MADROÑO

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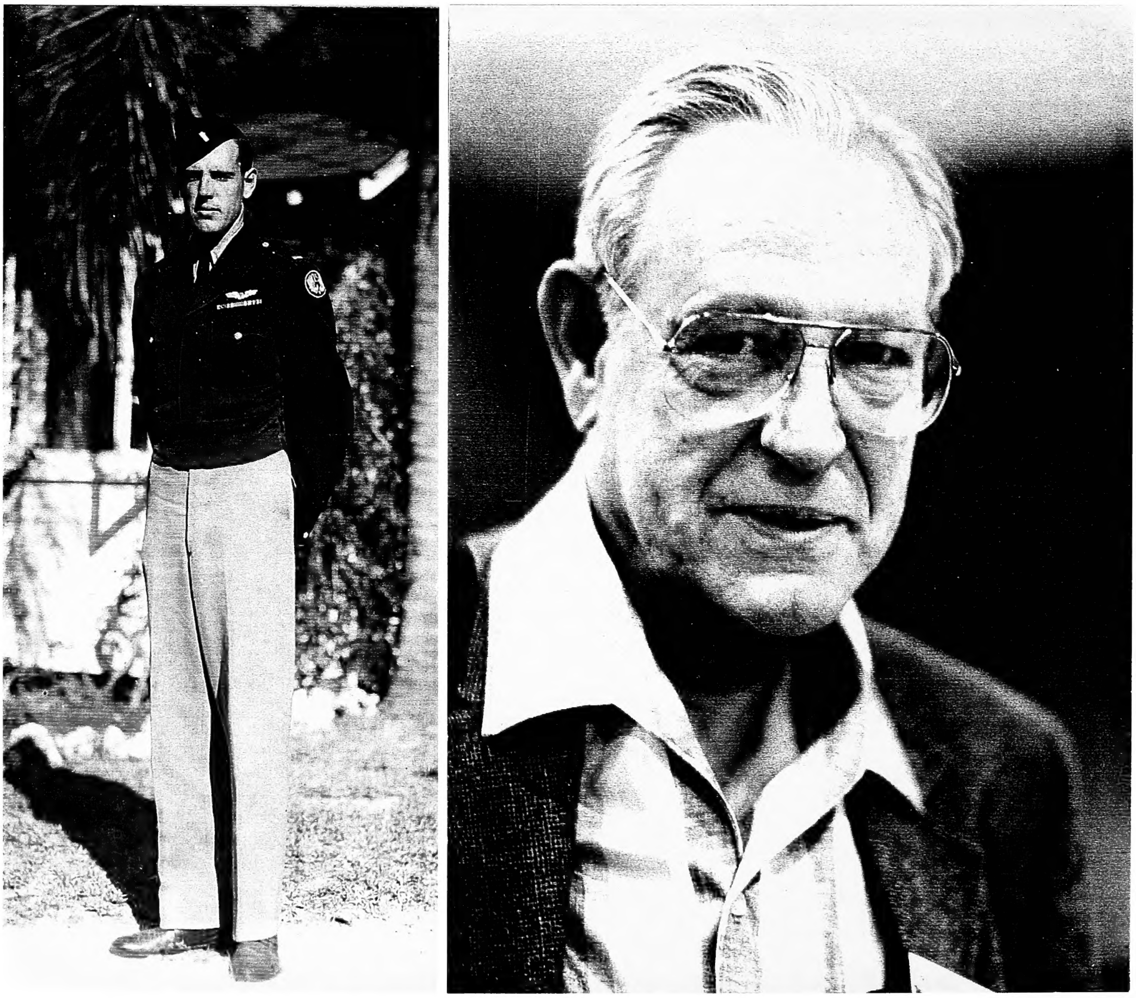
DEDICATION

Robert Folger (Bob) Thorne was born at Spring Lake, N. J., 13 July 1920, a community near the family home in Belmar. When he was two, the family moved to a second home at Gulfport, Florida, where they wintered, returning each summer to Belmar. Thus, he was reared within walking distance of saltwater, which accounts, no doubt, for his life-long addiction to sea food and marine aquatics! Learning to swim helped him later. Bob's father, Harry, was a professional portrait photographer and long served as the official photographer of both the New York Yankees and Boston Red Sox during their spring training activities at St. Petersburg, Florida. One of Bob's prized mementos of this era is a large photograph autographed by both Babe Ruth and Lou Gehrig and dedicated to his father. Bob graduated from St. Petersburg Senior High School in 1937 and in the same year entered Dartmouth College with aspirations of becoming a linguist; fortunately for botany, he discovered plants during his freshman year, and the rest, as they say, is history. He studied at Dartmouth with tuition scholarships where his academic prowess brought him membership in Phi Beta Kappa; he received his A.B. summa cum laude in 1941. Under the auspices of a Cramer Fellowship he moved on to Cornell University where he gained his M.S. in Botany in 1942.

As so often happened in those days, Bob was invited to enter the service. Although he doubtless could have collected and observed numerous plants as a member of one of the several ground forces, he chose instead, following his enlistment in 1942, to fly. He was trained as a navigator in the U. S. Army Air Force and served in the European Theater of Operations. His tenure with the 15th Air Force, 461st Bomb Group Heavy stationed in Italy, was not without considerable excitement, and he still recalls the names and nature of many of his flying comrades



Robert F. Thorne. Back from military service in Europe, October, 1944 (left). At the International Botanical Congress, Berlin, 1983 (right).

and the often harrowing times they shared. While on his 11th bombing mission into Axis territory, his plane, a B24 Liberator, was shot up over Austria and went down off the coast of Yugoslavia. Fortunately, he and his crew parachuted to "safety" on the Dalmatian island of Vis and were rescued by partisans—Bob landed in the Adriatic and managed to swim ashore despite the burden of a parachute and a wet uniform. Soon back with his unit in Italy, he was so "admired" for his efforts that he was "asked" to take part in 29 more missions before being allowed to return to the states in September 1944 and ultimately released from service shortly after the war in Europe ended early in 1945.

Bob resumed his formal training in botany under the guidance of Professors Walter Muenscher and Arthur Eames at Cornell, receiving his Ph.D. in 1949. He married his wife of 52 years, the former Mae Zukel, in 1947. His doctoral thesis was a floristic study of southwestern Georgia and resulted in a long paper that brought him a share of the first George Cooley Award presented at the American Society of Plant Taxonomy meeting in 1955.

Before graduation, Bob accepted an Assistant Professorship in Botany at the University of Iowa, Iowa City, becoming Associate Professor in 1954 and Professor in 1961. During his years at Iowa, he distinguished himself not only as organizer and curator of a herbarium but also as a teacher and as a mentor of numerous graduate students. Not incidentally, he developed his basic philosophy regarding the principles underlying angiosperm phylogeny and biogeography, and laid the groundwork for his becoming what he is today—a world leader in the study of plant geography, phylogeny, and floristics.

Of great significance to western botany was Bob's move from Iowa to the Rancho Santa Ana Botanic Garden in 1962 where he became Taxonomist and Curator of the Herbarium as well as Professor of Botany in the Claremont Graduate School. Within a relatively short time, through diligent work both in the herbarium and in the field, he mastered the California flora to a degree that amazed many long-time students of the region. During his long tenure at the garden not only did he have continued success as teacher and researcher but also, under his guidance, the herbarium grew and prospered, becoming one of the outstanding repositories of plants from the western United States and elsewhere. And his studies, alone or with others, have contributed greatly to our knowledge of the biogeography and flora of California.

Bob's writings on geography, floristics, and phylogeny have brought him international renown. The "Thorne system" of the higher-level classification of plants is accepted and used by many botanists throughout the world, and it is the standard against which much modern-day research is compared. More often than not in the light of today's molecular and cladistic studies, it stands up to critical scrutiny. His botanical studies and explorations have involved not only diverse regions of the United States, Mexico, and Jamaica in the New World but many parts of the Old World as well—Australia (Fullbright Research Scholar, 1959–1960; NSF Senior Postdoctoral Fellow, 1960), Tasmania, New Caledonia, New Guinea, Indonesia, Taiwan, India, China, Iran, and Scandinavia.

Bob has been accorded many honors for his scientific studies and academic accomplishments. He has been elected Foreign Member of the Royal Danish Academy, Fellow of the Linnean Society of London, and Fellow of the French Societé de Biogeographie. He is a member of numerous societies, including The American Institute of Biological Sciences; The American Society of Plant Taxonomists (Secretary, 1957–1958; Council, 1961–1967; President, 1968); The Botanical Society of America (Chmn. of the Central States Section, 1956, the Systematic Section, 1957–1958; and the Pacific Section, 1977); The California Botanical Society (Vice-President, 1966); The Southern California Botanists (President, 1966; Council, 1963–1987; Vice-President, 1975–1977). He is a member of Sigma Xi, Phi Kappa Phi, and was National Treasurer of Gamma Alpha, 1954–1957. In 1996, he received a Botanical Society of America Merit Award in recognition of his contributions to the field of plant systematics.

Although Bob formally retired in 1987, he has continued his studies at the garden nearly full time. He is as enthusiastic as ever, relentlessly searching for new items to add to his unparalleled plant-stamp collection and continuing his many and varied botanical pursuits. The latter includes a never-ending perusal of the botanical literature in search of all new information having valid bearings on his system of classification, which he does not hesitate to upgrade as needed from time to time, even at the expense of long-held opinions. For his distinguished service to the botany of California, and to the world for that matter, it is entirely fitting that this volume of *Madroño* be dedicated to Robert Folger Thorne.

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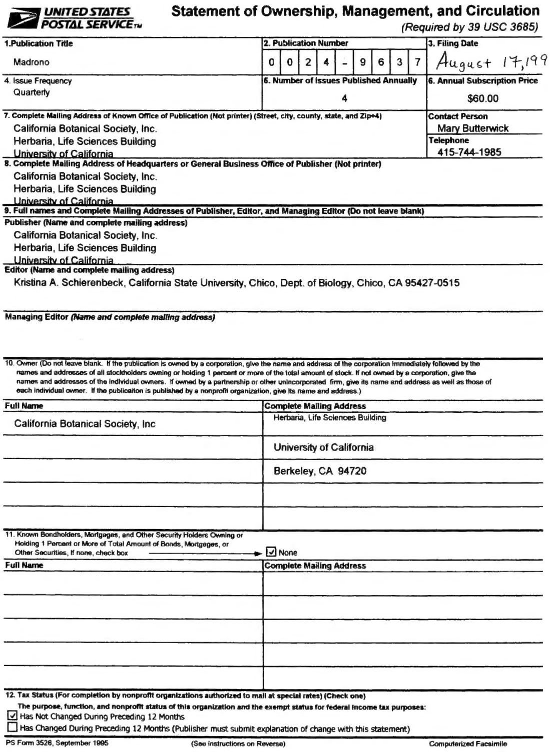

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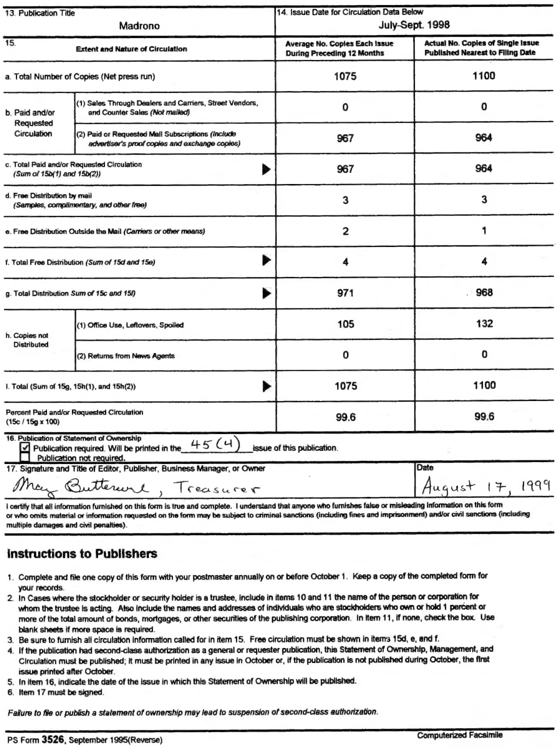

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560 YEARS OF VEGETATION CHANGE IN THE REGION OF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Pollen evidence from two sites in the Santa Barbara region show evidence of vegetation changes following European settlement in California. In the Santa Barbara coastal region, oak woodland populations (dominated by *Quercus agrifolia*) remained stable during the pre-European period; however, in the last century woodland densities have increased. At higher elevations along the oak woodland/pine forest ecotone, pines are becoming dominant. Reduction in fire frequency has probably been the main factor contributing to density increases. The pollen record does not show any evidence of an expansion of chaparral over the last 200 years; however, there is weak evidence for an increase in coastal-sage scrub since the early 1800's. The transformation of the California grassland appears to have begun particularly early with the invasion of *Erodium cicutarium* in the region even before the first Spanish settlement in California.

With the settlement of Spanish Missionaries, beginning in 1769, the California landscape has been radically altered by human-caused environmental change. The exact nature of these changes is not always readily apparent, since descriptions of the pre-European vegetation are sketchy at best, and by the time reliable botanical records were gathered, much of the landscape had already been altered. The vegetation we see today represents the dynamic result of two centuries of response to various changes, including changes in fire regime, introduction of livestock, invasion of alien species, and land clearing for agriculture and urban development. Understanding how vegetation has changed in response to these impacts can provide valuable information for present-day conservation efforts.

Of particular concern recently has been the affect of human-caused environmental changes in oak woodlands (Muick and Bartolome 1987; Bolsinger 1988). To date, no high resolution paleoecologic studies have been conducted that document environmental change in regions dominated by California oak woodland. A variety of methods have been used to reconstruct past change in California oak woodlands, including age structure studies (White 1966; Vankat and Major 1978; Anderson and Pasquinelli 1984; McClaran 1986; McClaran and Bartolome 1989; Mensing 1992), historical records (Mayfield 1981; Rossi 1980), analysis of aerial photographs (Brown and Davis 1991), and resurveying of permanent plots (Holzman 1993). These studies have contributed significant information on oak woodland history; however, they are generally restricted to the last 200 years and reveal little about the pre-European period.

Pollen analysis from an estuarine sediment core on Santa Rosa Island in the Santa Barbara Channel has documented the invasion of exotic taxa and changes in native vegetation following the settlement of the island in the late 1800's (Cole and Liu 1994). Radiocarbon dates from the top three meters of core however are influenced by old carbon effects which suggest that the bulk sediment dates may be 1200 years too old. The chronology for the historic period therefore was extrapolated from exotic pollen types. Oak pollen was only a minor component of the pollen sum and is not discussed by the authors.

In this paper I use pollen evidence from two sites in the Santa Barbara region to reconstruct vegetation history for the last 560 years. The sites include the Santa Barbara Channel, just off the coast of Santa Barbara, and Zaca Lake in northern Santa Barbara County (Fig. 1). Oak woodland, chaparral, coastal-sage scrub, and grassland comprise the majority of the vegetation in the region. This area was one of the earliest settled by Spanish missionaries and provides an opportunity to identify the effects of European impacts on vegetation. Repeat photography is used to help illustrate changes in the last century.

STUDY AREA

Santa Barbara Basin. The Santa Barbara Basin (34°11′–34°16′N; 120°01′–120°05′W), is located between mainland California and the Channel Islands (Fig. 1). The center of the basin has a maximum depth of ca. 590 m and the bottom waters are normally anoxic. Because of the absence of a bottom fauna seasonal differences in sediment density are preserved as varves, and these have been used to establish a high resolution chronology of the last 560 years (Soutar and Crill 1977; Schimmelman et al. 1990).

The source region for pollen deposited in the Santa Barbara Basin is the coastal plain and Santa Ynez Mountains. *Quercus agrifolia* appear dominant on north-facing slopes, in canyons, and in mesic sites along the coastal marine terrace. West and

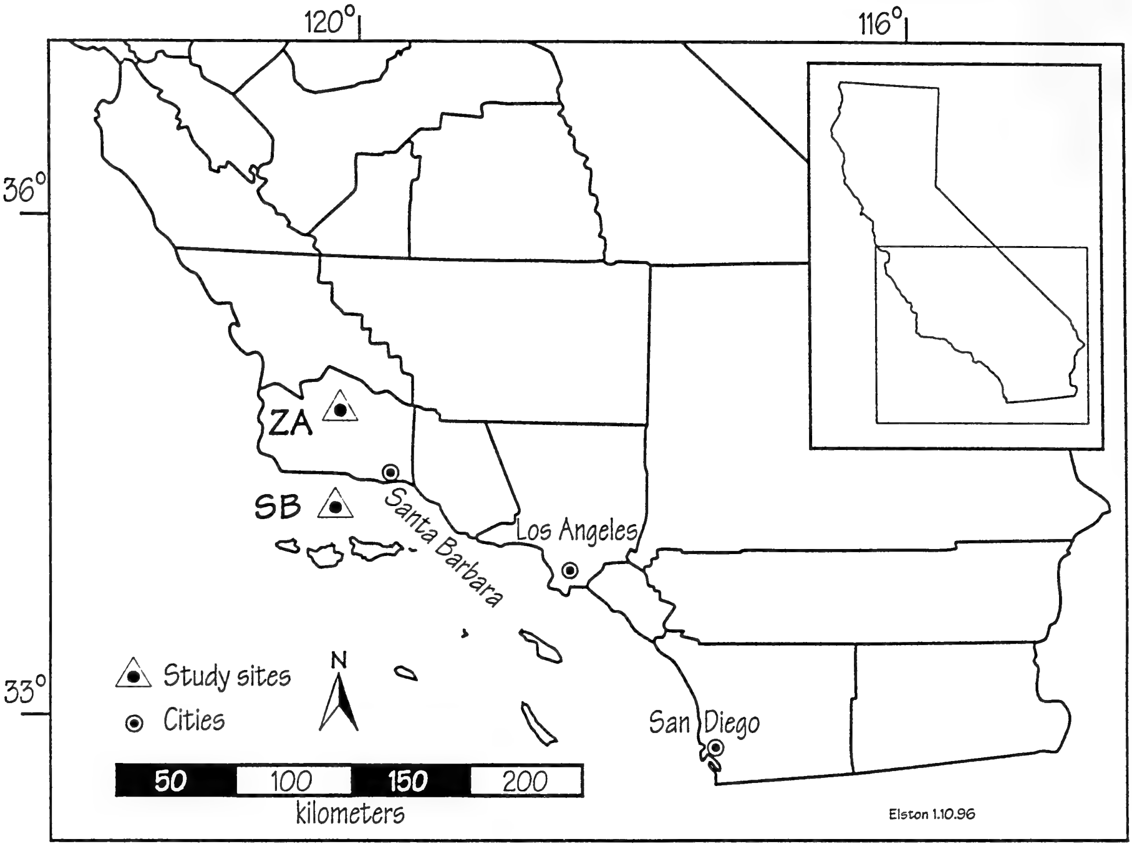

FIG. 1. Location map of the Santa Barbara Basin core site (SB), and Zaca Lake (ZA).

south facing slopes are dominated by chaparral, and coastal-sage scrub. Along the coastal plain introduced grasses and herbaceous plants are common (Ferren 1985). *Pinus muricata* grows in the Santa Ynez Mountains northwest of Santa Barbara although its distribution is restricted (Griffin and Critchfield 1976).

Zaca Lake. Zaca Lake (34°36′36″N; 120°02′17″W, elev. 730 m) is in the San Rafael Mountains, within the Los Padres National Forest, approximately 50 km northwest of Santa Barbara. Two massive Quaternary landslides blocked Zaca Creek to form the lake (Hall 1981). The lake is steep-sided and slopes to a flat bottom 13 meters in depth. Surface area is 6.9 ha. and the maximum length is 350 m.

The lake lies at the transition zone between oak woodland at lower elevations and pine forest at higher elevations. *Quercus agrifolia, P. coulteri, P. ponderosa,* and *P. sabiniana* are co-dominants around the lake. South-facing slopes are characterized by *Ceanothus* spp., *Arctostaphylo* spp., *Yucca* spp., *Salvia* spp., and *Artemisia californica.* Canyons include small stands of *Q. douglasii, Q. chrysolepis,* and *Calocedrus decurrens.* Small patches of exotic pines remain as a legacy of tree planting at the turn of the century (Blakely personal communication). Ornamental conifers planted near the lake include *Sequoia sempervirens* and *Cedrus deodara* (Peterson 1980).

METHODS

Santa Barbara Basin cores SABA 87-1 and 88-1 were recovered by researchers from Scripps Institute of Oceanography with a Soutar Box Corer and a Kasten Corer (Schimmelman et al. 1990). All cores were initially sampled at near annual resolution, but the pollen analysis was based on sub-samples which represented consecutive, ca. 5 year intervals. An equal weight of sediment was taken from each annual sub-sample. Fifty-nine samples were analyzed from the period 1425 to 1985.

Two sediment cores were recovered from Zaca Lake in May, 1992 using a modified square-rod Livingstone piston corer fitted with a 5 cm diameter plastic tube liner; a 910 cm core (core C) and an overlapping 865 cm core (core D). While still in the plastic tube, cores were X-radiographed at the University of California Museum of Paleontology to record stratigraphy and density changes. Magnetic susceptibility and Gamma-ray analyses were carried out at the United States Geologic Survey laboratories in Menlo Park. Sediment samples (0.5 cc) were then removed for pollen analysis.

Standard techniques were used to concentrate pollen (Faegri and Iversen 1975). A known quantity of *Lycopodium* spores was introduced as a control to calculate absolute pollen concentration and accumulation rate (Stockmarr 1971). A minimum of 400 pollen grains were counted for each level. For Zaca Lake, aquatic and riparian pollen types were counted but excluded from the pollen sum.

RESULTS

Santa Barbara Basin

Chronology. The Santa Barbara Basin varve chronology has been corroborated by radiometric dating, cross-correlation with tree-rings and correlation with hydrological data (Soutar and Crill 1977; Koide et al. 1972; Krishnaswami et al. 1973; Hulsemann and Emery 1961). The chronology used here is that of Schimmelman et al. (1990), and Schimmelman et al. (1992). Varve counts were made using high quality X-radiographs and age assignments were checked against distinctive marker layers of known events such as El Niño periods, floods, and oil spills. The estimated precision of the time scale is ±1 year for 1900 to 1987, ±2 years from 1900 to 1840, ±5 years from 1840 to 1750, and ±10 years at the 1425 level.

Taxonomy. Taxonomic nomenclature follows Hickman (1993). Forty-eight pollen and spore types were identified (Mensing 1993). Percentage abundance of the nine most important types is shown in Figure 2. *Quercus* probably represents *Q. agrifolia,* by far the dominant tree species in the region. Additional, but less important sources may include *Q. lobata,* which is important in the Santa Ynez drainage, *Q. durata* and *Q. dumosa* which are found in association with chaparral, and *Q. tomentella* from the Channel Islands. *Pinus* would primarily be *P. muricata, P. sabiniana, P. coulteri,* and *P. ponderosa.* Following Heusser (1978), the taxonomically difficult group including Rhamnaceae and Rosaceae are combined. These taxa include many chaparral species and probably represent the genera *Ceanothus, Rhamnus, Adenostoma, Cercocarpus, Prunus,* and *Heteromeles. Artemisia* is primarily *Artemisia californica.* Other Asteraceae are difficult to identify below family level and have been combined in Figure 2. Poaceae and Polemoniaceae also are not identified below the family level. Several native taxa from the Brassicaceae are present in small quantities early in the record; however, alien taxa became important in California in the early 19th century and the pollen increase probably represents introduced species. *Erodium* has been identified to the species *Erodium cicutarium,* a Mediterranean annual (Mensing and Byrne in press).

Pollen analysis. Below 1760, *Quercus* shows few changes; however, after 1760 the record becomes increasingly variable. Beginning in 1870, *Quercus* steadily increases from 20% to 42%, twice as high as the average during the pre-European period. *Pinus* remains below 10% through most of the record, and shows virtually no change. Although Rhamnaceae and Rosaceae show high variability, no long term trends appear over the 460 year period. *Artemisia* averages 7% and shows little variability for the first 400 years of the record, then, from 1820 to 1985 it increases to an average of 10%.

Asteraceae averages 20% from 1435 to 1700, but then begins to decline, dropping to only 7% percent in 1970. Poaceae declines at a slow but fairly constant rate through most of the record, but clearly increases between 1945 and the present. The Polemoniaceae are primarily insect pollinated, consequently only small quantities of pollen reach the Santa Barbara Basin. Polemoniaceae is present in virtually every level between 1425 and 1795, averaging nearly 1% of the pollen sum. In the last two centuries, Polemoniaceae is commonly absent, Brassicaceae is infrequent prior to 1825, but increases substantially in the modern period, most likely due to the introduction of European Brassicaceae. *Erodium* first appears in the pollen record in 1755 and is continuously present after that date.

Zaca Lake

Chronology. The Zaca Lake chronology was developed using core D (0–0.5 m depth) and core C (0.5–2.75 m depth). Both cores clearly record a complex stratigraphy of laminations, dark silty layers, and dense clay layers described in earlier studies (Caponigro 1976; Peterson 1980). X-radiographs were used to correlate core stratigraphy with that described by Caponigro and Peterson. The chronology was developed using core-to-core correlation, radiocarbon dating, and the first appearance of two exotic pollen types (*Erodium* and *Cedrus*).

The base of the core section analyzed gave a radiocarbon age of 2510 ± 70 BP (Beta-55301) (Calendar calibration B.C. 661 ± 150, Stuvier and Reimer 1986) (Fig. 3). The first occurrence of *Erodium* at 110 cm depth is assigned a date of 1830 ± 40. The data and error estimate are approximated from the Santa Barbara Basin data (Mensing and Byrne in press), and the species dispersal ability. The date of 1953 at the 47 cm depth is based on a ^{137}Cs peak identified by Caponigro (1976). The first appearance of *Cedrus* pollen at 35 cm dates to 1964 assuming a 15 year maturation period following the first planting in 1949 (Peterson 1980). The disparity in sedimentation rate between the upper core (110 cm in 160 years) and the lower core (165 cm in 1500 years) suggests that the radiocarbon age may be artificially old. Even assuming no changes in sedimentation rate, the lower half of the core would span at least two centuries of vegetation history prior to Spanish settlement.

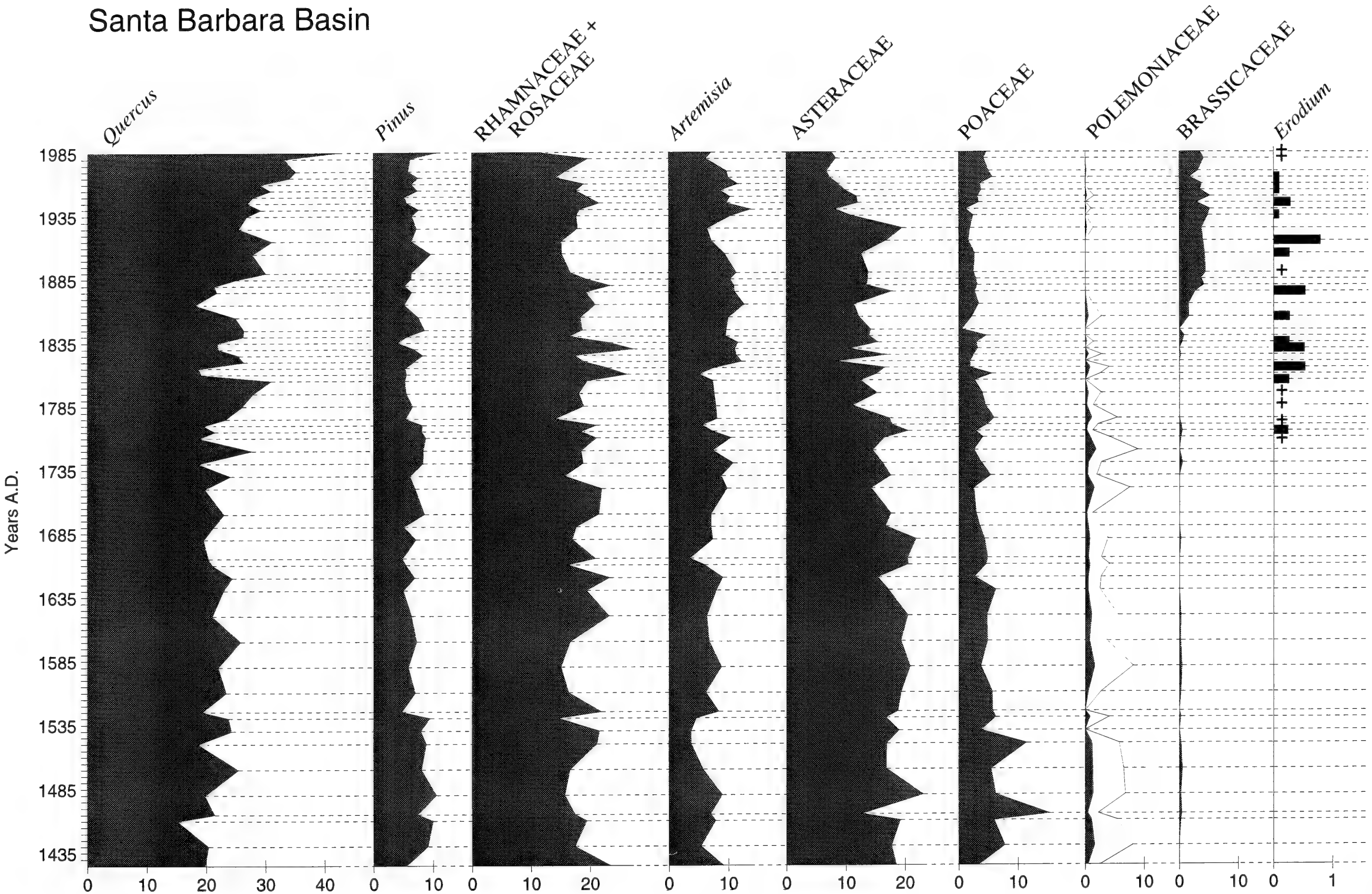

FIG. 2. Selected pollen types from the Santa Barbara Basin. Sums are expressed as a percentage of total pollen and spores excluding poorly preserved unidentified grains. The unshaded area under Polemoniaceae represents five times exaggeration. Note the scale change for *Erodium* (+) represents a level where *Erodium* pollen was identified by scanning (Mensing 1993).

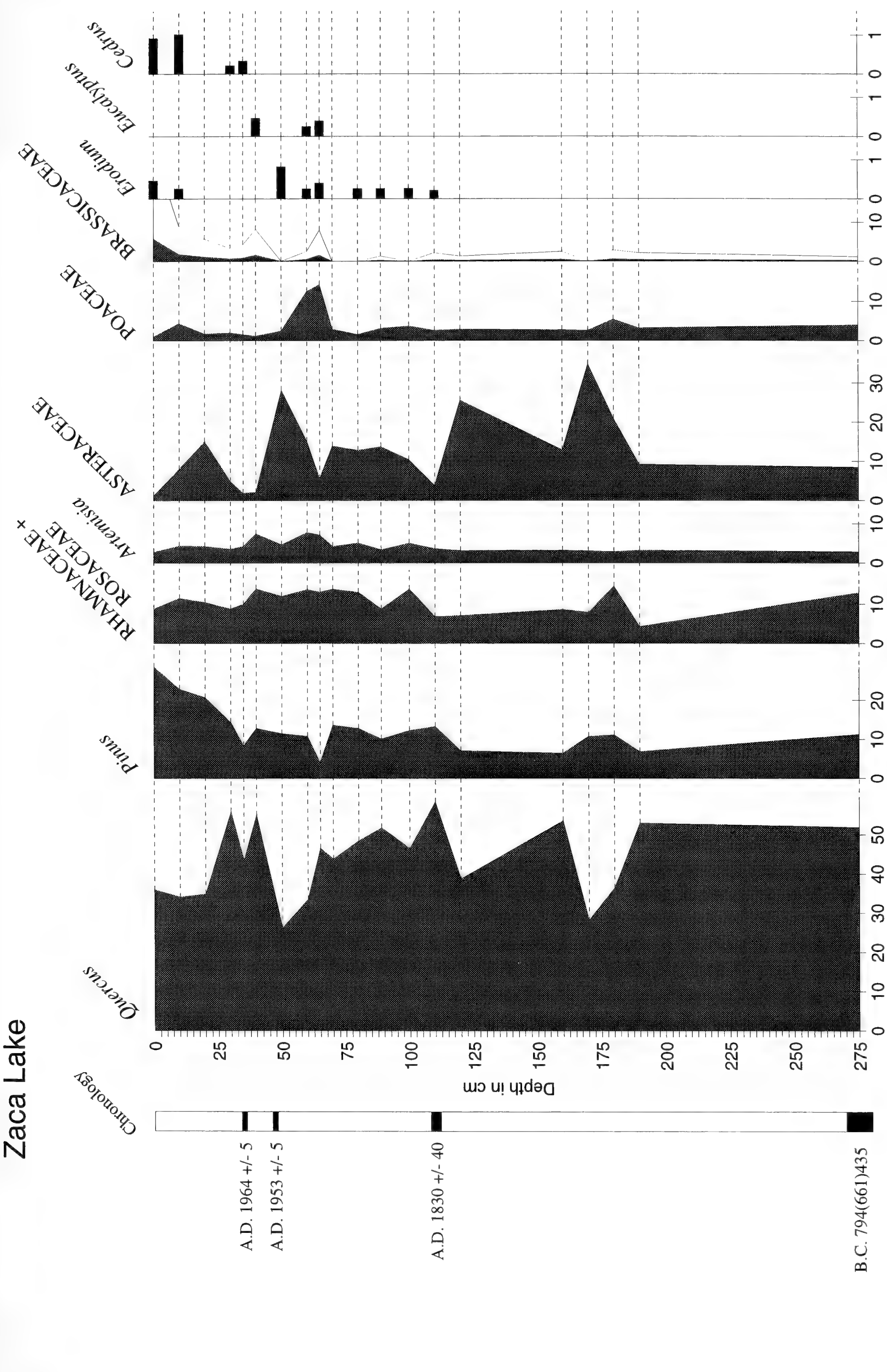

FIG. 3. Selected pollen types from Zaca Lake. Sums are expressed as a percentage of total pollen and spores excluding aquatics (*Typha*, Cyperaceae, and *Ruppia*), riparian taxa (*Salix* and *Platanus*) and poorly preserved unidentified grains. The unshaded area under Brassicaceae represents five times exageration. Note the scale change for *Erodium*, *Eucalyptus*, and *Cedrus*.

Taxonomy. Fifty-four pollen and spore types were identified (Mensing 1993), of which ten taxa are graphed in Figure 3. Species of oaks in the region that most likely contribute pollen to the site include *Q. agrifolia, Q. lobata, Q. durata, Q. chrysolepis, Q. wislezenni,* and *Q. douglasii.* Of these species *Q. agrifolia* and *Q. lobata* dominate the region today. *Pinus* includes *P. ponderosa, P. sabiniana,* and *P. coulteri* as well as *P. attenuata,* planted around the turn of the century. Rhamnaceae/Rosaceae includes taxa similar to those described for the Santa Barbara Basin as well as *Cercocarpus betuloides, Prunus ilicifolia, Heteromeles arbutifolia.* Asteraceae around Zaca Lake primarily represent herbaceous taxa. Brassicaceae probably include introduced mustards in the post-European period. *Erodium* was identified as *Erodium cicutarium. Eucalyptus* is no longer present at the site and the type is unknown. *Cedrus* is from *Cedrus deodora* planted near the lake.

Pollen analysis. Twenty-six levels were analyzed at approximately 10 cm intervals. Six levels were excluded from the analysis because of extremely high percentages of Asteraceae pollen presumably associated with erosion events. Dense clay layers are present in the core at 130–150 cm and 200–240 cm depth. These lenses are associated with above average magnetic susceptibility and generally low organic content (Mensing 1993). High magnetic susceptibility readings generally result from deposition of iron bearing sediments. Peterson (1980) hypothesized that these layers may be associated with periods of higher than average erosion. Asteraceae pollen is particularly resistant to biodegradation and during periods of high runoff, pollen accumulated on the soil surface may have been washed into the lake biasing the sample.

For most of the record, *Quercus* pollen remains between 40–50%. Low percentages are seen at the 50–60 cm 120 cm and 170–180 cm depths. The declines are mirrored by increases in Asteraceae. These strata are not clay layers; however, they show above average magnetic susceptibility suggesting that they may also be associated with erosion events. Organic rich lake sediments (gytja) commonly had 50% *Quercus* pollen. In the upper part of the record, from about 1970 to the present, *Quercus* averages 35%. Unlike previous decreases in *Quercus,* Asteraceae also declines during this time.

Pinus values remain stable at about 10% through most of the core then begin to increase rapidly to 29% in the mid 1900's. The Rhamnaceae/Rosaceae curve shows little variation averaging about 12%. Similarly, *Artemisia* varies little, reaching as high as 7% between 40–65 cm, but remaining at less than 4% for most of the record.

Asteraceae is the most important herbaceous pollen type. The record is highly variable, ranging from 1% to 34%. Poaceae, which remains fairly constant at about 2–3% for most of the core shows an interesting short term increase at the 60 and 65 cm levels (ca. 1920 to 1930), jumping up to 14%. *Zea mays* (corn) pollen was also found in the 65 cm level, suggesting a period of local cultivation. Brassicaceae is present at about 1% in the core section below 65 cm (ca. 1920). From 65 cm up to the surface level, Brassicaceae steadily increases from 1% up to 6%. *Erodium* first appears in the core at 110 cm depth and is present in ten levels. *Eucalyptus* is present in three levels with approximate dates of 1920, 1930, and 1960. *Cedrus* first appears in 1964 and increases in abundance in the surface samples.

DISCUSSION

Oak woodlands. The Santa Barbara pollen record shows no significant vegetation changes during the pre-European period. The evidence suggests that oak woodland populations remained stable for up to four centuries. Beginning around 1870 and continuing until 1985, percent *Quercus* pollen steadily increases to its highest level in 560 years. Principal components analysis of pollen accumulation rates indicates that the abundance of *Quercus* pollen has indeed increased over the last century (Mensing 1993). The twofold increase of *Quercus* pollen during the last century strongly suggests an increase in oak woodlands in the Santa Barbara region. This increase may be from an increase in woodland density, expansion of oak woodland habitat, or a combination of the two.

The Zaca Lake record is less clear concerning oak woodlands. For most of the record, *Quercus* is the dominant pollen type with maxima averaging 50 percent. Periodic declines in *Quercus* consistently correspond with increases in Asteraceae. An increase in individuals of the Asteraceae, locally composed primarily of herbaceous annuals, would not displace oak woodlands. Since decreases in *Quercus* are not associated with increases in woody taxa, I suggest that oak populations in this area remained stable prior to the mid-1900's. Since 1950 another woody taxon, *Pinus,* has increased substantially. The increase in the importance of *Pinus* recorded in the pollen record is confirmed by repeat photography (Fig. 4). Scattered pine groves, visible on the distant slopes in the 1895 photograph, now appear as dense forest. Today, the understory surrounding the lake is thick with young pines and oaks, but pines over-top oaks in most places. Zaca Lake is located at the transition between oak woodland and coniferous forest. Although oaks may be increasing to some extent at this site, the primary signal in the pollen record, supported by evidence from repeat photography, is an increase in the importance of pines.

This study presents the first high-resolution paeloecologic records to document changes in California oak woodlands from the pre-European period to the modern period. Of significance here is that

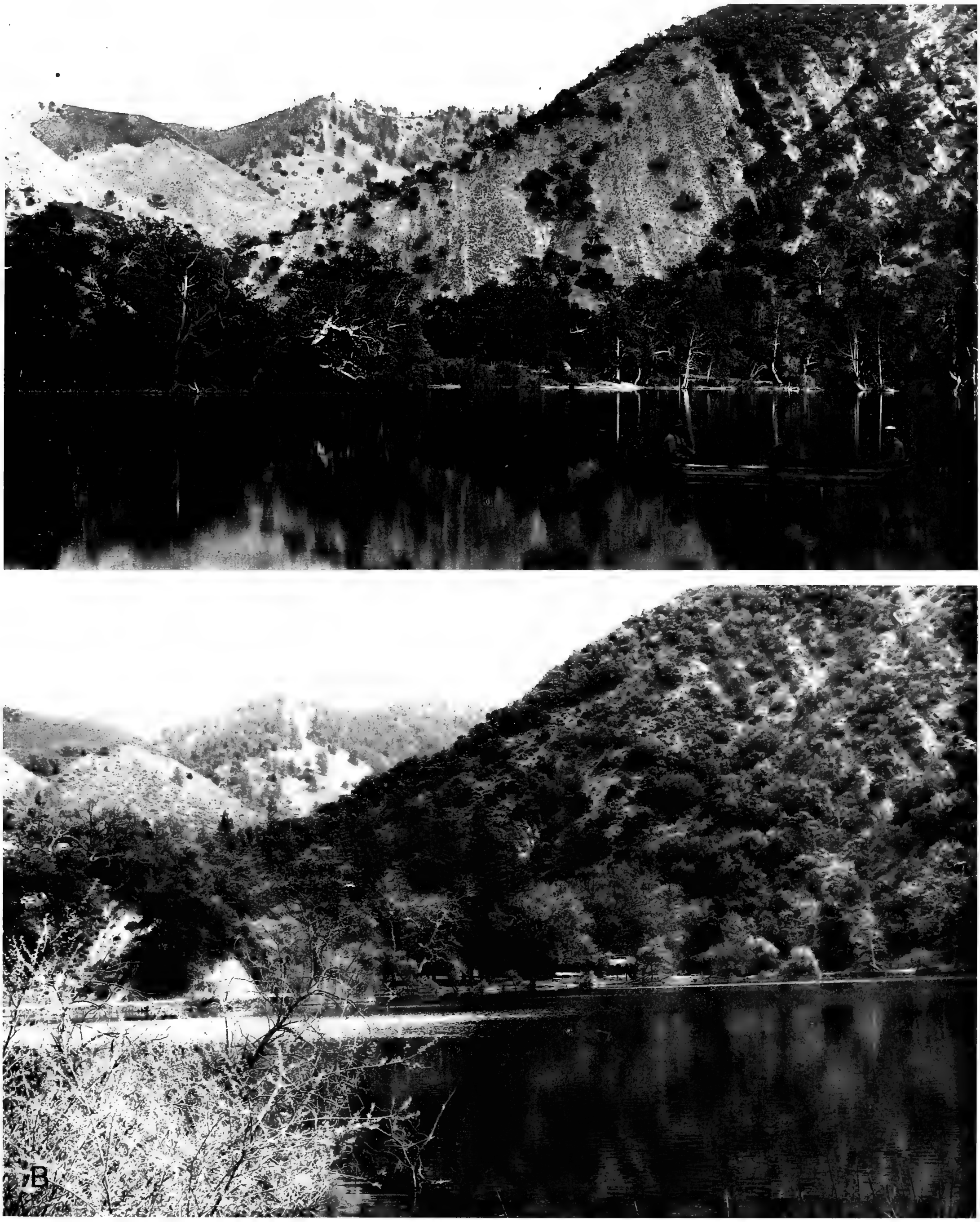

FIG. 4. Repeat photography of Zaca Lake taken from the north shore looking east. The upper photograph was taken by a local Santa Barbara photographer ca., 1895 (courtesy Santa Barbara Historical Society Museum). The lower photograph is by the author, 1992.

Q. agrifolia populations in the Santa Barbara area have increased in the recent century, after a long period with no apparent changes. Other studies, primarily stand age analyses of *Q. douglasii,* have also documented increases in woodland density (White 1966; Vankat and Major 1978; Mensing 1992); however, these studies do not extend to the pre-European period. A resampling of permanent plots in northern California found that *Q. douglasii* have increased over the last 60 years, with live oaks beginning to emerge as co-dominants (Holzman 1993).

In general, there is concern that California oak woodlands are in decline. A recent assessment of

Q. douglasii found that 87% of the study locations were experiencing a net loss in both tree density and canopy cover (Sweicki et al. 1993). Studies have documented negative impacts of human-caused environmental change to oak woodlands throughout the state including direct loss of woodlands through clearing (Bolsinger 1988; Rossi 1980) and poor regeneration as a result of livestock grazing, invasion of annual grasses, and other changes (Griffin 1971; Bartolome et al. 1987; Borchert et al. 1989; Harvey 1989; Gordon and Rice 1993; Muick 1995).

To understand the full extent of these changes on California oak woodlands, it is valuable to have data on how current populations compare with those from the pre-European period. In this regard, paleoecologic studies provide important information to understand the long term implications of human-caused environmental change. This study suggests that *Q. agrifolia* populations in the Santa Barbara region have increased during the modern period, a time of significant human-caused environmental change.

The increase in *Q. agrifolia* is most apparent in the 1900's. I believe that the environmental change most likely to have resulted in an increase of oak woodland is a change in fire regime. In the absence of fire, *Q. agrifolia* tends to increase. Density and canopy cover for *Q. agrifolia* at Burton Mesa in Santa Barbara County was found to be highest on sites without recent fires (Davis et al. 1988). McBride (1974) examined plant succession in the Berkeley hills and suggested that in the absence of recurrent fires, *Q. agrifolia* and *Umbellularia californica* would succeed *Baccharis pilularis.* In a comparison of vegetation dynamics on burned and unburned plots at Gaviota State Park west of Santa Barbara, Callaway and Davis (1993) found that chaparral was being converted to oak woodland at a rate of 0.12% per year in the absence of fire. They predicted that with the absence of fire and grazing, oak woodland would dominate a larger proportion of the landscape.

The Chumash regularly set fires along the coastal plain, and this practice continued even after establishment of the missions (Timbrook et al. 1982). Many of these grass fires probably burned through the understory of adjacent oak woodlands, killing oak seedlings and saplings. Trees of less than 7.5 cm diameter breast height have bark approximately 0.6 cm thick and may be killed by low intensity fires (Plumb and Gomez 1983). This process would have maintained open oak woodlands similar to the oak parks typically described by early Spanish explorers. Since the turn of the century, urban and agricultural development has concentrated in areas dominated by grassland and oak woodland. Although urban and agricultural development have been responsible for clearing oaks, fire protection in developed areas favors oaks in nearby wildland settings (Davis et al. 1988; Callaway and Davis 1993). The Santa Barbara Basin pollen record suggests that the last 100 years have produced such an increase in oaks in the Santa Barbara region.

Reduction in fire frequency may also be responsible for the recent increase in woodland and shrub cover at Zaca Lake. Fires have been systematically recorded in the Los Padres National Forest since 1911. Three fires have burned on the chaparral slopes to the northwest of the lake; however, no fires larger than a few acres have burned the wooded slopes in the upper Zaca Lake watershed (Los Padres National Forest Fire Statistical Database). Here, absence of fire appears to have favored pines over oaks. Zaca Lake is located at the pine/oak ecotone. The tendency for pine to invade oak woodland following fire suppression has been clearly demonstrated in Yosemite Valley where open oak meadows were converted to closed coniferous forest after fire suppression (Reynolds 1959; Gibbens and Heady 1964; Anderson and Carpenter 1991). The Zaca Lake pollen record suggests that at upper elevation sites where coast live oak grows with pines, coniferous forest will replace oak woodland in the absence of frequent fire.

Chaparral, coastal-sage scrub, and herbaceous vegetation. There is some debate concerning the impact of European settlement on chaparral, coastal-sage scrub, and herbaceous vegetation. Dodge (1975) argued that grassland was much more extensive during the pre-European period because frequent low-intensity fires cleared out young shrub seedlings. He concluded that heavy grazing and fire suppression have reduced low-intensity fires and permitted shrub invasion of vast areas formerly dominated by grasses. Timbrook et al. (1982) echoed this sentiment and concluded that chaparral has increased in density and extent over the last 200 years because of suppression of grassland burning. Furthermore, they suggested that a grassland which dominated the Santa Barbara coastal plain and foothills has been largely replaced by coastal-sage scrub as a result of fire suppression.

The pollen record does not support the idea that chaparral has expanded over the last 200 years. The Rhamnaceae/Rosaceae curve from each site show virtually no consistent trends (Figs. 2, 3). If anything, the Santa Barbara Basin diagram shows a modest decline in chaparral taxa in the recent century. The pollen record suggests that chaparral has not expanded its range in response to European impacts.

There is some evidence to suggest a modest increase in the importance of coastal-sage scrub over the last 200 years. *Artemisia* averages 7% of the pollen sum from the period between 1425 and 1820 (Fig. 2). However, beginning in 1820, it increases to 12%, and averages 10% between 1820 and 1985. Pollen percentage remains at the higher levels except for two brief declines centered on 1920 and 1980. At Zaca Lake *Artemisia* averages 2.7% prior to about 1800, then increases to an average of 5.0% in the upper core (Fig. 3). Although this may represent a true increase, it is difficult to interpret too much from such a small change.

Comparison of burned and unburned plots in Santa Barbara County found that coastal-sage scrub invaded grassland in the absence of fire, but frequent fire favored grassland (Callaway and Davis 1993). Westman (1976) also found that coastal-sage scrub replaced undisturbed grassland when fire was removed. In northern California, *Baccharis pilularis* was found to invade grassland during periods of low fire frequency (McBride and Heady 1968). Reduced fire frequency along the coastal plain may have favored a slight expansion of coastal-sage scrub; however, there is no evidence that this impact affected the distribution or abundance of chaparral.

Pollen evidence of herbaceous taxa shows that the invasion of alien species into grasslands began very early. *Erodium* first appears in the pollen record in 1760, nearly a decade prior to the first Spanish settlement in San Diego and more than 20 years before the founding of the Mission Santa Barbara (Fig. 2). The pollen has been identified as *Erodium cicutarium* (Mensing and Byrne in press), a Mediterranean native, and provides evidence that the invasion and transformation of herbaceous vegetation began prior to European settlement. Polemoniaceae averages nearly 1% and is consistently present through the 1700's. Asteraceae, the dominant herbaceous pollen type, averages 18% in the pre-European period. Both taxa decline markedly in the modern period. The decline becomes particularly pronounced after the arrival of alien Brassicaceae which became widespread along the coastal plain in the early 1800's (Cleland 1951).

CONCLUSIONS

The evidence from this study suggests that oak woodlands in the Santa Barbara region have increased during the last 100 years. The nature of this increase varies between sites. In the Santa Barbara area, *Q. agrifolia* appears to have increased beginning in the late nineteenth century. Fire suppression on the coastal plain has probably been the main factor contributing to this increase. The Chumash are reported to have periodically set fires; however, with an increase in settlement and development, burning has been suppressed. In the absence of fire, *Q. agrifolia* has increased in density. A policy of fire suppression appears to favor *Q. agrifolia,* and where fire return intervals are long, oaks would be expected to continue to increase in density.

At higher elevations where *Q. agrifolia* grow alongside pine, such as at Zaca Lake, fire suppression appears to have favored pine over oak. Here, coniferous forest is expanding into oak woodland. The taller pines may eventually shade out the slower growing oaks if the present trend continues.

The pollen record shows that prior to European settlement, oak populations had been stable for at least three centuries. In the past two centuries, oak populations have changed in response to European impacts, including the introduction of grazing, suppression of fire, and a shift in understory composition. In some cases, these changes appear to have favored oaks, creating woodlands more dense than during the pre-European period.

Chaparral does not appear to have expanded significantly in response to European land use changes. Coastal-sage scrub may have expanded some; however, the evidence for this change is weak. Invasion and transformation of grassland appears to have begun particularly early with the first alien taxa reaching the area even before the first Spanish settlement of California.

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SUCCESSIONAL PATTERNS OF THE LOWER MONTANE TREELINE, EASTERN CALIFORNIA

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ABSTRACT

Stand age patterns of pinyon woodlands along the lower montane treeline ecotone (LMTE) in eastern California suggest that prior to European settlement, woodlands were very open (41 trees/ha) and were mostly restricted to xeric topographic settings with shallow, coarse-textured soils. Since European settlement in about 1861, pinyon woodlands have rapidly increased in density, expanded downslope, and invaded more mesic topographic sites.

The lower montane treeline ecotone (LMTE) forms the lower elevation extent of montane vegetation communities in the Intermountain West. In Inyo and Mono Counties the LMTE is dominated primarily by open woodlands of *Pinus monophylla* Torr. and Frem. (single-needle pinyon pine) with an understory of predominantly Great Basin shrub species such as *Artemisia* spp. (sagebrush), bitterbrush (*Purshia* spp.), and rabbitbrush (*Chrysothamnus* spp.) (Vasek and Thorne 1977). The pinyon woodland occurs mostly between 1900 m–2900 m elevation. In the eastern Sierra Nevada, Sweetwater Mountains, and Glass Mountain Ridge, the upper elevations of pinyon grade into montane forests and woodlands of Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus murrayana*), and white fir (*Abies concolor*). In the White Mountains and Bodie Hills, a sagebrush shrubland dominates the cover immediately above the pinyon woodlands. In the White-Inyo Range, subalpine woodlands of bristlecone pine (*Pinus longaeva*) and limber pine (*Pinus flexilis*) occur above the upper sagebrush zone (St. Andre et al. 1965; Spira 1991; Vasek and Thorne 1977).

The pinyon woodland in eastern California is unusual in the rarity of Utah juniper (*Juniperus osteosperma*), which commonly codominates with pinyon to form a pinyon-juniper woodland throughout the central Great Basin (West et al. 1978). Utah juniper co-occurs with pinyon in eastern California primarily in the White-Inyo Range where it is largely restricted to sites on alluvial soils (St. Andre 1962; Mooney 1973). Of the 521 trees sampled in this study, only two are Utah juniper, and the remainder are single-needle pinyon.

Throughout the Intermountain and Rocky Mountain west, observers have noted that the lower montane woodlands have been expanding downslope and have become denser within their elevational range since the late 1800's (Cottam and Stewart 1940; Blackburn and Tueller 1970; Burkhardt and Tisdale 1969, 1976; Rogers 1982; Vale 1975). Early observations, historic photographs, and stand age data suggest that lower montane woodlands were formerly savanna-like, with trees restricted to rocky outcrops or steep slopes with coarse-textured soils. Many of these topographic sites with existing trees have subsequently converted to fully-stocked stands while much of the range expansion of pinyon and juniper has been onto gently sloping or valley bottom sites with deeper, finer-textured soils (Cottam and Stewart 1940; Burkhardt and Tisdale 1969, 1976; Miller 1921; Miller and Rose 1995; Phillips 1909; Woodbury 1947).

While the ecology of pinyon and juniper woodlands has been extensively investigated, patterns and processes along the LMTE have received little study. Most previous workers have been concerned with larger-scale relationships of mature woodlands, and so have avoided sampling and describing ecotonal or early successional stands (Koniak 1986; Meeuwig and Cooper 1981; Tausch et al. 1981; Tueller et al. 1979; West et al. 1978). Blackburn and Tueller (1970) described and classified the range expansion of single-needle pinyon and Utah juniper in eastern Nevada, but did not investigate differences in stand age and dominance in relationship to the landscape topography. In this work I present pinyon age and dominance data in relation to topographic settings along the LMTE.

METHODS

The study areas are all within Inyo and Mono Counties, California; and sites were located in the Bodie Hills, Glass Mountain Ridge, the White Mountains, the Sherwin Summit area just east of the Sierra Nevada, and at Tuttle Creek, at the base of the southern Sierra Nevada. Sites were selected where the LMTE occurs in each area. Elevations ranged from 1900-2000 m elevation. Sampling areas were usually small drainage basins. Plots were randomly placed on a variety of topographic positions with a maximum of 50 m elevation difference within a sampling area. At this small scale, it was assumed that soil moisture variation is primarily a function of soil texture and topographic position, and that the influence of elevation is a constant.

The LMTE is highly interdigitated with respect to topographic position. The woodland is more developed and extends further downslope on topographic convexities, such as ridges, and steep slopes. To measure the influence of topographic position on stand variables, the sampling frame was stratified based on topographic position using the Topographic Relative Moisture Index (TRMI) (Parker 1982). The TRMI is a scalar index (0–60, 0 = most xeric topographic sites, 60 = most mesic) designed for mountainous terrain in the western United States, and offers a way to stratify the landscape into topographic position based on slope angle, configuration, aspect, and position on the slope. Individual plots were placed randomly within each landscape unit, such as valley bottom, ridge top, toe slope, and upper slope. This stratified random sampling process sometimes resulted in the placing of field plots where trees were absent; however, a sampling frame based on vegetative characteristics would not reflect the topographic influence on stands. Each plot was checked visually to insure that it did not include anomalous vegetative cover relative to the rest of the landscape unit.

To examine the hypothesis that pinyon existed as open woodlands primarily on xeric sites prior to European settlement, and then invaded onto mesic sites, I separated the plots into 22 xeric (low TRMI, <30) and 22 mesic (high TRMI, >30) sites. While there is a gradation between xeric and mesic sites, the combined weight of the slope variables (topographic position, slope steepness, and slope configuration) made them more important than aspect in determining whether a site was classified as mesic or xeric. In general, sites described as xeric are mostly located on topographic convexities and steeper slopes, and the mesic sites are located in draws, valley bottoms and other topographic concavities. Soil variables are not incorporated into the TRMI; however, within each study site, there is a strong positive correlation between shallow, coarse-textured soils and xeric sites as determined by the TRMI excluding aspect (Vaughn 1983).

Plots were 30 m × 30 m in all areas except the White-Inyo Range, where 50 m × 20 m plots were used to be consistent with previous field work (St. Andre 1962). All lives trees rooted in the plot >1.5 m height were cored at 30 cm for aging, and all trees were measured for basal area, crown projection area, and height. Understory cover was measured by the line-intercept placement of a 30 m transect through the plot. Percent cover was calculated as the percent distance intersected vertically by the line. In each study area, cross-sections were cut from juvenile trees <1.5 m height to determine the age to coring height. The average age at 30 cm was found to be 12.24 yrs (n = 30), so 12 years were added to the ring count age of each tree. To gain a representation of the age patterns of juveniles <1.5 m height, a simple linear regression equation was used to predict their ages. The best equation to predict age was based on stem radius and tree height (both measured in centimeters) using data from the cross-sectioned trees and cored trees <3 m height. The simple linear regression equation is

$$\text{Age} = 8.19(\text{radius}) + 0.169(\text{height});\ n = 122,\ r^2 = 65\%,\ p < 0.0005.$$

Growth rates are highly variable for immature trees due to their greater sensitivity to soil moisture fluctuations (Barton 1993), variations in overstory canopy shade, and the potential influences of nurse shrubs (Drivas and Everett 1988). Consequently, the predicted ages of juvenile trees are not reliable in determining actual dates of recruitment or seedling establishment, but they do offer a relatively accurate picture for interpreting overall reproductive status of the stand.

Finally, while there is no evidence of historic wood cutting on the sites, such as stumps, and the sampled stands are not within the known woodsheds of historic mining centers in the area, the possibility exists that some mature trees may have been cut for wood use in the past, and are now absent from the stands.

RESULTS AND DISCUSSION

At the LMTE, topographic position explains more variation in pinyon age and dominance patterns than elevation or aspect. Figures 1a and b illustrate tree ages from the 44 plots, and Table 1 summarizes stand age and density data. Of 381 trees aged by ring counts and 140 juvenile ages predicted through linear regression, 23% on all sites, 29% on xeric and 13% on mesic sites, predate European settlement. The mean (and median) tree ages of all sites today is 97.2 (79) years, on xeric sites 106.6 (81) years, and on mesic sites 83.6 (78) years. Currently and in 1861, pinyon stands on xeric sites are significantly older than trees on mesic sites along the LMTE (two-tailed t-test, $p < 0.005$). There was no difference in statistical significance when ages from cored only, or cored and predicted juvenile ages, were used.

Prior to the establishment of permanent European ranching and mining settlements in Inyo and Mono Counties in 1861 (Chalfant 1933; Sauder 1994), the data suggest that pinyon woodlands were largely restricted to xeric habitats, such as topographic convexities and steep slopes with thin, rocky soils. From stand age reconstructions, xeric sites supported an average of 45 trees/ha in 1861. Draws and other topographic concavities with deeper, finer-textured soils supported 13 trees/ha on average. Today, xeric sites support 156 trees/ha, and mesic sites 107 trees/ha. Estimated average tree ages in 1861, however, show stronger contrasts in tree dominance: 41 years in mesic sites, with one

Figure 1a. Tree establishment dates, high TRMI (mesic) sites.

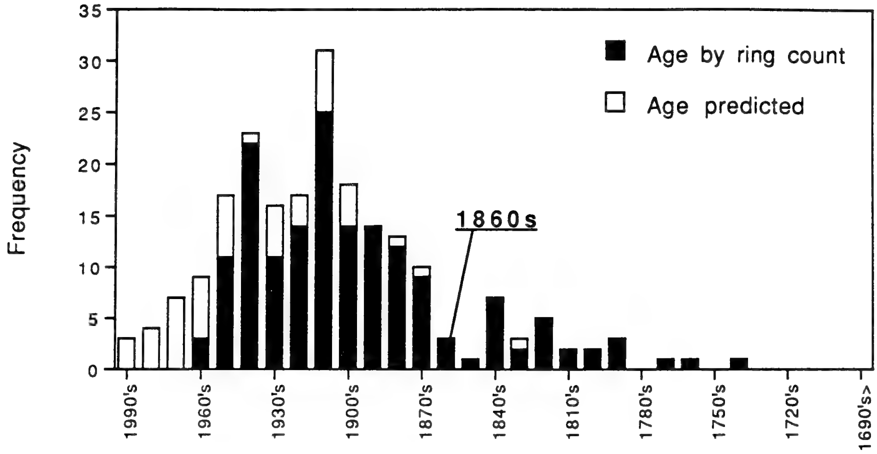
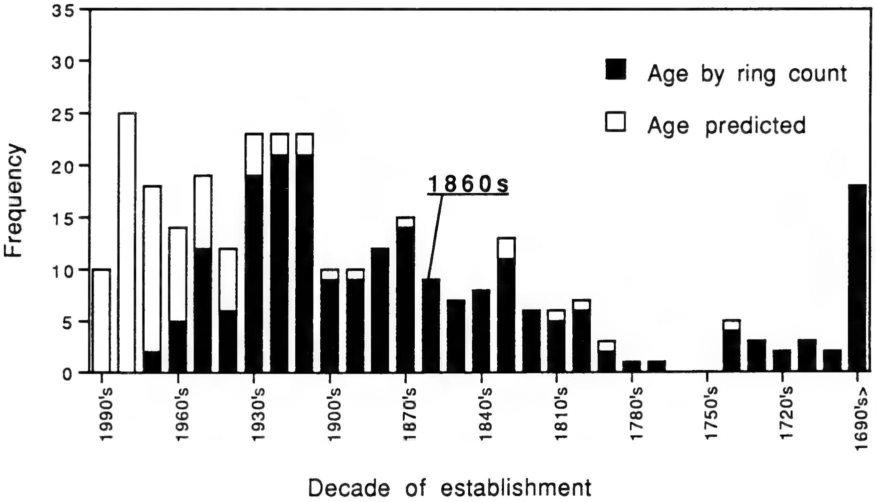


Figure 1b. Tree establishment dates, low TRMI (xeric) sites.



FIGS. 1a, b. Tree establishment dates of pinyon by decade, mesic (TRMI > 30) and xeric (TRMI < 30) sites along the lower montane treeline ecotone, Inyo and Mono Counties, California.

tree (0.5/ha) over 100 years old; and 92 years on xeric sites, with 33 trees (17 trees/ha) over 100 years. The average 41 year old pinyon today is about 125–150 cm tall, which is similar to the average shrub height in most of the plots. With 17/45 trees per hectare over 100 years old on xeric sites in 1861, ridges and slopes may have visually appeared as open, savanna-like stands consisting of predominantly mature, widely-spaced trees. Valley bottoms and draws may have appeared to be wholly absent of trees in 1861.

Both xeric and mesic sites have had considerable seedling recruitment since European settlement. In the last 135 years, estimated tree density has increased 400% on xeric sites and 800% on mesic sites. This is consistent with early observations that lower montane woodlands were primarily restricted to topographic convexities prior to 1861, and that existing stands were formerly more open and contained largely mature trees. As pinyon cover has increased on all topographic settings, understory shrub, grass and herb cover has decreased. Current understory total vegetation cover in xeric sites is 14% on average, whereas mesic sites support 31% understory cover. While these values of understory cover may also reflect different soil moisture regimes and edaphic settings, and not simply relationships to woodland canopy cover or competition with pinyon, the negative relationship between understory vegetation cover and tree density or can-

Table 1. Pinyon Stand Data for Xeric and Mesic Sites at the LMTE.*

	Number of trees		Tree density		Mean age (years)		Mature trees, 1861 (trees >100 years)	
	Current	1861	Current	1861	Current	1861	No.	Density
Xeric sites (TRMI < 30)	309	91	156/ha	45/ha	106.6	92	33	17/ha
Mesic sites (TRMI > 30)	212	28	107/ha	13/ha	83.6	41	1	0.5/ha
All sites	512	119	130.3/ha	29/ha	97.2	80	34	8.8/ha

* For all measures, stands on xeric sites are significantly different than mesic stands ($p < 0.01$).

opy cover is well-documented (Austin 1987; Everett and Koniak 1981; Pieper 1990).

At the larger scale of the entire elevational gradient of mountain ranges in the Great Basin, a coarse-grained view would show the altitudinal zonation of vegetation is largely influenced by effective soil moisture as determined by climatic variables, such as average precipitation and temperature (Daubenmire 1943; Billings 1951). However, a finer-grained view of the small scale topographic relationships along the LMTE suggests an inverse relationship of pinyon to topographically influenced moisture patterns. Greater pinyon stand development on xeric topographic settings along the LMTE is contrary to previous reports that montane tree species become increasingly restricted to mesic topographic settings towards the lower ecotone (Parker 1980; Peet 1988; Rourke 1988; Whittaker and Niering 1965). Two factors may have produced this inverse pattern: shrub and grass competition prior to 1861 may have excluded trees from the sites with deeper, finer-textured soils and more favorable moisture status; and, the greater density and biomass of shrubs and grasses may have supported more frequent fires, causing the mortality of invasive trees (Burkhardt and Tisdale 1969, 1976; Cottam and Stewart 1940; Blackburn and Tueller 1970). The introduction of livestock grazing in the West reduced competitive cover and fuel to carry fires, which may have allowed trees to become established, and then survive into maturity.

Acknowledgements

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CURRENT STATUS, STRUCTURE, AND PLANT SPECIES COMPOSITION OF THE RIPARIAN VEGETATION OF THE TRUCKEE RIVER, CALIFORNIA AND NEVADA

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ABSTRACT

Although riparian areas are a critical component of biodiversity in arid lands, our knowledge of many major rivers of the western United Startes remains limited. The Truckee River of California and Nevada is typical, with a general lack of published data on its riparian vegetation. Cover type mapping of eight reaches shows that the relative proportions between natural vegetation and cultural land-use types vary. Despite impacts from logging, railroad and highway construction, and water resource development, riparian vegetation along the upper three reaches is currently dominated by native riparian species. In the remaining reaches large proportions of the floodplain have been converted to urban and industrial or agricultural uses, or have been disturbed and are dominated by introduced weeds. Downstream reaches have also been more affected by flow regulation, water diversions, and related impacts. The lower reaches also, however, offer the greatest opportunities for restoration and enhancement of the riparian corridor. Data is also presented on the current plant species composition and structure of natural riparian vegetation which, in conjunction with hydrological data, can help land managers and biologists to formulate strategies for wildlife habitat enhancement.

Riparian areas are a critical component of biodiversity within the arid lands of the western United States and their importance is amplified by the minor proportion of the overall area which they occupy (Carothers 1977). Despite an increasing emphasis on the ecology and management of western riparian ecosystems over the past two decades (e.g., Johnson and Jones 1977; Warner and Hendrix 1984; Johnson et al. 1985; Knopf et al. 1988; Abell 1989; Clary et al. 1992), there remains a striking lack of published basic ecological data on many major western rivers. The Truckee River, one of three large rivers which drain eastward from the Sierra Nevada to sinks in western Nevada is typical, with refereed publications infrequent and of narrow focus. Papers have appeared regarding food preferences and demographics of beaver (Hall 1960; Busher et al. 1983), local flora (Savage 1973; Smith 1984), historical avifaunal changes along the lower Truckee River (Klebenow and Oakleaf 1984), and seed germination in *Salix* (Martens and Young 1992).

The Truckee River drains a 3100 km^2 basin in the Sierra Nevada into Pyramid Lake (elevation 1160 m), Nevada (Fig. 1). From Lake Tahoe (elevation 1899 m), the river flows 174 km through steep mountain canyons and narrow valleys, passes highly urbanized areas near the city of Reno, and continues through high desert canyons and irrigated agricultural land in broader valleys to its terminus. Significant development of natural resources in the Truckee River drainage began in the 1860's with extensive logging to provide timber to the nearby mining boomtown, Virginia City, and for railroad ties and snowsheds along the route of the Central Pacific Railroad (California Department of Water Resources 1991). Much of the Lake Tahoe Basin and the surrounding area was stripped of trees and the logs were transported by flumes along the river, as well as down the river channel itself.

Prior to the turn of the century, numerous dams had been built at the outlets of lakes, including one at the outlet of Lake Tahoe constructed in the early 1870's (California Department of Water Resources 1991). Subsequent to the passage of the Reclamation Act of 1902, the U.S. Bureau of Reclamation became the major developer of water projects on the Truckee River. Derby Dam, downstream of Reno, was this agency's first construction project (Fig. 1). Completed in 1905 as part of the Newlands Project, the dam and its conveyance canal were designed to transfer water from the Truckee River to arable land with little rainfall in the adjacent Carson River drainage. Irrigation water supplied by the project continues to be the single largest use of Truckee River water.

As a result of this water diversion, a steep decline in the water surface elevation of Pyramid Lake began in about 1910. The lake elevation reached a low point in the late 1960's at about 23 m below its pre-Derby Dam diversion level. In response, the lower eight km of the river channel widened and incised into its floodplain, stranding the adjacent river terraces (Born 1972; Water Engineering & Technology, Inc. 1991). Channelization of the river during the 1960's led to further

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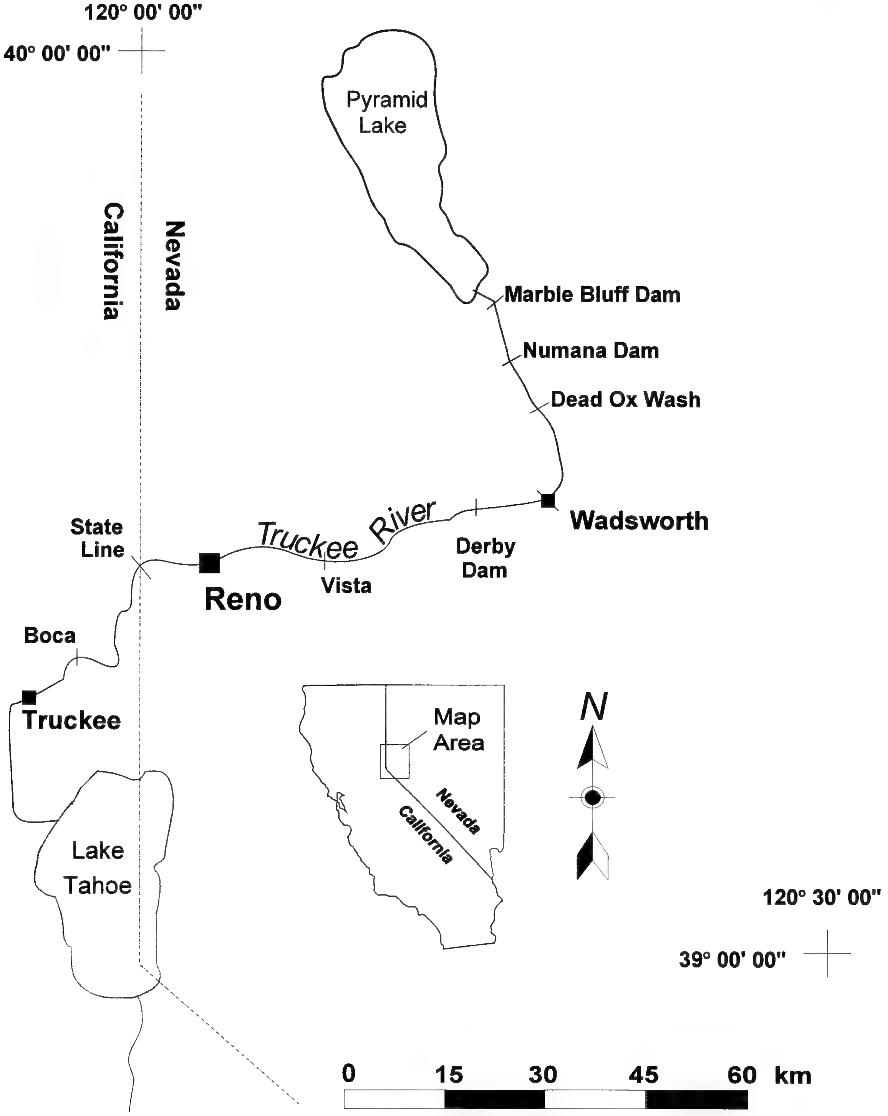


FIG. 1. Location of the study area along the Truckee River, California and Nevada. Urban areas and boundaries of the eight reaches are shown.

incision downstream of Wadsworth (Glancy et al. 1972). Since about 1990, the lake elevation has been about 15 m below the pre-Derby Dam level.

Federal reservoirs for water storage and flood control in the Truckee River watershed and their construction dates include Boca (1937), Prosser Creek (1962), and Stampede Reservoir (1970), all owned by the Bureau of Reclamation, and Martis Creek (1971), owned by the U.S. Army Corps of Engineers. These reservoirs combined provide about 317,000 acre-feet of usable storage. Numerous smaller non-Federal reservoirs and diversions are located in the Truckee River watershed.

In an attempt to reduce water loss due to evapotranspiration, beaver (*Castor canadensis*) were introduced to the drainage in the late 1940's (Hall 1960). Evidence of beaver activity, primarily gnawed trunks, is present throughout the river corridor although serious impacts seem highly localized.

This study was restricted to the riparian corridor along the 174 river kilometers of the mainstem of the Truckee River from Lake Tahoe Dam to Marble Bluff Dam. In this paper, I present baseline data on the vascular plant species composition, structure, and areal extent of the existing riparian vegetation of this area in order to provide a framework for future ecological research.

METHODS

Terminology. Throughout this paper, the terms "riparian" and "riparian corridor" are used in the functional sense of a "three-dimensional zone of interaction between terrestrial and aquatic ecosystems" (Gregory et al. 1991). As such, the riparian zone includes, at a minimum, the low-flow and active river channels and the inferred historic floodplain. Because of the vertical component of the definition, the riparian zone upstream of State Line may also include, as a minor component, lower hillslopes supporting coniferous forests. It is important to note that "riparian" as used in this paper is not synonymous with "wetland" in a jurisdictional sense. In most areas downstream of Reno, and especially downstream of Derby Dam, flow regulation and water diversion have altered the natural hydrography of the river and contributed to lowered groundwater tables with a consequent shift toward a less hydrophytic vegetation. As noted earlier, this effect has been most profound in the lower eight km of the river upstream of Pyramid Lake.

Cover type mapping. The 174 km river corridor was subdivided into eight reaches based on morphological, geological, and hydrological characteristics. The reaches vary in length, stream gradient, floodplain area, and the ratio between floodplain area and reach length (Table 1). The latter is an indicator of the local constraints imposed on the channel and valley floor by geomorphic features and, by extension, the width of the riparian corridor (Gregory et al. 1991). Natural vegetation and land use types within the riparian zone were mapped on acetate overlays of enlarged black-and-white aerial photography at a scale of 1:1200. Source photos for these enlargements were flown on November 4, 1991; the scale of the original photos was 1:12,000. Cover type polygons were manually delineated. The minimum mapping criterion for forested types was at least six trees (as defined below) in an area of 0.2 ha. The overlays were scanned into AUTOCAD and areas were calculated for each cover type by polygon. Areas adjacent to, and enroute to, field sample sites were field checked for boundary and classification accuracy and revised accordingly. Because of interpretation difficulties, some non-forested areas outside of the historic floodplain may have been incorrectly included. These inaccuracies are believed to have resulted in only minor overestimates of the extent of the riparian zone downstream of Reno.

Data collection. Data on plant species composition and abundance were collected only from natural vegetation types, excepting marshes and ponds, along 31 transects at 11 sites. Sites were chosen to be representative of general conditions with the study reaches and to isolate, to the extent possible, river hydrology as a controlling variable for vegetation from other hydrological influences (e.g., irrigated pastures above channel banks, unlined irrigation canals, springs, sewage effluent runoff, and significant grading and fill placement). An additional constraint was relative proximity to stream

TABLE 1. RIVER LENGTH, CHANGE IN ELEVATION, RIVER GRADIENT, RIPARIAN ECOSYSTEM AREA, AND THE RATIO OF FLOODPLAIN AREA TO RIVER LENGTH FOR THE EIGHT TRUCKEE RIVER STUDY REACHES. The ratios are measures of stream gradient and width of the riparian corridor, respectively. Lake Tahoe outlet dam lies at 1899 m, Marble Bluff Dam at 1176 m.

Reach	Length (km)	Elevation change (m)	Gradient (m/km)	Area (ha)	Corridor ratio (ha/km)
Lake Tahoe to Boca	37.03	222.20	6.00	166.37	4.49
Boca to State Line	20.93	152.40	7.28	206.81	9.88
State Line to Vista	37.03	183.88	4.97	393.86	4.96
Vista to Derby Dam	27.37	60.96	2.23	537.97	19.66
Derby Dam to Wadsworth	17.71	30.48	1.72	403.32	22.77
Wadsworth to Dead Ox	16.10	39.62	2.46	505.24	31.38
Dead Ox to Numana Dam	6.44	15.24	2.37	72.76	11.30
Numana to Marble Bluff Dam	11.27	18.22	1.62	422.18	37.46
Total	173.88	723.00	4.16	2708.51	15.58

gages so that channel hydraulics could be calculated in order to relate flow rates to topographic inundation. Areas with extensive recent activity by beavers were avoided, as were areas of recent logging or fuelwood cuttings. The transects were oriented perpendicular to the river channel and varied in length according to the width of the riparian zone. A total length of 3380 m was sampled. Data were collected by structural layer according to the following definitions and procedures:

Tree layer.—Single- or multiple-stemmed woody plants ≥ 6 m in height and ≥10 cm diameter-at-breast height (dbh). Data were collected on dbh and density within 15 m of the transect (i.e., a 30 m belt transect). Stand canopy coverage was estimated by species at random locations along the transect using a spherical densiometer. Average stand canopy height was estimated using a clinometer.

Shrub layer(s).—All woody plant species < 6 m in height or < 10 cm dbh. Canopy coverage was estimated visually along each transect using the line-intercept method (Mueller-Dombois and Ellenberg 1974). Data were collected in three height classes: tall shrubs (>3 m), medium shrubs (>1 m and ≤3 m), and low shrubs (≤1 m).

Herbaceous layer.—Non-woody species including herbs, grasses, and graminoids. Canopy coverage visually estimated by species using the line-intercept method.

Ground surface.—Ground surface data on brush-piles, litter, and bare ground was tallied using the line-intercept method. Bare ground was further recorded as clay, sand, gravel, cobbles, or boulders.

Other information collected included site elevation (taken from topographic maps), transect orientation (measured from aerial photos), current land use, and evidence of recent disturbance (e.g., grazing, beaver activity). The taxonomic reference for all plant scientific names is Hickman (1993).

Data analysis. The areal coverage of individual vegetation and land use types was calculated by reach. Vegetation data from the transects were summarized for transect segments stratified by physiognomic type (forest, shrub, herbaceous). Each segment was treated as a sample of its physiognomic type. The total of 178 samples were subjected to Two-way Indicator Species Analysis (TWINSPAN), a hierarchical classification procedure (Hill 1979; Gauch and Whittaker 1981); the TWINSPAN output was further refined based on the field experience and professional judgement of the investigator.

RESULTS

Physical characteristics. Physical characteristics of each of the eight reaches are provided in Table 1. The disparity in reach lengths is due to the variety of geologic and topographic settings through which the Truckee River passes along its course from the Sierra Nevada to Pyramid Lake. This is also reflected in the river gradient which generally decreases from Lake Tahoe to Pyramid Lake. There is a corresponding general increase in the width of the riparian corridor. Exceptions to this trend occur in the State Line-Vista and Dead Ox-Numana Dam reaches, where the river passes through narrow bedrock canyons.

Cover type mapping. Four major categories of aquatic ecosystem, natural vegetation, and cultural types were mapped (Fig. 2). These include: 1) the active channel of the river including the low-flow wetted channel; 2) riparian forest and riparian shrub communities on the floodplain; 3) cultural types on the floodplain; and, 4) upland forest and upland shrub communities. The boundaries of the low-flow wetted channel were based on the area covered by water on the November 4th date of the aerial photographs. Also occurring within the active channel were sparsely-vegetated cobble bars and patches of graminoids and herbs, here referred to as the vegetated streambed. There is a dynamic relationship among these three elements of the active channel. The boundaries of the low-flow wetted channel expand and contract in response to annual climatic variation, and water regulation or diversion. Channel scour during high flows leads to an increase in the amount of cobble bars. Conversely, the absence of scouring flows results in an increase in the total area of vegetated streambed. Because this study was conducted during the sixth consecutive year of drought, the ratio of vegetated streambed within the active channel was greater than normal, when compared to either the cobble bars or the low-flow wetted channel. Overall, the active channel comprises about 25% of the riparian corridor, although in the steep, narrow canyons which characterize the Lake Tahoe-Boca and Dead Ox Wash-Numana Dam reaches, this value increases to 51% and 38%, respectively (Fig. 2).

Riparian forest and riparian shrub communities occur on the floodplain of the river in most reaches. Deciduous riparian forests comprise between 2% and 20% of the riparian corridor upstream of Reno, with the lowest percentage occurring above Boca (Fig. 2). Downstream of Reno, the range is narrower (6% to 18%), although no riparian forest occurs in the Dead Ox-Numana Dam reach (Figs. 2, 3). A similar pattern is seen in the riparian shrub communities. Upstream of Reno, riparian shrub communities comprise 22% to 28% of the riparian corridor (Fig. 2). Downstream of Reno, riparian shrub communities comprise 5% to 14% of the riparian corridor (Figs. 2, 3).

Cultural types were defined to include agricultural fields and facilities, urban and industrial areas, sites dominated by the noxious weed *Lepidium latifolium,* and other disturbed areas. The proportions of the riparian corridor occupied by these habitats is low to moderate (7%–29%) in the upper three reaches, high (45–60%) in the middle three reaches,

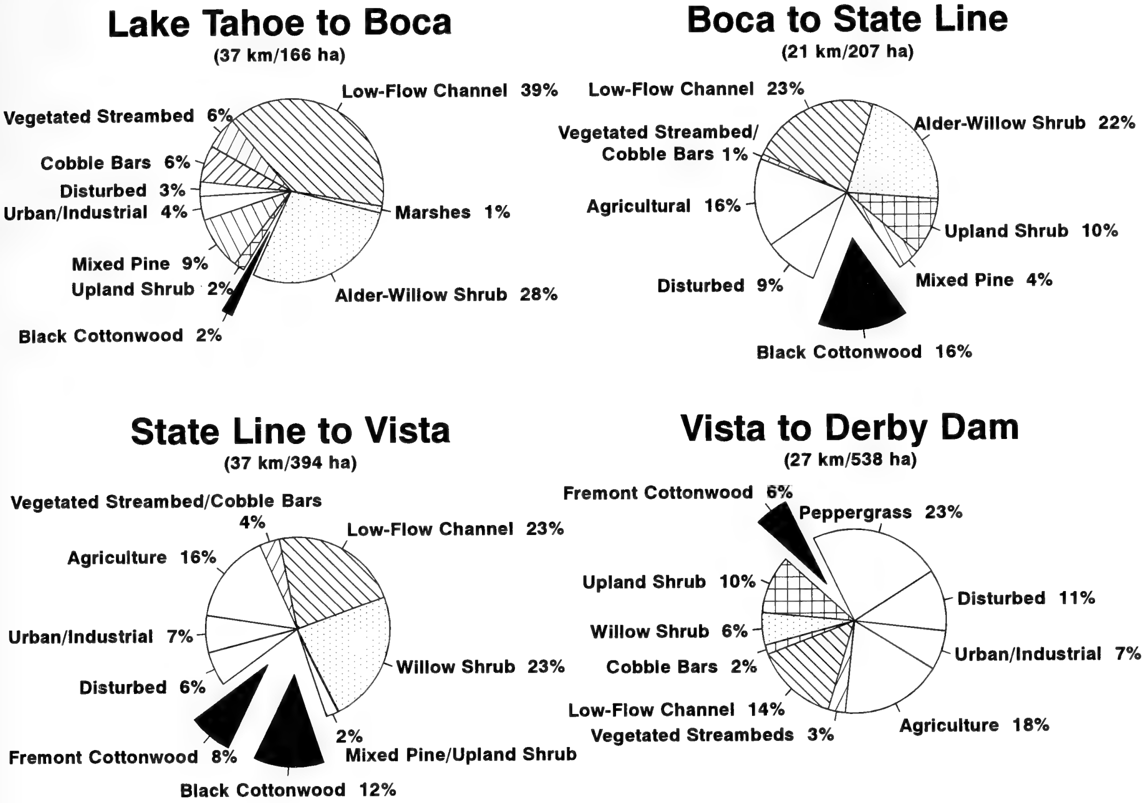


FIG. 2. Percentages of vegetation, aquatic, and land-use types for the upper four study reaches along the Truckee River. The length and area of riparian corridor is provided for each reach in parentheses.

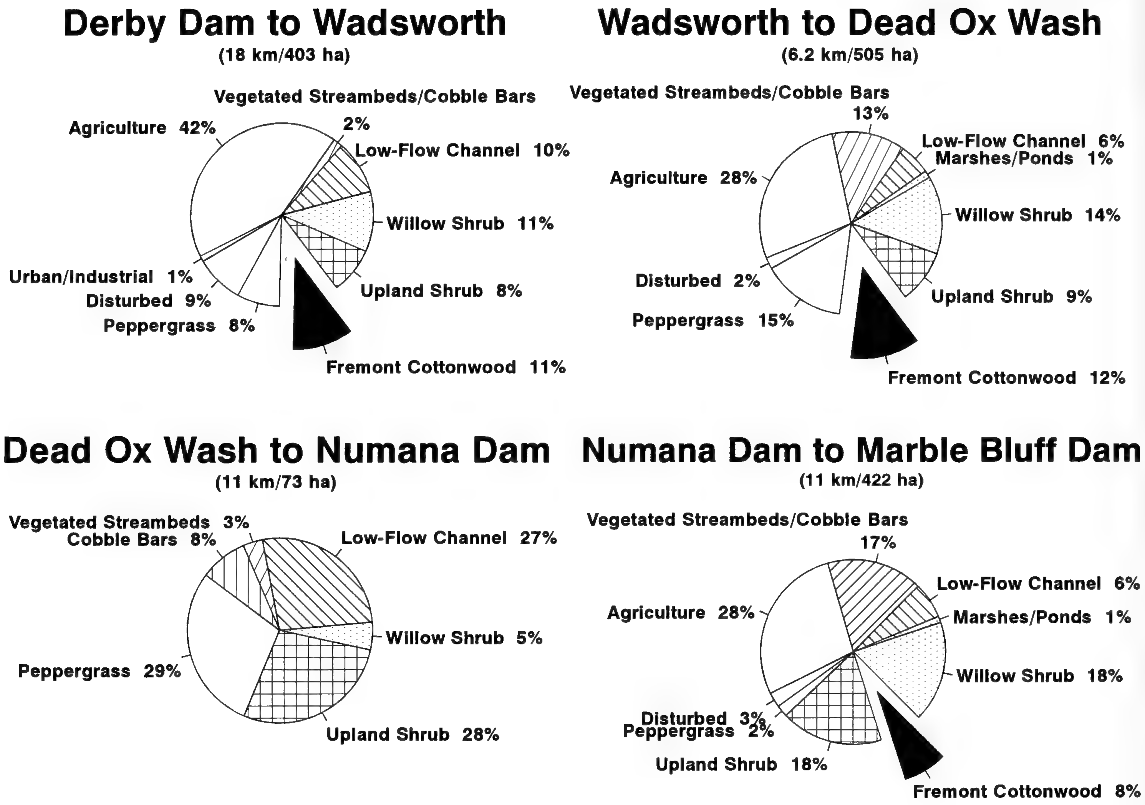
and moderate (29–33%) in the lower two reaches (Figs. 2, 3).

Mixed pine communities occur on lower hillslopes adjacent to the floodplain only along the upper three reaches where they comprise 2% to 9% of the riparian corridor (Fig. 2). Upland shrub communities occur on the floodplain in all reaches where they account for 2% to 10% of the riparian corridor, except along the lower two reaches where they comprise 18% and 28% of the corridor (Fig. 3). Marshes and ponds occur in several reaches, but they never account for more than 1% in any reach in which they occur (Figs. 2, 3).

Species composition and abundance. The results of the TWINSPAN analysis supported distinctions between groups of samples of riparian forest, riparian shrub, vegetated streambed and cobble bar communities based on their occurrence upstream or downstream of Reno (Tables 2, 3). Upstream of Reno samples correspond roughly to the upper three study reaches, while samples downstream of Reno correspond to the lower five study reaches. Upland shrub communities showed no such distinction, perhaps due to the infrequent occurrence of this type along transects upstream of Reno. Upland mixed pine forests occur only along the upper three reaches.

Populus trichocarpa ssp. *balsamifera,* with 80% canopy coverage, is the dominant tree species in deciduous riparian forests along the upper three reaches (Table 2). A tall shrub layer with 15% cover, dominated by *Salix lutea,* is present. The only other riparian shrubs present are *S. exigua* and saplings of *P. trichocarpa* ssp. *balsamifera,* each with only a few percent cover. Minor amounts of upland shrubs also occur in this type. The understory is dominated by *Elymus trachycaulus* and *Poa pratensis* with 19% and 14% coverage, respectively. *Conium maculatum* and *Urtica dioica* are the dominant herbaceous species.

Both *Populus trichocarpa* ssp. *balsamifera* and *P. fremontii* ssp. *fremontii* (Fremont cottonwood) dominate individual deciduous riparian forest patches in the State Line-Vista reach, although no mixed stands of these species as canopy dominants were observed. Downstream of this reach, *P. fremontii,* with 70% canopy coverage, is the sole dominant tree in the riparian forests (Table 3). There is a conspicuous dearth of riparian shrubs in these forests, where tall shrubs of *P. fremontii* provide only about 8% cover. *Artemisia tridentata* ssp. *tridentata* is present in small amounts, and there is a sparse understory of *Elymus trachycaulus* and *Lepidium latifolium.*


Derby Dam to Wadsworth (18 km/403 ha)

Wadsworth to Dead Ox Wash (6.2 km/505 ha)

Dead Ox Wash to Numana Dam (11 km/73 ha)

Numana Dam to Marble Bluff Dam (11 km/422 ha)

FIG. 3. Percentages of vegetation, aquatic, and land-use types for the lower four study reaches along the Truckee River. The length and area of riparian corridor is provided for each reach in parentheses.

A shift occurs in the dominant species of the riparian shrub communities which corresponds to that seen in the riparian forest, although the transition is more gradual. Upstream of Reno, tall and medium height shrubs of *Alnus incana* ssp. *tenuifolia* dominate this community, although numerous other riparian shrubs typically occur with it (Table 2). A wide variety of grasses, graminoids, and herbaceous plants make this the most diverse of all the habitats investigated. *Alnus incana* ssp. *tenuifolia* is much less common downstream of Reno, where the dominant species in the riparian shrub community is *Populus fremontii* ssp. *fremontii* of medium and low stature (Table 3). Numerous other riparian shrubs are associated with this type, and there is a well-developed grass, graminoid and herbaceous layer dominated by *Lepidium latifolium* with 21.8% coverage.

Vegetated streambed communities in the upper three reaches were dominated by *Poa pratensis* and *Elymus trachycaulus,* with 10.7% and 9.4% coverage, respectively (Table 2). *Carex aquatilis* and *C. utriculata* are common associates. Downstream of Reno, vegetated streambed communities are dominated by *Eleocharis acicularis* and *Lepidium latifolium* with 29.4% and 29.8% coverage, respectively (Table 3). *Scirpus americanus* and *Melilotus alba* are the most abundant associated species. Cobble bars are only sparsely vegetated in all reaches, but still differ distinctly in species composition. Upstream of Reno, *Carex utriculata* and *Glyceria striata* are the most abundant species (Table 2). Downstream of Reno, the most abundant species on cobble bars is *Lepidium latifolium* (Table 3).

Upland forests along the upper three study reaches are generally comprised of mixtures of *Abies concolor, Pinus jeffreyi,* and *P. contorta* ssp. *murrayana,* although pure stands of the latter species can be found. *Populus balsamifera* ssp. *trichocarpa* occurs infrequently in these forests (Table 2). Upland shrubs comprise about 26% coverage, while grasses and graminoids dominate the understory. Upland shrub communities are the predominant vegetation adjacent to the riparian corridor along the five lower reaches, where they occasionally extend onto the floodplain. *Artemisia tridentata* ssp. *tridentata* is the dominant species in this community (Table 3). The most abundant associated shrub species are *Chrysothamnus viscidiflorus* and *Shepherdia argentea.* Associated grasses include *Leymus cinereus* and *Bromus tectorum.* Because this study was conducted during the sixth consecutive year of drought, the abundance of the latter species

TABLE 2. PLANT SPECIES COMPOSITION AND ABUNDANCE IN RIPARIAN VEGETATION TYPES ALONG THE UPPER TRUCKEE RIVER, CALIFORNIA/NEVADA. Abundance values are absolute percent canopy coverage. Introduced species are marked with an asterisk. Total and mean transect lengths, and ground surface characteristics for each type are also included.

Name	Cobble bars (n=15)	Vegetated streambed (n=17)	Riparian shrub (n=40)	Riparian forest (n=4)	Mixed pine forest (n=12)
Total/mean transect length (m)	93.3/8.5	170.0/10.0	371.2/9.3	208.5/52.1	84.4/10.6
Trees					
Populus balsamifera ssp. *trichocarpa*	—	—	—	80.1	1.1
Abies concolor	—	—	—	—	16.7
Pinus jeffreyi	—	—	—	—	13.8
Pinus contorta ssp. *murranyana*	—	—	—	—	15.5
Layer Total	—	—	—	80.1	47.1
Tall Riparian Shrubs					
Alnus incana ssp. *tenuifolia*	—	—	19.1	—	—
Salix lutea	—	0.5	1.5	12.8	—
Salix melanopsis	—	0.6	0.7	—	—
Populus balsamifera ssp. *trichocarpa*	—	—	2.5	2.3	—
Layer Total	—	1.1	23.8	15.1	—
Medium Riparian Shrubs					
Alnus incana ssp. *tenuifolia*	—	1.4	23.0	—	1.1
Populus balsamifera ssp. *trichocarpa*	—	—	1.7	0.5	—
Salix lucida ssp. *lasiandra*	—	0.5	7.0	—	—
Salix lutea	—	—	5.4	1.5	—
Salix exigua	—	—	0.1	0.2	—
Salix melanopsis	—	—	0.5	—	—
Cornus sericea	—	—	0.3	—	—
Layer Total	—	1.9	38	2.2	1.1
Low Riparian Shrubs					
Salix exigua	0.6	0.1	1.4	—	—
Salix lutea	—	—	0.2	—	—
Populus balsamifera ssp. *trichocarpa*	0.1	0.3	1.9	0.2	2.4
Alnus incana ssp. *tenuifolia*	—	—	0.5	—	—
Salix lucida ssp. *lasiandra*	—	—	0.4	—	—
Cornus sericea	—	—	0.3	—	—
Salix melanopsis	—	—	0.1	—	—
Layer Total	0.7	0.4	4.8	0.2	2.4
Upland Shrubs					
Artemisia tridentata ssp. *tridentata*	0.1	0.8	0.1	0.1	5.5
Rosa woodsii var. *ultramontana*	—	1.3	2.7	0.3	5.8

TABLE 2. CONTINUED

Name Total/mean transect length (m)	Cobble bars (n=15) 93.3/8.5	Vegetated streambed (n=17) 170.0/10.0	Riparian shrub (n=40) 371.2/9.3	Riparian forest (n=4) 208.5/52.1	Mixed pine forest (n=12) 84.4/10.6
Chrysothamnus nauseosus	1.1	0.4	—	—	0.6
Chrysothamnus viscidiflorus	—	—	0.7	0.8	—
Ribes viscosissimum	—	—	0.4	—	3.4
Populus tremuloides	—	—	1.4	—	—
Amelanchier alnifolia var. *pumila*	—	—	—	—	6.5
Symphoricarpos rotundifolius	—	—	—	—	3.1
Purshia tridentata var. *tridentata*	—	—	—	—	0.7
Layer Total	1.2	2.5	5.3	1.2	25.6
Grasses and Graminoids					
*Poa pratensis**	1.5	10.7	6.1	14.1	2.2
*Hordeum brachyantherum**	0.2	2.3	0.2	4.6	8.8
Carex subfusca	1.0	1.7	4.7	—	—
Glyceria striata	2.3	0.4	4.6	—	—
Carex athrostachya	1.0	3.3	0.6	—	—
Alopecurus aequalis	0.2	2.2	0.8	—	—
Agrostis exarata	0.1	2.9	0.6	—	—
Juncus mexicanus	1.4	—	—	0.2	1.6
*Dactylis glomerata**	0.6	—	—	—	—
Scirpus microcarpus	0.5	—	0.5	—	—
Carex utriculata	6.7	5.1	1.0	—	—
Carex aquatilis	—	5.1	1.1	—	—
*Phalaris arundinacea**	—	1.2	0.9	—	—
Juncus effusus	—	—	0.4	—	—
Carex lenticularis	—	—	0.2	—	—
Carex lanuginosa	—	—	0.2	—	—
Achnatherum occidentalis	—	—	0.1	—	0.2
Elymus trachycaulus	—	9.4	5.9	19.4	5.1
Juncus balticus	—	—	0.1	0.2	—
*Bromus tectorum**	—	—	0.6	2.2	2.8
Calamagrostis rubescens	—	—	—	—	3.1
Layer Total	15.5	44.3	28.6	40.7	23.8
Herbs					
Epilobium ciliatum	1.8	0.1	0.6	—	—
Mimulus guttatus	0.3	2.0	0.5	—	—
*Melilotus alba**	0.4	1.4	0.3	—	—
Sphenosciadium capitellatum	0.2	—	—	—	—
*Lepidium latifolium**	0.1	0.3	—	—	—

TABLE 2. CONTINUED

Name Total/mean transect length (m)	Cobble bars (n=15) 93.3/8.5	Vegetated streambed (n=17) 170.0/10.0	Riparian shrub (n=40) 371.2/9.3	Riparian forest (n=4) 208.5/52.1	Mixed pine forest (n=12) 84.4/10.6
Rumex triangulivalvis	0.3	0.3	—	—	—
*Plantago lanceolata**	0.1	0.2	—	—	—
Lupinus sp.	0.5	—	—	—	—
Equisetum arvense	0.7	5.3	5.3	0.3	—
Artemisia ludoviciana	0.3	0.1	0.5	1.2	—
Solidago canadensis	1.2	0.5	1.3	—	—
*Trifolium repens**	0.2	—	0.3	—	—
*Verbascum thapsus**	—	0.2	0.6	—	—
*Tragopogon dubius**	—	0.2	—	0.3	—
Arnica amplexicaulis	—	1.1	—	—	—
Smilicina stellata	—	1.4	—	—	—
Potentilla glandulosa	—	0.3	—	—	—
Galium triflorum	—	0.1	—	—	—
Equisetum fluviatile	—	0.1	0.6	—	0.4
Hypericum anagalloides	—	0.1	0.1	—	—
Cicuta douglasii	—	2.8	1.6	—	—
*Cirsium arvense**	—	1.9	0.2	2.3	—
*Conium maculatum**	—	1.7	3.7	8.5	0.7
Artemisia dracunculus	—	—	0.7	—	—
Fragaria virginiana	—	—	0.1	—	—
Phacelia heterophylla	—	—	0.1	—	—
Urtica dioica	—	—	0.3	4.5	—
Vicia americana	—	—	—	0.3	—
Heracleum lanatum	—	—	0.1	—	1.7
Wyethia mollis	—	—	—	—	0.2
Sidalcea glaucescens	—	—	—	—	0.3
Polygonum douglasii	—	—	—	—	0.1
Eriogonum umbellatum	—	—	—	—	0.1
Penstemon sp.	—	—	—	—	0.1
Layer Total	6.1	20.1	16.9	17.4	3.6
Ground Surface					
Litter	14.1	56.3	65.2	63.1	75.1
Boulders	15.6	3.9	4.7	5.6	1.5
Cobbles	49.5	19.7	1.3	1.2	—
Gravel	10.1	—	—	—	0.5
Sand	—	2.1	—	6.4	6.3
Silt/clay	3.6	—	0.2	—	—
Brush piles	—	1.0	7.8	3.7	—
Ground Surface Total	92.9	83.0	85.0	80.0	83.4

TABLE 3. PLANT SPECIES COMPOSITION AND ABUNDANCE IN RIPARIAN VEGETATION TYPES ALONG THE LOWER TRUCKEE RIVER, NEVADA. Abundance values are absolute percent canopy coverage. Introduced species are marked by an asterisk. Total and mean transect lengths, and ground surface characteristics for each type are also included.

Name Total/mean transect length (m)	Cobble bars (n=20) 545.0/27.3	Vegetated steambed (n=25) 238.7/9.6	Riparian shrub (n=15) 107.0/7.1	Riparian forest (n=13) 271.3/20.9	Upland Shrub (n=17) 215.2/12.7
Trees					
Populus fremontii ssp. *fremontii*	—	—	—	70.1	—
Tall Riparian Shrubs					
Populus fremontii ssp. *fremontii*	—	—	0.9	7.8	—
Alnus incana ssp. *tenuifolia*	—	—	5.1	—	—
Eleagnus angustifolius	—	—	3.6	—	—
Layer Total	—	—	9.6	7.8	—
Medium Riparian Shrubs					
Populus fremontii ssp. *fremontii*	0.2	—	18.6	0.9	—
Salix exigua	—	—	4.8	—	—
Salix lutea	—	—	1.2	—	—
Salix lucida ssp. *lasiandra*	—	—	1.3	—	—
Alnus incana ssp. *tenuifolia*	—	—	1.0	—	—
Eleagnus angustifolia	—	—	0.9	—	—
Populus balsamifera ssp. *trichocarpa*	—	—	0.8	—	—
Layer Total	0.2	—	28.6	0.9	—
Low Riparian Shrubs					
Populus fremontii ssp. *fremontii*	0.1	0.3	19.5	—	—
Salix exigua	0.3	—	2.1	0.4	—
Salix lucida ssp. *lasiandra*	0.1	—	2.0	—	—
Alnus incana ssp. *tenuifolia*	—	—	0.5	—	—
Salix lutea	—	—	0.3	—	—
Layer Total	0.5	0.3	24.4	0.4	—
Upland Shrubs					
Artemisia tridentata ssp. *tridentata*	1.3	0.1	—	3.8	42.4
Chrysothamnus viscidiflorus	0.2	—	—	—	5.5
Sarcobatus vermiculatus	0.2	—	—	—	0.3
Prunus andersonii	0.1	—	—	—	0.1
Gutierrezia sarothrae	0.1	—	—	0.1	0.1
Chrysothamnus nauseosus	—	—	1.8	—	0.7
Shepherdia argentea	—	—	—	—	6.0
Layer Total	1.9	0.1	1.8	3.9	55.1

TABLE 3. CONTINUED

Name Total/mean transect length (m)	Cobble bars (n=20) 545.0/27.3	Vegetated steambed (n=25) 238.7/9.6	Riparian shrub (n=15) 107.0/7.1	Riparian forest (n=13) 271.3/20.9	Upland Shrub (n=17) 215.2/12.7
Grasses and Graminoids					
*Bromus tectorum**	0.3	1.1	0.7	—	1.9
Leymus cinereus	0.3	0.2	—	0.1	3.3
Carex lenticularis	0.1	—	—	—	—
Carex douglasii	0.1	0.2	—	—	—
Juncus balticus	0.4	0.5			
*Poa pratensis**	0.4	—	2.0	—	—
Eleocharis acicularis	—	29.4	1.0	—	—
Scirpus americanus	—	4.3	1.3	—	—
*Polypogon monspielensis**	—	2.7	2.4	—	—
Juncus effusus	—	0.9	0.8		
*Holcus lanatus**	—	0.9	2.0	—	—
Carex utriculata	—	—	1.1	—	—
*Phalaris arundinacea**	—	—	1.0	—	—
Carex athrostachya	—	—	0.4	—	—
*Hordeum brachyantherum**	—	—	0.1	—	—
Elymus trachycaulus	—	0.1	1.1	4.8	—
Distichlis spicata	—	—	—	0.1	0.3
Layer Total	1.6	40.3	13.9	5.0	5.5
Herbs					
*Lepidium latifolium**	4.4	29.8	21.8	6.8	1.0
*Melilotus alba**	0.4	5.3	9.1	—	—
Artemisia dracunculus	0.1	0.4	1.0	—	—
Epilobium ciliatum	0.1	1.6	0.6	—	—
*Trifolium repens**	0.3	0.8	1.3	—	—
*Salsola kali**	0.1	—	—	—	—
Artemisia ludoviciana	0.1	—	—	—	—
Xanthium strumarium	—	2.8	—	—	—
Mimulus guttatus	—	0.2	0.3	—	—
*Conringia orientalis**	—	—	3.1	—	—
Castilleja minor	—	—	0.2	—	—
*Plantago lanceolata**	—	—	0.1	—	—
Urtica dioica	—	—	0.2	—	—
Cicuta douglasii	—	—	0.1	—	—
Equisetum arvense	—	—	0.1	—	—
Layer Total	5.5	40.9	37.9	6.8	1.0

Table 3. Continued

Name	Cobble bars (n=20)	Vegetated steambed (n=25)	Riparian shrub (n=15)	Riparian forest (n=13)	Upland Shrub (n=17)
Total/mean transect length (m)	545.0/27.3	238.7/9.6	107.0/7.1	271.3/20.9	215.2/12.7
Ground Surface					
Litter	30.8	20.1	40.9	65.3	51.1
Boulders	0.9	—	—	—	—
Cobbles	28.4	4.0	13.8	1.0	2.3
Gravel	3.8	—	—	1.3	1.5
Sand	31.3	32.7	27.0	25.2	33.9
Silt/clay	1.6	30.2	—	—	—
Brush piles	0.3	—	3.0	1.2	0.3
Ground Surface Total	97.1	87.0	84.7	94.0	89.1

was substantially reduced from its typical abundance during wetter periods.

Discussion

The conversion of the riparian corridor of the Truckee River to urban, industrial, and agricultural uses, water resource development, and other human activities has led to a significant decline in the biological resources of the riparian corridor. Although some areas have recovered from earlier impacts, the type, degree, and extent of recovery from these actions varies among the study reaches. For example, the Lake Tahoe-Boca reach was intensively logged in the last half of the 19th century. Today, much of the riparian corridor in this area has natural vegetation with only 7% in either urban and industrial uses or otherwise disturbed.

In the downstream reaches between Boca (CA) and Vista (NV), human activities continue to directly impact between 25% and 29% of the riparian corridor. For the lowermost of these two reaches, which contains the city of Reno, this is a significant underestimate of the historic losses within the riparian corridor since the river in this area is contained between flood control levees.

The riparian corridor in the two reaches between Vista and Wadsworth is dominated by agricultural and industrial uses, or is otherwise disturbed. Only about 40% of the riparian corridor in these reaches remains in natural condition. Downstream of Wadsworth, the proportion of natural vegetation increases to between 55% and 70%.

Two aspects of the data are of particular interest in regard to ecological restoration within the riparian corridor. These are: 1) the relative impacts of introduced plant species; and, 2) the potential amount of habitat available for restoration. With respect to introduced plant species, the habitats vary when compared to each other as well as among reaches. Along the upper Truckee River, introduced plants include only grasses and herbs (Table 2). They are most abundant in the understory of the riparian forests where they comprise 47% of the total vegetative cover. Three species, *Poa pratensis, Hordeum brachyantherum,* and *Conium maculatum* account for most of this cover.

Along the lower Truckee River, the introduced shrub *Eleagnus angustifolius* is a minor component of the riparian shrub community, but here are numerous introduced grasses and herbs. Individual species of introduced grass comprise only a few percent of any community. The predominant introduced herb is *Lepidium latifolium,* which dominates the herbaceous layer of all natural vegetation but the upland shrub community. Overall, it accounts for 33% to 72% of the total understory cover, and is most abundant in the vegetated streambed and riparian shrub communities.

If one assumes that the total area currently occupied by agricultural and otherwise disturbed areas (including areas dominated solely by *Lepidium latifolium*) represents the maximum amount of area potentially available for habitat restoration, the three lower river reaches between Vista and Dead Ox Wash offer the most potential for restoration, with 280 ha, 238 ha, and 227 ha of these habitats, respectively. This is not, however, to say that potential restoration opportunities are not available, or should not be pursued, in other reaches. Opportunities are most limited in reaches where the floodplain is restricted to a relatively narrow canyon bottom. Examples include upstream of the town of Truckee where the already narrow floodplain is constrained by a highway and an increasing number of residences, and in the narrow gorge between Dead Ox Wash and Numana Dam. Urban and industrial areas in the vicinity of Reno also offer limited restoration opportunities.

The presence of suitable habitat is not the only factor constraining restoration opportunities. Aside from the obvious need for the cooperation of private landowner's, ecological processes must also be considered. As noted in the introduction, downstream of Numana Dam the river has incised deeply into floodplain terraces which formerly supported extensive stands of cottonwood forest. The scattered skeletons of dead trees and the few decadent living cottonwood trees which remain on these terraces suggest that groundwater levels in this area have dropped beyond that necessary to maintain trees.

Serious constraints on restoration potential also exist upstream of the area where significant channel incision has occurred. Flow regulation and water diversions have altered the magnitude, timing, frequency, and duration of flows in the river. These changes have had the greatest effect downstream of Derby Dam where the interbasin diversion of water to the Carson River drainage takes place. River terraces which currently support cottonwood forests are no longer flooded with the historic frequency, so conditions conducive to cottonwood (and willow) seed germination are less frequent. This partially accounts for the paucity of replacement cottonwoods in the shrub layers of the cottonwood forests, as well as the absence of any associated riparian shrubs. This absence, and the fact that *Artemisia tridentata* ssp. *tridentata* is the only shrub present in these forests, suggests that groundwater levels are below the effective rooting depth of riparian shrubs for an insufficient length of time to allow the establishment of any seedlings that might germinate during wet springs.

The existing riparian shrub communities along the lower river occur primarily on sandy deposits along the edge of the active channel. These communities, dominated by cottonwood saplings, were established after a period of high runoff in 1983 (Lisa Heki, personal communication, August 1998). In 1995, an estimated 50,000 new cottonwoods regenerated along the active channel in this area as a result of experimental flows patterned on a natural flow regime (Christensen 1996). Flow management in 1996 and 1997 resulted in additional channel reshaping and creation, and the establishment of an estimated 15 to 20 million cottonwood seedlings downstream of Wadsworth (L. Heki, personal communication, August 1998).

I had earlier expressed concerns that high flows might remove saplings already established in the active channel (U.S. Fish and Wildlife Service 1993). These concerns now appear unwarranted. Although the 1997 flood reached 23,000 cubic-feet-second, and removed some saplings that had established in 1983, many of these uprooted trees were deposited downstream where they resprouted after being buried in sediment. In addition, the flood rearranged channels and created side channels that provided additional habitat for cottonwood recruitment. This newly created habitat more than compensates for cottonwood regeneration lost to the flood flows (L. Heki, personal communication, August 1998).

Such remarkable short-term successes make the long-range prospects for the restoration and enhancement of the lower Truckee River appear highly favorable. With continued flow management directed toward maintenance of the regenerated cottonwoods in the active channel, riparian forests can be expected to develop and eventually provide suitable habitat for riparian forest associated plant and animal species. In addition, the erosive action of floods will be decreased by the network of roots associated with these forests and their aboveground vegetation (Gregory et al. 1991). Increased sediment deposition resulting from the enhanced retention of material in transport may lead to an increase in the general elevation of the streambed, thereby restoring the hydrological connection to the uppermost river terraces. In time, the river valley may once again resemble the one described over 120 years ago as consisting of "meadowlands . . . studded with fine large cottonwood trees . . . which were here and there grouped into delightful groves, sometimes unencumbered, but generally with a shrubby undergrowth, amongst which the "buffalo-berry" (*Sheperdia argentea*) was conspicuous" (Ridgeway 1877).

CONCLUSION

This paper provides basic information on the species composition, structure, and areal extent of riparian vegetation along the Truckee River. These data, along with an understanding of hydrological processes such as flow magnitude, frequency, timing, and duration can guide land managers and biologists in their efforts to restore and enhance these habitats. Such actions will become increasingly important as the urban and rural populations of the west continue to grow.

Acknowledgments

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DEMOGRAPHY OF NATURAL AND REINTRODUCED POPULATIONS OF *ACANTHOMINTHA DUTTONII,* AN ENDANGERED SERPENTINITE ANNUAL IN NORTHERN CALIFORNIA

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ABSTRACT

The purpose of this study was to 1) demographically monitor the only remaining natural population of the rare serpentinite annual plant *Acanthomintha duttonii* (Lamiaceae); 2) attempt to reintroduce a new, experimental population within historic range; and 3) evaluate the new population by comparing its demographic characteristics with those of the natural population. The natural population of *A. duttonii* at Edgewood Park significantly and progressively increased in abundance and density between 1990 and 1994, then began a decline that lasted through 1997. In general, high density and high yield (reproductive plants produced from previous year's nutlet production) were associated with average or below-average years of precipitation while low densities and yields were associated with above-average rainfall years. During the entire study period, survivorship to reproduction remained fairly high and consistent, indicating that population trends were due to variations in nutlet production and the influence of cryptic factors that operate in the seed bank. The experimental population at Pulgas Ridge differed in several critical respects from the natural population, including low germination, low and variable survivorship, low nutlet production and perhaps high nutlet mortality. These features reduced the potential for self-sustained growth in the experimental population, which is likely to be extirpated within the next few years. This failure to produce a self-sustaining population of *A. duttonii* emphasizes the urgent need for in situ preservation of self-sustaining natural populations of serpentinite species.

Serpentinite endemics comprise the largest single edaphic category of rare plants in the native flora of California (Pavlik and Skinner 1994). They tend to occur in low elevation grassland and chaparral habitats on rocky outcrops, gravel colluvium and alluvial clays throughout the California Floristic Province, especially in the coast ranges and Sierra Nevada foothills (Kruckeberg 1984; Fiedler 1992). These same localities are also favored by land developers who build houses at the edges of rapidly expanding cities. The increasing development pressure on serpentinite habitats requires more effective conservation strategies if we are going to maintain these species as wild populations in California. Among those strategies are the preservation of remaining natural populations on managed reserves (Reznicek 1987; Lessica and Allendorf 1992; Pavlik 1996) and the creation of new populations within historic range (i.e., reintroduction) to decrease the overall probability of species extinction (Pavlik 1994; Guerrant and Pavlik 1997). Reintroduction has also been used in a mitigation context, attempting to ameliorate the destruction of natural populations by transporting propagules onto protected sites. Reintroduction in any context is fraught with difficulties and uncertainties (see Falk et al. 1996), but is especialy so when conducted under the fiscal, temporal, and political constraints imposed by mitigation (Howald 1996).

The San Mateo Thornmint, *Acanthomintha duttonii,* is among California's most endangered plant species (York 1987). This state- and federally-listed plant occurs in a single, fragmented population at Edgewood County Park on the San Francisco peninsula (Sommers 1984; Skinner and Pavlik 1994). The population has a particularly high risk of extinction because of its small areal extent, proximity to high density suburbs and altered water runoff patterns from upslope development. Once a popular spot for off-road motor vehicle recreation, the site now experiences only sporadic disturbance by hikers and mountain bikers.

Other than being an annual plant restricted to serpentinite grasslands, relatively little is known about the demography, ecology, and genetics of *A. duttonii.* No demographic monitoring (*sensu* Pavlik 1987; Pavlik and Barbour 1988; Pavlik 1994) has been conducted on this or any other species of *Acanthomintha.* Surveys of *A. duttonii* at its only remaining natural population have recorded large fluctuations in population size. In 1984, fewer than 5000 individuals were found, while estimates in 1981 and 1986 were closer to 3000 (Sommers 1986; CNDDB 1989). An apparent high of 6000 during 1985 was reported by McCarten (1986). Although such fluctuations are to be expected in populations of annual plants, the responsible factors have yet to be identified and related to management of this endangered species.

The purpose of this study was to 1) institute demographic monitoring to determine general trends and limiting factors in the only remaining natural population of *A. duttonii* at Edgewood County Park, 2) attempt to reintroduce a new, experimental population within historic range and appropriate habitat, and 3) evaluate the new population by comparing its demographic characteristics with those of the natural population.

MATERIALS AND METHODS

Study Species and Study Sites

The most recent taxonomic treatment of the genus *Acanthomintha* (Lamiaceae) has been done by James Jokerst for the Jepson Manual (Hickman 1993). He recognized four species (*A. ilicifolia, A. obovata, A. duttonii,* and *A. lanceolata*) on the basis of style morphology, corolla morphology, stamen fertility, leaf morphology, geographic distribution, and substrate preference (Jokerst 1991). *Acanthomintha duttonii* is an annual, frequently unbranched herb with dense glomerules subtended by spineless bracts (in contrast to the spine-tipped cauline leaves). The bilabiate corolla is white or tinged with lavender and contains 4 stamens with reddish anthers. Each flower is capable of producing a maximum of 4 nutlets.

Nothing is known about the genetic structure of the population. *Acanthomintha duttonii* is primarily a self-pollinating species (Steeck 1995), although visits to the corolla by small insects are frequent during the spring. As inferred from electrophoretic studies of other inbreeding plants, intrapopulation allelic variation would probably be relatively low and interpopulation variation would have been high prior to extirpation (Hamrick et al. 1991). This pattern is typical of habitat specialists whose populations are isolated from each other by significant barriers to gene flow.

Ecologically, *A. duttonii* is restricted to mesic serpentine grasslands that receive an average 500 mm of precipitation per year. At Edgewood Park, site of the only remaining natural population, mean annual temperature is 15°C with a mean annual temperature range of 11.1°C. Frosts are rare, with freezing temperatures occurring in less than 0.5% of the hours of the year (estimated from a Bailey nomogram). It is associated with more widespread grassland dominants, such as *Nasella pulchra, Lolium multiflorum, Delphinium hesperium* and *Hemizonia congesta* var. *luzulifolia* (nomenclature follows Hickman 1993).

McCarten (1986) conducted detailed surveys of actual and potential habitat of the species in San Mateo County. He did extensive soil sampling and found that the deep serpentinite clay of the Edgewood site was moist, chemically unusual, and rather uncommon in the county. Using these data and a wealth of field experience, McCarten and others (especially Susan Sommers, Toni Corelli and Ken Himes) mapped several possible sites for creating new populations. Pulgas Ridge, largely composed of serpentinite clay, lies along the eastern edge of the San Andreas Rift Zone and was identified as a general location suitable for reintroduction of *A. duttonii.*

The process of selecting microsites for new *A. duttonii* populations took many factors into consideration, including the ecological (macroclimate, soil, exposure, community associates, habitat size and degree of disturbance), and the logistic (land use history, road access, property ownership). A microsite on Pulgas Ridge was selected because of its apparently high quality habitat (mesic grassland on serpentinite clay soil), its public status as watershed lands operated by the San Francisco Water Department, and because it is very close to, if not within, the historic range of the target species. In many ways Pulgas Ridge resembles the Edgewood Park site, although its serpentinite areas are much larger and less fragmented by intrusions of non-serpentinite vegetation (e.g., oaks and annual grassland). The soil at Pulgas Ridge also compared favorably with soils at Edgewood Park (Pavlik et al. 1992) because it was found to be rich in clay (high saturation percentage) and chemically typical of local serpentinite (low nitrogen, low calcium/magnesium ratio, high nickel).

In addition to the ecological and logistic criteria discussed above, the microsite was selected to be; 1) large enough to allow a total of 24, 26 × 28 cm quadrats, separated by row and column spaces (access paths) 2) relatively homogeneous with respect to microhabitat factors (soil depth, slope, associated species, etc.), 3) accessible but reasonably concealed to reduce the potential for vandalism or other human disturbance, and 4) surrounded by suitable habitat so as not to constrain population growth in the future. We chose an east-west trending channel of a small intermittent stream, with gently-sloping (25%) banks of serpentinite clay. Plant cover was relatively sparse and open and would not excessively shade or otherwise crowd the new *A. duttonii* plants.

Monitoring the Natural Population at Edgewood Park

Seedling density and survivorship to reproduction in situ. Estimates of adult plant densities in the natural population were made in May–June in the years 1990–1997. A total of thirteen 0.125 m^2 circular quadrats were used to map the population and to record the densities of other species (e.g., *Lolium multiflorum* and *Avena fatua*) on and off the serpentinite clay. Given the lack of security and high visitation at Edgewood Park, we decided to leave very few, cryptic markers for mapping locations within the population. Consequently, only five permanent quadrats were randomly positioned during May 1990 in the belief that more markers would have increased the probability of vandalism. An X-Y grid was superimposed on the population and used to determine the positions from coordinates generated by a random numbers table. In addition, eight transient quadrats were distributed around the permanent quadrats at that time, increasing the number of density estimates for our maps. In following years, the locations of transient quadrats were approximated. After flooding had promoted downslope colonization during the winter of 1991–1992, two new permanent quadrats were established. The quadrats were used to determine the mean density of reproductive plants and to estimate total population size (when multiplied by the area of the population, about 42 m^2).

The same permanent plots were also used to estimate survivorship to reproduction during the 1991 to 1997 growing seasons. Fifty seedlings of *A. duttonii* were marked within each permanent plot when germinules were at the 4–6 leaf stage (January–February). The plots were revisited in June and the number of marked, reproductive plants were tallied.

Plant size and nutlet production. During peak flowering period (May–June) of 1990 to 1996, whole plants of *A. duttonii* were non-randomly selected to represent the complete range of plant sizes within a variety of microhabitats. These plants were clipped at ground height, sealed in individual bags and taken back to the laboratory. Stem length was measured from the clipped point to the base of the lowest glomerule. Forty-three plants were collected in 1990 and 25 plants were collected in each of the following years. Correlations between stem length and reproductive output were established using methods developed during studies of other endangered plants (Pavlik and Barbour 1988; Pavlik et al. 1993). Linear and non-linear models were applied to the data in each year, but the former produced higher correlation coefficients in most years and was, therefore, consistently applied across all data sets.

In June of each year, all plants that survived to reproduce within the permanent survivorship quadrats were measured for stem length and number of glomerules. These parameters were used to estimate mean plant size and nutlet output for the natural population and to generate frequency distributions of plant size for comparison with similar data collected for the experimental population.

Reintroducing the Experimental Population

Characteristics of the founder nutlets. The propagules (=nutlets) of *A. duttonii* used were collected from Edgewood Park in May–June of 1990 to 1994. Nutlets were taken from at least 40 individuals that represented the complete size range and microenvironmental amplitude of the natural population. The collection would be likely to contain, therefore, a representative sample of the existing genetic variation (Falk and Holsinger 1991). Nutlets were stored at 4°C in paper pouches within sealed plastic bags until they were sown in the field.

Laboratory germination trials were conducted in 1991 to 1993. Nutlets from each year's crop were tested the following January using three replicates of 25 nutlets each. A replicate consisted of a plastic petri dish (5.5 cm diameter) containing a filter paper disk that was kept moist with distilled water. Nutlets were spread across the paper disks and kept in a dark room in which the temperature averaged 25°C. Replicates were checked every day for 12 days, noting germination (protrusion of the radicle through the pericarp) and removing germinules with a paintbrush.

Installation. The population installed at Pulgas Ridge during the early winter of 1991 consisted of two sets of 12 plots each. A removable wooden frame containing a 7 × 7 grid of 49 holes was used as a template to precisely sow *A. duttonii* nutlets. The holes allowed exact placement and subsequent monitoring of germinules and juvenile plants. This "precision-sowing" technique has been successfully used by Pavlik and Manning (1993) to establish and monitor new subpopulations of the endangered *Oenothera deltoides* ssp. *howellii* and *Erysimum capitatum* var. *angustatum* and by Pavlik et al. (1993) to establish and monitor new populations of *Amsinckia grandiflora.*

In 1992 a total of 1176 nutlets of *Acanthomintha duttonii,* half from the 1990 crop at Edgewood and half from the 1991 crop, were sown into the 24 plots at Pulgas Ridge. Six additional precision-sown plots were established in the late fall of 1992. We also used a streak method for sowing five plots with 250 more nutlets on a small clay lens 30 m away from the stream bank. A linear furrow was cut in the soil with a blunt nail and sown with 50 seeds before covering it over with native soil. Streak plots did not allow for strict demographic measurements, but they were easier to establish and quicker to monitor. Additional enhancements to the reintroduced population were added in the falls of 1993, 1994 and 1995 in the form of ten more streak plots per year within 10 m of the demographic plots. All plots were sown in September–November of each year and no supplements of water or nutrients were applied. A summary of the nutlet inputs to all plots is presented in Table 3.

Monitoring and evaluation. The fate of each precision-sown nutlet was followed during the January to June growing season by repositioning the wooden frames on each plot and searching for seedlings. The condition of each seedling was recorded on plot-specific data sheets to allow calculation of critical demographic parameters (Pavlik 1994). Those parameters included field germination, stress factors (desiccation, etiolation, grazing by microherbivores), mortality, phenology, survivorship to reproduction, and plant size (number of glomerules and stem length). Streak plots were checked three times during the growing season for seedling emergence and each plant was measured at peak flowering period (May–June) for number of glomerules and stem length.

During the early summer of 1994, ten whole

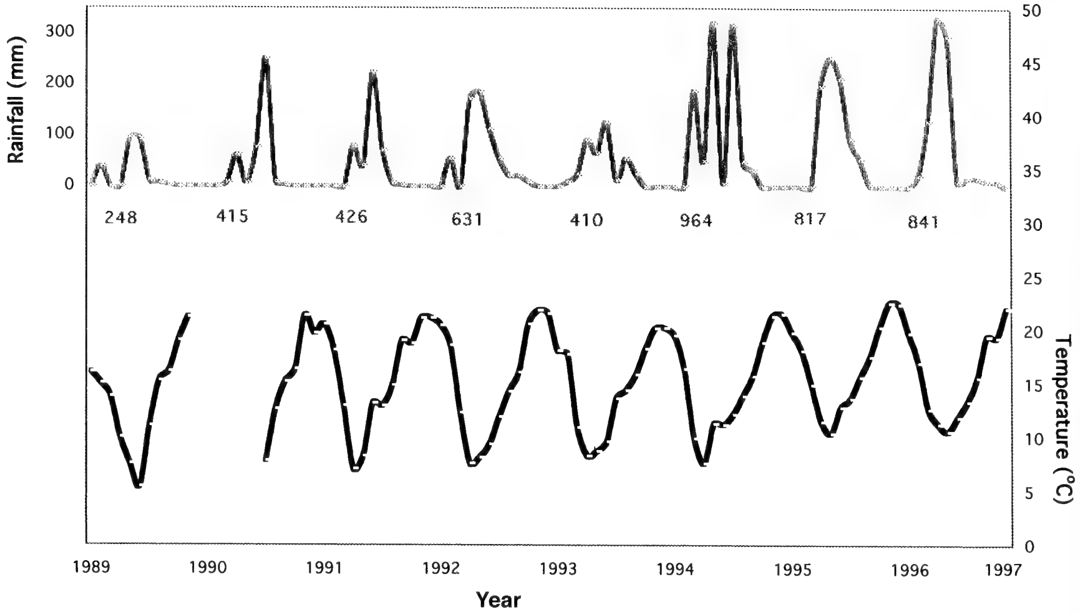

FIG. 1. Patterns of monthly precipitation and air temperature near the natural population of *Acanthomintha duttonii* at Edgewood County Park, 1990–1997. Rainfall totals for a growing season (November to November) are shown.

plants of *A. duttonii* were collected from the Pulgas Ridge experimental population. Stem length was measured from the clipped point (at soil surface) to the base of the lowest glomerule. Correlations between stem length and reproductive output were then calculated.

RESULTS AND DISCUSSION

Environmental Patterns 1990–1997

Rainfall varied significantly from year to year, but the seasonal patterns and magnitudes of mean monthly air temperature seemed to be similar for all years of the study (Fig. 1). Pronounced drought occurred during 1990 (November 1989–June 1990 growing season) when less than 300 mm was received in the vicinity of Edgewood Park. The years 1991, 1992 and 1994 were also dry relative to normal (about 500 mm), while 1993 was wetter than average. The years 1995, 1996 and 1997 were extremely wet, each exceeding 800 mm during the growing season. The overall pattern during the study, therefore, was one of low rainfall during the first five years (1989–1994) and extremely high rainfall during the last three years (1994–1997). Flooding of the natural population may have occurred during all wet years, but during the winter of 1991–1992 a single, intense storm had facilitated seed dispersal. This storm evidently caused soil erosion and downslope movement of nutlets into an adjacent patch of serpentinite clay that previously did not support *A. duttonii.* The newly-colonized area was subsequently included in the monitoring program. Flooding of some portions of the experimental population was prolonged during the extremely wet 1994–1995 growing season.

Another form of disturbance to the population was observed each late spring and summer. As the serpentinite clay soil dried and shrank, large surficial cracks began to open, sometimes as much as 4 cm wide and 30 cm deep. Mature nutlets would drop from adjacent plants into the gaping crevices. These cracks fill with water and clay during the next winter rain, perhaps burying a large number of nutlets at depths too great for seedling emergence. It is likely that these cracks significantly reduce potential population growth, but it is also likely that some nutlets remain viable for long periods of time within the seed bank. Observations made on a small, transient colony of *A. duttonii* in an adjacent portion of Edgewood Park have confirmed that nutlets can produce plants after 8 years of quiescence in situ. That quiescence, during which no adult plants were observed, was associated with high rainfall, *El Nino* climatic events during the early 1980's (Sommers 1986, Pavlik and Espeland 1994).

Demography of the Natural Population at Edgewood Park

Density and survivorship. During eight years of observation at Edgewood Park, mean density of the reproductive *A. duttonii* population could vary by a factor of 5 (Table 1), with a low of 230 plants/m^2 (1991) and a high 1106 plants/m^2 (1994). A 64% decline in density occurred between 1994 and 1995, with stepwise decreases through 1997. Spa-

TABLE 1. CHARACTERISTICS OF NATURAL AND EXPERIMENTAL POPULATIONS OF *ACANTHOMINTHA DUTTONII*, 1990–1997. Population size for natural population was estimated using the mean density and population area. Survivorship and density shown as means ± SD. Yield estimates were obtained dividing present population size by the previous year's nutlet production (Table 2).

	Emergence (%)	Reproductive survivorship (%)	Reproductive density (#plants/m2)	Reproductive population size (#plants/site)	Yield
Natural Population (Edgewood)					
1997	—	36.6 ± 11.5	63 ± 58	5289	0.128
1996	—	36.3 ± 12.1	89 ± 68	6885	0.126
1995	—	56.0 ± 32.7	390 ± 210	20,280	0.048
1994	—	52.0 ± 18.0	1106 ± 589	53,136	0.110
1993	—	62.9 ± 21.2	794 ± 756	36,279	0.305
1992	—	59.4 ± 29.4	302 ± 294	18,772	0.025
1991	—	54.8 ± 14.9	230 ± 78	9660	0.073
1990	—	—	689 ± 704	12,864	—
Experimental Population (Pulgas)					
1997	—	28.0	23	52	—
1996	—	39.0	35	77	—
1995	1.7	13.6	54	145	—
1994	10.9	53.2	66	158	—
1993	34.0	63.0	81	181	—
1992	27.0	38.0	68	120	—

tial variations in density were high (Fig. 2), with unique patterns found in each of the permanent plots. Patterns of increased abundance during drought years (Fig. 1), are supported by observations made on some species of common annual forbs (*Plantago erecta* and *Lotus subpinnata*) from serpentinite sites at nearby Jaspar Ridge (Armstrong and Huenneke 1992).

In contrast, survivorship to reproduction was fairly constant over time (~50%, Table 1) for the

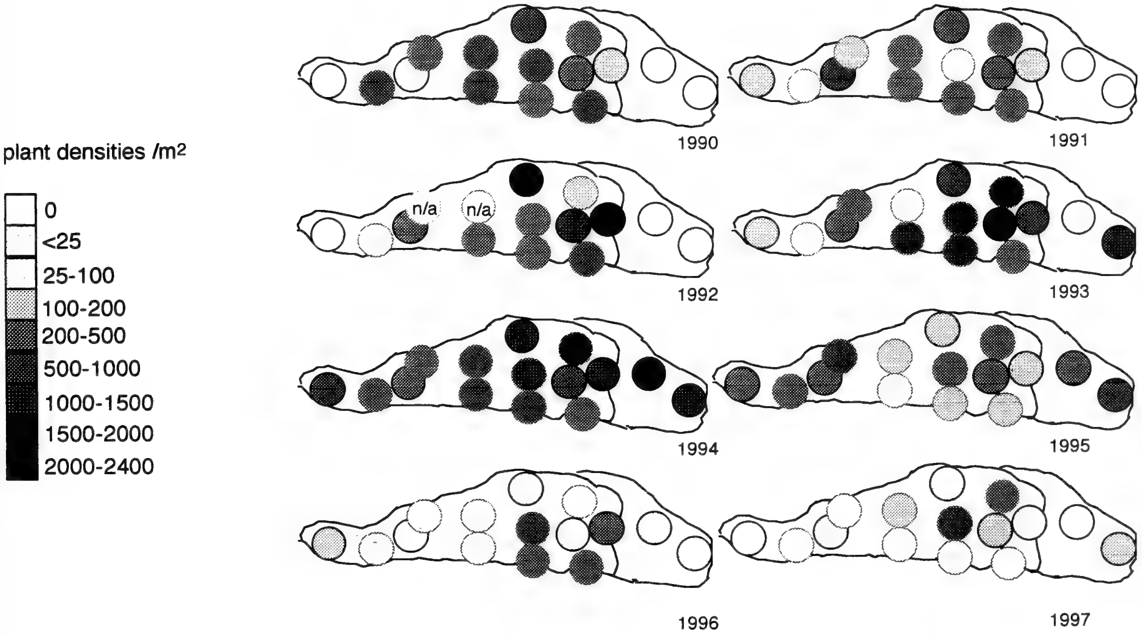

FIG. 2. Spatial pattern of reproductive plant density of the only remaining natural population of *Acanthomintha duttonii* at Edgewood County Park, 1990–1997. The smaller lobe of the population's outline (to the right) is the downslope addition colonized after flooding in the winter of 1991–1992. n/a = data not available.

TABLE 2. REPRODUCTIVE CHARACTERISTICS OF NATURAL AND EXPERIMENTAL POPULATIONS OF *ACANTHOMINTHA DUTTONII*, 1990–1997. Nutlet output estimated using #nudets/plant = m(stem length) + b. Nutlet production is the product of nutlet output and population size (Table 1). [a] = estimated using 1996 nutlet output correlation for the site [b] = estimated using 1994 nutlet output correlation for the site.

	Correlation between nutlet output (y) and stem length (x)					Mean plant size in plots		Estimated nutlet output (#/plant)	Estimated nutlet production (#/site)
	m	b	r	P	n	Stem length (cm)	n		
					Natural Population (Edgewood)				
1997	—	—	—	—	—	4.1 ± 3.8	206	56[a]	3.0×10^5
1996	3.23	42.8	0.30	ns	25	5.3 ± 2.7	211	60	4.1×10^5
1995	3.51	8.1	0.39	<0.05	25	5.1 ± 3.3	198	26	5.4×10^5
1994	2.25	27.3	0.51	<0.05	25	4.0 ± 3.2	155	25	1.3×10^6
1993	2.86	36.1	0.45	<0.05	25	4.5 ± 2.4	220	49	1.8×10^6
1992	1.88	3.1	0.85	<0.01	25	6.9 ± 7.1	150	16	3.0×10^5
1991	9.00	−5.1	0.92	<0.01	6	9.2 ± 3.6	25	78	7.5×10^5
1990	2.83	21.1	0.71	<0.01	43	4.7 ± 2.5	188	34	4.4×10^5
					Experimental Population (Pulgas)				
1997	—	—	—	—	—	4.5 ± 3.4	55	30[a]	1560
1996	2.99	16.5	0.52	<0.05	15	9.4 ± 6.1	75	45	3375
1995	—	—	—	—	—	3.6 ± 2.8	145	27[a]	3045
1994	2.53	22.4	0.74	<0.05	25	5.2 ± 4.8	158	36	5688
1993	—	—	—	—	—	4.4 ± 2.5	181	34[b]	8869
1992	—	—	—	—	—	3.5 ± 1.5	315	42[b]	3150

population as a whole, tending to be slightly higher downslope in the newly colonized area and slightly lower upslope. Variations in plant density, therefore, are probably influenced by cryptic factors that operate in the seed bank (nutlet density, nutlet mortality, germination, emergence) rather than more obvious factors that control seedling growth and mortality.

Estimated total population size progressively increased from a low of 9660 reproductive individuals in 1991 to a peak of 53,136 in 1994. The ratio of reproductive population size to estimated nutlet production in the previous year (yield) was commonly between 0.07 and 0.13, with a single peak of 0.30 in the spring of 1993. The peak in population size was followed by a 60% decline in 1995, with no evidence of catastrophic flooding or anthropogenic disturbance. In years of decline there were intrusions of *Hemizonia congesta* var. *luzulifolia, Perideridia* sp., and *Lolium multiflorum* into the body of the population. Therefore, the recent decline in population size of *A. duttonii* appeared related to decreasing density across the entire habitat, with losses of potential habitat to common, serpentinite-tolerant species during especially wet years.

Plant size and nutlet production. The output of nutlets by individual *A. duttonii* plants in the natural population was linearly related to the sum of the stem lengths per plant in most years (Table 2). The slopes and intercepts of the relationship varied from year to year, but again there was no obvious correlation with environmental patterns or plant density. Mean stem length was greatest in 1991 and 1992 (years of below normal rainfall), but again there was no correlation between plant size and total yearly precipitation. Regardless of year, the large majority of plants in the population fell into the one glomerule or short-stem size categories and few were large and well branched (data not shown).

The total nutlet production of the population could be estimated using the nutlet output correlation along with estimates of mean plant size, population density, and population area for each year. Average plants usually output between 16 and 80 nutlets (Table 2), but the largest plants could make between 150 and 200 nutlets each. In June of 1992 an extremely large individual was found to produce 662 nutlets (from 232 flowers in 18 glomerules, with 66 cm of stem length in eight branches). Given the high density of the population in most years of the study, nutlet rain ranged between 10,300 nutlets/m^2 (1990) and 36,800 nutlets/m^2 (1993) (data not shown). Consequently, the total nutlet production of the natural population was in the range of 10^5–10^6.

Reintroduction at Pulgas Ridge

Laboratory germination of the founding nutlets. Nutlets of *A. duttonii* had moderate to high rates of germination in the laboratory. Germination averaged 87% for 1990 nutlets, 63% for 1991 nutlets and 71% for 1992 nutlets, even though all crops were approximately seven months old at the time the tests were conducted. There was a strong after-ripening requirement that prevented any germination during the six months following collection (June through December). Late winter germination appears to be characteristic of this species, owing to a rigid endogenous control mechanism that stratification, pericarp scarification, fire, wet-dry cycling, and red light cannot override (Pavlik and Espeland 1991). Perhaps such a mechanism prevents germination before a thorough saturation of the clay substrate takes place, thus avoiding the possibility of seedling desiccation during warm days in fall and early winter (also discussed in Armstrong and Huenneke 1992). Percolation is slower within clay substrates and so a higher proportion of the falling rain is likely to run off. Furthermore, clay particles require much more water than sands and gravels to bring soil water potentials into the tolerable range of −0.1 to −1.5 MPa for most seedlings.

Emergence in the field. Total emergence (in situ germination) during the late December 1991 to early April 1992 period was low compared to concurrent laboratory germination on the same seed lots. On average, only 27% of all sown nutlets emerged (Table 1), with the majority occurring by the end of January. In subsequent years, emergence was as high as 34.0% (1993) and as low as 1.7% (1995). It is likely, therefore, that nutlets remained dormant or died within the seedbank, and constituted a significant constraint on growth of the founding population.

Seedling establishment and mortality. A total of 315 live seedlings and established plants were found over the entire 1991–1992 growing season, corresponding to densities between 150 and 175 plants/m^2 (comparable to the natural population at Edgewood Park [Table 1]). Physical contact and shading between the seedlings and other plants were minimal because of the 1) virtual absence of annual grasses, 2) relatively large spaces between *Nassella pulchra* bunches and 3) the open or lax growth forms of the common herbs (e.g., *Perideridia kelloggii, Delphinium virgatum*) in this serpentinite grassland.

Despite this moderate production of seedlings at Pulgas Ridge, fewer than half survived to reproduce by early June 1992 (Table 3). Only 120 individuals completed fruit formation, or 38% of the total plants produced during the growing season and 10% of the total nutlets sown (the initial yield). Overall, survivorship to reproduction was low in the experimental population compared to that observed in the natural population at Edgewood Park. Mortality began early, with weekly mortality rates as high as 16.9% per week during the 28 January to 10 March period. The principle cause was difficult to identify from observations of grazing, desiccation, and etiolation stresses. Grazing by microherbivores (insects, snails, etc.) was the most commonly observed stress, affecting 4–34% of all live plants within plots during the growing season. Other stresses, including pathogens, may also be important during the early phases of population growth, but these were not assessed during this study.

TABLE 3. NUMBER OF NUTLET SOWN IN EXPERIMENTAL PLOTS (INPUT) DURING REINTRODUCTION AT PULGAS RIDGE AND THE NUMBER OF REPRODUCTIVE PLANTS SUBSEQUENTLY PRODUCED IN THOSE PLOTS AT PULGAS RIDGE, 1991–1995. Initial yield is the ratio of first year reproductive plants in spring to the number of nutlets input during the previous fall.

Fall input		Number of reproductive plants produced in spring				Spring initial
Year	Nutlets	1992	1993	1994	1995	yield
1991	1176	120	64	17	5	0.102
1992	514	—	117	29	4	0.228
1993	2000	—	—	112	25	0.056
1994	6450	—	—	—	111	0.017

Mean survivorship increased during 1993 and 1994 (63 and 53% respectively), but decreased to 13.6% in 1995. The decrease was caused by flooding in the ephemeral creek channel which inundated some of the reintroduction plots. Such large variation in survivorship, biased towards the low end of the range, characterizes the experimental population at Pulgas Ridge and not the natural population at Edgewood Park.

Plant size and nutlet production. Mean plant size at Pulgas Ridge in 1992 was less than that measured at Edgewood Park (3.5 ± 1.5 cm vs. 6.9 ± 7.09 cm), but only if the large colonizing plants of the natural population were included in the latter estimate (Table 2). Colonizing plants were those found downslope in a previously unoccupied, contiguous area (Fig. 2). By excluding the colonists, mean plant size of the introduced population compared favorably with that of the natural population (3.5 cm vs. 4.0 cm, respectively). During other years, mean plant size and nutlet output in the experimental population at Pulgas Ridge was comparable to those observed in the same years at Edgewood Park. Missing from Pulgas Ridge were the few, large, fecund individuals observed primarily as colonists in the new area at Edgewood Park. This indicates that although the general conditions for reproduction at Pulgas Ridge were suitable, they were not optimal. Perhaps optimal microhabitat patches do exist at the Pulgas Ridge reintroduction site, but they were not sown with nutlets during these reintroductions. Such patches can have a disproportional effect on population growth by producing a few, highly fecund individuals that generate hundreds, rather than tens, of nutlets each.

Persistence of reintroduced cohorts. Although the initial yields of reproductive plants could be as high as 23% at Pulgas Ridge (relative to the number of sown nutlets) and mean plant size was comparable to that of the natural population, none of the founding cohorts was able to increase in size during the study period (Table 3). Reductions in cohort population size between years were between 50 and 90% regardless of how the nutlets were sown (precision or streak) or the patterns of yearly precipitation (dry or wet). Despite a total input of more than 10,000 founding nutlets, fewer than 150 reproductive plants were found during the springs of 1995, 1996 and 1997. Again, we believe that post-dispersal factors, including high nutlet mortality and poor conditions for germination, were probably responsible. Even after a year such as 1994, when the natural population at Edgewood Park was flourishing, the reintroduced population was not able to increase its numbers. Progressive declines during unfavorable years with high rainfall indicate that the reintroduction of *A. duttonii* to Pulgas Ridge is unlikely to have conservation value or evolutionary potential and must be considered a biological failure.

We do expect, however, that germination from a declining but persistant seed bank at Pulgas Ridge will continue for a few more years. Ex situ studies have shown that nutlets of this species are long-lived (data not shown), and in situ observations have confirmed that nutlets can produce plants after 8 years of quiescence during periods of extraordinary annual rainfall. Perhaps the persistence of this population, as viewed from the standpoint of its ability to produce reproductive plants, is better judged by the long-term activity of the seed bank. If that seed bank were much larger (in the range of 10^5–10^6), the adult population produced even in unfavorable years might be enough to provide reproductive recharge. Collecting many nutlets from the natural population in order to boost the long-term activity of the seed bank may be another approach towards spreading the risk of extinction between multiple populations. If the Edgewood seed bank is as large as production measures indicate (Table 2), as much as 50% of the nutlet crop in a "good year" (e.g., total averaged 1.6 million in 1993/1994) could be harvested and transferred because the remaining crop would be equivalent to maximum production in a "bad year" (750,000 in 1991). The effects of harvest on the natural population would have to be monitored, but the very large existing seed bank should be able to buffer the impact for a few, non-successive years (Guerrant 1996). Careful spreading of these nutlets across the Pulgas site may also increase the probability of contacting optimal, but otherwise invisible, microsites that encourage the growth and persistence of the seed bank.

CONCLUSIONS

The natural population of *Acanthomintha duttonii* at Edgewood Park significantly increased in abundance and density during the 1990–1994 period. There were no strong correlations between density with overall temperature or precipitation patterns, but in general, high density and high yield were associated with average or below-average years of precipitation and the declines were associated with above-average rainfall years. Survivorship to reproduction remained fairly high and consistent, indicating that the trends were due to variations in nutlet production and the influence of cryptic factors that operate in the seed bank (nutlet mortality, germination). Nutlet production was in the range of 10^5–10^6 per year for the population as a whole and it is likely that the lens of suitable serpentinite clay habitat at Edgewood Park can become saturated with *A. duttonii* nutlets.

The experimental population at Pulgas Ridge differed in several critical respects from the natural population at Edgewood Park. First, the cryptic seed bank factors at Pulgas Ridge, especially low germination (emergence) and perhaps high nutlet mortality, may have placed a severe constraint on population growth. Secondly, survivorship to reproduction was more variable and more likely to be low at Pulgas Ridge. Finally, total nutlet production at Pulgas Ridge was on the order of 10^3 per year, even though plant size and nutlet output compared favorably with the natural population. These three features combined to reduce the potential for self-sustained growth in the experimental population. The reintroduction plots established in the winter of 1991 had 120 plants in the spring of 1992, but only 64 reproductive plants in 1993, 17 in 1994 and 5 in 1995. Similar patterns of decline in abundance were observed in the plots in all other years. It is likely, therefore, that the experimental population at Pulgas Ridge will be extirpated within the next few years depending on the activity of the seed bank. This failure to produce a self-sustaining population of *A. duttonii,* despite having taken great care in site selection, sowing and monitoring of the reintroduction, emphasizes the urgent need for in situ preservation of self-sustaining natural populations of annual serpentinite species.

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REVEGETATION AFTER FOUR STAND-REPLACING FIRES IN THE LAKE TAHOE BASIN

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ABSTRACT

Low and moderate intensity surface fires have been accepted as a natural and beneficial part of the upper montane mixed conifer forests in the northern Sierra Nevada, both in terms of reducing risk of crown fires and improving the ecological health of forests. Stand-replacing fires have not generally been considered ecologically significant, in part because they have been assumed to be historically unimportant. However, high intensity stand-replacing fires did occur prior to fire suppression and may have affected vegetation structure more than previously thought.

The occurrence of an extensive, pre-suppression, stand-replacing fire at the south end of Lake Tahoe on Angora Ridge was supported using historical evidence, aerial photographs, and stand age analysis. Data was gathered on the structure and composition of current vegetation on Angora Ridge and three subsequent stand-replacing fires using randomly selected plots. The post fire vegetation on these sites were compared in regard to species diversity, fuel accumulation, stand density, and composition.

Results indicate that a long period of herb and shrub domination occurred on Angora Ridge after the 1890's fire. The treeless period was followed by simultaneous recruitment of fir and pine. The sites of the three later fires have developed little forest canopy up to the present, and currently remain dominated by shrubs and small trees. While surface fuel accumulation and the density of standing dead trees were higher on Angora Ridge than on the other fire sites, species diversity was lower.

The prevalence of small, low intensity, surface fires in the Sierra Nevada before European settlement has been widely accepted (Kilgore 1981; Boyce 1921; Show and Kotock 1924). The exclusion of fire through suppression has resulted in a number of structural and compositional changes to forests throughout the Sierra Nevada, including the Lake Tahoe Basin. These changes include an increase in fuel load (Lunan and Habeck 1973; Minnich 1983, 1989; Wagel and Eakle 1979); a reduction in species richness (Baker 1992; Bock et. al. 1978; Murray 1992); and changes in species composition. Shade tolerant and non-fire resistant species such as *Abies concolor* (Gordon & Glend.) Lindley (white fir) tend to increase in dominance (Lunan and Habeck 1973; Phillips and Sure 1990), while species that require disturbance for germination, and tend to be more fire resistant, such as *Pinus jeffreyi* Grev. & Balf. (jeffrey pine) and *P. ponderosa* Laws. (ponderosa pine) decrease in frequency. The high density of forest stands that results from total fire suppression may also be a contributing factor in the tree mortality presently occurring in the Lake Tahoe Basin.

Low intensity surface fires are presently being used to reduce surface fuel and repress the development of understory in the forests around Lake Tahoe. The California Department of Parks and Recreation has been using prescribed surface fire on 10 to 40 ha per year in Lake Tahoe area parks to reduce fuel loading and enhance wildlife habitat (Rice 1988, 1990; Walter 1992). The USDA-Forest Service has used non-broadcast techniques such as machine and hard-pile burning for fuel reduction on 80–360 ha per year in the Lake Tahoe Basin (Swanson 1993). The importance of fire is also being considered in its relation to management of Lake Tahoe Basin forest ecosystems by the Tahoe Regional Planning Agency (TRPA) Forest Health Consensus Group (Swanson 1993; Sweeney 1993).

Concern about the ecological condition of the forested lands surrounding Lake Tahoe has been growing in recent years due to the visible decline of a large number of forest trees. This decline can be attributed to a number of factors, including an extended drought coupled with species conversion from drought tolerant pine to drought susceptible fir, high forest density, and the activity of bark beetles (Wenz and DeNitto 1983; Williams et al. 1992). Recent bark beetle outbreaks, though these beetles are a natural part of affected ecosystems, have resulted in unprecedented interest and commitment by both private citizens and public agencies toward the development of management policies and goals for the Lake Tahoe Basin forests. The TRPA Forest

TABLE 1. FIRE AREA CHARACTERISTIC. The forest type for all four fire areas was upper montane mixed conifer. The designations ABCO and PIJE stand for the dominant tree species on those sites, *Abies concolor* and *Pinus jeffreyi* respectively.

	Angora Ridge	Cathedral Creek	Cascade Lake	Luther Fire
Date	~1890	1937	1978	1987
Hectares	100	21	6.5	8
Elevation	1950–2190	1950–2190	1950–2190	2010–2190
Soil type	Meeks-Talac	Meeks-Talac	Meeks-Talac	Meeks-Talac
Forest type	ABCO	ABCO	PIJE	ABCO

Health Consensus Group, which includes private land owners and representatives of public agencies, has concluded that the forests should be managed toward their pre-European state (Swanson 1993; Sweeney 1993).

The historical occurrence of low and moderate intensity surface fires in Sierra Nevada montane forests is well accepted. However, due to their rarity larger and more intense stand-replacing fires, as defined by Romme (1980), have not been considered an important ecological factor in the evolution of these forests. Though it is true that surface fires were much more common than stand-replacing fires before European settlement and fire suppression, stand-replacing fires did occur (Kilgore and Taylor 1979) and their effect on forest structure may have been profound (Agee 1974). For example, recruitment of species that have high light requirements for seedling establishment is increased by stand-replacing fires through the opening of large canopy gaps. Habitat heterogeneity and species diversity may also be increased by crown fires (Baker 1992; Minnich 1983, 1989). In addition, gaps exceeding 10 ha caused by crown fire may be important in determining the structure and composition of the Sierra Nevada forests. Therefore, stand-replacing fires must be considered in understanding pre-European disturbance regimes.

This paper presents the findings in a study focusing on four stand-replacing fires in the south Lake Tahoe area. Our purpose is to demonstrate the existence of a stand-replacing fire that occurred prior to systematic fire suppression and to determine the development of vegetation after such fire.

FIG. 1. Angora Ridge taken from Upper Angora Lake in 1917 (Scott 1973). The southeast side of the ridge, and the denuded fire area is clearly visible.

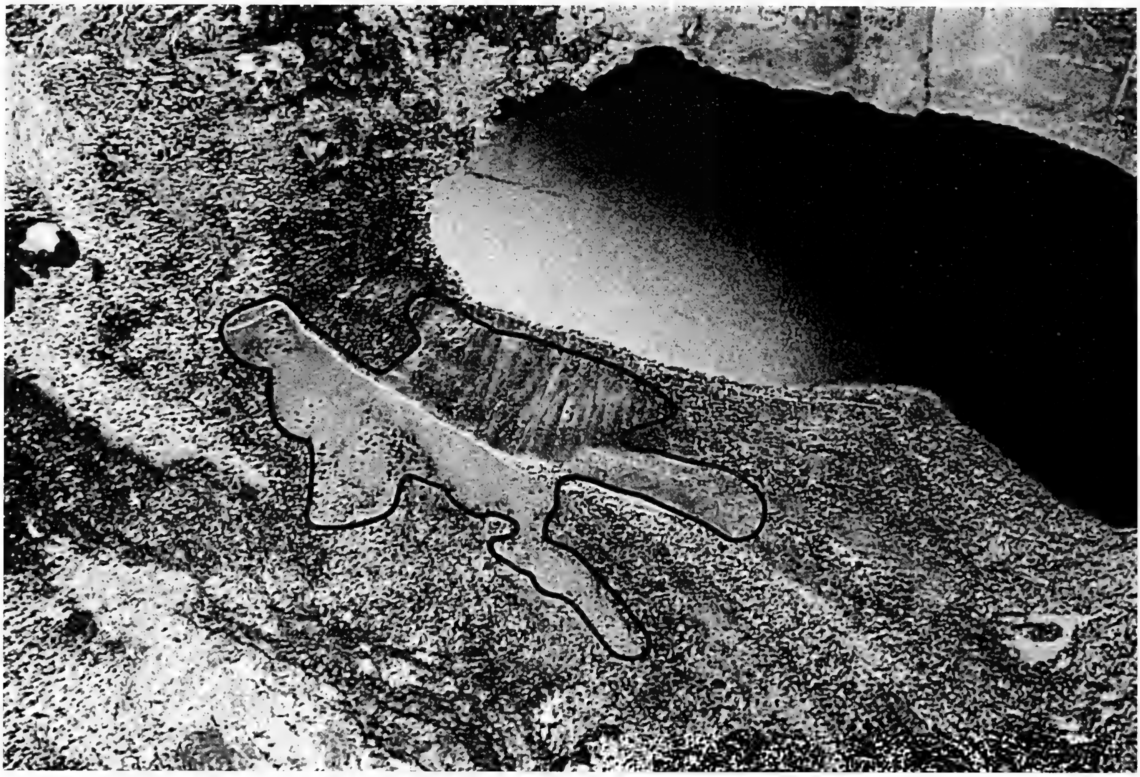

FIG. 2. This is the earliest available aerial photograph of Angora Ridge taken in July 1940. The fire area is clearly visible particularly on the south east side. The area appears to be dominated by shrubs.

METHODS

Location of study sites. The location and perimeter of four stand-replacing fires (Table 1) were determined through interviews with USDA Forest Service fire management personnel (Swanson 1993) and long-term residents of the area (Craven 1993; Gwinn 1993; Hildinger 1993), and through interpretation of historical and aerial photographs (1917–1983) (USDA-For. Serv. aerial photos).

The Angora Ridge Fire burned approximately 100 years ago, covered approximately 100 ha, and was located on both sides of Angora Ridge between the present location of the Angora lookout tower and lower Angora Lake. The fire ran from 1950 to 2190 m in elevation burning both the northwest and the southeast sides of Angora Ridge. The area's vegetation is currently dominated by a *Abies concolor-Pinus jeffreyi* mixed conifer forest type with *Calocedrus decurrens* (Torrey) Florin (incense cedar) included at the lower elevations, *Abies magnifica* Andr. Murray (red fir) becoming more prominent at higher elevations, and occasional occurrences of both *Pinus monticola* Douglas (western white pine) and *P. contorta* ssp. *murrayana* (Grev. & Balif.) Critchf. (lodgepole pine).

The Cathedral Creek Fire burned in 1937, covered approximately 21 ha, and was located in the Cathedral Creek drainage on the southeast slope above Fallen Leaf Lake, from 1950 to 2190 m in elevation. The same forest type dominates the area surrounding both fires, and both have soils of the Meeks-Tallac formation type (USDA 1974).

The Cascade Lake Fire burned in 1978, covered approximately 6.5 ha and was located on the southeast slope above Cascade Lake, from 1950 to 2190 m in elevation. The forest type surrounding this fire is similar to those above with more abundant *Pinus jeffreyi.*

The Luther Fire burned in 1987, covered approximately 8 ha, and was located on the northwest slope above Christmas Valley, from 2010 to 2190 m in elevation. Vegetation and soil types are similar to those in the other three fire areas.

Sampling techniques. Stand structure data was collected using 10 m by 20 m rectangular plots that were randomly selected along elevational gradients and distance from center of site within each study site. Within each plot slope, aspect, elevation, and forest type were recorded as well as information on size and identification of all live and dead standing trees present. The number of seedlings (trees less than 61 cm in height) and saplings (trees less than 10 cm in diameter) of each species were also recorded. Canopy cover was determined for the four cardinal directions at the center of each plot with a spherical densiometer. Fuel load was determined

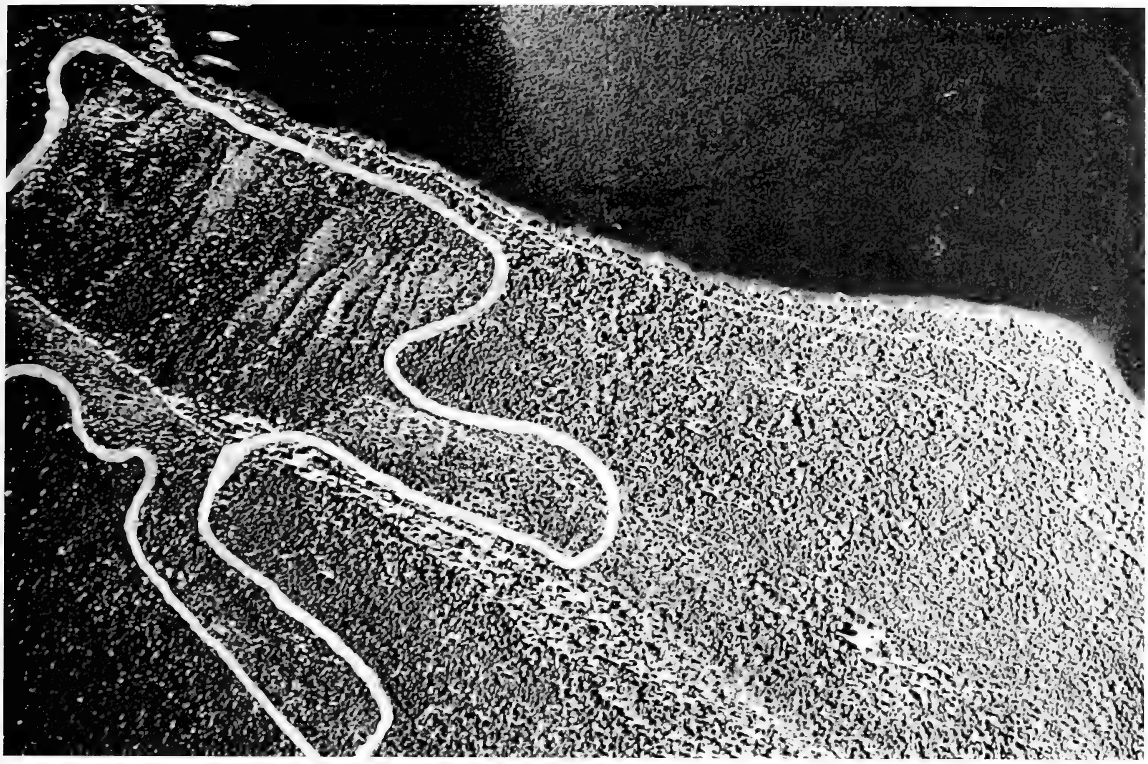

FIG. 3. This 1983 photograph shows Angora Ridge in a state similar to its present condition, with high density forests on both sides of the ridge.

using a natural forest residue photo series (Blonski and Schramel 1981). Stand age was determined by taking a core sample from the largest tree of each species present on each plot.

Three 1.8 m diameter circular nested plots were used within each 10 m by 20 m rectangular plot to sample herbaceous and shrub species. For all shrubs present, cover class was determined using a standard cover scale (Daubenmire 1959, 1968). The presence of all herbaceous and shrub species on 1.8 m plots was recorded.

Stand structure analysis. Data collected on 65 timber plots and 195 herbaceous-shrub plots yielded the total and relative frequency and density of each tree species, the total and relative frequency and density of standing dead trees, the total and relative frequency and density of seedlings and saplings of each species, the average canopy cover for each study site, the average percent cover of each shrub species, the average fuel load (metric tons/ha) for each study site (Blonski and Schramel 1981), and three measures of species diversity (species richness, species evenness, and the Shannon diversity index).

RESULTS

Interpretation of aerial photographs. Aerial photographs of the Angora Ridge indicate that a long interval occurred before tree cover developed following the fire in the 1890's. There is little or no tree canopy visible in aerial photographs in the fire area before 1952. Historical photographs taken in 1917 (Fig. 1) and aerial photographs taken in 1940 (Fig. 2) show that the post-burn was dominated by brush fields.

Aerial photographs taken in 1952 and 1966 show the gradual development of tree canopy on Angora Ridge. By 1976 (Fig. 3) aerial photographs indicate that a significant forest canopy has developed but there are still areas of shrub domination.

Stand age. Tree ages for the dominant tree on each plot ranged from 21 to 95 years on Angora Ridge. The modal age was 70 years for all species with no significant difference in age between *Abies concolor, A. magnifica,* and *Pinus jeffreyi.* This is consistent with the existence of a 100 year old stand-replacing fire. The 30 year delay in tree recruitment is consistent with shrub domination during the same period. As sheep grazing was common in the study area during the period in question it may have influenced vegetation recruitment patterns, however, the occurance of shrub domination on the Cascade Lake fire and Luther fire areas suggests that grazing is not necessarily a factor.

On the Cathedral Creek Fire area the dominant tree age on each plot ranged from 20 to 54 years

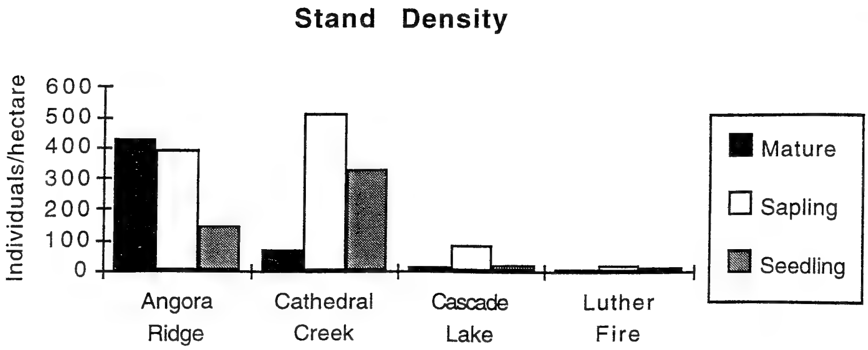

FIG. 4. Stand density.

with a modal age of 39 years. There was no significant difference in age between *Abies concolor* and *Pinus jeffreyi.* This result is consistent with a 56 year old fire.

Neither the Cascade Lake Fire area nor the Luther Fire area had enough tree recruitment to determine stand age through coring. Both areas are dominated by shrubs. Because of their recent occurrence, however, the age of the burns were easily determined through fire records and interviews with USDA Forest Service fire suppression personnel (Johnson 1993).

None of the sites studied received artificial replanting treatments so that stand age reflects natural recruitment and development.

Structural analysis. The density of mature trees was much higher on the Angora Ridge Fire site than on the Cathedral Creek, Cascade Lake, and Luther Fire sites (Fig. 4). This difference in the density of mature trees was associated with other structural differences such as canopy and shrub cover. Canopy cover averaged 72% on Angora Ridge and less than 10% on each of the other three fire sites. Shrub cover dominated these three sites (Cathedral Creek = 88%; Cascade Lake = 76%; Luther Fire = 87%) while Angora Ridge exhibited only 13% shrub cover. These results suggest that the balance between tree and shrub cover is a function of the time interval since fire and the ability of trees, once they become established, to shade out shrubs.

A difference in species diversity occurred between the Angora Ridge and the other three fire areas as is indicated by species richness counts and the Shannon diversity index (Fig. 5) which were higher on the three younger sites. Though the number of tree species is relatively consistent on all of the sites, the abundance of herbaceous and shrub species was lower in the older fire area. This is due primarily to increased shading resulting from greater tree canopy on that site.

The accumulation of fuel also varied between the older site and the three younger sites with the highest fuel accumulation occurring on Angora Ridge (Fig. 6).

Results indicate a pattern of vegetation development consistent with conventional models of post-fire succession in mixed conifer forests (Lyon and Stickney 1976; Kercher and Axelrod 1984). However, the proportional abundance of the two major genera of trees, *Abies* and *Pinus,* was about the same for Angora Ridge, Cathedral Creek, and the Luther fire (Table 2) with white fir clearly the dominant species. In the Cascade Lake Fire area, however, *Pinus* was clearly dominant. The relative dominance of *Abies* and *Pinus* on these sites is likely the result of seed availability rather than a result of post-fire competition and succession. This is further demonstrated by a comparison of the relative density of mature fir and pine to seedlings and saplings (Table 2). The earliest recruitment of fir ap-

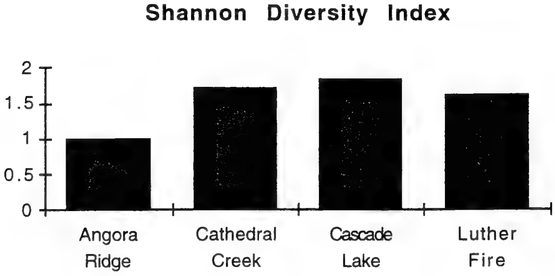

FIG. 5. Shannon diversity index.

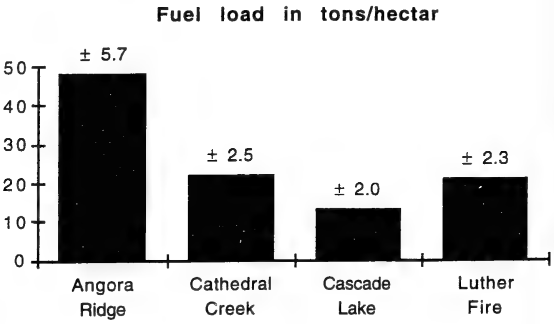

FIG. 6. Fuel load.

TABLE 2. RELATIVE DENSITY. ABMA = *Abies magnifica,* ABCO = *A. concolor,* PIJE = *Pinus jeffreyi,* PICO = *P. contorta* (ssp. *murrayana*).

	Angora Ridge			Cathedral Creek			Cascade Lake			Luther Fire		
Species	Mat	Sap	Seed	Mat	Sap	Seed	Mat	Sap	Seed	Mat	Sap	Seed
ABMA	3.5	2.3	4	—	1	—	—	—	—	—	—	—
ABCO	89	93	96	79	83	99	—	4.5	—	—	86	83
PIJE	8.5	4.7	—	21	16	1	—	91	100	—	14	17
PICO	—	—	—	—	—	—	—	4.5	—	—	—	—

pears to have coincided with the earliest recruitment of pine. There does not appear to be a requisite period of pine domination on these sites as was described for a similar site in the Sierra Nevada (Bock and Bock 1969; Bock et al. 1976). The continuous regeneration of *A. concolor* found in this study is comparable to that found by Conard and Radosevich (1982).

Mortality. The total density of dead trees and the relative mortality of individual species may be useful in predicting the future direction of vegetation change. Clearly the density of dead to live trees were much higher on the Angora Ridge than on the other three sites (Fig. 7) suggesting that mortality may be connected to stand density. The mortality of *A. concolor* was much higher than that of any other species resulting from the high density of this species. All trees that were recorded as dead on both fire sites showed evidence of bark beetle activity.

CONCLUSIONS

The Angora Ridge fire occurred at a time before the implementation of systematic fire suppression (Craven 1993; Gwinn 1993; Hildinger 1993). The existence of this fire and the ecological information collected within its perimeters indicates that not only did stand-replacing fires exist before fire suppression, but that the process of forest development after such fires can be lengthy, including a long period with minimal forest canopy cover. In addition, results point to a number of other interesting conclusions including a lack of a post-fire pine domination period on the sites studied, higher species diversity on the more recent fire sites, and higher fuel accumulation on the oldest fire site.

Simultaneous recruitment of pine and fir occurred on the four fire sites during their post-fire periods. Fir and pine did not follow the traditional successional sequence after large fires that usually includes a period of pine domination followed by increasing fir domination (Bock and Bock 1969; Bock et al. 1976; Lyon and Stickney 1976; Kercher and Axelrod 1984). It appears that there was no obligatory period of post-fire pine domination in the study areas, and that fir regenerated with as much facility as pine.

The higher species diversity on the more recent fire sites is important in that diversity seems to decline as canopy cover increases. This supports the notion that in some communities diversity has an inverse relationship to secondary successional development of forests after fire (Shafi and Yarranton 1977).

Higher fuel accumulation and a high density of standing dead on the older fire site suggests that the long fire-free interval has increased the probability of another high intensity fire.

In the quest to determine the proper role of fire in the forest management scheme in the Tahoe Basin, stand-replacing fires need to be understood as part of the pre-European fire regime. In addition to periodic surface fires, stand-replacing fires have been instrumental in the formation of canopy gaps, and the maintenance of habitat heterogeneity and species diversity. Including stand replacing-fire as a part of forest management in the Lake Tahoe Basin may be unpopular socially and politically, and difficult to implement. However, suppression of all

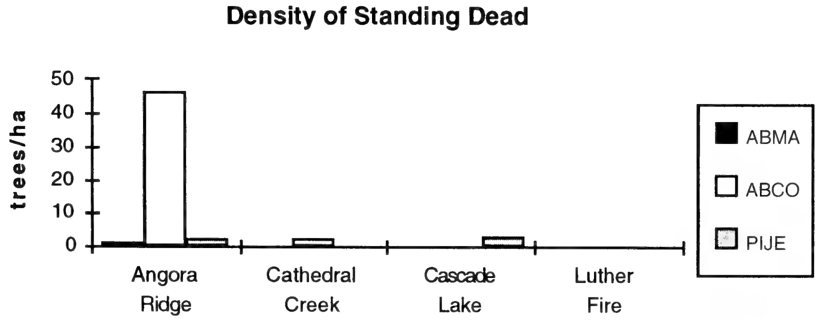

FIG. 7. Standing dead.

stand-replacing fires, in the long run, may be more costly than their careful management.

ACKNOWLEDGMENTS

We thank Dr. Lester Rowntree of the Environmental Studies Department at San Jose State University for his role as adviser on the Master of Science thesis project from which this study originated. We thank the USDA Forest Service for financial support and the technical support of John Swanson and Katherine Culligan. For their comments on the manuscript we thank Dr. Robert Sweeney and Dr. V. Thomas Parker (San Francisco State University), Scott Stevens (University of California Berkeley), and John Swanson (USDA Forest Service, Lake Tahoe Basin Management Unit).

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FIRE REGIME OF THE LODGEPOLE PINE FOREST OF MT. SAN JACINTO, CALIFORNIA

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ABSTRACT

The objective of this study of the 1000 ha lodgepole pine (*Piñus contorta* ssp. *murrayana*) forest of Mt. San Jacinto, California, is to typify several components of the fire regime, including intensity, size, frequency, and the relationship of fire with weather and its seasonal timing. We analyzed several lines of evidence, including fire occurrence from suppression records, fire dates from scarred *P. contorta* ssp. *murrayana,* forest structure as it relates to past disturbances, forest fuel loading, dendroclimatological modeling as it relates to past fire occurrences, and fire-igniting weather characteristics. The lodgepole pine forest of Mt. San Jacinto has a regime of fires that are typically of low intensity and that typically burn small areas (<10 ha). Lightning ignites fire somewhere within this forest as frequently as every few years, but given that lightning is a spatially random process and that fires typically burn areas less than 10 ha in size, the mean fire interval for any 10 ha area is more likely on the order of 100 years. Atypically large fires (20 ha or larger) are possible, but they have burned infrequently in the past. Fires appear to be more common during years when surface and ground fuels are relatively dry (a result of below-average winter precipitation), and fires occur primarily late in or after the growing season. Mt. San Jacinto State Park managers should always prepare for lightning fires, but they can probably safely allow most lightning fires to burn naturally within this ecosystem. Because the possibility exists for fires to burn large areas, fires should probably be monitored closely to protect a unique resource of very old *P. contorta* ssp. *murrayana* trees.

RESUMEN

El objetivo de este estudio en un bosque de mil hectáreas de *Pinus contorta* ssp. *murrayana* en Monte San Jacinto, California, es describir varios componentes del régimen de incendios, incluyendo la intensidad, el área, la frecuencia, las asociaciones entre incendios y el tiempo, y su sincronización estacional. Analizamos varias líneas de evidencia, incluyendo la ocurrencia de incendios según los registros de supresión, fechas de incendios según los pinos con heridas de incendio, la estructura forestal en relación a las pasadas perturbaciones, la cantidad de combustible forestal, modelos dendroclimatológicos en relación a pasadas ocurrencias de incendios, y las características climáticas iniciadoras de incendios. El bosque de *Pinus contorta* del Monte San Jacinto tiene un régimen de incendios que típicamente arden con una intensidad baja y en áreas menores de 10 ha. Los rayos inician incendios en cualquier parte dentro de este bosque con una frecuencia de 4 a 7 años, pero dado que los rayos que acompañan las tormentas son un proceso espacialmente al azar y que los incendios típicamente queman áreas menores de 10 ha, el intervalo promedio entre incendios en cualquier punto es probablemente del orden de 100 años. Incendios atípicamente grandes (decenas de hectáreas o más) son posibles, pero han ocurrido con poca frecuencia. Los incendios parecen ser más comunes durante años cuando los combustibles forestales en la superficie y el suelo están relativamente secos (a causa de precipitación invernal menor que la normal), y los incendios ocurren principalmente hacia el final o después del período vegetativo. Los guardabosques de Monte San Jacinto deben estar siempre preparados para incendios producidos por rayos, pero probablemente pueden permitir arder naturalmente la mayoría de estos incendios dentro de este ecosistema. Debido a que existe la posibilidad de incendios que queman áreas amplias, los incendios deben ser vigilados atentamente para proteger este recurso único de *Pinus contorta* longevos.

INTRODUCTION

The first step in formulating a fire management plan for a wilderness or natural area is determining the natural role of fire for the area (Agee 1974). Knowledge of the natural fire regime forms the basis for predicting fire behavior and responding to fires, helps illustrate the inevitability of fire in natural areas, and aids in the application and public interpretation of fire management plans (Mutch 1980). The (lodgepole pine) *Pinus contorta* ssp. *murrayana,* forest of the Mt. San Jacinto State Wilderness, California, has ample evidence of past fires in the form of abundant living, fire-scarred *P. contorta* ssp. *murrayana* located throughout the forest (Hamilton 1983). However, few of the details of the behavior of past fires can be inferred merely from the presence of fire-scarred trees. Our objective here is to typify several components of the regime of lightning-ignited fires of this forest, including intensity, size, frequency, the relationship of fire with weather, and seasonal timing of fires. To meet this objective, we analyzed multiple lines of evidence, including fire occurrence from suppression records, fire dates from scarred *P. contorta* ssp. *murrayana,* forest structure as it relates to past disturbances, forest fuel loading, dendroclimatological modeling

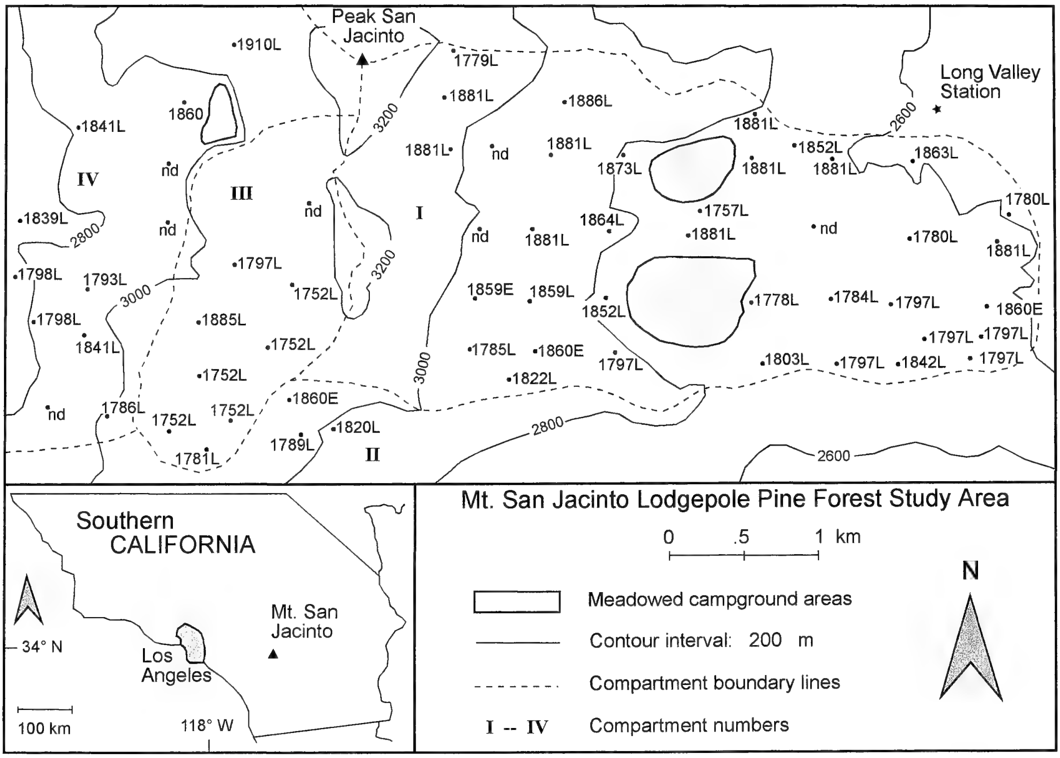


FIG. 1. Lodgepole pine forest of Mt. San Jacinto, Southern California. Dots mark plot locations, year values indicate the years when fire-scarred *P. contorta* ssp. *murrayana* were burned, and "nd" indicates fire-scar samples that were not crossdateable. "L" indicates a fire that occurred late in or after the growing season, and "E" indicates a fire that occurred early in the growing season; dates with neither letter indicate that the seasonal timing of the fire could not be unequivocally determined.

as it relates to past fire occurrences, and fire-igniting weather characteristics.

To accommodate the natural fire ecology of this lodgepole pine forest, Mt. San Jacinto State Park managers may use information from this study when formulating or amending policies for managing fire within their broader management goals of maintaining natural disturbance processes and protecting unique natural resources that include *P. contorta* ssp. *murrayana* up to several hundreds of years old (Hamilton 1983). This study also adds to the understanding of the ecology of *P. contorta* ssp. *murrayana* which occurs throughout the Sierra Nevada, Transverse, and Peninsular Ranges of California and in Baja California and is thought to have a stable ecological role and distribution that is not related to fire (Lotan and Critchfield 1990).

MATERIALS AND METHODS

Study site. Mt. San Jacinto (33°49′N, 116°41′W) is 160 km east of Los Angeles, California (Fig. 1, inset). Between 2550 to 3200 m elevation *P. contorta* ssp. *murrayana* forms a xerophytic and depauperate forest (Thorne 1988) covering approximately 1000 ha. This forest is a topoedaphic climax with relatively minor amounts of other species (Hamilton 1983). At its lower elevations (2550 to 2900 m), *P. contorta* ssp. *murrayana* is mixed with *Abies concolor* (white fir), which extends to lower elevations beyond the range of *P. contorta* ssp. *murrayana.* At its higher elevations (2900 to 3200 m), *P. contorta* ssp. *murrayana* is mixed with *Pinus flexilis* (limber pine) in a sparse forest with an open canopy. The understory consists predominantly of *Ceanothus cordulatus* (snow bush) and *Chrysolepis sempervirens* (bush chinquapin).

Climate is mediterranean (cold, wet winters and warm, dry summers; Bailey 1966). Soils are derived from granitic parent material and are classified as lithic Xerorthents: They are shallow, coarse-textured with a large volume of rock fragments and outcrops, well drained, and very low in water holding capacity and fertility (Cohn, B. R. and J. G. Retelas, unpublished soil survey on file with the San Bernardino National Forest, California).

The fire regime and structure of this forest probably reflect little influence by Native Americans of the past. The Cahuilla Indians had the strongest presence in the study area (Smith 1957), but their main territory was the Cahuilla Valley at 1200 m elevation (Barrows 1900), considerably below the lodgepole pine forest. Summer and fall encampments were common in lower canyons (Aschmann 1959) but less common on higher ridges (James 1960; Bean and Saubel 1972). The Cahuillas rarely if ever used fire as a hunting aid (Drucker 1937).

Although there was some cattle grazing on Mt. San Jacinto, it ended by about 1940. Anecdotal accounts indicate that grazing was limited in the lodgepole pine forest and essentially restricted to the largest of the three meadow areas (Fig. 1; Hamilton 1983). While we recognize the potential impact of grazing on fire regimes of ecosystems in general (Savage and Swetnam 1990), we believe that the specific impact of grazing on the lodgepole pine forest of Mt. San Jacinto was not substantial.

Field sampling took place during the summers of 1983 and 1984. We divided the 1000 ha lodgepole pine forest study site into compartments by aspect (Fig. 1): Compartment I faces east, II faces south, III is a relatively flat plateau, and IV faces west. Meadowed campground areas were excluded because of the potential impacts of heavy recreational use on the fire regime, fuel loading, and forest structure. Within each compartment we located transects perpendicular to contours (Arno et al. 1993). Transects were 200 m apart, and sample points were 500 m apart along each transect. The fire-scarred *P. contorta* ssp. *murrayana* (Mitchell et al. 1983) nearest each sample point (usually no more than a few tens of meters away) was chosen as the center point for a 0.04 ha (20 m × 20 m) sample plot. Occasionally a plot contained more than one fire-scarred *P. contorta* ssp. *murrayana* up to five in one case.

For each plot, we recorded elevation, slope, and aspect, and we estimated forest fuel loading using a photo series of woody residues as quantified by Blonski and Schramel (1981) for this forest type. Within each plot, we measured diameter at breast height of all trees and counted trees, saplings, and seedlings shorter than breast height. We extracted increment cores from scarred *P. contorta* ssp. *murrayana* to dendrochronologically date the fires that caused the scars (Sheppard et al. 1988). We also cored old, unscarred *P. contorta* ssp. *murrayana* throughout the study site to develop a site- and species-specific reference chronology for crossdating purposes.

ANALYSIS

Fire occurrence from suppression records. Although San Bernardino National Forest fire suppression records extend back to 1912, early records appear to be incomplete and we restricted this analysis to the period since 1945. We tabulated information on the suppression of lightning fires in the lodgepole pine forest of Mt. San Jacinto. We chronologically listed all years with at least one recorded lightning fire and calculated the mean time period between years when fires occurred.

Fire dates from scarred lodgepole pines. We crossdated (Stokes and Smiley 1968) cores from unscarred *P. contorta* ssp. *murrayana* (two cores per tree from twenty trees) and measured ring widths to the nearest 0.01 mm. We removed growth trends from each ring-width series by dividing each measurement by the corresponding value of a trend line estimated from either a modified negative exponential or a linear fit (Fritts 1976). We then autoregressively modeled the detrended series into residual series of white noise (Cook 1985), which were averaged into the reference index chronology. We verified the crossdating of this chronology against a tree-ring chronology from bigcone *Pseudotsuga macrocarpa* (Douglas-fir) growing 20 km from the study site (Keen Camp Summit, 33°43′N, 116°05′W, 1432 m elevation; Drew 1972).

Scarred trees were exclusively single-scarred, which allowed the effective use of increment cores to date the fires by crossdating ring-width series with the reference chronology (Sheppard et al. 1988). To establish the year of formation of the outermost ring before the fire, we crossdated nondisturbed ring growth that preceded the scar. Our crossdating of scarred samples was checked by another dendrochronologist. Additionally, we determined the general seasonal timing of the fire from the relative completeness of the outermost ring before the scar on samples for which this was possible (Baisan and Swetnam 1990). A complete or nearly complete ring (with at least some latewood cells) indicated a fire that burned after or late in the growing season (late July through early September). An incomplete ring (no latewood cells) indicated a fire that burned early in the growing season (early June through mid-July).

Pinus contorta *ssp.* murrayana *structure as related to disturbance regime.* We evaluated the histogram of diameters of sampled *P. contorta* ssp. *murrayana* from throughout the study site to determine the placement of this forest along the continuum of relatively even- to uneven- or all-aged structures (Hanley et al. 1975; Despain 1983; Lorimer and Frelich 1984). The use of diameters instead of actual ages requires that diameter and age be related such that age need not be determined for all trees sampled. To test for this relationship, we compared ages to diameters for a subset of *P. contorta* ssp. *murrayana* located throughout the study site for which pith dates were determined (Fig. 2). Based on this relationship, size is sufficiently related to age to use a histogram of diameters to characterize the age structure of *P. contorta* ssp. *murrayana* in this forest.

Relationship between fire occurrence and weather. We dendroclimatically modeled (Fritts 1976) the Keen Camp Summit tree-ring chronology with monthly weather data for the NOAA climatic division #7 (southeastern deserts) of California. This tree-ring chronology correlates well with precipi-

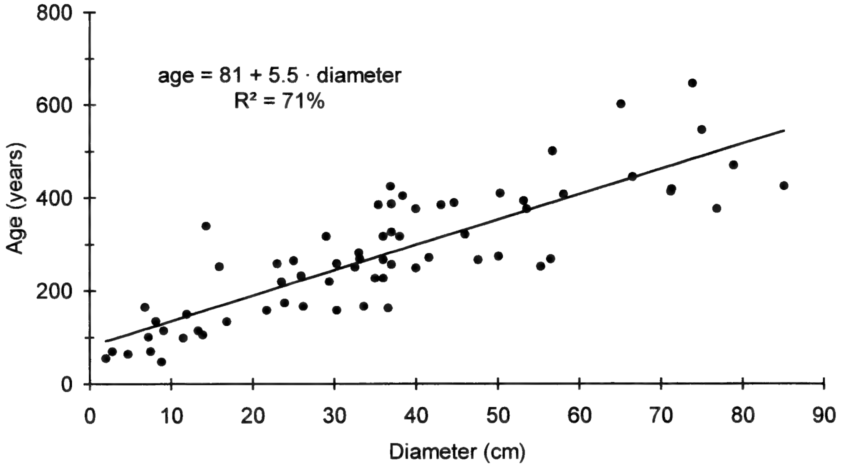


FIG. 2. Age-diameter relationship for *P. contorta* ssp. *murrayana* of Mt. San Jacinto.

tation of the winter prior to the growing season (Fig. 3a). When the December through March precipitation totals are summed, the winter season correlation with the chronology is 0.60 ($P < 0.01$). We extended the Keen Camp Summit tree ring chronology, which ends in 1966, by appending to it an indexed series of winter (December through May) precipitation at Idyllwild, California (1700 m elevation, 8 km south of Peak San Jacinto). We then assessed the relationship between fire occurrence and winter precipitation by comparing the average chronology index value for years when fire occurred to the average index value for the chronology (1.0 by definition, Fritts 1976).

Seasonal timing of fire risk. We searched the daily weather records from the Long Valley Ranger Station (2585 m elevation; Fig. 1) and the Idyllwild Fire Station for evidence of lightning occurrence for the entire study site. Combining data from these two stations located on opposite sides of the study site accounted for the local and sporadic nature of summer convection storms. Mid-May through mid-September is the period of likely convection storms (Tubbs 1972), and any day within this period with data or comments about rain, thunder, or lightning was considered to have had lightning possible. We grouped counts of these days into half-month periods and averaged across years for which complete records exist for both stations (1965 to 1974 and 1979 to 1984).

RESULTS

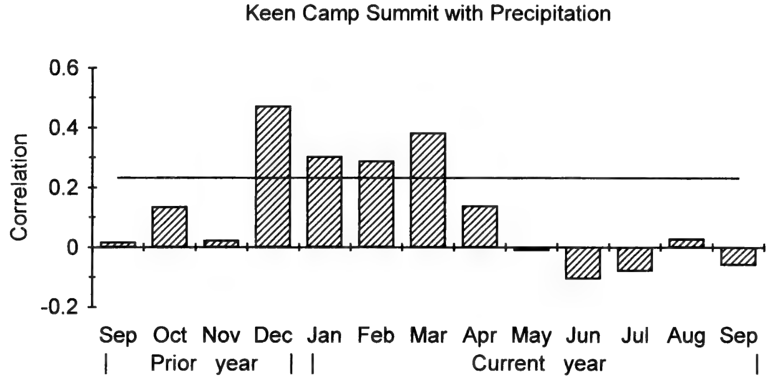
Fire occurrence from suppression records. The mean time period between years with at least one suppressed lightning fire is 5.2 ± 1.1 years (all error estimates are 95% confidence intervals) for the 1000 ha lodgepole pine forest from 1945 to 1987 (Table 1). Notably, 6 distinct fires were recorded for 1972, including two within the same survey section (259 ha) on each of two different days. Most of the listed fires occurred after mid-July (81%). Furthermore, all of the listed lightning fires were declared as spot fires—less than 0.4 ha in size at the time they were suppressed.

Fire dates from scarred P. contorta *ssp.* murrayana. We were able to crossdate 56 (88%) of the scarring events that we sampled (Table 2). Within plots with more than one fire-scarred *P. contorta* ssp. *murrayana,* all crossdatable samples dated the fires to the same year. We were able to determine the season of scarring in 52 scar samples, most of which (92%) contain at least some latewood cells in the outermost prescar ring and thus indicate fires that burned late in or after the growing season (Fig. 1).

Many of the fires dated from scarred *P. contorta* ssp. *murrayana* appear to be independent of each other, either by date and/or location (Fig. 1). For example, the year 1860 is represented by four plots that are widely separated from one another. To quantify the degree of this independence, we compared fire dates within each pair of adjacent plots, and most pairs (79%) have fire dates that differ from one another. Most adjacent pairs with the same fire date are located within three different clumps in the study site: five 1797 dates are located in the southeastern edge of Compartment I, nine 1881 dates in the northern half of Compartment I, and five 1752 dates in Compartment III (Fig. 1).

Our collection of fire scars includes only one date in the 20th century (1910). The lack of fire scars dating in the 20th century contradicts the suppression record (Table 1), which indicates frequent natural fires during the 20th century, especially since 1945. We attribute this apparent inconsistency to a bias of sampling visually obvious, larger scars of fires that burned further back in time. These *P. contorta* ssp. *murrayana* respond to fire scarring

(a)



(b)

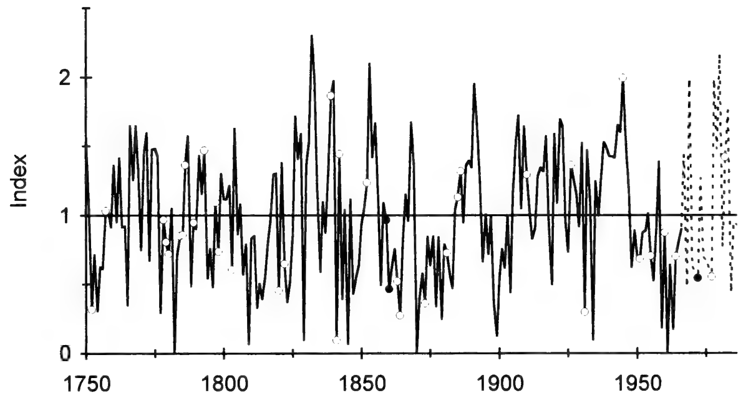


FIG. 3. (a) Correlations of the bigcone Douglas-fir index chronology from Keen Camp Summit to total monthly precipitation for NOAA climatic division 7 (southeastern deserts) of California. Reference lines indicate critical value for significance for alpha = 0.05, n = 71. (b) Winter (December through March) precipitation index chronology. The solid line (1750 to 1966) is the Keen Camp Summit chronology, the dashed line (1967–1986) is from the actual meteorological data from the Idyllwild station, and the reference line of 1.0 indicates average winter precipitation. Open dots indicate all years with evidence of fires, and closed dots indicate years with evidence of early-season fires.

with very slow growth rates after the scar, and scars from fires during the 20th century are small and inconspicuous such that we probably under-sampled them relative to older fire scars. Because of this sampling bias, we restricted our interval analysis of fire-scar dates to the period from 1752 to 1886, and the mean time period between years with fire anywhere in the 1000 ha forest is 5.0 ± 2.2 years (Table 2).

Pinus contorta ssp. *murrayana structure as related to disturbance regime.* The histogram of diameters of all sampled lodgepole pines is adequately fit by a negative exponential curve pattern (Fig. 4a). The three areas with several adjacent plots with the same fire dates (1752, 1797, and 1881; Fig. 1) warrant closer scrutiny, and we evaluated size histograms of *P. contorta* ssp. *murrayana* located within plots burned during those years. In the case of 1752, the size histogram is shaped broadly in a negative exponential pattern (Fig. 4b), and it has a slope coefficient that does not differ substantially from that of the *P. contorta* ssp. *murrayana* size histogram for the entire forest. In the case of 1797, the size histograms are not shaped in a negative exponential pattern (Fig. 4c). In the case of 1881, the size histogram is shaped broadly in a negative exponential pattern, but the number of individuals in the smallest size class is overestimated (Fig. 4d).

Forest fuel loading. The fuel loading within this lodgepole pine forest averages 18.9 ± 2.9 tonnes/ha, similar to the estimate of 15.4 tonnes/ha reported for a single area near the smallest meadowed campground area (Fig. 1; Compartment IV; Hanawalt and Whittaker 1976). The general fuel type of the lodgepole pine forest of Mt. San Jacinto is best described as Model H of the National Fire-Danger Rating System (Deeming et al. 1977), in which conifer trees pre-dominate; duff, litter, and branchwood are the primary ground fuels; and needles are less than 5 cm long. Additionally, as an indicator

TABLE 1. SAN BERNARDINO NATIONAL FOREST SUPPRESSION RECORDS (1912 TO 1989) OF LIGHTNING FIRES WITHIN THE LODGEPOLE PINE FOREST OF MT. SAN JACINTO[a]. All of these fires were listed as spots, smaller than 0.4 ha when suppressed. Mean time period between years with fire = 5.2 ± 1.1 years[d]. [a] The reports included all fires that burned within the San Jacinto District, but only lightning fires within the lodgepole pine forest were considered pertinent to this study. [b] All sections are approximately 259 ha (1 mi^2) and are within Township 4S, Range 3E of the San Bernardino Meridian. [c] This was not calculated for years prior to 1945 because of the incompleteness of the records for that time period. [d] For the period 1945 to 1987 and for the 1000 ha lodgepole pine forest.

Section location[b]	Date	Return interval (yrs)[c]	Section location	Date	Return interval (yrs)
27	August 4, 1926				8
			20	June 2, 1972	
29	September 4. 1931		21	June 2, 1972	
			21	June 2, 1972	
21	September 8, 1945		23	July 30, 1972	
		6	23	July 30, 1972	
21	September 28, 1951		23	July 31, 1972	
		4			5
23	August 14, 1955		23	August 16, 1977	
		5			5
23	September 7, 1960		22	July 25, 1982	
		4			5
30	July 26, 1964		21	September 1, 1987	

of the living fuel loading, the average stocking density of this forest is 375 ± 73 stems/ha for all species.

Relationship between fire occurrence and weather. For the period from 1752 (earliest fire-scar date) to 1986 (last year of our chronology of winter precipitation), fires have occurred only slightly more commonly during years of below-average winter precipitation (Fig. 3b). The average chronology index value for years with fire is 0.887 ± 0.120, which is not significantly different from the average index value of 1.0. Eight of the ten years for which we have more than one fire scar (Table 2) or fire-suppression evidence of multiple ignitions (Table 1) had below-average winter precipitation. Similarly, all 3 years for which we have evidence of early-season fires (1859, 1860, and 1972), had below-average winter precipitation (Fig. 3b).

TABLE 2. CHRONOLOGICALLY SORTED YEARS FOR WHICH A FIRE SCAR FROM *PINUS CONTORTA* SSP. MURRAYAMA WITHIN THE LODGEPOLE PINE FOREST OF MT. SAN JACINTO WAS DENDROCHRONOLOGICALLY DATED. Mean time period between years with fire = 5.0 ± 2.2 years[b]. [a] The number in parentheses for some years is the number of trees scarred during that year; years without parentheses have just one scarred tree. b For the period 1752 to 1886 and for the 1000 ha lodgepole pine forest.

Year	Return interval (yrs)	Year	Return interval (yrs)	Year	Return interval (yrs)	Year	Return interval (yrs)
1752(5)[a]			1		2		3
	5	1786		1822		1863	
1757			3		17		1
	21	1789		1839		1864	
1778			4		2		9
	1	1793		1841(2)		1873	
1779			4		1		8
	1	1797(7)		1842		1881(9)	
1780(2)			1		10		4
	1	1798(2)		1852(2)		1885	
1781			5		7		1
	3	1803		1859(2)		1886	
1784			17		1		24
	1	1820		1860(4)		1910	
1785							

Seasonal timing of fire risk. On average, 78% of all days with evidence of lightning occur after mid-July (Fig. 5). Thus, the natural fire regime of this lodgepole pine forest includes lightning risk that occurs primarily late in or after the growing season.

DISCUSSION

Fire intensity. Given that the thin bark of *P. contorta* ssp. *murrayana* cannot protect trees from fires of moderate or high intensity (Minore 1979; Ryan and Reinhardt 1988), a fire scar on living *P. contorta* ssp. *murrayana* indicates low intensity for that fire. By extension, the abundance of living, fire-scarred *P. contorta* ssp. *murrayana* of Mt. San Jacinto suggests that fires typically burned with low intensity. The exclusively nonserotinous nature of *P. contorta* ssp. *murrayana* of Mt. San Jacinto also indicates a regime of low intensity fires (Brown 1975; Lotan 1976).

At 375 stems/ha, the lodgepole pine forest of Mt. San Jacinto is sparsely stocked and therefore has a highly discontinuous living fuel load. *Pinus contorta* ssp. *murrayana* generally has an open crown

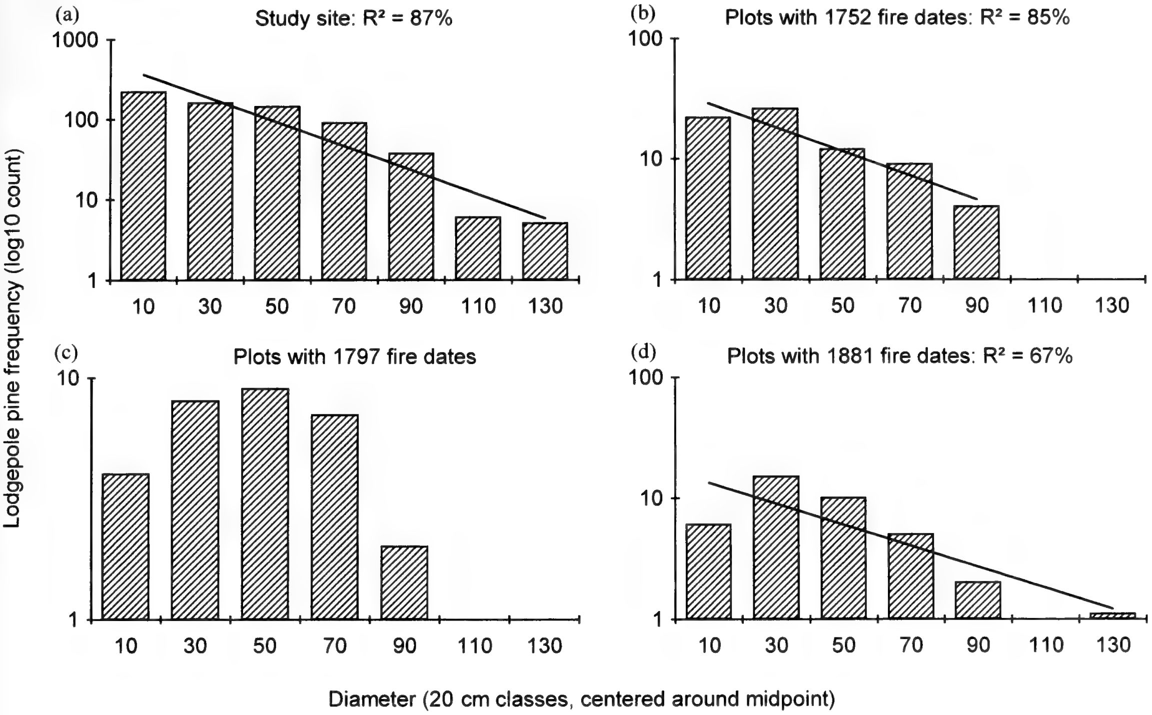


FIG. 4. Size histograms of *P. contorta* ssp. *murrayana* within (a) the entire lodgepole pine forest of Mt. San Jacinto, and plots burned in (b) 1752, (c) 1797, or (d) 1881.

form and foliage with low flammability (Minore 1979), which results in discontinuous ladder fuel loading with little potential for crown fires (Fahnstock 1970). The average ground fuel loading of 18.9 (±2.1) tonnes/ha for the lodgepole pine forest of Mt. San Jacinto is also light, and the Model H fuel type supports fires that typically spread slowly and are not intense except possibly in areas of concentrated downed woody material (Deeming et al. 1977). Furthermore, rock outcrops (common throughout the lodgepole pine forest) act as natural firebreaks that isolate live and dead fuels. This light and discontinuous fuel loading indicates a regime of low intensity fires (Philpot 1977) within the lodgepole pine forest of Mt. San Jacinto.

The forest-wide structure of abundant young trees and exponentially fewer old trees (Fig. 4a) indicates that the lodgepole pine forest of Mt. San

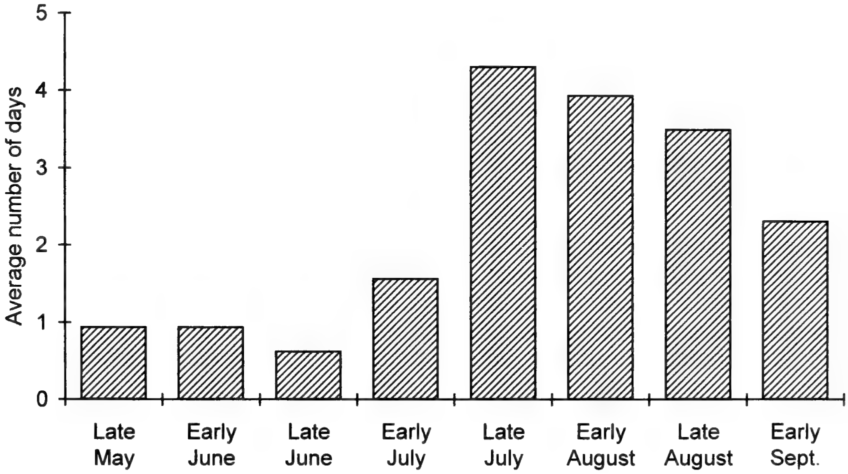


FIG. 5. Frequency of weather with possible lightning somewhere over the lodgepole pine forest of Mt. San Jacinto. Data are summarized from daily records (1965–1974 and 1979–1984) from the Idyllwild and Long Valley stations.

Jacinto is all-aged and self-perpetuating (Lorimer 1980) and that it has not experienced intense disturbances in the past few to several hundred years (Schmelz and Lindsey 1965; Brown 1975; Renkin and Despain 1992). These traits are similar to some Sierra Nevada subalpine forests where *P. contorta* ssp. *murrayana* forms stable populations of zonal dominants on sites beyond the ecological range of more tolerant competitors (Parker 1988) and where canopy or crown fires are virtually absent (Parker 1986). These results and interpretations are also similar to those for some lodgepole pine forests of Yellowstone National Park that have been described as nonpyrogenous, with fire as a disturbance process of low intensity (Despain 1983).

There is some structural evidence for fires of relatively higher intensity. Notably, *P. contorta* ssp. *murrayana* size histograms for the 1797 and 1881 fires are not shaped in a negative exponential pattern, indicating unusually intense disturbances. This is consistent with the fact that many forested ecosystems have regimes of typically low intensity fires with occasional fires of higher intensity (Kilgore 1981).

Fire area. The fact that all suppressed lightning fires were listed as spot (0.4 ha or smaller) suggests natural fires do not typically expand in size quickly. It can be argued, of course, that suppressed fires remained small because they were suppressed. However, remote fires in wilderness areas are inherently difficult to access, and fire crews may have taken more than a day to reach some of these fires, especially before the availability of airborne access. That none of the listed fires grew larger than 0.4 ha before being suppressed suggests that fires typically burn small areas.

Our strategy for field sampling fire scars (transects 200 m apart with grid points every 500 m along each transect) limited our minimum resolvable fire area to approximately 10 ha (Arno et al. 1993). If past fires typically burned areas exceeding 10 ha, we would expect a majority of pairs of adjacent sampling plots to have the same fire date. In contrast to that interpretation, most adjacent pairs of sampling plots have different fire dates, indicating that these fires typically burned areas of less than 10 ha.

The three areas containing several plots with the same fire dates (1752, 1797, and 1881; Fig. 1) have at least two possible interpretations. One is that several small, spatially independent fires ignited and burned during those years. The fire suppression record for 1972 (six fires independent of one another by date or location; Table 1) indicates that this scenario is at least possible because of frequent lightning ignitions. A valid alternative scenario is that a single, large fire burned during those years. Given that higher intensity disturbance processes generally impact larger areas (Sousa 1984) and that forest structure results for plots burned in 1797 and 1881 indicate that those fires may have been relatively intense, it is probable that those fires were relatively large (20 ha or larger).

Frequency. We cannot precisely quantify mean fire interval, defined as the average of all fire intervals between successive fires of a designated area (Romme 1981), because the fire-suppression records and our fire-scar data do not indicate more than one fire date for any particular area. However, if we define the designated area as any single area 10 ha in size (our minimum resolvable fire area), and if lightning ignites fires randomly throughout the entire 1000 ha forest, then a natural fire should burn any designated area only once every 100 years. At this spatial scale, this regime qualifies as one of infrequent (mean fire interval of >25 years) fires of low intensity, similar to other subalpine forests of the Sierra Nevada (Kilgore and Briggs 1972; Kilgore 1981).

In contrast to the mean fire interval of at least 100 years, the mean time interval between fires anywhere in the lodgepole pine forest—not necessarily any particular area—since the mid 18th century is approximately 4 to 7 years (5.2 ± 1.1 years for the fire suppression record of 1945 to 1989, Table 1; and 5.0 ± 2.2 years for the fire scar record 1752 to 1886, Table 2); thus, natural fires occur somewhere throughout the lodgepole pine forest fairly frequently. If this interval analysis is restricted to include only those fires that appear to have burned atypically large areas (as was possible for 1752, 1797, and 1881), then the mean time interval between large fires somewhere throughout the lodgepole pine forest is 64 years, much longer than the 4 to 7 years between fires of any size. The fact that large fires occur infrequently conforms to the general principle that large disturbance events are relatively rare (Sousa 1984).

Relationship of fire with weather. For the lodgepole pine forest of Mt. San Jacinto, evidence that fires, especially most large fires and all early-season fires, occur more commonly during years with below-average winter precipitation is consistent with results from other Southwestern forest ecosystems where natural fires occur more commonly during dry years (Swetnam and Betancourt 1990). These results support the intuitive notion that moisture content of ground and surface fuels is an important factor in fire occurrence and behavior.

Seasonal timing of fire. As indicated by daily weather records and by both the suppression and scar records of fire, lightning and/or fires in the lodgepole pine forests of Mt. San Jacinto commonly occur late in or after the growing season (after mid-July). This temporal pattern of lightning risk is similar to that of the entire Peninsular Range of southern California (Tubbs 1972), but it differs from the pattern found in Southwestern forest ecosystems where lightning fires occur more commonly during June and early July (Baisan and Swetnam 1990).

MANAGEMENT IMPLICATIONS

Given that lightning fires occur fairly frequently somewhere within the lodgepole pine forest of Mt. San Jacinto, State Park Wilderness managers should always expect and be prepared for fires, especially during the latter half of the growing season and during summers preceded by below-average winter precipitation. However, because fires typically burn small areas with low intensity, managers can expect to safely allow most lightning fires to burn naturally, as has been suggested for other forests (Heinselman 1970). Larger fires are possible, of course, and monitoring fires will continue to be prudent, especially for Mt. San Jacinto because of its unique natural resource of very old *P. contorta* ssp. *murrayana.*

ACKNOWLEDGMENTS

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A NEW *STIPA* (POACEAE: STIPEAE) FROM IDAHO AND NEVADA

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ABSTRACT

Stipa shoshoneana is a new grass species principally from east-central Idaho, but with a disjunct population in the Belted Range of southern Nevada. *Stipa shoshoneana* is allied with Eurasian species of *Stipa* L. sect. *Lasiagrostis* (Link) Hackel, and with North American stipoids historically assigned to *Oryzopsis sensu amplo.* Vegetative features, panicles, glumes, anthoecia, and flowers approximate *Stipa canadensis* Poir., but the lemma callus and awn morphology resemble *Oryzopsis pungens* (Torr.) A.S. Hitchc.

INTRODUCTION

During 1978, three grass specimens were collected (*D. M. Henderson 4432*) within the Salmon River Canyon of Lemhi County, Idaho, that possess a unique combination of micro- and macromorphological character-states, but with clear alliance to Eurasian species of *Stipa* L. sect. *Lasiagrostis* (Link) Hackel (≡*Achnatherum* P. Beauv. *sensu stricto*), and to a group of North American stipoids historically assigned to *Oryzopsis sensu amplo.* Vegetative features, spikelet arrangement, glumes, anthoecia (lemma and palea without callus or awn) and flowers approximate *Stipa canadensis* Poir. (≡*Oryzopsis canadensis* [Poir.] Torr.), but the lemma callus and awn parallel *Oryzopsis pungens* (Torr.) A. S. Hitchc.

Over 200 subsequently collected specimens of this enigmatic grass confirmed the presence of more than just a few anomalous plants. Fourteen widely separated populations are known within the Salmon River Mountains and Lemhi Range of east-central Idaho, and a small disjunct population exists in the Belted Range of southcentral Nevada.

The known geographical range of this undescribed species occurs beyond the spatial extent of any close tribal relative. *Stipa canadensis* and *Oryzopsis pungens,* both species of Canada and the northeastern United States, are presently unknown within Idaho, although both occur nearby in southern British Columbia and Alberta. *Oryzopsis micranthum* (Trin. & Rupr.) Thurber (≡*Piptatherum micranthum* [Trin. & Rupr.] Barkworth) is locally frequent to common throughout the Great Basin, central Rocky Mountains, and northern Great Plains, but is known within Idaho from only one site in southwestern Clark County (Moseley and Henderson 1994) ca. 30 km by air northeast across Birch Creek Valley from the closest population of the undescribed species. *Oryzopsis exigua* Thurber is present at several sites across the Salmon River Mountains and Lemhi Range, but has not been found with the undescribed species.

Twelve other stipoids occur within the geographical extent of the undescribed species: *Stipa comata* Trin. & Rupr. (≡*Hesperostipa comata* [Trin. & Rupr.] Barkworth); *S. viridula* Trin. (≡*Nassella viridula* [Trin.] Barkworth); *S. hymenoides* R. & S.; *S. lettermanii* Vasey; *S. nelsonii* Scribn.; *S. nevadensis* B. L. Johnson; *S. occidentalis* Thurber; *S. pinetorum* M. E. Jones; *S. richardsonii* Link; *S. thurberiana* Piper; *S. webberi* (Thurber) B. L. Johnson; and *Oryzopsis swallenii* C. L. Hitchcock & Spellenberg. Note that the last ten species were all recombined in *Achnatherum* by Barkworth (1993). The undescribed species is, however, ecologically segregated from all twelve, as it occurs only on or at the base of near-vertical cliffs not occupied by any other stipoid.

Although these populations from east-central Idaho and southcentral Nevada constitute a previously undescribed species, ready assignment to *Oryzopsis* is now incongruous with recent generic realignments in the American Stipeae (Barkworth 1983, 1990, 1993; Barkworth and Everett 1987) that 1) excluded *Stipa* L. from North and South America; 2) treated *Oryzopsis* as a unispecific genus comprising only *O. asperifolia* Michx.; 3) reassigned several North American *Oryzopsis* to other genera; and 4) temporarily retained *S. canadensis, O. exigua,* and *O. pungens* in *Oryzopsis* as an informally recognized group, "Boreobtusae", with uncertain generic affinity. Anthoecial morphology and lemma epidermal cell patterns expressed by the "Boreobtusae" are traceable to Miocene stipoids of present-day Nebraska (Thomasson 1980).

For the past decade, we have delayed the formal naming of this new species while these generic realignments have transpired. Without question, Stipeae systematics are very complex and likely involve reticulate evolution among ancestral ge-

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[1] Deceased 1996. During 1993 and 1994, Henderson participated in the writing and editing of previous drafts.

nomes, as first discussed by Johnson (1945, 1972). The recognition of *Oryzopsis sensu amplo* has long been problematic owing to the obvious heterogeneity within the genus, and to the lack of consistent macromorphological difference from *Stipa sensu amplo* (Johnson 1945, 1972; Hoover 1966; Hitchcock and Spellenberg 1968; Spellenberg and Mehlenbacher 1971; Maze 1972; Kam and Maze 1974; Freitag 1975, 1985; Barkworth and Everett 1987). While it is clear that the North American "Boreobtusae" are only partially similar in macromorphology to *O. asperifolia,* an alternative generic grouping is not readily evident, as species of "Boreobtusae" are macromorphologically dissimilar.

Obvious qualitative differences in floral, spikelet, and vegetative morphology exist among the four species of "Boreobtusae," including the undescribed species. Both *O. pungens* ($2n=22$, Johnson 1945) and *O. exigua* ($2n=22$, Hitchcock and Spellenberg 1968) share with *O. asperifolia* ($2n=46$, Johnson 1945; $2n=48$, Bowden 1960) the combination of a fused style column bearing two or three stigmata, together with obovate glumes both shorter than or equal to the lemma body apex and divaricate at fruit dissemination. However, the florets of *O. pungens* and *O. exigua* differ markedly from each other (Table 1). Both *S. canadensis* and the undescribed species have free styles along with elliptical glumes longer than the lemma body apex and non-divaricate at fruit dissemination. But again, the florets of *S. canadensis* and the undescribed species are otherwise dissimilar (Table 1).

To better evaluate taxonomic placement of both the enigmatic "Boreobtusae" and the undescribed species, we reassessed the central argument espoused by Barkworth and Everett (1987) for generic monophyly as based on putatively autapomorphic lemma epidermal cell patterns first discussed by Thomasson (1976, 1978a).

METHODS

Laminar, lemmatal, and paleal abaxial epidermal patterns were observed from material prepared following the sodium hydroxide/chlorozol black clearing/staining method detailed by Thomasson (1978b). Descriptions of all laminar and lemmatal preparations follow Ellis (1976, 1979). Embryos were dissected from mature fruits first immersed in boiling water removed from a hot plate and then left to cool overnight. Mitotic chromosome counts were made upon root-tips removed from fruits germinated on filter paper in petri dishes, pretreated in distilled water vials kept on ice for 48 hours, and subsequently fixed/stained in aceto-orcein. Meiotic counts were obtained from anthers fixed in 3:1 ethanol : acetic acid and stained in aceto-carmine. Observations and drawings were made through a Zeiss Standard 18 microscope with a camera-lucida attachment. Voucher specimens for chromosome counts are deposited at CAS.

TABLE 1. SPECIES OF "BOREOBTUSAE".

	Stipa shoshoneana	*Stipa canadensis*	*Oryzopsis pungens*	*Oryzopsis exigua*
Proximal glume length	Longer than lemma body apex	Longer than lemma body apex	Shorter than lemma body apex	Shorter than lemma body apex
Anthoecium profile in fruit	Obovate	Obovate	Obovate	Elliptic
Lemma awn	subterminal, caducous, 1—2.5 mm long, ± straight spirally contorted < 1 revolution	terminal, persistent, 10–20 mm long, twice-geniculate, proximal segment spirally contorted > 2 revolutions	subterminal, caducous, 1–2.5 mm long, ± straight, spirally contorted < 1 revolution	dorsal, somewhat persistent, 3–8 mm long, once-geniculate, proximal segment spirally contorted < 1 revolution
Lodicules	3	3	3	2 (3)
Anthers	penicillate, 1.5–2.2 mm long	glabrate, 1.5–2.0 mm long	glabrate, 1.5–2.0 mm long	penicillate, 1.5–3.0 mm long
Styles	2, free throughout	2, free throughout	2, fused proximally	3, fused proximally
Stigmata	2, plumose, exserted laterally	2, plumose, exserted laterally	2, papillate, exserted apically	3, papillate, exserted apically
$2n =$	20 (This paper)	22 (Johnson 1945; Spellenberg 1970)	22 (Johnson 1945) 24 (Bowden 1960; Löve and Löve 1981)	22 (Hitchcock and Spellenberg 1968)

For our morphometric comparisons among "Boreobtusae" species, we examined and measured 204 specimens of the undescribed species, 64 specimens of *O. exigua* at ID, IDS, and UTC, and 470 specimens of other "Boreobtusae" (76 *S. canadensis,* 157 *O. micrantha,* and 237 *O. pungens*), borrowed from CAN, MIN, and RM.

RESULTS AND DISCUSSION

A discussion of generic relationships and realignments will be presented in another paper. In brief, we conclude that the undescribed species and *S. canadensis* are probably best placed with species of *Stipa* L. sect. *Lasiagrostis* (Link) Hackel (≡*Achnatherum* P. Beauv. *sensu stricto*). As for the placement of *O. exigua* and *O. pungens,* we remain at an impasse. If both are transferred to *Stipa* or to *Achnatherum,* then either genus would incorporate species combining fused styles and short glumes, making the exclusion of *O. asperifolia,* the genertype of *Oryzopsis,* even less-tenable. Perhaps both *O. exigua* and *O. pungens* should remain in *Oryzopsis* despite their incongruities otherwise with *O. asperifolia.*

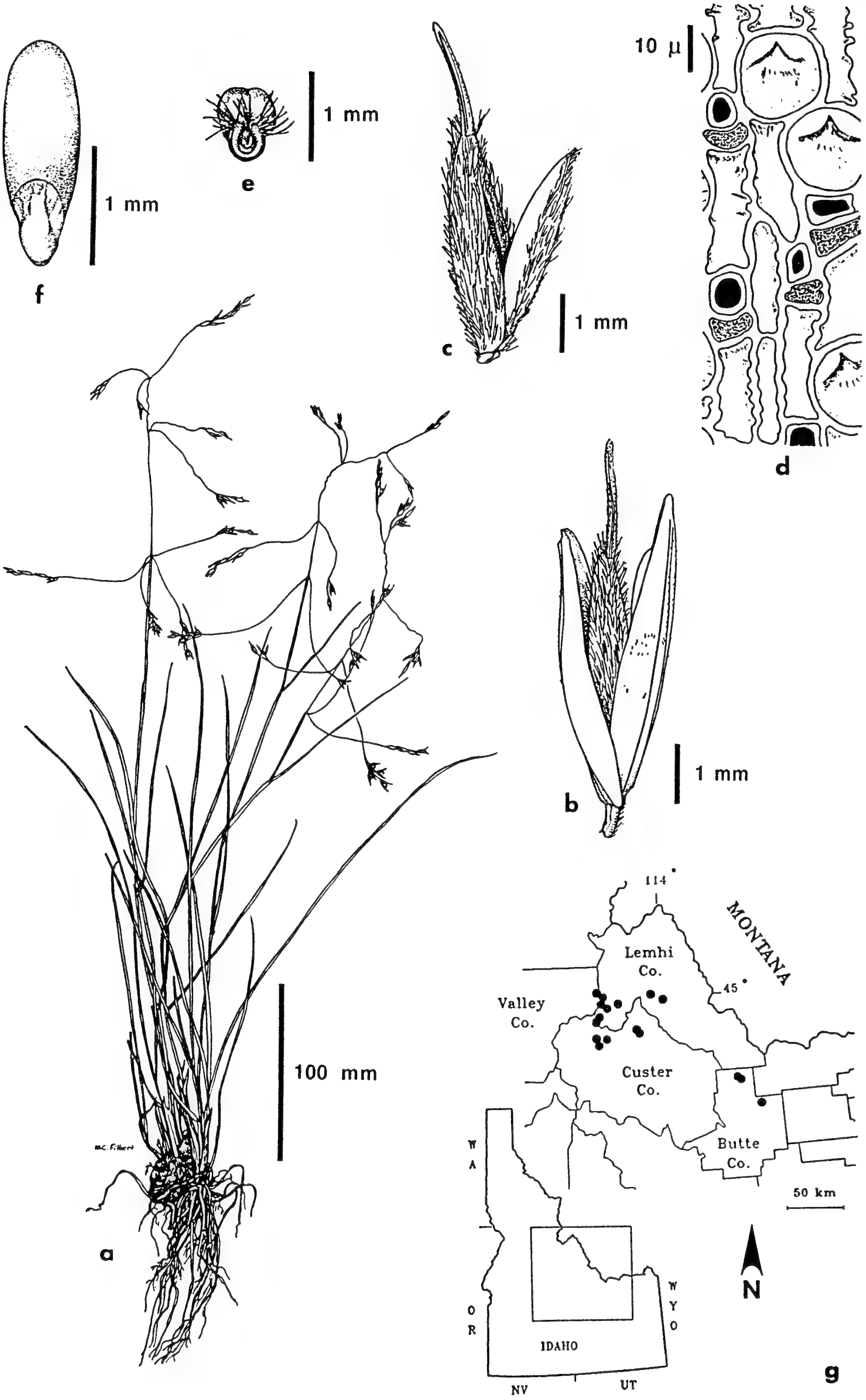
Achnatherum sensu stricto, the greatly enlarged and heterogeneous *Achnatherum sensu* Barkworth (1993), and the newly recognized Australian segregate genus *Austrostipa* S.W.L. Jacobs & J. Everett (1996), form a macromorphological continuum with *Stipa*; and are not globally circumscribable Linnean genera with any greater coherence or predictive utility than *Stipa sensu amplo.* Although others may emphasize differences among modes of variation by segregating smaller genera, we choose to recognize the continuum among these modes by using subgenera within *Stipa sensu amplo,* as did Freitag (1975), Clayton and Renvoize (1986), and recently Vázquez and Devesa (1996).

We anticipate that others will likely recombine this new species in segregate genera. Thus, we have selected a specific epithet that presents no nomenclatural barrier to direct transfers. Table 1, and a phenetic key, enable discrimination of the new species from similar regional stipoids.

Stipa shoshoneana Curto & D.M. Henderson, sp. nov. (Fig. 1). —TYPE: USA, Idaho, Salmon River Mts, ca. 15 km N of Challis, Morgan Creek Canyon ca. 7 km NW of US Hwy 93, near 44°39′47″N, 114°13′19″W, Gooseberry Creek 7.5 min quadrangle, T15N R19E S4 SW¼ of NE¼, el. ca. 1675 m, aspect SW, along N side of road in cracks of near vertical cliffs with *Cercocarpus ledifolius* Nutt., *Heuchera grossulariifolia* Rydb., *Elymus spicatus* (Pursh) Gould, and *Poa interior* Rydb., 30 June 1987, *L. Eno 17* (holotype: CAS; isotypes: BRY, ID, K, MIN, MO, NY, RM, UC, US, UTC, WTU; all to be distributed).

Stipa canadensis Poir. affinis, cujus habitum, anthoecia, et flores habet, sed differt callis lemmatum brevibus, aristis curtis caducis, antheris penicillatis, et chromosomatum numero aequante 20.

Plants rhizocarpic, iteroparous perennials. *Culms* herbaceous, 20–50 cm tall, densely tufted, slender, geniculate or ascending to erect; unbranched distally; nodes 2–3, glabrate, internodes hollow, antrorsely scabridulous; innovations intravaginal. *Leaves* mostly basal, few cauline; vernation convolute. *Sheaths* exauriculate; margins free; cross-section rounded; transverse septae absent; abaxial surface scabridulous. *Ligules* adaxial; membranous throughout; 1.8–5.5 mm long, apex acute, often lacerate. *Lamina* narrowly elongate, the length : width ratio > 30:1; planar or involute with drying, stiff, scabridulous along veins and margins. *Synflorescences* terminal, ebracteate or with a solitary linear bract at the proximal nodes; paniculate, ultimately diffuse, rachis and branches persistent; rachis nodes 3–7; rachis 33–220 mm long; most-proximal rachis internode 0.5–63.0 mm long; branches persistent, terminating at spikelets, slender to subcapillary, irregularly quadrangular, scabridulous; primary branches 1–2(–4) per node, most-proximal primary branches 18–116 mm long, distance to initial secondary branch 4–76 mm long; reflexed 90°–270°, bearing axillary pulvini; secondary and tertiary branching strictly dichotomous, branches bearing axillary pulvini and divaricate pre- and post-anthesis; penultimate and ultimate branches adpressed. *Spikelets* borne as distinctly pedicellate monads, adpressed in fruit; florets and flowers 1, bisexual; 3.3–5.3 mm long excluding lemma awn; pre-anthesis anthoecial profile elliptical, obovate in fruit; pre-anthesis anthoecial compression subterete, somewhat dorsoventrally compressed in fruit; rachilla terminating at floret attachment; disarticulation distal to the glumes. *Glumes* two, persistent, size and shape subequal, both extending beyond lemma body apex, rounded abaxially, membranous to chartaceous, evident veins 1–9, green and purple proximally, colorless distally, glabrate or with midvein scabridulous distally; proximal (first or lower) glume 3.2–5.1 mm long, profile asymmetrically lanceolate or oblongly lanceolate, apex acute to acuminate, awnless; distal (second or upper) glume 3.3–5.3 mm long, profile asymmetrically ovate, apex acute to acuminate, awnless. *Lemma Callus* obconic relative to pedicel, ≤0.3 mm long abaxially, blunt, glabrate, articulation scar round, slightly excavated, peripheral ring raised. *Lemma Body* 2.2–3.8 mm long; profile broadly elliptical; margins symmetrically involute, juxtaposed parallely with spikelet axis prior to anthesis, gaping in fruit; apex emarginate about excurrent midvein; rounded abaxially; germination flap absent; texture coriaceous at anthesis; veins 5–7; evenly antrorsely hirtellous throughout, trichomes simple, ≤0.5 mm long, colorless initially, aging tawny. *Lemma Awn* terminal, unbranched, straight or slightly arcuate, antrorsely scabridulous, 1.0–2.5 mm long; caducous. *Palea*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2.1–3.6 mm long; length, texture and vestiture subequal to lemma; profile broadly elliptical; margins planar; apex bifid, minutely biaristate; rounded abaxially; veins 2(3); disarticulating with respective lemma; abaxial epidermal pattern similar to lemma pattern. *Lodicules* three, free, adaxial pair obovate, 0.75–1.25 mm long, abaxial linear, 0.5–1.0 mm long. *Stamens* three; filaments free, evanescent to marcescent; anthers free, penicillate, 1.75–2.2 mm long, yellow. *Ovularium* obovate, glabrate; styles two, subterminal, free, short; stigmata two, exserted laterally, white. *Caryopsis* obovoid, compression dorsoventral, length ca. 2 mm long; enclosed within, but free from anthoecium; exocarp smooth and glossy; hilum linear, ca. ⅞ caryopsis length; endosperm solid; embryo F+FF, ⅖ to ½ caryopsis length. *Seedling* mesocotyl lengthy; first leaf lamina narrow, erect, 7- to 15-veined. *Chromosomes* relatively small, 2–4 μ long, $n=10$, $2n=20$ (fruits from *Eno 17,* CAS), $2n=20$ (fruits from *Eno 18,* CAS).

Lamina Abaxial Epidermis without microhairs or papillae; costal/intercostal zonation conspicuous; *costal regions:* short-cells solitary, paired or in short rows, silica bodies round, square, horizontally nodular-elongate, irregulary dumbbell- or saddle-shaped, hooks infrequent, central, medium, prickles infrequent, single file, small to medium, barb pointing toward blade apex; *intercostal regions:* long-cells elongated, mostly 75–150 μ long, walls moderately thickened, side-walls parallel, undulations moderate, U-shaped, end-walls angled or interlocking, distributed in alternating long-cell/short-cell files with occasional short-cell pairs, intercostal short-cells square, rectangular, or irregular, silica body shape similar to cell shape, stomata low-dome-shaped, arranged in single or double rows along costal zones, one or two interstomatal long-cells between successive stomata, these occasionally separated by square to rectangular short-cells; transverse section exhibiting prominent adaxial ribs, midrib generally indistinguishable from others; sclerenchyma abundant interior to both epiderms, forming ab- and adaxial vascular bundle girders.

Lemma Abaxial Epidermis achnatheroid, costal/intercostal zonation absent; microhairs absent; papillae absent; stomata absent; long-cells ca. 10–30 μ long, walls moderately thickened, side-walls irregularly undulating, end-walls irregular, arranged in files as long-cell/short-cell/long-cell, long-cell/short-cell/suberin-cell, or long-cell/prickle/long-cell; silica bodies horizontally oblong or squarish, ca. 5–10 μ long; silico-suberose couples occasional, suberin-cells crescentic, ca. 5 μ long; prickles 20–25 μ long, barb short.

Paratypes. USA, Idaho: Butte Co., Lemhi Range, ca. 35 km (air) NNW of Howe, Bunting Canyon above Badger Mine, 44°06′21″N, 113°07′48″W, T9N R28E S16 SW¼, 2255 m, 12 July 1979, *S. & P. Brunsfeld 1132* (ID); *loc. cit.,* 16 June 1981, *J. Civille 251d* (ID); *loc. cit.,* 13 June 1987, *L. Eno 6* (ID); *loc. cit.,* 26 June 1987, *L. Eno 11* (ID); Lemhi Range, ca. 12 km (air) NNE of Howe, Middle Canyon, 43°53′30″N, 112°57′29″W, T7N R29E S26/35, 1950–2255 m, 17 June 1978, *D. M. Henderson 4629, S. & P. Brunsfeld* (ID, UTC); *loc. cit.,* 16 June 1981, *J. Civille 260* (ID); *loc. cit.,* 10 June 1987, *L. Eno 4,* (ID); *loc. cit.,* 25 June 1987, *L. Eno 9* (ID); Custer Co., Salmon River Range, Loon Creek ca. 500 m N of Bennett Creek Bridge, 44°47′34″N, 114°48′02″W, T17N R14E S22 SE¼, 1400 m, 18 May 1988, *L. Eno 25* (ID); ca. 4 km (air) SE of Cougar Creek Ranch along Hood Creek, 44°43′38″N, 114°52′38″W, T16N R13E S16 NE¼, 2000 m, 20 June 1982, *J. Civille 309* (ID); Loon Creek ca. 1.5 km NE of Tin Cup Campground, 44°36′41″N, 114°47′50″W, T15N R14E S26 NW¼, 1700 m, 2 July 1987, *L. Eno 18* (ID); ca. 14 km (air) N of Challis, Morgan Creek Road ca. 5 km NW of US Hwy 93, 44°38′39″N, 114°12′32″W, T15N R19E S10 NE¼ SW¼, 1600 m, 14 June 1987, *L. Eno 7* (ID); Lemhi Co., Salmon River Range, Middle Fork Salmon River Canyon ca. 4.5 km N of Bernard Creek Guard Station, ca. 800 m S of Jack Creek confluence, 45°00′22″N, 114°43′14″W, T19N R14E S11 NW¼, 1150 m, 19 July 1982, *J. Civille 335* (ID); ca. 55 km (air) NW of Challis, Middle Fork Salmon River Canyon at Camas Creek confluence, 44°53′31″N, 114°43′25″W, T18N R15E S16 SW¼, 1160 m, 15 July 1982, *J. Civille 332* (ID); ca. 55 km (air) NW of Challis, Middle Fork Salmon River watershed, Camas Creek ca. 400 m E of Macarte Creek Camp, 44°53′03″N, 114°41′36″W, T18N R15E S22, 1200 m, 10 June 1982, *J. Civille 289* (ID); *loc. cit.,* 19 May 1988, *L. Eno 26* (ID); ca. 55 km (air) NW of Challis, Middle Fork Salmon River watershed, Camas Creek between Dry Gulch and Forage Creek, 44°53′30″N, 114°34′57″W, T18N R16E S15 SW¼, 1700 m, 7 July 1981, *D. M. Henderson 5990* (ID); ca. 13 km WNW of US Hwy 93, jct Salmon NF Roads 045 (Iron Creek Rd) & 088 [*sic,* 046?], 44°55′20″N, 114°06′43″W, T18N R20E S4 NW¼, on quartzite cliffs, 3 July 1987, *P. M. Peterson 4764 & C. R. Annable* (ID, UTC); Salmon River Canyon, ca. 55 km N of Challis, US Hwy 93 ca. 500 m N of mile 279, 400 m SE of highway opposite Iron Creek, 44°53′00″N, 113°57′56″W, T18N R21E S15 SE¼ SW¼, 1400 m, 14 June 1978, *D. M. Henderson 4432* (ID); *loc. cit.,* 12 July 1981, *J.*

←

FIG. 1. *Stipa shoshoneana.* a) habit; b) spikelet; c) floret; d) lemma abaxial epidermis; e) lemma callus; f) caryopsis, abaxial view; g) distribution of largest Idaho populations.

Civille 276 (ID); *loc. cit.,* 21 June 1987, *L. Eno 8* (ID); *loc. cit.,* 28 June 1987, *L. Eno 13* (ID); Salmon River Range, Middle Fork Salmon River watershed, Loon Creek ca. 3 km NW of Falconberry Guard Station, between Mearney Creek and Burn Creek, 44°42′07″N, 114°46′41″W, T16N R14E S24 SW¼ NW¼, 1500 m, 6 July 1982, *J. Civille 330* (ID); Valley Co., Middle Fork Salmon River, W side ca. 1.5 km N of Golden Creek, Tombstone Rock, 45°09′44″N, 114°43′26″W, T21N R14E S15 SE¼ NE¼, 1025 m, 20 May 1988, *L. Eno 27* (ID); Nevada: Nye Co., Belted Range, N of Cliff Spring, 37°30′45″N, 116°05′15″W, T5S R53E S8, 2170 m, infrequent at cliff base, 18 June 1995, *F. J. Smith 3936* & *J. Heers* (UNLV).

Distribution. Stipa shoshoneana is known principally from canyons of the Middle Fork of the Salmon River and from its eastern tributaries, Camas and Loon Creeks, extending ca. 160 km by air southeast to the southern Lemhi Range (Fig. 1). *Stipa shoshoneana* is also curiously disjunct near Cliff Spring in the Belted Range of south-central Nevada about 750 km by air southwest of the most southern Idaho population. This disjunction suggests possible presence in the intercalary ranges of eastern Nevada. Searches by Curto at some potential sites in the Jarbidge, Independence, Ruby, Schell Creek, Snake, White Pine, and Quinn Canyon Ranges of eastern Nevada found populations of *O. exigua* or *O. micrantha,* but no *S. shoshoneana* populations.

Habitat. Stipa shoshoneana is nearly always found within moist crevices of intrusive or extrusive igneous, metamorphic, or sedimentary cliffs and rock walls. Typical associate species include: *Heuchera grossulariifolia* Rydb., *Ribes cereum* Dougl., *Potentilla glandulosa* Lindl., *Elymus spicatus* (Pursh) Gould, *Poa interior* Rydb., and *Poa secunda* K. B. Presl, with other taxa, such as *Pseudotsuga menziesii* (Mirb.) Franco, *Cercocarpus ledifolius* Nutt., *Artemisia tridentata* Nutt., *Amelanchier alnifolia* Nutt., *Glossopetalon spinescens* A. Gray, *Mimulus cusickii* (Greene) Piper, *Petrophyton caespitosum* (Nutt.) Rydb., and the east-central Idaho endemics, *Astragalus amnis-amissi* Barneby, *Cryptantha salmonensis* (Nels. & Macbr.) Pays., or *Draba oreibata* Macbr. & Pays., being locally common at some sites.

Chromosome number significance. Stipa shoshoneana plants possess the fewest chromosomes ($2n=20$) of all North American Stipeae counted to date, and the second-lowest somatic number ever reported for the tribe; Prokudin et al. (1977) reported $2n=18$ for *S. bromoides* (L.) Doerfler (as *Achnatherum bromoides* [L.] Nevski). Chapanov and Yurtsev (1976) reported $2n=20$ for the Asian species *Piptatherum vicarium* (Grig.) Roshev., although all other reports indicate $2n=24$ for this species, the common number of *Piptatherum* sect. *Piptatherum.*

Epithet etymology. The specific epithet refers to the Northern and Western Shoshone people whose ancestral lands encompass the entire known distribution of this species.

PHENETIC KEY

1 Styles fused proximally, persisting as a centric "beak" upon caryopsis; proximal glume length shorter than or equal to anthoecium length.

2 Lemma awn 1–2.5 mm long, exserted subapically, straight or weakly arcuate, often absent on herbarium specimens; anthers glabrate or rarely penicillate distally; stigmata 2 . . . . *Oryzopsis pungens*

2′ Lemma awn 3–8 mm long, exserted abaxially, recurved or geniculate at midlength, some usually present on herbarium specimens; anthers penicillate distally; stigmata 3 . . . . *Oryzopsis exigua*

1′ Styles free throughout, persisting as lateral "horns" upon caryopsis, or with no visible persistence; proximal glume length longer than anthoecium length.

3 Anthoecium averaging ≤ 3 mm long, glabrate or sparsely antrorsely puberulent, trichomes adpressed . . . . *Oryzopsis micrantha*

3′ Anthoecium averaging > 3 mm long, evidently evenly antrorsely hirtellous to hirsute, trichomes deflexed.

4 Ligule ≤ 1.0 mm long, longer laterally than medially.

5 Palea $\geq$ ¾ lemma body length; lemma awn ≤ 7 mm long, contorted < 1 revolution, weakly once-geniculate, caducous; primary panicle branches short, erectly adpressed to rachis at maturity . . . . *Oryzopsis swallenii*

5′ Palea $\leq$½ lemma body length; lemma awn 18–30 mm long, contorted > 1 revolution proximally, twice-geniculate, persistent; primary panicle branches elongate, deflexed from rachis at maturity . . . . *Stipa richardsonii*

4′ Ligule ≥ 1.5 mm long, acute to attenuate.

6 Lemma awn persistent until fruit maturity or thereafter, 8–20 mm long, stout, once- or twice-geniculate, proximal segment distinctly spirally contorted; anthers glabrate . . . . *Stipa canadensis*

6′ Lemma awn caducous, 1–2.5 mm long, straight or weakly arcuate; anthers penicillate . . . . *Stipa shoshoneana*

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SYSTEMATIC STUDIES AND CONSERVATION STATUS OF *CLAYTONIA LANCEOLATA* VAR. *FLAVA* (PORTULACACEAE)

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ABSTRACT

A biosystematic study of *Claytonia lanceolata* and related taxa in the Rocky Mountains was undertaken to evaluate the taxonomic status of *C. lanceolata* var. *flava*. This study was part of a broader assessment to determine the need for protection of the latter taxon under the federal Endangered Species Act. Electrophoretic and morphological studies revealed that *C. lanceolata* var. *flava* in southwestern Montana and northwestern Wyoming represents a distinct diploid species ($n=8$) whose populations consist of yellow- and/or white-flowered plants. Morphological, allozyme, and cytological data all indicate that this taxon does not belong in the *C. lanceolata* complex, but is best placed in the group of narrow-leaved species that includes *C. rosea*, *C. tuberosa*, and *C. virginica*. Numerous populations of *C. lanceolata* var. *flava*, most often consisting of the white-flowered phenotype, were found in Montana and Wyoming, and legal protection is not warranted at this time. In some cases, actions to conserve endangered plant taxa must be preceded by an evaluation of their taxonomic status; this study illustrates the utility of biosystematic techniques in conducting such evaluations.

INTRODUCTION

A need for accurate taxonomic evaluations of rare plant species has frequently arisen as conservation of biological diversity has become a priority on the part of government agencies and private organizations. Such evaluations are critical to ensuring that the limited funding available for plant conservation is devoted to taxa that are deserving from a biosystematic perspective.

Claytonia lanceolata Pursh (Portulacaceae) is a common, wide-ranging species of western North America (Hitchcock et al. 1964). *Claytonia lanceolata* var. *flava* (A. Nels.) C. L. Hitchc. has been applied to yellow-flowered populations in the northern Rocky Mountains (Hitchcock et al. 1964; Davis 1966). The type collection of this variant was made in 1899 by Aven and Elias Nelson (*5488*, RM), near the northwest corner of Henry's Lake in Fremont County, Idaho (Nelson 1900). From 1911 to 1988, it was collected at five additional stations in southwestern Montana (Shelly 1989) and one station in northwestern Wyoming (Marriott 1986). It was rediscovered at the type locality in 1986 (D. Atwood personal communication). The infrequency of collection and the relatively restricted geographic range of these yellow-flowered populations led to the designation of *C. lanceolata* var. *flava* as a candidate for listing under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1985, 1993).

The taxon was initially described as *C. aurea* (Nelson 1900). Rydberg (1922) reduced this name to a synonym of *C. chrysantha* Greene (=*C. lanceolata* var. *chrysantha* (Greene) C. L. Hitchc., a yellow-flowered form of the latter species occurring in western Washington (Douglas and Taylor 1972)), undoubtedly based on the shared flower color. *Claytonia aurea* was later renamed *C. flava*, the former name having already been used by Kuntze in 1891 (Nelson 1926). Rydberg (1932) also subsequently recognized it as *C. flava*. Since that time, *C. flava* has been reduced to a variety of *C. lanceolata* on two separate occasions (Hitchcock et al. 1964; Davis 1966). The latter revision was perhaps an oversight of the Hitchcock treatment, and Davis has occasionally been cited as the author of this change. Boivin (1968) placed *C. flava* as a variety of *C. caroliniana* Michx. More recently, the taxon has again been treated as a species (Dorn 1984).

We conducted two studies to evaluate the need for listing of *C. lanceolata* var. *flava* under the federal Endangered Species Act. In the first study, we

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used isozyme electrophoresis and field morphological analyses to compare *C. lanceolata* var. *flava* with sympatric populations of *C. lanceolata* var. *lanceolata.* The purpose of this study was to assess the current taxonomic treatment of the yellow-flowered populations as a variety of the latter, common taxon. During initial field work, surveys of known Montana populations of *C. lanceolata* var. *flava* revealed the presence of narrow-leaved, white-flowered plants that were morphologically very similar to the yellow-flowered individuals. These white-flowered plants did not fit the descriptions of typically broader-leaved *C. lanceolata* var. *lanceolata.* Thus, we also examined the degree of isozyme differentiation between white- and yellow-flowered individuals of these narrow-leaved plants, and whether any other morphological differences aside from petal color exist between them. Yellow- and white-flowered individuals of these narrow-leaved plants are biotically sympatric, occurring in intermixed populations, in four of the five study locations. Furthermore, these narrow-leaved plants are either biotically or neighboringly sympatric (occurring in closely adjacent but non-overlapping populations) with *C. lanceolata* var. *lanceolata* in all five study locations.

In the second study, we undertook herbarium morphological analyses in an initial attempt to place the narrow-leaved *Claytonia* populations of the northern Rocky Mountains in a broader context with respect to other congeneric taxa. In addition to *C. lanceolata* vars. *flava* and *lanceolata,* other taxa included in this herbarium study were *C. lanceolata* var. *chrysantha* (Greene) C. L. Hitchc., *C. lanceolata* var. *multiscapa* (Rydb.) C. L. Hitchc., and *C. rosea* Rydb. This second study did not include electrophoretic analyses, as it was intended to be a preliminary assessment of the wider affinities of *C. lanceolata* var. *flava* within the narrow-leaved *Claytonia*s.

The taxonomy of *Claytonia* is currently being revised for the Flora of North America project (Miller and Chambers in mss.). Pending publication of this treatment, throughout this paper the name *C. lanceolata* var. *flava* will refer to populations of both the white and yellow flower color phenotypes of the narrow-leaved taxon, except when citing previous alternative treatments.

MATERIALS AND METHODS

Five populations of *C. lanceolata* var. *lanceolata* and seven of var. *flava* (four consisting of plants with both yellow and white flowers, two including only white-flowered plants, and one consisting of only yellow-flowered plants) were sampled for morphological and isozyme electrophoretic studies. All five populations of var. *lanceolata* were included in both studies. For var. *flava,* five of the seven populations were included in both studies; the two exceptions were the Boulder and Burton Park populations (consisting of only the white-flowered phenotype in both cases), which we were unable to include in the electrophoretic analysis. The study populations are located in southwestern Montana and northwestern Wyoming (Fig. 1, Table 1).

Morphological studies. Morphological studies were conducted with live plants in the field and with herbarium specimens. We emphasized characters that are easily examined on living plants and pressed specimens, and that have been used in past keys treating some or all of the taxa of interest.

In the field, morphological data were collected from 720 living plants, representing five populations of *C. lanceolata* var. *lanceolata* and seven populations of var. *flava* (four including both yellow- and white-flowered plants, two with white-flowered plants only, and one with yellow-flowered plants only). In each population (and for each color phenotype in the mixed populations of var. *flava*), 45 plants were examined for the following characters: stem height, leaf length and width, petal length and width, and sepal length. Stem height was measured in centimeters, from ground level to the point of attachment of the uppermost pedicel; all other lengths were measured in millimeters. For statistical analyses, length/width ratios of the leaves and petals were also calculated.

One hundred eighty-four herbarium collections, representing *C. lanceolata* vars. *lanceolata, flava, multiscapa,* and *chrysantha,* as well as *C. rosea,* were examined from the following herbaria: MONTU, OSC, RM, UA, UAL, WS, WTU. In addition to the characters listed above, the petal/sepal length was calculated, and petal apex outline and cauline leaf venation were scored for the herbarium specimens (see Table 4 for scoring criteria).

Isozyme Electrophoresis. A total of 679 individuals from 10 populations (five of *C. lanceolata* var. *lanceolata,* four of var. *flava* consisting of both the yellow- and white-flowered phenotypes, and one strictly yellow-flowered population of the latter) was sampled. Both color phenotypes were sampled in the mixed populations of var. *flava.* Whole flowering stems, including the cauline leaves, were collected by clipping the plants at ground level. These were kept chilled in the field for one to several days until placement in ultracold storage (−80°C).

Leaves were ground immediately upon removal from the ultracold freezer, in the Tris HCl-PVP crushing buffer of Soltis et al. (1983) with 6% PVP. Nineteen putative loci, coding for twelve enzymes, were resolved using three electrophoretic buffers. A morpholine buffer, pH 6.4 (Odrzykoski and Gottlieb 1984) was used to resolve glyceraldehyde-3-phosphate dehydrogenase (G3PDH), malate dehydrogenase (MDH), and phosphoglucomutase (PGM). Buffer 8 of Soltis et al. (1983), as modified by Haufler (1985), was used to resolve alcohol dehydrogenase (ADH), aspartate aminotransferase (AAT), leucine aminopeptidase (LAP), phospho-

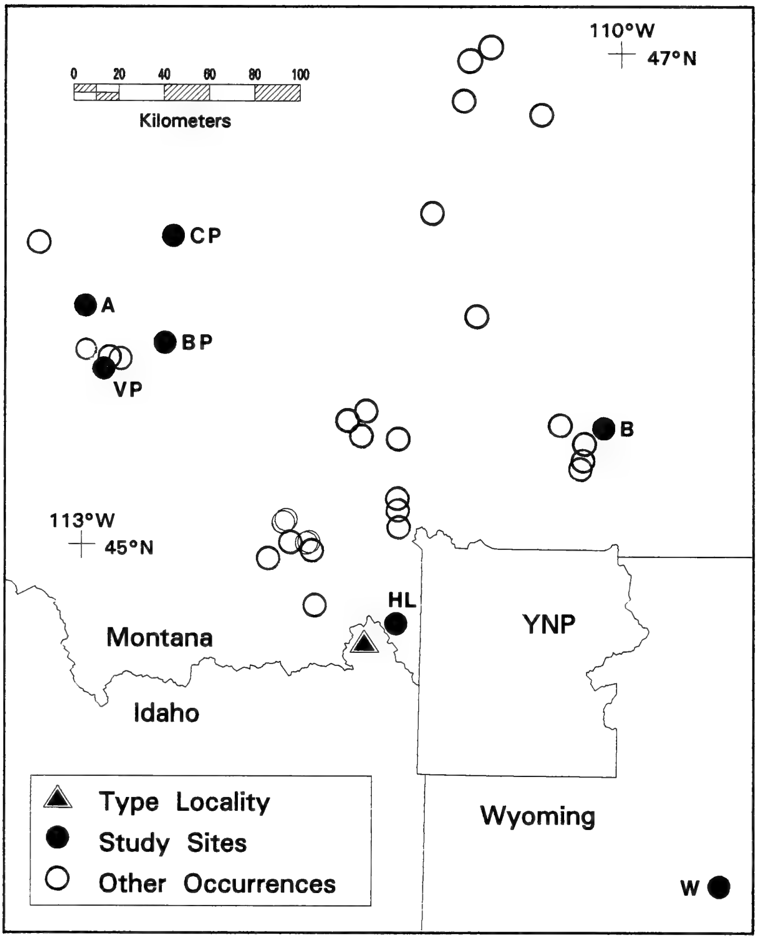

FIG. 1. Distribution of *Claytonia lanceolata* var. *flava* in Montana, Idaho and Wyoming, and locations of study populations (A = Anaconda; B = Boulder; BP = Burton Park; CP = Champion Pass; HL = Hebgen Lake; VP = Vipond Park; W = Wyoming; YNP = Yellowstone National Park). Open circles indicate additional occurrences of yellow- and/or white-flowered populations, as recorded by the Montana Natural Heritage Program; the type locality, in Idaho, has only been observed to contain yellow-flowered individuals.

glucoisomerase (PGI), and triosephosphate isomerase (TPI). Buffer 11 of Soltis et al. (1983) was used to resolve isocitrate dehydrogenase (IDH), menadione reductase (MNR), shikimate dehydrogenase (SkDH), and 6-phosphogluconate dehydrogenase (6PGD). The stain recipe for ADH was that described by Wendel and Weeden (1989). All other staining protocols were those of Soltis et al. (1983).

Data analysis. We assessed the morphological distinctiveness of the taxa using principal components analysis (PCA) and discriminant analysis of the characters listed above. These analyses were performed using SYSTAT (Wilkinson 1986), and were based on log-transformed values for the characters listed above.

Electrophoretic data were analyzed using the computer program BIOSYS-1 (Swofford and Selander 1981). Two separate analyses were performed: 1) allele frequencies at 19 loci were entered for all ten populations (14 samples total, since both color phenotypes were included from the four mixed populations of var. *flava*) and analyzed for genetic variability statistics and Nei's genetic identity between populations of *C. lanceolata* vars. *lanceolata* and *flava,* and between the nine populations of var. *flava* (five yellow- and four white-flowered); and 2) eight *C. lanceolata* var. *flava* populations, from all localities except Hebgen Lake (yellow-flowered phenotype only), were entered as genotype numbers and analyzed for population substructuring, to examine differences between color phenotypes within localities. An unweighted pair group method (UPGMA) was used for cluster analysis of Nei's genetic identity relationships.

RESULTS

Field studies. Taxon means, ranges, and standard deviations for the eight quantitative characters measured on living plants are given in Table 2.

TABLE 1. POPULATIONS OF CLAYTONIA LANCEOLATA VARS. FLAVA AND LANCEOLATA ANALYZED IN ISOZYME AND FIELD MORPHOLOGICAL STUDIES. Flower color phenotypes of var. *flava* were sampled as separate "populations" where they are biotically sympatric (Anaconda, Champion Pass, Vipond Park, and Wyoming). Vouchers are deposited at MONTU; * = duplicates deposited at OSC. + = the Boulder and Burton Park populations of white-flowered *flava* were not included in the electrophoretic study.

Taxon	Abbreviation	Collection data
Claytonia lanceolata var. *flava*	ANACONDA WHITE	Montana, Deer Lodge Co. *Shelly & Lesica 1412**
	ANACONDA YELLOW	Montana, Deer Lodge Co. *Shelly & Lesica 1413**
	BOULDER WHITE+	Montana, Sweet Grass Co. *Shelly 1617*
	BURTON PARK WHITE+	Montana, Silver Bow Co. *Shelly, Schassberger & Schitoskey 1504*
	CHAMPION YELLOW	Montana, Jefferson Co. *Shelly 1417**
	CHAMPION WHITE	Montana, Jefferson Co. *Shelly & Lesica 1423**
	HEBGEN YELLOW	Montana, Gallatin Co. *Shelly & Lesica 1419**
	VIPOND YELLOW	Montana, Beaverhead Co. *Shelly & Scow 1444**
	VIPOND WHITE	Montana, Beaverhead Co. *Shelly & Scow 1445**
	WYOMING YELLOW	Wyoming, Fremont Co. *Shelly & Lesica 1446**
	WYOMING WHITE	Wyoming, Fremont Co. *Shelly & Lesica 1447**
Claytonia lanceolata var. *lanceolata*	ANACONDA LANCEO	Montana, Deer Lodge Co. *Shelly & Lesica 1411*
	CHAMPION LANCEO	Montana, Jefferson Co. *Shelly & Lesica 1422*
	HEBGEN LANCEO	Montana, Madison Co. *Shelly & Lesica 1420**
	VIPOND LANCEO	Montana, Beaverhead Co. *Shelly 1201*
	WYOMING LANCEO	Wyoming, Teton Co. *Shelly & Lesica 1448**

PCA of the living-plant morphological characters other than flower color revealed that white-flowered and yellow-flowered forms of *C. lanceolata* var. *flava* are indistinguishable from each other but are easily separable from *C. lanceolata* var. *lanceolata* (Fig. 2). The first principal component accounted for 46% of the variation and had strong contributions by petal width, leaf length, stem height, leaf length/width ratio, sepal length, and petal length/width ratio. The second component had strong loadings by leaf width and petal length and accounted for 20% of the variation (Table 3).

The cross-validation error rate for the discriminant analysis comparing white- and yellow-flowered individuals of *C. lanceolata* var. *flava* was 0.42; there is only a 58% chance of correctly identifying the two flower color phenotypes of *C. lanceolata* var. *flava* based on the morphological characters used in the analysis. Thus, the two phenotypes cannot be reliably discriminated on characters other than flower color.

Herbarium studies. Taxon means, ranges, and standard deviations for the eight quantitative and two qualitative characters examined on the herbarium collections are given in Table 4.

PCA of the herbarium morphological characters other than flower color also revealed that white-flowered and yellow-flowered forms of *C. lanceolata* var. *flava* are indistinguishable from each other, and are very similar to var. *multiscapa* and *C. rosea,* but that specimens of all three latter taxa are easily separable from *C. lanceolata* var. *lanceolata* (including *C. lanceolata* var. *chrysantha*; Fig. 3). The first principal component accounted for 33% of the variation and had strong contributions by leaf venation, petal apex outline, leaf length/width ratio, leaf width, petal/sepal length ratio, and sepal length. The second component had strong loadings by petal width and length and accounted for 22% of the variation (Table 5).

Isozyme electrophoresis. Coding of populations of *C. lanceolata* var. *flava* was straightforward, as

TABLE 2. TAXON MEANS, RANGES AND STANDARD DEVIATIONS FOR FIELD MORPHOLOGICAL DATA, CLAYTONIA LANCEOLATA VARS. FLAVA AND LANCEOLATA.

	Yellow *flava*	White *flava*	*lanceolata*
No. of specimens	225	270	225
Height (cm)			
Mean	7.6	9.6	4.1
Range	3.5–16.9	4.0–27.2	1.4–10.8
SD	2.1	1.3	1.5
Leaf length (mm)			
Mean	36.0	42.8	26.3
Range	13.0–76.0	14.0–111.0	14.0–46.0
SD	11.7	18.4	6.8
Leaf width (mm)			
Mean	5.4	5.9	9.1
Range	2.5–11.5	3.0–13.5	4.0–19.0
SD	1.6	1.9	2.7
Sepal length (mm)			
Mean	5.0	5.1	4.0
Range	3.0–8.5	3.5–8.0	2.0–6.0
SD	0.98	0.83	0.79
Petal width (mm)			
Mean	5.3	5.7	4.2
Range	3.0–8.5	3.0–9.0	2.5–9.0
SD	0.96	0.97	0.84
Petal length (mm)			
Mean	8.6	9.2	8.8
Range	6.0–12.0	6.5–13.5	4.5–12.5
SD	1.2	1.1	1.3
Leaf length/width ratio			
Mean	6.8	7.5	3.0
Range	3.3–14.2	2.6–18.5	1.6–6.3
SD	2.0	2.6	0.9
Petal length/width ratio			
Mean	1.7	1.6	2.1
Range	1.1–2.3	1.1–2.3	0.5–3.0
SD	0.2	0.2	0.3

simple diploid expression was observed in all cases. However, *C. lanceolata* var. *lanceolata* expressed more complex banding patterns indicative of tetraploidy. To make comparisons among varieties and flower-color phenotypes at each locality, it was necessary to code allele frequencies for *C. lanceolata* var. *lanceolata.* This was done by assuming that each individual was tetraploid and possessed four allelic doses per locus. Some individuals, therefore, expressed more than two alleles at a locus. Relative staining intensities were used to determine dosage effects (Wolf 1988). Allele frequencies are given in Table 6.

Differences between varieties. The UPGMA cluster analysis of Nei's genetic identity values is shown in Figure 4. All five populations of *C. lanceolata* var. *lanceolata* were completely separated from the nine populations of *C. lanceolata* var. *flava* (represented by samples of both white- and yellow-flowered plants). The mean genetic identity between populations of these two taxa was 0.69.

Differences among populations of C. lanceolata var. *flava.* The UPGMA cluster analysis also indicates the level of differentiation among populations of *C. lanceolata* var. *flava* (Fig. 4). With the color phenotypes pooled within localities, genetic identity values among the five study localities ranged from 0.913 to 0.979. The genetic identities correspond to geographic proximity; the more southerly populations (Hebgen Lake and Wyoming) clustered together, as did the northern populations (Anaconda, Champion, and Vipond).

Differences between color phenotypes within localities of C. lanceolata var. *flava.* In the four cases where they are biotically sympatric, yellow- and white-flowered "populations" of *C. lanceolata* var. *flava* were always more similar allozymically to each other than to allopatric populations of the same flower color (Fig. 4). The Nei's genetic identity values between color phenotypes within localities were high, ranging from 0.995 (Vipond Park) to 1.00 (Anaconda). By contrast, interpopulation genetic identity values within color phenotypes ranged from 0.935 to 0.987 for the yellow form, and from 0.910 to 0.989 for the white form.

DISCUSSION

Morphological studies and isozyme electrophoresis revealed that populations ascribed to *C. lanceolata* var. *flava* represent a diploid species ($2n=16$; Marriott 1986) that is distinct from the *C. lanceolata* complex. *Claytonia lanceolata* displayed banding patterns suggestive of autopolyploidy in the populations we sampled. Tetraploid populations ($n=16$) of *C. lanceolata* have been reported from Utah (Halleck and Wiens 1966; Stewart and Wiens 1971), and populations with $n=8$, 12, 18, 22, 24, and 32 have been found in other Rocky Mountain populations of this species (Davis and Bowmer 1966; Halleck and Wiens 1966).

In past treatments, petal color, described as "golden yellow" by Davis (1952, 1966) and "deep yellowish-orange" by Hitchcock et al. (1964), was the primary character used to distinguish *C. lanceolata* var. *flava* from related taxa at the level of species (as *C. flava*; Davis 1952) or variety (Hitchcock et al. 1964; Davis 1966). However, PCAs of our morphological data indicated that the characters most important for distinguishing *C. lanceolata* var. *flava* from typical *C. lanceolata* are related to leaf morphology (length/width ratio and venation) and petal shape (length/width ratio and apex outline).

Davis (1952) described the leaves of *C. lanceolata* var. *flava* as "linear or lance-linear," as compared to "stem leaves lanceolate" in *C. lanceolata.* Similarly, Hitchcock et al. (1964) described the stem leaves of *C. lanceolata* var. *flava* as "lanceolate or narrowly oblong, several times longer than broad" and those of *C. lanceolata* (represented by

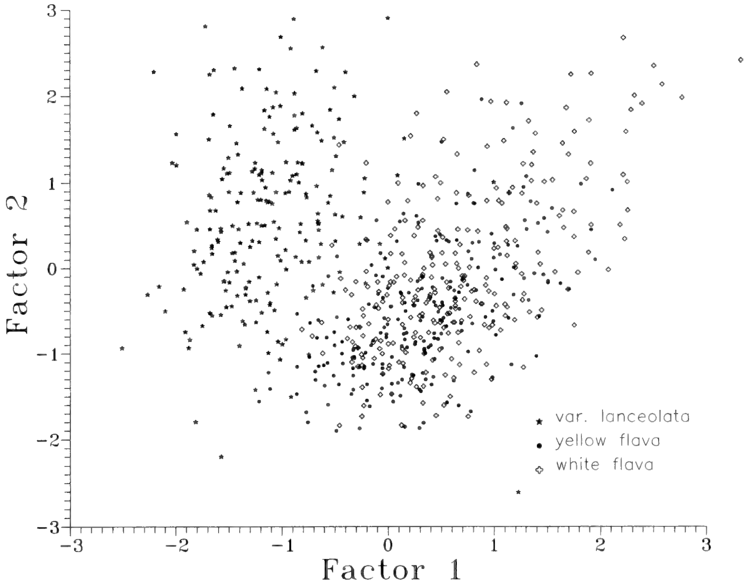

FIG. 2. Scatter diagram of individuals of *Claytonia lanceolata* var. *flava* (yellow- and white-flowered) and *C. lanceolata* var. *lanceolata* on principal components 1 and 2. Based on morphological data collected from living plants in the field.

var. *chrysantha*) as "broadly elliptic to ovate, (1)1.5–2.5(4) cm long, usually over ⅓ as broad." Our study showed that the leaves of *C. lanceolata* var. *flava* average approximately seven times longer than wide, whereas those of typical *C. lanceolata* average three times as long as wide (Table 2). These numeric differences are in accordance with the earlier, largely qualitative leaf shape differences described for these taxa.

Rydberg (1922) recognized the patterns in leaf venation that distinguish the narrow-leaved species of *Claytonia* (i.e., *C. virginica, C. rosea,* and *C. multiscapa*) from *C. lanceolata.* He observed that the former group has leaves "1-ribbed or indistinctly 3-ribbed," whereas the latter species has leaves that are "distinctly triple-ribbed." Our results uphold this as a valid and important means of distinguishing the narrow-leaved *Claytonia* populations from those of *C. lanceolata* in the northern Rocky Mountains; the leaves of *C. lanceolata* var. *flava* have only the distinct midvein, whereas populations of typical *C. lanceolata* have leaves with two prominent lateral veins in addition to the midvein (Table 4).

TABLE 3. LOADINGS OF THE FIRST TWO PRINCIPAL COMPONENTS FOR THE QUANTITATIVE CHARACTERS MEASURED IN THE FIELD MORPHOLOGY STUDIES.

	Component	
Character	1	2
Petal width	0.832	0.114
Leaf length	0.807	0.177
Height	0.789	0.033
Leaf length/width	0.755	−0.426
Sepal length	0.700	0.202
Petal length/width	−0.646	0.395
Leaf width	−0.189	0.847
Petal length	0.474	0.702

Davis (1952) also distinguished *C. lanceolata* var. *flava* from typical *C. lanceolata* by petal apex outline, describing the former as having petals "rounded at the apex," and the latter with petals "retuse or emarginate." Our studies confirmed that the petals of *C. lanceolata* var. *flava* are rounded at the apex, while those of typical *C. lanceolata* are usually retuse or emarginate (Table 4). In addition, the results of both the field and herbarium morphological studies confirmed that the petals of *C. lanceolata* var. *flava* are more nearly oval in shape, whereas those of *C. lanceolata* are most often obovate, and frequently narrowly so. These results also concur with the descriptions by Davis (1952).

Isozyme electrophoresis also clearly indicated that *C. lanceolata* var. *flava* is distinct from typical *C. lanceolata* and warrants recognition as a distinct species. The mean genetic identity between *C. lanceolata* var. *lanceolata* and populations representing *C. lanceolata* var. *flava* (I = 0.69) is close to the mean between congeneric species (I = 0.67) presented in several reviews (Gottlieb 1981; Crawford 1983). This value contrasts greatly with mean values for conspecific populations of var. *flava* (I = 0.91 to 0.98) and for populations of typical var. *lanceolata* (I = 0.89 to 0.99).

The diploid taxon represented by populations assignable to *C. lanceolata* var. *flava* includes conspecific yellow- and white-flowered plants. In this

TABLE 4. TAXON MEANS, RANGES AND STANDARD DEVIATIONS FOR QUANTITATIVE AND QUALITATIVE MORPHOLOGICAL CHARACTERS FROM HERBARIUM SPECIMENS, *CLAYTONIA LANCEOLATA* VARS. FLAVA, LANCEOLATA, AND MULTISCAPA, AND *C. ROSEA*. For some characters, the number of accessions was less than that shown in the first line; exceptions are given in parentheses after the means. * Petal apex outline scores: 0—retuse/emarginate, 1—rounded; ** Leaf venation scores: 0—lateral veins inconspicuous or absent, 1—lateral veins conspicuous.

	flava	*lanceolata*	*multiscapa*	*rosea*
No. of accessions	17	124	8	35
Leaf length (mm)				
Mean	41.6	32.6	43.4	44.0
Range	18–71	13–59	29–56	17.5–84
SD	3.1	0.9	3.7	2.8
Leaf width (mm)				
Mean	5.2	10.4	5.9	5.1
Range	2.4–8.4	2.8–26	2.3–10.6	1.3–14
SD	0.4	0.4	1.1	0.5
Leaf length/width ratio				
Mean	8.3	3.5	8.7	10.8
Range	4.7–15.1	1.7–12.5	5.2–13.0	4.0–32.8
SD	0.6	0.1	1.2	1.2
Sepal length (mm)				
Mean	4.4	3.8	4.8	4.7
Range	3.3–5.7	2.0–6.6	4.0–5.9	2.9–7.0
SD	0.2	0.1	0.3	0.2
Petal width (mm)				
Mean	4.3	4.0 (123)	4.6	4.1 (32)
Range	3.0–5.4	1.8–6.2	2.9–6.0	2.7–5.5
SD	0.2	0.1	0.3	0.1
Petal length (mm)				
Mean	9.5	9.1	9.2	9.3 (34)
Range	6.8–11.8	5.2–14.0	7.5–11.3	5.8–12.7
SD	0.3	0.1	0.6	0.3
Petal length/width ratio				
Mean	2.3	2.4 (123)	2.1	2.3 (32)
Range	1.5–3.1	1.6–3.7	1.3–2.6	1.5–3.2
SD	0.1	0.1	0.2	0.1
Petal/sepal length ratio				
Mean	2.2	2.4	1.9	2.1 (34)
Range	1.6–2.8	1.2–3.7	1.3–2.5	1.2–3.7
SD	0.1	0.1	0.1	0.1
Petal apex outline*				
Mean	0.9 (16)	0.1 (118)	1.0	0.9
Leaf venation**				
Mean	0.0	0.9 (123)	0.1	0.1 (34)

and other cases, flower color has been found to be of limited use in delineating true phylogenetic relationships within *Claytonia.* Elsewhere in North America, several other predominantly white- or pink-flowered taxa in *Claytonia* include named or unnamed yellow-flowered forms. Examples include *C. lanceolata* var. *chrysantha* (Douglas and Taylor 1972), *C. virginica* L. var. *hammondiae* (Kalmbacher) Doyle, Lewis and Snyder (Snyder 1992), and a recently discovered population of *C. caroliniana* in Maryland that contains yellow-flowered plants in addition to typical white- to pink-flowered plants (Snyder 1992). Such color forms are probably best viewed as minor variants within their respective taxa. They probably do not typically warrant taxonomic recognition, except in cases where their populations are correlated with ecological, genetic, geographic, and/or further morphological segregation (as is the case for *C. virginica* var. *hammondiae*) (Snyder 1992). In the case of *C. lanceolata* var. *chrysantha,* Douglas and Taylor (1972) found that, based on morphological, ecological, and biochemical analyses, ". . . there is no significant difference between the yellow and white forms of *Claytonia lanceolata,* other than petal color," and that "(t)he difference in petal color is most likely

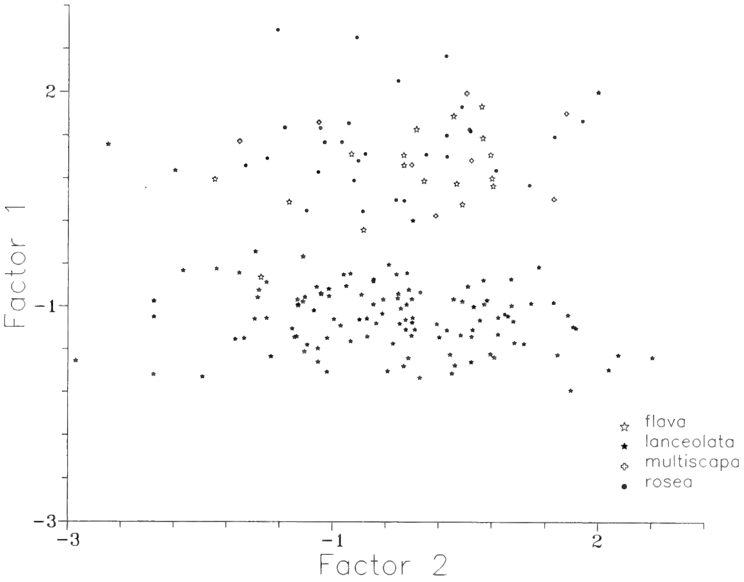

FIG. 3. Scatter diagram of individuals of *Claytonia rosea* and *C. lanceolata* vars. *flava, lanceolata* (including var. *chrysantha*), and *multiscapa* on principal components 1 and 2. Based on morphological data collected from herbarium specimens.

due to one or very few genes, as evidenced by the virtual lack of intermediate color forms." They concluded that "... there is no basis for the recognition of var. *chrysantha* ..." (Douglas and Taylor 1972). Our results indicate the same situation with respect to the yellow and white flower color phenotypes of "*C. lanceolata* var. *flava.*" Plants of the two color phenotypes are biotically sympatric in at least four populations in the northern Rocky Mountains, and these phenotypes reflect little or no morphological or isozyme differentiation within or among those populations. While there was some genetic differentiation among populations of *C. lanceolata* var. *flava,* plants of the two flower color phenotypes are undoubtedly conspecific; at the four sites where they are biotically sympatric, individuals of the two phenotypes are nearly or completely identical genetically. This suggests that in such cases they are part of the same breeding population, that flower color represents simple genetic differences (i.e., determined by one or a few genes), and that flower color does not warrant taxonomic recognition. The allozyme data also suggest separate origins of the yellow flower phenotype in each locality where it occurs.

TABLE 5. LOADINGS OF THE FIRST TWO PRINCIPAL COMPONENTS FOR THE QUANTITATIVE AND QUALITATIVE CHARACTERS USED IN THE HERBARIUM MORPHOLOGY STUDY.

Character	Component 1	Component 2
Venation	−0.840	0.039
Petal apex outline	0.830	−0.051
Leaf length/width	0.775	−0.061
Leaf width	−0.630	0.472
Petal/sepal length ratio	−0.607	0.121
Sepal length	0.588	0.450
Petal width	0.069	0.872
Petal length	−0.095	0.778
Leaf length	0.344	0.500
Petal length/width	−0.174	−0.409

The morphological comparison among species of *Claytonia* revealed a strong similarity between *C. rosea* and *C. lanceolata* vars. *flava* and *multiscapa* (Fig. 3). The latter variety, all collections of which are white-flowered, is reported by Hitchcock et al. (1964) as occurring in "Yellowstone National Park and vicinity." The morphological similarity of var. *multiscapa* to var. *flava,* and its complete geographic overlap with stations of white- and/or yellow-flowered populations of the latter entity, support the notion that var. *multiscapa* is the same taxon as the white-flowered form of var. "*flava.*" The more southerly white- to pink-flowered *Claytonia rosea* probably represents a similar, closely related narrow-leaved taxon (J. Miller personal communication). Like the populations of *C. lanceolata* var. *flava* sampled in Montana and Wyoming, numerous Colorado populations of *C. rosea* are diploid ($n=8$; Halleck and Wiens 1966).

In summary, electrophoretic and morphological data clearly revealed that *C. lanceolata* var. *flava* does not belong in the *C. lanceolata* complex. Rather, its affinities lie with the narrow-leaved group of species that includes *C. rosea, C. tuberosa* Pallas ex Willd. and *C. virginica.* Furthermore, *C.*

TABLE 6. ALLELE FREQUENCIES AT 19 ENZYME LOCI FOR 14 POPULATIONS OF CLAYTONIA LANCEOLATA. [1] = white-flowered phenotype of *C. lanceolata* var. *flava* is not represented at Hebgen Lake. [2] y = yellow-flowered phenotype of *C. lanceolata* var. *flava*; w = white-flowered phenotype of *C. lanceolata* var. *flava*; lanc = *C. lanceolata* var. *lanceolata*. [3] = number of individuals per taxon or flower color morph sampled at each location.

		Study locations													
		Hebgen Lake[1]		Anaconda			Champion Pass			Wyoming			Vipond Park		
Locus	Allele	y[2] 50[3]	lanc 50	y 50	w 50	lanc 50	y 50	w 30	lanc 49	y 50	w 50	lanc 50	y 30	w 40	lanc 30
Mdh-1	a	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0
	b	0	0.81	0.05	0.01	0.98	0.08	0.10	0.98	0	0	1.00	0.10	0.06	1.00
	c	1.00	0.19	0.95	0.99	0	0.92	0.90	0.02	1.00	1.00	0	0.90	0.94	0
Mdh-2	a	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
	b	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	100	1.00	1.00	1.00	1.00
Mdh-3	a	0	0.06	0	0	0	0	0	0.21	0	0	0.18	0	0	0
	b	0	0.94	0	0	1.00	0	0	0.64	0	0	0.65	0	0	1.00
	c	1.00	0	0.96	0.97	0	1.00	1.00	0.15	1.00	1.00	0.11	0.95	0.97	0
	d	0	0	0.04	0.03	0	0	0	0	0	0	0.06	0.05	0.03	0
Pgm-1	a	0.90	1.00	1.00	1.00	1.00	0.62	0.53	1.00	1.00	1.00	1.00	1.00	0.97	1.00
	b	0.10	0	0	0	0	0.38	0.47	0	0	0	0	0	0.03	0
Pgm-2	a	0.64	0.01	0	0	0	0	0	0.04	0.55	0.54	0	0	0	0
	b	0.10	0.65	0.75	0.90	0.37	0.88	0.93	0.46	0.06	0.06	0.18	0.27	0.42	0.40
	c	0.26	0.21	0.06	0.03	0.57	0.03	0.02	0.48	0.39	0.42	0.77	0.52	0.18	0.49
	d	0	0.13	0.19	0.07	0.06	0.03	0.05	0.02	0	0	0.05	0.21	0.40	0.11
G3pdh	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Lap	a	0	0.01	0	0	0.03	0	0	0	0	0	0.08	0	0	0.06
	b	1.00	0.36	1.00	0.95	0.87	0.99	1.00	0.97	1.00	1.00	0.44	0.98	1.00	0.55
	c	0	0.63	0	0.05	0.10	0.01	0	0.03	0	0	0.48	0.02	0	0.39
Aat	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Adh	a	0	0	0	0	0.01	0.02	0	0	0.46	0.36	0	0	0.02	0
	b	1.00	0	1.00	0.98	0.28	0.98	1.00	0.02	0.54	0.64	0.10	0.98	0.94	0
	c	0	1.00	0	0.02	0.71	0	0	0.98	0	0	0.90	0.02	0.04	1.00
Pgi-1	a	1.00	1.00	1.00	0.99	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	b	0	0	0	0.01	0	0	0.02	0	0	0	0	0	0	0
Pgi-2	a	0	0.04	0	0	0.01	0	0	0.02	0	0	0.05	0	0	0.06
	b	0.04	0.44	0.32	0.29	0.55	0.12	0.07	0.55	0.31	0.39	0.70	0.02	0.06	0.43
	c	0.96	0.52	0.68	0.71	0.44	0.88	0.93	0.43	0.69	0.61	0.25	0.98	0.94	0.51
Tpi-1	a	0.01	0.01	0.06	0.06	0.01	0	0	0	0	0	0	0.05	0	0
	b	0.81	0.71	0.91	0.92	0.81	0.91	0.87	0.96	0.92	0.86	0.99	0.93	0.96	0.96
	c	0.15	0.28	0.03	0.02	0.18	0.09	0.13	0.04	0.08	0.14	0.01	0.02	0.04	0.04
	d	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
Tpi-2	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Tpi-3	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mnr	a	0	1.00	0	0	1.00	0.02	0	0.46	0.07	0.20	0.98	0	0	0.89
	b	0.94	0	0.53	0.50	0	0.52	0.55	0.54	0.93	0.80	0.02	0.27	0.39	0.04

TABLE 6. CONTINUED

		Study locations													
		Hebgen Lake[1]		Anaconda			Champion Pass			Wyoming			Vipond Park		
Locus	Allele	y[2] 50[3]	lanc 50	y 50	w 50	lanc 50	y 50	w 30	lanc 49	y 50	w 50	lanc 50	y 30	w 40	lanc 30
	c	0.06	0	0.47	0.50	0	0.46	0.45	0	0	0	0	0.73	0.61	0
	d	0	0	0	0	0	0	0	0	0	0	0	0	0	0.07
Skdh	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6pgd-1	a	0.22	0	0.51	0.55	0	0.41	0.63	0	0.23	0.20	0	0.58	0.58	0
	b	0.78	0	0.49	0.45	0	0.59	0.37	0	0.76	0.79	0.10	0.40	0.42	0.53
	c	0	1.00	0	0	1.00	0	0	1.00	0.01	0.01	0.90	0.02	0	0.47
6pgd-2	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00
	b	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0
Idh	a	0	0.03	0	0	0.13	0	0	0.05	0	0	0	0	0	0.07
	b	0	0.97	0	0	0.87	0.35	0.31	0.95	0	0	1.00	0	0	0.93
	c	0.98	0	0.99	1.00	0	0.65	0.69	0	0.91	0.95	0	0.75	0.77	0
	d	0.02	0	0.01	0	0	0	0	0	0.09	0.05	0	0.25	0.23	0

lanceolata vars. *flava* and *multiscapa* would best be treated conspecifically as *C. multiscapa* (J. Miller personal communication); such a proposed treatment is supported by the results of our herbarium morphological study, as well as the entirely overlapping geographic ranges, of the plants currently bearing these names from the Yellowstone and surrounding areas. Formal nomenclatural changes are not made here, but left for publication of a complete revision of the genus (Miller and Chambers in mss.).

Conservation status. In the northern Rocky Mountains, narrow-leaved populations of *Claytonia* consisting wholly or partially of yellow-flowered individuals remain relatively uncommon (ten such populations are now known from Idaho, Montana, and Wyoming). However, the morphologically and allozymically highly similar white-flowered populations are more common and widespread. These white-flowered populations occur over a larger area in northwestern and north-central Wyoming, and south-central to southwestern Montana; a population has also recently been confirmed in the Sweetgrass Hills of north-central Montana (B. Heidel personal communication). Populations of both flower color phenotypes are usually very large in size and areal extent, and at least 30 populations consisting of one or both forms have been documented in Montana (Montana Natural Heritage Program unpublished data). Because these yellow and white flower color phenotypes are "contaxonomic," *C. lanceolata* var. *flava* is not in need of protective listing, regardless of its eventual taxonomic disposition.

When necessary, legal protection and management of putatively endangered taxa should be preceded by accurate evaluations of their phylogenetic relationships and taxonomic status (Avise and Nelson 1989). Biochemical and molecular techniques will continue to be increasingly useful for ensuring that the limited funds available for endangered species conservation are correctly focused on evolutionarily deserving taxa in the endeavor to maintain biological diversity.

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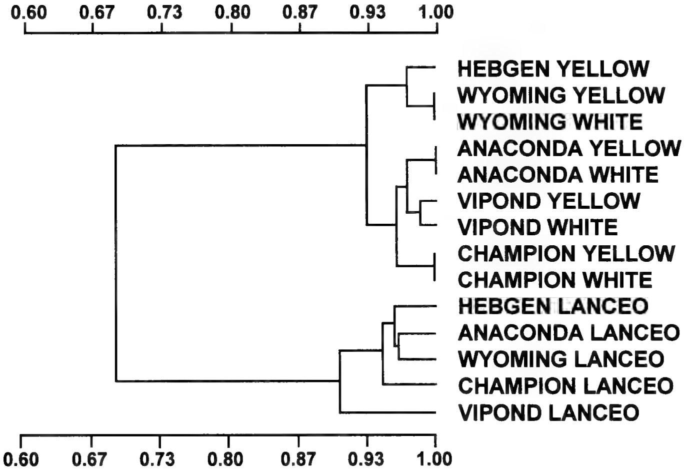

FIG. 4. Phenetic relationships among populations of *Claytonia lanceolata* var. *flava* (yellow- and white-flowered) and *C. lanceolata* var. *lanceolata,* based on cluster analysis (UPGMA) of Nei's genetic identity values.

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EFFECTS OF CLIMATIC VARIABILITY ON HERBACEOUS PHENOLOGY AND OBSERVED SPECIES RICHNESS IN TEMPERATE MONTANE HABITATS, LAKE TAHOE BASIN, NEVADA

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ABSTRACT

Surveys of herbaceous flora found in flower in the eastern central Sierra Nevada (Nevada) demonstrated the influence of climate variability on herbaceous phenology and observed species richness. Mid-summer surveys conducted in two climatically different years showed differences in number of flowering species (greater in the wetter year) and their characteristic phenological class (more early- vs. late-flowering species in the wetter year). Between year variation in phenology and species richness appeared to be keyed to snowpack duration, spring and summer moisture availability, and early growing season temperatures. Responses in mesic habitats were greater than in xeric sites. Phenological responses to climate variability can be interpreted in terms of displacement, compression, and amplification of the phenological cycle. Comparison of the two surveys suggests that both displacement and amplification generated observed differences. In the wetter year, late snowpack and lower spring temperatures delayed flowering times and greater spring and early summer moisture resulted in greater observed species richness. Sensitivity of herbaceous species in these montane habitats to year-to-year differences in climate highlights the importance of considering effects of climate variability on phenology and population dynamics in short-duration plant biodiversity surveys and long-term monitoring programs.

INTRODUCTION

Climate variability strongly affects population, community, and ecosystem processes in herbaceous systems (e.g., Tilman and El Haddi 1992; Walker et al. 1994). Stand phenological responses to interannual variability in thermal, moisture, and light regimes can be dramatic, reflecting seasonal dynamics of species reproductive cycles, community composition, and plant production. Understanding the herbaceous response to interannual climate variability and identification of key surface climate factors controlling this response can reveal the sensitivity of the herbaceous component of plant communities to short-term climate variation and directional climate change. This understanding can, in addition, aid in evaluating the representativeness of rapid biodiversity assessments and design of long-term monitoring studies.

In temperate regions, soil and air temperature, moisture availability, photoperiod, and, in areas receiving snow, snowpack duration are common controls over growth initiation and timing of subsequent phenophases (Holway and Ward 1963, 1965; Lieth 1974; Dickinson and Dodd 1976; Pitt and Heady 1978; Schemske et al. 1978; Bertiller et al. 1990). In mountain environments of western North America, one of the strongest interannual climatic signals is that of winter snowpack. The strength of this signal is derived from the effect of quasi-periodic interannual variations in tropical and mid-latitude Pacific sea surface temperatures on the strength and tracks of winter storms, such as associated with El Niño and the North Pacific Oscillation (Ropelewski and Halpert 1986; Sheaffer and Reiter 1985).

The objective of this study was to understand the phenological response of the herbaceous component of several montane communities in the eastern central Sierra Nevada (Nevada) to interannual snowpack variation and associated variation in temperature. The approach was to analyze changes between two plant surveys, one conducted in a low snowpack year and the other in a high snowpack year, in terms of (1) differences in the number of species found in flower and predominant phenological class of these species and (2) whether these responses varied by habitat.

METHODS

Study area. The plant surveys were conducted in the Sierra Nevada montane forest belt on the eastern side of the Lake Tahoe Basin, Nevada. The study area covered four watersheds: Skunk Harbor, Slaughterhouse Canyon, Marlette Creek, and Spooner Lake (Fig. 1). These sites were chosen to capture a wide variety of vegetation types characteristic of this montane region. The predominant type is East-slope Jeffrey Pine Forest as described by Rundel et al. (1980), with dominance shared by *Pinus jeffreyi, P. ponderosa, Abies concolor,* and *Calocedrus decurrens.* The forest is generally open, reflecting a relatively xeric environment.

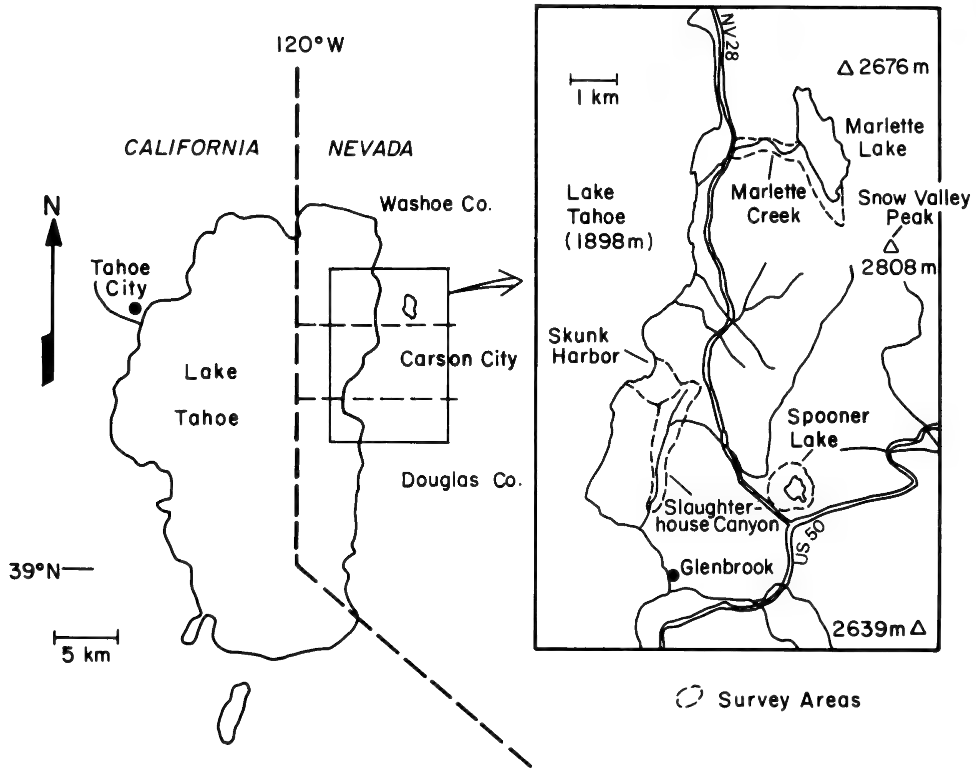

FIG. 1. Location of the survey area in the Lake Tahoe Basin, California-Nevada. The four survey sites are indicated by enclosed short-dashed lines on the detailed map.

Each watershed also contains varying amounts of other vegetation types. Skunk Harbor (elevation range 1900–2000 m) includes narrow riparian communities and montane chaparral with *Arctostaphylos patula* and *Chrysolepis sempervirens* (see Smith 1973; Ornduff 1974). The Slaughterhouse Canyon site (1920–1990 m) has extensive montane meadows and adjacent stands of *Pinus contorta* ssp. *murrayana.* Vegetation of the Marlette Creek watershed (1970–2440 m) is predominantly Jeffrey Pine Forest with a transition at higher elevations to Red Fir (*Abies magnifica*) Forest (Rundel et al. 1980). The Spooner site (2120–2150 m) includes a large meadow surrounding Spooner Lake, that grades from wet meadow dominated by *Carex* spp. to dry meadow (Rundel et al. 1980; Smith 1973), and an adjacent sagebrush scrubland (Smith 1973) dominated by *Artemisia tridentata.*

Surveys. Gordon and Dossman (1968) undertook a presence-absence survey of non-graminoid herbaceous species across the study area in 1968. In the following year, I repeated their survey to evaluate how the findings of such efforts might vary between two climatically-different years (Kittel 1969). Both 1968 and 1969 surveys spanned the first week of July. One observer from the first survey (J. Gordon) assisted in the second. This facilitated consistency in both diversity and areal coverage of vegetation types sampled within each watershed. The surveys recorded presence or absence of non-graminoid herbaceous species that were in flower during repeated walk-throughs in each area. As an indicator of species habitat, the surveys recorded vegetation type (e.g., wet meadow, Jeffrey Pine Forest, montane chaparral) for each species recorded. The original taxonomic authority was Munz and Keck (1973); taxonomy presented in this paper was updated to Hickman (1993).

Differences between years in total area sampled across watersheds and by vegetation type could not be quantified, potentially limiting the significance of results. However, coverage of the study area was extensive, widely sampling each watershed and vegetation type in both years. In general, sampling of each vegetation type was continued until no or very few additional species were found on visits to different parts of a watershed. As a result, between-year differences in the total area surveyed within a watershed or by vegetation type likely had only small systematic effects on the number and phenological class of species found.

Climate data. As representative measures of climate for the region, I used monthly and daily temperature and precipitation data for Glenbrook, Nevada (elevation 1915 m; Fig. 1) and precipitation and snow depth data from Spooners Station (2142

m) near Spooner Lake (U.S. Environmental Data Service 1967, 1968, 1969a, b, 1970, 1973; U.S. Weather Bureau 1965). I calculated growing degree days from mean daily temperatures with a base temperature of 0°C.

Analyses. I classified the species into early- and late-flowering taxa based on flowering times given by Munz and Keck (1973). While the given flowering times span those observed over the elevational extent of a species, they indicate a species' tendency toward early- vs. late-flowering. Because the surveys were made in early July, I defined early-flowering species as those with flowering periods centered on June or earlier and late-flowering species as those with flowering periods centered on July or later. I included species with June–July flowering periods in the early-flowering class. I omitted from the classification 21 species with broadly specified flowering times overlapping this division.

I compared the 1968 and 1969 frequency distributions of early- vs. late-flowering classes for in-flower species that were unique to a year for each of the sites. I used a chi-square (χ^2) test for independence (Conover 1980; SPSS and Norušis 1986) to test the null hypothesis that the distribution of unique species between early- and late-flowering categories was the same for the two years.

In addition to the site-by-site analysis, I employed three analyses on data combined across sites. First, in a combined-flora analysis, I determined whether a species was unique to a year based on 1968 and 1969 species lists combined across all sites. I evaluated flowering class distributions of these unique species in a χ^2 analysis as in the site-by-site analysis. This test was more conservative than the site-by-site analysis because species unique to a year at one site were omitted if they were present for the other year at other sites.

Second, in a pooled-distribution analysis, I summed the distributions of flowering time classes across all sites and evaluated the pooled distribution with a χ^2 test. This was a more powerful test than the combined-flora analysis because the response patterns of each site were represented in the analysis.

In a third cross-site analysis, I evaluated whether habitat influenced phenological responses to climate variability across the study area. I stratified unique species into two habitat classes based on broadly-defined "mesic" and "xeric" groupings of vegetation types. This stratification reflects a simple but clear distinction in habitats across the study area. I analyzed pooled flowering class distributions for each habitat class with a χ^2 test. Habitat classes based on vegetation type were as follows: mesic habitats included forest-meadow edge, wet and dry meadow, and riparian areas, while xeric habitats included conifer forest, chaparral, and sagebrush scrubland. Although vegetation type is only one descriptor of a species' habitat, vegetation type tended to co-vary across the landscape with other site characteristics (slope, aspect, drainage, and soil). Mesic vegetation types tended to be on less well drained sites with more developed finer soils. Xeric types were found on steep slopes with poorly developed coarse soils (e.g., decomposed granite). A benefit of this analysis is that stratification by habitat class helped to remove possible systematic differences between years in areal coverage of vegetation types.

RESULTS

Mean climate. The long-term mean maximum temperature for the warmest month (July) at Glenbrook was 28.2°C and mean minimum for the coldest month (January) was −5.0°C (Fig. 2a). Long-term mean annual precipitation for Glenbrook was 487 mm. The seasonal cycle of precipitation has a winter maximum characteristic of Mediterranean climates (Fig. 2a). Winter precipitation is generated by mid-latitude cyclonic storms from the Pacific and generally falls as snow at this elevation. There is a second, smaller precipitation peak in late spring (around May) that is evident in records for individual years (Fig. 2b). This peak is not distinguishable in the mean pattern (Fig. 2a) because of variability in its timing. This secondary maximum is common at higher elevations of the central and southern Sierra Nevada and is largely due to convective precipitation associated with greater surface heating and conditionally unstable air associated with late spring weak cyclones from the Pacific (Pyke 1972). Summer climate is dominated by dry subsiding air from the eastern Pacific subtropical high pressure center, with only occasional rainfall from convective storms.

Climate variability. There was high variability in monthly precipitation and temperatures among years 1967, 1968, and 1969 at Glenbrook (Fig. 2b). For the 1967–1968 water year (July–June), that is, for the 12 months prior to the 1968 survey, precipitation totalled 443 mm, or 91% of the long-term mean. In contrast, the 1968–1969 water year precipitation was 771 mm, or 158% of the mean. This interannual difference was also reflected in Spooners Station precipitation and snow depth records (Fig. 3). Snowpack was greater in 1969 than in 1968 (e.g., 152 cm on 15 February 1968 vs. 221 cm on the same date in 1969; Fig. 3a). Snow cover lasted at Spooners through early April in 1969 versus through the end of February in 1968 (Fig. 3a).

Timing of the spring precipitation maximum at Glenbrook was one month later in 1969 than in 1968 (June vs. May, Fig. 2b). The month shift in 1969 spring precipitation was not an artifact of dividing the record into months when constructing means: daily precipitation data showed that the spring minimum and maximum in each year were well centered in the indicated months. Timing of

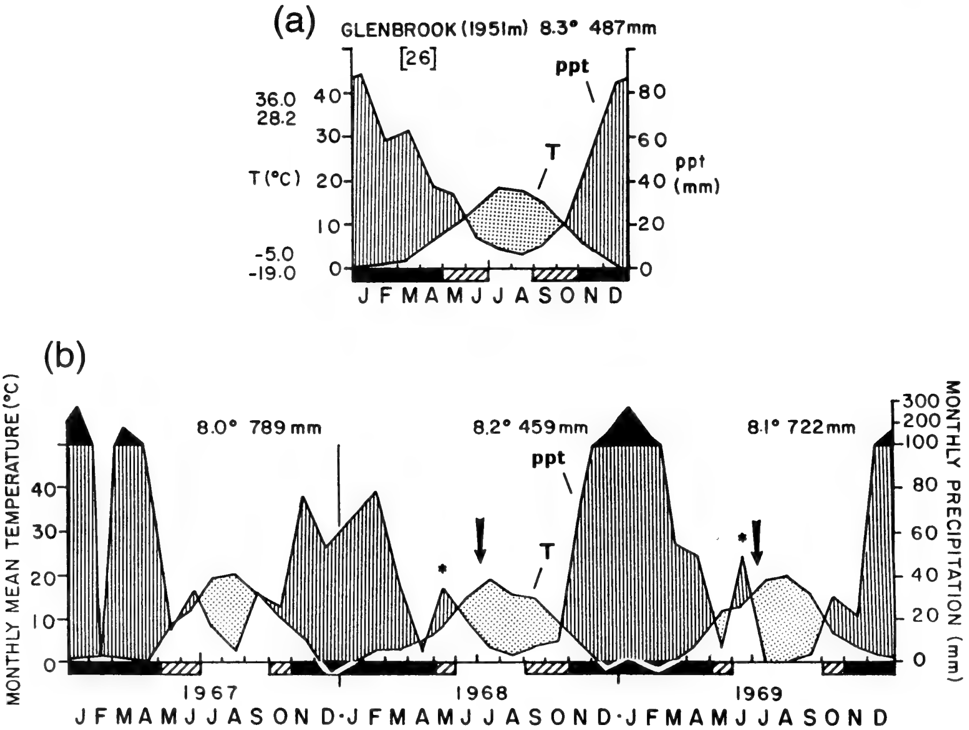

FIG. 2. Walter (1985) climate diagrams for Glenbrook, Nevada. (a) Long-term (1945–1970) mean temperature (T; left axis) and monthly precipitation (ppt; right axis). (b) Monthly mean temperature and monthly precipitation for 1967, 1968, and 1969. Arrows mark survey periods (first week in July) and asterisks (*) indicate the spring precipitation maxima preceding each survey. Vertically-hatched areas indicate periods of water surplus and stippled areas those of water deficit as defined by Walter (1985). Bars under the x-axis show months with mean daily minimum temperature < 0°C (solid bar) and months with absolute monthly minimum < 0°C but mean daily minimum > 0°C (diagonally-hatched bar). Solid area under the precipitation curve in (b) denotes a scale change in the precipitation axis. The two values above each year's plot in (a) and (b) are the mean annual temperature (°C) and annual precipitation (mm/y). In (a), the value given in square brackets is the number of years in the record, and values to the left of the plot are, from top to bottom, highest temperature in the record, mean daily maximum of the warmest month, mean daily minimum of the coldest month, and lowest temperature in the record.

the spring maximum is critical because it generally marks the end of the precipitation season.

Between year variability in early season temperatures was reflected in growing degree-days. 1968 had more growing degree-days from January through June than did 1969 (1136 vs. 1019°C-days). Average temperature in June, the month just prior to the surveys, was greater in 1968 than in 1969 (15° vs. 13.3°C). In summary, the water year prior to the 1968 survey was warmer, drier, and snow-free earlier than that preceding the 1969 survey.

Survey comparison. The surveys identified 105 species in 30 families (Table 1). The survey in 1969 found significantly more species (88 species) than that in 1968 (75 species; $P < 0.0015$, df = 3, 1-tailed paired Student's t-test). The number of both early- and late-flowering species also increased significantly from 1968 to 1969 ($P < 0.0001$ and 0.05, respectively). Of the total number of species found combined from both years, a higher portion was unique to the 1969 survey than to the 1968 survey (29% vs. 16%). At individual sites, species unique to the 1969 survey accounted for up to more than half of the species found (Table 1).

Early-flowering species dominated both surveys, but more so in 1969 than in 1968. The ratio of early- to late-flowering species was 1.15 in 1968 and 1.56 in 1969. For species unique to each survey, the frequency distribution of flowering times differed between years (Fig. 4a). At each site, unique species were predominantly late-flowering in 1968 and early-flowering in 1969. The strength of this relationship varied between sites, ranging from statistically significant at the 0.05 level (Spooner Lake) to not significant (Marlette Creek) (Fig. 4a). The shift in dominance across sites from late to early species from 1968 to 1969 was strongly supported by the combined-flora analysis ($\chi^2 = 4.3$, $P < 0.05$, df = 1; Table 2) and the pooled-distribution analysis ($\chi^2 = 10.6$, $P < 0.0015$, df = 1).

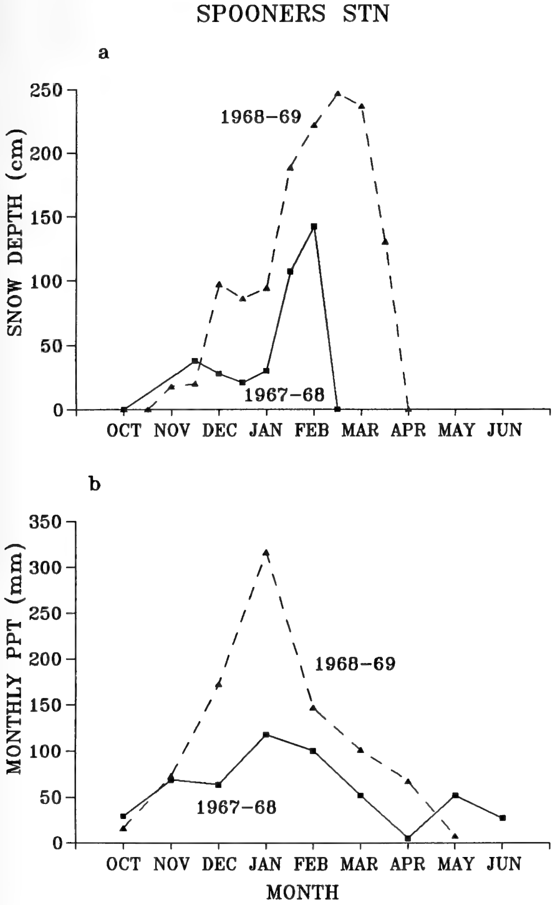

FIG. 3. (a) Biweekly snow depth and (b) monthly precipitation at Spooners Station for 1967–1968 and 1968–1969 winters. X-axis ticks in (a) mark the 15th of each month. Precipitation data for June 1969 were not available.

TABLE 1. NUMBER OF SPECIES, TOTAL AND UNIQUE, FOR THE 1968 AND 1969 SURVEYS AND FOR BOTH YEARS COMBINED. The percent of unique species relative to the combined total is given in parentheses.

Site	Combined total	1968 Survey Total	1968 Survey Unique to year	1969 Survey Total	1969 Survey Unique to year
Skunk Harbor	49	25	6 (12%)	43	24 (49%)
Slaughterhouse Canyon	71	41	7 (13%)	64	30 (42%)
Spooner Lake	75	45	14 (19%)	61	30 (40%)
Marlette Creek	57	26	5 (9%)	52	31 (54%)
All sites	105	75	17 (16%)	88	30 (29%)

Weak differences at the site level may have arisen from the variety of habitats within sites and because different habitats responded differently to climate variability. Consequently, phenological shifts may have been stronger than observed, but were blurred because sampling at each site ranged across habitats. In the analysis by species' habitat pooled across sites, both habitat classes showed a significant difference in flowering class frequencies between years (Fig. 4b). The response was stronger for mesic habitats ($\chi^2 = 11.4$, df = 1, $P < 0.001$) than for more xeric habitats ($\chi^2 = 6.0$, df = 1, $P < 0.015$). In addition, both habitats showed an increase from 1968 to 1969 in the number of unique species found, with xeric habitats having a larger increase (from 12 to 50 species pooled across sites) than mesic habitats (9 to 26).

The effect of habitat on flowering class response was also reflected at the site level. Slaughterhouse Canyon and Spooner Lake sites, dominated by wetter habitats (meadow and riparian), had greater flowering class shifts, as shown by the magnitude of corresponding χ^2's (4.5 and 3.7, respectively; Fig. 4a), than Skunk Harbor ($\chi^2 = 2.6$) and Marlette Creek ($\chi^2 = 0.5$), dominated by conifer forest and montane chaparral.

DISCUSSION

Modes of phenological response to climate variability. Phenological response of herbaceous species to variation in climate can be in terms of altered phenophase timing (displacement), duration (phase compression or extension), and amplitude (phase amplitude modulation) (Fig. 5). In displacement, timing of phenophases is delayed or advanced, so that the flowering season occurs later or earlier in the year (Fig. 5a). On the other hand, if the growing season is shortened or lengthened, the duration of phenophases may be compressed or extended, respectively (Fig. 5b). With compression, for example, the phenological cycle is completed more rapidly so that the flowering period starts later and ends earlier. In amplitude modulation, the timing and length of the phenological cycle are not altered, but the number of individuals per species and number of species observed in a given phenophase is amplified or reduced (Fig. 5c). In amplification, favorable conditions enhance plant growth, flower production, or other physiological and population factors that increase the number of species observed in flower at a given time.

Comparison of the 1968 and 1969 surveys suggests that both displacement and amplitude modulation were important in generating observed differences. In 1969, prolonged snowpack and later spring precipitation delayed plant phenologies so that substantially more early-flowering than late-flowering species were in flower during July. In 1968, below normal winter and spring precipitation and more growing degree-days advanced plant phenologies and increased the number of late-flowering species in blossom in July. Other studies have observed phenological displacement in winter-snow environments, where delayed snowpack melt delayed initiation of growth and flowering in early

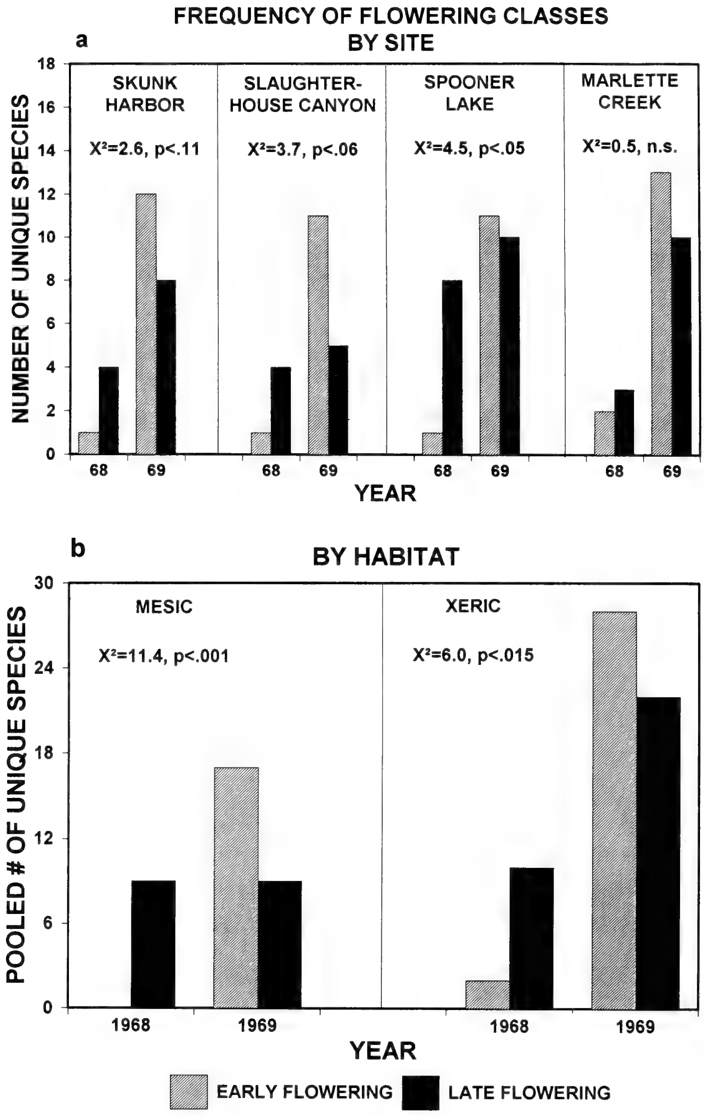

FIG. 4. Frequency distribution of early- and late-flowering classes for species unique to either 1968 or 1969 surveys (a) by site and (b) by mesic vs. xeric habitats pooled across sites. Chi-square values (χ^2) and significance levels (p) are given (df = 1). ns = not significant. In (b), the y-axis is number of unique species pooled (summed) across sites.

season species (Holway and Ward 1965; Owen 1976).

The greater number of both early- and late-flowering species found in flower in 1969 may have resulted from phenophase amplification. Better spring and early summer moisture conditions in that year possibly resulted in greater population sizes or greater flower production, increasing the likelihood of less common species being included in the 1969 survey. Jackson and Bliss (1984) also found phenophase amplification in a subalpine meadow where greater mid-season precipitation increased recruitment, growth, flowering, and seed set.

Phenophase duration responses may have also occurred but cannot be demonstrated by the 1968–1969 comparison because of the short, single sampling period used by the surveys. This response has been observed in other winter-snow environments including alpine communities (Holway and Ward 1965; Billings and Bliss 1959). In the extremes, a severely shortened growing season can lead to truncation of phenologies for late season species (Holway and Ward 1963), while an unusually prolonged growing season can lead to early season species completing all or part of a second cycle in a year (Holway and Ward 1965; Dickinson and Dodd 1976).

While analysis of phenological responses in terms of these three modes is a useful approach for understanding observed variation as a function of

TABLE 2. SPECIES UNIQUE TO EITHER 1968 OR 1969 SURVEYS BY EARLY VS. LATE-FLOWERING CLASS ACROSS ALL SITES. Species with broadly defined flowering periods were omitted. Nomenclature follows Hickman (1993). Growth habit (from Hickman 1993) is given: A = annual, B = biennial, P = perennial, and P/ = perennial, dies after flowering once; introduced (I) or possibly introduced (I?) species are also indicated.

Collection year	Early flowering		Late flowering	
	Species	Habit	Species	Habit
1968 only	*Brassica rapa* L.	A (I)	*Angelica breweri* A. Gray	P
	Lepidium virginicum L. var. *pubescens* (E. Greene) Thell.	A	*Antennaria rosea* E. Greene	P
	Tragopogon porrifolius L.	B (I)	*Ipomopsis aggregata* (Pursh) V. Grant	P/
			Phacelia hastata Lehm. ssp. *compacta* (Brand) Heckard	P
			Polygonum amphibium L. var. *stipulaceum* Coleman	P
			Pterospora andromedea Nutt.	P
			Pyrola minor L.	P
			Stachys ajugoides Benth. var. *rigida* Jepson & Hoover	P
			Trifolium monanthum A. Gray	P
			Veronica cusickii A. Gray	P
1969 only	*Allophyllum gilioides* (Benth.) A.D. Grant & V. Grant ssp. *violaceum* (A.A. Heller) Day	A	*Chamaesyce serpyllifolia* (Pers.) Small	A
	Camissonia contorta (Douglas) Raven	A	*Eriogonum spergulinum* A. Gray	A
	Collinsia parviflora Lindley	A	*Mimulus breweri* (E. Greene) Cov.	A
	Delphinium nuttallianum Walp.	P	*Mimulus mephiticus* E. Greene	A
	Descurainia pinnata (Waller) Britton ssp. *intermedia* (Rydb.) Detl.	A	*Montia chamissoi* (Sprengel) E. Greene	P
	Galium aparine L.	A (I?)	*Penstemon gracilentus* A. Gray	P
	Lewisia nevadensis (A. Gray) Robinson	P	*Saxifraga nidifica* E. Greene var. *nidifica*	P
	Linanthus ciliathus (Benth.) E. Greene	A	*Urtica dioica* L. ssp. *holosericea* (Nutt.) Thorne	P
	Madia minima (A. Gray) Keck	A		
	Mentzelia congesta Torrey & A. Gray	A		
	Paeonia brownii Hook.	P		
	Ranunculus alismifolius Benth.	P		

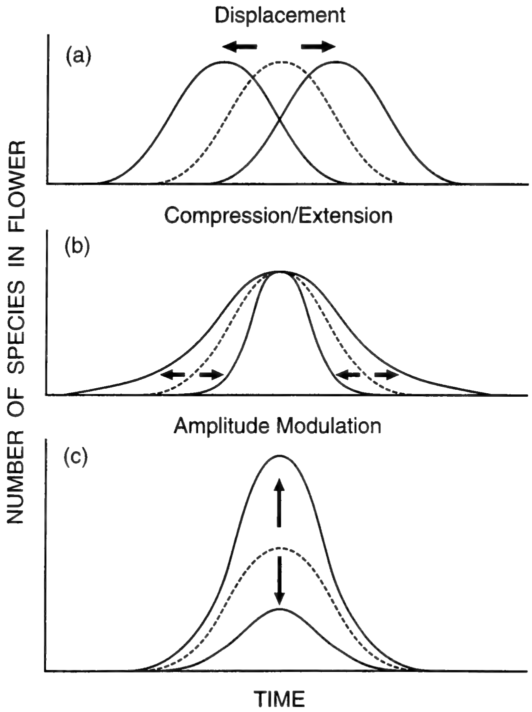

FIG. 5. Idealized phenological response curves. Phenophase (a) displacement, (b) compression and extension, and (c) amplitude modulation are illustrated in terms of number of species in flower during the course of a growing season.

climate, responses may be complex combinations of these modes arising from multiple and interactive effects of temperature and moisture on plant physiology (Walker et al. 1994; Holway and Ward 1965; Jackson and Bliss 1984). Additional complexity arises at the community level because responses are an admixture of species-specific responses moderated by species interactions (Jackson and Bliss 1984). In addition, climate conditions in one year have important carry-over effects to the next through seed set, belowground shoot meristem production in perennial herbs, and, in non-herbaceous taxa, flower primordia production (Scott 1977; Jackson and Bliss 1984; Billings and Mooney 1968; Holway and Ward 1965).

Habitat effects. Habitat type influenced the magnitude of phenological response to climate variability. Phenologies were more delayed in less well drained sites, where higher soil moisture (and cooler soil temperatures) likely persisted longer into the 1969 summer following heavy snowpack and late spring precipitation. In contrast, forest and chaparral areas on slopes with poorly developed soils (primarily decomposed granite) likely dried out earlier, i.e. by mid-summer, than did wetter sites in both years. At these drier sites, greater winter snowpack, late spring rainfall, and associated cooler temperatures in 1969 appear to have resulted in a large increase in the number of flowering species (indicating phase amplification), but a smaller delay in herbaceous phenologies (Fig. 4b).

Key abiotic factors. Differences in survey floras and climate for 1968 and 1969 suggest that herbaceous phenology and observed species richness in the Sierra Nevada montane region are controlled by snowpack amount and duration and early growing season precipitation and temperature. Studies of alpine systems indicate that thawing of soil is the key control over initiation of growth and timing of subsequent phenophases (Billings and Bliss 1959; Billings and Mooney 1968; Holway and Ward 1965; Ram et al. 1988). Increased soil moisture in high snowfall years is an additional control over phenology in these systems, increasing production and delaying senescence on drier sites (Holway and Ward 1965).

Interaction among abiotic factors is critical to understanding seasonal dynamics of montane herbaceous communities because direct effects of changes in a factor may be either amplified or countered by indirect effects. For example, years with greater winter precipitation tend to have greater and more persistent snowpack, cooler early season temperatures, and greater growing season soil moisture. The negative impact of spring snowpack on growing season length can be more than offset by the positive effect of greater soil moisture (Walker et al. 1994).

Implications for plant biodiversity surveys. Between-year changes observed in this study demonstrate that surveys of herbaceous species need to be designed to account for phenological variability and population and community dynamics driven by climate variability. In rare and endangered plant surveys, effects of climatic variability must be considered to avoid misleading assessments of populations (Gruber et al. 1979; Clark and Dorn 1981; Tilman and Wedin 1991). Weather driven within-season shifts in phenology and population sizes can limit the utility of rapid "snapshot" biodiversity assessments. Likewise, because climate variability can force year-to-year shifts in community composition (Tilman and El Haddi 1992; Pitt and Heady 1978; Borchert et al. 1991), such effects must be considered in long-term studies monitoring the status of plant communities facing threats from local to global environmental change.

These responses emphasize the need to understand the role of climate variability in population and community dynamics that influence the preservation of rare species and maintenance of community diversity. Such environmental variation can play a key role in maintaining species diversity (Jackson and Bliss 1984; Grime 1973) or, in the case of extreme climate events, cause local extinctions of individual species, reducing community richness in the long term (Tilman and El Haddi

1992). The sensitivity of the central Sierra Nevada montane herbaceous species to interannual climate variability suggests that population, community, and ecosystem processes will respond rapidly to climate fluctuations and directional climate change.

ACKNOWLEDGEMENTS

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NOTEWORTHY COLLECTIONS

CALIFORNIA

QUERCUS ENGELMANNII Greene (FAGACEAE).—Orange Co., San Joaquin Hills, upper Coyote Canyon, ca. 4 km from coastline along a drainage bottom in a small valley just north of Signal Peak. Found in association with *Quercus agrifolia* var. *agrifolia, Q. berberidifolia, Rhus integrifolia,* and *Heteromeles arbutifolia* in southern oak riparian woodland, adjacent to annual (non-native) grassland. Hybrids involving *Q. berberidifolia* and *Q. engelmannii* were observed in close proximity to the solitary *Q. engelmannii* (Engelmann oak); ca. 33°37′N, 117°49′W, elev. ca. 250 m, 11 June 1991, *R. A. Erickson s.n.* (RSA), verified by F. M. Roberts, Jr. Additional specimens obtained on 17 Oct 1996 (*J. E. Harrison 500,* RSA).

Previous knowledge. Recognized distribution is generally from southern base of San Gabriel Mts. in eastern Los Angeles Co. south to northwestern Baja California (F. M. Roberts, Jr., Illustrated Guide to the Oaks of the Southern Californian Floristic Province, pp. 60–63, F. M. Roberts Publ., Encinitas, CA, 1995). Overall distribution is patchy, with several disjunct populations of varying size and configuration; the vast majority of individuals are found in interior foothills and valleys of western, cismontane San Diego Co. Scattered occurrences in eastern Orange Co. are known from Casper's Regional Park and on private lands (i.e., Rancho Mission Viejo) (F. M. Roberts, Jr., Rare and endangered plants of Orange County, Crossosoma 16(2):3–12, 1990). Extent to which distribution of this species may have been influenced by Native Americans is unknown, but is potentially significant.

Significance. First record in San Joaquin Hills of Orange Co; next closest population ca. 20 km east. This specimen documents the San Joaquin Hills distribution of *Q. engelmannii* mapped by Roberts (1995). Following the October 1993 Laguna Canyon Fire and recent construction activities, significant hybrids are apparently no longer present. Remaining Engelmann oak is charred, with the trunk split to the base, and the entire tree has fallen. Resprouting up to 2.5 m in height has occurred at base of remaining trunk (*J. E. Harrison 500*). Roberts (1990) noted that non-hybrid Engelmann oaks are very rare in Orange Co. Currently, *Q. engelmannii* has no federal or State status, but is designated as "List 4: Plants of Limited Distribution—A Watch List" by the California Native Plant Society.

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CALIFORNIA

MADIA MADIOIDES (Nutt.) E. Greene (ASTERACEAE).—San Diego Co., NW Palomar Mountains, Agua Tibia Mountains, Cleveland National Forest, Agua Tibia Wilderness Area, W slope of Agua Tibia Mountain, SSW of the Crosley Saddle, N branch of upper Agua Tibia Creek, E of large drainage coming from the W before the confluences of branches of the Creek, N of the Wilderness boundary, T9S R1W, NE/4, SW/4, sect. 15, elev. 3120 ft, 13 June 1995, *Darin L. Banks & Steve Boyd 0618* (RSA), verified by Dr. B. Baldwin (JEPS).

Previous knowledge. Known from redwood forest, north coastal coniferous forest and mixed coniferous forest of the outer southern coast ranges and northern high Sierra Nevada, north to British Columbia (J. C. Hickman [ed.], The Jepson manual: higher plants of California, 1993; P. A. Munz and D. D. Keck, A California flora, 1959).

Significance. First report for California south of San Luis Obispo Co., and first record for San Diego Co. Plants are associated with a relictual *Arbutus menziesii* population in the northern Palomar Mountains.

SENECIO ASTEPHANUS E. Greene (ASTERACEAE).—San Diego Co., NW Palomar Mountains, Agua Tibia Mountains, Cleveland National Forest, Agua Tibia Wilderness, E slope of Agua Tibia Mountain, along the Arroyo Seco Drainage, SE of the Crosley Trail, where the two forks of upper Arroyo Seco converge in Section 11, T9S R1W, SE/4, NE/4, sect. 11, elev. 3120 ft, 27 June 1995, *Darin L. Banks & Steve Boyd 0723* (RSA); Palomar Range, Agua Tibia Wilderness Area, northeastern flank of Agua Tibia Mountain, Arroyo Seco tributary at the north base of Eagle Crag, from the Wildhorse Trail east to the main trunk of Arroyo Seco, T9S R1W S½ N½ sect. 11, Near 33°24′37″N 116°57′30″W, elev. ca. 3200 ft, local in moist shaded side draw on north-facing slope in understory of *Quercus agrifolia,* near center of section 11, 6 April 1995, *Steve Boyd & Darin L. Banks 8448* (RSA).

Previous knowledge. Known from chaparral and steep rocky slopes of the San Gabriel and San Bernardino Mountains, west to Ventura Co. and north to San Luis Obispo Co. (J. C. Hickman 1993, *loc. cit.*; P. A. Munz, A flora of Southern California, 1974).

Significance. First reports for California south of the Transverse Ranges and first records for San Diego County and the Palomar Mountains.

FESTUCA CALIFORNICA Vasey var. PARISHII (Piper) A. Hitchc. (POACEAE).—San Diego Co., NW Palomar Mountains, Cleveland National Forest, Agua Tibia Wilderness Area, N peak of Agua Tibia Mountain on the NE corner of the peak, just S of the Riverside County boundary, in a very steep bowl shaped depression on the N flank of Agua Tibia Mountain, T9S R1W, SE/4, NW/4, sect. 4, 33°25′18″N–116°57′24″, elev. 4200 ft, 1 June 1995, *Darin L. Banks & Steve Boyd 0509* (RSA); Palomar Range, Agua Tibia Wilderness Area, western crest of Agua Tibia Mountain at the head of a steep draw in the Pechanga Creek watershed, just northwest of the large *Quercus agrifolia* woodland about the junction of the Palomar Divide and Dripping Springs trails, T9S R1W, SW¼, NW¼, sect. 4, near 33°25′10″N 116°59′38″W, elev. ca. 4500 ft, locally common on more mesic exposures with some afternoon sun, 25 April 1995, *Steve Boyd 8508* (RSA); Cleveland National Forest, Agua Tibia Wilderness Area, E face of Eagle Crag, S of upper Arroyo Seco, W of the Cutca Valley, along the Palomar-Magee Trail, T9S R1W, NE/4, SW/4, sect. 14, elev. 4600 ft, 10 May 1995, *Darin L. Banks & Steve Boyd 0429* (RSA); NW Palomar Mountains, Agua Tibia Mountains, Cleveland National Forest, Agua Tibia Wilderness Area, NE face of Eagle Crag, SE of the Crosley Saddle, S of the Cutca Trail along drainage that parallels the trail, E of upper Arroyo Seco, T9S R1W, SE/4, SE/4, sect. 14, elev. 4520 ft, 15 June 1995, *Darin L. Banks & Steve Boyd 0684* (RSA).

Previous knowledge. Considered endemic to the San Bernardino Mountains, where known from dry chaparral and yellow pine forest. (P. A. Munz 1974, *loc. cit.*).

Significance. First report for California south of the San Bernardino mountains and first record for San Diego County and the Palomar Mountains.

Polypogon maritimus Willd. (Poaceae).—Riverside Co., Magnesium Canyon [possibly Magnesia Springs Canyon], north base of Santa Rosa Mountains, 29 May 1955, *C. K. Buechner C73* (RSA); NW Palomar Mountains; Agua Tibia Mountains; Cleveland National Forest, Agua Tibia Wilderness Area, along lower Arroyo Seco, S of the Dripping Springs Campground, along the narrow benches where Arroyo Seco turns to the E, just W of the Metasedimentary hills, T8S R1W, SW¼, NE¼, sect. 27, elev. 1720 ft, 17 October 1995, *Darin L. Banks & Steve Boyd 0816B* (RSA).—San Diego Co., NW Palomar Mountains, Agua Tibia Mountains, Cleveland National Forest, Agua Tibia Wilderness Area, E slope of Agua Tibia Mountain, SW of the Crosley Homestead, W of Arroyo Seco Drainage, along the Wildhorse Trail, T9S R1W, NW/4, SE/4, sect. 2, 33°25′15″N 116°57′02″W, elev. 2790 ft, 12 June 1995, *Darin L. Banks & Steve Boyd 0588* (RSA); NW Palomar Mountains, Agua Tibia Mountains, Cleveland National Forest, along the Cutca Trail, E of Cutca Valley, approximately 1.3 km W of the Aguanga Trail junction, T9S R1E, SE/4, NW/4, sect. 16, 33°23′39″N 116°53′27″W, elev. 3540 ft, 27 October 1995, *Darin L. Banks & Steve Boyd 0838* (RSA).

Previous knowledge. Known from moist areas of northwestern California, east to the Sierra Nevada foothills, and south to the San Francisco Bay area and throughout the San Joaquin Valley. Introduced from Europe and Africa (J. C. Hickman [ed.] 1993, *loc. cit.*; P. A. Munz and D. D. Keck 1959, *loc. cit.*).

Significance. First reports for California south of the Transverse Ranges and first records for Riverside and San Diego Counties. Attempts to identify this taxon using *A flora of Southern California,* Munz (1974), will result in misidentification as *Polypogon monspeliensis* (L.) Desf.

—Darin L. Banks and Steve Boyd, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

Oregon

Lomatium foeniculaceum (Nutt.) J. M. Coult. & Rose ssp. *fimbriatum* Theob. (Apiaceae).—Malheur Co., Rome ash beds, 4 miles west of Rome on Hwy 95. T31S R41E sect. 32 SE¼, (42°49′5″N, 117°42′45″W), growing on heavy clay outwash south of a barren gray ash outcrop, 1120 m, 26 April 1997, F. Wernette 28 with D. Mansfield and Field Botany class (CIC, OSC).

Previous knowledge. Well distributed across southcentral Nevada from eastern California to western Utah.

Significance. First record for Oregon. Population is ca. 400 km north of northern most Nevada population.

—Donald H. Mansfield, Department of Biology, Albertson College of Idaho, 2112 Cleveland Blvd., Caldwell, ID 83605.

Oregon

Carex crawfordii Fernald (Cyperaceae)—Coos Co., OR, SW of Floras Lake, 2.5 km W of U.S. Route 101, elev. 15 m, T31S R15W S20, 21 August 1997, *P. F. Zika 13357 & B. Wilson* (OSC; MICH), naturalized weed in cranberry crop fields, on sandy banks and ditch margins, with *Rubus ursinus, Spergula arvense,* and *Vaccinium macrocarpon*; Jackson Co., OR, Spruce Lake, 13 air km WNW of Wizard Island (Crater Lake), Crater Lake National Park, W slope of Cascade Mts., elev. 1450 m, T30S R4E S12 NW¼, 30 August 1995, *P. F. Zika 12703* (Crater Lake National Park Herbarium [hereafter abbreviated CLNP]; OSC), grassy receding shorelines on moist sunny soil, with *Agrostis hyemalis* var. *scabra* and *Carex lenticularis* var. *impressa*.

Previous knowledge. A transcontinental boreal species, *C. crawfordii* ranges south in Washington State to Snoqualmie Pass (Hitchcock *et al.* Vascular Plants of the Pacific Northwest, Part 1., Univ. Washington Press, Seattle, 1969.), 500 km N of Crater Lake.

Significance. First records of Crawford's sedge for Oregon. The coastal site appears to be a weed introduced with rooted cranberry stock from a Great Lakes or New England source of commercial *Vaccinium.*

Festuca ovina L. s. str. (Poaceae)—Klamath Co., OR, Mazama Campground, 5 air km NE of Union Peak, Crater Lake National Park, E slope of Cascade Mts., elev. 1830 m, T31S R5E S13 SW¼, 24 August 1994, *Wilson (7526), Zika & Kuykendall* (CLNP, OSC, det. B. Wilson), dry sunny gravel roadsides and parking lot margins, weed among *Sitanion hystrix, Carex inops.*

Previous knowledge. At one time, a broad *F. ovina* species concept included what are now considered five native Oregon taxa (*F. brachyphylla* Schultes & Schultes, *F. idahoensis* Elmer var. *idahoensis, F. idahoensis* var. *roemeri* Pavlick, *F. occidentalis* Hook., and *F. saximontana* Rydb.). However, *F. ovina* s. str. (sheep fescue) is a Eurasian bunchgrass cultivated in the Pacific Northwest. It occasionally escapes and may become naturalized. The species is probably under reported due to identification difficulties.

Significance. First record as an escaped plant for Oregon.

Festuca trachyphylla (Hackel) Krajina—Klamath Co., OR, Route 62, 3.9 air km S of Crater Peak, Crater Lake National Park, E slope of Cascade Mts., elev. 1570 m, T32S R6E S10 SE¼, 9 July 1995, *Zika 12497* (CLNP, OSC), sunny dry gravelly roadside weed, with *Carex subfusca, Collomia tinctoria, Madia minima, Poa secunda,* and *Sitanion hystrix.*

Previous knowledge. A bunchgrass native to Eurasia, *F. trachyphylla* (hard fescue) is cultivated in the Pacific Northwest and occasionally escapes. This taxon should not be confused with *F. rubra* var. *trichophylla* Gaudin. See Darbyshire and Pavlik (*Phytologia* 82:73–78, 1997) for justification for use of the name *F. trachyphylla* for this taxon rather than the later names *F. longifolia* Thuill. or *F. brevipila* Tracey.

Significance. First record for Oregon.

ACKNOWLEDGMENTS

We are grateful to the Native Plant Society of Oregon, National Park Service, the Oregon Nature Conservancy, and the Crater Lake Natural History Association for partial funding of field work in Crater Lake National Park.

—PETER F. ZIKA and BARBARA WILSON, Carex Working Group, Herbarium, Dept. of Botany and Plant Pathology, Oregon State Univ., Corvallis, OR, 97331.

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OBITUARY

LAURAMAY TINSLEY DEMPSTER
(1905–1997)

Lauramay Tinsley Dempster, who died at home in Orinda, California, on November 14, 1997, started her botanical career at the University of California, Berkeley as a freshman when she was sixteen and finished this career at the same institution almost eighty years later! Her active life—a balancing of personal and professional—is indeed a salutory reflection of distinguished women in science during the twentieth century.

Born on May 11, 1905, in El Paso, Texas, daughter of creative parents (her mother a writer, her father a telescope builder), she grew up in the San Francisco Bay area, with an early interest in natural history. Encouraged by her mother and grandmother, she became a botany student at Berkeley in 1921 and soon was active both in and out of class, joining enthusiastic fellow students to create the University's first field botany club, *Calypso.* The club would draw faculty and pupils together for memorable junkets into the natural bounty of California for almost two decades, an antidote for what William Morton Wheeler once called "the dry rot of biology."

Lauramay's undergraduate course in "phaenogamic botany" from Professor Willis Jepson about 1923 launched an academic relationship which would flourish on and off for more than two decades. Upon graduation in 1925, she was urged by Jepson, who was working on the mustard family for his monumental *Flora,* to consider doing a master's with him, focusing on *Lepidium* for a thesis, undoubtedly not the most exciting genus in the botanical world. But the challenge resulted in a superb, comprehensive monograph, which contained many maticulous line drawings (photographed for the thesis by her father) and was a portent for this budding botanical artist. Said Jepson, when Lauramay completed her master's work, "If it were up to me, I would give you a doctor's degree." Lauramay's lifetime regret was that she didn't published that thesis—"a terrible mistake"; but Jepson's regret would be rectified by Lauramay's eventual professional accomplishments.

Meanwhile, while a university senior Lauramay had met and fallen in love with her future husband, Everett Ross Dempster, an engineering student and native of San Francisco, two years her elder. The Dempster clan had a retreat at Inverness, and the Dempster family young people shared Lauramay's love for the out-of-doors. Indeed, part of the summer before she started her graduate work had been spent on an extended Dempster hiking hagiera in the southern Sierra.

Miss Tinsley received her master of arts degree early in 1927 and then served as a research assistant for the rest of the academic year. Everett would not complete his engineering program until 1928, but already the couple was looking forward to a wedding in the autumn of 1927. Lauramay decided to explore the science teaching profession in the interim. During the summer of 1927 she taught biology at a Fresno State College field session at Huntington Lake (a job which had been turned down by Herbert Mason). She was the youngest teacher there, expressed some concerns about her abilities, but at least reveled in the botany of the mountain area, adding to her personal herbarium and wondering if she could do some collecting for Professor Jepson.

On October 8, 1927, Lauramay Tinsley and Everett Dempster were married at Berkeley's First Unitarian Church; and Lauramay, who had always had a distinct disgust for housework, began the combination of being a housewife and working in biology, continuing to assist Jepson with his research as well as creating a new household. By early May of 1928, she was perceptibly ready to conclude, in a note to Dr. Jepson: "How could a married lady be a botanist even if so inclined?"

The ensuing academic-year (1928–1929), as Everett pursued an engineering job with Magnavox in Oakland, Lauramay tackled teaching again, this time a beginning botany course for seven young people at Cora Williams Institute on College Avenue in Berkeley. She flunked six of the seven students both semesters, incurring the wrath of administrators and parents alike. But she was later vindicated, since the six who flunked went on to the University of California, where they also flunked. Lauramay's ultimate reaction to pedigogy after these teaching experiences: "teacherly ambitions do not in any way harmonize with my plan of life."

Everett's electrical engineering position with Magnavox Company now took the young couple to Chicago in late May of 1929, where they were "installed" in a tiny apartment in the heart of a big city. Lauramay complained to Jepson that "There is very little here to tease the eye of a botanist, though the new weeds in vacant lots might prove interesting." She thought of visiting the University of Chicago and Northwestern University Botany Departments in the event that there might be some botanical occupation, and Jepson suggested she go to the Department of Botany at the Field Museum, where Jepson's casual acquaintance Paul Stanley was curator. Alas, although she enjoyed the Field Museum exhibits, she was bluntly told that "there was no room for me. . ."

The only appealing Middle West experience came during a vacation trip with Everett by second-hand canoe northward in Wisconsin and into Lake Michigan, where the canoe eventually swamped and the couple had to return to Chicago by train. Also, Lauramay visited New York and New Jersey, finding the countryside in the latter state superior in every way to Illiois. But, as she reflected, "I am more than ever impressed with the uniqueness of California, geographically and climatologically. Compared with it, all the rest of the country that I have seen is nearly monotonously alike. Simultaneously, my longing for California increases . . .. Hoping to come back some day."

Everett's engineering job would shift him from Chicago to Fort Wayne, Indiana, back to Chicago, and to England for a time. But eventually he and Lauramay did return to Berkeley, in 1933, where, of all unexpected things, Everett gave up his engineering profession and decided to become a biologist like his wife. He began taking the necessary background courses and started his pursuit of a Ph.D. in genetics, meanwhile commencing his own teaching career as a botanical assistant in 1935. Dempster received his Ph.D. in 1941 and in his botanical career would go on to become chairman of the Department of Genetics at Berkeley for many years.

Thus it was that Lauramay Tinsley Dempster again became a research assistant to Professor Willis Lynn Jepson in 1933. To be specific, she was his "botanical dissector and preparateur of details for drawings," working part-time for him on the *Flora* and to a greater extent as somewhat of a personal secretary, especially when Jepson was off campus, handling his correspondence, reading proof, toiling over the index of *Madroño,* visiting the library and herbarium, coping with students, visitors, and other assistants. Incidentally, Jepson was continually piqued beyond measure that he, supposedly unlike his academic colleagues, never had a full-time secretary. Unfortunately, this working arrangement which was beneficial to both Jepson and Lauramay came to an end by early 1936 as Lauramay anticipated the birth of her second child (she had lost her first several years earlier).

Although over ensuing years, until World War II, Lauramay did keep in contact with Jepson, and indeed casually did little jobs for him such as proof reading sections of the *Flora* as they appeared, she increasingly devoted her life to Everett and their growing family. As she wrote Dr. Jepson in 1939, "My botany is at present petty and quite avocational . . . but has not been dropped altogether."

While Everett Dempster was advancing at the University of California from instructor in 1941 to assistant professor of genetics in 1944, Lauramay again commenced helping Jepson with his *Flora,* "far from an expert typist but improving," spending about an hour every evening, typing and proof-reading. As she informed him, "Welcome though the money is [from Jepson's university grant], I have enjoyed feeling that I was helping you in a way that relatively few people would be able to do. Indeed it is a pleasure to know that I have contributed, however slightly to so great a work." A friend noted at this time that although Lauramay did "have her hands full" with her family, she "wouldn't do anything for anybody else but for Jepson, she'd give him whatever time she could manage." Everett, incidentally, had not been too happy about his wife working for Jepson, even part-time, because her "job at home is more than man-sized already."

Willis Lynn Jepson died in 1946, his great *Flora* uncompleted; but provisions of his will provided for continuing pursuit of the project. And on October 8, 1951, Lauramay was employed by the University of California as Herbarium Botanist, part-time, fittingly on the Jepson Endowment Fund, a position which she would occupy until the summer of 1963. With the establishment of the Jepson Herbarium in 1951, she became the assistant of the first curator, Dr. Rimo Bacigalupi, and was initially charged with organizing Jepson's botanical books into the herbarium library. Later, between 1959 and 1967, she also received an appointment as Research Geneticist at 60% of full time.

During these years, Lauramay and Everett's own family was growing up, but an "extended family" and befriended friends (Everett was always known for putting students "first"), initially at the house in Berkeley and then in the new oak-woodland suburban home at Orinda and the Inverness retreat, made continuing demands on the Dempsters Their residence, as a friend once commented, was "like Grand Central Station!"

Nevertheless, despite familial distractions, Lauramay was increasingly able to pursue what through the years she had longed to pursue, the professional life of a taxonomic botanist. She had been continuing her work on revision of Umbelliferae, and, thinking "there is great danger in devoting all of one's attentions to a single group," was also pursuing Hydrophyllaceae, had worked on Scrophulariaceae, Solanaceae, and *Gilia.* In 1958 she published her first major paper, "Dimorphism in the fruits of *Plectritis* [a genus in the Verbenaceae family] and its taxonomic implications", in *Brittonia.* It was Dr. Bacigalupi who first suggested that Lauramay tackle the revision of that difficult Rubiaceae genus *Galium,* and she would eventually become world famous for this research.

Shortly before Jepson died, Lauramay had written him that "All my life I have craved land, as many people do the seas. In fact there is no type of land that I do not love, and the plants upon it are only its most charming manifestations." Starting in the 1950's, alone or with other companions, she was to see lands—and their natural history—that encompassed the Biosphere. It was across Africa, Europe from France to Sweden, the Alaskan highway through Canada to Fairbanks and Mt. McKinley, the diversity of Australia from the tropics of Darwin to the Red Center at Alice, the alpine tundra of the Snowy Mountains and the coastal rainforests of Queensland; New Zealand, Malayasia . . . and of course North, Central, and South America. In 1988 the continent of Antarctica was added to Lauramay's geographical roster.

At home in California her botanical research and writing accelerated. From 1959–1964, with National Science Foundation grants and especially in close association with Ledyard Stebbins, she was almost continually in the field spring-summer-and-fall the length of the Golden State and elsewhere, working on *Galium.* Publications began appearing, in *Madroño, University of California Publications in Botany, Allertonia, Phytologia, Boletin de la Sociedad Botanica de Mexico, Great Basin Naturalist, Fieldiana, Brittonia, Leaflets of Western Botany, Sida.* Her biographical sketch appeared in the 1965 edition of *American Men of Science.* In 1968 Lauramay Dempster was designated as a Research Associate with the Jepson Herbarium and Library, an appointment which she would hold until her death. Commented Robert Ornduff with respect to this unpaid appointment: "Mrs. Dempster holds an M.A. degree from this institution but does not have Ph.D. Nevertheless, I believe that the quality and volume of her research work are equivalent to that of a person holding a doctorate, and exceed that of a number of doctoral products of our department." Ornduff added that much of her research was carried out without financial support. When the new Jepson *Manual* appeared in 1993, Lauramay was author for not only Rubiaceae, but also Apocynaceae, Caprifoliaceae, most of Valerianaceae and Convolvulaceae, not to mention the genus *Lewisia.* Her definitive treatment of *Galium* for the *Flora of North America* was completed in 1996, seventy years after she was doing research on *Lepidium* for her master's thesis.

The shy young co-ed in the photograph of a Calypso Club excursion in the mid-1920's, Lauramay Tinsley then, would over the decades become more than a distinguished taxonomic botanist. For one who detested housework, Lauramay learned to put on a memorable Thanksgiving spread for 30 people. But on the other hand, when Dr Jepson came to her parents' home for dinner, Lauramay spilled a platter of bisquits on his head. Her tenacity at driving her car from Orinda through the tunnel to the University when over ninety years old was probably a latter-day manifestation of her youthful love for motorcycles. Yet despite spending much leisure time along the northern California coast, she was not partial to boats. No wonder that when she went overboard while floating the Colorado River through the Grand Canyon, her husband had to pull her back aboard by the hair. Although quiet spoken and self-contained, she was chairman of the Society of American Geographers for three years, an active member of University Women's Club, California Botanical Society, American Society of Plant Taxonomists, and the Amphion Club . . . not to mention a founding member of the Calypso Club.

Lauramay was accomplished at playing the recorder and was remembered for her duets on the oboe with a dog. Her plant anatomy drawings were detailed and exquisite; in the Orinda home her colorful wall-sized murals of tropical rainforest and of flowers were overwhelming. Although many an hour and day were spent indoors over a typewriter, a manuscript, a dried plant specimen, Lauramay was an outdoorswoman, a world traveler, a committed conservationist of the natural world. Although she refused to snoop around another botany professor's office for Jepson, on the other hand Jepson rarely offered her credit in publication for her research contributions. But she forgave him. "He was always ready to give me attention if I asked for it, but for the most part he left me alone. Left me to use my own judgement. And I think he couldn't have done better!"

When Lauramay Dempster died this past November, her surviving contemporaries were few. Many who had received a coveted Ph.D. diploma during those bygone days, and were entitled to spend a lifetime at research and/or teaching in the hallowed Halls of Ivy, are now both gone and forgotten. Miss Tinsley need no longer regret that she couldn't have been one of them. Dividing her many years between a pursuit of botany and a commitment to family and society, she succeeded in transcending them all.

—RICHARD G. BEIDLEMAN

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY
18TH GRADUATE STUDENT MEETINGS

SATURDAY, 20 FEBRUARY 1999

CALIFORNIA POLYTECHNIC STATE UNIVERSITY
SAN LUIS OBISPO

These meetings provide an opportunity for current and recent graduate students in all aspects of plant science to meet and exchange ideas regarding proposed research, research in progress, or completed research. Interested parties (not limited to graduate students) are encouraged to attend the presentations.

The California Botanical Society Annual Banquet will be held following the graduate student meetings.

Guest Speaker: Dr. Sherwin Carlquist
Santa Barbara Botanic Garden

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November 10, 1998

RESOLUTION BY THE CALIFORNIA BOTANICAL SOCIETY ON TRANSPLANTATION

Whereas:

I. **native plants and their habitats have experienced increased threat from development and other land use practices on public and private lands and,**

II. **relatively few permanently protected areas exist that support natural populations of native plants and their habitats, and,**

III. **studies have shown that transplant attempts of native plants back into habitat are mostly unsuccessful and long-term monitoring of such transplants are currently completely inadequate.**

The California Botanical Society strongly urges all appropriate agencies, organizations, and individuals involved with the protection of native plants, including both common and rare taxa, for the purpose of maintaining plant diversity to:

4. **develop and implement policies that make protection of natural populations of native plants the first and foremost priority for mitigation and other preservation activities, and,**
5. **restrict the use of transplantation for mitigation of native plants and populations as a last resort and least preferred option for protection, and,**
6. **when transplant mitigation is chosen as the last resort option, that a scientific study of known habitat conditions and species biology be completed prior to transplantation, and,**
7. **a quantitative demographic monitoring study of mitigation transplants be implemented annually for a period of not less than seven years.**

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MADROÑO

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NATIVE PLANT DIVERSITY IN RIPARIAN COMMUNITIES OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

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ABSTRACT

Riparian ecosystems in the mountains of southern California are characterized by unusually dynamic conditions of fluvial disturbance, fire, landslides, and other physical processes. Riparian communities and associated wetland habitats make up less than 1% of the land area of the Santa Monica Mountains of southern California but are the primary habitat for nearly 20% of the native vascular plant flora. While the conditions responsible for such high biodiversity has not been well investigated, the dynamic disturbance regime and seasonal availability of water in riparian ecosystems are two critical factors. In comparison to the total native flora of the Santa Monica Mountains, riparian specialists (i.e., those species with their primary ecological occurrence in such habitats) showed a higher relative frequency of herbaceous perennials, and a lower relative frequency of woody shrubs, geophytes, and annuals. Winter deciduous growth habit characterizes nearly 80% of the woody riparian specialists, a far higher level than in comparable non-riparian species. Compound to the total flora, riparian specialists were found to have relatively broader geographic patterns of distribution within California. No rare or endangered species are included in the riparian-specialist flora of the mountains. Biological diversity of native plant species in riparian communities appears to be negatively impacted by human disturbance. Habit modification, weedy exotic species introductions, stream channel modification, and heavy recreational use all appear to lead to sharp reductions in plant species diversity. Without additional knowledge of the demography and ecology of potentially keystone riparian species, it is impossible to accurately model the impact of anthropogenic disturbance regimes on the structure and stability of these riparian ecosystems.

Riparian ecosystems play a critical role in a variety of ecosystem processes. Situated at the interface between terrestrial and aquatic ecosystems, these ecosystems act to buffer hydrologic and erosional cycles, control and regulate biogeochemical cycles of nitrogen and other key nutrients, limit fire movements, and create unique microclimates for animal species (Gregory et al. 1991; Clary and McArthur 1992; Naiman et al. 1993; Malanson 1993). Both terrestrial and aquatic wildlife depend on riparian ecosystems with their year-round availability of water, nutrients, food sources, and organic sediments. In addition to these critical components of food resources, riparian ecosystems provide wildlife with a structural complexity that includes mosaics of shade and sun, shelter, and protected corridors between adjacent plant communities. It is not surprising, therefore, that riparian ecosystems are centers of high biodiversity (Nilsson et al. 1989; Gregory et al. 1991).

The ecological significance of riparian zones is accentuated in the semi-arid mediterranean-climate regions of southern California where water resources are strongly limiting for plant growth. Riparian communities of the Santa Monica Mountains occur in an unusually dynamic geomorphic and climatic environment. The southern California mountains are subject to impacts of fluvial disturbances from flooding and associated sediment deposition and/or erosion (Rice and Foggin 1971), as well as nonfluvial impacts from adjacent upland areas in the form of fire, landslides, and other alterations to their physical structure. Wildfires burn through the chaparral and woodlands of the Santa Monica Mountains at intervals of 10–30 years or more (Radke et al. 1982), with near total removal of upland vegetation cover and litter layers, as well as significant impacts on the canopy cover of woody species in riparian habitats. Flood cycles frequently follow fires when vegetation cover has been strongly altered, causing sharp increases in runoff with associated erosion, soil slippage, and mudflows. Fluvial disturbances from flooding can be particularly severe in irregular years with strong El Niño/Southern Oscillation events when rainfall of remarkable intensity occurs over short periods of time. Added to this are a geologically young landscape, steep terrain, and a high frequency of geological faulting and associated earthquakes as further factors in destabilization of hydrologic drainage zones. Thus the riparian ecosystems of the Santa Monica Mountains are subject to extreme but unpredictable events of catastrophic disturbance.

Do dynamic environmental disturbance regimes and the associated structural diversity of riparian ecosystems produce habitats with high diversity of native species? Despite the importance of such a question in understanding the environmental significance of these zones and thus developing effective and objective policies of resource management for riparian habitats, there has been little study of the significance of native plant species diversity within riparian ecosystems of southern California. In this paper we address this question of biodiversity of native vascular plant species in riparian communities of the Santa Monica Mountains, and evaluate this diversity in relation to the life-forms and biogeographic distribution of the species present. We further discuss the potential significance of disturbance regimes, both natural and anthropogenic, as important factors in influencing the structural and ecological diversity of riparian communities. Nonnative species, an increasingly important component of riparian community structure, are not included in this study.

MATERIALS AND METHODS

The Santa Monica Mountains form the most southwestern component of the east-west trending Transverse Ranges of southern California. They extend for 73 km from the Oxnard Plain on the west to the Los Angeles River on the east. Elevations range from sea level to 948 m. This small elevational range and a generally semi-arid mediterranean-climate regime restricts overall plant species diversity because of the relative rarity of permanent water supplies in the summer months (Raven et al. 1986). Chaparral, coastal sage scrub, oak woodlands, and valley grasslands cover most of the range. Significant wetlands are present, however, in the form of riparian woodlands and limited areas of freshwater marsh, salt marsh, and aquatic communities.

A checklist of wetland and/or riparian species existing in the Santa Monica Mountains was prepared from field observations and from habitat information presented in Raven et al. (1986). This checklist was restricted to native species whose characteristic habitat was a wetland type. Riparian habitat specialists were defined as those species whose characteristic habitat was riparian zones, flood plains, ravine bottoms, and springs. Taxa present in wetland habitats but equally or more characteristic of other habitats were not included. Thus a species such as *Quercus agrifolia* Nee which is abundant along riparian corridors was not included since it is widespread on slopes and flats away from true wetland habitats.

The life-form and biogeographic distribution of each wetland species was classified using information in Hickman (1993). Life-forms used were annual (therophyte), herbaceous perennial (hemicryptophyte), suffrutescent subshrub (most chamaephytes), and woody shrub and tree (phanerophytes). Biogeographic distributions in California for these species were divided into eight regions: Northwestern, Cascade Ranges, Sierra Nevada, Great Valley, Central Western, Southwestern, Great Basin, and Desert.

The distribution and extent of wetland types in the Santa Monica Mountains and adjacent area of the Santa Monica Bay drainage basin have been described by Josselyn et al. (1993) in a study for the Santa Monica Bay Restoration Project. Restricting the Santa Monica Mountains to those areas contained within the Newbury Park, Triunfo Pass, Thousand Oaks, Point Dume, Calabasas, Malibu Beach, Canoga, Topanga, Van Nuys, Beverly Hills, Burbank and Hollywood 7.5 minute USGS quadrangles, these investigators calculated the existence of 1066 ha of wetlands. This estimate was made using an analysis method based on digitized quadrangle maps to determine aerial coverage or length of each wetland type. Length of stream systems was converted to area using a standardized width for each stream type.

Wetland communities in the Santa Monica Mountains were divided into six types by Josselyn et al. (1993). Channelized streams with little or no vegetation were classified as riverine habitats and included 16.9% of all wetland areas. Intermittent streams with vegetation cover and surface flow for only part of the year but permanently wet soils comprised 23.8% of the wetlands. Streams in Topanga, Little Sycamore, and Solstice Canyons are examples of such intermittent streams. Perennial streams with woody vegetation corridors, such as Malibu Creek and Las Virgenes Creek, made up 18.0% of the wetland area. Freshwater marshes and permanently moist flood plains away from stream channels are relatively uncommon in the Santa Monica Mountains, and totaled only 6.5% of existing wetlands. Lakes, ponds, and reservoirs comprised the largest area of wetlands covering 357 ha or 33.5% of the total. These areas, however, are largely made up of Metropolitan Water District reservoirs above Hollywood and Beverly Hills, and artificial lakes near Thousand Oaks. These reservoirs and lakes support little natural vegetation or species diversity. The final category of wetlands are salt marshes and estuaries which are largely formed by Malibu Lagoon, with a small area near Point Dume. Salt marshes make up only 13.3 ha, or 1.2% of all wetlands.

Taxonomic names used in this study follow Hickman (1993).

RESULTS

Based on this analysis by Josselyn et al. (1993), the total wetland area of 1066 ha in the Santa Monica Mountains is only 1.1% of the total area of 98,500 ha (Raven et al. 1986). Excluding salt marsh and lake/reservoir habitats, riparian areas of all types including freshwater wetlands comprise only 0.7% of the area of the mountains. There are certainly small areas of springs and first and second order streams that contain riparian species but could not be mapped at the scale used in this study. Nevertheless, it seems doubtful that the addition of such habitats would raise the total area of riparian habitats in the Santa Monica Mountains beyond 1–2% of total land area.

Despite the small relative area of wetland habitats in the Santa Monica Mountains, the signifi-

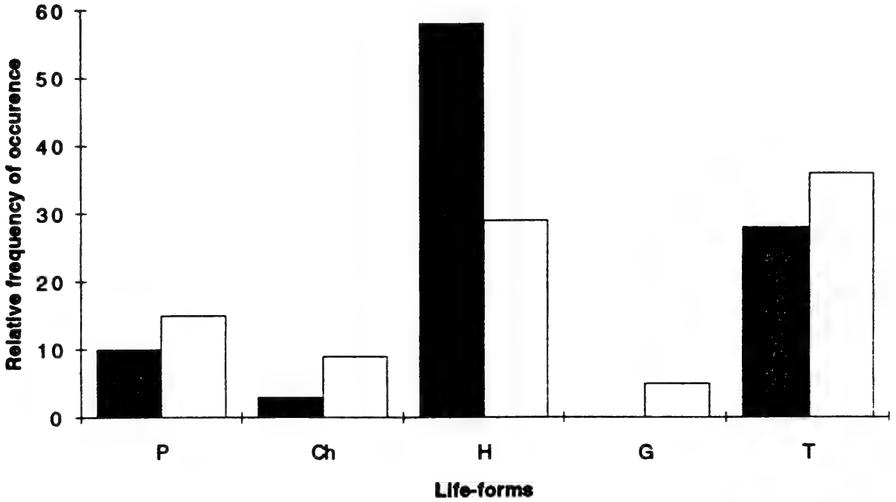

FIG. 1. Relative distribution of plant life-forms within the riparian (dark bars) and total vascular plant floras (open bars) of the Santa Monica Mountains. Only native species are included in these summaries. Abbreviations for life-forms are as follows: P = phanerophytes (woody plants above 50 cm height), CH = chamaephytes (woody or semi-woody plants below 50 cm in height), H = hemicryptophytes (perennial plants dying back to ground level annually), G = geophytes (perennial herbs dying back to below-ground fleshy tissues), and T = therophytes (annuals).

cance of these habitats as centers of biodiversity is surprisingly high. Of the total native vascular plant flora of 644 species within the mountains (Raven et al. 1986), 161 are characteristically wetland species. This amounts to 25% of the flora. Salt marsh habitats are relatively poor in vascular plant diversity, with only 24 species in the Santa Monica Mountain region. Excluding obligate salt marsh species, three marine angiosperms, and aquatic species that occur in freshwater lakes and pools, riparian habitats and associated moist flood plains and freshwater marshes form the primary habitats for 125 species (19.4% of the flora) in only a tiny fraction of the surface area of the region (Appendix).

Although woody species form the dominant aspect of riparian vegetation, trees and shrubs made up only a small part of the overall diversity of riparian species. There are ten riparian-specialist trees in the flora of the Santa Monica Mountains. These, together with four characteristically riparian shrub species, form 11% of the riparian flora (Fig. 1). This group includes ten deciduous tree species (*Acer macrophyllum* Pursh, *Alnus rhombifolia* Nutt., *Fraxinus velutina* Torrey, *Platanus racemosa* Nutt., *Populus fremontii* S. Watson ssp. fremontii, *P. balsamifera* L. ssp. *trichocarpa* (Torrey & A. Gray) Brayshaw, *Salix exigua* Nutt., *S. laevigata* Bebb, *S. lasiolepis* Benth. and *S. lucido* Muhlenb. ssp. *lasiandra*) and one evergreen tree (*Umbellularia californica* (Hook. & Arn.) Nutt.). The facultative riparian tree *Quercus agrifolia,* one of the most abundant and ecologically significant trees in riparian habitats, is also an evergreen species. Two deciduous shrubs (*Cornus glabrata* Benth. and *Holodiscus discolor* (Pursh) Maxim.) and two evergreen shrubs (*Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers. and *Myrica californica* Cham. & Schldl.) are the additional woody plants characteristic of riparian habitats.

Herbaceous perennials (hemicryptophytes) form the largest single group (58%) of riparian specialists. Next are annuals with 28%, followed by suffrutescent subshrubs (chamaephytes) with 3% of the riparian flora. This relative distribution of life-forms among the riparian flora of the Santa Monica Mountains differs notably from the life-form spectra of the total native flora. Woody shrubs, suffrutescent subshrubs, and annuals are proportionally less common among the riparian specialist flora than the total flora, while herbaceous perennials are far more common (Fig. 1). No riparian-specialist geophytes occur in the Santa Monica Mountains.

The biogeographic range of distribution for most riparian species in the Santa Monica Mountains is broad. Two-thirds or more of this riparian flora can also be found in riparian areas of the Northwest Coast, Sierra Nevada, Central Valley, and Central Coast phytogeographic regions of California. (Fig. 2, Appendix). Even the arid Great Basin and Mojave/Sonoran Desert regions share more than 40% of the riparian species from the Santa Monica Mountains.

Only 4% of riparian species from the Santa Monica Mountains are restricted in distribution in California to the Southwestern phytogeographic region (SW), while 56% of the riparian species occur in six or more of the regions (Fig. 3). Nearly a quarter of the riparian species occur in all eight phytogeographic zones. These data can be compared with data for the total flora of the large and ecologically diverse family Asteraceae in the Santa Monica

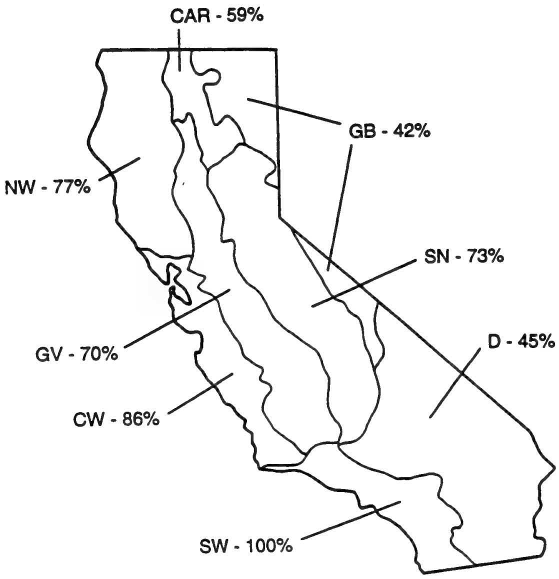

FIG. 2. Relative presence of riparian species from the Santa Monica Mountains in each of the eight major phytogeographic regions of California (*sensu* Hickman 1993). Each value shown is the percent of the 132 riparian/wetland species from the Santa Monica Mountains that also occur naturally in each region. NW = northwestern, CaR = Cascade Ranges, SN = Sierra Nevada, GV = Great Valley, CW = Central Western, SW = Southwestern, GB = Great Basin Province, and D = Desert Province.

Mountains, where 5% of the species are restricted to the southwestern region in California, but only 40% occur in six or more regions.

DISCUSSION

The small percentage of total land area occupied by riparian habitats in the Santa Monica Mountains is wholly consistent with relative cover of such communities elsewhere in California, as well as the western United States. Omart and Anderson (1986) have estimated that riparian habitats make up approximately 0.5% of land area in the West. The ability of such small areas to support high levels of biodiversity for both plant and animal species has been attributed to a variety of reasons (Hubbard 1977; Brode and Bury 1984; Klebenow and Oakleaf 1984; Nilsson et al. 1989; Gregory et al. 1991; Clary and Medin 1992). Primary among these causes is structural diversity in plant above-ground architecture, derived from the multiple selective pressures operating in the dynamic riparian landscape. Resource availability in riparian habitats throughout the year is also important.

The relative differences in life-form distribution between riparian species and the total flora of the Santa Monica Mountains may provide clues to the significance of disturbance regimes in maintaining high plant species diversity within riparian communities. Despite the availability of water resources and high plant biomass, riparian habitats have lower diversity in woody shrubs than the overall flora of the Santa Monica Mountains. This lower diversity in shrubs may reflect the impacts of intense flooding and attendant streambank and streambed scouring on the establishment and long-term survival of low-growing woody species.

However, the association of a tree growth form with mesic habitats in the Santa Monica Mountains is highly pronounced. Ten of the 14 native tree species in the Santa Monica Mountains (71% of the total number) are riparian specialists. Of the remaining four tree species, *Quercus agrifolia, Quercus lobata* Nee, and *Juglans californica* S. Watson all favor conditions with high moisture availability as indicated by the deep root systems of the two oak species which tap underground water supplies (see Griffin 1967; Rundel 1980) and the association of *J. californica* with areas of seepage or high soil moisture availability. Only the rare *Juniperus californica* Carrière occurs on seemingly xeric sites among the tree species in the Santa Monica Mountains.

It is interesting to note that 11 of the 14 species of riparian-specialist woody shrubs and trees (10 trees and four shrubs) are winter deciduous. This phenological pattern is relatively uncommon among woody shrubs in the Santa Monica Mountains where the majority of shrubs are evergreen chaparral species or drought-deciduous species associated with coastal sage scrub. The success of such a winter deciduous phenology suggests that water availability throughout the dry summer months is a critical element of the success of woody riparian species, while cool winter temperatures may limit potential photosynthetic gain during the leafless period for these species.

Annual plants (therophytes), another group poorly represented in the riparian-specialist flora, typically require soil seed pools for continued establishment in mediterranean-climate regions. Flood and erosion cycles along streams and water channels may not favor native species in this group, although non-native annual species can be widespread. Herbaceous perennials (hemicryptophytes) form the most diverse life-form of riparian specialists, with a relative frequency well above that of the group for the total flora of the Santa Monica Mountains. Individuals of these species have the ability to persist for many years along streambanks or streambeds, and to rapidly resprout or reestablish themselves after disturbance.

Adaptations for survival in dynamic riparian communities appears to result from generalist strategies that work well in riparian zones across broad mesoclimatic gradients. Patterns of biogeographic distribution for the riparian-specialist flora of the Santa Monica Mountains clearly indicate that these species are commonly widespread in distribution. This is not surprising given that the relatively high availability of water in riparian habitats decouples

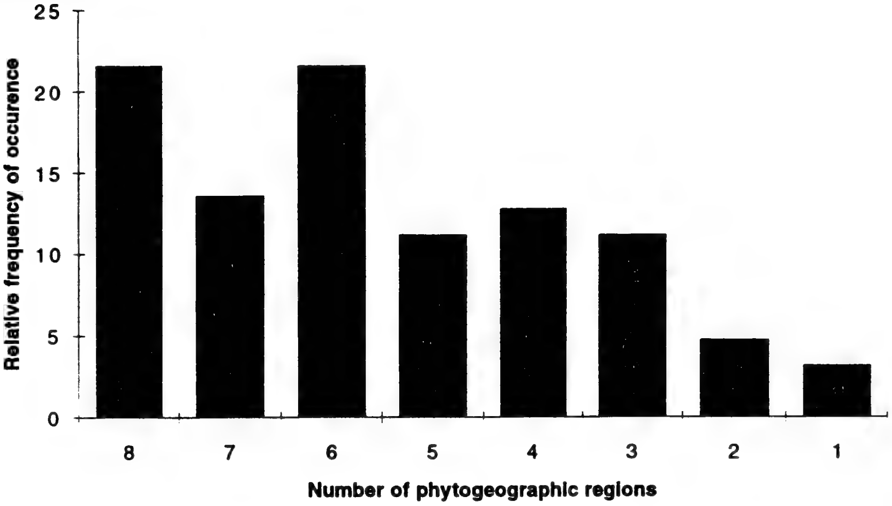

FIG. 3. Relative biogeographic distribution of riparian species of the Santa Monica Mountains among the eight major phytogeographic regions of California. The values shown are the percent of these riparian species that are restricted to each number of phytogeographic regions.

many plant species from regional rainfall regimes. None of the specialist riparian flora of the Santa Monica Mountains is included as rare or endangered for the California flora (Skinner and Pavlik 1994).

Despite generalist adaptations to disturbance regimes, riparian zone plants are highly sensitive to human impacts. Vegetation clearance, trampling, stream channel modifications, altered fire regimes, grazing, and recreational activities have significant impacts on the structure and diversity of riparian communities in the Santa Monica Mountains. These impacts come about through physical changes in the environment as well as secondarily by the introduction of exotic species which choke out the growth of natives. We have noted that riparian plant species diversity is commonly inversely correlated with levels of disturbance, while frequency of exotic plant occurrences is directly related to disturbance (Rundel and Sturmer unpublished). We know very little, however, about the relationship between biodiversity and ecological function in riparian ecosystems. Non-native species appear to be increasing in diversity and abundance in riparian habitats in the Santa Monica Mountains. Some of these species, particularly *Arundo donax* L., have the potential to profoundly impact these ecosystems.

Woody riparian species of *Salix* spp., *Platanus racemosa* Nutt. and *Alnus rhombifolia* Nutt., as well as *Quercus agrifolia* are keystone species providing the structural stability and biological productivity of riparian zones in the Santa Monica Mountains. Yet our knowledge of the demographic pattern of seed dispersal, seedling establishment, and sapling growth in relation to natural and anthropogenic disturbance regimes remains poorly studied. Process-based models of the dynamics of flood and fire cycles impacting the structure and function of riparian ecosystems in the mediterranean-climate regions of California are critically needed if we are to effectively manage riparian community resources for the future.

Given the dynamic changes of fire and flood cycles that alter the physical environment of riparian ecosystems in southern California, it is not surprising that riparian plant communities are highly irregular in structural and compositional diversity. Riparian communities reflect not only the effects of both individual and cumulative disturbance regimes along their stream channels, but also the impacts of landscape processes affecting adjacent chaparral and woodland communities. Structural and compositional complexity presents problems in developing workable classification systems based on species dominance for riparian plant communities in California (Holland 1986; Sawyer and Keeler-Wolf 1995). The impacts of irregular disturbance regimes, geomorphic history and structure are now being considered in developing new classification systems for riparian communities in the coastal mountains of Southern California (Ferrin et al. 1994).

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Appendix. Vascular Plant Species Characteristic of Riparian and Adjacent Freshwater Marsh Habitats in the Santa Monica Mountains, California, and Their Life Forms and Biogeographic Distributions. Taxonomy follows Hickman (1993). See text for discussion of life forms and distributions. Life forms are phanerophytes (Ph), hemicryptophytes (H), therophytes (Th), and chamaephytes (Ch). Phytogeographic regions are as illustrated in Figure 2. [1] Also found in fresh water marshes. [2] Also found in salt marshes.

Species			Life form				Phytogeographic region							
Family	Genus	Species	Ph	H	Th	Ch	NW	CaR	SN	GV	CW	SW	GB	D
Aceraceae	*Acer*	*macrophyllum*	+				+	+	+		+	+		
Alismataceae	*Alisma*	*plantago-aquatica*		+			+	+	+	+	+	+		
	Echindorus	*berteroi*			+		+			+	+	+		
Amaranthaceae	*Amaranthus*	*californicus*			+		+	+	+	+	+	+	+	+
Apiaceae	*Berula*	*erecta*		+			+	+	+	+	+	+	+	+
	Hydrocotyle	*umbellata*		+			+	+	+	+	+	+		
	Oenanthe	*sarmentosa*		+			+		+		+	+		
Apocynaceae	*Apocynum*	*cannabinum*		+			+	+	+	+	+	+	+	
Aspleniaceae	*Asplenium*	*vespertinum*		+										

APPENDIX. CONTINUED

Species			Life form				Phytogeographic region							
Family	Genus	Species	Ph	H	Th	Ch	NW	CaR	SN	GV	CW	SW	GB	D
Asteraceae	*Ambrosia*	*scanthicarpa*			+		+		+					
	Artemisia	*douglasiana*				+	+	+	+	+	+	+		
	Aster	*subulatus*			+					+	+	+		
	Baccharis	*douglasii*				+	+		+	+	+	+		
	Baccharis	*salicifolia*	+				+	+	+	+	+	+		+
	Bidens	*frondosa*			+		+			+		+	+	
	Bidens	*laevis*			+					+	+	+		+
	Euthamia	*occidentalis*[1]		+			+	+	+	+	+	+	+	
	Gnaphalium	*leucocephalum*			+							+		
	Gnaphalium	*palustre*				+	+	+	+	+	+	+	+	+
	Helenium	*puberulum*		+	+		+		+	+	+	+		
	Hemizonia	*pungens*			+			+		+	+	+		
	Lepidospartum	*squamatum*				+			+		+	+		+
	Madia	*elegans*		+			+	+	+	+	+	+	+	
	Madia	*exigua*		+			+	+	+	+	+	+		
	Pluchea	*odorata*		+	+				+	+	+	+		+
	Psilocarphus	*tenellus*			+		+	+	+	+	+	+		+
Betulaceae	*Alnus*	*rhombifolia*	+				+	+	+		+	+	+	+
Blechnaceae	*Woodwardia*	*fimbriata*		+			+	+	+		+	+		
Brassicaceae	*Barbarea*	*orthoceras*		+			+	+	+	+	+	+		
	Guillenia	*lasiophylla*			+		+	+	+	+	+	+	+	+
	Rorippa	*curvisiliqua*			+		+	+	+	+	+	+		
Campanulaceae	*Lobelia*	*dunnii*		+							+	+		
Chenopodiaceae	*Chenopodium*	*macrospermum*			+		+			+	+	+		
Cornaceae	*Cornus*	*glabrata*	+				+	+	+	+	+	+		
Cyperaceae	*Carex*	*barbarae*		+			+	+	+	+		+		
	Carex	*praegracilis*		+			+	+	+	+	+	+		
	Carex	*senta*		+					+	+	+	+		
	Carex	*spissa*		+							+	+		
	Cyperus	*eragostis*		+			+	+	+	+	+	+		
	Cyperus	*erythrorhizos*		+			+	+	+	+	+	+	+	+
	Cyperus	*esculentus*			+		+	+	+	+	+	+	+	+
	Cyperus	*niger*		+			+	+	+	+	+	+	+	
	Cyperus	*odoratus*			+					+		+		+
	Eleocharis	*macrostachya*		+			+	+	+	+	+	+	+	+
	Eleocharis	*montevidensis*		+			+				+	+		
	Scirpus	*acutus*		+			+	+	+	+	+	+	+	+
	Scirpus	*americanus*		+			+	+	+	+	+	+	+	+
	Scirpus	*californicus*		+			+			+	+	+		+
	Scirpus	*cernuus*		+			+			+	+	+		
	Scirpus	*maritimus*[2]			+		+			+	+	+	+	+
	Scirpus	*microcarpus*		+			+	+	+	+	+	+	+	
Datiscaceae	*Datisca*	*glomerata*			+			+	+	+	+	+	+	
Equisetaceae	*Equisetum*	*hyemale*		+			+	+	+	+	+	+		
	Equisetum	*laevigatum*		+			+	+	+	+	+	+	+	+
	Equisetum	*telmateia*		+	+		+				+	+		
Euphorbiaceae	*Chamaesyce*	*serpyllifolia*			+		+	+	+	+	+	+	+	+
Fabaceae	*Glycyrrhiza*	*lepidota*		+			+	+	+	+	+	+	+	+
	Hoita	*macrostachya*		+			+	+	+	+	+	+		
	Lotus	*oblongifolius*		+			+	+	+	+	+	+		+
	Rupertia	*physodes*		+			+				+	+		
	Trifolium	*obtusiflorum*			+		+		+		+	+		
	Trifolium	*variegatum*			+		+	+	+	+	+	+		
Hydrophyllaceae	*Nama*	*stenocarpum*			+							+		
Juncaceae	*Juncus*	*balticus*		+		+	+	+	+	+	+	+	+	
	Juncus	*bufonius*			+		+	+	+	+	+	+	+	+
	Juncus	*macrophyllus*		+							+	+		+
	Juncus	*mexicanus*[2]		+			+	+	+		+	+	+	+
	Juncus	*patens*		+			+				+	+		
	Juncus	*phaeocephalus*		+			+		+		+	+		
	Juncus	*textilis*		+							+	+		
	Juncus	*torreyi*		+								+	+	+
	Juncus	*xiphioides*		+			+	+	+	+	+	+	+	+

APPENDIX. CONTINUED

Species			Life form				Phytogeographic region							
Family	Genus	Species	Ph	H	Th	Ch	NW	CaR	SN	GV	CW	SW	GB	D
Lamiaceae	*Mentha*	*arvensis*		+			+	+	+	+	+	+	+	
	Stachys	*ajugoides*		+			+	+	+	+	+	+	+	
	Stachys	*albens*		+			+		+	+	+	+	+	
	Stachys	*bullata*		+							+	+		
Lauraceae	*Umbellularia*	*californica*	+				+	+	+		+	+		
Lemnaceae	*Lemna*	*gibba*			+		+	+	+	+	+	+	+	+
	Lemna	*triscula*			+			+	+			+	+	+
Liliaceae	*Lilium*	*humboldtii*		+				+	+			+		
Lythraceae	*Ammannia*	*coccinea*			+			+	+	+	+	+		+
	Lythrum	*californicum*			+		+		+	+	+	+		+
	Lythrum	*hyssopifolium*		+	+		+	+	+	+	+	+		
Myricaceae	*Myrica*	*californica*	+				+				+	+		
Oleacea	*Fraxinus*	*velutina*	+						+			+	+	+
Onagraceae	*Epilobium*	*brachycarpum*			+		+	+	+	+	+	+	+	
	Ludwigia	*peploides*[1]		+			+		+	+	+	+		+
	Oenothera	*laeta*		+				+	+	+	+	+	+	+
Orchidaceae	*Epipactis*	*gigantea*		+			+	+	+		+	+	+	+
Platanaceae	*Platanus*	*racemosa*	+						+	+	+	+		
Poaceae	*Agrostis*	*exarata*		+			+	+	+	+	+	+		
	Andropogon	*glomeratus*		+			+		+	+		+		+
	Hordeum	*brachyantherum*		+			+	+	+	+	+	+		
	Leptochloa	*fascicularis*			+					+		+	+	+
	Leptochloa	*uninervia*			+				+	+		+	+	+
	Panicum	*capillare*			+		+	+	+	+	+	+	+	+
	Phragmites	*australis*		+			+	+	+	+	+	+	+	+
	Poa	*palustris*		+			+	+				+	+	
	Polypogon	*interruptus*		+			+	+	+	+	+	+	+	+
Polygonacae	*Polygonum*	*amphibium*			+		+	+	+	+	+	+		+
	Polygonum	*hydropiperoides*		+	+		+	+	+	+	+	+		
	Polygonum	*lapathifolium*		+			+	+	+	+	+	+	+	+
	Polygonum	*punctatum*		+			+	+	+	+	+	+	+	+
	Rumex	*crassus*		+			+				+	+		
	Rumex	*salicifolius*		+			+	+	+	+	+	+	+	+
Polypodiaceae	*Polypodium*	*californicum*		+			+				+	+		
Primulaceae	*Samolus*	*parviflorus*		+						+	+	+		
Pteridaceae	*Adiantum*	*capillus-veneris*		+			+	+	+		+	+	+	+
Ranunculaceae	*Ranunculus*	*cymbalaria*		+			+	+	+			+	+	+
Rosaceae	*Holodiscus*	*discolor*	+				+		+	+	+	+		
Salicaceae	*Populus*	*balsamifera*	+				+	+	+	+	+	+	+	
	Populus	*fremontii*	+				+	+	+	+	+	+	+	+
	Salix	*exigua*	+				+	+	+	+	+	+	+	+
	Salix	*laevigata*	+				+	+	+	+	+	+	+	+
	Salix	*lasiolepis*	+				+	+	+	+	+	+	+	+
	Salix	*lucida*	+				+	+	+	+	+	+	+	
Saxifragaceae	*Boykinia*	*occidentalis*		+			+		+		+	+		
	Boykinia	*rotundifolia*		+							+	+		
Scrophulariaceae	*Castilleja*	*spiralis*			+		+		+	+	+	+		
	Mimulus	*cardinalis*		+			+	+	+	+	+	+		
	Mimulus	*floribundus*			+		+	+	+	+	+	+		
Solanaceae	*Petunia*	*parviflora*			+						+	+		
Thelypteridaceae	*Thelypteris*	*puberula*		+								+		
Typhaceae	*Typha*	*domingensis*		+			+			+	+	+	+	+
	Typha	*latifolia*		+			+	+	+	+	+	+	+	+
Urticaceae	*Urtica*	*dioica*		+			+			+	+	+	+	+
Vitaceae	*Vitis*	*girdiana*										+	+	+

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EARLY PRIMARY SUCCESSION ON DUNES AT BODEGA HEAD, CALIFORNIA

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ABSTRACT

Field examination of dune hillocks (nebkas) showed that changes in nebka topography and spread, sand texture, vascular plant and cryptogram cover, and species prescence were correlated with nebka ages between 15 and 135 yr. We determined age by a series of aerial photographs dating back to 1955 and topographic maps drawn as early as 1862. Development of a cryptogamic crust was significant during this range of time; on the oldest nebka it contributed 43 g biomass m^{-2} of nebka surface, which represented 3% of total above-ground biomass. Nebkas at Bodega grew in height 4 cm yr^{-1} during the past century, whereas non-vegetated areas were deflated at the same rate. Sucession is driven by sand-stilling attributes of *Ammophila arenaria,* introduced to northern California in the mid-ninteenth century and additionally planted at Bodega in the mid-twentieth century. By reference to the 1862 map we concluded that *A. arenaria* has built a prominent, continuous foredune and hinddune since the time of its arrival.

Some of the earliest American concepts about succession came from studies of coastal dunes (Cowles 1901), and the Pacific coast dunes were one of the first Californian ecosystems to be monographed (Cooper 1936, 1967). Despite this history, most published information about primary succession on California dunes is largely anecdotal and inferrential (Barbour and Johnson 1988; McBride and Stone 1976; Barbour et al. 1981; Holton and Johnson 1979).

California dunes have been invaded in this century by *Ammophila arenaria* (L.) Link (European beachgrass) to the point that the prior dominant, *Leymus mollis* (Trin.) Pilger ssp. *mollis* (American dunegrass), has been virtually eliminated from many dune locations, with consequent changes in dune topography, species richness, and (probably) primary succession. Furthermore, no attention has been paid to the role of cryptogams in California dune succession, even though the broad importance of biological crusts to ecosystems with sand substrates is well known (e.g., Danin 1996; Dor and Danin 1996; St. Clair and Johansen 1993).

Our objective was to begin a study of dune succession, with a focus on changes in dune topography, sand texture, vegetation cover, species richness, and growth forms.

MATERIALS AND METHODS

Study area. Our study location is the Bodega Marine Reserve (Fig. 1), property managed by the University of California for the purpose of biological research and teaching. The physical and biological setting of Bodega Head have been described in detail by Barbour et al. (1973), Koonig (1963), Light et al. (1967), Lipps and Moores (1971), Standing et al. (1975), and Diamond and Kennedy (1975).

The reserve consists of 132 ha in the middle of Bodega Head Peninsula, located approximately 80 km north of San Francisco at 38°19′N latitude and 123°04′W longitude. The rocky, granitic headland is abruptly truncated within the Reserve's boundaries by the San Andreas Fault. Northeast of the fault is a 0.7–1.7 km by 3.5 km swath of relatively open dunes jointly administered by the University of California and the California Department of Parks and Recreation. Climate type is maritime-moderated-mediterranean. Annual precipitation is 78 cm, about 80% of which falls in the months November through March. Daily and seasonal amplitudes of temperature are modest and frosts are rare. Mean annual air and surface water temperatures are both 12°C. The majority of summer days have morning and evening fog. Prevailing winds are from the northwest and average 15 kph; spring

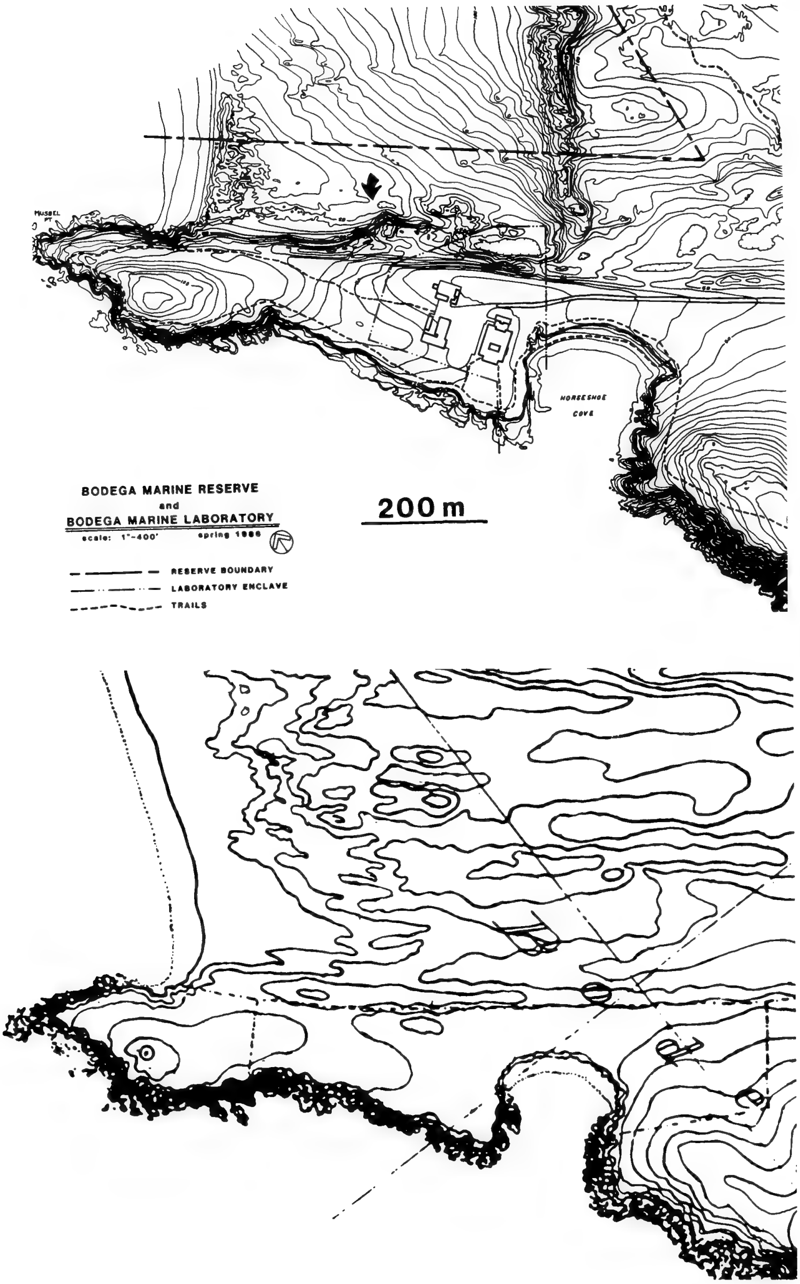

FIG. 1. Paired contour maps of a portion of Bodega dunes. The 1986 map (top) has 5 ft contours; the 1862 map (bottom) has 20 ft contours. The intersection of lines on the 1862 map, just above (north of) Horseshoe Cove, corresponds to 38°19′N latitude × 123°03′W longitude. The approximate location of our 30 × 150 m study plot is shown by the arrow (top). Scale for both maps is shown on the 1986 map.

is the windiest season, with afternoon northwest winds averaging 30–50 kph on many days. Dune sand originates as material eroded from northern watersheds and carried south by ocean currents.

Bodega Head and the adjacent dunes were occupied by Coast Miwok for at least the past 3000 yr, judging from well-documented artifacts including shell middens (Colley 1970; Greengo 1951). Russian settlers established a farming settlement early in the nineteenth century, but retreated to Alaska in the 1840's. American settlers since that time have used the area mainly for dairy cattle grazing, farming, and sheep pasture. It is probable that dune plant cover declined as a result of grazing and farming, and that the dunes became more mobile than they were during Indian occupation. Sand encroachment into Bodega Harbor this century has required periodic dredging to keep shipping lanes open. Between the 1920's and 1950's, extensive portions of the dunes were planted to European beachgrass in an attempt to stabilize the sand and minimize the need for repeated dredging.

Now, the dunes are a mosaic of densely vegetated areas, barren blowouts, swales, and scattered hillocks which have some degree of vegetative cover. We will hereafter call hillocks "nebkas," a north-African term meaning a topographic feature created by the sand-stilling nature of vegetation rooted in sandy substrate. Our focus is on a relatively open, 500-m-deep region, between a 5 m tall foredune and a 45 m tall hinddune. The foredune and hinddune vegetation cover is dominated by *A. arenaria* and the shrub *Lupinus arboreus* Sims (bush lupine, a California native here near its natural northern limit; Davidson and Barbour 1977). Aerial photographs and historical information both confirm that this study area was not included in the *A. arenaria* plantings of this century.

An 1862 topographic map of the dune area (Fig. 1; Rodgers and Kerr 1862; original scale 1:10,000), compiled before any *A. arenaria* was present, shows neither a foredune nor a hinddune, and instead details a series of low, broken dune ridges running perpendicular to the coast. Evidently, Bodega dune topography has been modified by the past century's displacement of native vegetation by *A. arenaria* in much the same way Cooper (1967) concluded *A. arenaria* had changed other parts of the Pacific coast.

Field sampling methods. Our intention was to select a series of adjacent nebkas of varying age. Using a series of aerial photographs of the dunes taken in 1955, 1971, 1977, 1988, 1990, and 1991, we identified four adjacent nebkas (Fig. 2A–D) that appeared at different times. These four occurred in a 30 × 150 m rectangular area with long dimension perpendicular to the shore, parallel to prevailing winds and remnants of nineteenth century dune ridges. Prevailing wind direction is from nebka A to nebka D. Nebka D is the windward portion of a ridge, hence differs in its present form from the island-like nebkas A, B, and C.

In the late spring of 1995, we mapped each nebka's edges to scale. The edge was identified by a congruence of: significant change in slope, plant cover, and surface coarseness. The high point of each nebka was marked with a pole and transect tapes were laid out in the four cardinal compass directions (N, E, S, W). We measured transect lengths to nebka edges. Using an inclinometer, we calculated nebka height relative to the edge. We sampled plant and cryptogamic cover by taking a point sample along north and east transects, the directions typically with highest plant cover due to aspect or protection from prevailing winds. If no species covered a point the point was recorded as bare, and total percent cover was calculated as the percent of points with vegetation.

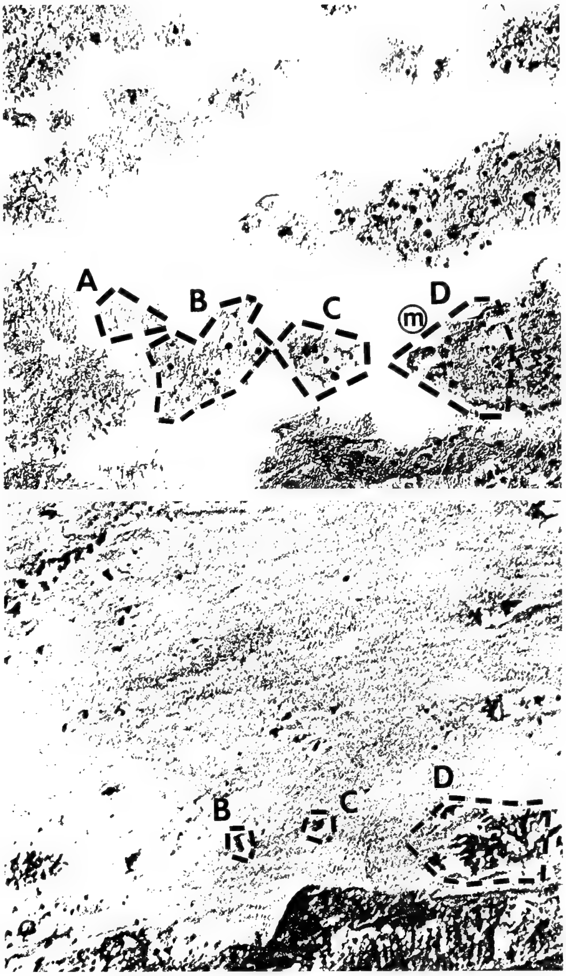

FIG. 2. Paired aerial photographs of our study plot taken in 1991 (top) and 1955 (bottom). The 1991 photograph shows nebkas A–D and an exposed midden (m), whereas the 1955 photograph shows only nebkas B–D. The shore (west) lies to the left, just out of view. The area of nebkas A–D is approximately 30 × 150 m.

Cryptogams were sent to experts for determination: mosses to Bruce Allen, Marshall Crosby, and Alan Whittemore of the Missouri Botanical Garden, and to Dan Norris of the University of California, Berkeley; and lichens to Clayton Newberry of the University of California, Berkeley. Reference specimens are deposited in those herbaria. Determined vascular plant taxa and specimens are deposited in both the University of California, Davis and the Bodega Marine Laboratory herbaria. Vascular plant nomenclature follows Hickman (1993).

We collected sand samples of 500–1000 g size at two depths and nine locations for each nebka: from the surface 2 cm and the subsurface 10–12

FIG. 3. Metal frame device used to extract plugs of cryptogamic crust 2 cm thick and 5 × 5 cm in area.

cm at the nebka center, midway along each of the four transects, and at the end of each transect. An equal number of random samples were collected from internebka locations. Samples were oven-dried at 105°C for 48 hr, then shaken on a reciprocating shaker for 3 min through a sequence of standard sieves: 2.0, 0.5, 0.25, and 0.05 mm. These sizes separated five fractions as: gravel, coarse sand, medium sand, very fine sand, and silt + clay, respectively (Gee and Bauder 1986; USDA 1951).

We also sampled the biotic crust for organic matter content and sand texture. We constructed a metal sampling device (Fig. 3) to extract a plug of crust 5 × 5 cm square and 2 cm deep. The top 3–4 mm of the plug consisted of green moss or lichen matter, whereas the rest consisted of living, pale-to-nongreen moss material. The top of the device was criss-crossed with fine wires, giving 16 intersections which could be used as points for making cover estimates. We chose sample locations subjectively to provide single-species samples of crusts dominated by the most abundant cryptogams: the fruticose lichens *Cladonia fimbriata* (L) Fr. and *C. macilenta* Hoffm. and the mosses *Brachythecium albicans* (Hedw.) BSG and *Didymodon vinealis* (Brid.) Zander. The only other cryptogam in the study site, the moss *Bryum capillare* Hedw., was restricted to a single nebka and therefore we did not sample its biomass. We also required that sampled crusts be exclusively comprised of one taxon only and that it covered 100% of a minimum area of 6 × 6 cm. We extracted three samples of each species of crust from each of three nebkas.

The samples were oven-dried at 105°C for 48 hr, at which time they ranged in weight between 50 and 140 g. Organic matter was chemically determined by potassium dichromate reduction and spectrophotometric measurement (a modified Wilkley-Black method; Nelson and Sommers 1982) and the samples were sieved to determine sand texture.

We measured changes in areas of nebkas A–D over time by examining sequential aerial photographs. We projected photographs onto a screen, traced nebka boundaries on graph paper, measured virtual areas, and converted them to actual areas by reference to the photograph's scale. We estimated our range of error to be <10%.

RESULTS

Nebka size, topography, and age. Present nebka height increased from <1 m for nebka A to >4 m for nebka D (Table 1). Present nebka area in general increased from A to D, although nebka B was larger than nebka C. Recall that nebka D was on the windward end of an old, elongate ridge; we arbitrarily defined the sample area as the most northwestern 4000 m^2 portion. Nebka area thus differed at the A and D extremes by an order of magnitude.

In 1955, nebkas B, C, and D were present, but B and C were very small (30–40 m^2 each), two orders of magnitude smaller than at present (Table 2 and Fig. 2). We estimate that the year of origin

TABLE 1. PHYSICAL TRAITS OF NEBKAS A, B, C, AND D, AS OF SPRING, 1995. Within a row, numbers with different superscript letters are statistically different at $P < 0.5$.

Trait	A	B	C	D
Area (m^2)	378	1256	908	4000
Height (m)	0.4	2.0	2.9	4.6
Coarse sand (%)	34.1^{a}	28.3^{b}	23.3^{b}	10.8^{c}
Very fine sand (%)	6.8^{a}	10.0^{b}	10.3^{b}	12.7^{b}

TABLE 2. APPROXIMATE AREA (m^2) OF EACH NEBKA AND OF A NEARBY MIDDEN OVER TIME. Based on interpretation of aerial photographs for all years prior to 1995, and on-the-ground-measurements in 1995. Nebka D, which remained constant at >4000 m^2, is not shown.

Year	Nebka A	Nebka B	Nebka C	Midden
1955	0	30	40	0
1971	0	160	115	100
1977	0	240	110	80
1988	290	1410	515	180
1990	470	2090	840	305
1991	440	2120	1120	375
1995	380	2205	910	400

for B and C did not long precede the 1955 photograph, and certainly was not equal to that of well-developed nebka D. Provisionally, we assigned an age of 45 yr to nebkas B and C. Nebka D—that is, the ridge to which it is the windward front—appears to have been present in the 1862 topographic map. Provisionally, we assigned an age of 135 yr to nebka D.

Nebka A did not appear until the 1988 photograph, at which time it measured nearly 300 m^2 in area. We interpret this relatively large size as indicating that its year of origin was closer to 1977 than to 1988. Provisionally, we assigned an age of 15 yr to nebka A. The present star-shaped appearance of nebka A may indicate that it was created by a single establishment event; that is, the star's rays are the results of *A. arenaria* rhizomatous spread from the single establishment locale.

The rate of growth in nebka area was unequal among the four nebkas (Table 2). It was essentially zero for nebka D. Nebkas A, B, and C grew in geometric fashion, slowly at first and then more rapidly over time. Within intervals, however, growth rates differed, nebkas A and C typically growing more slowly than nebka B (Table 2). Nebka B has increased in area 70-fold since 1955, whereas nebka C has increased only 25-fold. The current height of B, however, is nearly 1 m lower than that of C, thus aerial and vertical accretion seem to be uncoupled in this system. Growth for all three nebkas was slow in 1991–1995 compared to earlier periods of time.

Vegetative cover and richness of species and growth forms differed appreciably among the four nebkas (Table 3). Nebka A, the presumed pioneer

TABLE 3. VEGETATIVE COVER, IN 1995, ON THE FOUR NEBKAS. Data, in percent, are averages of two line transects, with point data taken every 50 cm. T = <0.1%; — = not present.

Growth form and species	Nebka A	Nebka B	Nebka C	Nebka D
Shrubs				
Lupinus arboreus	—	11.6	22.1	10.3
Baccharis pilularis	—	—	7.8	5.2
Herbs				
Ammophila arenaria	40.1	67.7	41.8	90.9
Cardamine oligosperma	4.9	5.7	5.2	10.8
Claytonia perfoliata	3.7	9.1	1.9	15.2
Lotus heermannii	2.4	—	—	—
Camissonia cheiranthifolia	T	0.7	1.4	—
Carpobrotus chilensis	T	—	—	—
Conyza canadensis	T	—	T	—
Brassica rapa	—	0.9	—	—
Gnaphalium purpureum	—	1.7	—	—
Ambrosia chamissonis	—	0.9	—	—
Crassula connata	—	3.0	1.9	—
Spergularia macrotheca	—	0.9	7.7	—
Erechtites minima	—	0.7	T	1.1
Carpobrotus edulis	—	—	4.1	—
Daucus pusillus	—	—	T	T
Juncus bufonius	—	T	—	—
Galium aparine	—	—	—	T
Poa douglasii	—	T	—	—
Solanum americanum	—	—	T	—
Cryptogams				
Bryum capillare	—	—	—	0.8
Didymodon vinealis	T	4.7	T	0.8
Brachythecium albicans	T	0.9	7.1	10.5
Cladonia fimbriata and *C. macilenta*	T	T	—	—
Total number of species	10	16	15	11
Bare ground (%)	49.0	17.9	25.3	8.2
Number of samples	61	135	63	115

TABLE 4. ORGANIC MATTER IN THE TOP 2 cm OF BIOTIC CRUST. Data are means of three samples, one sample per nebka. Within a column, data with a different superscript statistically differ at $P < 0.5$.

Dominant cryptogam	OM as %	OM as g m^{-2}
Cladonia spp.	30.3^a	497^b
Brachythecium albicans	29.6^a	408^b
Didymodon vinealis	31.9^a	269^c

phase, had the fewest species and the lowest vascular plant and cryptogamic cover. Nebka A lacked the presence of shrub taxa. Nebkas B and C had the most species and an intermediate amount of plant cover. Nebka D had almost as few taxa as nebka A, yet exhibited the most plant and cryptogam cover.

The contribution of cryptogams to plant cover increased from trace, to 5.6, to 7.1, and to 11.3% on nebkas A–D, respectively. Crytogamic cover was typically patchy, covering the entire surface in local 0.2–0.5 m^2 areas, while virtually absent elsewhere. The organic matter content of the topmost 2 cm in such patches averaged 30% by weight, or 391 g m^{-2} crust. There was significantly less biomass per unit area for the moss *D. vinealis* among the three cryptogams sampled (Table 4), but the other taxa were not statistically different from each other.

From Table 3, we can estimate that 11% of a mature nebka's surface would contain a biotic crust such as we sampled, and therefore the standing biomass would be $(0.11 \times 391 = 43 \text{ g m}^{-2})$.

Sand texture differed among nebkas, coarse sand (2.0–0.5 mm) and very fine sand (0.25–0.05 mm) fractions showing the most difference. Gravel (>2 mm) and silt + clay (<0.05 mm) fractions combined never accounted for >1% of any sample's weight. Surface and subsurface textures, however, were not statistically different, hence we have pooled those data in this paper. Textures at the nebka center and midway along the transects were insignificantly different among the nebkas, but they were different from texture at the nebka edge. Consequently, each nebka's texture data in this paper represent average data for ten samples: surface and subsurface samples at the nebka's center and midway along each of its four transects. Nebka sand texture was significantly finer than sand at nebka edges or at random internebka locations (Table 5).

One layer of coarse sand, approximately 2 m below the current surface of several ridges and of nebka D, was uniquely coarsest of all samples. We think this stratum was the result of a period of intense erosion during which finer particles were blown away. Our examination of the series of aerial photographs lead us to conclude that this coarse layer was at the surface just after 1955. One reason for our choice of 1955 was the presence of a midden mound adjacent to nebka D (Fig. 2 and Table 2) in the 1971 photograph, but not visible in the 1955 photograph. By 1995, the midden's exposed area had quadrupled from that in 1971, indicating that scouring of the unvegetated surface is continuing. The location of the coarse sand layer today, 2 m below the vegetated surfaces of ridges and nebka D, indicates an average sand accretion rate of 5 cm per year. This rate of accretion is modest compared to known rates for *A. arenaria* dunes elsewhere that approach 100 cm per yr (Barbour et al. 1985). At the same time, there must have been an equal amount of deflation between the ridges because the height of the coarse stratum is about 2 m above present internebka swales.

DISCUSSION AND CONCLUSIONS

The vegetation on nebkas A–D fits within the definition of dune scrub dominated by *A. arenaria* formally classified as "European beachgrass" series by Sawyer and Keeler-Wolf (1995) or as "*Ammophila-Erechtites*" and "*Ammophila-Baccharis*" communities by Parker (1974).

Ammophila arenaria today has a central importance to nebka formation, vegetation succession, and the composition of dune scrub on stabilized substrates at Bodega Head. We can presume that modern dune succession and dune scrub differ from that of the last century (when *Leymus mollis* was the dominant sand-stilling grass) because published studies show that *A. arenaria* grows more densely than *L. mollis* and that it suppresses species richness and cover from other taxa (Barbour and Johnson 1988; Barbour et al. 1976; Pavlik 1983).

Remnant areas of northern California dune scrub still dominated by *L. mollis* exist at Point Reyes National Seashore, Lanphere-Christensen Dunes

TABLE 5. SOIL TEXTURE. Coarse = a buried stratum found repeatedly beneath several nebkas and dune ridges. Internebka data come from five random samples within the 50 × 150 m study area. Edge = the surface and subsurface samples combined from 16 samples at nebka outer edges. Within = the surface and subsurface samples combined from 20 samples taken within nebkas. Data to the far right represent soil texture just beneath biotic crusts of *Cladonia, Brachythecium,* and *Didymodon.* Within a row, numbers with different superscripts are statistically different at $P < 0.5$.

Texture class	Coarse	Internebka	Edge	Within	Clad	Brach	Didy
Coarse sand	73.8^a	53.1^a	38.8^a	22.1^b	18.4^b	9.0^c	7.3^c
Very fine sand	7.7^d	11.7^d	8.9^d	10.0^d	15.3^e	21.4^e	26.3^e
No. samples	2	5	32	40	3	3	3

Preserve, just south of the mouth of Ten Mile River in Mendocino County, and in very local patches along Bodega Bay. This vegetation has been variously described as "native dunegrass," "yellow bush lupine," and "coyote brush" series by Sawyer and Keeler-Wolf (1995), as "*Baccharis-Scrophularia*," "*Poa-Lathyrus*," and "*Solidago spathulata-Lupinus* arboreus dune mat" communities by Parker (1974), or as "*Lupinus arboreus-Haplopappus* ericoides" association by Holton and Johnson (1979).

Vegetation on nebkas A–D are related by patterns commonly reported for progressive succession in general (Barbour et al. 1987). For example, total cover increases through the entire sere, but species richness peaks at an intermediate phase. We presume that the late-seral decline in species richness is due to growing dominance by *A. arenaria* and its homogenization of the microenvironment, reducing niche diversity.

The few studies of plant zonation and putative succession on California dunes suggest that the most highly correlated abiotic factors (possible drivers of succession) are: coarseness of the substrate, amount of soil organic matter, wind speed near the surface, intensity of salt spray, and degree of surface sand movement (Barbour 1992; Barbour et al. 1973; Barbour and DeJong 1977; Barbour 1978; Holton and Johnson 1979; Johnson 1963; McBride and Stone 1976; Parker 1974).

Our results corroborate and add detail to the published pattern of increasingly fine sand texture accompanying the progression of primary succession. The percent of coarse sand monotonically declined nearly an order of magnitude from internebka sand to sand at the edge of nebkas, to sand well within nebkas, and to sand within a cryptogamic crust on nebkas. At the same time, the percent of very fine sand more than doubled. Although we collected no data on the ecological effect of this textural cline, we can easily imagine that increasingly fine texture improves soil moisture retention. We can also infer that the driving factor for increasingly fine texture is declining surface wind speed, which allows smaller particles to settle out (Danin and Yaalon 1982; Danin 1996). Thus, gradients of sand movement, salt spray, and wind speed are all undoubtedly interdependent in this ecosystem.

Our observation of a widely distributed layer of exceptionally coarse sand gave us a possible datum from which to estimate rate of nebka building or internebka deflation. The 15-cm thick layer (Table 5; Fig. 4) had 39% more coarse sand and 34% less very fine sand than average internebka samples. It was visible at a consistent depth of about 2.0 m beneath stabilized ridges or large nebkas, and at a similar height above internebka swales and blowouts. The coarse layer may represent surface material prevalent prior to the widespread planting of *A. arenaria* and the creation of a foredune which has since slowed surface winds. It could have been present on the surface as recently as 1955 based on our interpretation of aerial photographs. If so, its burial has been the result of sand-stilling vegetation, trapping 2 m of sand in a span of 40 yr (average annual rate of accumulation = 5 cm). We know that short-term sand accumulation rates driven by the presence of *A. arenaria* may approach 1 m yr^{-1} along the foredune (Barbour and Johnson 1988; Barbour et al. 1985), but there are no published records of long-term sand accumulation rates in the lee of the foredune with which we can compare our deduced rate of 5 cm yr^{-1}.

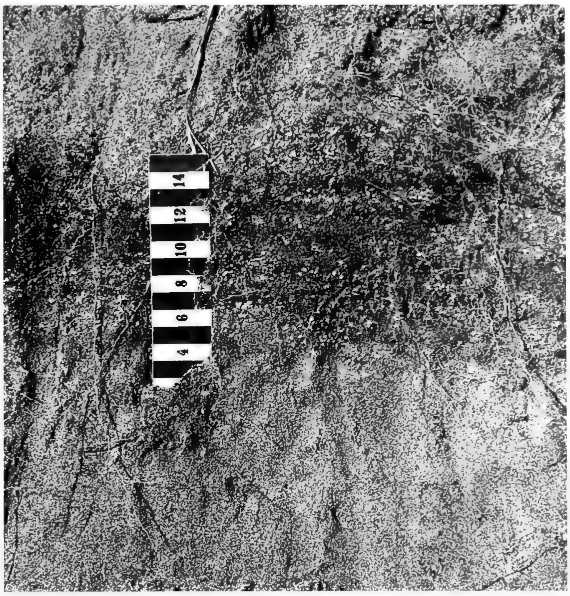

FIG. 4. Stratum of visibly coarse sand about 2 m below the current vegetated surface of ridges and mature nebkas.

Our study has shown that the role of cryptogams in nebka formation and vegetative biomass accumulation is significant. The percent cover of a crytogamic crust increased monotonically with presumed nebka age and physical complexity. On the presumed oldest nebka D, the 2-cm-thick crust contained an average of 391 g organic matter (biomass) per square meter of crust, or 47 g m^{-2} of nebka surface. This is not a trivial contribution to above-ground biomass. According to a more extensive California coast study by Barbour and Robichaux (1976) vegetation dominated by *A. arenaria* has a biomass of 1819 g m^{-2} dune surface when its cover is 100%. Nebka D had 91% cover by *A. arenaria*; ignoring any other plant cover, this would translate as (0.91 × 1819) 1655 g m^{-2} nebka surface. Thus, the cryptogamic biomass, 47 g m^{-2}, is 3% of total above-ground biomass. We expect that the contribution of biotic crust to biomass is even higher beyond the hinddune, where older and more stabilized dunes have a more continuous crust. However, there are no data yet collected for that part of the Bodega dunes ecosystem.

We have also been able to conclude that a continuous hinddune and foredune did not exist at Bodega Head prior to the introduction of *A. arenaria.* An 1862 survey map shows a gradual increase in base sand surface to the east and inland from tideline, reaching about 25 m elevation and—superimposed on this basal surface—a series of broken ridges running perpendicular to shore with maximum heights of 40 m. The distribution of peak ridge heights resembled a string of islands roughly parallel to shore and situated about 470–500 m inland. These peaks were approximately 100–150 m more shoreward of today's 45-m-tall hinddune that lies 600–650 m inland. The development of the hinddune was already substantially complete by 1958 according to a map prepared by Pacific Gas and Electric Company (PGE 1958), only a decade after wide-spread planting of *A. arenaria.* The impact of Ammophila on foredune topography thus matches that described recently for the northwest coast of North America in general by Wiedemann and Pickart (1996).

Finally, the rate of spread of *A. arenaria* on Bodega nebkas parallelled a pattern reported for more extensive dunes near Arcata, CA over the period 1939–1989 (Buell et al. 1995). In that study, *A. arenaria* first spread slowly, then entered a phase where the square root of area was linearly related to time in years. Bodega nebkas B and C (Table 2) showed a similar slow phase of increasing area between 1955 and 1971, then a linear increase phase thereafter. The linear phase exhibited an average increase of 100 m^2 yr^{-1} per nebka.

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HYBRIDIZATION BETWEEN *CERCIDIUM FLORIDUM* AND *C. MICROPHYLLUM* (FABACEAE) IN CALIFORNIA

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ABSTRACT

Cercidium floridum A. Gray ssp. *floridum* and *C. microphyllum* (Torrey) Rose & I. M. Johnston (Fabaceae) hybridize where they have overlapping distributions in an area between Earp, and Parker Dam, CA. In this area, the two species have substantially overlapping blooming times, but are normally ecologically separated by habitat requirements with *C. floridum* ssp. *floridum* preferring the sandy washes and *C. microphyllum* preferring the volcanic rocky slopes of the Whipple Mountains immediately adjacent to the washes. The hybrids tend to be found only on the sandy terraces between the wash and the mountains or on the sand dunes in the area. The best diagnostic traits for distinguishing the parental species and their hybrids include leaflet length, banner petal width and color, legume shape in cross section, the degree of constriction between seeds in the legume, and the seed shape in cross section. Introgression from *C. microphyllum* into *C. floridum* ssp. *floridum* may be occurring, but there is presently only limited evidence of any reciprocal introgression. The taxonomic and evolutionary significance of hybridization between these two taxa is discussed.

RESUMEN

En un área entre Earp, California, y la represa Parker se han encontrado híbridos entre *Cercidium floridum* A. Gray ssp. *floridum* y *C. microphyllum* (Torrey) Rose & I. M. Johnston. Estas dos especies se encuentran separadas ecologicamente ya que el habitat preferido por *C. floridum* ssp. *floridum* esta representado por lechos arenosos mientras que *C. microphyllum* prefiere las laderas montanosas de la cadena Whipple formadas por roca volcánica que bordean dichos lechos de río. Sin embargo, en esta zona la distribución de estas dos especies tienen una distribución superpresta y además comparten un período de florecimiento común. Los híbridos se encuentran primordialmente en las terrazas arenosas localizadas entre las montañas y los lechos arenosos o en las dunas que se encuentran en el área. Los razgos característicos mas apropiados para distinguir entre las especies paternas y los híbridos incluyen el largo de las hojuelas foliolos, el ancho y color del petalo central superior, la forma del corte transversal de la vaina, el grado de constricción la vaina entre las semillas, y la forma del corte transversal de la semilla. Aunque se observa una aparente introgresión de *C. microphyllum* en *C. floridum* ssp. *floridum*, evidencia introgresión recíproca es limitada. El significado entre la taxonomía y la evolución de hibridación de estas taxas se discuten.

While examining specimens of *Cercidium floridum* A. Gray ssp. *floridum* and *C. microphyllum* (Torrey) Rose and I. M. Johnston in the herbarium at Rancho Santa Ana Botanic Garden for a study of differences in ultraviolet (UV) floral patterns that act as a pre-pollination isolating mechanism (Jones 1978), we discovered a specimen collected by G. Wolf in 1940 that was annotated by him as a possible hybrid between these two species. The specimen (*Wolf 9722,* RSA) was collected about 11 miles (18 km) north of Earp, along the road to Parker Dam in San Berdardino County, CA. A field examination of this area in May 1972 revealed some interesting plants that had leaf characters that appeared to be intermediate between *C. floridum* ssp. *floridum* and *C. microphyllum.* The area was reinvestigated in April 1973 when both species were in full flower and we identified several possible hybrid individuals.

The vegetative and reproductive characters of the hybrids and their parental species have been described elsewhere (Jones 1978) and the parental species have been discussed and described by Carter (1974a, b) and by Carter and Rem (1974). Carter (1974a), in her work on the genus *Cercidium* in the Sonoran Desert of Mexico and the Southwestern United States, indicated that she had found very few hybrids between *C. floridum* ssp. *floridum* and *C. microphyllum.* She cites only two herbarium specimens as examples, one of which was the *Wolf 9722* (RSA) and the other was *Kamb 2014* from Molina Crater, northwest of Sierra Pinacate in Sonora, Mexico. Because we had found several plants that appeared to be morphologically intermediate between these two species in the area around Earp, we decided to investigate the possibility that these individuals represented several additional examples of hybrids. Herein we describe our determination of these plants as hybrids based on distributional overlap and sympatry of the two parental species (Carter 1974a; Jones 1978), morphological intermediacy, ultraviolet floral pattern differences (as previously reported in Jones 1978), and reproductive potential as determined by pollen stainability,

TABLE 1. COLLECTION DATA FOR THE FIVE SAMPLE POPULATIONS OF *CERCIDIUM.*

Population	Taxon represented	# of plants sampled	Locality
1	*C. floridum* ssp. *floridum*	10	Base of the Whipple Mountains, adjacent to the Colorado River, 16.8 km north of Earp, on State Hwy. 62 toward Parker Dam, elevation 60.96 m, San Bernardino Co., CA.
2	*C. floridum* ssp. *floridum*	10	4.83 km south of the Iron Mountains, along north side of State Hwy. 62, elevation 610 m, Riverside Co., CA.
3	*C. microphyllum*	11	Same location as no. 1.
4	*C. microphyllum*	11	47.15 km south of Mexicali, Baja California, on Mex. Hwy. 5 near El Faro, in wash on side of road.
5	*C. floridum* ssp. *floridum* × *C. microphyllum* (hybrid)	12	Same location as no. 1.

seed germination, and artificial hybridization studies.

MATERIALS AND METHODS

Field studies were conducted during spring and early summer months from May 1972 through July 1976. Five populations were selected for study (Table 1) and every *Cercidium* plant within these populations was examined. The Earp populations (1, 3 and 5) were selected to represent sympatric individuals of *C. floridum* ssp. *floridum* and *C. microphyllum* and possible hybrids. Populations 2 and 4 were selected to represent allopatric individuals of the parental species. The distributions of the parental species and the locations of the population sites are shown in Figure 1. Herbarium specimens of the 54 plants analyzed from the five populations are deposited in the Faye A. MacFadden Herbarium (MACF) at California State University, Fullerton.

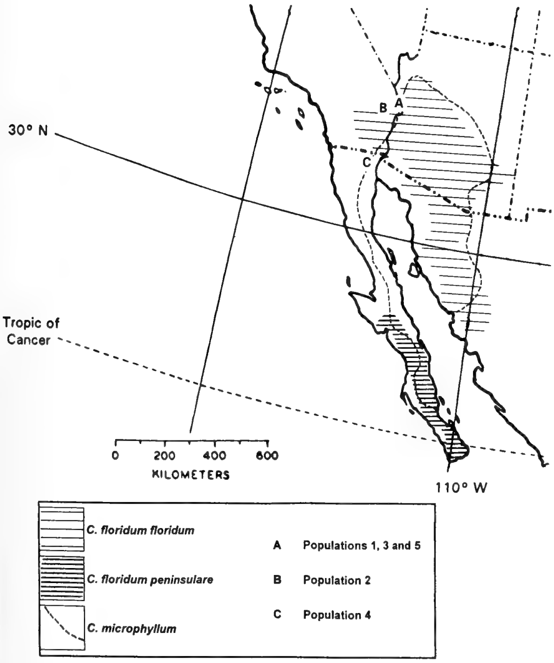


FIG. 1. Study sites and distribution of *Cercidium floridum* ssp. *floridum, C. floridum* ssp. *peninsulare* and *C. microphyllum.* Map based on Carter (1974a).

After an extensive examination of field samples and a careful review of the detailed descriptions and analyses provided by Carter (1974a, b) and Carter and Rem (1974), 12 quantitative and 13 qualitative characters were chosen for study (Table 2). Dial calipers, accurate to 0.01 mm, were used to make the 12 quantitative measurements illustrated in Figure 2. Five measurements per plant were taken for each quantitative character. Ultraviolet floral patterns were determined using techniques described by Jones (1978). Student's t-tests or one-way ANOVA were completed to determine if significant differences exist between character states in allopatric versus sympatric populations. Variation in the morphological characters for all plants from the five populations were analyzed graphically using a pictorialized scatter diagram and we used the hybrid index technique (Anderson 1949) to determine which plants to use for our artificial crosses. Characters and index values assigned to each are presented in Table 2.

Nectar samples taken from both parental types and the hybrids were sent to Drs. Irene (now deceased) and Herbert Baker at the University of California, Berkeley for analysis.

Pollen viability was estimated for each sample plant by staining the pollen with Cotton Blue (1% aniline blue in lactophenol) for at least 24 hours. Pollen from at least five separate flowers for each plant was used and a minimum of 400 grains were counted per plant. Those grains that stained dark blue and were of normal size and shape were considered viable, whereas those that stained faintly or not at all or were misshapen were considered inviable (Lawrence 1963).

Seeds were collected from every plant sampled. At least 100 seeds from each plant were scarified by soaking in concentrated sulfuric acid for three

TABLE 2. COMPARATIVE CHART OF MORPHOLOGICAL CHARACTERISTICS ILLUSTRATING THE INTERMEDIACY OF THE PUTATIVE HYBRIDS BETWEEN *CERCIDIUM FLORIDUM* spp. *FLORIDUM* AND *C. MICROPHYLLUM*. The mean and the range, in parentheses, are given for each quantitative character. Characters used to construct the morphological hybrid index are indicated with an asterisk. Values assigned to the hybrid index characters are zero (0) for *C. floridum* ssp. *floridum*, two (2) for *C. microphyllum* and one (1) for the intermediate state.

	C. floridum ssp. *floridum*	Hybrid	*C. microphyllum*
Hybrid index value	0	1	2
Character			
Branchlet tips*	without spinescent tips	variable	spinescently tipped
Branchlet surfaces*	glabrous	variable	pubescent
Axillary spines*	present	present or absent	absent
Branch color*	blue-green	green to yellow-green	yellow-green
Leaflet color*	blue-green	green to yellow-green	yellow-green
Banner petal color*	yellow	cream	white
Banner petal orange dots*	present	present or absent	absent
Ovary*	glabrous	variable	pubescent
Apex of legume*	broadly acute	intermediate	long accuminate
Pod shape*	flattened	somewhat rounded	rounded
Fruit*	not constricted between seeds	intermediate	constricted between
Seed shape*	oblong, flattened	intermediate	elliptic, rounded
Leaflets, # of pairs*	2.8 (2–4)	3.6 (2–5)	6 (5–9)
Leaflets, length (mm)*	4.1 (2.0–7.0)	3.3 (1.8–6.0)	1.6 (0.05–2.5)
Banner petal length (mm)	11.9 (9–15)	11.1 (8–14)	8.7 (4–10)
Banner petal width (mm)*	9.5 (7–12.5)	7.3 (4–14)	4.9 (3.1–7)
Flower diameter (mm)*	22.5 (18–26)	20.2 (16–27)	16.0 (12–21)
Anther length (mm)	2.0 (1.5–2)	2.1 (1.9–3)	2.0 (1.8–2.2)
Rachis length (mm)	27.7 (14–45)	22.1 (11–35)	31.1 (12–52)
Sword length (mm)	9.0 (3–19)	14.1 (4.5–37)	16.3 (7–34)
Length of pedicel, base of sepals to abscission layer (mm)*	3.3 (1.5–5.5)	2.1 (1.5–4)	1.5 (1.0–3)
Length of pedicel, abscission layer to rachis (mm)	7.0 (4–10)	7.1 (4.5–14)	5.0 (3–8)
Seed length (mm)	10.3 (8.8–12.2)	9.8 (8.2–12.4)	9.2 (7.0–11.9)
Seed width (mm)	7.2 (5.1–8.4)	6.5 (5.3–8.2)	6.4 (5.4–7.6)
Seed thickness (mm)	3.9 (3.3–4.9)	4.0 (3.1–5.1)	4.9 (3.9–6.1)
Pollen stainability (%)	77.4 (39–97)	77.3 (54–93)	85.7 (21–98)
Seed germination (%)	83.8 (58–100)	84.7 (46–99)	80.7 (32–96)

hours, then rinsed with distilled water and planted in small plastic pots filled with standard potting soil mix. The percent germination was calculated for each plant.

Artificial crosses were conducted in the field using pollinator exclusion bags from Wards (Wards No. 20W-7300, which are no longer available). Both crosses between the parental species and backcrosses to the putative hybrid were attempted. Branches having numerous unopened floral buds were bagged and the buds allowed to open. Flowers to be used as the female parent, or pollen recipient, were emasculated in the bud. Pollination was accomplished by removing pollen from mature anthers with a dissecting needle and placing it on the stigma of an emasculated flower. After pollination, the pollinator exclusion bags were replaced. The bags were periodically examined and all fruits that developed were harvested at maturity. The seeds from these crosses were treated, and percentage germination was determined, as described for the wild-collected seed.

RESULTS

Comparative morphology. Twenty-two of the 25 morphological characteristics studied (Table 2) were shown to be of some value in the delineation of the parental taxa and in the establishment of the intermediacy of their hybrids. However, certain characters such as leaflet length, banner petal width and color, legume shape in cross section, the degree of constriction between seeds in the legume, and seed shape in cross section proved to be more diagnostic.

Analysis of population samples. Variation exhibited in allopatric and sympatric populations of the parental species is represented in Figure 3. Squares represent allopatric individuals of each parental species, and circles represent sympatric individuals of each. Group (A) represents *C. microphyllum* (populations 3 and 4) and Group (B) represents *C. floridum* ssp. *floridum* (populations 1 and 2). Based on the morphological characteristics employed in this study the two species are quite distinct, al-

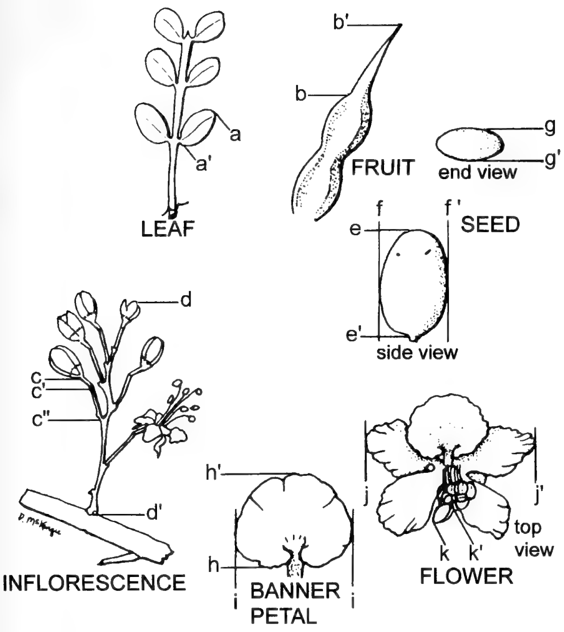


FIG. 2. Quantitative measurements of morphological characteristics as follows: a–a′, leaflet length; b–b′, legume sword length; c–c′, length of pedicel from base of sepals to abscission layer; c–c″, length of pedicel from abscission layer to rachis; d–d′, length of rachis; e–e′, length of seed; f–f′, width of seed; g–g′, thickness of seed; h–h′, length of banner petal; i–i′, width of banner petal; j–j′, diameter of flower; and k–k′, length of anther.

though there is greater range of variability in *C. floridum* ssp. *floridum* in most of the quantitative characteristics analyzed than in *C. microphyllum.* The differences between the allopatric and the sympatric populations of *C. floridum,* ssp. *floridum* as reflected in Figure 3 and based on leaflet length and banner petal width, are in marked contrast to the lack of variation between the allopatric and the sympatric populations of *C. microphyllum.* Using a Student's t-test, the leaflet length is significantly different at the 0.05 level ($t = 2.78$, $df = 9$) when the allopatric and the sympatric populations of *C. floridum* ssp. *floridum* are compared. Significant differences were not found when a comparison of allopatric and sympatric populations of *C. microphyllum* was completed.

Similar influence of *C. microphyllum* on *C. floridum* ssp. *floridum* in sympatry is exhibited in banner petal length (comparison of allopatric vs. sympatric populations of *C. floridum* ssp. *floridum* were significant ($P = 0.05$, $t = 2.38$, $df = 9$). Although not significant at the 0.05 level, the diameter of the flowers showed a similar trend.

In Figure 4, leaflet length and banner petal width are plotted for the hybrids, (represented by triangles) along with the parental types. This figure clearly demonstrates the intermediacy, in leaflet length and banner petal width, of these hybrids between the parental species.

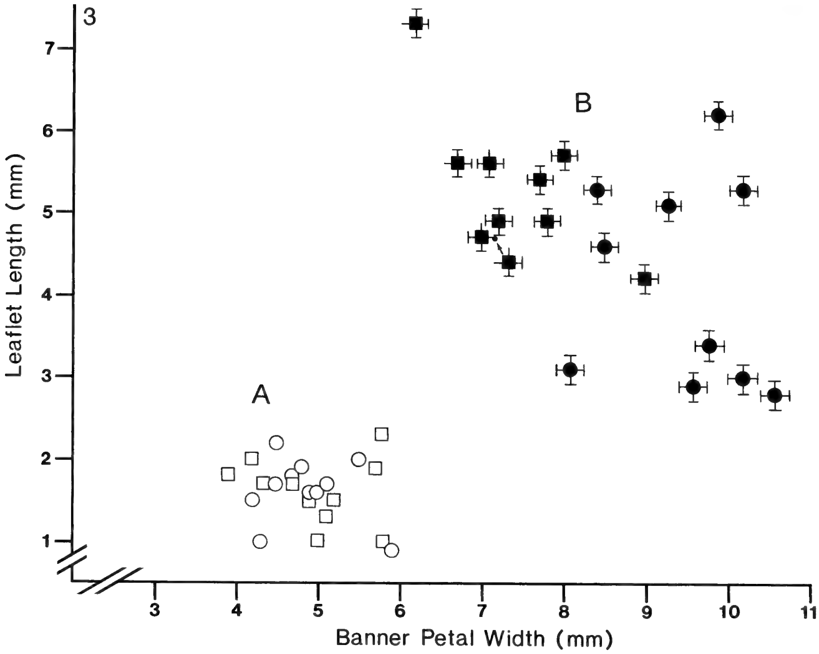
Nectar analysis. Table 3 summarizes the analysis of the nectar from both parental species and a putative hybrid. These data indicate that in amino acid content the putative hybrid sampled (# 1016) is identical to the plant of *C. microphyllum* sampled (# 4010). *Cercidium floridum* ssp. *floridum* differs in lacking lysine and tryptophan and in having a somewhat reduced concentration of threonine. In sugar content, the putative hybrid has more fructose and glucose, but considerably less sucrose than either parental species.

Fertility, experimental crosses and seed germination. The range and average pollen stainability and seed germination for both parental species and the hybrids were so similar that no statistical tests were done. These results are included in Table 2. All of the F_1 and backcrosses attempted between *C. floridum* ssp. *floridum* and *C. microphyllum* or their hybrid produced viable seed. The results of attempted crosses are presented in Table 4. The hybrid index value (HI) is given for each parent and the pollen stainability is reported for the male parent in each cross.

DISCUSSION

Cercidium floridum ssp. *floridum* and *C. microphyllum* have many obvious distinguishing characters (Carter 1974a; Carter and Rem 1974; Jones 1978; Siemens et al. 1994), illustrated in Figure 5, including size and number of leaflets; position and size of branch spines; size and coloration of flower parts; degree of constriction between seeds in fruits; and shape, size, and color patterns of seeds. The hybrids tend to be intermediate in most of these characters (see also Siemens et al. 1994).

It should be noted that some of the variation in flower color attributed to *C. microphyllum* in previous studies (Carter 1974a, p. 48) is probably due to post-pollination changes in banner petal color and is not typical of unpollinated flowers. Carter (1974a) notes, "Flowers of *C. microphyllum* differ also in having the limb of the long-clawed upper petal [banner petal] white, or occasionally cream or pale yellow . . ." Upon completion of pollination, the flowers of both *C. microphyllum* and *C. floridum* ssp. *floridum* undergo significant changes in floral color or symmetry that result in these flowers no longer being visited by the pollinating bees. In *C. microphyllum,* the change in banner petal color from white to cream or even yellowish is the result of a simple pH change. This change was duplicated by placing white banner petals in a weak sodium hydroxide solution and was reversed by immersing these treated petals in a weak solution of hydrochloric acid. In *C. floridum,* ssp. *floridum* on the other hand, the color of the banner petal does not change, but the banner petal folds down over the stamens, thus changing the symmetry of these spent flowers. This latter type of post-pollination change was previously reported for *Caesalpinia eriostach-*


3
B
A
Leaflet Length (mm)
1
2
3
4
5
6
7
3
4
5
6
7
8
9
10
11
Banner Petal Width (mm)

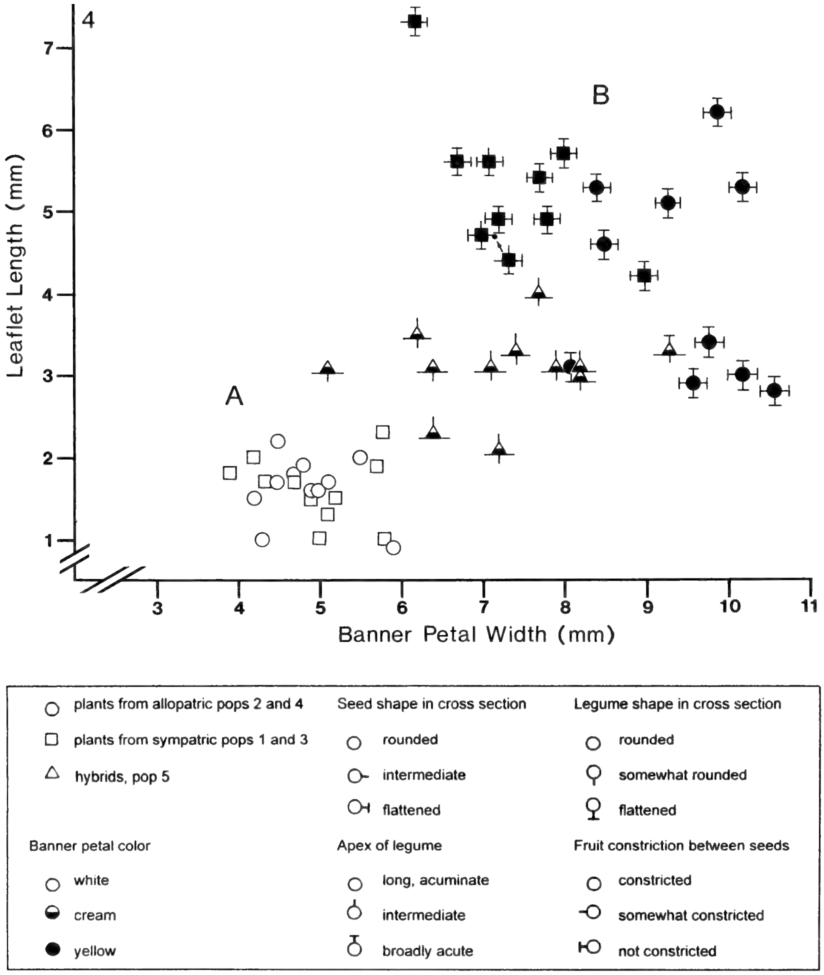

4
B
A
Leaflet Length (mm)
1
2
3
4
5
6
7
3
4
5
6
7
8
9
10
11
Banner Petal Width (mm)
plants from allopatric pops 2 and 4
plants from sympatric pops 1 and 3
hybrids, pop 5
Banner petal color
white
cream
yellow
Seed shape in cross section
rounded
intermediate
flattened
Apex of legume
long, acuminate
intermediate
broadly acute
Legume shape in cross section
rounded
somewhat rounded
flattened
Fruit constriction between seeds
constricted
somewhat constricted
not constricted

TABLE 3. A BREAKDOWN OF THE MAJOR COMPONENTS OF THE NECTAR OF *CERCIDIUM MICROPHYLLUM*, *C. FLORIDUM* ssp. *FLORIDUM* AND THEIR PUTATIVE HYBRID. + indicates presence, ++ indicates abundance, +/− indicates traces and − indicates absence. [1] Osmic acid test. [2] 2-6 dichlorophenol-indophenol test. [3] Dragendorff test. [4] Brom-phenol test. [5] p-nitraviline test.

	C. microphyllum	Hybrid	*C. floridum* ssp. *floridum*
Collection no.	4010	1016	4011
Sugars			
Fructose	16%	27%	22%
Glucose	25%	32%	23%
Sucrose	59%	37%	50%
Maltose	—	4%	5%
Amino acids			
mg/ml	1.17	1.17	0.78
Alanine	+	+	+
Arginine	++	++	++
Asparagine	+/−	+/−	+/−
Aspartic acid	+	+	+
Glycine	++	++	++
Histidine	++	++	++
Lysine	+	+	−
Proline	+	+	+
Serine	++	++	++
Threonine	++	++	+
Tryptophan	+	+	−
Lipids[1]	+	+	+
Antioxidants[2]	−	−	−
Alkaloids[3]	−	−	−
Protein[4]	+	+	+
Phenolics[5]	deep yellow	deep yellow	pale yellow

ys (Jones and Buchmann 1974). In the hybrids, the banner petal in some flowers folds down over the stamens; and in other flowers, on the same plant, it stays erect and changes in color from cream to yellowish.

As noted in Jones (1978), the two parental species differ in corolla size and in their response to ultraviolet light. The petals and stamens of the small-flowered *Cercidium microphyllum* are entirely absorbtive, whereas only the banner petals and stamens of the large-flowered *C. floridum* ssp. *floridum* absorb UV while the lateral petals are reflective. The hybrid plants display large corollas similar to those of *C. floridum* ssp. *floridum* but the flowers are entirely absorbtive (Fig. 5).

Although not considered in this paper, it should be pointed out to other taxonomists who might consider the use of UV floral patterns as a taxonomic characteristic, that such patterns, if determined from herbarium specimens and depending on which flavonoid pigments are involved in the UV absorption portion of the pattern, may change when the flowers are dried. These changes appear to commonly occur when the UV absorbing pigments are anthochlors (Scogin, Young, and Jones 1977). Since anthochlor pigments are known to be associated with UV floral patterns in the genus *Cercidium* (Hiegel and Jones unpublished), caution should be exercised in making taxonomic judgments based on these traits; such changes can result in spurious variation. When extensive variation in UV floral patterns is detected from herbarium specimens, such as Carter (1974b) found in *Cercidium praecox* and *C. sonorae*, a thorough investigation of living material should be undertaken to determine if such variation exists in living plants.

The flowers of *C. floridum* ssp. *floridum* have smaller banner petal widths when in sympatry with *C. microphyllum* and more closely resemble those found in *C. microphyllum*. The differences found in the banner petal width of *C. floridum* ssp. *floridum* collected from different populations may be

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FIG. 3. Pictorialized scatter diagram for *Cercidium* populations 1–4. Grouping (A) represents *C. microphyllum* and (B) *C. floridum*. ssp. *floridum*.

FIG. 4. Pictorialized scatter diagram for *Cercidium* populations 1–5 with hybrids plotted as triangles. Key to symbols the same as in Fig. 3.

Table 4. Results of Artificial Crosses Attempted Between *Cercidium floridum, C. mcirophyllum* and Their Putative Hybrids. * +Female parent is listed first. ** Fruits and seeds eaten by rodents.

	Female parent		Male parent						
Taxa	Coll. #	HI	Coll. #	HI	% pollen stainability	# flowers pollinated	# fruits developed	# seeds produced	Percent germination
*C. floridum** × *C. microphyllum*	1020	4	1019	33	97.5	57	2	3	—**
C. floridum × *C. microphyllum*	5011	5	5012	33	93.0	35	9	17	81.3
C. floridum × hybrid	1020	4	1018	15	91.5	41	5	8	62.5
C. floridum × hybrid	5011	5	5010	18	74.0	16	1	1	0.0
Hybrid × *C. floridum*	5010	18	5011	5	71.5	58	3	4	50.0
Hybrid × *C. floridum*	1018	15	2011	2	96.5	23	4	6	—**
Hybrid × *C. floridum*	2010	19	2011	2	96.5	19	1	0	—
Hybrid × *C. microphyllum*	2010	19	1019	33	97.5	29	4	7	42.9
Hybrid × *C. microphyllum*	5010	18	5012	33	93.0	21	3	5	60.0
C. microphyllum × hybrid	1019	33	2010	19	85.5	24	2	3	33.0
C. microphyllum × hybrid	5012	33	5010	18	74.0	37	6	8	50.0
C. microphyllum × *C. floridum*	1019	33	2011	2	96.5	32	6	9	44.4
C. microphyllum × *C. floridum*	5031	32	5001	5	81.0	17	2	3	66.7

best attributed to the influence of *C. microphyllum* on *C. floridum* ssp. *floridum* as mediated through the hybrids. The differences in leaflet length might be attributed to habitat moisture differences between the allopatric and the sympatric populations of *C. floridum* ssp. *floridum,* which were not present in *C. microphyllum* populations. *Cercidium floridum* ssp. *floridum* exhibits an ecological preference for desert washes, whereas *C. microphyllum* tends to be found up out of the washes on the plains or hillsides (Carter 1974a; Jones 1978). The sympatric site (population 1) for *C. floridum* ssp. *floridum* is along the Colorado River and although no exact quantification was undertaken, these washes appear to be more mesic than the washes where the allopatric population of *C. floridum* ssp. *floridum* (population 2) was sampled.

Although there is no evidence of hybrid *Cercidium* progeny successfully outcompeting the parental species in the sympatric zone in California (Jones 1978), the differences in floral morphology described above suggest the remote possibility of introgression through the hybrids of *C. microphyllum* and *C. floridum* ssp. *floridum* (see also Siemens et al. 1994). This interpretation, although the antithesis of an earlier study (Jones 1978), is supported by the observation that the peak flowering of the hybrids shows greater synchronism with *C. floridum* spp. *floridum* than with *C. microphyllum.* This greater synchronism of flowering seems to be of greater importance than the fact that the hybrid and *C. floridum* ssp. *floridum* have distinct UV and visible floral patterns.

The sugars, amino acids, and other components present in the nectar of the hybrid appear to represent simply a summation of those present in the two parental species (Baker and Baker 1976). The hybrid resembles *C. microphyllum* in amino acid and phenolic content but presents novel proportions of the simple sugars, and the presence of maltose reveals the genetic contribution of *C. floridum* ssp. *floridum.* Further evidence of hybridization was demonstrated by Siemens et al. (1994) using two-dimensional flavonoid spot patterns of both species and hybrids.

Viable seed can be produced from interspecific crosses involving *C. floridum* ssp. *floridum* and *C. microphyllum* and from artificial backcrosses (Table 4). It is of interest to note that although there is little evidence of any influence of backcrossing on *C. microphyllum,* such backcross progeny are possible. In both parental species and the hybrids a large range of pollen stainability percentages was encountered. This may indicate an otherwise cryptic influence of introgression on *C. microphyllum,* as well as further evidence for backcrossing between *C. floridum* spp. *floridum* and the hybrids, because most of the lower pollen stainability counts were derived from sympatric individuals of the two parental species.

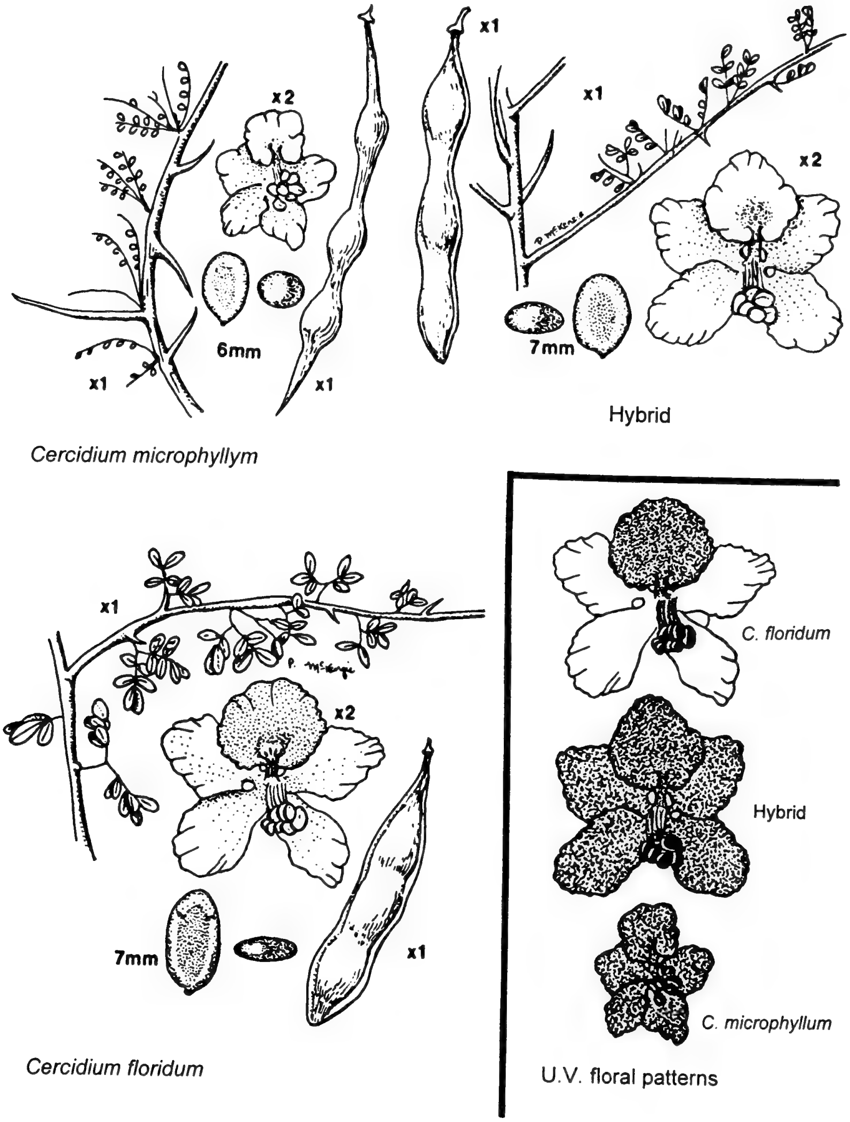

FIG. 5. Distinguishing characteristics of *Cercidium floridum* ssp. *floridum, C. microphyllum* and their hybrid.

Hybridization between *C. microphyllum* and *C. floridum* ssp. *floridum* either is an uncommon event or environmental pressures prevent the hybrids from becoming established in greater numbers. The average frequency of hybrids found in the various populations studied in the area of sympatry in California was only 3.2% (range 1.0–9.97%). This frequency of hybrids is particularly low given that these species are long-lived perennials living up to 400 years in age (Benson and Darrow 1944). Although the frequency of hybrids compares favorably with the frequency of "mistakes" made by pollinating bees in areas of sympatry (Jones 1978), it should be emphasized that in species with such slow replacement rates, minor differences in ecological requirements exhibited by these two species may result in significant selective pressures for the maintenance of certain genotypes in the population. As a result of such pressures, even fertile hybrid progeny would be eliminated from all but the rather extensive, naturally disturbed, floodplain, intermediate habitats. Most of the hybrids were found in this habitat. This may help explain the very cryptic evidence of introgression found in the population of *C. floridum* spp. *floridum* that was sympatric with *C. microphyllum.*

Although our work has substantially increased the knowledge about the number of known, naturally-occurring hybrid progeny between *C. floridum* spp. *floridum* and *C. microphyllum,* it appears that hybridization is limited to some peripheral sympatric zones; and as such is probably of little evolutionary consequence for these species. However, it would be of interest to thoroughly examine other zones of sympatry to see if hybridization is occurring. For example, the specimen collected by Kamb (*Kamb 2014*) and cited by Carter (1974a) as a hybrid from Sonora, Mexico, would serve as a start for more detailed studies on the extent over the vast area of sympatry of these two species. A collection trip in 1997 revealed another possible area of hybridization, between Quartzite, AZ and Blythe, CA where individuals of both species were simultaneously in bloom. Isozymic studies of the two parental species and their hybrids are currently underway and we anticipate the agreement of these data with our morphometric analyses (Mary Sampson unpublished). Additionally, our work complements a monographic study of *Cercidium* and *Parkinsonia* completed by Dr. Julie Hawkins that suggests the possibility of widespread hybridization. At the present time, we agree with Carter (1974a) and Hawkins (1996) that the species are well-delimited entities and should be recognized as separate taxa.

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THE ROLES OF SOIL TYPE AND SHADE INTOLERANCE IN LIMITING THE DISTRIBUTION OF THE EDAPHIC ENDEMIC *CHORIZANTHE PUNGENS* VAR. *HARTWEGIANA* (POLYGONACEAE)

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ABSTRACT

Understanding the ecological factors that cause narrow geographic range and habitat specificity is essential for the conservation of rare species of edaphic endemic plants. Here we investigated the relative roles of soil and light in limiting the distribution of *Chorizanthe pungens* Benth. var. *hartwegiana* Rev. & Hardham (Polygonaceae), an annual plant endemic to open patches of low nutrient soils in the sandhills habitat of the Santa Cruz Mountains, Central Coastal California. Seedlings were grown in a controlled pot experiment under three light conditions and five soil treatments. The growth, survival, and reproduction of individual plants were compared.

Plants were least successful when grown on their native low nutrient soil, suggesting that soil type is not a limiting factor in the taxon's distribution. However, when grown under high shade, survivorship, growth, and reproduction of individuals were low. This suggests that shade intolerance is the major cause of this taxon's restriction to open, sandy areas. Thus management to preserve this federally endangered species should include artificial or natural disturbances to prevent populations from being extirpated due to encroachment of taller, shade-producing species.

The geographic distributions of plant species are determined by many factors. While history, geographic barriers, and isolation all influence the distribution of species, the ultimate determinant of where a taxon can be found is its inherited tolerance to environmental factors (Kruckeberg and Rabinowitz 1985). Climatic, biotic, and edaphic characteristics of a given environment determine the constraints or opportunities an individual plant faces, depending on its genetically determined physiologic capabilities (Mason 1946; Baskin and Baskin 1988). The question of what limits plant distributions is important both to biogeography and in assessing the threats to populations of rare species.

Among the most striking of geographic factors affecting plant distribution are unique edaphic conditions, including unusual bedrock outcrops (e.g., serpentinite), nutrient poor soils, and varying water regimes (e.g., vernal pools). Areas with these unusual conditions, which are considered inhospitable to the growth and reproduction of most plant species, are often inhabited by unique assemblages of specialized, morphologically distinct plant taxa. Due to their narrow habitat specificities and small geographic ranges, these endemic taxa are often among the rarest of plants (Rabinowitz 1981). Furthermore, small population sizes, limited geographic distributions, and generally poor competitive abilities render edaphic endemic plants highly vulnerable to extinction due to stochastic events, habitat degradation, and invasion by weedy species (Harper 1981; Kruckeberg and Rabinowitz 1985; Janzen 1986; Falk 1991; Schemske et al. 1994). Here we report the results of an experiment designed to determine the relative roles of soil and light in limiting the distribution of a rare taxon endemic to the Zayante soils of Central Coastal California.

Recent studies on edaphic endemic plants have attempted to determine the specific factors that allow them to inhabit their typically harsh habitats, as well as the factors that confine them to those habitats (Latham 1983; Baskin and Baskin 1988; Buchele et al. 1989; Snyder et al. 1994). Three general hypotheses have been advanced to explain the habitat restriction of edaphic endemic plants. First, edaphic endemics may have specific chemical, physical, or biological requirements that are met only on a particular substratum (Walker 1954). Second, edaphic endemics may tolerate, though not require, the inimical conditions where they typically occur, while they are excluded from more hospitable habitat due to competitive interactions with other species. In particular, these often diminutive species may be limited to open communities where they are unshaded by taller, more competitive species that thrive in adjacent habitats (Baskin and Baskin 1988; Collins et al. 1989; Ware and Pinion 1990). Finally, edaphic endemics may be highly susceptible to soil pathogens found in nutrient-rich soils, and thus limited to low productivity areas in

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which their exposure to pathogens is decreased (Tadros 1957; Latham 1983). In addition to these three ecological factors (soil requirements, shade intolerance, and susceptibility to soil pathogens) low genetic diversity has been suggested as the root cause of the poor competitive abilities hypothesized for edaphic endemics (Stebbins 1942).

Little evidence supports the hypothesis that edaphic endemics are restricted to their habitats due to specific chemical, physical, or biological requirements. Most edaphic endemic plants can be cultivated more successfully in soils which do not contain the unique edaphic material in which they normally grow (Walker 1954; Kruckeberg 1954; Hart 1980; Ware and Pinion 1990). In studies of edaphic endemic plants, many species were found to have relatively high levels of genetic variation, suggesting that a lack of genetic diversity is also unlikely to be a common factor restricting many edaphic endemic plants to edaphically inhospitable and sparsely vegetated areas (Baskin and Baskin 1988; Collins et al. 1989; Menges 1992).

Although previous work has implicated light competition as a common limitation of edaphic endemics, the relative importance of competition for light and the influence of various soil factors, including competition for nutrients and the limiting effects of soil pathogens, has not been thoroughly evaluated for any single species. In this study, we chose to examine the composite effects of soil types in combination with varying shading levels on a highly restricted edaphic endemic. To compare the effects of different limiting factors and to understand the importance of interaction among these factors, we grew individuals of the federally endangered edaphic endemic, *Chorizanthe pungens* Benth. var. *hartwegiana* Rev. & Hardham (Polygonaceae) (the Ben Lomond Spineflower) in a controlled growth experiment in which we varied shade levels and soil types. By measuring growth, survivorship, and reproduction of this rare annual plant, we were able to evaluate the combined importance of shading and soil factors in limiting performance of this highly restricted species, thus providing a functional understanding of its distributional limits.

We chose a controlled growth experiment as a complementary approach to a previous study examining the demographic performance of *C. pungens* var. *hartwegiana* through a reciprocal transplant experiment in the field (J. Kluse and D. Doak personal communication). Experimental manipulation of environmental conditions allowed us to examine the specific effects of soil and shade while controlling for other factors. We note at the onset that we did not attempt to control or measure individual aspects of soils. Instead, given that each soil type is very distinct, our goal was to evaluate the multiple effects of soil characteristics in their entirety.

METHODS AND MATERIALS

The study species. Chorizanthe pungens var. *hartwegiana* is a diminutive annual plant found on many of the 'islands' of sandhills soils of the Santa Cruz Mountains, including the Bonny Doon Ecological Reserve, located at 37°03′N latitude, 122°08′W longitude. The taxon is further restricted to open, sandy, and frequently disturbed areas of this soil type. Due to its limited population size, narrow geographic range, and habitat degradation, *C. pungens* var. *hartwegiana* was listed as federally endangered in February of 1994 (Federal Register 1994). Though not noted as a separate species in The Jepson Manual, both the United States Fish and Wildlife Service and the California Native Plant Society recognize *C. pungens* var. *hartwegiana* as distinct.

The population biology of *C. pungens* var. *hartwegiana* previously has not been described in a peer-reviewed publication. Although little is known about the phenology of this rare plant, the basic seasonal pattern is similar to that of other winter-spring annuals. Seeds germinate in late fall after the first substantial rain in this region. The plants mature through the wet winter, then bolt and produce branches, flower in April and May, and die soon after seed production in June.

To date, researchers have considered habitat destruction to be the predominant threat to the taxon's existence (Morgan and Marangio 1987). Sand quarrying has already greatly reduced population numbers, and at least half of the sandhills habitat currently occupied by *C. pungens* var. *hartwegiana* is on property owned by sand and gravel companies with plans to expand mining operations. Residential development on smaller parcels also has eliminated populations and fragmented the remaining habitat (Federal Register 1994). The reduction in habitat area and the resulting decrease in population size greatly increases the likelihood of extinction due to environmental and demographic stochasticity (Falk 1991). Changes in the disturbance regimes (e.g., fire suppression) appear to be further reducing populations of *C. pungens* var. *hartwegiana* by allowing for the encroachment of larger, more competitive species such as *Arctostaphylos silvicola* Jepson & Wiesl. (personal observation).

The study site. The vegetation of the Santa Cruz Mountains of the Central California Coast is comprised of two main plant communities: Redwood Forest and Hardwood Forest-Oak Woodland (Barbour and Major 1977). Interspersed within these two vegetation types are small islands of deep, coarse sand derived from the highly erodible Zayante soil series, which were formed from weathered marine sediment of Santa Margarita sandstone (Soil Conservation Survey 1980). Over fifty separate islands, comprising approximately 8000 acres, of sandhills habitat have been mapped in the Santa Cruz Mountains (Marangio 1985). Managed by the

California Department of Fish and Game, the Bonny Doon Ecological Reserve (BDER) contains approximately 120 acres of sandhills habitat set aside for preservation and ecological research.

The well-drained, low nutrient soil of the sandhills habitats supports the sandhills plant communities—unique assemblages of species found primarily or exclusively on these soils (Marangio 1985). Analogous to the distinct communities found on serpentinite soil, the sandhills flora consists of many diminutive annuals and shrub species, several of which are state or federally listed (Morgan and Marangio 1987).

Three distinct types of sandhills vegetation are found on the BDER: maritime coast range ponderosa pine forest, the endemic *Arctostaphylos silvicola* (manzanita) mixed chaparral, and sparse assemblages of low-growing herbaceous species populating the open, sandy areas. *Chorizanthe pungens* var. *hartwegiana* occur almost exclusively in this last community type.

The soils of the BDER are comprised mainly of the Zayante coarse sands derived from weathered marine sediment of Santa Margarita sandstone. However, the soil within each of the three plant communities is distinct in color, content, and humus level. In open areas of the reserve, the sands have remained relatively free of organic addition. However, in the manzanita and ponderosa pine areas, organic matter from the overstory has created sandy loams. The redwood soil is composed of slightly acidic loams with high levels of organic matter characteristic of the Lompico-Felton complex. Similarly, the oak soil is composed of sandy loams of the Ben Lomond-Felton complex with a subsoil of clay loams (Soil Conservation Survey 1980). The upper layers of both soils are rich with decaying redwood and oak duff, respectively.

Experimental design. To determine the relative effects of edaphic factors and light levels on *C. pungens* var. *hartwegiana,* we conducted a controlled growth experiment at the University of California, Santa Cruz Arboretum. For this experiment, the plants were grown in five soil types. We chose to test performance in the three most predominant soils of the sandhills habitat (pure sand, manzanita, and pine) as well as the two most widespread soils bordering the BDER (oak and redwood forest). On 22 January 1994, we collected approximately 57 liters of each soil type from three sites within a single 10 × 10 m area, homogenizing it before use. The redwood soil was collected in a grove 3 km from the reserve's northern border and the oak soil from an oak woodland 5 km east of the reserve. The sand, pine, and manzanita soils were collected within the reserve. To collect all soils, we cleared away any leaves, duff, or herbaceous ground cover and then removed the top 10 cm of soil.

On 25 January 1994 we collected *C. pungens* var. *hartwegiana* seedlings from the open, sandy areas of the BDER by removing blocks of sand containing 10 to 30 seedlings each. The plants were transported in plastic bags and transplanted into standard 4 liter (15.2 cm rim diameter) pots within 4 h after removal from the reserve.

We planted 5 seedlings in each of 12 pots of each soil type for a total of 300 individuals. Five seedlings were planted in a circle within each pot such that each individual was 6 cm from the nearest neighbor and 3 cm from the edge of the pot. Plants for each pot were taken from several of the collected blocks of sand in order to mix the seedling sources. Extra plants were planted in separate pots for later use as replacements.

The pots were placed in two protective wire cages in an unshaded field at the University of California at Santa Cruz Arboretum. On 1 February 1994, shade treatments were established by suspending neutral shade cloth 30 cm above the top of the pots. Two different densities of shade cloth were used to create the low and high shade treatments. Each cage contained one block of each of the three shade treatments (high, low, and no shade) and two pots of each soil type were placed under each shade treatment. Both the placement of the pots within each shade treatment and the placement of the shade treatments within each cage were randomized. Each plant was assigned a number so that we could record and track the fate of each of the 300 plants individually (20 plants per treatment combination).

In order to prevent water from being a limiting factor in growth, plants were kept moist by watering with tap water whenever any one pot showed significant drying.

In a second transplant on 3 February 1994, one week after initial transplanting, we replaced any seedlings which were dead or dying. Five days following the second transplant initial size measurements of all 300 seedlings were taken. For each plant, we recorded the length of the longest leaf, a measure shown to have a strong positive correlation with total aboveground biomass in this taxon (Kluse 1994). Intermediate measurements were taken on 12 February, 13 March, and 11 April 1994. We recorded deaths and observations of plants infected by an unidentified rust common among *C. pungens* var. *hartwegiana* at the BDER.

Plants in our experiment flowered between 21 April (78 days after transplant) and 12 June (118 days after transplant). As each plant flowered, we recorded a final measurement of longest leaf length and then harvested it by cutting the plant at ground level, taking care not to disturb the other plants in the pot. Plants were dried to a constant mass then weighed to obtain final aboveground biomass.

Since the closed cages in our experiment prevented natural pollinator visitation, we could not measure seed production directly. However, *Chorizanthe* spp. are known to produce a single, one-seeded flower within each involucre (Hickman

1993). Thus, we counted the number of involucres produced by each individual and used this as our measure of reproductive output.

In order to compare the light levels under our shade treatments with those in the field, we measured photosynthetically active radiation (400–700 nm) using an LAI-2000 Plant Canopy Analyzer. Photon flux measurements above and below each canopy type were considered in our experiment. These values were compared to percent transmittance measurements in our three shade treatments.

To test for significant soil or shade effects on growth, we performed a 2-way analysis of variance (ANOVA) on longest leaf length measurements recorded throughout the experiment. Similarly, we used 2-way ANOVA to test for soil and shade effects on the reproduction and final biomass of *C. pungens* var. *hartwegiana* using (number of involucres)^2 and ln (final mass) as dependent variables (transformations to achieve normality). Due to the significant effect of initial seedling size on final biomass ($P = 0.02$), we performed all subsequent analyses of final biomass as ANCOVAs, using initial leaf length measurements as a covariate. Pairwise post-hoc comparisons (Tukey-Kramer) were then conducted to determine significant differences between means of final biomass and reproduction in the various shade and soil treatments. Finally, we used G-tests to test for treatment effects on survivorship to final harvest.

RESULTS

Light measurements. Percent light transmittance values for sand, manzanita, pine, redwood, and oak habitats were 99.5%, 26.2%, 59.4%, 1.6%, and 3.2% respectively (SD = 1.2, 16.4, 30.2, 0.4, and 1.8, respectively). The no shade treatment allowed complete light transmittance, the low shade 38.6% transmittance, and the high shade 19.7% (SD = 2.4 and 0.5, respectively).

Morphological observations. Throughout the growth period, substantial variation in plant morphology and time to flowering among the different treatments was observed. Plants in full sun grew prostrate with no basal stem and showed much secondary branching. Their leaves were short, wide, had crinkled edges and turned deep orange to red with age. Low shade plants also were prostrate, yet had fleshier, smoother (lacking crinkled edges) leaves which did not redden with age. Low shade plants showed less secondary branching. The high shade conditions produced etiolated plants with highly elongated basal stems. These plants lacked the three-branched pattern typical of the species' natural growth pattern. Their leaves were elongated, thin, fleshy, and very light in color.

Although there was overlap among flowering times in all treatments, plants that received more sunlight flowered earlier. Plants grown in full sun flowered first, as early as 21 April, 78 days after initial transplantation. The low shade plants began to flower a week later. However, most of the high shade plants did not flower until the last week of harvest.

Survivorship. Shading level had a significant effect on the survival ($G = 30.6$, 2 df, $P < 0.005$) with 48% of the plants surviving under full sun, 55% under low shade, and 20% under high shade conditions (Fig. 1a). In contrast, soil type did not significantly affect survival ($G = 6.6$, 4 df, $P = 0.127$), but certain treatment combinations of soil and shade yielded incongruent results. For example, plants in oak soil under high shade conditions had the lowest survivorship (10%), while those in oak soil in low shade had one of the highest survival rates overall (65%; Fig. 1c). While this pattern suggests a possible interaction between soil and shade treatments, there was no significant interaction effect ($G = 11$, 8 df, $P = 0.202$). In addition, high mortality of plants in oak soil under high shade resulted in a small sample size (i.e., two plants) for this treatment, thus caution must be taken in interpreting these data.

Reproduction. Shade had a highly significant effect on the number of flowers produced ($P < 0.001$; Fig. 2a). The low shade plants averaged significantly higher flower output than both high shade and no shade plants ($P = 0.001$ and $P = 0.049$, respectively). While plants grown under no shade produced a greater average number of flowers than the high shade plants, this result was not significant.

There was no significant effect of soil on flower output ($P = 0.109$; Fig. 2b) when the interaction effect between soil and shade is included in the analysis. However, when the interaction effect, which was not significant, was removed from the model, there was a significant effect of soil on flower output ($P = 0.012$). Plants in oak soil produced dramatically more flowers than those in any other treatments while plants in sand produced the fewest flowers; however pairwise comparisons showed no significant difference between flower output in any of the soil types.

In all five soil types, low shade plants generated the greatest number of flowers, high shade plants the fewest, and no shade plants an intermediate number (Fig. 2c), paralleling the result that shade and soil did not significantly interact in their effects on reproduction.

Final biomass. Analysis of the ln(mass) by ANCOVA, using initial leaf length of transplanted seedlings as a covariate, showed that final mass was affected by shade treatment ($P = 0.036$, Fig. 3a). Plants in the low shade accumulated the greatest mass while no shade plants reached moderate masses and plants in the high shade had the lowest masses. However, the only significant difference by pairwise comparison was between the low shade and the high shade ($P = 0.027$).

Final biomass also was strongly affected by soil

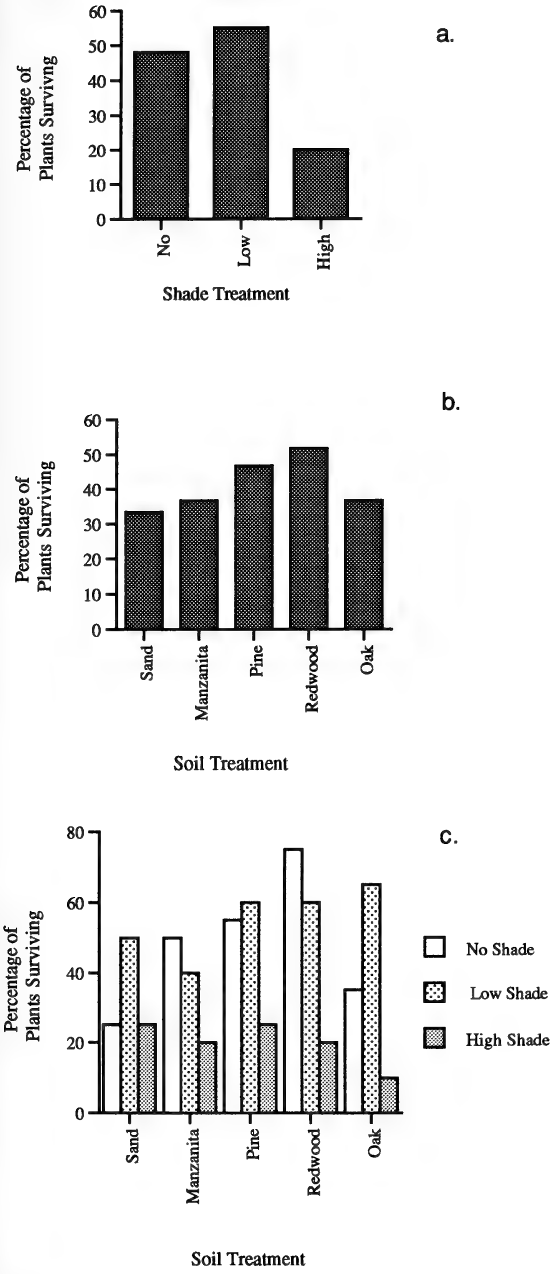

FIG. 1. Survivorship of plants: a) in the three shade treatments; b) in the five soil treatments; c) grown in the 15 different soil and shade treatment combinations. All values plotted are the percentages of *C. pungens* var. *hartwegiana* in each treatment which survived until harvest.

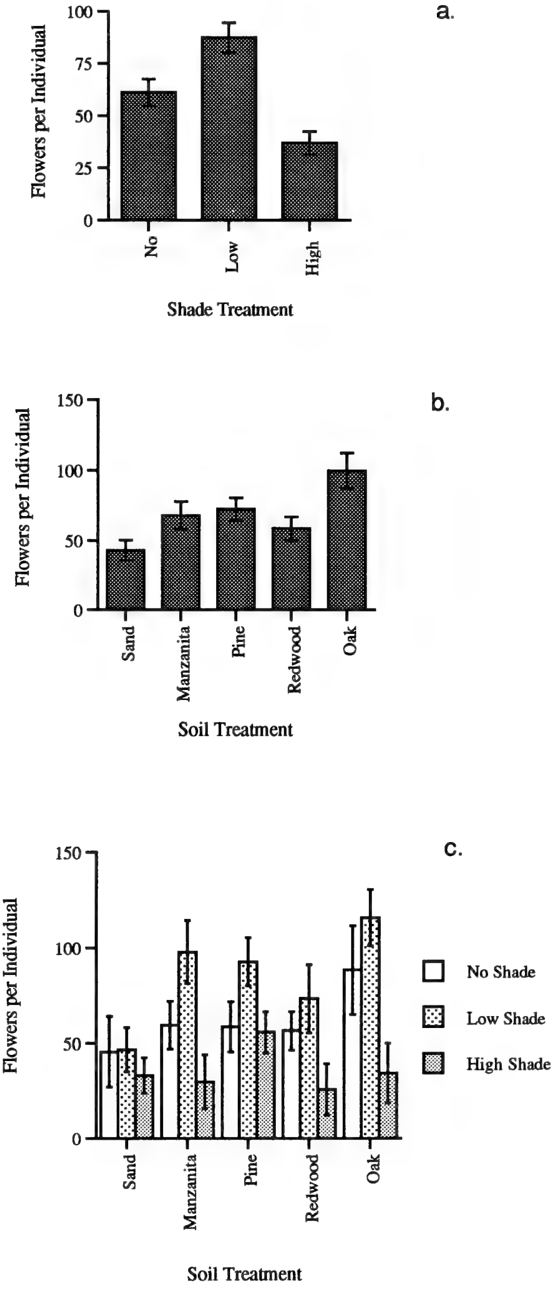

FIG. 2. Mean number of flowers per plant: a) in the three shade treatments; b) in the five soil treatments; c) in the 15 different soil and shade combinations. All values plotted are the mean number of flowers produced by each plant ± one standard error. Sample sizes ranged from two to fifteen among the different treatment combinations.

type ($P = 0.004$, Fig. 3b). Plants grown in the non-sandhill soils had the greatest final biomass with the biomass for plants grown in pine and manzanita soils intermediate, and plants in sand soil remaining, on average, very small. Both pine and redwood soils yielded plants with significantly higher biomass than sand soil ($P = 0.008$ and $P = 0.015$, respectively). Although plants grown in oak soil attained the highest average mass, pairwise comparisons showed no significant differences in biomass between oak and the other soil treatments. This is most likely due to the low sample size which resulted from high mortality in oak soil.

There was no significant interaction effect be-

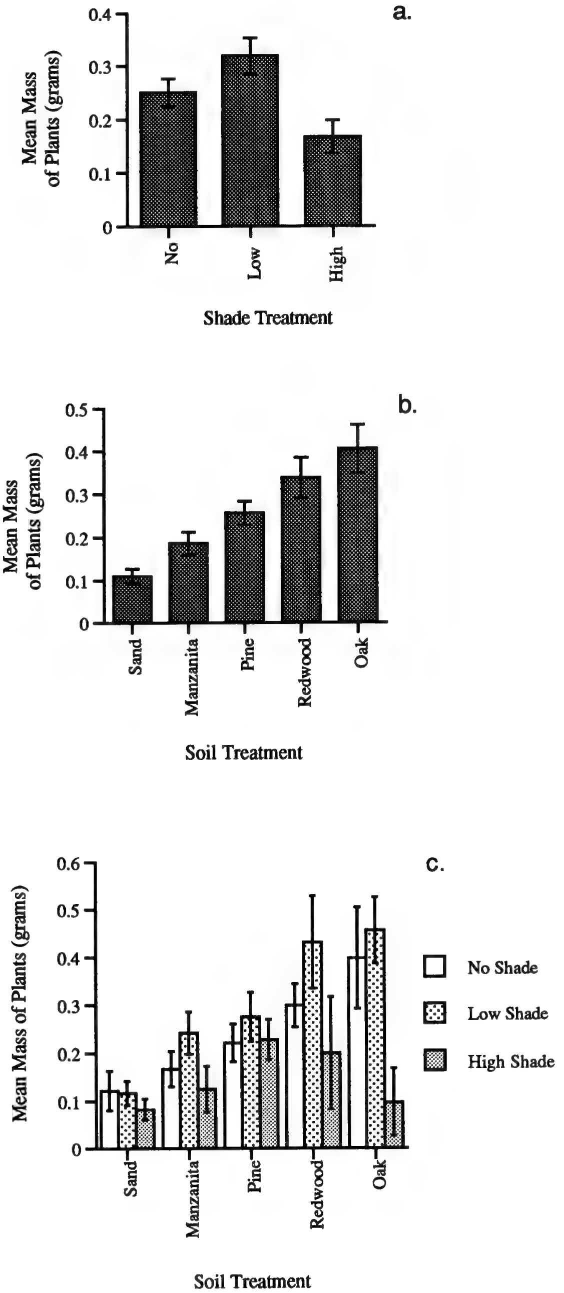

FIG. 3. Mean final aboveground biomass of *C. pungens* var. *hartwegiana:* a) in the three shade treatments; b) in the five soil treatments; c) in the 15 different soil and shade treatment combinations. Values plotted are the mean dry weights of plants ± one standard error. Sample sizes ranged from two to fifteen among the different treatment combinations.

tween soil and shade treatments on biomass. However, when grown under low shade, plants in oak soil averaged the largest biomass; yet, when grown under high shade, plants in oak soil had the second to smallest final biomass (Fig. 3c).

Table 1 shows the percentage of the variance (measured as percentage of total sum of squares from a two way ANOVA) in the longest leaf length explained by the variables soil, shade, and the interaction of soil and shade at each of the three intermediate measurements times in our study. By the eleventh day of the experiment, the interaction effect between soil and shade treatment accounted for the greatest amount of variance not due to error (16%). Although they accounted for a small amount of variance, the separate effects of shade (7.8%) and soil (5.5%) were statistically significant. By the forty-fifth day of the experiment, the amount of variance caused by the interaction effect had decreased to 10%, while the influence of both shade (8.7%) and soil (7.6%) had increased. This trend continued until the final measurement 113 days after transplanting, when the effect of soil became the most prominent cause of variance (18.8%), and shade had increased slightly, to 8.9%, leaving the interaction effect to account for only 2% of the variance.

DISCUSSION

Ecological implications. Our results implicate shade as a primary factor in limiting the distribution of *C. pungens* var. *hartwegiana.* Soil treatment also had significant effects on performance but, because atypical soils were most conducive to growth, survival, and reproduction, soil per se cannot be viewed as a limiting factor in the distribution of *C. pungens* var. *hartwegiana.* Instead, results showing that high shade levels correlated with relatively low survivorship, reproduction, and final biomass implicate shade intolerance as the primary cause of the species' restriction to open sandy areas.

The relative importance of the shade regime, soil treatment, and their interaction upon individual performance varied throughout the growing season. We note here that while the initial sample size was 100 plants for each shade treatment and 60 plants for each soil type, only 20 plants comprise each soil/shade treatment combination. Therefore, caution should be used when considering results of interaction tests. The interaction between soil and shade diminished during the course of the study. Conversely, the variation in plant size accounted for by both the shade and soil treatments increased throughout the experiment, with the soil effect more than tripling by the last measurement (Table 1). However, changes in the percentage of the variance explained by the soil, shade, and interaction effect may be an artifact of the change in plant growth form that occurred throughout the experiment. From the time that the plants bolted, additional growth in the form of increased branch length, and subsequently flowers, was observed, while leaf length remained constant.

Our results show that the distribution of *C. pungens* var. *hartwegiana* is not restricted by soil char-

TABLE 1. PERCENTAGE OF VARIANCE IN SIZE OF THE PLANTS EXPLAINED BY SOIL, SHADE, AND THEIR INTERACTION EFFECT AT THREE TIME INTERVALS DURING THE EXPERIMENT. Variance is measurement of the percentage of the total sum of squares accounted for by each independent variable in a two-way ANOVA on the longest leaf length, a measure of plant size. Both of the main effects and the interaction effect were significant at each sampling date ($p<0.05$).

	Time elapsed since transplant (percent)		
Source of variance	Day 11 (3/13/94)	Day 45 (4/21/94)	Day 113 (5/20/94)
Soil	5.5	7.6	18.8
Shade	7.8	8.7	8.9
Soil by Shade	16.2	10.1	2.6
Interaction Error	70.5	73.7	69.7

acteristics. In fact, all of our measures of performance were highest for individuals grown in the four soils where *C. pungens* var. *hartwegiana* does not naturally occur. The higher mass and flower number of plants in the manzanita, oak, pine, and redwood soils is perhaps due to the comparatively higher organic contents and greater water retention capacities of these soils relative to the sand soil. Many previous studies have used the addition of specific nutrients to controlled soil conditions to test the performance of edaphic endemics (Kruckeberg 1954; Baskin and Baskin 1988). However, we chose to use actual soils from the habitat adjacent to the naturally occurring populations in order to infer plant performance in these habitats. The success of *C. pungens* var. *hartwegiana* in the four test soils does not support the hypothesis that chemical, physical, or biological requirements of this taxon are met only on the sandy soil.

Although the soils with higher organic content, which have an inherently greater water holding capacity, significantly increased final biomass (Fig. 3b), growth in these soils did not result in strong or consistent increases in reproduction over the plants grown in the sand soil (Fig. 2b). Instead, only shade level had a significant effect on flower number through its effect on plant morphology. Plants grown in low shade and no shade treatments had multiple branches, and this translated into more inflorescences. *Chorizanthe pungens* var. *hartwegiana* growing naturally at the Bonny Doon Ecological Reserve were morphologically similar to those in the no shade treatment (personal observation).

Plants grown under the low shade treatment did consistently better in all three measurements of performance (biomass, survivorship, and reproduction) than plants grown in the no shade control treatment, which closely resembled natural light conditions. Low shade probably decreased water loss from evaporation and evapotranspiration while the corresponding decrease in light did not significantly reduce plant performance. In contrast, plants in the high shade showed drastically reduced success compared with individuals in the full sun treatments as high shade conditions caused etiolation, poor survival (Fig. 1a), low flower output (Fig. 2a), and small biomass (Fig. 3a).

These results support our hypothesis that *C. pungens* var. *hartwegiana* is shade intolerant. Increased growth, survival and fecundity of plants in the manzanita, oak, pine, and redwood soils, indicates that they are restricted from these areas because they are unable to compete for light with robust, common species that naturally occur on these soils. This helps to explain the distribution of *C. pungens* var. *hartwegiana* in the sandhills communities of the Bonny Doon Ecological Reserve, where the taxon is restricted to otherwise unvegetated, pure sand soils.

Management implications. The combination of habitat specificity and narrow geographic range of *C. pungens* var. *hartwegiana* renders the species vulnerable to extinction from both habitat degradation and the encroachment of other more competitive species. Habitat destruction by sand quarrying and residential development have been considered the major threats to the persistence of populations. Our results indicate additional threats to species' survival even within protected areas. In particular, shade intolerance increases vulnerability to extinction due to chaparral community succession and the encroachment of alien species. The taxon's inability to compete for light could explain its restriction to monospecific stands or open areas where it grows in association with other diminutive annual plants such as *Navarretia hamata* E. Greene.

At the Bonny Doon Ecological Reserve, the distribution of *C. pungens* var. *hartwegiana* currently is limited to open, physically disturbed areas, such as trails and old roads, where chaparral species have not become established. Such open habitats are transitory and disappear in the absence of disturbance by fire, wind, or sand movement. Historically, the open areas of the sandhills were probably maintained by frequent fires (Potts 1993). However, fire suppression in the Santa Cruz Mountains may have allowed for the spread of chaparral species such as *Eriodictyon californicum* (Hook & Arn.) Torrey and *Arctostaphylos silvicola,* a sandhills specialist species, into formerly open, unshaded areas. Even in areas with partial shrub cover, *C. pungens* var. *hartwegiana* populations are generally sparse. We speculate that, in the absence of fire or other physical disturbance, succession will result in widespread extirpation of *C. pungens* var. *hartwegiana.*

The invasion of alien weedy species poses a similar threat. These exotics not only create shade, but could also alter soil composition through nutrient addition (Vitousek 1990; Janzen 1986). Huenneke et al. (1990) found that increasing nutrient availability through fertilizing classically low-nutrient serpentinite soils resulted in increased biomass of the serpentinite endemic vegetation. By the second year, however, this addition of nutrients had allowed for the invasion and eventual dominance of non-native vegetation.

As native or exotic plants invade the pure sand areas of the sandhills, the deposition of nutrients can further facilitate the establishment of shade-producing species that were previously excluded due to low nutrient availability. The current invasion of smaller grasses (e.g., *Vulpia myuros* (L.) C. Gmelin) on the open sand areas of the Bonny Doon Ecological Reserve may not outcompete *C. pungens* var. *hartwegiana* for light; however, the cumulative alteration of the soil by this denser vegetation could facilitate the invasion of larger, shade-producing species such as *Genista monspessulanus* (L.) L. Johnson. Encroachment by invasive species is especially threatening to the sandhills because of their small size and island-like geography. In particular, the large edge to area ratio of small habitat fragments increases their susceptibility to invasion by aggressive species in surrounding habitats (Schierenbeck 1995).

Given the shade intolerance of *C. pungens* var. *hartwegiana* and current threats of invasion, we suggest a management strategy aimed at the maintenance of unvegetated, open areas in the sandhills through controlled burning and intentional mechanical disturbance. Because little is known about the fire ecology of *C. pungens* var. *hartwegiana,* small scale field tests and seed viability analyses should be conducted prior to implementing controlled burn management. However, due to its close association with chaparral vegetation and the frequent fire history of the sandhills prior to suppression, it is likely that the taxon is fire tolerant.

Alternatively, a mechanical method of disturbance (e.g., bulldozing or hand clearing) could maintain open, unshaded areas required by *C. pungens* var. *hartwegiana.* Indeed, the largest populations of *C. pungens* var. *hartwegiana* currently at the Bonny Doon Ecological Reserve exist on old road cuts and human trails. However, disturbance is a double-edged sword, as it often allows for the invasion of weedy species (Parker et al. 1993; Schierenbeck 1995). Local invasive exotics such as *G. monspessulanus,* and *V. myuros* are often found along the roads that border the reserve, apparently thriving because of disturbance. Future disturbance within the reserve could allow their spread into *C. pungens* var. *hartwegiana* habitat. To insure the viability of a disturbance-dependent plant, it is important to match the intensity and timing of novel disturbances with the natural disturbance regime to which the species is adapted (Pavlovik 1994). Therefore, we recommend further study on the responses of *C. pungens* var. *hartwegiana* to new disturbances prior to the widespread implementation of mechanical biomass removal or controlled burning.

In summary, the results of our study strongly suggest that a laissez faire approach to the conservation of the sandhills flora is not sufficient. Establishing reserves free of habitat conversion and destruction is the first step toward conservation of *C. pungens* var. *hartwegiana.* However, it is also essential to prevent the additional alterations in habitat caused by native chaparral succession in the absence of fire or alien species invasion from surrounding areas. Fortunately, the implementation of such management practices is feasible due to the small size of the sandhills habitats. Active conservation efforts aimed at controlling encroaching vegetation are likely to protect other similarly adapted endemics of the sandhills community in addition to preserving the remaining populations of *C. pungens* var. *hartwegiana.*

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ATRIPLEX LONGITRICHOMA (CHENOPODIACEAE), A NEW SPECIES FROM SOUTHWESTERN NEVADA AND EAST-CENTRAL CALIFORNIA

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ABSTRACT

Atriplex longitrichoma, a newly reported annual species from southwestern Nevada, and east-central California is described and illustrated. It is most abundant in Pahrump Valley, NV, in abandoned agricultural fields, in roadside borrow pits; and, in favorable years, occurs in contiguous, undisturbed sites. It is a tetraploid species, apparently most closely related to *Atriplex hillmanii* (Jones) Standley.

INTRODUCTION

In Pahrump Valley, Nye Co., NV and in neighboring Stewart Valley, Inyo Co., CA, there are several populations of a previously undescribed annual species: *Atriplex longitrichoma* sp. nov. It is most abundant within and around the community of Pahrump, NV, in abandoned cultivated areas, alongside roadways, and in other disturbed sites. In favorable years, it extends into neighboring, undisturbed, desert areas. In some localities, *A. longitrichoma* occurs as a near monoculture, in others it grows in association with several other species.

Atriplex longitrichoma Stutz, Chu, & Sanderson sp. nov. (Fig. 1)—TYPE: USA, Nevada: Nye Co., W side of Pahrump, T20S R53E S14, abundant. *S. Sanderson & G. L. Chu 95303* 26 May 1990 (holotype, BRY; isotypes, CAS, DAV, GH, MO, RENO, RSA, UC, UCR).

Herba annua. Caulis erectus, 10–20 cm altus, sparsim ramosus; rami basales plerumque decumbentes, 10–30 cm longi, teretes, leviter flexuosi, trichomatibus clavatis elongatis dense tectus. Folia sessilia vel inferiora aliquando petiolata; lamina anguste elliptica usque ovato-elliptica, 25–35 mm longa, 10–13 mm lata, integra, acuminato apice, cuneato base anguste, utrinque dense furfurascentes trichomatibus elongatis fragilibus, subtus cinereo-viridia, supra viridia; anatomia foliaris Kranz-typi. Staminati et pistillati flores in glomerulis mixti, axillares; perianthium floris staminalis hemisphaericum vel infundibuliforme, 1.5–2.0 mm diam., plerumque 5-partitum, apicibus segmentorum incurvatibus; antherae oblongae, ca. 0.6 mm longae, saepe purpureo-rubellae, leniter exsertae sub anthesi; filamenti filiformes, compressi, ca. 1.5 mm longi; bracteolae floris pistillati marginibus connatae infra medium; stigmata 2, filiformia, ca. 2 mm longa; stylus minus quam 1 mm, inconspicuus. Bracteae fructiferae oblongae usque late ovatae, 5–6 mm longae, 5–6 mm latae, trichomatibus elongatis fragilibus dense tectus, stipite brevi, basibus et areis centralibus induratis, marginibus dentibus lanceolatis irregularibus leviter curvis, utrinque appendicibus numerosis mollo-spinescentibus 2–3 mm longis ferentibus. Utriculus ovatus, 2–2.5 mm latus, pericarpio membranaceo. Semen flavo-brunneolum, perispermate duro; radicula supera.

Annual herb. Stem erect, 10–20 cm tall, sparsely branched, lower branches 10–30 cm long, usually decumbent, frequently longer than stem, terete, slightly flexuous, densely covered with clavate, single-cell, elongate trichomes (Figs. 2, 3). Leaves sessile or lower leaves sometimes petiolate; leaf blade narrowly elliptical to ovate-elliptical, 25–35 mm long, 10–13 mm wide, apex acuminate, base narrowly-cuneate, entire, becoming densely furfuraceous on both surfaces with elongate, fragile trichomes, gray-green abaxially, green adaxially; Kranz-type anatomy. Flowers in mixed axillary glomerules; male flowers most abundant in glomerules on the upper branchlets, perianth half-globose or funnel-shaped, 1.5–2.0 mm in diam., usually 5-parted, segment apices incurved, stamens as many as perianth segments, anthers oblong, ca. 0.6 mm long, frequently reddish purple, slightly exserted when flowering, filaments filiform, compressed, ca. 1.5 mm long; female flowers present in mixed glomerules throughout all branches, margin of bractlets united below the middle, stigmas 2, filiform, ca. 2 mm long, style very short, less than 1 mm. Fruiting bracts oblong to broad-ovate, 5–6 mm long with short stalk, 5–6 mm wide, center part and base indurate, with several soft-spiny 2–3 mm long

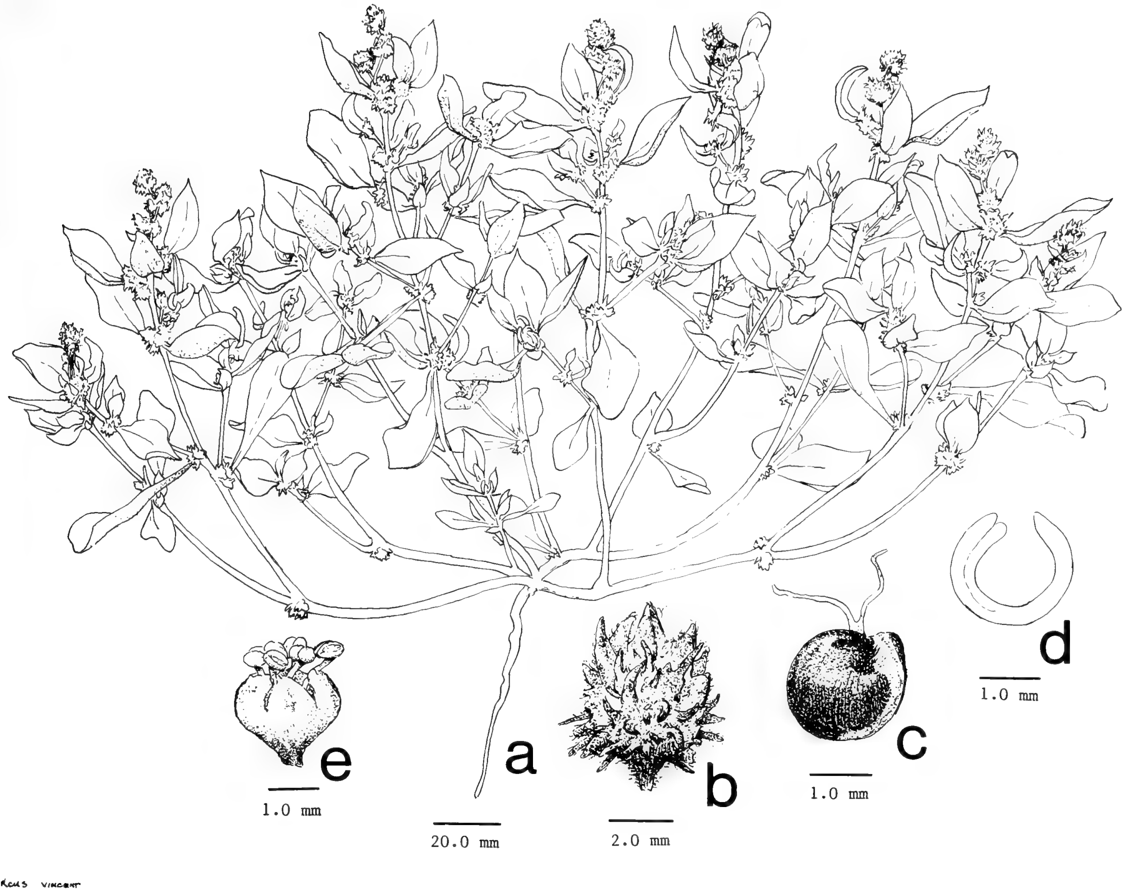


FIG. 1. *Atriplex longitrichoma.* a. Habit. b. Fruiting bract. c. Seed. d. Embryo. e. Male flowers. (Drawings by Marcus Vincent.)

appendages on both surfaces, margins with lanceolate, irregular, slightly curved teeth, densely furfuraceous with elongate, fragile trichomes. Utricle ovate, 2–2.5 mm broad, pericarp membranaceous. Seed yellow-brown, with solid perisperm; radicle superior. Flowering and fruiting period: April–June. Chromosome number: $2n = 36$.

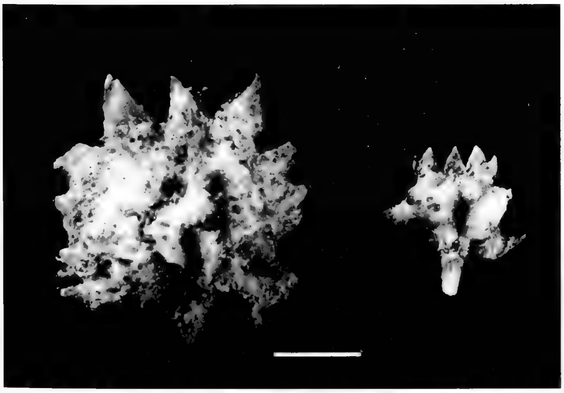
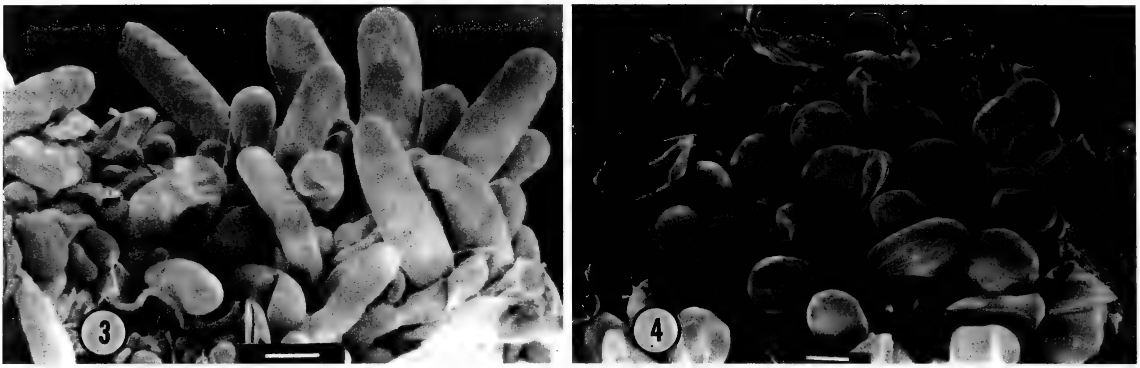


FIG. 2. Fruiting bracts of *Atriplex longitrichoma* (left) and *A. hillmanii* (right). Bar = 3 mm.

Paratypes. USA, California: Inyo Co., Stewarts Valley, Shoshone Road, on alkaline area, *R. S. Ferris 7365* 26 April 1928 (CAS, US); Stewarts Valley, E of Resting Spring Range, S of Dry Lake, ca. 2500 feet, *M. DeDecker 5463* 23 June 1983 (RSA); 20 mi E of Shoshone, *H. C. Stutz 95534* 3 June 1991 (BRY); Nevada, Nye Co., 5 mi W of Pahrump, *S. Sanderson & G. L. Chu 95301* 25 May 1990 (BRY); 5 mi. W of Pahrump, S 7st., *H. C. Stutz 95473* 17 April 1991 (BRY); W side of Pahrump, dense population covering ca. 10 acres but all ripe and dead, *H. C. Stutz & G. L. Chu 9760* 27 June 1995 (BRY).

Distribution and habitat. Atriplex longitrichoma is currently known only from a small area in Pahrump Valley, Nye Co., NV, and neighboring Stewart Valley, Inyo Co., CA. It is abundant in and around Pahrump, NV, occurring in open desert communities, alongside roadways, and in agricultural fields. The soils are gypsiferous clays with pH of ca. 6.5.



FIGS. 3, 4. Scanning electron micrographs of trichomes of *Atriplex longitrichoma* and *A. hillmanii* (scale bars = 100 μm). 3. *A. longitrichoma*. 4. *A. hillmanii*.

Taxonomic relationships. Atriplex longitrichoma appears to be most closely related to *A. hillmanii* (Jones) Standley but differs in several conspicuous characteristics including much larger fruiting bracts (5–6 mm long, 5–6 mm wide, vs. 3–4 mm long, 3–4 mm wide), bearing large, curved, marginal teeth (Fig. 2); decumbent branching habit in which the lower lateral branches are longer than the central branches; and the presence of a copious coating of elongate trichomes on all stems, leaves, and fruits (Fig. 3). Trichomes of *A. hillmanii* are spherical (Fig. 4). So abundant and conspicuous are the trichomes of *A. longitrichoma* that when plants are collected and placed in a container such as a paper sack, the deciduous trichomes accumulate in the bottom of the sack in quantities sufficient to permit them to be picked up with the fingers or by the spoonful.

Atriplex longitrichoma also differs from *A. hillmanii* in having narrow-elliptic to ovate-elliptic vs. oval-deltoid leaves. The leaf margins of *A. longitrichoma* are always entire whereas the leaf margins of *A. hillmanii* are often, but not always, sparingly toothed.

Atriplex longitrichoma differs from *A. argentea* Nutt. by its copious deciduous trichomes, narrower leaves (10–13 mm vs. 25–35 mm) and terete vs. quadrate branches. Fruiting-bract appendages of *A. longitrichoma* are flat or conical, whereas those of *A. argentea* are often folded.

Chromosomally, *A. argentea* is diploid ($2n = 18$), *A. longitrichoma* is tetraploid ($2n = 36$), and *A. hillmani* is mostly tetraploid ($2n = 36$), although some plants are diploid ($2n = 18$) and others are hexaploid ($2n = 54$).

Associated species. Atriplex longitrichoma sometimes grows as a near monoculture but most often grows in association with *Atriplex canescens* (Pursh) Nutt., *Atriplex confertifolia* (Torrey & Frémont) S. Watson, *Bromus madritensis* L. ssp. *rubens* (L.) Husnot, *Hordeum marinum* Hudson, *Larrea tridentata* (DC.) Cov., *Prosopis glandulosa* Torrey, *Salsola tragus* L., or *Suaeda moquinii* (Torrey) E. Greene.

Phenology. Flowering and fruiting of *Atriplex longitrichoma* is in early spring (April and May). By mid-June the fruits are fully mature and the plants are mostly dead. In early June, 1996, no living plants of *A. longitrichoma* could be found anywhere. However, many dead plants, left over from 1995, were present in most areas where they had been found earlier. Apparently they were unable to grow during the severe drought of 1996. Since such droughts occur quite often in these deserts, seeds very likely remain dormant in seed banks during unfavorable years.

Plants grown in the greenhouse and nursery at Brigham Young University, Provo, UT, from seed collected from populations near Pahrump, NV, showed the same characteristics as plants growing in the native populations, indicating high heritability of the distinctive features.

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EARLY SECONDARY SUCCESSION FOLLOWING CLEARCUTS IN RED FIR FORESTS OF THE SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Vegetation was quantified for clearcuts, age 4–32 yr, of *Abies magnifica* Andr. Murray old-growth forests along the west face of the central Sierra Nevada. TWINSPAN analysis of 113 sites × 87 common taxa generated six ecofloristic units mainly related to each other on a time-since-harvest basis, but also exhibiting correlations with slope, elevation, latitude, soil depth, harvest area, and ratio of edge-to-area. Nearly half the taxa showed non-random distributions among the TWINSPAN units, but only a minority of those could be related to time since harvest. The herbs *Gayophytum diffusum* Torrey & A. Gray, *Phacelia hydrophylloides* A. Gray, and *Sidalcea glaucescens* E. Greene were most significantly associated with pioneer sites age 4–10 yr since harvest, whereas the shrubs *Ceanothus cordulatus* Kellogg and *Ribes roezlii* Regel and the herb *Viola pinetorum* E. Greene were most significantly associated with later seral sites 16–32 yr since harvest. CCA ordination diagrams arranged the 113 sites along a continuum, rather than breaking them up into units, and this approach also revealed a strong relationship between site vegetation and time since harvest. The general path of early succession did not show dramatic floristic shifts nor was there any significant change in species richness over time. The first 32 yr of secondary succession probably represents only one-seventh the time necessary to attain old-growth status.

Abies magnifica Andr. Murray (California red fir) is a dominant of upper montane conifer forests of northern California at elevations between 2000 and 3000 m (Barbour and Minnich 1999; Barbour et al. 1991; Laacke 1990; Potter 1994; Rundel et al. 1988). The range of *A. magnifica* extends into southern Oregon and western Nevada but is largely within the boundaries of California, and its range accounts for 2% of the state's area. The autecology of *A. magnifica* and the dynamics of forests it dominates are poorly known, although *A. magnifica* has recently become a subject of research (e.g., Chappell and Agee 1996; Taylor 1993; Taylor and Halpern 1991).

The pattern and rate of succession from logging are unreported in the general literature, even though *A. magnifica* has been harvested this century at increasing intensities over time. A study by the Sierra Nevada Ecosystem Project Science Team (SNEP 1996) estimated that 65% of historic old-growth red fir forest acreage has been harvested by a combination of clear-, seed tree-, and select-cut methods. Some clearcuts have been slow to be invaded by *A. magnifica,* 1–3 decades passing before young red firs, 1–2 m tall, are present (Donald Potter personal communication; Barbour et al. 1998). The objective of this study is to describe the course of floristic succession during those first three decades following clearcut harvest.

METHODS

Over the course of three field seasons, we interviewed virtually every district silviculturalist in five national forests (hereafter, NF) in the central Sierra Nevada, regarding the location of clearcuts in old-growth red fir forests that met the following criteria: 1) the clearcut was 1–35 yr in age and >2 ha in area; 2) the stand harvested was >80% *A. magnifica* in tree composition; 3) the clearcut was located on the west side of the range, to keep climate uniform; 4) the stand harvested had not been previously disturbed by crown fire, blowdown, or selective logging; and 5) there was no record of post-harvest shrub suppression or tree thinning. (Some clearcuts had records of planting fir or pine seedlings after harvest, but mortality was consistently 100% (Barbour et al. 1998) allowing us to safely accept this form of post-harvest treatment as having no effect.) Once acceptable clearcuts were identified on maps and aerial photographs, they were visited and sampled. A total of 113 clearcuts are included in our analysis.

Each clearcut was described as to slope steepness, slope face, topographic profile (convex, concave, uniformly level, or mixed), elevation, latitude, soil depth, longitude, and national forest; and then a photograph was taken of the site. Data on clearcut area, shape, year of harvest, and subsequent post-harvest treatments were obtained from stand record cards (or whatever fragmentary records did exist, including the memory of long-term employees; typically clearcuts older than 35 yr had too few records for us to be sure that they satisfied our selection criteria).

Unless the clearcut was a narrow strip, it was

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TABLE 1. MEANS AND RANGES OF ENVIRONMENTAL VARIABLES AMONG THE 113 SITES.

Variable	Mean	Minimum	Maximum
Slope (°)	14.7	3.0	30.0
Aspect (°)	221.7	11.0	360.0
Soil depth (cm)	28.9	10.0	58.0
Elevation (m)	2273	1969	2656
Latitude (°N)	38.6	37.0	40.1
Area (ha)	6.7	2.0	27.9
Perimeter (m)	1185	580	3610
Edge (m/m^2)	0.023	0.006	0.066
Time (yr)	19.9	4.0	32.0
Herb cover (%)	5.8	0.0	52.5
Shrub cover (%)	3.8	0.0	9.4
Non-red-fir tree cover (%)	3.9	0.0	54.1
Red fir tree cover (%)	5.5	0.0	41.1
Red fir density (per 25 m^2)	3.9	0.0	63.0
Red fir average age (yr)	12.4	0.0	41.1

divided into four equal subareas and each was sampled with one 5 × 5 m plot, located randomly within the subarea in such a way that it fell halfway between the margin of the clearcut and the center of the subarea. If the clearcut was a strip, the plots fell along the center line of the strip.

In each plot, we recorded cover of all herb, shrub, and tree sapling species to the nearest tenth of a percent. Soil depth to rock was estimated at each plot corner by pounding a length of rebar into the ground until it reached an obstruction. In one 500 m^2 area, subjectively located in the center of the clearcut, all stumps >30 cm at the cut surface were tallied by species as a check on our criteria that *A. magnifica* was dominant, and also as a means of identifying the stand according to a classification of upper montane Sierran forests by Potter (1994). Additional information, to aid this classification process, was provided from an adjacent, uncut stand that we presumed was similar to the stand harvested. We sampled a 20 × 20 m area of that stand, noting the composition and relative species importance in overstory and understory strata. We used Potter's classification because it is much more detailed than the series descriptions of Sawyer and Keeler-Wolf (1995) and community/habitat descriptions of Robert Holland (unpublished, but see Barbour and Major, 1988). Voucher specimens were collected for all herbaceous species at each site. Nomenclature follows the Jepson Manual (Hickman 1993) and vouchers are housed in the Tucker Herbarium at the University of California, Davis.

Our analysis of successional dynamics followed two approaches. We used both the classicial approach of searching for discrete seral stages and the continuum approach of relating each site individualistically to gradients of environmental factors. For the first approach, we utilized TWINSPAN, a commonly used divisive computer program which sorts species into maximally different, but minimum in number, groups (Hill 1979; van Groenewoud 1992). These groups were then statistically correlated with site factors by ANOVA (analysis of variance) tables. For the second approach, we utilized an ordination technique called canonical correspondence analysis (CCA), first described by Ter Braak (1987).

RESULTS AND DISCUSSION

Overview of all sites. Our sample of 113 stands was nearly exhaustive, rather than random. We could have sampled more replicate clearcuts clustered within the same harvest unit, but we sampled all harvest units that fit our criteria. We assume that these sites are representative of mature, old-growth *A. magnifica* stands elsewhere in the range, stands which by chance have not yet been harvested. We have no evidence to support the possibility that only the most productive or unusual sites were harvested; rather, it is more likely that the logged stands were simply closest to already existing roads, making their exploitation less costly.

The distribution of our sites was neither uniformly distributed across the range of red fir forest nor was it random, because the use of clearcuts as a harvest technique has not been uniformly applied across all five forests, nor has the distribution of harvests been constant over time. Of our 113 clearcuts, 46 were in Tahoe NF, 42 in Stanislaus, 16 in Sierra, 7 in Eldorado, and 2 in Plumas. Thus, the latitudinal extremes (Sierra NF in the south, Plumas NF in the north) were the least intensively sampled. The latitudinal span of samples extended from 37 to 40°N (Table 1). Because of the NW-SE trend of the mountain range, longitude (119–121°W) is strongly linked with latitude and can't be treated as an independent variable in our analysis.

The span of clearcut age extended from 4 to 32 yr (Table 1). Younger clearcuts tended to fall toward the north, in Tahoe NF, whereas older clear-

TABLE 2. TWINSPAN ECOFLORISTIC UNITS. N = number of the 113 sites which fell in each unit. Assignment of the percentage of N sites to early, mid, and late is by age of the clearcut: 4–10 yr old is early-successional, 11–25 is mid-successional, and 26–32 is late-successional.

		Percentage of N sites by clearcut age		
Unit	N	Early	Mid	Late
1	12	17	33	50
2	10	0	40	60
3	35	11	43	46
4	26	15	62	23
5	16	60	28	12
6	14	100	0	0

cuts tended to fall toward the south, in Stanislaus and Sierra NFs. The correlation of clearcut age with latitude was highly significant ($r = -0.38$, $P = <0.0001$). More than half the Tahoe clearcuts were <11 yr old, whereas two-thirds of the Stainslaus clearcuts were >24 yr old. Clearcuts in the other three forests were more evenly distributed among the range of ages.

Clearcut areas varied more than an order of magnitude, from 2 to 28 ha, averaging nearly 7 ha (Table 1). Clearcut shapes ranged from long, narrow strips to roughly rectangular, square, and circular. "Edge"—the ratio of perimeter to area—varied by more than an order of magnitude, from 0.006 to 0.066 m/m^2. Clearcut elevations were between 1768 and 2591 m, increasing to the south somewhat faster than the Sierra-wide ecological displacement of 172 m per degree latitude (Parker 1994). Slopes were generally modest, 3–30°, and their topographic profiles were diverse (Table 1). All aspects were represented. Soil depth varied nearly six-fold, from 10 to 58 cm. We did not determine soil series or geologic substrates for use as variables in this study, as they were overwhelmingly Inceptisols on granitic parent material.

Herb cover was 0–52%, shrub cover was 0–80%, and tree cover (mostly *A. magnifica*) was 0–54% (Table 1). *A. magnifica* sapling density ranged from 0.5 to 387 per 25 m^2 (equivalent to 200–155,000 ha^{-1}, averaging 82,000 ha^{-1}). Average sapling age on all 113 sites was 13 yr, younger than the average site age of 20 yr (Table 1), which is another indication that there is a many-year lag between the time of harvest and the time of red fir invasion. The average age of other tree species in the sites was insignificantly different from that of *A. magnifica*: 12 yr for *Pinus contorta* Loudon ssp. *murrayana* (Grev. & Balf.) Critchf., 11 yr for *P. jeffreyi* Grev. & Balf., and 9 yr for *Abies concolor* (Gordan & Glend.) Lindley. Stumps of harvested trees (all taxa combined) averaged 160 ha^{-1} and the average age of the largest *A. magnifica* stumps was 350 yr (the oldest was 425 yr).

Uncut forests adjacent to the clearcuts fell into six associations described by Potter (1994): 70 sites fit his red fir association, 29 fit his red fir-white fir association, 9 fit his red fir-western white pine association, 2 fit his mountain hemlock association, and 1 each fit his red fir-western white pine-lodgepole pine and his white fir-sugar pine-red fir associations. Given the overwhelming preponderance of sites within one association, we did not attempt to analyze succession by separating out original associations harvested.

TWINSPAN analysis. A total of 208 vascular species were present in the 113 clearcuts. In order to statistically analyze patterns of change over time, a given species had to occur in at least five sites; only 87 of those taxa fulfilled this requirement. Included among the 87 were five tree species (*A. magnifica, A. concolor, Pinus monticola, P. jeffreyi, P. contorta* ssp. *murrayana*) and ten shrub species (*Arctostaphylos nevadensis* A. Gray, *A. patula* E. Greene, *Ceanothus cordulatus* Kellogg, *C. velutinus* Hook., *Prunus emarginata* (Hook.) Walp., *Ribes cereum* Douglas, *R. roezlii* Regel, *R. viscosissimum* Pursh, *Sambucus racemosa* L., and *Symphoricarpos mollis* Nutt.). Shrub species contributing the highest average cover were *Ribes roezlii, R. viscosissimum,* and *Ceanothus cordulatus,* in that order. The remaining 72 herb taxa were almost evenly split between monocots and dicots. Those contributing the highest average cover were *Phacelia hydrophylloides* A. Gray, *Elymus elymoides* (Raf.) Swezey, *Gayophytum diffusum* Torrey & A. Gray, and *Sidalcea glaucescens,* in that order.

TWINSPAN analysis of the 113 sites × 87 taxa resulted in six ecofloristic units, which we numbered 1–6 (Table 2). As a first approach towards understanding the units, we assigned their member sites to several discrete time classes. We subjectively created three equal groups of sites by dividing the 113 sites into three age spans: 4–10 yr (35 sites), 11–25 yr (35 sites), and 26–32 yr (43 sites).

It is apparent, from Table 2, that the six units do represent a time gradient, with the sequence from youngest to oldest: 6 to 5 to 4 to 1 to 3 and 2. Unit 6, for example, has 100% of its 14 sites in the youngest age category of 4–10 yr, whereas unit 2 has none of its 10 sites in that youngest category and 60% of its sites are in the oldest category of 26–32 yr.

In an attempt to refine our interpretation of the units, we performed ANOVA's of units against abiotic variables. Only four variables showed a statistically significant pattern (P = <0.05): slope, elevation, latitude, and time. Two biotic variables (shrub cover and tree sapling cover) also showed statistically significant differences among the six units. Three other abiotic variables just missed the significant cutoff (P = 0.06): soil depth, clearcut area, and edge. Thus, the six TWINSPAN units do reflect successional time, but they also reflect non-seral microenvironmental differences.

A cursory examination of the raw unit × taxa table (not included here) showed the following taxa to be most characteristic and abundant in the "older" units 1, 2, and 3: the shrubs *Ceanothus cordulatus, Ribes cereum,* and *R. roezlii*; the forbs *Hackelia nervosa* (Kellogg) I. M. Johnston, *Viola bakeri* E. Greene, and *V. purpurea* Kellogg, and the grasses *Achnatherum occidentalis* (Thurber) Backworth, and *Poa bolanderi* Vasey. No species, however, appeared to be characteristic of the younger units 4, 5, and 6.

A more powerful search for relationships between taxa and units is to subject each of the 87 common taxa to ANOVA, in essence asking the question: are they distributed among the six units randomly, by chance, or do any of them exhibit a non-random pattern? Nearly half exhibited a non-random distribution (P = <0.05): *A. magnifica, A. concolor, Achnatherum nelsonii* (Scribner) Backworth ssp. *dorci* (Backworth & J. Maze) Backworth, *Antennaria rosea* E. Greene, *Arabis sparsiflora* Torrey & A. Gray, *Arctostaphylos nevadensis, A. patula, Bromus carinatus* Hook & A. M., *Carex fracta* Mackenzie, *Ceanothus cordulatus, Chamaesaracha nana* (A. Gray) A. Gray, *Cirsium andersonii* (A. Gray) Jepson, *Collinsia torreyi* A. Gray, *Cryptanthus glomeriflora* E. Greene, *Elymus glaucus* Buckly, *Eriogonum spergulinum* A. Gray, *Hackelia nervosa, Lotus purshianus* (Benth) Clements & E. G. Clements var. *purshianus, Lupinus andersonii* S. Watson, *Monardella odoratissima, Pedicularis semibarbata* A. Gray, *Phacelia hydrophylloides, Pinus contorta* ssp. *murrayana, P. jeffreyi, P. monticola, Poa bolanderi, Polygonum douglasii* E. Greene, *Potentilla glandulosa* Lindley, *Ribes cereum, R. roezlii, Sidalcea glaucescens, Stephanomeria lactucina* A. Gray, *Symphoricarpos mollis* Nutt., *Viola bakeri* E. Greene, *V. pinetorum* E. Greene, *V. praemorsa* Douglas, and *V. purpurea* Kellogg. None of these, however, exhibited a statistically significant least-significant difference (Tukey's test, P = 0.05) between any two of the six units.

Ordination analysis. The ordination diagram (Fig. 1) shows the 113 sites distributed along three axes. Each site is represented as an open circle. The ordination program adds lines radiating from the center of the clusters which statistically relate to site factors. The direction of the line shows the direction of the relationship, relative to the axes, and the length of the line shows the statistical strength of the relationship (the longer the line, the stronger the relationship).

Axes 1 and 2 reveal that latitude and time were the abiotic factors which had the most effect on site similarity (circles close to each other) or difference (circles far apart). Axes 1 and 2 also show that the most important biotic factors for site similarity or difference were herb, shrub, and tree cover. The same biotic and abiotic variables were highlighted by axes 1 and 3 and 2 and 3 (Fig. 1). The outliers in the ordination diagram are all unique in that these sites had very rapid, massive invasion by *A. magnifica* seedlings, and in that they had a concave topography.

Taxonomic and functional species change over time. When we performed ANOVA's on the 87 common taxa × three age classes of sites, 15 exhibited significantly non-random distributions (Table 3). Those which peaked in cover in early succession (yr 4–10) were: *Cryptantha glomeriflora, Gayophytum diffusum* Torrey & A. Gray, *Phacelia hydrophylloides, Sidalcea glaucescens,* and *Symphoricarpos rotundifolius* A. Gray. Those which peaked in yr 11–25 were: *Arabis platysperma* A. Gray, *Elymus elymoides* (Raf.) Swezey, *Hieracium albiflorum* Hook. *Pinus monticola,* and *Ribes viscosissimum* Pursh. Those which peaked in yr 26–32 were: *Ceanothus cordulatus, Pinus jeffreyi, Ribes roezlii,* and *Viola pinetorum.* Even though these species trends are statistically significant, they involve relatively small amounts of cover, and the ecological significance or impact of the changes on community function are uncertain.

The general path of succession during the first 32 yr after harvest did not reveal dramatic changes, nor did it reveal trends widely reported elsewhere. For example, when species richness was regressed against site age, there was no significant linear or curvilinear relationship. Our data showed a flat relationship, with an average of 23 taxa per site, plus considerable "noise" (maximum richness was 49 taxa for a site 27 yr after harvest and minimum was 3 for a site 8 yr after harvest). In his recent summary of succession, Robert Peet (1992) concluded that species diversity and species richness both continually rise during successional time, peaking either at or just prior to the climax/equilibrium phase. Such functional attributes as growth forms, "strategies" (e.g., C, S, R of Grime 1979), and metabolic specialists (N-fixers, helophytes vs sciophytes, etc.; see Barbour et al. 1998) also typically change during succession, but our clearcut sites only showed an increase in shrub cover and total plant cover. There were no trends over time, for example, of annuals to perennials, N-fixers to non-fixers, grasses to forbs, nor in pollination or seed dispersal syndromes.

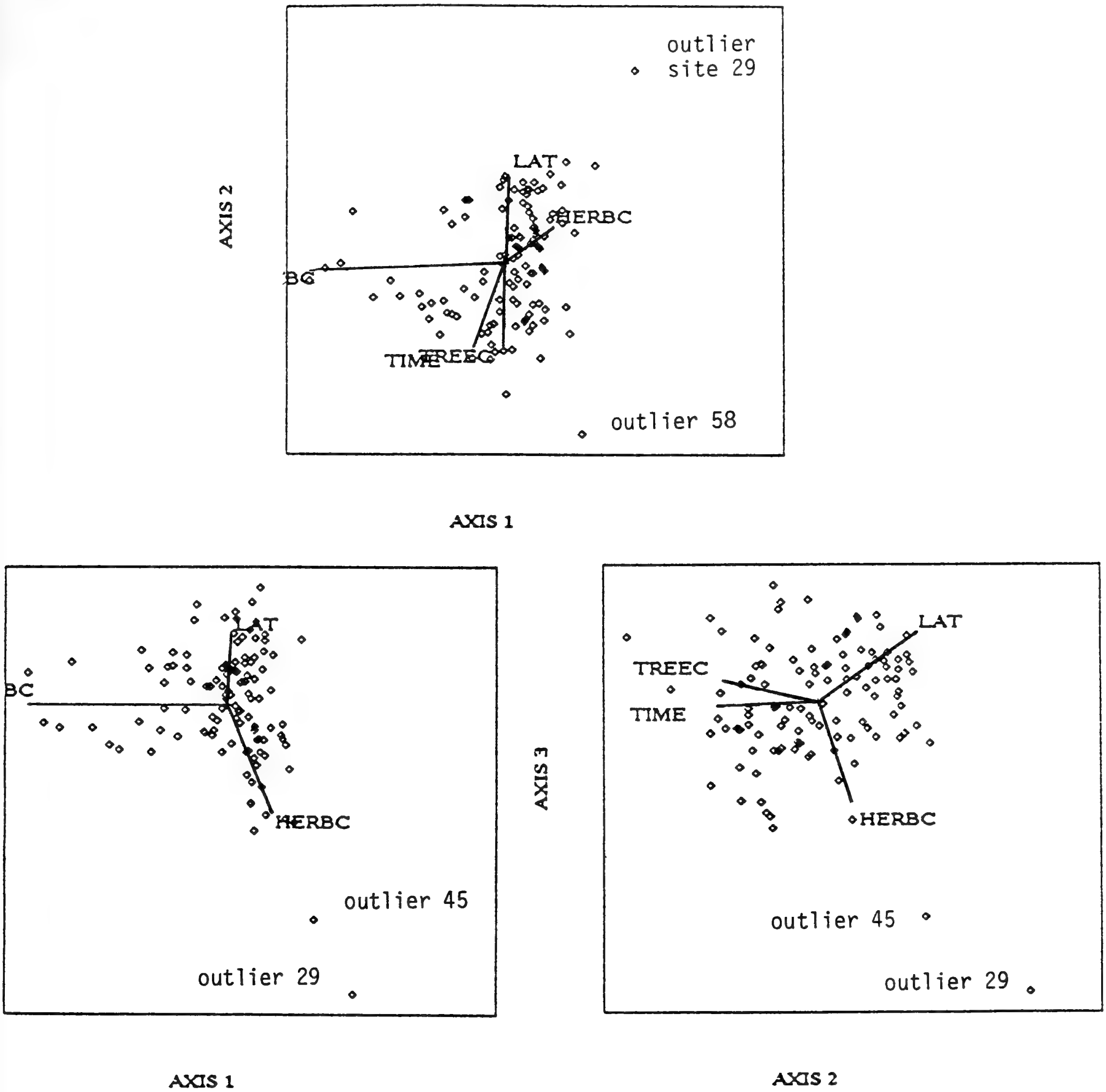

FIG. 1. Ordination of 113 sites by canonical correspondence analysis along three axes. The lines show correspondence with the site variables latitude (LAT), herb cover (HERBC), tree cover (TREEC), shrub cover (BC), and age of the clearcut (TIME). The longer the line, the stronger the correspondence.

Possibly the magnitude of change is modest because tree canopy (sapling canopy) cover is modest, even 32 yr after harvest (refer to Table 1, which shows that maximum tree cover was only about 50%). Our companion publication on *A. magnifica* regeneration for these sites (Barbour et al. 1998) showed that *A. magnifica* percent cover, when regressed against time, was = (0.21) (time, in yr) + 1.42. The positive slope was statistically significant ($P = 0.006$) even though the relationship accounted for only 7% of the variance. If the entire course of succession were similarly linear, 270 yr would be required to attain mature tree cover of 60% (average for old-growth red fir forests as reported by Barbour and Woodward, 1985). No doubt, there is an eventual curvilinear relationship between cover and time, where it rises more steeply, but there are no data yet to show when this might occur, or how steeply the cover might increase.

Based on the general age of trees in old-growth stands as reported in the literature, and stand data from our own unpublished data, secondary succession for red fir forests probably requires more than 200 yr. The portion of secondary succession investigated in this paper, then, is a rather small fraction, about one-seventh, of seral time.

TABLE 3. SPECIES WHICH EXHIBITED A NON-RANDOM DISTRIBUTION (ANOVA, $P < 0.05$) AMONG AGE CLASSES OF STANDS. Early-successional = 4–10 yr old sites, mid-successional = 11–25, late-successional = 25–32. Data are percent cover. Figures in the same row which share the same superscript do not differ at $P < 0.05$.

Species	Early	Mid	Late
Arabis platysperma	0.0^{a}	0.02^{b}	0.01^{ab}
Ceanothus cordulatus	0.8^{a}	8.9^{ab}	13.3^{b}
Cryptantha glomieriflora	0.04^{a}	0.0^{b}	0.02^{ab}
Elymus elymoides	0.0^{a}	0.31^{b}	0.27^{ab}
Gayophytum diffusum	0.95^{a}	0.22^{b}	0.28^{b}
Hieracium albiflorum	0.02^{ab}	0.06^{a}	0.02^{b}
Pedicularis semibarbata	0.01^{a}	0.0^{b}	0.01^{ab}
Phacelia hydrophylloides	1.1^{a}	0.1^{b}	0.2^{b}
Pinus jeffreyi	0.04^{a}	1.6^{b}	1.9^{b}
Pinus monticola	0.03^{ab}	1.3^{b}	0.1^{b}
Ribes roezlii	1.7^{a}	0.7^{a}	4.5^{b}
Ribes viscosissimum	0.2^{a}	1.9^{b}	0.7^{ab}
Sidalcea glaucescens	0.35^{a}	0.20^{ab}	0.05^{b}
Symphoricarpos rotundifolius	0.5^{a}	0.0^{a}	0.0^{a}
Viola pinetorum	0.01^{a}	0.03^{a}	0.5^{b}

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Donald Potter, Zone Ecologist for the USDA Forest Service, provided valuable advice about the biology and ecology of *Abies magnifica* as well as the identity of helpful agency silviculturalists and timber sale specialists. Fred Hrusa identified many of our voucher specimens. Financial support was provided by the USDA Competitive Grants Program, award No. 92-87101-7420.

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A NEW *GILIA* (POLEMONIACEAE) FROM LIMESTONE OUTCROPS IN THE SOUTHERN SIERRA NEVADA OF CALIFORNIA

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ABSTRACT

Gilia yorkii, a new species discovered in the southern Sierra Nevada, is restricted to limestone outcrops. From its morphology *G. yorkii* is identified as a member of *Gilia* sect. *Saltugilia,* and within the section it appears most like *G. scopulorum* M. E. Jones, a desert species. The two species differ in several characters, including different corolla proportions and some contrasting trichome details.

From recent explorations on xeric limestones (marbles) in the southern Sierra Nevada a new species of *Gilia* has been discovered. *Gilia yorkii* is scattered primarily over the southern exposures of a large north-south trending limestone ridge. At its highest point, this sheer-walled limestone formation rises more than 1000 m above the South Fork of Kings River. It occurs just east of Horseshoe Bend along both sides of the river canyon. This interesting new species was discovered by Dana York on 31 July 1995 in Monarch Wilderness, while exploring the steep and rugged limestone terrain.

Gilia yorkii Shevock & A. G. Day, sp. nov. (Fig. 1)—TYPE: USA, CA, Fresno Co, 86 km E of Fresno, Sequoia National Forest, Monarch Wilderness, 1 km S of Boyden Cave on S side of Kings River Canyon, 36°48′20″N, 118°48′40″W; T13S, R29E, S10, NW ¼ of SW ¼, 1290 m. 27 June 1996, *York & Shevock 949* (holotype CAS; isotypes JEPS, FSC).

Herba annua inter species sect. *Saltugilia* V. Grant & A. D. Grant trichomatibus a foliis multiseptatis et translucidis, calyce glanduloso, corollae lobulis lavandulis, capsula late ovoidea, inclusa, et seminibus in loculis 2–3, ad *G. scopulorum* M. E. Jones accedens sed differt foliis basalibus paucis, foliis paucilobis, vel interdum foliis integris, trichomatibus curvus, eglandulosis (nec patentibus nec glandulosis), trichomatibus pedicello et calyce glandulosis minutus incoloribus (nec magnus nec nigris), corolla minor, tubo incluso (nec exserto nec exserto longissimo).

Annual herb 10–25 cm high, with one or two somewhat spreading branches arising near base of main stem, sometimes vigorous plants becoming diffusely branched and to 4 dm high. Stems pubescent below middle or near base, with multiseptate, translucent, eglandular trichomes; upper stems densely glandular-puberulent. Basal and lower cauline leaves 2–8, with basal mostly drying and falling early, thus only vigorous, immature plants with unexpanded internodes show a definite basal rosette. Lower leaves pubescent on ventral side, densely so in their axils, trichomes very fine, multiseptate, eglandular, broad at base, fine-tapered near tip, shining, translucent, often ± bent at septa (Fig. 1D). Basal and lower cauline leaves 1.5–2.5 cm long, 1-pinnate or entire, oblanceolate, rachis linear below, broadened between lobes, lobes 5–7 in ascending, subopposite pairs, 3–5(7) mm long, elliptic, acute, entire or with 1–2 teeth near apex. Upper cauline leaves glandular-puberulent, elliptic, generally with two narrow, spreading, basal lobes, uppermost leaves reduced, entire. Upper stems, pedicels and calyces densely glandular-puberulent, trichomes stipitate, glands minute, (0.05 mm diam.), colorless, stipe narrower than gland, ca. twice as long as diameter of gland. Inflorescence loose, cymose, pedicels 3–10 mm in flower, in subequal to unequal pairs, or in 3's, elongating and divergent spreading in fruit to 5–33 mm. Calyx 3–3.6 mm long in flower, accrescent, ribs, lobes and membrane glandular-puberulent or rarely in earliest flowers calyx trichomes longer, non-glandular, as on lower leaves, ribs 0.2 mm wide, green, or in age red-streaked, connected by sinus membrane in lower half, membrane at maturity splitting between ribs to near base. Corolla 7–8.5 mm long, tube and throat together ±4 mm long, included in calyx, or upper throat exserted, tube and lower throat white, sometimes lavender-tinged, upper throat and lobes lavender to white; lobes spreading, 3–5 mm long, 2.5–4 mm wide, elliptical to broadly elliptical, apex rounded. Stamens inserted equally 0.5 mm below sinuses, filaments 0.2–1 mm long, anthers 0.9–1.5 mm long, maturing in or slightly above orifice, pollen blue. Style exserted beyond anthers, stigmas 1–1.5 mm long, spreading, tips curling downward toward, or touching anthers. Capsule broadly ovoid, 3–4.5 mm long, 1.4–1.7× as long as wide, equal to, or slightly exceeded by calyx, dehiscing by

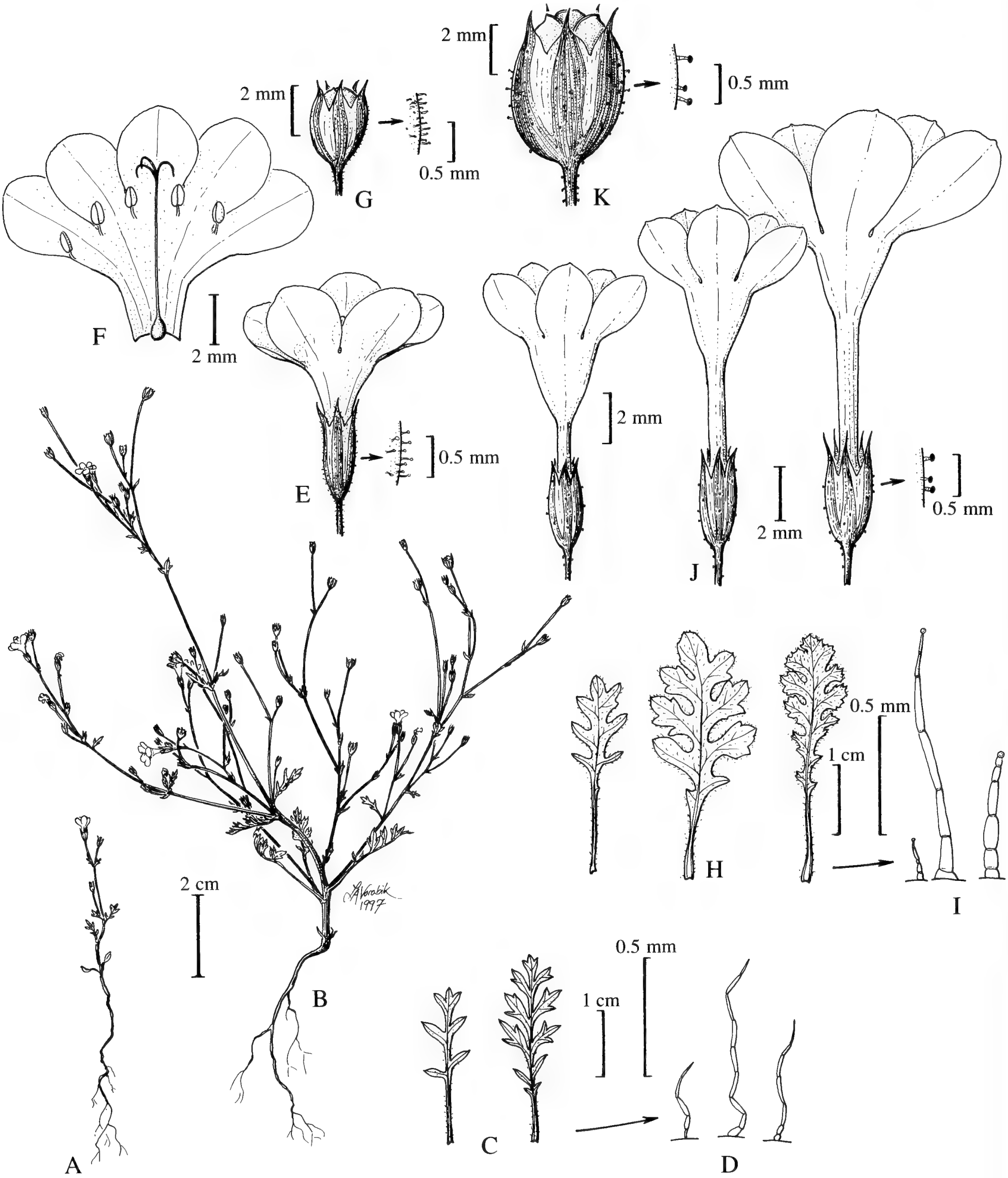

FIG. 1. Habit of *Gilia yorkii* Shevock & A. G. Day, with details shown in comparison with *G. scopulorum* M. E. Jones. A–G. *Gilia yorkii,* from holotype collection: A–B. Plant habit; A. young plant in early flower, with cotyledons present; B. Mature plant in flower and fruit; C. Basal and lower cauline leaves; D. leaf trichomes; E. *Flower with detail of calyx trichomes; F. Dissected corolla with stamens and style; G. Calyx with mature, included capsule. H–K. *G. scopulorum:* H. Variation in basal leaves, (l to r) *Darrow s.n.* (CAS 336894), *Prigge 994* (CAS 615000), *Raven 11790* (CAS 517748); I. leaf trichomes; J. *Flowers from three different collections, showing variation in corolla, and detail of calyx trichomes, (l to r) *Pinzl 2611* (CAS 637910), *Raven 11790* (CAS 517748), *Prigge et al. 769* (CAS 606023); K. Calyx with mature, included capsule, *Prigge 994* (CAS 615000).

Note: Corolla lobes are shown erect for comparisons of size and form. In real life, as in other Gilias, the lobes are spreading. This is shown in views of two flowers in the habit drawing of *G. yorkii* (B).

splitting between valves from apex to near base. Seeds 0.8–1.5 mm long, brown, verrucate, ± oblong, 2–3 per locule, mucilaginous when wet. Pollen grains ± spheroidal, zonocolporate, colpi 7–8, exine striate.

Paratypes. USA, CA, Fresno Co., Monarch Wilderness, vicinity of Boyden Cave, 31 Jul 1995, *York & Shevock 107* [CAS]; 31 Jul 1995, *York & Shevock 112* [CAS, FSC, JEPS]; 13 Oct 1995, *York 207* [CAS].

Distribution, Habitat and Phenology

Gilia yorkii is known only from the southern Sierra Nevada in Fresno Co., California, from limestone outcrops in the vicinity of Boyden Cave in the Kings River Canyon. Plants grow in fissures, ledges, and terraces in sandy or gravelly soils developed from weathered limestone, at elevations from 1290 to 1830 m. Within its habitat *G. yorkii* can easily be overlooked because the pale lavender flowers blend in with the surrounding limestone. Plant size may vary widely, depending on the timing and amount of late spring to early summer rain. In a year with early as well as late rains, plants may become tall and spreading, diffusely branched and abundantly flowered. In a more normal year, however, plants are apt to be smaller at maturity and to have fewer flowers.

The exposed limestone habitat occupied by *G. yorkii* is very arid, and during summer plants are subjected to daily ambient temperatures in excess of 34°C. The time of anthesis, depending upon the particular seasonal conditions, appears to range from May to July.

While the number of *G. yorkii* plants has not been estimated, the population could number in the thousands under optimum conditions. Only a portion of the potential habitat has been surveyed because of the rugged nature of the area.

This habitat is dominated by many petrophilous taxa along with species generally located within chaparral and foothill woodland plant communities. Prominent among these are woody associates including three *Cercocarpus* species: *C. intricatus* S. Watson, *C. betuloides* Torrey & A. Gray, and *C. ledifolius* Nutt. var. *intermontanus* N. Holmgren; and also *Garrya flavescens* S. Watson, *Pinus monophylla* Torrey & Frémont, *Rhamnus tomentella* Benth., *Umbellularia californica* (Hook. & Arn.) Nutt., and *Yucca whipplei* Torrey.

Other common associates, including annuals, ferns, and other perennial herbs are the following: *Argyrochosma jonesii* (Maxon) M. D. Windham, *Asclepias fascicularis* Decne., *Astragalus congdonii* S. Watson, *Avena sativa* L., *Bromus madritensis* L. ssp. *rubens* (L.) Husnot, *Cheilanthes cooperae* D. Eaton, *Cirsium occidentale* (Nutt.) Jepson var. *californicum* (A. Gray) Keil & C. Turner, *Clarkia rhomboidea* Douglas, *Eriogonum nudum* Benth. (*sensu lato*), *Erysimum capitatum* (Douglas) E. Greene, *Heterotheca monarchensis* York, Shevock & Semple, *Heuchera rubescens* Torrey var. *alpicola* Jepson, *Mentzelia laevicaulis* (Hook.) Torrey & A. Gray, *Mimulus floribundus* Lindley, *Nemacladus interior* (Munz) G. Robb., *Petrophyton caespitosum* (Nutt.) Rydb. ssp. *acuminatum* (Rydb.) Munz, *Selaginella asprella* Maxon, *S. hansenii* Hieron., and *Streptanthus fenestratus* (E. Greene) J. Howell.

The general aspect of the vegetation is markedly different at the borders of the limestone habitat, where reddish metamorphic rock outcrops support canyon live oak woodland with scattered *Torreya californica* Torrey and chaparral elements, but not *Gilia yorkii.*

Relationships

From its morphology *Gilia yorkii* fits readily into *Gilia* sect. *Saltugilia,* and within the section it appears rather like *G. scopulorum* M. E. Jones, sharing characters concerning pubescence, seed-number, and capsule form. They have a similar leaf type, as seen in the venation pattern, with the lobes, and their veins ascending. The lobes are toothed on both sides (Fig. 1C, H), but the leaves of *G. yorkii* are smaller, more delicate, and with lobes sparingly toothed. The two species also show some similarity in habitat, both commonly occurring in limestone areas. However, *Gilia scopulorum* has also been found on volcanic substrates.

In the Jepson Manual key to *Gilia* (Day 1993) *G. yorkii* would fall near the *G. scopulorum* position. A segment of that key, shown below, has some added details, and a new dichotomy to include *G. yorkii.* The important differences between *G. yorkii* and *G. scopulorum* are illustrated in Figure 1.

Gilia scopulorum leaf lobes tend to be large, and many-toothed, but sometimes are ± reduced, as in *G. yorkii,* entire or with 1–2 teeth. A stout, erect, leading stem above a well-developed rosette of basal leaves is the usual condition in *G. scopulorum.* However, this is not found in mature plants of *G. yorkii,* which lack a definite basal rosette of leaves, and have a shorter, generally several-branched central stem.

Other important differences are the shorter, included corolla tube of *G. yorkii* (Fig. 1E), and differences in size and gland-type of trichomes borne on the calyx and lower leaves and stems of the two species (Fig. 1E, J).

The importance of trichomes in differentiating species and larger taxonomic units of Polemoniaceae has been well demonstrated, as in *Gilia* sect. *Arachnion,* named for a characteristic trichome type, making up a fine arachnoid pubescence of all the member species (Grant and Grant 1956), and which is not found elsewhere in the genus.

Within sect. *Saltugilia* all species have multiseptate trichomes on the lower leaves, but as the key indicates, they are not all alike. Usually the multiseptate trichomes are coarsely translucent, often ± glandular, and straight or variously curving; but in

G. stellata A. A. Heller they are opaque-white, eglandular and markedly geniculate. In *G. yorkii* the multiseptate trichomes (Fig. 1D) have yet another variation: although translucent, they are very fine, eglandular, and often bent at the septa, or curving, but not markedly geniculate as in *G. stellata.*

The densely glandular-puberulent calyx of *G. yorkii* is unique in the section. The calyx in other species is either glabrous (*G. splendens* H. Mason & A. D. Grant group) or coarsely glandular-dotted (*G. scopulorum* and *G. stellata*). The scattered, large black glands on the calyx of *G. scopulorum* (Fig. 1J) contrast with the closely-spaced, minute, colorless calyx glands in *G. yorkii* (Fig. 1E).

Corolla proportions are variable in *G. scopulorum* (Fig. 1J). Usually the corolla tube is long-exserted; but a variant with a short, slightly-exserted corolla tube was collected several times in Mohave Co., Arizona and in south-western Nevada (Fig. 1J, flower no. 1). This approaches the form of the *G. yorkii* corolla, but the tube is exserted. In *G. yorkii* the tube, as well as the throat, or part of it, are included in the calyx (Fig. 1E). In all significant characters the above variant of *G. scopulorum* differs from *G. yorkii.*

KEY TO *GILA* SECT. *SALTUGILIA,* (IN PART) (Modified from The Jepson Manual, Key to *Gilia* (Day 1993))

1. Calyx glabrous; capsule narrowly ovoid, exceeding calyx; capsule valves 2–3× longer than wide; seeds 7–23 per locule. . . . . *G. splendens, G. australis* and *G. caruifolia.* (For key to this species group see Day, 1993: 830.)

1′ Calyx glandular-dotted; capsule broadly ovoid, included in calyx, capsule valves <2× longer than wide; seeds 2–6 per locule.

5. Trichomes on lower leaves opaque-white, eglandular, geniculate; corolla throat with purple spot below each lobe; seeds 3–6 per locule . . . *G. stellata*

5′ Trichomes on lower leaves translucent, straight or ± curved, glandular or eglandular; corolla throat not spotted; seeds 2–3 per locule.

6. Corolla 7–8.5 mm long, tube and throat (or part of throat) included in calyx; calyx and pedicels densely glandular-puberulent, glands minute, colorless; trichomes on lower leaves and stems few, scattered, denser in leaf axils, very fine, eglandular, variously curving. Rare endemic. Sierra Nevada, CA., Kings River Canyon . . *G. yorkii*

6′ Corolla 9–17 mm long, tube exserted, generally 2× calyx or longer; calyx and pedicels glandular-dotted, glands large, black; trichomes on lower leaves and stems dense, coarse, gland-tipped, ± straight, spreading. Desert mountains E of Sierra Nevada, CA to AZ, UT . . . . . *G. scopulorum*

DISCUSSION

Gilia yorkii and *G. scopulorum* are allopatric, being geographically isolated. *Gilia scopulorum* occurs in desert mountains of the Great Basin, Mojave, and Sonoran deserts from Utah and Arizona to California, but it does not extend to the Sierra Nevada. *Gilia yorkii* occurs only in the southern Sierra Nevada, west of the summit divide. However, this particular Sierran habitat is arid and desert-like, which is also indicated by the dominant species, and is quite unlike surrounding areas in the Kings River Canyon.

The two species show relationship in the numerous morphological characters that they share, but their recognition as distinct species is justified by their differences with respect to a number of other characters: trichome types, corolla proportions, plant habit, etc., and because no intermediates between them have been found.

RARITY

Gilia yorkii, previously unknown and uncollected, is an extremely rare species due to its lithophytic nature on limestones, a relatively uncommon substrate in the southern Sierra Nevada. While additional occurrences may well be discovered in steep canyons and rocky slopes, expansion of the distribution is unlikely to extend beyond the existing limestone outcrops in the Kings River basin. This species, therefore, is expected to remain a rare and localized endemic worthy of conservation efforts. Fortunately this new species, limited to its limestone habitat, is located within the Monarch Wilderness in very steep and rugged terrain. For these reasons anthropogenic impacts are likely to be few.

It is a pleasure to name this species for a colleague and friend who is actively exploring the Kings River Basin for the purpose of developing a floristic treatment for the region. His field work has already led to the discovery of three additional new taxa: *Heterotheca monarchensis* York, Shevock and Semple, and two as yet unnamed species of *Carex* and *Eriogonum.*

ACKNOWLEDGMENTS

We are grateful to Linda A. Vorobik for her excellent illustration comparing the species. We also thank Diana L. Lusk for her kind assistance in translating the diagnosis to Latin; and Dana York for sending photos and specimens of young *G. yorkii* plants that he grew from seed. We thank the reviewers, Robert W. Patterson and Dieter H. Wilken for their numerous helpful comments and suggestions. We appreciate the courtesies extended by the herbarium staff of the California Academy of Sciences (CAS/DS), and of the University of California at Berkeley (UC).

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WATER POTENTIALS OF *SALVIA APIANA, S. MELLIFERA* (LAMIACEAE), AND THEIR HYBRIDS IN THE COASTAL SAGE SCRUB OF SOUTHERN CALIFORNIA

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ABSTRACT

Shrubs in the genus *Salvia* are often dominants in Coastal Sage Scrub communities throughout southern and central California. *Salvia mellifera* E. Greene (black sage) tends to be more abundant near the coast with a more northerly distribution, whereas *S. apiana* Jepson (white sage) tends to occur farther inland and ranges much farther south. In areas of local sympatry in southern California, *S. apiana* is more frequently observed on south-facing slopes. It has been suggested to be better able to withstand drought conditions than *S. mellifera,* because *S. apiana* occurs in what appear to be more xeric sites. In addition, in areas of sympatry, somewhat fertile, morphologically intermediate hybrids form. We tested the hypothesis that *S. apiana* is better able to withstand drought than *S. mellifera,* and that hybrids are physiologically intermediate, by measuring predawn and midday water potential every month over 15 months at a site in the Santa Ana Mountains. *Salvia apiana* had statistically higher water potentials than *S. mellifera* during summer drought, and the hybrid exhibited intermediate values. The ability of *S. apiana* to maintain water potentials of 3 to 4 MPa greater than *S. mellifera* supports the hypothesis that *S. apiana* can better avoid summer drought. This difference in water relations may account in part for the distributional patterns of these two species.

Salvia apiana Jepson (White Sage) and *S. mellifera* E. Greene (Black Sage) are widespread species of summer deciduous shrubs that often dominate Coastal Sage Scrub (CSS) communities of central and southern California (Epling 1938; Harrison et al. 1971; Axelrod 1978; Kirkpatrick and Hutchinson 1980; Westman 1981) [botanical nomenclature follows Hickman (1993)]. The center of the geographical range of *S. apiana,* however, is over 300 km south of that of *S. mellifera*; where their ranges overlap in southern California, *S. apiana* can occur about 15–30 km farther inland extending into the western margins of the Mojave and Colorado deserts (Fig. 1). Over much of its range, therefore, *S. apiana* experiences a hotter, drier climate than *S. mellifera.* In areas where they are locally sympatric, *S. apiana* exhibits greater relative abundance on more xeric sites (interior, south-facing, well-drained, etc.); whereas, *S. mellifera* is often relatively more abundant in somewhat less xeric sites (Epling 1947; Anderson and Anderson 1954; Kirkpatrick and Hutchinson 1980; Westman 1981; DeSimone and Burk 1992). These distributional differences suggest that *S. apiana* can somehow better withstand summer drought conditions than *S. mellifera,* but this idea has not been tested.

Somewhat fertile hybrids will form where *S. apiana* and *S. mellifera* are sympatric (Epling 1938; Grant and Grant 1964) and the hybrids exhibit clearly intermediate reproductive and vegetative characteristics (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987). The large leaves of *S. apiana* are covered with dense, white pubescence, the smaller, narrower leaves of *S. mellifera* are glabrous and green, and those of the hybrid are intermediate in size, shape and degree of pubescence (Webb and Carlquist 1964). Survival of these hybrid populations primarily at disturbed sites has been used to infer that the hybrids are less competitive than either parent in the absence of disturbance (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987), however, very little is known of the physiological ecology of hybrid plants growing in natural environments (Rieseberg 1995).

Much of the original CSS habitat has been adversely impacted by agriculture and urbanization and is being reduced to increasingly smaller habitat islands (Westman 1981; O'Leary 1990). In spite of these environmental concerns, very little data exists on the physiological ecology of the summer deciduous plants composing this rapidly disappearing community (Mooney 1977; Westman 1981). The purpose of this study is to investigate seasonal patterns of water potential of *Salvia apiana, S. mellifera* and their hybrids in a CSS site where they cooccur. Studying these taxa in a single site where they all experience essentially the same rainfall and environmental conditions is a useful investigative approach, since differences in water potentials will indicate ecophysiological differences in drought response. The specific null hypothesis we tested was that water potentials of these three taxa would not differ (H_o: *S. apiana* = hybrid = *S. mellifera*). If *S. apiana* can maintain significantly more positive water potentials while receiving the same amount of precipitation, this would support the hypothesis

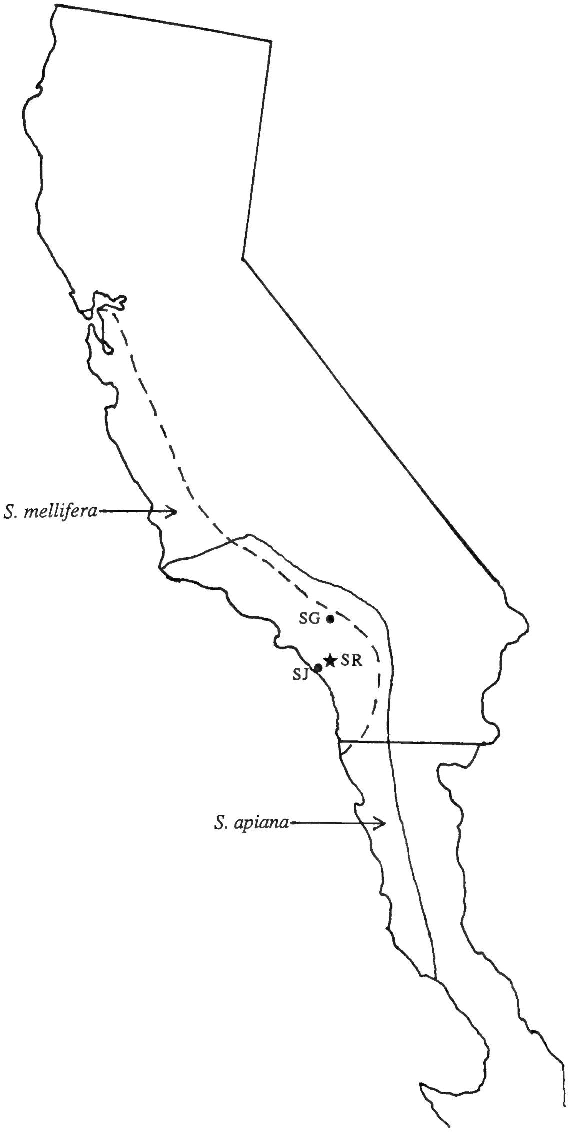

FIG. 1. The geographical ranges of *Salvia apiana* (solid line) and *S. mellifera* (dashed line) based on Figure 1 in Epling (1947), and data in Epling (1938) and Jepson (1939). The primary study site was located at Starr Ranch National Audubon Sanctuary (SR), while secondary sites were located in the San Joaquin Hills (SJ) and in San Gabriel Canyon (SG).

that *S. apiana* is better able to avoid summer drought than *S. mellifera.*

METHODS

The study site was located at Starr Ranch National Audubon Sanctuary in southeastern Orange Co., CA (Fig. 1) which has large stands of relatively intact CSS (DeSimone and Burk 1992). The mediterranean climate is characterized by warm (21°C mean air temperature), dry summers and cool (12°), wet winters with an annual precipitation of 36 cm with most falling from November to April. The primary research site (ca. 1.5 ha) was located at 370 m elevation on a west-facing slope (290° azimuth, 19° slope). The well-drained soils throughout the site are from the Gabino gravelly clay loam series (DeSimone and Burk 1992). The vegetation at the time of the study was about 15 years old and was dominated by *Artemisia californica* Less. and codominated by both species of *Salvia,* several other species of shrubs, and by a fairly high cover of native, perennial bunchgrass (*Nassella* sp.). The *Salvia* taxa were distributed throughout the site with no apparent differences in microhabitat selection.

In early February 1995, 10 sets (=blocks) of plants were selected, with each block containing one individual each of *Salvia apiana, S. mellifera,* and their hybrid all growing within 10 m of one another. Individuals within each block of plants were thus experiencing environmental conditions as similar as is possible in the field. Plants were assigned to respective taxa based on inflorescence structure, and on the size, shape and extent of pubescence of leaves (see Epling 1947; Anderson and Anderson 1954; Webb and Carlquist 1964; Meyn and Emboden 1987). Based on these criteria the hybrids appeared to be F_1's or first generation backcrosses toward *S. mellifera.* A random sample of 5 of these sets was selected for water potential measurements. Predawn and midday water potentials (WP) were measured monthly on 3 shoots per plant using a Scholander-style pressure chamber (Ritchie and Hinckley 1975). Every 2–3 months we switched to the other 5 sets of plants to minimize possible effects of harvesting shoots on plant vigor. Rainfall data were obtained from a gauge at the Starr Ranch headquarters about 1 km away and 70 m lower in elevation.

To confirm the generality of WP responses obtained in the primary site at Starr Ranch, WP was also measured in the summer of 1996 (23–25 June, 10 weeks since last spring rain) at two additional sites in southern California. The San Joaquin Hills site was located about 20 km SW near the Pacific Ocean and the San Gabriel Canyon site was about 60 km NNE in the interior foothills of the San Gabriel Mountains. Mean midday WP of *Salvia apiana, S. mellifera,* and their hybrids was measured on 3 shoots from five plants of each taxa except at the San Gabriel Canyon site where only three hybrid individuals could be located.

To test for differences among species (=taxon effects) and blocks (=microsite effects), data were analyzed using two-way analysis of variance (GLM procedure) on raw data since the data met the assumptions for homogeneity of variance (Levene's test, Minitab 1995). Microsite effects were not significant so all subsequent analysis was based on one-way analysis of variance (one-way procedure) and when significant ($P < 0.05$) taxon-level differ-

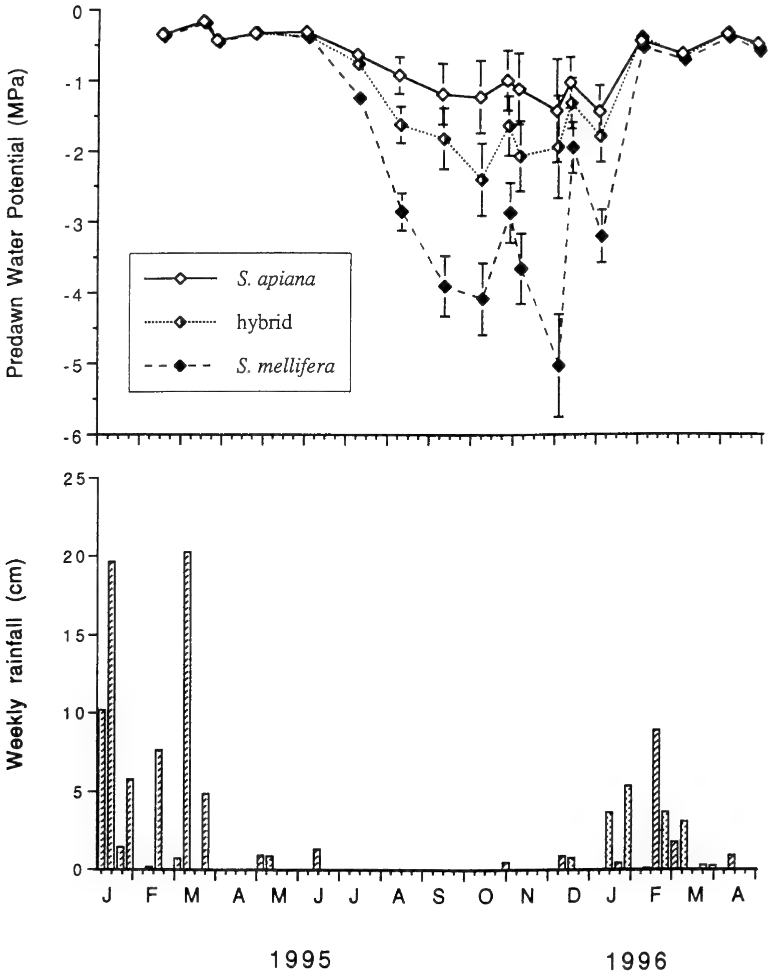

FIG. 2. Rainfall and predawn water potential of *Salvia apiana, S. mellifera,* and their hybrid at the Starr Ranch site. Rainfall is expressed as weekly total (cm), and water potential as the mean (±1 pooled SD) of five plants of each taxa, from January 1995 through April 1996. When no error bars are observed the pooled SD is smaller than the plotted symbol.

ences were detected, Fisher's aposteriori test was used to compare means (Minitab 1995). Data are expressed as means (±1 pooled standard deviation; $1\ \mathrm{SD}_{\mathrm{pooled}} = \sqrt{\text{mean square error}}$ from the ANOVA).

RESULTS

From February through early June of 1995 there were no significant differences in predawn water potential (WP) among taxa, with WP of all taxa being greater than −0.5 MPa (Fig. 2). After the last rain of the season, WP of all taxa started to decline as water loss began to exceed uptake. During summer drought conditions, *S. mellifera* experienced more negative WP than *S. apiana* and the hybrids were intermediate. On all 9 sampling dates from mid-July through early January 1996, WP differed significantly ($P < 0.01$) among taxa and the mean values always ranked in the order of *S. apiana* > hybrid > *S. mellifera.* Following an early autumnal rain of 0.46 cm on 2 November, WP of all taxa rapidly increased within 36 hours (Fig. 2). With no additional rain for two months, WP again declined showing the same pattern of differences among taxa. By early December, WP of *S. mellifera* was 3.6 MPa less than *S. apiana.* This same pattern of increasing and decreasing WP occurred again after a mid-December rain and a subsequent month-long dry period. After the middle of January 1996, relatively large rainstorms occurred almost every week and by early February WP of all taxa increased to above −0.5 MPa as had occurred the previous spring. There were no significant differences among taxa during the wet period from February through the end of the study in late April 1996 (Fig. 2).

The seasonal pattern in midday water potentials among these three taxa throughout the study was

TABLE 1. MEAN MID-DAY WATER POTENTIALS (MPa) OF *SALVIA APIANA, S. MELLIFERA,* AND THEIR HYBRID IN LATE JUNE 1996 AT THREE DIFFERENT SITES: STARR RANCH, SAN JOAQUIN HILLS, AND SAN GABRIEL CANYON (SEE METHODS). Overall significance levels (P) for taxon effects were determined by ANOVA; means within a site sharing the same superscript did not differ significantly ($P < 0.05$) as determined by Fisher's aposteriori comparison of means.

	Starr Ranch	San Joaquin Hills	San Gabriel Canyon
S. apiana	-1.86^a	-1.87^a	-1.15^a
Hybrid	-2.90^b	-3.07^b	-2.64^b
S. mellifera	-3.46^b	-4.76^c	-3.10^b
Pooled SD	±0.49	±0.82	±0.42
P	<0.001	<0.001	<0.001

the same as for predawn values, with all taxa experiencing midday depressions in WP of about −0.4 to −0.6 MP relative to predawn (data not presented). In addition, to confirm the generality of the results obtained at the Starr Ranch site, WP was measured during the early summer drought (23–25 June 1996, 10 weeks since last spring rain) at two additional sites in southern California. At all three sites there were significant differences among taxa, with higher WP exhibited by *S. apiana,* intermediate values by the hybrids, and the most negative values by *S. mellifera* (Table 1).

DISCUSSION

When these taxa co-occur at the same site, *S. apiana* maintains a significantly higher WP during summer drought than *S. mellifera* (Fig. 2, Table 1). The values of WP of *S. mellifera* obtained here are similar to other published reports of decreases from −5 to −9 MPa by the end of the summer drought (Mooney 1977; Gill and Mahall 1986; Kolb and Davis 1994). In San Diego Co., WP for *S. apiana* had decreased to −3.7 MPa at the end of summer drought, whereas WP in *Artemisia californica,* another dominant at many CSS sites, decreased to < −6.5 MPa (Poole and Miller 1975). This limited data from the literature on WP of CSS species also suggest that *S. apiana* does not experience WP as negative as *S. mellifera* or *A. californica. Salvia apiana* appears to be able to "avoid" summer drought relative to *S. mellifera,* which appears to be able to "tolerate" prolonged periods of very low WP (avoidance/tolerance *sensu* Mooney and Dunn 1970). The ability of *S. apiana* to maintain much higher WP during summer drought could account in part for distribution patterns of these species, apparently permitting survival of *S. apiana* in drier sites.

The functional basis for these different responses to summer drought does not appear to be related to summer deciduousness. By the end of summer, *S. apiana* retains ca. 50% of its spring-time leaf area, whereas *S. mellifera* becomes close to fully deciduous (Gill and Mahall 1986). Another possible explanation could be rooting depth. While most CSS species are apparently shallowly rooted, very little quantitative data is available. Hellmers et al. (1955) present limited data which indicate that *S. apiana* (n = 1) may have slightly greater rooting depth than *S. mellifera* (n = 2), 1.5 m compared to 0.6 m deep, respectively. The greater rise in WP immediately after the first rain of the season by *S. mellifera* (Fig. 2) also suggests that at least some of the roots of *S. mellifera* are shallower than those of *S. apiana*; however, it seems unlikely that small differences in rooting depth alone could account for the large differences in WP between the species during summer drought. Perhaps *S. apiana* has more conservative rates of transpirational water loss. Whole-leaf absorptance of photosynthetically active radiation (400–700 nm) is about 0.60 for the whiter leaves of *S. apiana* and almost 0.85 for the green leaves of *S. mellifera* (Ehleringer and Comstock 1989). Lower leaf absorptance in *S. apiana* (pubescent leaves, interior distribution) than *S. mellifera* (glabrous, more maritime) may help reduce leaf temperatures and transpirational demand in ways analogous to pubescent versus glabrous species of *Encelia* (Ehleringer and Cook 1990).

During summer drought, the hybrids exhibited WP intermediate between the parental species (Fig. 2, Table 1). We are aware of few studies on comparative WP of natural hybrids and parental species. In a study of *Arctostaphylos patula* E. Greene (generally more mesic), *A. viscida* C. Parry (generally more xeric), and their hybrids in the Sierra Nevada, the hybrids tended to have WP intermediate between parental species (Ball et al. 1983). The tissue osmotic potentials and elastic modulus of hybrids of two species of *Dubautia* in Hawaii also exhibited values intermediate between parental species, but WP was not measured (Robichaux 1984).

The hypothesis that these hybrids are competitively inferior to the parental species except in disturbed sites (Epling 1947; Anderson and Anderson 1954; Meyn and Emboden 1987) is difficult to test since necessary levels of disturbance were not specified. However, based on seasonal changes of WP at our study sites (Fig. 2, Table 1) it appears that hybrid individuals are not inferior to parental species in terms of competition for soil moisture at least among adult plants. Current hybridization between *S. apiana* and *S. mellifera* has produced individuals that are intermediate relative to parental species in terms of ability to avoid experiencing very low WP during summer drought. Controlled crosses could help elucidate the genetic basis for the different responses to summer drought of these two important CSS species.

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INVENTORY OF THE VASCULAR FLORA OF THE BLAST ZONE, MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

Mount St. Helens is an active volcano located in the Cascade Range of southwestern Washington. The volcano erupted in 1980 and created a wide array of devastated landscapes. Since the eruption, vegetation has been colonizing these new landscapes. In the summers of 1993 and 1994 we inventoried plant species and their relative abundance on the Pumice Plain, Plains of Abraham, Toutle Debris Avalanche, Toutle Ridge, and the crater. We distinguished plants as those found in primary successional uplands and wetlands and in refugia. Refugia are defined as habitat where plants survived the eruption as rootstock. The principal refugia are located between the Pumice Plain and Plains of Abraham.

The current flora is dominated by wind-dispersed invasive species, mainly those in the families Asteraceae, Poaceae, Cyperaceae, and Onagraceae. Large-seeded, late-successional understory species are common in refugia and, to a limited extent, have spread into primary substrates. The species documented comprise 341 species in 178 genera and 53 families. These species comprise 4 Sphenophyta, 6 Pterophyta, 9 Coniferophyta, and 322 Anthophyta (221 Dicotyledonae and 101 Monocotyledonae). Fifty-seven of the species are non-native. Species were surveyed for relative abundance on a three way scale—widespread, locally common, and infrequent. This checklist provides a baseline to judge future composition of the flora and plant invasion patterns.

Mount St. Helens is an active volcano located in the Cascade Range of southwestern Washington in the southern Cascade physiographic Province (46°12′N, 122°11′W). Pre-eruption forests were typical of the montane *Abies amabilis* (Douglas) James Forbes zone (Franklin and Dyrness 1988). After 130 years of inactivity, a major series of eruptions occurred beginning with a violent eruption on 18 May 1980. These eruptions created a diversity of devastated landscapes, and since the eruption, vegetation has been slowly colonizing these new landscapes. The many studies that have been conducted on Mount St. Helens have dramatically increased our understanding of primary successional processes, i.e., the patterns of revegetation of a devastated landscape (del Moral and Bliss 1993; del Moral et al. 1995; del Moral and Wood 1993a, b; Frenzen et al. 1994; Tsuyuzaki and Titus 1996; Wood and del Moral 1987, 1988). However, since no baseline inventory of the taxa present on the mountain has been available for use in assessments of the vegetation, we inventoried the vegetation of the primary-successional substrates on the mountain to provide a base-line species list for future studies.

Cascade Range volcanoes are isolated from other areas of similar elevation. These volcanoes are high elevation islands surrounded by mountain ranges which are more than 1000 m below the volcanic peaks. Thus, a species list of Mount St. Helens vegetation may also be useful in understanding the biogeography of the Cascades volcanoes.

Plant inventories of primary successional environments on volcanoes are infrequent. Tsuyuzaki (1995) provides a species list for Mt. Usu in Japan, which erupted in 1977 and 1978. Other Cascade volcanoes, which erupted thousands of years ago, have been surveyed and the results are contained in Burnett (1985) for Mt. Hood, Wynd (1936) and Applegate (1939) for Mt. Mazama (Crater Lake), Cooke (1940) for Mt. Shasta, Gillett et al. (1961) and Oswald et al. (1995) for Mt. Lassen, Ireland (1968) for the Three Sisters, Jones (1938) for Mt. Rainier, and St. John and Hardin (1929) for Mt. Baker. Other primary successional environments are occasionally inventoried, such as the Thompson and Wade (1991) checklist of the vegetation of a 12-year-old surface-mined coal area in Kentucky.

Plants that successfully invade primary successional landscapes usually have seeds which are

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dispersed over long distances. These small, aerially-dispersed seeds, however, are only marginally capable of developing viable seedlings under harsh conditions. Large-seeded species, although more adapted to surviving as seedlings under harsh conditions, are slower to reach these devastated landscapes (Wood and del Moral 1987; del Moral 1993; del Moral and Bliss 1993). Plants which invade these landscapes fall into groups of functional traits (Tsuyuzaki and del Moral 1995). Functional traits are attributes or life history characteristics that groups of species exhibit in response to similar environmental pressures, and can be used to infer constraints imposed by the environment. Thus, an inventory of the species present on Mount St. Helens provides an opportunity to study ecological traits of invading species.

Environmental Conditions on Mount St. Helens

Climate. The climate of the Mount St. Helens area is montane maritime, i.e., cool, wet winters with a significant snowpack at higher elevations, and warm dry summers. The climate is characterized by abundant yearly precipitation and short periods of drought, typically in July and August. Annual precipitation averages 2373 mm, yet often less than 5% of this falls between June and August. The snow-free growing season extends from April or May until late September, but it usually begins in June and ends by early September. Temperatures range from mean monthly minima of −4.2°C in January and 7.3°C in August to maxima of 0.5°C in January and 22.2°C in July (Spirit Lake Ranger Station (987 m), Anon. 1969; Reynolds and Bliss 1986). Summer temperatures range from 0 to 35°C with a mean ca. 12°C (Reynolds and Bliss 1986). Considerable variation is an important aspect of the Mount St. Helens climate. Precipitation shows dramatic annual variation for the summer months of July and August. Surface soil temperatures are often high on the devastated landscapes, approaching 50°C on tephra surfaces near Spirit Lake (Reynolds and Bliss 1986).

The eruption. The eruption of May 18, 1980, created a wide range of disturbances including tephra (all airborne materials ejected from a volcano, in this case pumice of different sizes), pyroclastic flows (masses of hot dry rock flowing suspended in air), hot airblasts, and lahars (unsorted mud and debris flows). Some of the features created by these disturbances include a pyroclastic flow into Spirit Lake, a 550 km^2 area of blown-down trees bordered by 96 km^2 of scorched trees, a 60 km^2 debris avalanche, and massive mudflows down the major streams draining the area (Lipmann and Mullineaux 1981). Most areas in the perimeter of the devastation were salvage logged and replanted. Because the major force of the eruption was directed laterally to the north, vegetation on the southern flank of the volcano was not destroyed except in a few locations by lahars. The eruption reduced the height of the cone from 2950 m to 2550 m.

The focus of this study is on those areas where the vegetation was essentially eliminated and revegetation was dependent upon the dispersal of propagules from outside the site. These areas are: the Pumice Plain directly north of the cone; the Plains of Abraham to the east of the cone; refugia areas with surviving plants between the Pumice Plain and the Plains of Abraham; the crater breach area where the crater wall was demolished by the lateral eruption; the crater proper, which contains the lava dome; the Toutle Debris Avalanche; and Toutle Ridge between the North and South forks of the Toutle River (Fig. 1). The Pumice Plain, Toutle Debris Avalanche, and the breach contain a variety of both upland and wetland habitats. The Toutle Ridge contains refugia where the vegetation was shielded from the blast. The refugia between the Pumice Plain and Plains of Abraham contains many species which survived the eruption as rootstock.

Pumice Plain

The Pumice Plain ranges in elevation from 1150 to 1300 m and occupies an area of approximately 20 km^2 immediately north of the crater. This area was formed by the deposit of over 100 m of material from the debris avalanche, subsequent pyroclastic flows, and incandescent pumice depositions. It was also repeatedly impacted by later lahars (Lipmann and Mullineaux 1981). The current surface is generally flat or gently sloping with numerous gullies formed by water-erosion dissecting the surface. Before the eruption, the Pumice Plain was vegetated by open coniferous forest (Kruckeberg 1987) with timberline 600–800 m below its climatic limit (Lawrence 1938). Now the area is blanketed by pumice ranging in depth from 10 to 200 m (Lipmann and Mullineaux 1981). Surface pumice particles range in size from 1 mm to 10 cm. Surface colors range from light to dark gray with high surface albedo (Reynolds and Bliss 1986). The surface layer of pumice acts as a mulch that impedes evaporation from below; thus, considerable moisture may be present at lower depths while surface layers may be very dry. In the summer, the surface pumice dries quickly between rains. Therefore, most Pumice Plain habitats probably do not remain moist long enough to allow seedling establishment. At greater depths, however, the soil remains moist so that adult plants rarely suffer from drought (Reynolds and Bliss 1986; Chapin and Bliss 1988; Pfitsch and Bliss 1988; del Moral and Bliss 1993). Substrates with fine particles contain more moisture than areas with coarse particles, and the erosion rills were slightly moister than other microsites (del Moral and Bliss 1993). The Pumice Plain soils are pedologically immature with very low concentrations of N, K, P, organic matter, and microbial biomass (Nuhn 1987; Halvorson et al. 1991, 1992).

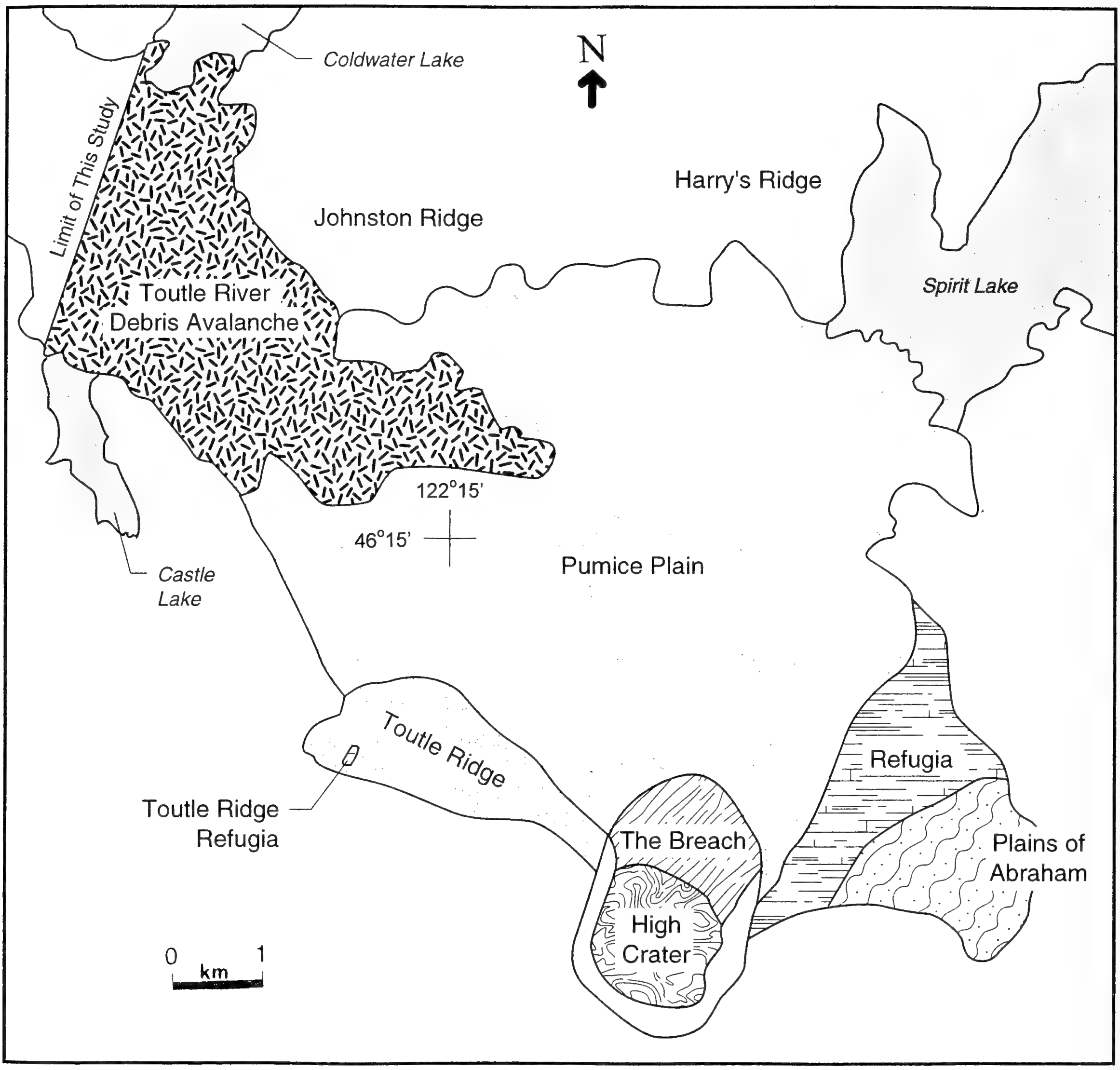

FIG. 1. Map of the study areas on Mount St. Helens, Washington.

Although seed sources for the Pumice Plain are distant (>3 km), the seed rain is dense with the seeds of species commonly found in upwind clearcuts (del Moral and Bliss 1993). In the post-eruption landscape, vegetation is sparse and was, until recently, confined to rills, but has now spread across the Plain. High surface soil temperatures and frequent summer droughts may explain why seedling establishment has been very low in many places on the Pumice Plain since the eruption (del Moral and Bliss 1993).

Four upland habitat types were recognized on the Pumice Plain by del Moral et al. (1995). These were refugia, pumice barrens, pyroclastic surfaces, and drainages. In this study refugia are treated as a separate habitat type, and the other three upland habitats were combined due to high floristic similarity. Scattered on the pyroclastic and stable drainage surfaces are sites that developed dense patches of *Lupinus lepidus* Douglas within two years after the eruption. Initially, these patches were nearly monospecific, but eventually they created biological oases that facilitated invasions of open-site species (Wood and Morris 1990; del Moral 1993; del Moral and Wood 1993a). Since the large seeds of *L. lepidus* are too heavy to be wind dispersed, the patches apparently originated from a few individuals which survived the eruption (Bishop 1996).

The wetland areas of the Pumice Plain are found primarily along permanent and seasonal creeks and in or near springs. Both hot and cold water springs are found near Spirit Lake and both support lush wetland vegetation. The waters of Spirit Lake itself support aquatic vegetation.

Refugia

Refugia exist on north-facing slopes close to the cone. During the eruption, these snow-covered areas provided refuge for many species and enabled them to survive the eruption as rootstock, particularly late-successional forest understory species. These areas were usually steep, and thus erosion quickly removed the pumice layer and exposed the rootstock for resprouting. Refugia have also been invaded by open-site species characteristic of the Pumice Plain (del Moral et al. 1995). Soils of refugia are richer in nutrients than the Pumice Plain (J. H. Titus unpublished) and contain mycorrhizae, which are essential to the survival of many of the late-successional forest understory species (Titus 1995).

Plains of Abraham

The Plains of Abraham is at an elevation of 1400–1450 m in an area of gentle topography, and was barren prior to the eruption (Kruckeberg 1987). Although the main fury of the 1980 eruption was directed northward, the Plains of Abraham, located to the east of the cone, was also devastated by the blast and the resulting pyroclastic flows and lahars (Foxworthy and Hill 1982). In 1980 the Plain was covered by tephra and pockets of silt, and vascular plants were absent. By 1987 wind erosion had removed all fine materials so that the surface now consists of coarse pumice generally 2–5 cm in diameter. Water erosion initiated numerous shallow rills in the pumice-dominated landscape. The pumice on the Plains of Abraham is of pre-1980 origin. Thus soil nutrient levels are higher than on the Pumice Plain because the substrate was formed prior to the most recent eruption (del Moral and Bliss 1993). As on the Pumice Plain, rills were moister than surrounding flat sites, and fine textured soils had twice the moisture content of coarse soils (del Moral and Bliss 1993). Over time, the pumice weathers to a fine sand. Wind removes much of this material so that a "desert pavement" is formed. Areas not eroded by water are essentially smooth, lack sites where seeds might lodge, and dry rapidly. Primary succession on the Plains of Abraham is proceeding under highly stressful conditions, and plant cover is still relatively sparse. Microsite variation is distinct with plants much more prevalent on rill edges (del Moral and Wood 1993a).

Toutle River Debris Avalanche

The debris avalanche was formed by a massive landslide of the north flank of the mountain that occurred during the eruption. The debris material averages 45 m in depth, 2 km in breadth, and extends 25 km from the crater along the North Fork of the Toutle River (Lipman and Mullineaux 1981). Plant devastation on the debris avalanche was virtually complete (Adams et al. 1982); however, rare individuals of at least 20 species survived on the debris deposit, the most widespread being *Epilobium angustifolium* L. ssp. *circumvagum* Mosq., *Cirsium arvense* (L.) Scop., and *Lupinus latifolius* J. Agardh. These individuals apparently resprouted from plant fragments that had been transported by the debris slide. The most common woody species to survive were willows, which regenerate readily from root and stem fragments. These willows were found primarily in the western portion of the avalanche and farthest from the crater (Dale 1986). Recovery of the vegetation was initiated within the first year after the eruption, and rapid colonization by *Alnus rubra* Bong. and other riparian species has occurred since that time (Adams et al. 1987). Recovery has been slow in other areas, however, especially in areas closer to the mountain. The primary seed source for the debris avalanche is seed rain from adjacent scorched pre-eruption clearcuts, heavily vegetated by herbaceous perennials that produce copious light, wind-dispersed plumed seeds (Franklin et al. 1985; Dale 1989).

Debris avalanche soils have an adequate balance between moisture retention and aeration properties, and percent organic matter is low but adequate for plant growth (Adams and Dale 1987). The soils are sandy or silty sand with the greater than 2 mm fractions comprising about 65% of soil samples.

A massive reseeding effort was conducted in 1980 and 1981 on the Toutle River debris avalanche using non-native grasses and forbs to reduce erosion. Many of the seeded species did not grow well on the new substrates, and there is no evidence that erosion was reduced (Dale 1989; Tsuyuzaki 1995). However, many other seeded species survived and now dominate much of the mudflow. This dominance by invasive non-native species may be slowing natural succession. Our survey was conducted on the eastern portion of the mudflow and terminated at a line roughly connecting the south side of Coldwater Lake to the northwest side of Castle Lake. This boundary line is at an elevation of approximately 760 m (Fig. 1) and was selected so as to avoid heavily artificially seeded areas. Much of the habitat west of our study area is dominated by non-native species, particularly legumes.

Wetlands on the Toutle debris avalance appear to be unique and have not been studied. Four distinct types can be distinguished based on hydrological and physical characteristics. Deep potholes created by large masses of entrained ice are now occupied by wetlands composed of temporary snow melt and rain water ponds or permanent spring-fed ponds. Broad cattail-dominated marshes spread across the mudflow. Riparian vegetation along many creeks is abundant, and numerous springs on the mudflow support a diverse flora. Two types of riparian habitat are found on the debris avalanche: unstable riparian areas that support a sparse herbaceous vegetation, and more stable riparian areas dominated by dense willow thickets.

Toutle Ridge

Toutle Ridge is an elevated area located between the North and South Forks of the Toutle River. This area was devastated by the eruption, although in a somewhat peripheral manner similar to that of the Plains of Abraham. There are two small refugia on the Ridge, but no wetlands. The study area ends to the west of the Ridge where blown-down trees are common and the devastation was less intense.

Crater

Since the creation of a crater by the eruption of 1980, a lava dome has been growing in its center. The crater can be separated into two parts: the breach, which is a wide area where the lateral eruption removed the north face of the mountain, and the high crater, which contains the lava dome. The breach contains both upland and wetland habitats from small springs. Creek banks are too unstable to support vegetation. The high crater is mostly barren upland. Very small wetland areas were created on the lava dome where stream from fumaroles continues to condense. These condensation areas principally support moss and algae, but a few wind dispersed vascular plants have also colonized these unusual sites.

METHODS

Census technique. To complete the current inventory, surveys were conducted during the summers of 1993 and 1994. The entire inventory area was examined several times over the season, and locations were recorded for all species present. The species list was compiled from observations noted during these surveys. Species were categorized into three abundance categories: widespread, locally common, and infrequent. These are qualitative rankings and are not based on quantitative data although in some cases quantitative data assisted in assigning the abundance rank. "Widespread" indicates that the plant was abundant throughout the inventory area. "Locally common" indicates a plant that was only locally common or occasionally a plant with a more scattered distribution. "Infrequent" describes plants which were difficult to detect.

Determinations and nomenclature. Species determinations were made using the *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973) with updated nomenclature from *The Jepson Manual: Higher Plants of California* (Hickman 1993). Voucher specimens were deposited at the University of Washington herbarium.

Pre-eruption Conditions

Before 1980, the 2950 m Mount St. Helens was surrounded by a patchwork of forested and clearcut land in varying stages of reforestation. The forests were typical of the *Abies amabilis* zone (Franklin and Dyrness 1988), composed primarily of *Abies amabilis, Abies procera* Rehder, *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii,* and *Tsuga heterophylla* (Raf.) Sarg. (Lawrence 1938). Clearcut land was generally replanted with *P. menziesii* and *A. procera* seedlings and had a lush cover dominated by herbs (e.g., *Epilobium angustifolium* and *Anaphalis margaritacea* (L.) Benth. & Hook.) and shrubs (e.g., *Acer circinatum* Pursh and *Rubus ursinus* Cham. & Schldl.). The riparian vegetation along the Toutle River was comprised primarily of deciduous trees (*Alnus rubra, Populus balsamifera* L. ssp. *trichocarpa* (Torrey & A. Gray) Brayshaw, *Salix scouleriana Hook.* and *Salix sitchensis* Bong.).

Before the eruption the vegetation on the Plains of Abraham was sparse (Kruckeberg 1987), and timberline was 600–800 m below its climatic limit. The forest that occurred was composed only of scattered conifers dominated by *Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa, Polygonum newberryi* Small, and *Penstemon cardwellii* (Lawrence 1938).

Previous botanical exploration. The pre-eruption Mount St. Helens flora was considered to be depauperate in species richness in comparison with other Northwestern Pacific volcanic summits due to geologically recent eruptions and mudflows (Kruckeberg 1987; del Moral and Wood 1986, 1988). This geological activity caused the volcano to have a suppressed timberline (Lawrence 1954). Since the eruption, researchers have sought an accurate picture of the pre-eruption assemblage of individual plant species, the plant communities in which they resided, and how those plant communities related to other nearby volcanic massif communities. Unfortunately, no comprehensive flora exists. A relatively complete pre-eruption flora is inferred by inventories contained within three publications, *Flora of the State of Washington* (Piper 1906), *The Flora of Mt. St. Helens* (St. John 1976), and *Plant Life on Mount St. Helens before 1980* (Kruckeberg 1987).

The first organized botanical exploration of Mount St. Helens and vicinity was conducted in 1898 by Dr. F. V. Colville, principal botanist of the U.S. Department of Agriculture. However, no flora was published until Harold St. John researched Colville's journals and published a brief accounting (St. John 1976). According to the journal, Colville traveled and collected throughout Oregon and Washington. His collections of the Mount St. Helens area appear to be limited to the south side of the mountain since he approached from the south via the Lewis River, camped at Merrill Lake, and then proceeded up the Kalama River to Three Buttes Camp (1220 m) at the southwest base of Mount St. Helens on 19 August 1898. From there he ascended and collected on the mountain. He listed 77 species; a partial collection of these are deposited at the Smithsonian Institution. Colville's flora remains unpublished, but his collection was used by C. V. Piper to construct a flora of the state of Washington, published by the U.S. National Herbarium in 1906 (Piper 1906).

The most comprehensive inventory of the Mount St. Helens flora was conducted in 1925 by Harold St. John and students including C. S. English, Jr. During an eleven-day visit in August 1925, they collected 315 plant species. Eight days were spent botanizing the region surrounding Spirit Lake and the north slope of the mountain, and one day climbing to the summit. An additional two days were spent collecting on the south side, exploring the upper valley of the Lewis River and the area around the present town of Cougar. The result of the inventory was not published until 1976, fifty years after the fieldwork was completed (St. John 1976). The collection is stored at the Washington State University Marion Ownbey Herbarium in Pullman, Washington.

The last documented botanical exploration of Mount St. Helens prior to the eruption was conducted in 1979 by Dr. Arthur Kruckeberg and eighteen members of the Washington Native Plant Society (Kruckeberg 1979). They identified approximately 86 plant species. They limited their investigation to timberline and above, beginning at Timberline Camp and the adjacent parking lot (1340 m—this area is now part of the Pumice Plain), and ascending to just below Sugar Bowl on the NE face (2075 m). Additional observations were made on a second day's traverse of Windy Pass (1495 m) and across the Plains of Abraham to the head of Ape Canyon (1280 m) on the southeast flank of the mountain.

DESCRIPTION OF CURRENT VEGETATION

Mount St. Helens is surrounded by thousands of hectares of recent clearcuts that are thickly vegetated with weedy wind-dispersed invasive species. The clearcuts provide a seed source for the recently created landscapes found on the volcano (del Moral and Bliss 1993). Thus, weedy invasive species typical of clearcuts were found at all sites examined during our surveys. Upland primary successional landscapes were similar in vegetation, except for the Toutle River Debris Avalanche which had additional dense stands of non-native legumes. The refugia have a vegetation distinct from the primary successional landscapes. Tree species were infrequent or only locally common. However, dense groves of trees did not occur on the Toutle River Debris Avalanche.

An unusual species that occurred in several of the areas was *Salix exigua* Nutt. This species generally occurs to the east of the Cascades. The probable cause for the presence of this species is that the open primary successional habitats of Mount St. Helens provide colonization sites for widely dispersed wind-dispersed species such as *Salix* species.

TABLE 1. NUMBER OF NATIVE AND NON-NATIVE SPECIES IN HABITATS OF THE MOUNT ST. HELENS BLAST ZONE.

Habitat	Number of native species	Number of non-native species
Pumice Plain uplands	151	20
Pumice Plain wetlands	110	11
Refugia	160	10
Plains of Abraham	65	4
Toutle Debris Avalanche uplands	146	44
Toutle Debris Avalanche wetlands	114	42
Toutle Ridge uplands	86	5
Toutle Ridge refugia	93	6
Breach uplands	47	5
Breach wetlands	27	5
High Crater	14	3

Pumice Plain

Upland. The barren areas of the Pumice Plain are floristically consistent across the Plain and have low cover. *Anaphalis margaritacea, Hypochaeris radicata* L., *Lupinus lepidus, Epilobium angustifolium, Penstemon cardwellii* Howell, *Penstemon serrulatus* Menzies, *Hieracium albiflorum* Hook., *Carex mertensii* Prescott, *Carex spectabilis* Dewey, *Agrostis pallens* Trin., *Agrostis scabra* Willd., and *Juncus parryi* Engelm. are typically among the leading dominants in all barren sites. Densely vegetated areas of the Pumice Plain tend to be dominated by these same species. Across the barren areas of the Pumice Plain, *L. lepidus* also forms extensive densely vegetated patches. One hundred and seventy-three species were found on Pumice Plain uplands (Tables 1 and 2).

Wetland. Juncus and *Salix* species often dominate springs and wet areas, especially *Salix sitchensis* Bong., *Juncus bufonius* L., and *Juncus acuminatus* Michaux. *Equisetum arvense* L. also occupies broad wet areas. *Epilobium watsonii* Barbey, *Salix sitchensis,* and *Mimulis guttatus* DC. are common along creeks. The waters of Spirit Lake contain *Potamogeton natans* L., *Myriophyllum sibiricum* V. Komarov, and *Ranunculus aquatilis* L. Extensive algal mats occur in both thermal and cold water springs. Wetland areas are usually more thickly vegetated and diverse than upland areas. One hundred and twenty-one species were found in Pumice Plain wetlands.

Refugia

Refugia are dominated by woody species such as *Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A. Löve & D. Löve, *Ribes laxiflorum* Pursh, *Rubus*

TABLE 2. CHECKLIST OF VASCULAR PLANT SPECIES IN PRIMARY SUCCESSIONAL HABITATS ON MOUNT ST. HELENS. w = widespread; c = locally common; i = infrequent; 1 = Pumice Plains uplands; 2 = Pumice Plain wetlands; 3 = Refugia; 4 = Plains of Abraham; 5 = Toutle Debris Avalanche uplands; 6 = Toutle Debris Avalanche wetlands; 7 = Toutle Ridge uplands; 8 = Toutle Ridge refugia; 9 = Breach uplands; 10 = Breach wetlands; 11 = High Crater; E = exotic non-native species.

Species	1	2	3	4	5	6	7	8	9	10	11
Cupressaceae											
Thuja plicata	i				i						
Pinaceae											
Abies amabilis	i		i		i		i	i	i		i
Abies lasiocarpa			i	i					i		i
Abies procera	i		i	i	c		c	w	i		i
Pinus contorta var. *latifolia*	i			i	i		i	i			
Pinus monticola	i				i						
Pseudotsuga menziesii	c		i	i	i		i	i			
Tsuga heterophylla	i		i	i	c		i	i			
Tsuga mertensiana			i	i							
Equisetaceae											
Equisetum arvense	c	w			c	w					
Equisetum fluviatile						i					
Equisetum hyemale ssp. *affine*		i				i					
Equisetum palustre						i					
Blechnaceae											
Blechnum spicant	i	i	i	i	i						
Dennstaedtiaceae											
Pteridium aquilinum var. *pubescens*			i		i						
Dryopteridaceae											
Athyrium filix-femina	c	i	c	i	c		i	c	c	c	
Cystopteris fragilis			i		i						
Polystichum munitum	c	i	c	i	c	i	i	c	c	c	
Pteridaceae											
Cryptogamma cascadensis	i		i	i					i		
Aceraceae											
Acer circinatum					i			c			
Acer glabrum var. *douglasii*			i					c			
Acer macrophyllum	i										
Apiaceae											
Heracleum lanatum			c								
Lomatium martindalei	i		c				w	i	i		
Oenanthe sarmentosa		i	i								
Osmorhiza purpurea			i					c			
Araliacene											
Oplopanux horridum			i								
Asteraceae											
Achillea millefolium	c		w	i	c		w	w	i		
Agosteris aurantiaca	i		i	i	i		c	i	i	i	
Agoseris glauca var. *glauca*	i		i	i	i		c	i	i	i	
Agoseris grandiflora	i		i		i		i	i			
Agoseris heterophylla	i	i									
Anaphalis margaritacea	w	c	w	w	w	i	w	w	w	w	c
Antennaria rosea	i		i		i		i				
Antennaria umbrinella	i		i		i		c				
Arnica cordifolia var. *cordifolia*	i		i				i	i			
Arnica latifolia var. *gracilis*	c		c	c			c	c	w		
Arnica mollis	i										
Arnica nevadensis	i								i		
Aster brachyactis		i				i					
Aster frondosus		i									
Aster ledophyllus var. *ledophyllus*	c	i	i	i	i		w	w	c		
Aster modestus			i								
Cirsium arvense var. *horridum* (E)	c	w	c		c	c	i	i	c	i	
Cirsium vulgare (E)	i	i	i		c	c					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Conyza canadensis	i	i			c	c					
Crepis capillaris (E)					i	i					
Erigeron aliceae	i	i	i		i	i					
Erigeron peregrinus var. *callianthemus*	i	i	i		i	i					
Eriophyllum lanatum var. *lanatum*	i		c		i				i		
Gnaphalium canescens ssp. *thermale*	c				c	i					
Gnaphalium purpureum					i	i					
Gnaphalium uliginosum (E)	i	c			w	w					
Hieracium albiflorum	w		w	w	w	i	w	w	w	i	i
Hieracium gracile	c			i					i	i	
Hypochaeris radicata (E)	w	w	w	w	w	w	c	w	w	i	i
Lactuca muralis (E)	i	i			i	i					
Lactuca serriola (E)					i	i					
Lapsana communis (E)					i	i					
Leontodon taraxacoides spp. *taraxacoides* (E)			i		i	i					
Leucanthemum vulgare (E)	i				c	i					
Luina hypoleuca	i		i	i							
Petasites frigidus var. *palmatus*	i	w	i		c	c			c	i	
Senecio fremontii var. *fremontii*	i										
Senecio jacobaea (E)	i				c	i		i	i	i	
Senecio sylvaticus (E)	w	i	i	i	c	c	i	i	c	i	i
Senecio triangularis var. *triangularis*	i				i						
Senecio vulgaris (E)	i										
Solidago candensis ssp. *elongata*					i	i					
Sonchus arvensis (E)						i					
Sonchus asper ssp. *asper* (E)	i	w	i		i	w					
Sonchus oleraceus (E)						i					
Taraxacum officinale (E)	i		i		i	i					
Trimorpha lonchophylla		i									
Berberidaceae											
Achlys triphylla ssp. *triphylla*			i		i						
Vancouveria hexandra			c		i			c			
Betulaceae											
Alnus rubra	i		i		w	w					
Alnus viridis ssp. *sinuata*	w	i	w		i	i	i	w			
Boraginaceae											
Myosotis laxa					c	i					
Brassicaceae											
Cardamine oligosperma var. *oligosperma*			i		i	i					
Cardamine pensylvanica	i		c		i	i					
Draba verna					i	i					
Rorippa curvisiliqua var. *lyrata*		c			i	c					
Rorippa nasturtium-aquaticum		i				i					
Rorippa palustris var. *occidentalis*		i									
Callitrichaceae											
Callitriche stagnalis (E)						w					
Campanulaceae											
Campanula rotundifolia			i								
Campanula scouleri	i		c					i			
Caprifoliaceae											
Linnaea borealis var. *longiflora*								c			
Lonicera ciliosa					i						
Sambucus racemosa var. *arborescens*			w		i	i	i	w			
Caryophyllaceae											
Arenaria serpyllifolia ssp. *serpyllifolia* (E)	i		i	i	i	i					
Cerastium arvense			i		i			i			
Cerastium nutans			i		c	i		i			
Moehringia macrophylla		i			i	i		c			
Sagina saginoides		i				c					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Silene parryi	i										
Spergula arvensis ssp. *arvensis* (E)					i	i					
Spergularia marina						i					
Spergularia rubra (E)	i	i	i	i	i	i	i	i	i	i	i
Stellaria borealis ssp. *stichana*					c	c					
Stellaria calycantha	i	i	i		i	i					
Stellaria crispa	i	i	c		i	c	i	i			
Stellaria nitens					c	c					
Celastraceae											
Paxistima myrsinites					i						
Cornaceae											
Cornus canadensis					i			c			
Crassulaceae											
Sedum oreganum	i	i	i								
Ericaceae											
Arctostaphylos nevadensis	i		i	i			c	w			
Arctostaphylos uva-ursi								i			
Gaultheria ovatifolia			i		i						
Gaultheria shallon			c		i						
Menziesia ferruginea var. *ferruginea*			w								
Orthilia secunda					i						
Phyllodoce empetriformis			i								
Pyrola asarifolia			i								
Rhododendron albiflorum			i								
Vaccinium membranaceum	i		w	i	i		w	w			
Vaccinium ovalifolium			c				i	i			
Vaccinium parvifolium	i		i		i		i	i			
Fabaceae											
Cytisus scoparius (E)	i										
Lotus corniculatus (E)					w	c					
Lotus purshianus var. *purshianus*					w	w					
Lupinus latifolius var. *latifolius*	w	i	w	w	w	w	w	w			
Lupinus lepidus var. *lepidus*	w	i	i	w	w	w	w		i		
Medicago lupulina (E)					w	w					
Melilotus alba (E)					w	w					
Trifolium microcephalum					i						
Trifolium pratense (E)					w	w					
Trifolium repens (E)	i	i			w	w					
Gentianaceae											
Centaurium erythraea (E)					i	w					
Grossulariaceae											
Ribes bracteosum			i								
Ribes howellii			c					i			
Ribes lacustre	i		w				i	w			
Ribes laxiflorum			w				i	w			
Ribes sanguineum var. *sanguineum*					i						
Ribes viscosissimum var. *viscosissimum*			i								
Halogaraceae											
Myriophyllum hippuroides		i				i					
Myriophyllum sibiricum		i				i					
Hydrophyllaceae											
Hydrophyllum fendleri var. *albifrons*					i						
Phacelia leptosepala	c		c	i	i		c	c			
Phacelia mutabilis	i		i	i	i		i	i			
Phacelia nemoralis ssp. *oregonensis*	c		c	i	i		i	i			
Hypericaceae											
Hypericum perforatum (E)					i						

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Onagraceae											
Circaea alpina ssp. *pacifica*						i					
Epilobium anagallidifolium	c		i	c	c	i	i	i	i	c	
Epilobium angustifolium	w	w	w	w	w	w	i	i	w	w	i
Epilobium brachycarpum	c	i			w	w			c		
Epilobium ciliatum ssp. *ciliatum*	i	w	i		c	w				w	
Epilobium clavatum	c	i	i	i			i	i	i	c	
Epilobium glaberrimum ssp. *fastigiatum*	i	i	i		i	i			i	i	
Epilobium glaberrimum ssp. *glaberrimum*	i	i	i		i	i					
Epilobium hornemannii ssp. *hornemannii*	i	i	i						i	i	
Epilobium lactiflorum	i	i	i						i	i	
Eiplobium luteum		i	i								
Epilobium minutum	c	i			c	i					
Oxalidaceae											
Oxalis oregana					i						
Papaveraceae											
Dicentra formosa	i		i								
Plantaginaceae											
Plantago lanceolata (E)	i					i					
Plantago major var. *major* (E)						i					
Polemoniaceae											
Collomia heterophylla					w	c					
Collomia larsenii							c				
Collomia tinctoria					i	i					
Phlox diffusa			i				w				
Phlox gracilis					i	i					
Polygonaceae											
Eriogonum pyrolifolium var. *coryphaeum*	w		i	w			w		i		
Polygonum douglasii ssp. *douglasii*	i				i						
Polygonum minimum	w	i	c	i	c	c	w	i			
Polygonum newberryi				i			w	i			
Polygonum persicaria (E)						i					
Rumex acetosella (E)	i		i			i	w	w			
Rumex crispus (E)						i					
Rumex obtusifolius (E)						i					
Portulacaceae											
Calyptridium umbellatum var. *caudiciferum*	w			w			w	i	w		i
Claytonia lanceolata var. *lanceolata*			i								
Claytonia sibirica		i	c		i	i		c			
Montia parvifolia var. *parvifolia*	w	c	i		i	i					
Primulaceae											
Trientalis latifolia			i		i						
Ranunculaceae											
Actaea rubra			i					i			
Aquilegia formosa			w								
Ranunculus aquatilis var. *capillaceus*		c				c					
Ranunculus aquatilis var. *hispidulus*		c				c					
Ranunculus sceleratus var. *sceleratus*		c				i					
Trautvetteria caroliniensis var. *occidentalis*			i								
Rosaceae											
Amelanchier alnifolia			c				i	i			
Aruncus dioicus var. *pubescens*	i		w	i	i		i	c			
Fragaria virginiana ssp. *platypetala*	i		w	i	c	c	w	w	i		
Holodiscus discolor	i				i						
Luetkea pectinata	w		w	w			w	i	c	w	
Potentilla anserina ssp. *anserina*						w					

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Potentilla glandulosa ssp. *glandulosa*	i										
Prunus emarginata					i						
Rosa gymnocarpa	i		i		i			i			
Rubus discolor (E)					i						
Rubus idaeus var. *gracilipes*					i						
Rubus laciniatus (E)					i						
Rubus lasiococcus	i		w	i	i		c	w			
Rubus leucodermis			i		i			i			
Rubus parviflorus	i		w	i	i		i	c			
Rubus spectabilis	i		w	i	i		i	w			
Sibbaldia procumbens							c				
Sorbus sitchensis var. *grayi*			w				i	w	i		
Spiraea betulifolia			i		i						
Spiraea densiflora var. *densiflora*			i								
Spiraea douglasii			i								
Rubiaceae											
Galium asperrimum					i						
Galium triflorum					i						
Salicaceae											
Populus balsamifera ssp. *trichocarpa*	c	i	i	i	w	c	i	i			
Populus tremuloides					c						
Salix commutata	i	i									
Salix exigua ssp. *exigua*		i			i	i					
Salix geyeriana					i	i					
Salix lucida ssp. *lasiandra*	i	c	i		i	c					
Salix scouleriana	i	i	i		i	i					
Salix sitchensis	w	w	w	c	w	w	w	c	c	c	i
Saxifragaceae											
Heuchera glabra	i	i	i		i	i					
Heuchera micrantha	i	i	i								
Mitella breweri	i	i	c								
Mitella pentandra	i	i	c								
Saxifraga arguta		i	i								
Saxifraga ferruginea var. *macounii*	w	i	w	w	c		i		c		
Saxifraga tolmiei var. *tolmiei*	i		i								
Tellima grandiflora			c								
Tiarella trifoliata var. *unifoliata*	i		c					c			
Tolmiea menziesii	i	i	c		i	i					
Scrophulariaceae											
Castilleja miniata ssp. *miniata*	c		w		i	i	w	w			
Digitalis purpurea (E)					i						
Mimulus floribundus		i									
Mimulus guttatus		c				c					
Mimulus lewisii		c	w								
Nothochelone nemorosa	c		c	i	c	i	c	c			
Parentucellia viscosa					i	c					
Pedicularis racemosa var. *racemosa*	i		i				c				
Penstemon cardwellii	w		w	w	w		w	w	i		
Penstemon confertus							i				
Penstemon rupicola	i		i								
Penstemon serrulatus	w		c	i	c	i	c	c			
Verbascum thapsus (E)					i						
Veronica americana						c					
Veronica officinalis (E)					i	c					
Veronica serpyllifolia ssp. *humifusa*					i	i					
Valerianaceae											
Valeriana sitchensis ssp. *sitchensis*			w					w			
Violaceae											
Viola sempervirens	i		c		i	i	i	i			

TABLE 2. CONTINUED

Species	1	2	3	4	5	6	7	8	9	10	11
Cyperaceae											
Carex canescens		i			i	i					
Carex deweyana ssp. *leptopoda*					i						
Carex illota	i										
Carex lenticularis var. *lipocarpa*		i				c					
Carex leporinella	i										
Carex mertensii	w	w	w	w	w	w	w	w	w	w	i
Carex microptera	w	w	c	w	w	i	w	c	c		
Carex ovalis	i										
Carex pachystachya	w	c	i	w	i	c	c				
Carex paysonis	w	c	w	w			w	w	i	i	i
Carex phaeocephala	c	c		i							
Carex praticola	c	i	c		c						
Carex preslii	i				i						
Carex proposita	i										
Carex rossii	i		w	i	i		w	c			
Carex spectabilis	w	w	w	w	w	c					
Carex stipata var. *stipata*	i										
Carex subfusca	c	c	c	i	c	i					
Eleocharis macrostachya		w				w					
Scirpus acutus var. *occidentalis*		c				c					
Scirpus americanus		i				c					
Scirpus maritimus		c				c					
Scirpus microcarpus		i				c					
Scirpus tabernaemontani		c				c					
Juncaceae											
Juncus acuminatus		w				w					
Juncus articulatus		w				w					
Juncus bolanderi		w				w					
Juncus bufonius	i	w				w					
Juncus effusus var. *gracilis*		c				w					
Juncus ensifolius var. *montanus*		w				w				w	
Juncus mertensianus	w	w	w	c	i	i	i	i	c	w	i
Juncus nevadensis var. *badius*			i								
Juncus parryi	w	w	w	w	i	i	c	i	w	w	
Juncus regelii	i	c	i			w				c	
Juncus tenuis var. *tenuis*	i	w				w					
Luzula hitchcockii	i										
Luzula multiflora ssp. *frigida*	i										
Luzula parviflora	w	w	w	i	i	i	w	i			
Lemnaceae											
Lemna minor						c					
Liliaceae											
Clintonia uniflora		i	w		i		c	w			
Disporum smithii			c					c			
Lilium columbianum			c		i						
Maianthemum dilatatum					i			i			
Smilacina racemosa	i		w				i	w			
Smilacina stellata	i	i	c				i	c			
Streptopus amplexifolius var. *americanus*	i		c								
Trillium ovatum ssp. *ovatum*			c								
Veratrum viride	i	i	w				i	w			
Xerophyllum tenax	i	i	w				i	i			
Orchidaceae											
Platanthera stricta	i		i								
Spiranthes romanzoffiana var. *romanzoffiana*	i	i			i	i					
Poaceae											
Achnatherum occidentale ssp. *occidentale*	c		i	i	i		w	w	i		i
Agrostis capillaris (E)	i				i	i					
Agrostis exarata ssp. *exarata*	i	w	i		c	w	c	c	c	c	

Table 2. Continued

Species	1	2	3	4	5	6	7	8	9	10	11
Agrostis exarata var. *monolepsis*	i	w	i		c	w	c	c	c	c	
Agrostis exarata ssp. *minor*	i	w	i		c	w	c	c	c	c	
Agrostis gigantea (E)					i	i					
Agrostis pallens	w	w	w	w	c	i	w	w	w	c	
Agrostis scabra	w	i	w	c	w	i	w	i	w	c	i
Agrostis stolonifera (E)					i	i					
Agrostis thurberiana	i	i	i		i	i					
Aira caryophyllea (E)					i						
Alopecurus geniculatus					i	i					
Anthoxanthum odoratum (E)					c	i					
Bromus sitchensis var. *sitchensis*	i		i		i		i	i			
Calamagrostis canadensis var. *canadensis*	i	c	i	i		i			c		
Calamagrostis howellii	c										
Calamagrostis sesquiflora	i		i	i							
Cinna latifolia	i	c	i		i	i	i				
Cynosurus echinatus (E)						c					
Dactylis glomerata (E)					c	i					
Danthonia intermedia	i	i			c	i					
Deschampsia atropurpurea	c	i	i	i			i				
Deschampsia danthonioides		i				i					
Deschampsia elongata	c	c			i	c					
Elymus elymoides ssp. *elymoides*	c		c	c	i		w	i	i	i	i
Elymus glaucus ssp. *glaucus*	i	i	i		i	i	i	i			
Elymus glaucus ssp. *jepsonii*	i		i		i	i					
Elymus glaucus ssp. *virescens*	i	i	c				i				
Elymus trachycaulus ssp. *subsecundus*	i		i		i						
Festuca arundinacea (E)	i				i	i					
Fesetuca idahoensis var. *idahoensis*							i				
Festuca occidentalis	i	i			i	i					
Festuca rubra var. *rubra*					i	i					
Glyceria elata	i	i			i	i					
Holcus lanatus (E)	i	i			w	w					
Hordeum jubatum		i									
Lolium multiflorum (E)					i						
Lolium perenne (E)					i						
Lolium temulentum (E)					i						
Phleum alpinum	i		i				i	i			
Phleum pratense (E)					i						
Poa compressa (E)		i									
Poa nervosa var. *nervosa*					i						
Poa pratensis ssp. *pratensis* (E)					i						
Poa secunda ssp. *secunda*	w		i	w			i	i			
Poa trivialis (E)					i						
Trisetum canescens	i								i		
Trisetum cernuum	i	i									
Trisetum spicatum	i		i	i	i		i	i	i	i	
Vulpia myuros var. *myuros* (E)					w	i					
Potamogetonaceae											
Potamogeton foliosus var. *macellus*		c				c					
Potamogeton natans		c				c					
Potamogeton pectinatus		c				c					
Typhaceae											
Typha latifolia		w				w					

spectabilis Pursh, *Rubus parviflorus* Nutt., *Vaccinium membranaceum* Hook., *Aruncus sylvester* Kostel., and *Penstemon cardwellii,* and herbs such as *Agrostis pallens, Lupinus latifolius, Luzula parviflora* (Ehrh.) Desv., *Carex rossii* Boott, and *Anaphalis margaritacea.* Overall, 174 species were found in the refugia. These areas are quite diverse and contain an assortment of late-successional forest understory species which have persisted since before the eruption as well as barren site species which have invaded the refugia (see del Moral et al. 1995).

Plains of Abraham

The sparse vegetation of the Plains of Abraham is also dominated by those species with seeds that disperse well on the wind. *Anaphalis margaritacea* is the most widespread species, with *Hypochaeris radicata* L., *Epilobium angustifolium, Hieracium albiflorum, Agrostis pallens* and *Calyptridium umbellatum* (Torrey) E. Greene also common. One *Pinus contorta* Loudon var. *latifolia* Engelm. survived the eruption on the Plains of Abraham. The Plains of Abraham does not contain *Lupinus lepidus* patches and is less diverse than the Pumice Plain with a total of 69 species detected.

Toutle Debris Avalanche

The Toutle Debris Avalanche has numerous and diverse landscapes. Non-native species, from artificial seeding and natural wind-dispersed invasion, dominate much of the mudflow, especially upland environments. Non-native species are less common in wetlands.

Uplands. The uplands are largely dominated by non-native herbaceous species. There are broad areas dominated by *Melilotus alba* Medikus, which was probably a constituent in seed mixes. *Lotus corniculatus* L., *Lotus purshianus* (Benth.) Clements & E. G. Clements var. *purshianus, Medicago lupulina* L., *Trifolium pratense* L., and *Trifolium repens* L. are prevalent across the uplands. The annual *Vulpia myuros* (L.) C. Gmelin is also common. *Anaphalis margaritacea, Hypochaeris radicata, Epilobium angustifolium, Epilobium brachycarpum, Agrostis pallens,* and *Collomia heterophylla* Hook. are widespread. *Alnus rubra* Bong. stands are prevalent, and *Abies procera* Rehder regeneration is plentiful in places. One hundred and ninety species were found on Toutle Debris Avalanche uplands. The lower elevation, greater proximity to seed sources, and artificial seedings of the Toutle mudflow created conditions which promoted much denser vegetation than is found on the Pumice Plain and Plains of Abraham. In addition, the Toutle River Debris Avalanche is located in a valley below heavily vegetated clearcuts which produce copious quantities of seeds (Dale 1986, 1989).

Wetlands. Typha latifolia L. marshes cover many hectares of the mudflow. *Equisetum arvense* carpets broad areas. Dense *Salix sitchensis* thickets are common along streams and around ponds with a wide variety of *Carex* and *Juncus* species. *Spiranthes romanzoffiana* Cham. occurs on wetland edges. One hundred and fifty-six species were found in Toutle Debris Avalanche wetlands.

Toutle Ridge

Toutle Ridge is also occupied by wind-dispersed invasive species similar to those found on the Pumice Plain and Plains of Abraham. Ninety-two species were found on Toutle Ridge uplands. *Sibbaldia procumbens* L., however, was unique to Toutle Ridge occurring in the high elevation (>1800 m) western portion of the Ridge. Unlike the other species on the Ridge it is a subalpine species (Hitchcock and Cronquist 1973). This species may have invaded from less disturbed ridges to the south or survived the eruption under a thick snow pack in a protected site. The small refugia are dominated by a typical forest understory flora similar to the larger refugia between the Pumice Plain and Plains of Abraham. Ninety-nine species were found in the Toutle Ridge refugia.

Crater

The crater is sparsely vegetated by herbaceous wind-dispersed species similar to those of upland areas of the Pumice Plain and Plains of Abraham. Vegetation, dominated by *Juncus* and *Epilobium* species, is dense in the seepage wetlands. In 1994 the first individual of *Lupinus lepidus* was found in the breach. This was the first large-seeded, non-wind-dispersed species found in the crater since the eruption. The crater proper, which surrounds the lava dome, is very barren. Only a few sparsely distributed, wind-dispersed species have become established. The highly unstable nature of the lava dome limits vegetation over most of the dome. Areas where steam from fumaroles condenses rarely support vascular plants, yet a few individuals of *Hypochaeris radicata* and *Salix sitchensis* were observed. Fifty-two species were found in the breach uplands, 32 species in the breach wetlands, and 17 species in the high crater.

Non-native Species

The second most widespread invader of upland successional landscapes on the Pumice Plain, Plains of Abraham, and Toutle Ridge (the most widespread is *Anaphalis margaritacea*) is the non-native *Hypochaeris radicata.* It is possible that the rate of succession has changed substantially because of the presence of this non-native species. Most of the other exotics, such as *Cirsium, Senecio,* and *Sonchus* species, do not dominate the landscape. Non-natives are less common in wetlands. The only *Cytisus scoparius* (L.) Link plant was located on the west edge of the Pumice Plain and was chopped down in 1994. *Cytisus scoparius* forms dense thickets on the Toutle Debris Avalanche outside of the range of this study. In all, 57 non-native species were found.

The Toutle River Debris Avalanche has vast areas completely dominated by non-native species to the complete exclusion of natives presumably due to the artificial seeding that was undertaken after the eruption for erosion control. Species such as *Lotus corniculatus, Medicago lupulina, Melilotus alba, Trifolium pratense, Trifolium repens,* and *Vulpia myuros* cover large areas of the Debris Avalanche. These species create extensive monocultures which exclude native species and prevent natural successional processes from occurring. For example, the entire mouth of Coldwater Lake is completely dominated by non-native species. Thus, the possibility of natural succession to a scrub-shrub or forested wetland lakeshore is reduced. Other non-natives on the lahar, such as *Hypericum perforatum* L., *Rubus discolor* Weihe & Nees, *Cirsium arvense* (L.) Scop., and *Cirsium vulgare* (Savi) Ten., probably arrived on their own via wind or animal dispersal.

CONCLUSION

The focus of this study was to investigate the recently devastated areas of Mount St. Helens. Species richness is difficult to compare with studies of other Cascade Range volcanoes in which the entire volcano, including relatively undisturbed areas, was surveyed. These other Cascade Range volcanoes have not been subjected to recent volcanic eruptions.

Because areas investigated during the study varied greatly in terms of current physical features, environmental conditions and size of area available for colonization, species richness varied across the landscape. The highest richness was observed in the Toutle Debris Avalanche uplands, probably due to the area's great size, diversity of physical features and proximity to seed sources of potential colonizers.

Richness on Mount St. Helens has increased greatly since 1980 when richness equaled zero (except in the refugia). Although most of the species currently dominant on the landscape are invasive species that characteristically have small wind-dispersed seeds, some large seeded plants such as *Lupinus lepidus* are common. No threatened, endangered or sensitive species or regional endemics were detected during our survey of the volcano. An interesting finding was the presence of *Salix exigua.* This species is not thought to occur west of the Cascades. The open primary successional habitats created by the volcanic eruption allow colonization by wind-dispersed species from great distances.

This study creates a baseline to judge changes to the landscapes of Mount St. Helens, and should also facilitate future studies of primary successional processes on the mountain.

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THE DISTRIBUTION OF VESICULAR-ARBUSCULAR MYCORRHIZAE ON MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

Vesicular-arbuscular mycorrhizae (VAM) occur in most terrestrial ecosystems and are crucial to understanding community structure and function. However, their role in primary succession is poorly understood. This study examined the distribution of VAM propagules, spores, and plants across the Pumice Plains of Mount St. Helens.

VAM colonized plants and propagules were common in sites with thick vegetation, such as areas of relict pre-eruption vegetation and lupine patches, but were very infrequent in barren areas which comprise nearly all of the Pumice Plain. The vegetation of the Pumice Plain is composed primarily of facultatively mycotrophic species which are currently nonmycorrhizal. Mycorrhizal plants occur in refugia and thickly vegetated areas. VAM spore density and richness was low and spores are essentially restricted to densely vegetated habitats.

The focus of this study is the distribution of VAM plants and VAM propagules across the Pumice Plain of Mount St. Helens, and their relationship with microsites. The relationship between VAM and microsites is of interest because microsites are crucial to the colonization dynamics on Mount St. Helens (del Moral and Bliss 1993, Titus 1995).

During primary succession on volcanic substrates, it is unlikely that pioneer species would depend on mycorrhizae (Allen 1991). Only non-host and facultatively mycotrophic species could invade these sites. Obligately mycotrophic species would be prevented from establishing until a population of VAM fungi was present in the soil, presumably having arisen in association with facultatively mycotrophic species. Seral sequences may reflect the mycorrhizal dependence of the colonizing species (Allen 1991). Thus, the pattern of VAM distribution across the primary successional landscape of the Pumice Plain may regulate plant invasion patterns (Allen 1988). However, previous to this study, the distribution of VAM propagules across the Pumice Plain was unknown.

VAM propagules are composed of spores, hyphae and VAM colonized roots. The two indices of VAM density, spore counts and degree of root colonization, are not necessarily correlated (Louis and Lim 1987; Johnson et al. 1991). Spore counts assess only one type of propagule while colonization indirectly estimates all types of propagules. Therefore, root colonization is a more accurate measure of total VAM density. In this study, the distribution of VAM has three facets: 1) The presence of VAM fungal propagules in the soil, i.e., the mycorrhizal inoculum potential (MIP), which is determined through a root bioassay; 2) the presence of VAM plants; and 3) the presence of VAM fungal spores in the soil. This study examines the distribution of these three components of VAM across the Pumice Plain.

METHODS

Study site. The Pumice Plain was formed by the 18 May, 1980 eruption of Mount St. Helens (46°12′N, 122°11′W). The Pumice Plain covers 20 km^2 immediately north of the crater between 1150–1300 m elevation. It was formed by the deposit of up to 200 m of material from a debris avalanche, subsequent pyroclastic flows, air-fall pumice, and was repeatedly impacted by later lahars. The Pumice Plain is blanketed by pumice that ranges in depth from 10 to 200 m. The surface is flat or gently sloping, with numerous gullies created by erosion dissecting the surface. Surface pumice particles range in size from 1 mm to 10 cm (del Moral and Bliss 1993).

The climate is maritime, with cool wet winters and warm, dry summers. Periods of drought often occur in July and August. Annual precipitation averages 2373 mm, yet usually less than 5% of this falls between June and August. The growing season begins in June and ends by early September. Temperatures range from mean monthly minima of −4.2°C in January and 7.3°C in August to maxima

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of 0.5°C in January and 22.2°C in July (Spirit Lake Ranger Station (987 m a.s.l.), Pacific Northwest River Basins Commission 1969). Summer temperatures range from 0 to 35°C with a mean ca. 12°C. Surface soil temperatures are often very high in the summer approaching 50°C on tephra surfaces (Reynolds and Bliss 1986).

Pumice Plain soil is immature, with very low concentrations of carbon, nitrogen, and microbial biomass (del Moral and Bliss 1993). Considerable variation in soil moisture values has been recorded between and within microsites. Substrates with fine particles contain more moisture than areas with coarse particles and erosion rills are more moist than other microsites (del Moral and Bliss 1993). In summer the surface tephra dries quickly between rains, thus, most Pumice Plain habitats do not remain moist for periods sufficient to allow seedling establishment. However, the surface layer of tephra acts as a mulch to impede evaporation and is capable of holding considerable moisture at lower depths so that adult plants rarely suffer from drought (Reynolds and Bliss 1986).

Microsites. The seven types of microsites in this study appear to differ in environmental characteristics on the spatial scale of an individual seed or seedling. They were chosen because personal observation and the literature both suggest them to be important to revegetation processes on the Pumice Plain. These sites are:

Flat—sites which have homogeneous gravel, sand or silt substrates in which the topography is level. Pumice particles are less than 5 cm in diameter. Flat sites occupy most of the Pumice Plain and are sparsely vegetated.

Rill—small gullies formed by erosive water action. These are linear habitats that marginally protect seedlings from wind, collect more snow, and have lower solar radiation (del Moral and Bliss 1993). Rill edges are more stable than rill bottoms and drainages.

Near-rock—adjacent to rocks larger than 25 cm in diameter. On exposed surfaces rocks protect seedlings from direct solar exposure, reduce wind and surface temperatures, and are more likely to trap seeds.

Ridges—sites located on small ridgetops where there is evidence of extensive wind erosion.

Lupinus patch—sites associated with dense patches of living and dead *Lupinus lepidus* Douglas. These sites contain higher levels of soil nitrogen and lupines effectively trap seeds and organic matter. *Lupinus* patches are described in Halvorson et al. (1992), del Moral and Bliss (1993), del Moral et al. (1995), Bishop (1996).

Crowded vegetation—sites located in thick vegetation on new volcanically emplaced surfaces which are not dominated by *L. lepidus.*

Refugia—sites with pre-eruption soil exposed by erosion in which some belowground plant organs survived and subsequently sprouted. Refugia are densely vegetated and are confined to the eastern fringe of the Pumice Plain on steep north facing slopes. Refugia vegetation is described by del Moral et al. (1995).

These sites were investigated to determine the distribution of VAM propagules and plants across the Pumice Plain. The first study looks at the distribution of VAM propagules, the second at the distribution of VAM plants and the third at the distribution of VAM spores.

Corn bioassay for assessing VAM propagule distribution. Soil samples were collected at 20 representative locations within each site (except refugia) in July 1991. Four 250 g samples from the upper 8 cm of soil were collected at each location and combined to form two composite samples. Soil was sifted to remove all particles larger than 4 mm, amended with 20% sterile perlite to increase porosity, and 650 g was placed into 10 cm by 10 cm freely draining plastic pots. Bioassays were conducted with non-fungicide treated *Zea mays* seeds. All pots were watered daily with tap water. Fertilizer was applied in 50 ml aliquots per pot of Colwell's solution minus phosphorus at planting and at weekly intervals throughout the experiment. Colwell's solution mimics natural proportions of nutrients in typical temperate soils (Colwell 1943; R. B. Walker personal communication). The control consisted of 20 pots of sterile greenhouse soil placed randomly among the treatment pots and planted with corn to determine if contamination by greenhouse VAM propagules occurred. Previous work showed that VAM propagules, if present, rapidly colonize corn in the greenhouse (Titus personal observation). Pots were randomized and maintained at the University of Washington Botany Greenhouse at 20–25°C, and rotated every 10 days. Bioassay plants were grown for 35 days from 20 July to 14 August 1991. Plants were harvested, roots washed, and frozen at −18°C until October 1991 at which time roots were assayed for VAM colonization. The quantity of inoculum in the soil, mycorrhizal inoculum potential (MIP), was estimated by percent colonization of corn roots (Moorman and Reeves 1979; Doerr et al. 1984; Johnson and McGraw 1988).

Staining. Roots were washed, cleared and stained with trypan blue (Brundrett et al. 1994; E. Cázares, Oregon State University, personal communication). Percent colonization was estimated by placing a grid of 1 cm squares below a petri plate which contained the root sample under a dissecting microscope. One hundred locations where a root crossed a line on the grid were scored for mycorrhizae. Many samples were examined under higher power to ascertain that the fungus was indeed VAM. Root segments containing vesicles, arbuscles or intercellular hyphal coils or hyphae were recorded as being colonized. The number of mycorrhizal "hits" is an estimate of the percent of the root colonized (Brundrett et al. 1994).

Mycorrhizal colonization of pioneer species. The roots of 14 plants of six major pioneer species were collected from each of the seven site types at different locations across the Pumice Plain. Most root samples were collected during July, 1992, and the remainder during July, 1993. All sampled plants were at least 4 m from their nearest neighbor, except for those in lupine patches, crowded vegetation and refugia. Species sampled were *Anaphalis margaritacea* (L.) Benth. & Hook., *Carex mertensii* Prescott, *Epilobium angustifolium* L. ssp. *circumvagum* Mosq., *Hieracium albiflorum* Hook., *Hypochaeris radicata* L. and *Penstemon cardwellii.* In addition to these target species, roots were collected from several other naturally occurring species where they occurred. Roots of these species were not collected in all microsite types because they only occurred in certain ones. Roots were washed when harvested and stored in alcohol until they were cleared and stained to assess VAM colonization as above.

Spore isolation. Soil samples were collected using two sampling regimes. For the first regime soil was collected from 20 representatives of each of the seven site types. Four 100 ml soil samples were collected from the top 8 cm of soil and combined to form a single sample during August 1993.

The second sampling regime was part of a larger study. Percent cover of each plant species in 150 100 m^2 circular plots was assessed across the Pumice Plain during summer, 1993. Vegetation of these plots were grouped into five habitat types based on substrate and vegetation (del Moral et al. 1995). In conjunction with vegetation sampling, 100 ml of soil were collected at each of four locations within each plot and combined into a single sample.

Soil samples were dried at room temperature and stored at 3°C in sealed plastic bags. Spores were extracted from two subsamples of the soil from each plot by the wet-sieving and decanting technique (Gerdemann and Nicolson 1963; Pacioni 1992; Brundrett et al. 1994). One hundred and fifty ml of soil were placed into a 1.651 mm mesh sieve above 0.417 and 0.052 mm mesh sieves. The soil was washed vigorously with water. Roots in the top sieve and soil from the fine mesh bottom sieve were examined in a petri dish under a dissecting microscope at 40× power for VAM spores.

In order to compare spore extraction techniques, the soil from ten samples with two replicates each were analyzed using both the wet-sieving with decanting technique and the differential water/sucrose centrifugation method (Ianson and Allen 1986). Selected soil samples were those likely to contain VAM spores. Spore isolation efficiency was not improved using the differential water/sucrose technique. Although Ianson and Allen (1986) found better spore isolation with the differential water/sucrose technique, the extremely low organic matter content of Pumice Plain soils obviated the need for improved resolution in the case of these soils.

TABLE 1. VAM CORN BIOASSAY FOR THE DETERMINATION OF MYCORRHIZAL INOCULUM POTENTIAL (MIP) OF PUMICE PLAIN SOIL. Soil MIP is shown by percent VAM colonization of corn roots. % plants colonized is the percentage of the plants of each species which were colonized by VAM. (mean ± standard deviation, n = 20 paired samples).

Microsite	MIP	% plants colonized
Flat	0	0
Near Rock	0	0
Ridge	0	0
Rill	0.3 ± 0.6	15
Lupine Patch	3.0 ± 3.3	60
Crowded Vegetation	4.3 ± 3.0	70

Spores were isolated and stored dry on filter paper. Spore types were determined from the experience of the third author and the use of spore identification guides (Mosse and Bowen 1968; Gerdemann and Trappe 1974; Trappe 1982; Morton 1988; Schenck and Perez 1990).

Data analysis. Mean percent mycorrhizal colonization was determined to yield MIP (Experiment I) and mean colonization (Experiment II). In Experiment III, spore density was averaged and richness determined for each site and for each habitat type. The preponderance of zeros precluded statistical data analysis, so values are reported only as observational data. Although both parametric and non-parametric techniques are robust for violations of their respective assumptions, the statistical techniques appropriate for analysis of this experimental design (e.g., one-way ANOVA or the Kruskal-Wallace test (Zar 1984)) are invalid for the analysis of data with many zeros. Even non-parametric statistics require homoscedastic variances. This aside, the patterns in the data are clearly apparent without statistical tests. Frequency of VAM colonization or spores are also reported.

RESULTS

Corn bioassay for assessing VAM propagule distribution. Ridge, flat, and near-rock substrates contained no detectable MIP. Rill microsites occasionally contained VAM propagules, whereas lupine patch and densely vegetated site soils usually contained mycorrhizal inoculum (Table 1).

Mycorrhizal colonization of pioneer species. Anaphalis margaritacea, Hieracium albiflorum and *Hypochaeris radicata* were without mycorrhizal colonization in flat, ridge and near-rock sites, but were mycorrhizal in rill, lupine patch, crowded vegetation and refugia (Table 2). *Carex mertensii* was without mycorrhizal colonization in all sites,

TABLE 2. VAM COLONIZATION OF PLANT SPECIES COLLECTED FROM MICROSITES ON THE PUMICE PLAIN. (mean ± standard deviation, n = 14). Flat, ridge and near rock microsites contained no VAM plants and are not shown.

	Microsite							
	Rill		Lupine patch		Crowded vegetation		Refugia	
Species	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized	% VAM colonization	% plants colonized
Anaphalis margaritacea	1.1 ± 2.6	36	8.3 ± 15.3	57	10.2 ± 12.6	86	6.4 ± 7.8	63
Carex mertensii	0	0	0	0	0	0	0.1 ± 0.4	14
Epilobium angustifolium	0	0	2.0 ± 5.6	29	0.4 ± 1.6	14	4.2 ± 6.6	36
Hieracium albiflorum	0.2 ± 0.8	14	4.9 ± 9.3	64	5.3 ± 12.3	64	8.9 ± 10.5	50
Hypochaeris radicata	0.9 ± 2.5	29	8.1 ± 11.8	64	8.0 ± 15.5	33	10.7 ± 13.7	50
Penstemon cardwellii	0.8 ± 2.8	7	3.2 ± 4.2	43	7.0 ± 7.8	79	15.7 ± 9.0	79

except for a trace of VAM in refugia. *Epilobium angustifolium* was not colonized in rill microsites, but was occasionally colonized in lupine patch, crowded vegetation and refugia. The species with the highest mycorrhizal colonization was *A. margaritacea,* and the site with the most VAM plants was crowded vegetation. Most of the VAM fungal hyphae observed were of the fine endophyte type. Non-target species were all nonmycorrhizal in flat, ridge and near-rock sites (Table 3). Only *Juncus parryi* Engelm. was mycorrhizal in rill microsites. *Juncus parryi* and *Lupinus lepidus* were mycorrhizal in lupine patches. Many species were mycorrhizal in crowded sites and refugia, and species restricted to refugia were usually mycorrhizal.

Spore distribution. No spores were found in flat, rill, or near-rock sites. Densities were variable where spores were found in dead lupine, crowded vegetation, and refugia (Table 4). Dead lupine and crowded vegetation microsites with VAM spores often were located far from refugia. Most refugia samples contained many spores.

Pumice barrens, pyroclastic surfaces and drainages (del Moral et al. 1995) rarely contained VAM fungal spores (Table 5). Samples containing spores were usually located near refugia. The only exception was an isolated barren pumice site which also contained a large willow. Lupine patches occasionally contained spores which, when present, were in high densities. Lupine patches which contained spores were widely spread across the Pumice Plain. Refugia almost always contained spores.

Three spore types were found: *Glomus macrocarpum* (Tul. and Tul.), *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe, and an *Acaulospora* type. The most common spores found were dead (which are empty), dark brown, brassy, or black. There was usually only one spore type present in a sample (not including dead spores which were usually present), however, all three spore types occurred in microsites and habitat types where spores were common.

DISCUSSION

VAM distribution. Based on observational data only, microsites differ in MIP and spore density, and pioneer species differ in mycorrhizal colonization depending on the microsite it inhabits. Sites with thicker vegetation contained more VAM propagules and VAM plants.

After the 1980 eruption, the Pumice Plain was free of VAM fungal propagules (Allen 1987). The VAM propagules detected in this study show that dispersal forces, most likely animals (Allen 1987), have been returning VAM propagules to this landscape. The invasion of VAM propagules is sporadic as some microsites contain more mycorrhizal propagules and more heavily colonized plants than do other microsites. This supports the patch-dynamic model which proposes that the pattern of VAM fungal propagules dispersed by animals searching among patches for food and cover in sparsely vegetated landscapes creates a patchy distribution of inoculum (Allen 1987, 1988). This patchiness may also result from the ability of certain microsites to effectively trap windborne or waterborne propagules.

VAM spores were uncommon across the Pumice Plain, but they are present in crowded and lupine patch microsites. The bulk of the Pumice Plain appears to remain VAM spore free. Evidence for a non-patchy landscape level spread of VAM fungi was observed in the plots adjacent to refugia in which VAM propagules were found. Since refugia are on steep slopes, VAM propagules could immigrate to adjacent barren and drainage habitats by erosion. Plant diversity is also slightly higher in areas adjacent to refugia (del Moral et al. 1995). However, one pumice barren plot distant from sites with high levels of VAM spores contained VAM spores. This is evidence for a patchy distribution of VAM spores and adds support to the patch-dynamic model (Allen 1988). This pumice barren site contained a large willow which is probably a locus for small mammal activity in a barren landscape. In

TABLE 3. VAM COLONIZATION OF PLANT SPECIES COLLECTED FROM MICROSITES ON THE PUMICE PLAIN. n = sample size. (mean ± standard deviation).

	Microsite								
	Flat			Ridge			Near rock		
Species	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized
Achillea millefolium									
Agrostis pallens	4	0	0	2	0	0	4	0	0
Agrostis scabra	7	2.3 ± 6.1	14	2	0	0	7	0	0
Blechnum spicant									
Calyptridium umbellatum	4	0	0				3	0	0
Carex pachystachya	3	0	0	3	0	0	3	0	0
Carex phaeocephala	3	0	0	3	0	0	3	0	0
Cirsium arvense							2	0	0
Epilobium anagallidifolium	5	0	0	2	0	0	4	0	0
Epilobium brachycarpum									
Epilobium ciliatum									
Eriogonum pyrolifolium									
Fragaria virginiana									
Gnaphalium uliginosum									
Juncus mertensianus									
Juncus parryi	10	0	0				2	0	0
Luetkea pectinata									
Lupinus latifolius	4	0	0				4	0	0
Lupinus lepidus	17	0	0	6	0	0	16	0	0
Luzula parviflora									
Phacelia hastata									
Polygonum minimum									
Ribes laxiflorum									
Rubus lasiococcus									
Rubus spectabilis									
Saxifraga ferruginea	5	0	0				4	0	0
Sambucus racemosa									
Senecio sylvaticus	8	0	0	4	0	0	6	0.7 ± 1.6	17
Smilicina racemosa									
Spergularia rubra	2	0	0	0	0	0	2	0	0
Vaccinium membranaceum									
Vancouveria hexandra									

addition, several of the crowded vegetation and lupine patch microsites which contained VAM spores were isolated across the Pumice Plain far from refugia, adding further support to the patch-dynamic model. The differences in spore counts for lupine patch and refugia between Tables 4 and 5 were not unexpected due to the large standard deviations and patchy nature of spore distribution (Anderson et al. 1983; St. John and Koske 1988).

Mycotrophic Status of Colonizing Species

Glomus tenuis. Glomus tenuis (Greenall) Hall is distinguished by hyphal diameters in the 0.5–1.5 μm range (Hall 1987). Other *Glomus* species have coarse (5–30 μm in diameter) hyphae (McGonigle and Fitter 1990; Wang et al. 1993). Therefore, only root colonizations caused by *G. tenuis* can be identified confidently in the absence of sporulating structures (Carling and Brown 1982; Hall 1987). Colonization by *G. tenuis* has been found to be highest in dry very low phosphorus environments (Rabatin 1979), low pH soils (Wang et al. 1993), and in alpine environments (Read and Haselwandter 1981; Mullen and Schmidt 1993). *Glomus tenuis* is also often the dominant VAM fungal species in pioneer species and disturbed environments (Daft and Nicolson 1974). In this study, fine endophyte hyphae were observed frequently, but no spores of *G. tenuis* were detected. *Glomus tenuis* spores may be too small (7–12 μm) to be extracted by the wet sieving technique (Hall 1987; Wang et al. 1993). Thus the possibility exists that these spores are common but were not detected. Although spores are the only way to identify *Glomus* species, they are not indicative of the actual infectivity of a soil and should be used only in conjunction with other indices. For example, no spores were detected in rill microsites, but there was some VAM colonization of corn roots and the target species in rills were occasionally VAM.

TABLE 3. EXTENDED

Microsite								
Rill			Lupine patch			Crowded vegetation		
n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonized	n	% VAM colonization	% plants colonnized
						2	6	100
4	0	0	4	0	0	12	8.0 ± 21.8	25
7	0	0	7	0	0	6	0.4 ± 0.9	17
2	0	0	1	0	0			
3	0	0	3	0	0	5	0	0
3	0	0	3	0	0	5	0	0
3	0	0	2	0	0	3	5.7 ± 4.0	100
			4	0	0	2	0	0
2	0	0				2	15.0 ± 7.1	100
						2	0	0
						1	0	0
						6	0	0
11	0.5 ± 1.5	9	8	9.0 ± 7.0	88	16	0.8 ± 2.6	13
1	0	0						
						5	0	0
16	0	11	19	0.2 ± 0.6	11	6	0.7 ± 1.6	77
						14	0	0
						2	4.0 ± 5.7	50
						2	0	0
5	0	0	1	0	0	2	1.0 ± 1.4	50
4	0	0	5	0	0	4	1.5 ± 1.9	50
2	0	0				0	0	0

Carex spp. are considered to be non-hosts (Powell 1975; Anderson et al. 1984), although mycorrhizal *Carex* spp. have been found in the alpine (Read and Haselwandter 1981; Allen et al. 1987) and in grasslands (Read et al. 1976). VAM *Carex mertensii* plants were only observed in two individuals in this study. *Juncus parryi* is generally thought to be in a non-host genus (Powell 1975). However, in this case it was heavily colonized by VAM in rill, lupine patch and crowded sites. Genera-wide generalizations of mycorrhizal dependence may be inaccurate and extensive examinations of the species must be conducted to ascertain mycotrophy (Read et al. 1976; Newman and Reddell 1987).

Annuals are often considered to be non-hosts (Trappe 1987; Boerner 1992; Peat and Fitter 1993), but in this survey *Senecio sylvaticus* was frequently mycorrhizal. Allen et al. (1992) found the annual *Epilobium paniculatum* to be mycorrhizal in a lupine patch. In this survey the species was found to be nonmycorrhizal.

Allen et al. (1992) found *Lupinus latifolius* J. Agardh. and *L. lepidus* to be mycorrhizal, while this survey found *L. lepidus,* but not *L. latifolius,* to be mycorrhizal. Avio et al. (1990) observed *Lupinus* to be a strongly non-host genus. O'Dell and Trappe (1992) found both *L. lepidus* and *L. latifolius* to be occasionally mycorrhizal. They located a mycorrhizal *L. latifolius* on Mount St. Helens but did not find a mycorrhizal *L. lepidus* on the volcano. O'Dell and Trappe (1992) suggested that VAM fungi may need to be established on a companion host before colonizing roots of lupines.

Most plant species now colonizing Mount St. Helens barren sites appear to be facultatively mycotrophic (Titus 1995). This status supports a broad range of tolerance to VAM, from rarely mycorrhizal to nearly always colonized depending upon the species, neighboring species and site conditions (Allen 1991; Boerner 1992).

VAM fungal species. VAM fungal richness was low, with only three spore types, but greater than the single species (*Glomus macrocarpum*) found in the blast zone by Allen et al. (1984), Allen and

TABLE 3. CONTINUED

	Microsite		
	Refugia		
Species	n	% VAM colonization	% plants colonized
Achillea millefolium			
Agrostis pallens			
Agrostis scabra			
Blechnum spicant	2	5.0 ± 0	100
Calyptridium umbellatum			
Carex pachystachya			
Carex phaeocephala			
Cirsium arvense			
Epilobium anagallidifolium			
Epilobium brachycarpum			
Epilobium ciliatum			
Eriogonum pyrolifolium			
Fragaria virginiana	3	8.3 ± 13.6	67
Gnaphalium uliginosum			
Juncus mertensianus			
Juncus parryi	0	0.5 ± 1.5	9
Luetkea pectinata	4	0	0
Lupinus latifolius			
Lupinus lepidus			
Luzula parviflora			
Phacelia hastata			
Polygonum minimum			
Ribes laxiflorum	4	15.0 ± 9.1	100
Rubus lasiococcus	2	0	0
Rubus spectabilis	4	16.0 ± 5.9	100
Saxifraga ferruginea			
Sambucus racemosa	4	20.0 ± 12.8	100
Senecio sylvaticus	2	4.0 ± 2.8	100
Smilicina racemosa	4	30.0 ± 14.1	100
Spergularia rubra			
Vaccinium membranaceum	4	25.0 ± 7.7	100
Vancouveria hexandra	2	0	0

TABLE 4. NUMBER AND RICHNESS OF VAM FUNGAL SPORES IN 150 ML SOIL SAMPLES FROM MICROSITES ON THE PUMICE PLAIN. (mean ± standard deviation for spore counts, n = 20 for each microsite type). [1] Mean richness is based only on samples which contained spores.

Microsite	Mean number of spores	% samples with spores	Mean richness[1]
Flat	0	0	—
Near Rock	0	0	—
Ridge	0	0	—
Rill	0	0	—
Lupine Patch	13.6 ± 29.2	55	1.4
Crowded Vegetation	18.4 ± 41.1	70	1.3
Refugia	20.7 ± 49.6	85	1.8

MacMahon (1988), and Allen et al. (1992). This indicates that VAM fungal species are invading the blast zone or at least proliferating into detectable densities. The preponderance of inviable spores found in this study is not unusual (Read et al. 1976; Berliner and Torrey 1989). The patchy nature of VAM species distribution is evidenced by the large variance in spore densities and by the presence of different spore types in different sites with little overlap. However, each species was present in the microsites and habitat types which had detectable spore populations. It is important to note the difference in sampling intensity between above- and belowground environments. Plot size in del Moral et al. (1995) was 100 m^2, where as the surface area of the belowground sampling effort was only approximately 400 cm^2, which is 0.0004 as large as the aboveground sampling area. Therefore, statements about patchy spore distributions must be regarded in the light of the small belowground sampling area (Anderson et al. 1983). In the few studies which address VAM species distribution, richness is usually low and density variable. It is therefore difficult to draw conclusions about successional patterns in VAM fungal types from the results presented here.

CONCLUSION

This study assessed both VAM colonization and VAM fungal propagules. The results are comple-

TABLE 5. NUMBER AND RICHNESS OF VAM FUNGAL SPORES IN 150 ML SOIL SAMPLES FROM HABITAT TYPES ON THE PUMICE PLAIN. Habitat types based on del Moral et al. (1995). "Near" indicates a site adjacent to a refugia, "far" indicates a site distant from a refugia. n = sample size. (mean ± standard deviation for spore counts). [1] Mean richness is based only on samples which contained spores.

Habitat type	n	Mean number of spores	% samples with spores	Mean richness[1]
Pumice Barrens–near	11	1.5 ± 3.0	4	1
Pumice Barrens–far	32	0.03 ± 0.2	3	1
Pyroclastic Surfaces	15	0	0	—
Drainages–near	4	0.3 ± 0.5	25	1
Drainages–far	15	0	0	—
Wetlands	23	0	0	—
Lupine Patches	16	10.5 ± 26.2	25	1.5
Refugia	26	14.5 ± 33.1	62	1.3

mentary and converge to the conclusion that the Pumice Plain remains essentially VAM free, except for the few isolated lupine patch and crowded sites. Refugia contain VAM fungal propagules and mycorrhizal plants. The sparse vegetation of the Pumice Plain is composed largely of facultatively mycotrophic species which are at present nonmycorrhizal.

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LATE-HOLOCENE VEGETATION CHANGES FROM THE LAS FLORES CREEK COASTAL LOWLANDS, SAN DIEGO COUNTY, CALIFORNIA

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ABSTRACT

The vegetation history of coastal southern California is incompletely known, due primarily to a lack of suitable sites for preservation of subfossil organic remains, and destruction of sites by recent human impact. One coastal site, along Las Flores Creek in San Diego County, has yielded a pollen record, enabling us to reconstruct vegetation and climatic changes for the last ca. 4300 radiocarbon years. Pollen from riparian plants, including *Typha* (cattail) and Cyperaceae (sedges), are common between ca. 4000 and 2600 years ago. *Cupressus,* or a closely related tree, may have grown along this riparian corridor, suggesting formerly larger range for this plant. By ca. 2600 years ago, a vegetation mosaic including elements of the coastal sage, chaparral, and grassland communities, were established near the site, persisting until the introduction of exotic weed and tree species within the last century.

The pollen record from Las Flores Creek provides information on the environment of the Native American population during the Late Holocene. Local plant species undoubtedly provided resources for seasonal occupation of the coast, which supplemented extensive shellfish collecting, especially after ca. 2000 years ago. An increase in pollen from the Chenopodiaceae at that time may correspond to local human-caused disturbances.

Analysis of pollen assemblages from stratigraphic profiles in southern California has lagged significantly behind studies in other parts of the state (Adam 1985). The primary reasons for this include a perceived lack of suitable sites, as well as generally poor pollen preservation from sites that have been analysed. Because traditional sites for pollen profiles (i.e., lakes or bogs) in this arid region are generally missing at low elevations in southern California, alternative sites, such as alluvial sections or estuaries, must be investigated in order to provide information on local vegetation changes for the coastal region.

Pollen recovery from alluvial and colluvial sections at locations in California and the American Southwest has been highly to moderately successful. For example, Anderson and Smith (1994) and Koehler and Anderson (1994) reported on montane alluvial/colluvial profiles at middle elevations in the Sierra Nevada. Pollen preservation was excellent in these sections, which occurred as low as 1509 m.

Holocene pollen profiles have been investigated as well from several coastal estuary sites in southern California, including Los Penasquitos Lagoon and Mission Bay in San Diego (Mudie and Byrne 1980), San Joaquin Marsh in Orange County (Davis 1992), and Abalone Rocks Marsh on Santa Rosa Island (Cole and Liu 1994). Pollen deposited in estuarine sediments contains assemblages from terrestrial, freshwater, and marginal marine plants, and has been used to infer changes in sealevel as well as the terrestrial record from the adjoining uplands. A late Pleistocene pollen record was also obtained from a rockshelter on San Miguel Island (West and Erlandson 1994).

In January 1994, we discovered a thick alluvial section near the mouth of Las Flores Creek, on Camp Pendleton Marine Base, San Diego County. Our investigations were part of ongoing archaeological excavations on the Base (Byrd 1996). Pollen preserved in this 4.75 m section has allowed us to reconstruct the vegetation history of the upland and riparian habitats near the shoreface, in contrast to those from the sub- and near-tidal marshes of southern San Diego, Orange, and Ventura Counties named above. The data from the Las Flores Arroyo not only provide a Late Holocene record from a region with inadequate paleoenvironmental coverage, but also provide an environmental context useful in archaeological reconstructions of the region.

Location and Characteristics of Site

The Las Flores Arroyo site is located along Las Flores Creek, at the mouth of Las Pulgas Canyon, on Camp Pendleton Marine Base (Las Pulgas Canyon USGS 7.5′ Quad; 33°17′30″N latitude; 117°27′30″W longitude; Fig. 1). The top of the section occurs at an elevation of ca. 6 m. The deposit is a deeply incised Holocene alluvial terrace, with stacked silts and sands comprising both alluvial deposits and paleosols (Fig. 2A, personal observations, and Waters 1996).

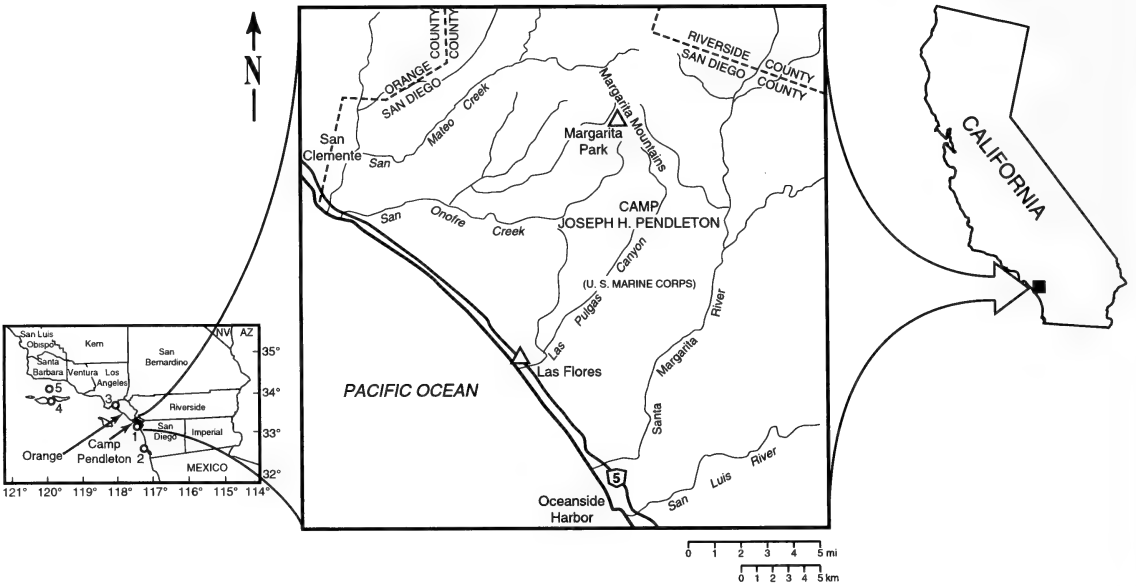

FIG. 1. Location of the Las Flores pollen site, San Diego County, California, as well as other nearby sites mentioned in the text. 1 = Las Flores profile (this paper); 2 = Los Penasquitos Lagoon and Mission Bay (Mudie and Byrne 1980); 3 = San Joaquin Marsh (Davis 1992); 4 = Abalone Rocks Marsh (Cole and Liu 1994); 5 = Santa Barbara Basin (Huesser 1978; Byrne et al. 1977).

The vegetation of Camp Pendleton and the adjacent coastal uplands was mapped by Pacific Southwest Biological Services, Inc. (1986); Zedler et al. (unpublished) has studied the community composition of the Base. At least four distinct plant communities occur within 500 m of the Las Flores site (Fig. 2B). Community composition and vegetation distribution on the Base is heavily influenced by past land use activities, including farming and grazing, fire, construction activities, and military training (Zedler et al. unpublished).

The arroyo itself presently supports Cottonwood/Willow Riparian Woodland. Common tree species in the riparian zone include *Populus fremontii* S. Watson ssp. *fremontii, P. balsamifera* L. ssp. *trichocarpa* (Torrey & A. Gray) Brayshaw, *Salix gooddingii* C. Ball, *S. lasiolepis* Benth. and *S. laevigata* Bebb. Typical associates include *Platanus racemosa* Nutt. (California sycamore), as well as *Artemisia douglasianna* Besser (mugwort), *Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers. (mule-fat), *Conium maculatum* L. (poison hemlock), *Xanthium strumarium* L. (cockle burr), *Urtica dioica* L. (stinging nettle) and *Vitis girdiana* Munson (wild grape) (Zedler et al. unpublished; Beauchamp 1986). The alluvial deposit itself is covered by Southern Willow Scrub. This vegetation unit includes the willows mentioned above, plus *Salix exigua* Nutt. Associated herbaceous species include *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene (poison oak), *Ambrosia psilostachya* DC. (ragweed), *U. dioica, X. strumarium, Artemisia douglasianna,* and the non-natives of *C. maculatum,* and *Foeniculum vulgare* Miller (sweet fennel).

On the headland immediately south of the arroyo is found a small patch of Diegan Coastal Sage Scrub, dominated by low (<2 m), soft-leaved, drought-deciduous shrubs (Zedler et al. unpublished). Plant composition is variable across gradients of exposure, elevation and soil type. However, dominant species include *Artemisia californica* Less. (California sagebrush), *Salvia mellifera* E. Greene (black sage), *Malosma laurina* (Nutt.) Abrams (laurel sumac), *Baccharis pilularis* DC (coyote brush), *Lotus scoparius* (Nutt.) Ottley (deerweed) and *Eriogonum fasciculatum* Benth. (California buckwheat). Chaparral species potentially occurring within this community include *Ceanothus crassifolius* Torrey (hoaryleaf ceanothus), *Rhamnus ilicifolia* Kellogg (holly-leaf redberry), *Rhus integrifolia* (Nutt.) Brewer & S. Watson (lemonadeberry), *Heteromeles arbutifolia* (Lindley) Roemer (toyon), and *Cercocarpus betuloides* Torrey & A. Gray (mountain-mahogany).

Non-Native Annual Grassland presently occupies a large area south of Las Flores. Common introduced grasses include *Bromus diandrus* Roth, *B. madritensis* L. ssp. *rubens* (L.) Husnot, *B. hordeaceus* (ripgut, foxtail chess and soft chess), *Avena barbata* Link, *A. fatua* L. (slender and wild oat), *Hordeum* spp. (wild barley), and *Lolium multiflorum* Lam. (Italian ryegrass).

METHODS

The Las Flores Arroyo wall face was sampled on 5 May 1994. Using an extension ladder to reach the

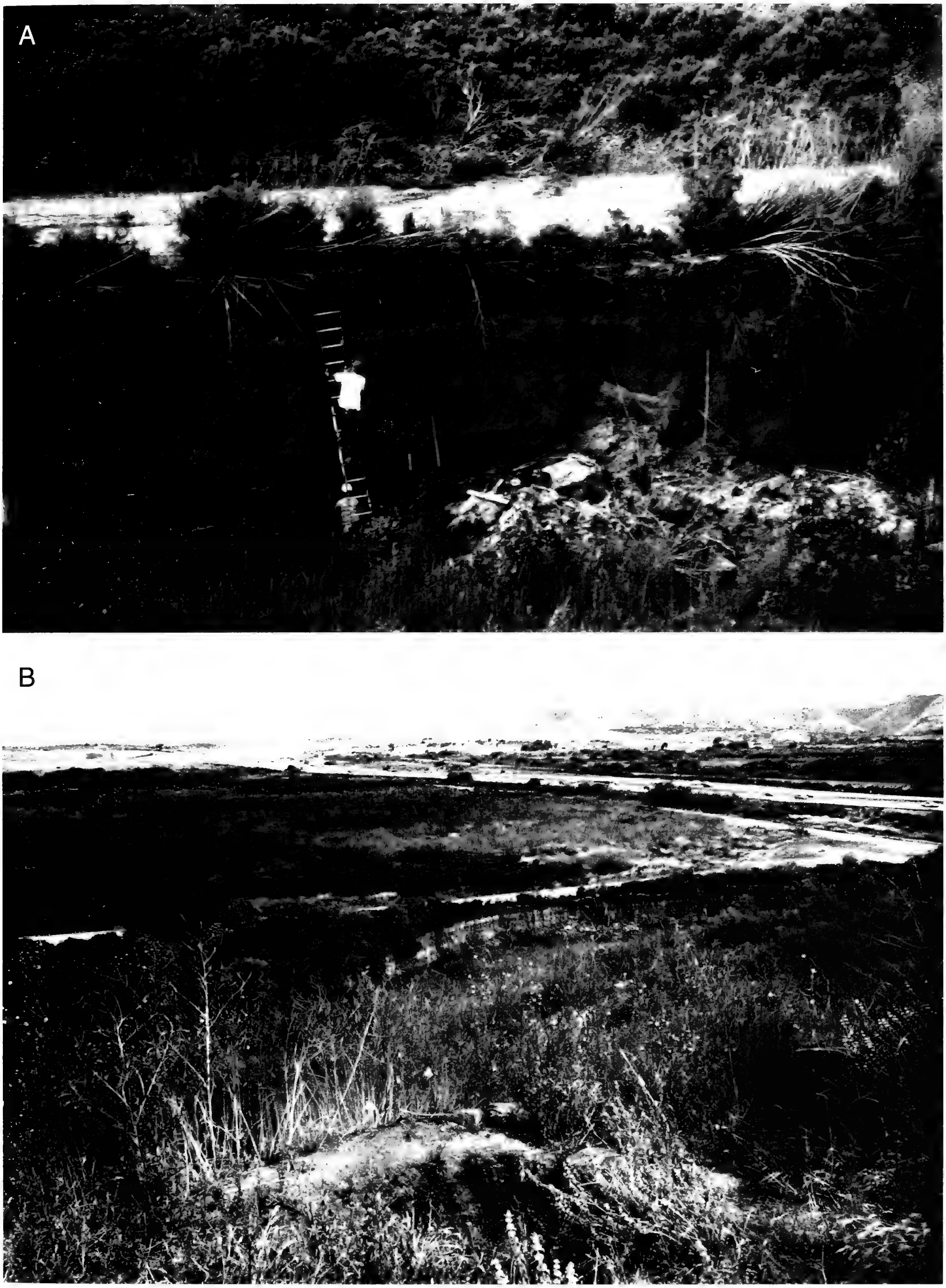

FIG. 2. A. Exposed section of the Las Flores Creek alluvial deposit. The man on the ladder is ca. 2 m tall for scale. B. Vegetation communities in the vicinity of Las Flores Creek. Most of the foreground and middle of the photo is coastal sage scrub and introduced species. Beyond Interstate-5 is coastal grassland; chaparral and oak woodland [Engelmann (*Quercus englemanni*) and coast live (*Q. agrifolia*) oaks] blanket the hills in the background. Sample site in Figure 2A is at center-right.

profile top, the arroyo face was scraped clean with a trowel, and samples of the sediment were collected with a hammer and chisel from the face. Samples were taken at ca. 25 cm intervals from the surface of the deposit to 475 cm depth (total of 20 pollen samples). Samples were placed in 1-gallon bags for transport back to the laboratory.

At Northern Arizona University's Laboratory of Paleoecology (LOP), the pollen samples were processed by a technique which included suspension of a 20 cc subsample of sediment in dilute HCl to dissolve carbonates. *Lycopodium* tracer tablets are added at this step to allow for the calculation of pollen concentration. Subsequent steps included overnite suspension in HF to dissolve silicates, and flotation of the pollen in $ZnBr_2$. The resulting pollen residue was washed with distilled water and placed in glycerol for examination on microscope slides. Each sample contained abundant charcoal, so a final step was added in which we suspended the pollen residue in sodium pyrophosphate and filtered it through an 8 μ mesh. This eliminated most of the charcoal, making the sample more easily counted. The resulting pollen samples were counted to a fixed pollen sum as necessary on a Leitz microscope, with reference to the modern pollen reference collection at the LOP. The pollen sum included all terrestrial pollen types (plus degraded and unknowns), and excluded aquatics (Cyperaceae, *Typha*), riparian trees (*Tamarix,* cf. *Platanus, Populus, Juglans, Alnus* and *Salix*), and spores.

Three samples were taken for radiocarbon dating, at 100, 170 and 370 cm depth. Radiocarbon dates were performed by Beta Analytic, Miami.

Conventions for pollen identifications. Forty-one pollen and four spore types were recognized, exclusive of deteriorated and unknown grains. Where possible, grains were assigned to the generic level, more rarely to the family level. Several groupings were further subdivided, including the Asteraceae, the genus *Pinus,* the Malvaceae, and the spores. The following conventions were used for those groups that were subdivided:

Asteraceae. Pollen of the Asteraceae were separated into 11 groups. Main groupings included *Ambrosia* (ragweed), *Artemisia* (sage), *Cirsium* (thistle), Liguliflorae (chicory), and other Asteraceae. However, since a majority of grains were in the other Asteraceae group, six morphotypes were recognized, based upon the size and shape of the spines, as well as the size of the grain itself. Based upon an unpublished list of plants growing on Camp Pendleton Marine Base, the following genera were included in the 11 Asteraceae subgroups. *Ambrosia*-type included *Ambrosia, Iva,* and *Xanthium. Artemisia*-type included only *Artemisia. Cirsium*-type included *Cirsium* and *Centaurea.* Liguliflorae included *Cichorium, Lactuca,* and *Taraxacum.* Each of these species has been introduced to the Base, thus ancient pollen grains must include additional species not presently near the site. *Baccharis*-type included *Baccharis, Brickellia, Conyza, Cotula, Encelia, Erigeron, Eriophyllum, Gutierrezia, Helianthus, Heterotheca, Pluchea,* and *Senecio. Coreopsis*-type included only *Coreopsis. Chaenactis*-type included *Bebbia, Chaenactis,* and *Viguiera. Solidago*-type included *Euthamia, Solidago,* and *Gnaphalium.* Two additional members of the Asteraceae include Type 4 and Type 6, not referable to other members of the family presently identified.

Pinus. Pine pollen was separated into diploxylon-type (*Pinus coulteri* D. Don and *P. ponderosa* Laws.; both presently occur on the Base), and undifferentiated pine-type.

Brassicaceae. Only one pollen type of mustard was recovered primarily in the most recent sediments. This was assigned to the genus *Brassica,* because of the ubiquity of the plant.

Apiaceae. Only one pollen type of umbel was recovered, primarily contemporaneous with *Brassica.* The pollen type is most similar to *Foeniculum,* which is also the most common umbel at the site today.

Malvaceae. Specimens of *Sphaeralcea* and an unknown Malvaceae occurred in the pollen assemblages.

Spores. Four types of trilete spores occurred in the assemblages. These were assigned to *Cheilanthes*-type, *Ophioglossum*-type and two unknowns.

RESULTS

Sediments. Sediments of the pollen profile were described in detail by Waters (1996). The column consists of six major units. Unit I (bottom-most unit) is a brown sandy clay with a paleosol at the top, containing calcium carbonate nodules and root casts. Unit II is a silty sand, also containing calcium carbonate nodules and root casts, capped by another paleosol. Unit III is a fining upward sequence with sand at the base, fining upward to sandy silty clay at the top. A third paleosol caps the sequence. Calcium carbonate was also present in these sediments. Unit IV, a silt and silty clay, again contained pedogenic features, including calcium carbonate. Unit V was a gray, bioturbated silt, with archaeological debris and marine shells throughout the deposit. The upper unit, VI, is highly disturbed, and may consist of spoil sediments.

Chronology. Three radiocarbon dates were obtained from this profile (Table 1). Beta-75375 (1800 ± 80 yr BP) came from Unit IVb, Beta-76432 (2610 ± 80; collected and submitted by Mike Waters) came from Unit IIIb, and Beta-75376 (4230 ± 60 yr BP) came from near the top of Unit Ib. The first and third samples contained low carbon content, and required extended counting. The low standard error suggests that little if any contamination by older or

TABLE 1. RADIOCARBON DATES FROM THE LAS FLORES POLLEN PROFILE.

Lab #	Depth (cm)	Conventional C14 age	Calibrated calendar yrs
Beta-75375	100	1,800 ± 80	AD 60–420
Beta-76432	170	2,610 ± 80	BC 905–515
Beta-75376	370	4,230 ± 60	BC 2920–2610

younger carbon was present, even though each sample consisted of bulk sediments.

Pollen. Forty-one pollen types were identified from the Las Flores pollen assemblages (Appendix Table 1). Pollen preservation varied from very good in levels near the surface, to very poor near the bottom. This was reflected both in the number of grains counted to achieve a rational pollen sum, as well as the pollen concentration from each of the samples. Pollen sums exceeded 300 grains in samples above 150 cm depth, were ca. 200 grains between 175 and 225 cm depth, dropped to below 100 grains from 250 to 300 cm, and were essentially barren below 330 cm depth (Appendix Table 1). Similarly, pollen concentrations (grains/cc) averaged 25,400 grains/cc (range = 888 to 83,700) in the top 150 cm, but dropped to 1815 grains/cc (range 521 to 6060) from 175–225 cm. Pollen concentrations below 225 cm were generally a couple of hundred grains/cc or less (Appendix Table 1).

Pollen zones. Based upon composition of the pollen assemblages, as well as pollen concentration values, five pollen zones are recognized. Pollen zones correspond largely to major breaks in sedimentary composition, as determined by Waters (1996). The pollen assemblages are described below:

Pollen Zone I (bottom of profile [475 cm] to 315 cm). Pollen is essentially absent from this section of the core (Fig. 3; Appendix Table 1). Individual grains of *Cupressus*-type, *Baccharis*-type, Brassicaceae, and Apiaceae were found, but their numbers were insufficient to warrant an interpretation. These sediments correspond largely to Waters' (1996) Units I and II. The single radiocarbon date from this unit is middle Holocene (4230 ± 60 yr BP).

Pollen Zone II (ca. 315–140 cm). Pollen concentrations increase substantially throughout the zone, from negligible amounts at the bottom to several thousand near the top. This trend is paralleled by an increase in degraded grains (see below). The dominant pollen type in the lower portions of the zone is *Cupressus*-type, but above ca. 225–250 cm *Cupressus* declines as several pollen types of the Asteraceae increase (Fig. 3). Prominent among these is the *Baccharis*-type, though *Solidago*-, *Coreopsis*-, and *Chaenactis* types also become important. Members of the *Ambrosia* group, as well as the Liguliflorae, are abundant. *Artemisia* and grasses also increase toward the end of the zone. Spores of several species are prominent during this zone, including *Cheilanthes, Ophioglossum,* and two unidentified types. Aquatic herbs are most abundant during the early portion of the zone. Pollen Zone II largely corresponds to Waters' (1996) Unit III. Waters collected a radiocarbon date near the top, dating 2610 ± 80 yr BP.

Pollen Zone III (ca. 140–100 cm). Pollen in this zone is little changed from Zone II below it, except in the relative absence of *Cupressus*-type and the increase for the first time in pollen of Chenopodiaceae-*Amaranthus* plants (Cheno-Am) (Fig. 3). The pollen assemblage is still dominated by members of the Asteraceae, though *Coreopsis*- and *Chaenactis*-types are less important. Other than a few grains of sedge (Cyperaceae) no aquatic or riparian pollen is found. This zone corresponds to Waters' (1996) Unit IV. The single radiocarbon date near the top of this unit is 1800 ± 80 yr BP.

Pollen Zone IV (ca. 100–40 cm). Major changes in the pollen profile begin in this zone. Pollen concentrations are the highest of any pollen zone, averaging 67,750 grns/cc. The pollen assemblage continues to be dominated by *Baccharis*- and *Solidago*-types, but Cheno-Am, *Artemisia,* and grasses remain prominent. *Cupressus* and *Ambrosia* are absent. One pollen type, *Eriogonum,* becomes most abundant in this zone, while a second, *Brassica*-type, is first recognized here. Riparian indicators (*Alnus, Salix,* and Cyperaceae) are also important once again. Pollen zone IV corresponds to Unit V of Waters (1996).

Pollen Zone V (ca. 40 cm to the profile top). This pollen assemblage is the most distinctive of any in the profile. The assemblage is dominated by *Brassica*- and *Foeniculum*-type pollen, both indicative of severe disturbance. Cheno-Am pollen, another disturbance indicator, reaches its maximum here. Tree pollen includes *Pinus,* and the introduced species *Eucalyptus, Olea,* and *Tamarix.* Riparian species include cf. *Platanus, Juglans, Salix, Alnus,* and Cyperaceae (Fig. 3). This zone corresponds to Waters' (1996) Unit VI.

DISCUSSION

We examined several sites along the Camp Pendleton coastline for potential reconstruction of Holocene paleoenvironments. Our reconnaissance, as well as those of Waters (1996), suggested that analysis of alluvial deposits provides the best opportunity for paleoecological reconstruction there. Waters (1996) and Waters et al. (in press) identified two types of stream systems operating along the coast. Some streams, like Santa Margarita Creek, have large drainage basins with through-flowing discharge capable of maintaining an open channel to the ocean. Other fluvial systems have considerably smaller drainage basins with smaller discharg-

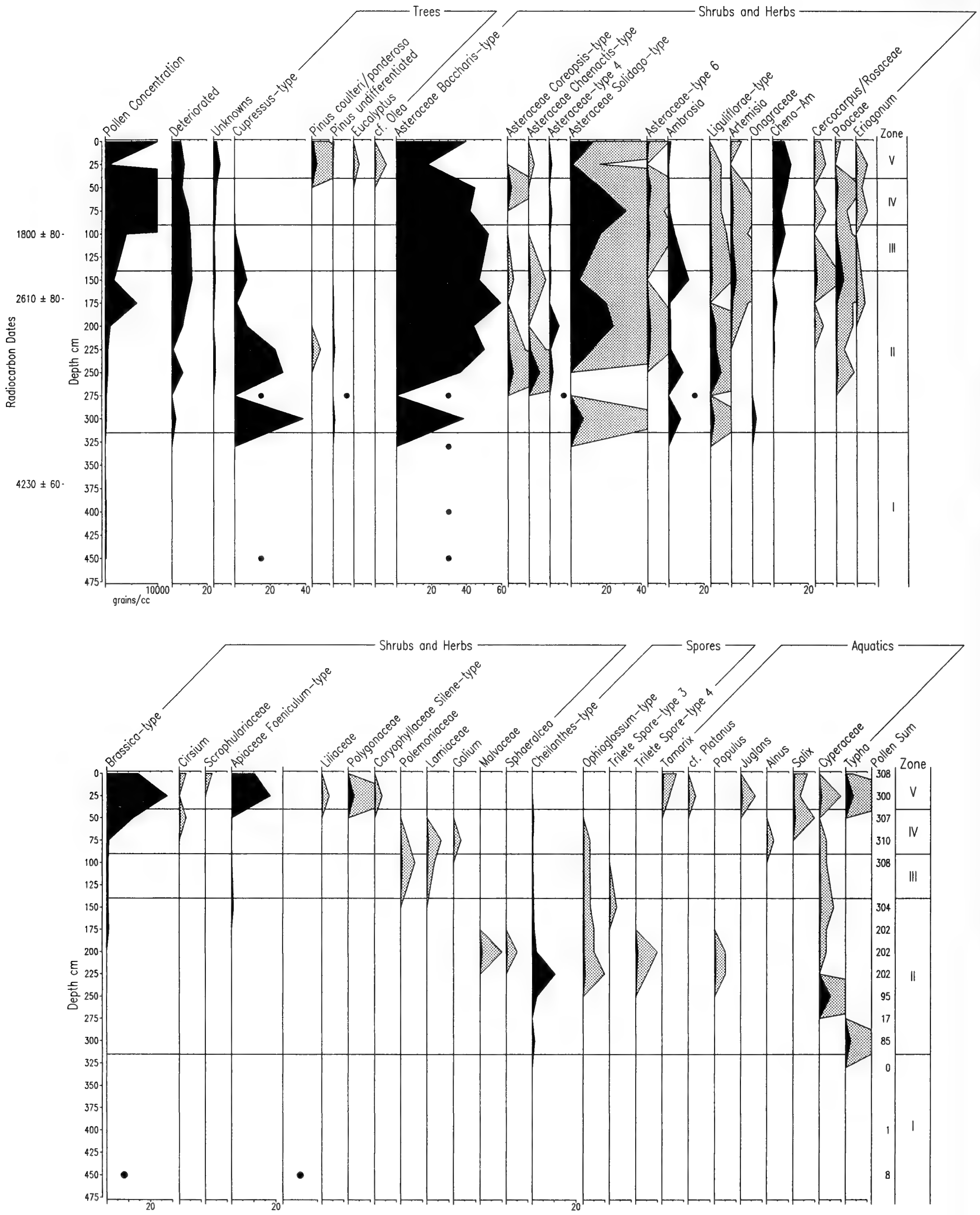

FIG. 3. Pollen percentage diagram for the Las Flores Creek pollen profile. Silhouettes are the pollen percentages ×10. Dots represent single-grain occurrences of the individual pollen types.

es, and do not terminate at the ocean. Instead, these drainages most often terminate in lagoons or sloughs, dammed by beach sand. During large storms when stream discharge increases, a channel cuts through the beach deposit, and the slough drains. Subsequently, shoreline processes restore the beach and the slough forms once again. The Las Flores Creek deposit falls in the latter category.

Differences of opinion exist between researchers regarding the interpretation of alluvial pollen assemblages. Hall (1985) reviewed the literature from alluvial sites in the Southwest. Though local vegetation changes can be interpreted from the data, Hall noted that many profiles contain unconformities, with pollen sequences typically beginning or ending during the late Pleistocene or middle Holocene, due to changes in sedimentation, erosion, or soil formation. Fall's (1987) work in Arizona suggested to her that alluvial pollen was unreliable for reconstruction of regional paleoenvironments. For most contexts, it should be assumed that alluvial pollen integrates vegetation occurring near the stream or channel. At a minimum, alluvial pollen records local vegetation changes, often associated with paleohydrologic changes, and tied to climate.

The record exposed along Las Flores Creek represents at least the last ca. 4300 years, perhaps longer. It is an important record since records from only three other coastal sites (Davis 1992; Cole and Liu 1994; Mudie and Byrne 1980) have together defined the Late Holocene sequence for southern California. Each of these studies record vegetation changes within coastal salt marshes, while the record from Las Flores Creek is largely from a coastal bluff. In addition, the Las Flores site exists alongside a prehistoric archaeological site occupied by Native Americans (during Pollen Zone IV).

The pollen changes presented here record some startling vegetation changes along the Las Flores corridor, though unfortunately, the record cannot be interpreted with any precision below ca. 315 cm depth. Pollen Zone I (sedimentary Units I and II), deposited primarily before ca. 4200 yr BP, record a basal and succeeding unit of deposition, each capped by soil development. Pollen preservation was largely unfavorable in these sediments. Poor preservation and low concentrations could result from intense decomposition during soil formation, or rapid sedimentation and dilution of pollen. Existing evidence cannot exclude either hypothesis.

However, during Pollen Zone II time (depositional Unit III), pollen preservation increased from bottom to top. Waters (1996) described this unit as a fining upward sequence, implying channel infilling and overbank deposition. The resulting pollen assemblage provides some support for this interpretation, as well as insight into the vegetation communities that existed along the banks of the ancient Las Flores Creek. Riparian indicators (*Typha,* Cyperaceae, *Ophioglossum*-type) are most prominent in the coarser sediments deposited near the opening of Zone II, and become less important with time. The increase in degraded grains near the top of the unit are indicative of intense soil formation. A third period of soil formation commenced sometime around 2600 years ago.

The occurrence of *Cupressus*-type pollen is of great interest, yet becomes problematic, for several reasons. *Cupressus* does not occur on Camp Pendleton today. The abundance of *Cupressus*-type pollen during this time is suggestive of a riparian gallery forest of *Cupressus,* or, alternatively, transport of the pollen from nearby upstream locations. The disappearance of *Cupressus*-type pollen during the waning stages of Zone II time could then represent movement of the stream away from the present profile site, or local extermination of the species, perhaps due to more frequent drying of the slough. Problematic is the fact that today *Cupressus guadalupensis* ssp. *forbesii* and *C. arizonica* ssp. E. Greene *stephensonii* are both found in chaparral foothills, though the former presently occurs as low as 150 m (Beauchamp 1986). A remnant population of the former grows in the Santa Ana mountains of Orange County (Vogl et al. 1988). The morphology of the grain is not referable to *Juniperus,* and is less like *Calocedrus,* both of which occur at higher elevations and away from the site today. All members of the Cupressaceae produce copious amounts of pollen, and the absence of *Cupressus*-type pollen higher in the profile suggests local extirpation of the plant.

Increases in pollen of *Artemisia, Eriogonum* and Poaceae, as well as the establishment of a large number of species in the Asteraceae family, suggest establishment of a vegetation mosaic, including coastal sage, chaparral and grassland communities, near the site by ca. 2600 years ago. This mosaic has largely persisted until the present, with allowances for recent introductions of non-native plants and changes associated with human disturbance. Pollen spectra from Santa Barbara Basin cores show similar increases in species of coastal sage scrub (*Artemisia, Eriogonum,* Labiatae) and chaparral (Rosaceae-Rhamnaceae-Anacardiaceae) during the Late Holocene (Heusser 1978). Since the source of pollen extracted from this marine core is the area drained by the Ventura and Santa Clara Rivers, we conclude that the record from Las Flores is a local example of a large-scale development of coastal vegetation in southern California. The Las Flores record is important in confirming this theory, and fixing the timing of the vegetation change.

The pollen assemblage of Zone III time largely represents continuation of conditions during Zone II, and a transition into Zone IV times. Sediments deposited during Zone IV time (Unit V of Waters, 1996) include a prehistoric archaeological occupation represented in the section by marine shells (dominated by *Donax gouldii*), fire-affected rock, and charcoal; a radiocarbon date suggests deposition centered around 1800 years ago. Archaeological excavations of this site directly to the north revealed an extensive coastal shell midden also radiocarbon dated between 1800 and 1500 years ago (Byrd 1996). This prehistoric occupation is part of a regional trend toward intensive exploitation of periodic *Donax* resurgences during the last 2000 years (Byrd, in press; Reddy 1996a; Laylander and Saunders 1993). These sediments are darker colored and considerably more organic than those below. This may have contributed to the higher concentration of pollen found during Zone IV time. Though the pollen is not significantly different from below, indicators of local disturbance (e.g., *Brassica*-type and Cheno-Am pollen) suggest human activity. (*Brassica*-type pollen probably includes several species or genera, and probably does not represent the same species found in Zone V above). The first occurrence of willow pollen suggests that the modern willow scrub community originated on the deposit surface during this time.

No pollen types indicative of aboriginal cultivation were found in these sediments. Recent investigations have demonstrated that aboriginal occupation patterns were probably not characterized by agriculture or horticulture (see Shipek 1989), but instead entailed intensive exploitation of wild plant and animal resources, of which shellfish, fish, small terrestrial mammals, grasses, and nuts were dietary staples (Byrd 1996; Glassow and Wilcoxon 1988; Jones 1991, 1992). The slowing of sea-level rise during the late Holocene converted the region's mainly rocky shorelines into larger stretches of sandy beach (Inman 1983), and caused a decline in shellfish productivity (Warren 1964). However, periodic exploitation of massive resurgences of sandy beach swelling *Donax* and offshore fishing during the last 2000 years provided a niche in which this area's coastline could be occupied for an extended period each year. Based on seasonality analysis of fish otoliths and paleoethnobotanical remains, this site along Las Flores Creek was occupied at least from March through October (Hudson 1996; Reddy 1996b). If abandoned during the winter, inland sites situated among oak groves would have provided an alternative seasonal niche to exploit.

The uppermost sediments and pollen are certainly recent in age, dating to the occupation of Europeans. Several pollen types confirm this interpretation. Dominating the pollen assemblage are *Foeniculum*-type (Apiaceae) and *Brassica*-type (Brassicaceae). *Foeniculum vulgare* and *Brassica nigra,* which today grow on the deposit surface, are both native to Europe (Beauchamp 1986). *Eucalyptus* trees, native to Australia, were imported to North America and planted in the San Francisco region prior to 1860 (Ingham 1908); they were first planted in San Diego County during the period 1902–1910 (Stanford 1970; Mudie and Byrne 1980). *Tamarix,* a native of the Middle East and Old World, was widely planted in the southwestern U.S., and has escaped along watercourses. Most of the plants in cultivation here were part of a clone established by J. J. Thornber in Arizona, during the early part of the 20th century (Benson and Darrow 1981; see also Baum 1967). Arroyo cutting probably intensified during Zone V time as witnessed by the increase in riparian pollen types (Fig. 3). This may have allowed the deposit surface to dry somewhat, causing weedy annuals to be favored.

Though timing of the Pollen Zone I/II transition is uncertain, interpolation between radiocarbon dates suggests that the major palynological change occurred ca. 3800 years ago, consistent with an increase in effective precipitation, following a drier middle Holocene. Abundant evidence from the Sierra Nevada and other locations suggest that effective precipitation increased during the late Holocene. Anderson and Smith (1994) reported wet meadow deposition originated in the Sierra by ca. 4500 years ago, indicating rising groundwater levels. Treeline was higher (warmer conditions) in the Sierra and adjacent White Mountains prior to ca. 3700 years ago (LaMarche 1973; Scuderi 1987). Along the coast, Cole and Liu (1994) inferred increased precipitation on Santa Rosa Island beginning ca. 3250 yr BP, while Davis (1992) inferred drier conditions. Cole and Liu (1994) suggested that the disparity might be due to the proximity of the Santa Rosa site to the ocean, which, like the Las Flores site, is less than 100 m from the shorefront, while San Joaquin Marsh (Davis 1992) is ca. 7 km inland.

Thompson et al. (1993) presented maps of the effective moisture for the western United States, depicting the maximum effective moisture for the entire Pacific Coast during the last ca. 3000 years. Unfortunately the only blank spot on the map lies in southern California. The data presented here suggest that southern coastal California has responded to climatic change in a manner similar to the rest of coastal California and the Pacific Northwest.

CONCLUSIONS

Analysis of pollen from a stratigraphic section along Las Flores Arroyo has allowed us to reconstruct the local paleoenvironment over the last several thousand years. The Las Flores data are important because they represent one of only a handful of Holocene paleobotanical sites along the southern California coast, and are the first attempt to reconstruct paleoenvironments from Camp Pendleton Marine Base.

In most cases, pollen changes can be correlated with sedimentary changes, as determined by Waters (1996). Declines in pollen concentration with depth are indicative of the increased length of time that the pollen has been subject to decomposition. Alkaline conditions, as shown by petrocalcic nodules, are unfavorable for pollen preservation; in general, the greater oxidation potential of sandy sediments also contributes to increased pollen decomposition.

Even so, the pollen evidence tells us that the paleoenvironment during Zone II time (near the end of the Middle Holocene) was considerably different from the modern environment. *Cupressus* (or a similar tree) probably grew along the watercourse. This suggests wetter conditions than occur today during the early part of Zone II, allowing the tree to grow at lower elevations. Subsequent stabilization of the surface and colonization by herbs occurred by about 2600 years ago. These conditions were maintained until the present.

During the archaeological occupation of the valley floor, Pollen Zone IV, the vegetation growing locally was little changed from earlier, but increased disturbance may be seen by elevated Cheno-Am pollen. No distinctly identified cultivars were noted, but pollen evidence suggests semi-permanent water nearby probably provided at least a seasonal freshwater supply.

The historic period is recorded in the top 30–40 cm of the profile by the occurrence of several pollen types of introduced species. We do not know the source of these sediments, but the high riparian pollen content suggests that the sediments either came from a different alluvial source of recent deposition, or that incision of the deposit occurred within the most recent 100 years or so.

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APPENDIX TABLE 1. LAS FLORES CREEK ALLUVIAL SECTION POLLEN PERCENTAGES.

	Sample depth (cm)														
	0	25	50	75	100	150	175	200	225	250	275	300	330	400	450
Tracers	41	456	8	5	100	245	45	276	523	253	101	523	1	7	59
Pollen Sum	308	300	307	310	308	304	202	202	202	95	17	85	0	1	8
Pollen Conc. grains/cc	10141.5	888.2	51806.3	83700.0	4158.0	1675.1	6060.0	988.0	521.4	506.9	227.2	219.4	0.0	192.9	183.1
Deteriorated	5.2	7.3	5.9	9.7	10.7	11.8	8.9	6.4	1.0	6.3	0.0	2.4	0.0	0.0	0.0
Unknowns	1.9	4.0	1.6	1.3	0.3	1.0	0.5	0.0	1.0	1.1	0.0	0.0	0.0	0.0	0.0
Cupressus-type	0.0	0.0	0.0	0.0	0.6	7.2	1.5	7.4	23.3	27.4	X	38.8	0.0	0.0	X
Pinus coulteri/ponderosa	1.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Pinus undifferentiated	0.6	0.3	0.0	0.0	0.0	0.0	0.5	0.5	1.0	0.0	X	1.2	0.0	0.0	0.0
Eucalyptus	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
cf. *Olea*	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceanothus	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0
cf. Solanaceae	0.0	0.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asteraceae *Baccharis*-type	40.6	18.7	45.3	42.6	52.9	47.7	59.9	44.6	50.5	36.8	X	38.8	X	X	X
Asteraceae *Coreopsis*-type	0.0	0.0	2.3	0.0	0.0	0.3	0.0	0.5	1.0	3.2	0.0	0.0	0.0	0.0	0.0
Asteraceae *Chaenactis*-type	0.0	0.3	0.0	0.0	0.0	1.0	0.5	0.0	1.0	6.3	0.0	0.0	0.0	0.0	0.0
Asteraceae type-4	0.0	1.3	0.0	1.3	0.3	0.7	0.0	5.4	0.5	2.1	X	0.0	0.0	0.0	0.0
Asteraceae *Solidago*-type	13.6	1.7	17.3	31.6	17.2	5.3	20.3	24.3	12.4	0.0	0.0	7.1	0.0	0.0	0.0
Asteraceae type-6	1.3	0.0	2.3	1.0	1.6	0.0	1.0	2.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0
Ambrosia	1.9	0.7	0.7	1.0	3.9	11.8	1.0	1.5	1.5	8.4	X	7.1	0.0	0.0	0.0
Cheno-Am	6.8	10.7	8.1	4.8	7.1	0.0	2.5	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Cercocarpus/Rosaceae	0.3	0.7	0.0	0.6	0.0	1.6	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Artemisia	0.6	0.0	1.0	1.6	1.0	3.3	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poaceae	0.3	0.0	1.6	0.6	1.0	4.9	1.0	1.0	0.5	1.1	0.0	0.0	0.0	0.0	0.0
Brassica-type	14.6	27.7	12.4	1.0	0.6	0.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	X
Cirsium	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scrophulariaceae	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apiaceae *Foeniculum*-type	10.4	17.3	0.3	0.0	0.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	X
Liliaceae	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Liguliflorae	0.0	0.7	0.7	0.6	1.0	1.3	0.0	3.5	3.5	6.3	0.0	2.4	0.0	0.0	0.0
Eriogonum	0.0	0.7	0.3	0.6	0.0	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polygonaceae	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caryophyllaceae *Silene*-type	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polemoniaceae	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lamiaceae	0.0	0.0	0.0	0.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Galium	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malvaceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaeralcea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Onagraceae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0
Tamarix	0.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
cf. *Platanus*	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Populus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0

APPENDIX TABLE 1. CONTINUED

	Sample depth (cm)														
	0	25	50	75	100	150	175	200	225	250	275	300	330	400	450
Juglans	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alnus	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Salix	0.6	0.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperaceae	0.0	1.0	0.0	0.3	0.3	0.6	0.3	0.3	0.0	5.3	0.0	0.0	0.0	0.0	0.0
Typha	0.3	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0
Cheilanthes-type	0.0	0.0	0.7	0.3	0.3	0.7	1.0	2.0	10.4	2.1	0.0	1.2	0.0	0.0	0.0
Ophioglossum-type	0.0	0.0	0.0	0.3	0.3	0.3	0.5	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Trilete Spore type-3	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trilete Spore type-4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0

MADROÑO, Vol. 45, No. 2, p. 183, 1998

REVIEW

Mojave Desert Wildflowers. Jon Mark Stewart. 1998. vi + 210 pages. $14.95. Published by the author. ISBN 0-9634909-1-5.

Mojave Desert Wildflowers is the second offering of photographer Jon Mark Stewart, following his *Colorado Desert Wildflowers.* Stewart fell under the spell of desert botany while a student, and he has maintained his interests through his photography. *Mojave Desert Wildflowers* is a recent addition to a wide array of photographic guides to plants of desert regions. The goals of most such guides include 1) provide an easy means to identify plants via photographs and/or drawings, and 2) display the beauty of form and color in the plants of the desert. Attainment of both of these goals, and the quality of the reproduction, varies from guide to guide, but Stewart's new addition is a notable success. Here is produced a set of very good photographs of many of the commoner, and several less common species that inhabit the Mojave Desert. What caught my attention immediately was the exceptional quality of most of the photos. They are in focus with great depth of field, brightness and contrast are very good, and the color of the plants is true. Too often photos in field guides, whether due to inadequate originals or diminished reproduction, appear over- or underexposed. Bright yellow or white flowers are especially difficult to photograph for publication without seeming glary. Not so in this book. Field guides, to be useful, must show clearly the details that distinguish and differentiate species, and in this aspect Stewart succeeds.

Mojave Desert Wildflowers covers 195 species organized by flower color, with the exception of the cacti, which are contained in their own chapter. The taxonomy follows The Jepson Manual (1993), the most recent comprehensive flora of the region. In the back of the book there is a useful cross-list of names used by Munz' Flora of California (1959) and Kearney and Peebles' Flora of Arizona (1960), for those of us who learned the names of desert plants prior to 1993. I didn't notice a reference to where Stewart got his common names, but I suspect that many of them came from Jaeger's (1940) Desert Wild Flowers. As is common with wildflower guides, common names of the better known species are well-known and widely accepted, while those of lesser known species often appear to be forced on the species. For example, *Linanthus parryae* is called "Parry gilia", dating from the 19th century when all species of *Linanthus* were recognized as species of *Gilia.* I doubt if (m)any botanists today would actually call *L. parryae* by that name. Nonetheless, as there are no rules by which use of common names are followed, any common name appears fair game.

At the end of the book there is a page describing the film, equipment, and methods used in the photography. I enjoyed reading about this—not so much because I use essentially the same materials as Stewart, but because I can have hope that someday I might be able to achieve the high standard of photography that is present in this book.

I took this book with my plant taxonomy class to the Mojave Desert, and the consensus among these advanced students of botany was that it was a keeper. Among the wide assortment of picture books *Mojave Desert Wildflowers* stands out. I recommend the book to all who collect and use field guides to desert plants.

—ROBERT PATTERSON, Department of Biology, San Francisco State University, San Francisco, CA 94132.

MADROÑO, Vol. 45, No. 2, p. 184–185, 1998

NOTEWORTHY COLLECTIONS

ARIZONA

CYMOPTERUS BECKII Welsh & Goodrich (Apiaceae).—Navajo Co., Tsegi Canyon, UTM E. 545000, UTM N. 4066000, near small spring, July, 1996, verified by Stan Welsh of Brigham Young University. Voucher specimen on file at Deaver Herbarium (ASC), Northern Arizona University, Flagstaff.

Previous knowledge. Listed as an endemic in San Juan and Wayne counties, Utah. First described in 1981 by Stan Welsh.

Significance. This is a first report for Arizona and represents a range extension of about one hundred ten kilometers. This plant is a candidate for the federal listing of rare and endangered species. It is found only near seeps and springs in the area and its occurrence is fairly rare.

—SUSAN HOLIDAY and TINA AYERS, Northern Arizona University, Box 5640, Flagstaff, AZ 86011.

CALIFORNIA

LIMNANTHES MACOUNII Trel. (LIMNANTHACEAE).—Abundant on ca 18 acres of a seasonally fallow field along the east side of Highway 1 just south of Moss Beach and opposite the Half Moon Bay airport, San Mateo Co. 24 March 1998. (UC); 12 April 1998. *E. Buxton s. n. R. Ornduff 10168* (UC). This large population was discovered by the first author in early February, 1998; flowering plants were present on the site until late May, 1998, when the field was plowed prior to planting cabbage.

Previous knowledge. Limnanthes macounii is otherwise restricted to a small portion of southern Vancouver Island and offshore islets in and near Victoria, British Columbia, Canada. Elsewhere the genus occurs in California and southwestern Oregon (*L. alba* Benth. has become locally established in Linn County, Oregon, where it is cultivated as an oilseed crop).

Signficance and comment. There were doubtless many more individuals of *L. macounii* in the Moss Beach population in 1998 than in all the British Columbia populations combined. The Moss Beach plants are unusually robust for *L. macounii,* producing decumbent fruiting stems that are up to 60 cm long. In certain foliar characters they differ somewhat from British Columbia specimens (A. Ceska, personal communication). Because the California population occurs in a field that is adjacent to and easily visible from a well traveled highway and is opposite an airport, we suspect that it is not native to the site but originated via an accidental introduction. The species is autogamous and thus successful establishment of a new population requires the introduction of only a single nutlet. We have no idea how long this population of *L. macounii* has occupied the field, but its large size suggests that it has been present since well before 1998. We thank Adolf Ceska for his helpful comments.

—EVA BUXTON, LSA Associates, Inc., 157 Park Place, Point Richmond, CA 94801; ROBERT ORNDUFF, Department of Integrative Biology, University of California, Berkeley, CA 94720-3140.

CALIFORNIA

SAGITTARIA RIGIDA Pursh (ALISMATACEAE).—Marin Co., Pt. Reyes Peninsula, dunes at SE end of Abbotts Lagoon, very abundant in small farm pond N of radio tower facility, associated with *Polygonum amphibium* L. var. *emersum* Michaux, *Hydrocotyle ranunculoides* L. f., *Cotula coronopifolia* L., etc., 38°06′30″N, 122°56′40″W, alt. ca. 6 m, 20 Jul 1987, *R. Raiche 70477* (JEPS). Tehama Co., in large stock pond on an unnamed tributary of Inks Creek ca. 1.3 air miles N of Dales Lake, 40°21′N, 122°3′55″W, T29N R2W NE¼ of SE¼ S22, alt. 185 m, ca. 1000 individuals growing in association with *Sagittaria latifolia* Willd, *S. sanfordii* E. Green, *Eleocharis macrostachya* Britton, and *Scirpus acutus* Bigelow var. *occidentalis* (S. Watson) Beetle, 26 May 1992, *Dean Wm. Taylor 12649* (UC!) & 21 Jul 1992, *C. Witham 450* (JEPS). Plumas Co., east side of Last Chance Marsh located at the north end of Lake Almanor, 40°20′5″N, 121°12′25″W, T29N R7E NW¼ of NE¼ S33, alt. 1365 m, ca. 1000 individuals in colonies scattered along 300 m of marsh in association with *Menyanthes trifoliata* L., *Nuphar lutea* (L.) Sibth & Sm. ssp *polysepala* (Engelm.) E. Beal, *Potamogeton natans* L., *Utricularia vulgaris* L., and other marsh vegetation, vegetative plant on 6 Sep 1994, *V. Oswald 6476* (CHSC) & flowering and fruiting plants on 22 Jul 1997, *V. Oswald 8768* (CHSC).

Previous knowledge. A plant of brackish and saline waters of eastern North America (Que. to MN south to KS, MO, VA).

Significance. First records for California and western North America. *S. rigida* can be separated from all other species of *Sagittaria* in California based on the three pistillate flowers and fruiting heads, which appear to be sessile in the lowest whorl of the inflorescence. All other *Sagittaria* in California have obviously pedicelled pistillate flowers and fruiting heads. Plants from all three populations have been annotated by Robert Haynes, The University of Alabama, who is coordinating the treatments of aquatic plants for the Flora of North America project. The three California populations of *S. rigida* are in artificial ponds and lakes separated by distances of from 72 to 282 km. How the plant arrived in California is open to conjecture, but it can now be expected to become more widely dispersed through the movements of waterfowl.

—VERNON H. OSWALD, Herbarium, Department of Biological Sciences, California State University, Chico, CA 95929-0515; ROGER RAICHE, 1 Maybeck Twin Dr., Berkeley, CA 94708-2037; CAROL WITHAM, 1028 Cypress Lane, Davis, CA 95616-1364.

CALIFORNIA

UTRICULARIA OCHROLEUCA R. Hartman (*U. occidentalis* Gray) Lentibulariaceae. Plumas Co., northern end of Lake Almanor, east side of lake north of Hwy. 36 bridge, T29N-R7E-sw sec. 28, 1437 m. Selected associate species: *Utricularia macrorhiza, U. minor, Nuphar polysepalum,* *Eriophorum gracile*; 24 June 1994, J. H. Rondeau 5169 (SJSU).

Previous knowledge. This species is very rare throughout the western U.S. with only three citations in Oregon (Rondeau, 1995) and two in Washington (Ceska & Bell, 1973). The nearest known location is 470 km northward at Gold Lake in central Oregon, although it may exist as far south as Bull Swamp in Klamath County (Rondeau, 1995).

Special thanks to Goran Thor (Swedish Univ. of Agric. Sciences, Uppsala, Sweden) for taxonomic assistance via quadrifid gland analysis.

Significance. First collection for California.

Literature Cited

Ceska, A. and M. A. Bell. 1973. *Utricularia* (Lentibulariaceae) in the Pacific Northwest. Madroño, 22:74–84.

Rondeau, J. Hawkeye. 1995. Carnivorous plants of the west, Volume II: California, Oregon, and Washington. San Jose, CA 95127.

Thor, G. 1988. The Genus *Utricularia* in the Nordic Countries, with special emphasis on *U. stygia* and *U. ochroleuca.* Nord. Jr. Bot. 8(3):213–225.

—J. Hawkeye Rondeau, "mybog@aol.com", 37 Sunnyslope Ave., San Jose, CA 95127.

Oregon

Carex diandra Schrank (Cyperaceae).—Lake Co., Dog Lake, 4.8 air km SSE of Dog Mountain, E of crest of Barnes Rim, Fremont National Forest, T40S R17E S22 SW¼, alt. 1583 m, floating mat in mid-lake, with *Carex utriculata, Typha latifolia, Scirpus acutus,* 20 July 1996, *Zika et al. 12917* (OSC).

Previous knowledge. Circumboreal and recorded sporadically south in our region, with collections from northern California, northern Washington, Idaho and Montana. An earlier Oregon report by Peck (A Manual of the Higher Plants of Oregon, 1961) stated: "bogs in the high mountains of eastern Oregon", but was unsubstantiated by herbarium collections.

Significance. First verified record for Oregon.

—Peter F. Zika, Keli Kuykendall, Danna Lytjen, and Nick Otting, Herbarium, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

Volume 45, Number 2, pages 93–185, published 5 May 1999

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MADROÑO

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MADROÑO, Vol. 45, No. 3, pp. 187–199, 1998

PHYLOGENY OF THE *ARCTOSTAPHYLOS HOOKERI* COMPLEX (ERICACEAE) BASED ON NRDNA DATA

STACI MARKOS[1], LENA C. HILEMAN[2], MICHAEL C. VASEY, AND V. THOMAS PARKER
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ABSTRACT

The *Arctostaphylos hookeri* G. Don complex is composed of five subspecies whose classification has been problematic. We investigated the monophyly of *A. hookeri* using sequence data from the ITS and 26S regions of nuclear rDNA. Several of the individual plants sequenced contained ITS sequence polymorphism. An investigation of 34 *Arctostaphylos* taxa, using RFLP data, demonstrated that polymorphism in the ITS region exists in several members of the genus. Collectively, our results indicate 1) the subspecies of *A. hookeri* are not monophyletic, 2) the current understanding of many species relationships within the genus and the circumscription of subgenera and sections need to be further investigated, and 3) a complex pattern of ITS sequence evolution is suggestive of either hybridization or sorting of ancestral polymorphism.

Arctostaphylos (Ericaceae: Arbutoideae) is a large and taxonomically complex genus composed of over 100 taxa (Wells 1991). Geographically, the distribution of *Arctostaphylos* is circumboreal but most of that distribution is accounted for by only one species, *A. uva-ursi* (L.) Sprengel. Most species are restricted to the California Floristic Province where approximately half of the taxa are considered rare, threatened, or endangered (Skinner and Pavlik 1994). Species diversity is highest in the coast ranges of California where more than 30 species occur (Fig. 1).

Arctostaphylos is considered to have originated in the Miocene, approximately 15 million years ago (Stebbins and Major 1965; Raven and Axelrod 1978). Based on the fossil record, radiation of the genus is considered to have begun during the Pleistocene, approximately 1.5 million years ago (Raven and Axelrod 1978). Diversification in the genus has been attributed to a number of abiotic and biotic influences which include: the development of diverse topography and soils, edaphic restriction (Wells 1993; Raven and Axelrod 1978), the presence of fire regimes characteristic of the California Floristic Province (Raven and Axelrod 1978), different life history strategies (Wells 1969; Raven and Axelrod 1978), polyploidy (Stebbins 1980), and hybridization (Shapin 1966; Gottlieb 1968; Kruckeberg 1977; Schierenbeck et al. 1992).

Determining evolutionary relationships in *Arctostaphylos* has challenged botanists. Currently, taxa thought to be closely related most often are classified as subspecies, as within *A. glandulosa* Eastw., *A. stanfordiana* C. Parry, *A. tomentosa* (Pursh) Lindley, and *A. hookeri* G. Don.

We tested the monophyly of *A. hookeri* (*sensu* Wells 1993). This complex of five subspecies was chosen for investigation because the subspecies have been allied with different species in earlier treatments (Table 1). Also, the subspecies of *A. hookeri* are all limited in distribution and are threatened by development. An understanding of their relationships is essential for their conservation.

An overview of the systematics of Arctostaphylos. Based on taxonomic treatments (Drude 1897; Busch 1952; and Thorne 1992) *Arctostaphylos* is one of six allied genera in the Ericaceae. These genera (*Arctostaphylos, Arbutus, Comarostaphylis, Arctous, Ornithostaphylos,* and *Xylococcus*) have been considered to constitute the tribe Arbuteae within the subfamily Vaccinioideae (Stevens 1971), but recent molecular studies support the placement of these genera as the subfamily Arbutoideae (Cullings 1994, 1996; Kron and Chase 1993; Kron 1996).

Current understanding of the genus *Arctostaphylos* has been enhanced greatly by the work of Jepson (1922, 1939), Eastwood (1934), Adams (1940), Roof (1976, 1978), and Wells (1968, 1988, 1992, 1993) who undertook systematic studies of the entire genus. Several subgeneric groups have been recognized in *Arctostaphylos.* These groups are reflected in the classification proposed by Wells (1992). He proposed two subgenera, subgenus *Micrococcus* and subgenus *Arctostaphylos.* Subgenus *Micrococcus,* once elevated to generic standing by Eastwood (1937), comprises only 4 taxa. There are three sections in the subgenus *Micrococcus,* two of which are monotypic. There are three sections in subgenus *Arctostaphylos*: *Foliobracteata, Arctostaphylos,* and *Pictobracteata. Arctostaphylos hookeri* is a member of subgenus *Arctostaphylos* sect. *Arctostaphylos.*

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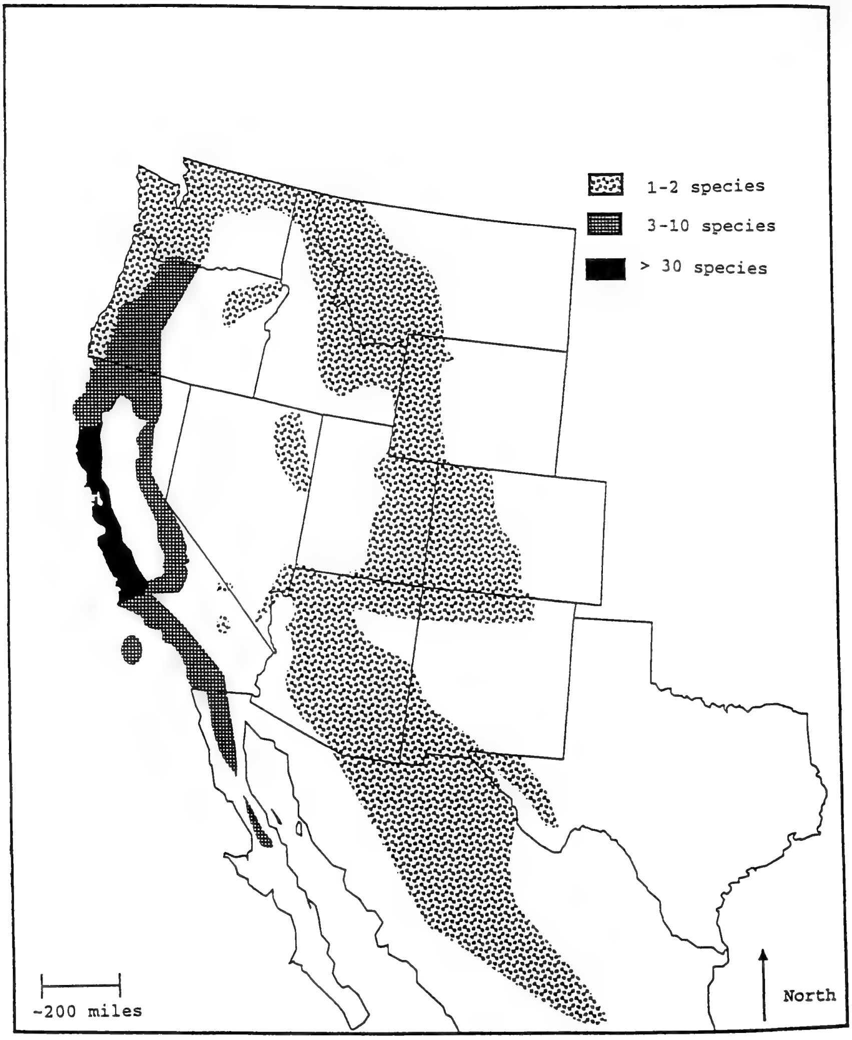

FIG. 1. Distribution of *Arctostaphylos* taxa in the western United States. *Arctostaphylos uva-ursi* has a circumboreal distribution which is not shown.

Systematics of Arctostaphylos hookeri. Arctostaphylos hookeri C. Don ssp. *hookeri* occurs in the hills, dunes, and forests near Monterey Bay. Roof (1980) stated that "... efforts to erect an '*Arctostaphylos hookeri* complex' seem unwise and impractical, since the synthesis requires the cross-placing of individuals of the *A. pungens* Kunth. alliance with those of the *A. uva-ursi* alliance." Accordingly, in Roof's (1976, 1980) treatments of the five taxa treated as subspecies of *A. hookeri* by Wells (1993), none fell within the circumscription of *A. hookeri.* Taxa that were previously treated as members of the *hookeri* complex were classified as infraspecific taxa of either *A. uva-ursi* or *A. pungens* (Table 1). *Arctostaphylos hookeri* was allied with *A. uva-ursi,* as *A. uva-ursi* ssp. *hookeri.* Wells (1993) recognized *A. hookeri* ssp. *hookeri,* reaffirming his concept of the *A. hookeri* complex. *Arctostaphylos hookeri* ssp. *hookeri* is listed as rare, threatened, or endangered in California by the California Native Plant Society (CNPS) (Skinner and Pavlik 1994).

Arctostaphylos hookeri ssp. *hearstiorum* (Hoover and Roof) P. Wells was described as *A. hearstiorum* by Hoover and Roof (1966). Wells (1968) reduced *A. hearstiorum* to a subspecies of *A. hookeri. Arctostaphylos hookeri* ssp. *hearstiorum* is endemic to grassy hills and mesas of the Arroyo de la Cruz area of San Luis Obispo County. It is listed as rare, threatened, or endangered in California by CNPS (Skinner and Pavlik 1994) and is State-listed as endangered.

Arctostaphylos hookeri G. Don ssp. *franciscana* (Eastw.) Munz was described as *A. franciscana* by Eastwood (1905) and was reduced to a subspecies of *A. hookeri* by Munz (1958). *Arctostaphylos hookeri* ssp. *franciscana* was known to occur on serpentine outcrops at three locations in San Fran-

TABLE 1. A SUMMARY OF THE TAXONOMIC HISTORY OF THE *A. HOOKERI* COMPLEX (*SENSU* WELLS 1993).

- *A. hookeri* ssp. *franciscana*
  - *A. franciscana* Eastw. (1905)
  - *Uva-ursi franciscana* Heller (1914)
  - *A. hookeri* G. Don ssp. *franciscana* (Eastw.) Munz (1958)
  - *A. uva-ursi* (L.) Spreng. var. *franciscana* (Eastw.) Roof (1980)
- *A. hookeri* ssp. *hearstiorum*
  - *A. hearstiorum* Hoover & Roof (1966)
  - *A. hookeri* G. Don ssp. *hearstiorum* (Hoover & Roof) Wells (1968)
  - *A. uva-ursi* (L.) Spreng. var. *hearstiorum* (Hoover & Roof) Roof (1980)
- *A. hookeri* ssp. *hookeri*
  - *A. hookeri* G. Don (1834)
  - *Uva-ursi hookeri* (G. Don) Abrams (1914)
  - *A. uva-ursi* (L.) Spreng. ssp. *hookeri* (G. Don) Roof (1980)
- *A. hookeri* ssp. *montana*
  - *A. montana* Eastw. (1897)
  - *Uva-ursi montana* Abrams (1914)
  - *A. pungens* HBK var. *montana* (Eastw.) Munz (1958)
  - *A. hookeri* G. Don ssp. *montana* (Eastw.) Wells (1968)
  - *A. pungens* HBK ssp. *montana* (Eastw.) Roof (1976)
- *A. hookeri* ssp. *ravenii*
  - *A. pungens* HBK var. *ravenii* (Wells) Roof (1976)
  - *A. hookeri* G. Don ssp. *ravenii* Wells (1968)

cisco (Roof 1976). It is now extinct in the wild and persists only in cultivation.

Arctostaphylos hookeri G. Don ssp. *ravenii* P. Wells was considered extinct in the wild until 1952 when it was rediscovered by Peter Raven at a previously unknown location, a serpentine outcrop in the San Francisco Presidio. *Arctostaphylos hookeri* ssp. *ravenii* has been treated as *A. pungens* var. *ravenii* (Roof 1976). *Arctostaphylos hookeri* ssp. *ravenii* is listed as rare, threatened, or endangered in California by CNPS (Skinner and Pavlik 1994) and is also listed as state and federally endangered.

Arctostaphylos hookeri G. Don ssp. *montana* (Eastw.) P. Wells was described as *A. montana* by Eastwood (1897). Munz (1958) later placed it within *A. pungens* as *A. pungens* var. *montana*. In 1968, Wells classified *A. pungens* var. *montana* as a subspecies of *A. hookeri* because of the "resemblance . . . in morphology, ecology, and chromosome number" to *A. hookeri* ssp. *ravenii*. Roof (1976) followed Munz (1958) and recognized *A. pungens* ssp. *montana*. In this same publication Roof disagreed with an observation made by Jepson (1939) that *A. pungens* ssp. *montana* ". . . has an affinity with *A. hookeri* and might be referred to as that species save for their thick leaves," and stated that this taxon should not be included in the *A. hookeri* alliance. Wells (1993) transferred *A. pungens* ssp. *montana* to *A. hookeri*. *Arctostaphylos hookeri* ssp. *montana* is restricted to serpentine-derived soils on Mount Tamalpais, Marin County. It is listed as rare, threatened, or endangered in California by CNPS (Skinner and Pavlik 1994).

MATERIALS AND METHODS

Terminal taxa in the phylogenetic analyses. ITS Region.—The ITS region of nine *Arctostaphylos* taxa was sequenced and subjected to phylogenetic analysis. The taxa included were all five members of the *A. hookeri* complex, the two taxa to which the subspecies of *hookeri* have been previously allied (*A. pungens* and *A. uva-ursi*), and two taxa presumably distantly related to *A. hookeri: A. tomentosa* ssp. *tomentosa* (a member of section *Foliobracteata*) and *A. nummularia* A. Gray (a member of subgenus *Micrococcus*) (Wells 1987). At least two individuals per taxon, from disparate parts of its range, were sequenced for all taxa except *A. tomentosa, A. nummularia,* and the outgroup (*Arbutus menziesii* Pursh) (Table 2).

26S Region.—The taxa included in the 26S study were two members of the *A. hookeri* complex (ssp. *hookeri* and ssp. *montana*), and 14 species representing five sections of *Arctostaphylos* (Table 2). One individual per taxon was sequenced.

In both analyses, the outgroup, *Arbutus menziesii,* was chosen based on results of a recent molecular phylogenetic study that placed *Arbutus* in a basally divergent position in the Arbutoideae (Hileman et al. 1994). The choice of outgroup was also well supported by morphological data and fossil evidence (Stevens 1971; Wehr and Hopkins 1994; Schorn personal communication). For all taxa sampled, taxonomic positions, collection localities, voucher information, and accession numbers are provided in Table 2.

Taxa included in the ITS-RFLP analysis. Thirty-four taxa were included in the ITS-RFLP study. These taxa represent all members of section *Arctostaphylos* and select taxa from sections *Foliobracteata* and *Pictobracteata,* and subgenus *Micrococcus* (Table 2).

DNA extraction. Total DNA's were isolated from dried leaves of individual plants. DNA extraction followed a simplified Doyle & Doyle CTAB extraction (1987). The protocol used is detailed in Cullings (1992).

Amplification and sequencing. ITS Region.—Double-stranded PCR products were amplified using the primers c28KJ (Cullings 1992) and "ITS 5" (White et al. 1990). The 25 μl reactions contained 14.9 μl water, 2.5 μl *Taq* enzyme buffer, 2.5 μl 25 mM MgCl$_2$, 0.475 μl 40 mM dNTP's, 1.25 μl 10 μm c28KJ, 1.25 μl 10 μm "ITS 5", 0.125 μl *Taq* polymerase (5 units/μl), and 2 μl genomic DNA (dilutions of genomic DNA ranged from 1:10 to 1:1000). Amplification parameters followed

TABLE 2. COLLECTIONS EXAMINED FOR ITS SEQUENCE (*) 26S SEQUENCE (●) AND ITS RFLP ANALYSES (▲). Taxonomic position of the individuals sampled is also indicated. Accession numbers refer to GenBank Libraries. Collector abbreviations: VTP, V. Thomas Parker; MV, Michael Vasey; SM, Staci Markos. Specimens will be deposited in SFSU.

	ITS	26S	RFLP	Taxon	Voucher	Locality	Accession number	
							ITS	26S
SUBG. MICRO								
Sect. Micro.								
			▲	*A. mendocinoensis* P. Wells	VTP&MV 0300	Mendocino Co., CA		
		●			VTP&MV 0037	Mendocino Co., CA		AF106803
	*		▲	*A. nummularia* A. Gray	MV&VTP 0398	Santa Cruz Co., CA	AF091949	
		●			MV&VTP 0040	Marin Co., CA		AF091974
Sect. Niss.								
			▲	*A. nissenana* Merriam	MV&VTP 0368	Eldorado Co., CA		
		●			MV&VTP 0490	Eldorado Co., CA		AF106804
SUBG. ARCTO.								
Sect. Arcto.								
			▲	*A. bakeri* Eastw.	VTP&MC 0071	Sonoma Co., CA		
			▲	*A. densiflora* Baker	MV&VTP 0069	Sonoma Co., CA		
			▲	*A. edmundsii* J. Howell	VTP&MV 0061	Monterey Co., CA		
			▲	*A. gabrielensis* P. Wells	P. Wells (s.n.)	Los Angeles Co., CA		
			▲	*A. glauca* Lindley	VTP&MV 0198	Riverside Co., CA		
		●			VTP&MV 0235	San Luis Obispo Co., CA		AF106805
			▲	*A. hispidula* Howell	VTP&MV 0360	Del Norte Co., CA		
	*		▲	*A. hookeri* G. Don ssp. *franciscana*	Tilden Regional Park	San Francisco Co., CA	AF106816	
	*			(Eastw.) Munz	Strybing Arboretum	San Francisco Co., CA		
	*		▲	*A. hookeri* G. Don ssp. *hearstiorum*	SM, VTP&MV 0603	San Luis Obispo Co., CA	AF106817	
	*			(Hoover & Roof) P. Wells	Strybing Arboretum	San Luis Obispo Co., CA		
	*	●	▲	*A. hookeri* G. Don ssp. *hookeri*	SM, VTP&MV 0607	Monterey Co., CA	AF106818	AF106806
	*				Tilden Regional Park	Monterey Co., CA		
	*	●	▲	*A. hookeri* G. Don ssp. *montana*	SM, VTP&MV 0601	Marin Co., CA	AF091951	AF091977
	*			(Eastw.) P. Wells	Tilden Regional Park	Marin Co., CA		
	*		▲	*A. hookeri* G. Don ssp. *ravenii*	Tilden Regional Park	San Francisco Co., CA	AF106819	
				P. Wells	Strybing Arboretum	San Francisco Co., CA		
			▲	*A. klamathensis* S. Edwards	R. Raiche 20804	Siskiyou Co., CA		
			▲	*A. manzanita* C. Parry ssp. *manzanita*	VTP&MV 0166	Sonoma Co., CA		
			▲	*A. mewukka* Merriam ssp. *mewukka*	VTP&MV 0333	Butte Co., CA		
			▲	*A. nevadensis* A. Gray	VTP&MV 0359	Del Norte Co., CA		
			▲	*A. parryana* Lemmon	MV&VTP 0189	Ventura Co., CA		
			▲	*A. patula* E. Greene	VTP&MV 0313	Sierra Co., CA		
		●			VTP&MV 0102	Glenn Co., CA		AF106807

TABLE 2. CONTINUED.

							Accession number	
	ITS	26S	RFLP	Taxon	Voucher	Locality	ITS	26S
			▲	*A. pumila* Nutt.	VTP&MV 0054	Monterey Co., CA		
	*	●	▲	*A. pungens* Kunth	Tilden Regional Park	San Diego Co., CA	AF106820	AF106808
	*				MV 0194	San Bernardino Co., CA		
			▲	*A. rudis* Jepson & Wiesl.	VTP&MV 0151	San Luis Obispo Co., CA		
		●			VTP&MV 0237	Santa Barbara Co., CA		AF106809
			▲	*A. stanfordiana* C. Parry	MV&VTP 0390	Napa Co., CA		
		●			MV&VTP 0468	Sonoma Co., CA		AF106810
	*	●	▲	*A. uva-ursi* (L.) Spregel	VTP&MV 0046	Monterey Co., CA	AF106821	AF106811
	*				MV 0019	San Mateo Co., CA	AF106822	
	*				VTP 0440	Ocean Co., NJ	AF091950	
		●	▲	*A. viscida* C. Parry	VTP&MV 0314	Plumas Co., CA		AF106812
Sect. Folio.								
			▲	*A. andersonii* A. Gray	VTP&MV 0086	Santa Cruz Co., CA		
		●			VTP&MV 0089	Santa Cruz Co., CA		AF091976
		●	▲	*A. canescens* Eastw.	MV&VTP 0179	Santa Cruz Co., CA		AF106813
			▲	*A. catalinae* P. Wells	VTP&MV 0155	Santa Barbara Co., CA		
			▲	*A. columbiana* Piper	VTP&MV 0299	Mendocino Co., CA		
			▲	*A. glandulosa* Eastw. ssp. *glandulosa*	VTP&MV 0157	Santa Barbara Co., CA		
			▲	*A. refugioensis* R. Gankin	VTP&MV 0156	Santa Barbara Co., CA		
	*		▲	*A. tomentosa* (Pursh) Lindley	MV&VTP 0243	Monterey Co., CA	AF106823	
		●			MV&VTP 0095	San Francisco Co., CA		AF106814
Sect. Picto.								
		●	▲	*A. pringlei* C. Parry ssp. *pringlei*	MV&VTP 0232	Puma Co., AZ		AF106815
Outgroup	*	●		*Arbutus menziesii* Pursh	U. C. Botanic Garden	Alameda Co., CA	AF086828	AF086829

Cullings (1992). Amplified products were stored in 1X LTE.

Asymmetric PCR using double-stranded template was performed with various combinations of the following primers: "ITS 2", "ITS 3", "ITS 4", "ITS 5" (White et al. 1990). The 50 μl reactions contained 5.8 μl water, 5.0 μl *Taq* enzyme buffer, 5.0 μl 25 mM $MgCl_2$, 2.0 μl 50% glycerol, 1.0 μl 100% DMSO, 0.950 μl 40 mM dNTP's, 2.5 μl primer #1 (10 μM), 2.5 μl primer #2 (diluted to proper ratio), 0.25 μl *Taq* polymerase (5 units/μl), and 25 μl double-stranded template taken from 1X LTE solution. Amplification parameters followed Cullings (1992). Single-stranded DNA products were purified using spin columns. Columns were loaded with G-50 sephadex equilibrated with 1X STE (Sambrook et al. 1989).

Both DNA strands were sequenced by the dideoxy method using the Sequenase dGTP kit (U.S. Biochemical). ^{35}S-dATP was used for isotopic labeling. The limiting primers in the single-stranded amplification were used as the sequencing primers. Samples were electrophoresed on an 8% polyacrylamide gel. Gels were fixed with a solution of 10% methanol and 10% acetic acid for 30 min, transferred to 3 MM Whatman paper, and vacuum dried at 80°C for 40 min. Gels were exposed to autoradiographic film for at least 12 hours.

26S Region.—Double-stranded PCR products were amplified using 28KJ (Cullings 1992) and either the universal primer 28C (Hamby and Zimmer 1988) or 28B (Hamby et al. 1988). The 50μl reactions contained 1X Promega PCR buffer (M190A), 0.75 mM dNTPs, 0.15–0.5 μM each primer, 1.0–2.5 mM $MgCl_2$, 1.25 units Promega *Taq,* and 5 μl extracted DNA (dilutions ranged from 1:10 to 1:10,000). Cycling conditions consisted of a 3 min. denaturation at 94°C, followed by 40–44 cycles of a 20 sec denaturation at 95°C, a 45 sec annealing at 55°C and a 1.5–2.0 min extension at 72°C, and a final extension at 72°C for 7 min. Amplified products were cleaned using the QIAGEN PCR product kit. Cleaned products were quantified by comparison to *Hind*III digested lamda on a 1.5% standard agarose gel.

Between 25 and 30 ng/μl of amplified product were subjected to 35 rounds of cycle sequencing using either the 28KJ primer or the 28B primer. Dye terminator chemistry was used according to manufacturers specifications with an annealing temperature of 51°C. Sequenced products were run on the ABI 377 automated sequencing system according to manufacturer specifications.

Sequence analysis. ITS Region.—ITS sequences were aligned with those of *Brassica napus* L. (Okumura et al. 1992) and *Daucus carota* L. (Yokota et al. 1989) to determine the boundaries of the coding and spacer regions. DNA sequences were aligned manually using the DNA alignment program MacDNASIS (1994). Alignment of the ingroup and outgroup taxa required the introduction of gaps to accommodate five indels. All five indels occurred in ITS 1. The placement and length of the indels was unambiguous. The indels did not vary within the ingroup and were entered into the data matrix as gaps.

26S Region.—The 26S fragment corresponds to bp positions 334–616 of the 26S region determined by unambiguous alignment to *Fragaria ananassa Ducheshe* (GenBank accession # X58118) and *Citrus limon* (L.) Burm. f. (GenBank accession # X05910)

Phylogenetic analysis. ITS Region.—ITS data were analyzed by Fitch parsimony as implemented in PAUP version 3.1.1 (Swofford 1993) using the branch-and-bound procedure to find all maximally parsimonious trees. All character-state changes were weighted equally. Bootstrap values were calculated from 100 replicate parsimony analyses (Felsenstein 1985) using PAUP heuristic searches, simple taxon addition sequence, TBR branch-swapping, and MULPARS.

Due to the number of polymorphic taxa in the data set, it was not practical to exclude all taxa with ITS polymorphism from the analyses. We therefore chose to conduct two analyses that differed in their treatment of polymorphism in the ITS sequence data. In the first analysis polymorphic sites were coded using the IUPAC-IUB ambiguity codes and multiple states were recognized as polymorphic rather than uncertain in PAUP. In the second analysis data were recoded from DNA data to multistate characters (Campbell et al. 1997). For example A = 1, G = 2 A/G = 3.

26S Region.—As with the ITS sequence data two analyses were conducted to account for 26S sequence polymorphism. In analysis one, polymorphic sites were coded using the IUPAC-IUB ambiguity codes and multiple states were recognized as polymorphic rather than uncertain in PAUP. In analysis two, data were recoded from DNA data to multistate characters (Campbell et al. 1997).

In both 26S analyses data were analyzed by Fitch parsimony using PAUP version 3.1.1 (Swofford 1993). Heuristic searches were conducted with 10 replicates of random addition sequence, TBR branch-swapping, and MULPARS in effect to find maximally parsimonious trees. All character-state changes were weighted equally. Bootstrap values were calculated from 1000 replicate parsimony analyses (Felsenstein 1985) using PAUP heuristic searches, random starting trees, and TBR branch-swapping.

Restriction digests of the ITS region. The ITS region was PCR amplified as described above. The approximately 700 bp fragment was subjected to digestion by two restriction endonucleases: *Alu* I and *Hha* I. These restriction endonucleases were chosen following a survey for phylogenetically informative restriction sites in the ITS sequences. Each reaction digest contained 4 μl double-stranded PCR products, 4 μl water, 1 μl 10X buffer, and 1 μl restriction endonuclease (diluted to ca. 7.5 units/μl). Reactions were left at the manufacturer's suggested incubation temperature for at least 16 h. Digested DNA was electrophoresed on 3% agarose gels using 1X TAE as the gel buffer.

RESULTS

Sequence analysis. ITS Region.—In the study taxa, ITS 1 was 253 bp long ITS 2 was 226 bp long, and the 5.8S was 164 bp long. These findings are similar to those found in other ITS studies of angiosperms (Baldwin et al. 1995). Of the aligned positions in ITS 1, ten sites (4.0%) were variable within the ingroup, seven were potentially informative phylogenetically. In ITS 2, two sites (0.88%) were variable and both were potentially informative phylogenetically. There were no variable sites in the 5.8S subunit (Table 4). Polymorphism within an individual, seen as two or more nucleotide states on the autoradiograph, was found to varying degrees throughout the taxa sequenced. Some taxa (e.g., *A. hookeri* ssp. *hookeri*) did not exhibit any polymorphic sites. Other taxa (e.g., *A. pungens*) were polymorphic at almost all variable sites (Table 4). At least two individuals per taxon were sequenced (excluding *A. tomentosa, A. nummularia,* and the outgroup). Variation among individuals of a single taxon was noted only in *A. uva-ursi.* All sequences obtained were included in the analysis (Table 2).

26S Region.—Two hundred and eighty-one bp of the 26S were sequenced and aligned. Of those 281 bp, 4 (1.4%) were phylogenetically informative (Table 4). Polymorphism was detected in three taxa, *A. pungens* and *A. stanfordiana,* and *Arbutus menziesii.*

Phylogenetic analysis. ITS Region.—In analysis one (multiple states at a position recognized as polymorphism), nine equally parsimonious trees were generated using a branch-and-bound search (with furthest taxon addition sequence). Each of the nine trees required 100 evolutionary steps and has a CI (excluding uninformative characters) of 0.595. The nine maximally parsimonious trees differ topologically in their placement of one taxon, *A. pungens. Arctostaphylos pungens* is polymorphic at 7 of 9 phylogenetically informative sites, so it is not surprising that its phylogenetic position is unresolved. When *A. pungens* was removed and the analysis was conducted as described above, the positions of the remaining taxa relative to each other did not change. One maximally parsimonious tree was generated (Fig. 2A). This tree required 93 evolutionary steps and has a CI (excluding uninformative characters) of 0.643. The analyses were also conducted with exclusion of the outgroup, *Arbutus menziesii.* The topology of the ingroup did not change with the omission of *A. menziesii.*

Analysis two (multiple states at a site rescored as a novel multistate characteristic) generated one tree of 96 steps with a CI (excluding uninformative characters) of 0.905 (Fig. 2B). The relative topology is almost the same as in analysis one, the only difference being the placement of *A. pungens.* In analysis one, when *A. pungens* was included it fell out in several places in the tree but in analysis two it is nested within the clade containing *A. hookeri* ssp. *franciscana, A. hookeri* ssp. *montana,* and *A. hookeri* ssp. *ravenii.*

In both analyses, the low amount of sequence divergence within the ingroup resulted in a lack of phylogenetic resolution and weak support of some clades. Despite these limitations, the results of the two analyses are nearly congruent (the only difference in topology is accounted for by *A. pungens*) and some conclusions can be drawn. Two monophyletic clades were resolved in *Arctostaphylos.* One clade includes *A. hookeri* ssp. *hookeri, A. hookeri* ssp. *hearstiorum, A. uva-ursi* from New Jersey, and *A. nummularia.* The other clade contains *A. hookeri* ssp. *ravenii, A. hookeri* ssp. *montana, A. hookeri* ssp. *franciscana,* (*A. pungens* in analysis 2) *A. uva-ursi* from California, and *A. tomentosa.* These data suggest that *A. hookeri* (*sensu* Wells 1993) is non-monophyletic, with subspecies found in two distinct clades that each include some representatives of other species in the genus. In addition, the widespread and variable *A. uva-ursi* also appears to be non-monophyletic.

26S Region.—Analysis one of the 26S sequence data (multiple states at a position interpreted as polymorphism) resulted in eight equally parsimonious trees. Each of the eight trees required 34 evolutionary steps and has a CI (excluding uninformative characters) of 0.537. Analysis two (multiple states at a site rescored as a novel multistate characteristic) resulted in three most parsimonious trees which required 24 evolutionary steps. The consistency index of each tree (excluding uninformative characters) was 1.00. The topologies of the consensus trees from the two analyses were identical and discussions therefore will be restricted to this common topology. One of the eight trees from analysis one was identical to the strict consensus trees (Fig. 3). Two distinct, moderately supported clades of *Arctostaphylos* taxa are present. Although there is no resolution among taxa within the two clades, some important results emerge: 1) *A. hookeri* is non-monophyletic, *A. hookeri* ssp. *hookeri* and *A. hookeri* ssp. *montana* fall into two distinct clades; 2) the results suggest that the subgeneric classification constructed by Wells (1992) does not represent phylogenetic relationships of the taxa, section *Arctostaphylos* is paraphyletic; 3) the two clades reconstructed using the 26S sequence data

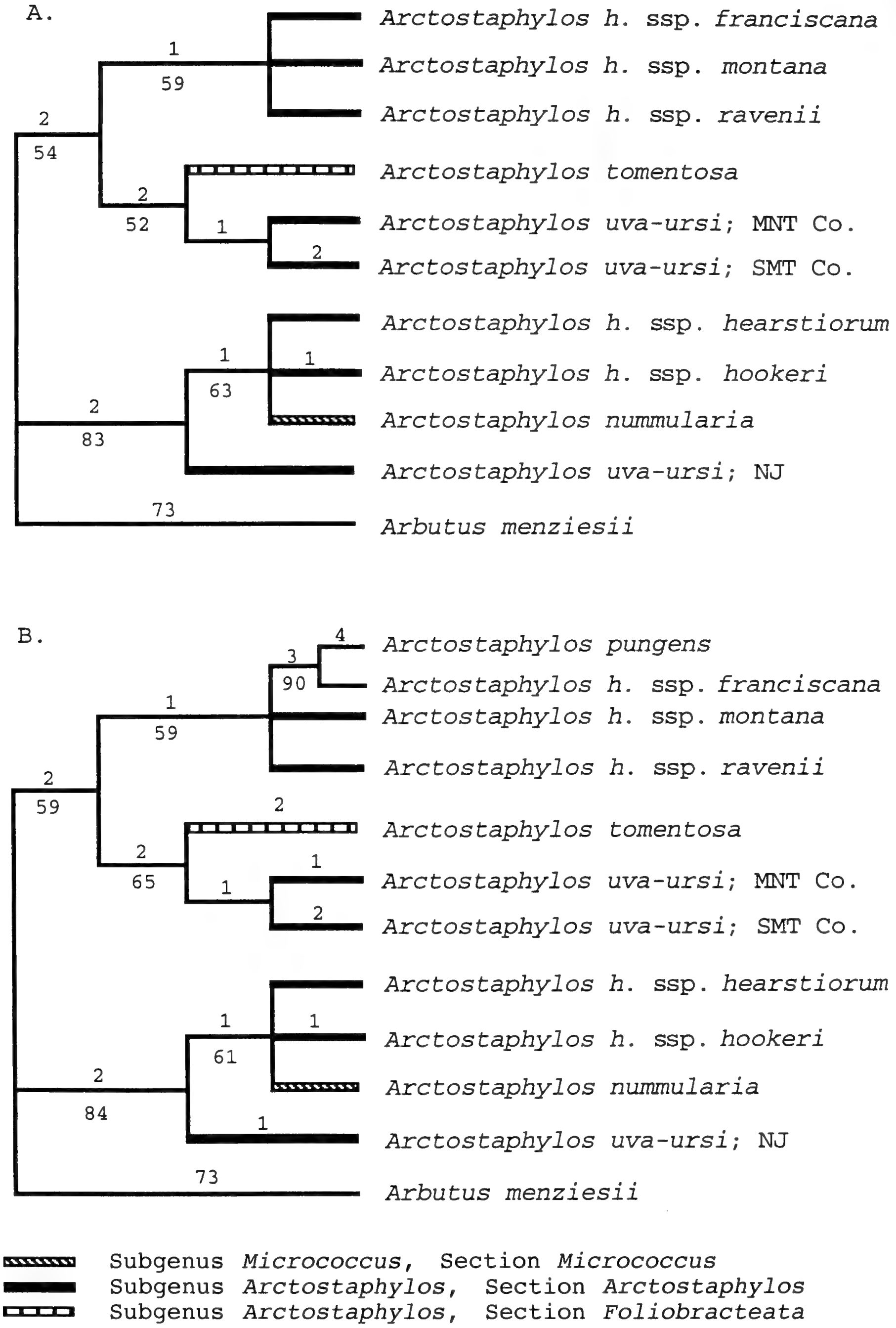

FIG. 2. The single most parsimonious trees produced from each of two analyses of data from the ITS region. Numbers above the lines represent the branch lengths and numbers below the lines represent bootstrap values. A) Analysis one, multiple states at a position recognized as polymorphic. Length = 93 steps. CI excluding uninformative characters = 0.643. RI = 0.905. RC = 0.885. *Arctostaphylos pungens* was not included in the analysis. B) Analysis two, multiple states at a position rescored into a novel multistate characteristic. Length = 96 steps. CI excluding uninformative characters = 0.905. RI = 0.920. RC = 0.901.

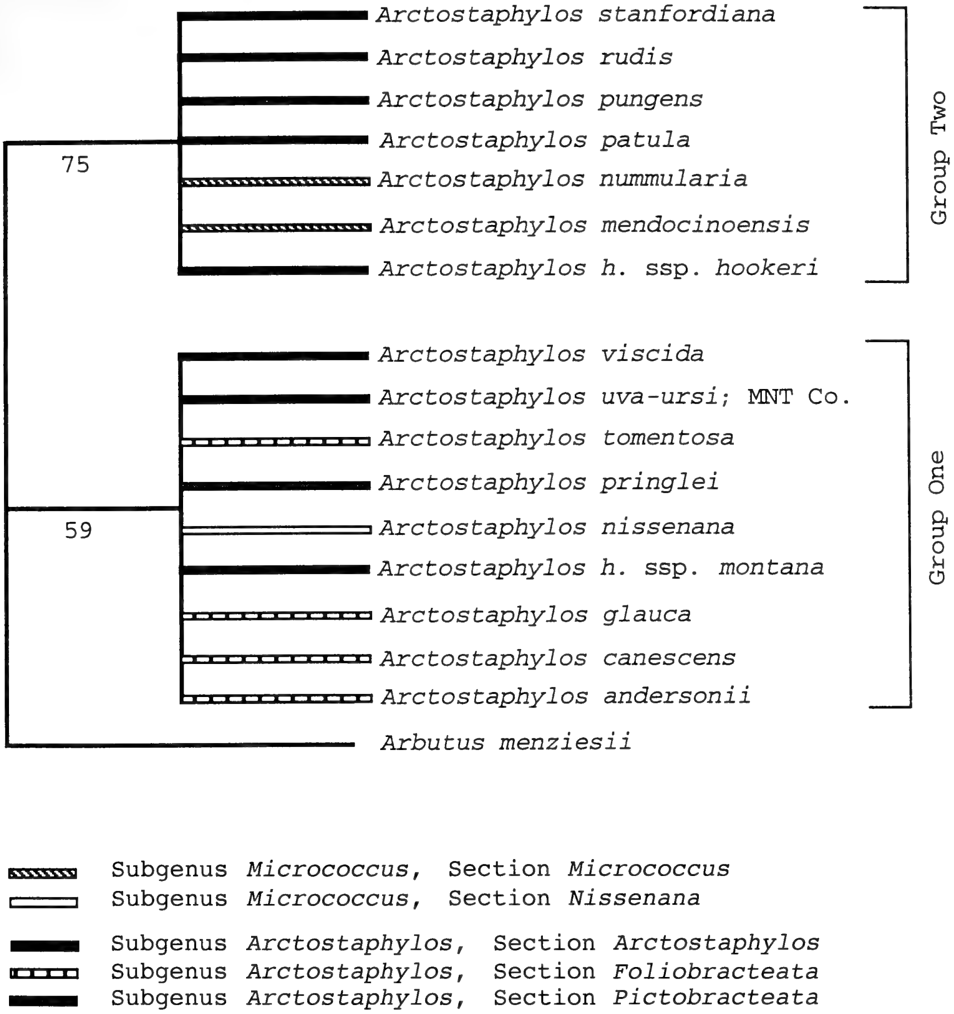

FIG. 3. One of the 8 most parsimonious trees produced in analysis one (multiple states at a position recognized as polymorphic) using data from the 26S region. The topology is identical to the strict consensus trees of both analysis one and analysis two of the 26S data. *Arbutus menziesii* was used as the outgroup. Bootstrap values are given below the lines. Length = 34 steps. CI excluding uninformative characters = 0.537. RI = 1.00. RC = 1.00.

correspond well to the two groups detected with the ITS-RFLP data (Fig. 3, Table 3).

ITS-RFLP results. The ITS region from 34 taxa was analyzed with 2 restriction endonucleases. Combining the data from the endonucleases, each taxon had one of three primary pattern types: Group One, Group Two, and Mosaic (Table 3). Taxa were placed in Group One if the *Alu* I site was absent and the *Hha* I site was either present or polymorphic. With one exception, taxa were placed in Group Two if the *Hha* I site was absent and the *Alu* I site was either present or polymorphic. Taxa were placed in the Mosaic Group if the recognition site for both *Alu* I and *Hha* I was absent. Only one taxon, *A. pungens,* was polymorphic at both the *Alu* I and *Hha* I sites and it was placed in Group Two based on data from analysis of the 26S sequence data.

DISCUSSION

The results of this study suggest that *A. hookeri sensu* Wells (1993) combines taxa that do not constitute a natural group. The five subspecies of *A. hookeri sensu* Wells are members of two distinct ITS lineages (Fig. 2). One lineage includes the three subspecies which occur in the San Francisco Bay Area on serpentine soil: *franciscana, montana,* and *ravenii.* Also included in this lineage are *A. tomentosa* and *A. uva-ursi* (from California). The second lineage consists of two subspecies, *hookeri* and *hearstiorum,* which occur along the central coast of California and *A. nummularia* and *A. uva-*

TABLE 3. NUCLEAR RIBOSOMAL DNA RESTRICTION SITE MUTATIONS OF 34 *ARCTOSTAPHYLOS* TAXA. Columns represent subgeneric taxa recognized by Wells (1992). The presence (1), absence (0), or polymorphic state (*) of restriction sites are shown.

			Subgenus *Arctostaphylos*								
Subgenus *Micrococcus*	A	H	Sect. *Arctostaphylos*	A	H	Sect. *Foliobracteata*	A	H	Sect. *Pictobracteata*	A	H
Group 1											
A. nissenana	0	1	*A. edmundsii*	0	1	*A. andersonii*	0	1	*A. pringlei*	0	1
			A. glauca	0	1	*A. columbiana*	0	1			
			A. h. montana	0	1	*A. refugioensis*	0	1			
			A. h. ravenii	0	1	*A. tomentosa*	0	1			
			A. klamathensis	0	1						
			A. manzanita	0	1						
			A. pumila	0	1						
			A. uva-ursi	0	1						
			A. viscida	0	1						
			A. bakeri	0	*	*A. canescens*	0	*			
			A. gabrielensis	0	*	*A. catalineae*	0	*			
			A. h. franciscana	0	*	*A. glandulosa*	0	*			
			A. nevadensis	0	*						
Group 2											
			A. h. hearstiorum	1	0						
			A. h. hookeri	1	0						
A. mendocinoensis	*	0	*A. densiflora*	*	0						
A. nummularia	*	0	*A. hispidula*	*	0						
			A. patula	*	0						
			A. stanfordiana	*	0						
			A. pungens	*	*						
Mosaic											
			A. mewukka	0	0						
			A. parryanna	0	0						
			A. rudis	0	0						

ursi (from New Jersey). At this time, the phylogenetic position of *A. pungens* is unresolved.

The ITS-RFLP data set also provides support for the presence of two distinct lineages in *Arctostaphylos* (Table 3). The two groups represented in the ITS-RFLP study correspond to the two clades seen in both trees based on the ITS sequence data (Fig. 2) and the 26S data (Fig. 3). These two groups were not represented in the subgeneric classification proposed by Wells (1992). Section *Foliobracteata* is the only section with members restricted to one group while members of section *Arctostaphylos* and subgenus *Micrococcus* are disassociated and occur in both primary groups.

Within-individual polymorphism was detected in the ITS region for several of the taxa examined. Polymorphism was seen in both the ITS sequence data (Table 4A) and in the ITS-RFLP study (Table 3). Although widespread, the presence of polymorphism does not seem to have dramatically altered the topology of the ITS tree (Fig. 2) or the interpretation of the ITS-RFLP data. With regard to the ITS sequence data, the position of only one taxon, *A. pungens,* changes with respect to the type of analysis done. All other taxa remain in the same relative phylogenetic position. In the ITS-RFLP study, with the exception of one taxon, the two primary groups seen (Group One and Group Two) (Table 3) correspond to the two lineages detected with both ITS and 26S sequence data (Figs. 2–4).

The 26S sequence data (Fig. 3) corroborate the finding that *A. hookeri* is not monophyletic. Although only two taxa of the *A hookeri* complex were sampled for 26S data, moderate levels of bootstrap support were found for the placement of *A. hookeri* ssp. *hookeri* and *A. hookeri* ssp. *montana* in two distinct clades each including representatives of other species of *Arctostaphylos.* Despite low levels of resolution, subgenus *Arctostaphylos* appears to be non-monophyletic, members are found in each of the two 26S clades (Fig. 3). The concordance between the ITS data and 26S data is not surprising given that the ITS region and 26S region are both part of the nrDNA 18S–26S repeat. The value of the 26S data to our study is not to provide an independent (un-linked) source of phylogenetic evidence, but to augment the limited number of variable ITS characters most of which are complicated by the presence of within-individual polymorphism—the 26S data provides more support for the two clades observed with the ITS data. Collectively, both lines of nrDNA data pro-

TABLE 4. VARIABLE NUCLEOTIDE POSITIONS IN A) THE ITS REGION AND B) THE 26S REGION. Symbols A, G, T, C, M = A/C, R = A/G, Y = C/T, K = G/T, W = A/T, S = C/G. Phylogenetically informative sites are indicated by (*).

```
A.                *     ***          *     *  *                *   *
                                 11111111111222222222333334444444444455555555555555555556666666666666666
                  12234444456667701122233444000233444089991334455566801123456777788889990001222223333 3
                  035112469002837539368010363583072684904683838457048256442400279134837818990458901589

A.menz.          GCCCACCCTTGGCCCCCCGGAGCGCCCTCCCTGCATCCCGGGCCGGGTGGACAGAGGCCCCCCTGGCCCCCCGCGGCGCGCGCC
A.franciscana    ACCTGTTACTTAGTTTATTAATTATCCCAMTCACTCTTGCAATTTCRGTTRTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.hearst.        ACCTGTTCCCTAGTTTATTAGTTATCCCACTCACTCTTGCAATTTCAGTTATGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.hookeri        ACTTGTTCCCTAGTTTATTAGTTATCCCACTCACTCTTGCAATTTCAGTTATGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.montana        ACCTGTTACTTAGTTTATTAATTATCCCAATCACTCTTGCAATTTCGGTTGTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.ravenii        ACCTGTTACTTAGTTTATTAATTATCCCAATCACTCTTGCAATTTCGGTTGTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.pungens        ACCTGTTMYYTAGTTTATTARTTATCCCAMTCACTCTTGCAATTTCRGTTRTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.nummularia     ACCTGTTCCCTAGTTTATTAGTTATCCCACTCACTCTTGCAATTTCAGTTATGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.tomentosa      ACCTGTTCMTTAGTTTATTAATTATMTCAATCASTCTTGCAATTTCGGTTGTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.u-u.MNT        ATCTGTTCATTAGTTTATTAATTATCTCAATCACTCTTGCAATTTCGGTTGTGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.u-u.SMT        ATCTGTTCMTTAGTTTATTAATTATCTCAATCACTCTTGCAATTTCAGTTATGCGATTTTTTTCATTTTTTTTGTATAAATATT
A.u-u.NJ         AYCTGTTCCCTAGTTTATTAATTATCCCACTCACTCTTGCAATTTCAGTTATGCGATTTTTTTCATTTTTTTTGTATAAATATT
```

```
B.                   *      *  *    *
                    11111111222222222222
                   211333356011344566667
                  1736568964179305401283

Arbutus menziesii GYGYYKRAGCRYCCCYCTYCRY
A.andersonii      GCGTTTACACATCCCCCATTGT
A.canescens       GCGTTTACACATCCCCCATTGT
A. glauca         GCGTTTACACATCCCCCATTGT
A.h.hookeri       NCGTTTACATATACTCCTTTGT
A.h.montana       GCGTTTACACATCCCCNATTGT
A.mendocinoensis  GCGTTTACATATACCCCTTTGT
A.nissenana       GCGTTTACACATCCCCCATTGT
A.patula .        GCGTTTACATATACCCCTTTGT
A.pringlei        GCGTTTACACATCCCCCATTGT
A.pungens         GCKTTTACAYATWCCCCWTTGT
A.rudis           GCTTTTACATATATCCCTTTGT
A.stanfordiana    GCKTTTACATATACCCCTTTGT
A.tomentosa       GCGTTTACACATCCCCCATTGT
A.uva ursi, MNT   GCGTTTACANATCCCCCATTGT
A.viscida         GCGTTTACACATCCCCCATTGT
```

vide strong evidence for the existence of at least two, previously unrecognized lineages in *Arctostaphylos.*

Despite the apparent phylogenetic pattern reconstructed using nrDNA data, a history of lineage sorting or hybridization may complicate the interpretation of apparent phylogenetic signal (Avise 1989; Rieseberg 1991; Doyle 1992). The polymorphism seen in the ITS data is suggestive of either hybridization or sorting of ancestral polymorphism. Some authors have interpreted patterns such as those seen in the ITS RFLP data as evidence of reticulate evolution (Sang et al. 1995; Rieseberg et al. 1990; Rieseberg 1991; Rieseberg and Brunsfeld 1992). Ellstrand et al. (1987) and Schierenbeck et al. (1992) have provided empirical evidence of introgression and hybridization between *Arctostaphylos* taxa. Others have also postulated that first generation hybrids, hybrid swarms, and taxa of hybrid origin exist in the genus (Dobzhansky 1953; Gottlieb 1968; Keeley 1976; Kruckeberg 1977). However, at this time we can not distinguish between patterns of reticulate evolution and lineage sorting in the taxa examined.

This is the first study to address phylogenetic relationships among *Arctostaphylos* taxa using molecular data. If the results presented here are indicative of the phylogenetic complexity of the genus as a whole, then uncovering phylogenetic patterns in the group may prove difficult. Furthermore, until phylogenetic analyses that include all of the recognized taxa are complete, taxonomic decisions regarding the circumscription of subgenera, sections, and species must be considered tenuous at best. A complete phylogenetic investigation is in progress that should help to build a better understanding of patterns of evolution in *Arctostaphylos.*

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MORPHOLOGICAL VARIATION IN CALIFORNIA ALPINE POLEMONIUM SPECIES

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ABSTRACT

Relationships between the two California alpine species of *Polemonium* (*P. chartaceum* H. Mason and *P. eximium* E. Greene) as well as their species limits have been uncertain for many years. We sought to clarify these issues through multivariate analysis of floral and foliar characters. We made 16 measurements on each of 159 plants from populations throughout the ranges of *P. chartaceum* and *P. eximium,* and from populations of two putatively related species, *P. elegans* E. Greene from the Cascade Range and *P. viscosum* Nutt. from the Great Basin and Rocky Mountains. We used multidimensional scaling (MDS) to summarize in three dimensions patterns of variation with regard to the 16 measured variables. We used discriminant analysis to test the robustness of patterns identified in heuristic interpretation of the MDS. Our results suggest populations from the Klamath Range, White Mountains, northern Sierra Nevada (Sonora Pass), and southern Sierra Nevada each form distinct morphological-geographical entities. Patterns of similarity among these groups suggest that *P. chartaceum* and *P. eximium* warrant taxonomic revision, and that populations of *P. chartaceum* from throughout its range have affinities closer to *P. elegans* than to *P. viscosum.*

Two alpine species of *Polemonium* are native to California: *P. chartaceum* H. Mason and *P. eximium* E. Greene. Both species, known commonly as sky pilots, are small herbaceous perennials with congested inflorescences and showy, blue-violet corollas. Both species are diploid (Pritchett 1993), and Grant (1959) reported that both are outcrossers, pollinated by bees and flies. Ranges of the two California species as well as sampling locations of two related species (*P. elegans* E. Greene and *P. viscosum* Nutt, discussed below) appear in Fig. 1. *Polemonium chartaceum* is on List IB (plants rare, threatened, or endangered in California and elsewhere) of the California Native Plant Society (Skinner and Pavlik 1994).

Unlike the Rocky Mountain *P. viscosum,* which has been the subject of considerable research (Galen 1990, 1985, 1983; Galen and Kevan 1980), the California species have received relatively little study. They have been examined only in the context of treatments of the entire genus or sections within it (Wherry 1942; Davidson 1950; Grant 1989; Pritchett 1993).

Despite the taxonomic treatments provided by past researchers, several questions of taxonomy and biogeography remain. The first question regards the circumscription of *P. chartaceum.* When Mason (1925) described the species, he considered it endemic to the White Mountains of eastern California. Davidson (1950) later included *Polemonium* from the Klamath Range in northwestern California in *P. chartaceum.* Only three collections from the Klamath Range were available for examination at that time (Pritchett 1994), and Davidson's treatment resulted in *P. chartaceum* showing an unusual and disjunct distribution (Fig. 1).

Monographers since Davidson (1950) have accepted this circumscription, although occasionally collections from the Klamath Mountains (e.g., Denton 4239—WTU) are assigned to *P. elegans* rather than to *P. chartaceum*; and Whipple (1981) noted that the degree of leaflet dissection in Klamath Mountains plants differed from that described by Munz (1973). The California Natural Heritage Database (Horner 1976) has called specifically for a re-evaluation of the relationship between Klamath Mountains populations and those in the White and Sweetwater Mountains.

A second series of questions exists regarding the taxonomic status of *P. chartaceum* and *P. eximium,* and relationships with regional congeners. Munz (1973) recognized *P. chartaceum* but wrote that it was "doubtfully specifically distinct from [*P. eximium*]." He considered *P. eximium* ssp. *chartaceum* as a likely alternative. Grant (1989) considered it "a matter of preference" as to whether to recognize *P. chartaceum* and *P. eximium* or to reduce them both to subspecies of their Rocky Mountain relative *P. viscosum,* following Murray (1983). Both Davidson (1950) and Wilken (personal communication) suggest a third possibility: that further examination might lead to reduction of at least *P. chartaceum* to a subspecies of the *P. elegans* of the Cascade Range.

Biogeographic patterns implicit in these proposed subspecific relationships differ considerably. Munz (1973) *P. eximium* ssp. *chartaceum* suggests that California taxa are most closely related to each other. *Polemonium elegans* ssp. *chartaceum,* however, suggests north-south relationships along the

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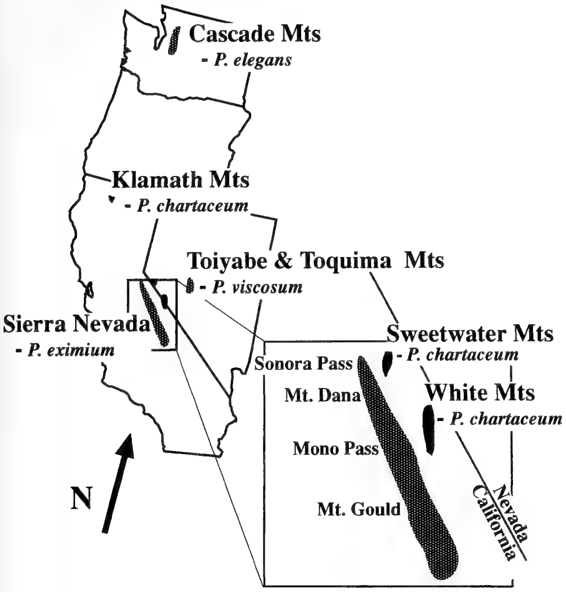

FIG. 1. Distribution and Sampling Map. *Polemonium chartaceum* occurs in the White, Sweetwater, and Klamath Mountains and was sampled in all three ranges. *Polemonium eximium* occurs in the Sierra Nevada and was sampled in the four labeled areas. *Polemonium elegans* occurs in the Cascade Range and was sampled on Mt. Ranier. *Polemonium viscosum* occurs in alpine areas throughout the Rocky Mountains and Great Basin and was sampled in the Toiyabe and Toquima Mountains. See Table 1 for precise collection localities.

Sierra Cascade axis, while *P. viscosum* ssp. *chartaceum* and *eximium* could suggest east-west relationships across the Great Basin to the Rocky Mountains.

As part of an examination of relationships among California alpine *Polemonium* species we assembled a data set of floral and leaflet measurements (Table 2). Measurements were made on plants collected from populations throughout the entire geographic ranges of both CA species as well as populations of *P. elegans* and *P. viscosum* (Table 1, Fig. 1). In this paper we describe patterns of morphological variation revealed in these data through techniques of multivariate analysis.

MATERIALS AND METHODS

Sampling. Inflorescences (one per plant) were collected from throughout each population visited—(Table 1, Fig. 1). After collections were pressed and dried, they were inspected for the presence of intact, 5-merous flowers in which the stigmas had spread apart. In large inflorescences several flowers typically met these criteria and the largest were chosen for dissection. This provided a simple means for consistent sampling among populations without lengthening the already-lengthy dissection and measurement protocol. We initially dissected four flowers per plant but were soon forced by constraints of inflorescence size and dissection time to reduce the number to two, and, in two cases, one.

Because we wished the individual plant to be the OTU rather than the individual flower we averaged

TABLE 1. SOURCES OF MATERIAL USED FOR MEASUREMENTS. Elevations are converted (1 ft = 0.3048 m) from those on U.S.G.S. 7.5′ and 15′ topographic maps. All collections made by DWP.

Mountain range	Location	# Plants measured	Collection number
Klamath	Trinity Co., Summit, 2658 m, 1.6 km. NW Mt. Eddy	6	101
Klamath	Trinity Co., Mt. Eddy Summit, 2751 m.	6	102
Klamath	Trinity Co., Summit 2707 m, 1.2 km. E Mt. Eddy	7	100
Sweetwater	Mono Co., Summit South Sister Peak, 3456 m	19	111
White	Mono Co., Marble Ck. Divide, 4084 m	6	115
White	Mono Co., Saddle 0.5 km. SE Mt. Dubois, 4072 m	6	105
White	Mono Co., SE slope White Mt. Peak, 4237 m	7	106
	TOTAL *P. chartaceum*	57	
Sierra Nevada (Sonora Pass)	Mono Co., Summit 3307 m., 1.2 km. SE Leavitt Lake	10	118
Sierra Nevada (Sonora Pass)	Mono Co., Summit Leavitt Peak, 3527 m	9	119
Sierra Nevada (Mt. Dana)	Tuolumne Co., Summit Mt. Dana, 3979 m	16	103
Sierra Nevada (Mono Pass)	Inyo Co., Ridge 0.4 km. SW Mono Pass, 3840 m	8	104
Sierra Nevada (Mono Pass)	Fresno Co., Ridge 1.6 km. W Pine Creek Pass, 3658 m	8	112
Sierra Nevada (Mt. Gould)	Fresno Co., SW slope Mt. Gould, 3810 m	8	107
Sierra Nevada (Mt. Gould)	Fresno Co., SW slope Kearsarge Pass, 3658 m	8	121
	TOTAL *P. eximium*	67	
Cascade	Pierce Co. (Wash.), Mt. Rainier, Panorama Pt., 2134 m	16	108
	TOTAL *P. elegans*	16	
Toiyabe	Lander Co. (Nev.), Big Creek Summit, 3374 m	10	109
Toquima	Nye Co. (Nev.), NW slope Mt. Jefferson, 3353 m	9	110
	TOTAL *P. viscosum*	19	

TABLE 2. MEANS AND RESULTS OF STUDENT-NEWMAN-KEILS MULTIPLE RANGE TESTS OF NINE GEOGRAPHIC GROUPS DEFINED FOR DISCRIMINANT ANALYSIS. Measurements are in mm. Number of leaflet lobes is a count after square root transformation. Anther exsertion is the sum of filament length and insertion distance, less corolla tube length. Stigma exsertion is corolla tube length less style length. Asterisks indicate measurements in which ANOVA showed means to differ significantly ($P < 0.05$) but for which multiple range tests resolved no groupings. Geographic codes: R = Mt. Ranier; K = Klamath Range; S = Sweetwater Mts; W = White Mts; L = Sonora Pass; D = Mt. Dana; C = Mono Pass; G = Mt. Gould; T = Toiyabe Range.

Species:	*elegans*	*chartaceum*			*eximium*				*viscosum*	
Geographic code:	R	K	S	W	L	D	C	G	T	Multiple range test
Measurement										
Corolla lobe perimeter	15.72	14.78	13.29	12.99	14.22	17.93	19.90	20.79	20.15	R K L S W < D < G C T
Corolla lobe length	5.11	4.94	4.22	4.31	4.42	5.41	5.66	6.02	6.37	L S W < R K D C < G < T
Corolla lobe width	4.12	3.81	3.62	3.26	3.95	5.32	6.17	6.55	5.67	R K L S W < D T < G C
Corolla lobe base	1.88	1.98	1.92	1.85	2.14	2.21	2.22	2.20	2.90	R K L D G C S W < T
Filament length	6.47	6.86	5.96	7.55	3.25	4.06	5.71	5.79	8.89	L < D < R K G C S < W < T
Insertion distance	2.85	3.39	3.06	2.40	5.63	4.72	2.99	2.79	2.42	R K G C S T W < D < L
Style length	7.81	9.63	6.71	7.81	6.32	3.24	3.72	3.56	11.03	D G C < L S < R W < K < T
Stigma length	1.59	1.62	1.61	1.90	1.68	2.10	2.25	2.05	1.78	*
Corolla tube length	6.69	6.72	6.42	6.21	8.25	10.55	10.82	11.18	8.95	R K S W < L < T < D G C
Corolla tube circumference	10.13	9.34	9.62	9.54	10.63	12.03	11.43	10.76	14.28	*
Corolla tube base	3.58	4.06	3.81	3.62	3.42	3.67	3.98	3.99	4.03	*
Calyx length	5.34	5.68	5.00	5.82	5.04	6.59	7.94	7.27	6.45	R K L S W < D T < G < C
Calyx lobe length	2.78	2.57	2.43	2.56	2.35	3.13	3.35	3.64	3.08	*
Calyx circumference	8.16	8.24	8.10	8.73	8.15	9.07	10.03	9.80	8.70	R K L D S T W < G C
Calyx base	5.80	5.28	5.39	5.37	5.34	5.84	6.21	6.27	6.59	*
Number of leaflet lobes	1.62	2.28	2.84	4.06	3.05	3.20	4.01	4.83	2.64	R < K < L D S T < C W < G
	n = 16	n = 19	n = 19	n = 19	n = 19	n = 16	n = 16	n = 16	n = 19	*
Stigma exsertion	−1.12	−2.91	−0.29	−1.60	1.92	7.31	7.10	7.61	−2.08	*
Anther exsertion	2.64	3.54	2.60	3.74	0.64	−1.77	−2.12	−2.60	2.36	*

all 15 floral measurements (Table 2) from each flower from a given plant. These 15 averages were combined with the count of maximum leaflet lobes per rachis node to obtain a set of 16 measurements to represent each plant in the data set. To meet Pimentel's and Smith's (1986) requirements that sample sizes (for multigroup discriminant analysis) equal or exceed the number of variables measured, we sampled at least 16 plants from every geographic region of interest.

Characters. We assembled a data set of floral and leaflet measurements (Table 2). We chose these characters because they have been used in various combinations by previous workers to distinguish alpine *Polemonium* species (Wherry 1942; Davidson, 1950; Grant 1989). We treated two important characters, however, in novel ways. A two-state character regarding anther exsertion (i.e., anthers exserted vs. anthers included) has been used to help distinguish *P. chartaceum* from *P. eximium* (Wherry 1942; Davidson, 1950; Grant 1989). Rather than record this two-state character we measured the floral components that define anther exsertion (i.e. filament length, filament insertion distance, and corolla tube length) (Table 2) and used the components—instead of the two-state character—in our analysis. Similarly, a two-state leaflet arrangement character, two-ranked vs. verticillate (Wherry 1942; Davidson 1950), or arranged in one plane vs. arranged in whorls (Grant 1989), has been used. Grant (1989) used this character to help define sections of the genus. Instead of recording this as a two-state character we sampled two well-developed leaves and counted the maximum number of leaflet lobes per rachis node. (The maximum—as opposed to the mean—number of lobes was used due to the extensive time and effort required to count leaflets at all nodes on a leaf to obtain a mean.) We made these changes in character treatments in search of finer resolution of morphological patterns and variation among plants examined for the analysis.

The measurements discussed above were made on plants sampled from populations throughout the entire geographic ranges of both California species, as well as populations of *P. elegans* and *P. viscosum* (Table 1, Fig. 1).

Dissection. After re-hydration, one longitudinal incision was made from the mouth of the corolla (between two corolla lobes) to the base of the corolla tube. The corolla tube was opened and flattened on a microscope slide. Corolla lobes were removed from the corolla tube (perpendicular to the long axis of the corolla tube) at their bases. The corolla lobes and tube were then mounted on the slide. The style was removed from the ovary and mounted on the slide with the three stigmas separated. Filaments were pulled up from the surface of the flattened corolla tube, bent back at the points of insertion and then flattened back on the surface of the corolla. This created at the point of insertion a distinct angle that was used as a landmark for measurement. Calyx tubes were dissected with a longitudinal incision, opened, and mounted on slides in a procedure analogous to that used for dissection of the corolla. Calyx lobes were not cut from the calyx tubes, however, as were corolla lobes.

Measurement. Dissected flowers were placed under a dissecting microscope with a camera lucida attachment. The camera lucida was used to project on the magnified image of the dissected flowers the image of the cross hairs of a mouse on an adjacent digitizing tablet. This enabled us to measure both straight-line distances and the lengths of perimeters of curved features. Straight-line distances between pairs of morphological landmarks were measured by placing the image of the cross hairs on each landmark, then clicking the mouse button. Curved shapes were measured by holding a mouse button down and "dragging" the image of the cross hairs of the mouse along the image of the particular feature to be measured. All floral measurements were made with the camera lucida and digitizing tablet using one of these two techniques, and were recorded directly on the microcomputer to which the digitizing tablet was connected.

Analytical techniques. We subjected character data to nonmetric multidimensional scaling [MDS]. This technique allowed us to summarize in three dimensions patterns of variation with regard to all 16 measurements. MDS has been shown to be effective for numerical taxonomy (Rohlf 1972 as cited in Pimentel 1979) and usually outperforms Principal Components Analysis (Pimentel 1979). To assess variation at both intra- and inter-specific scales, we examined measurements of plants assigned to *P. chartaceum* and plants assigned to *P. eximium* both separately and together.

Before performing each MDS we standardized floral measurements and calculated average Euclidean distances between all pairs of OTU's (plants). We used the resulting distance matrix first as the basis of a Principal Coordinates analysis. We then used the principal coordinates as an initial configuration (following the procedure of Rohlf (1993)) for an MDS of the average Euclidean distance matrix.

We also subjected the character data to multigroup discriminant analysis (MDA) (*sensu* Pimentel and Smith 1986) to test the robustness of patterns seen in results of MDS (Abbot et al. 1985). Herein, after square-root transformation of leaflet counts to correct for deviation from normality, we classified each OTU (plant) *a priori* to a group, and calculated linear combinations of measured variables in which distances among the a priori groups were maximized (canonical variates analysis). We then calculated the scores of the OTU's on the canonical variates axes and compared them to scores of the centroids of the original groups. This allowed computation of the probability of membership in each group for each OTU (Geisser classification). The extent to which predictions of group membership were successful was taken as evidence the particular circumscription of groups could be supported based on the variables measured. Classification results in MDA thus helped provide an idea of "how different is different" Pimentel (1979).

We used several different circumscriptions of groups for different iterations of MDA. Results presented below are based upon a geographic circumscription: each plant was assigned to one of nine groups defined by the population and/or region where the plant was collected. The assignment of plants to groups is shown by the nine values in the "Geographic Code" field in Table 2. Results of MDS suggested geographic patterning; these circumscriptions represented geographic grouping at the finest scale (in terms of group sample sizes vs. numbers of variables) the data could support (Pimentel and Smith 1986).

Other components of the MDA (in addition to the calculation of canonical variates and Geisser classifications mentioned above) included calculation of ANOVA's, Student-Newman-Keuls Multiple Range Test scores, and Generalized distances (Mahanobis Distance) among group centroids. These analyses aided interpretation of discriminant results by showing differences among the nine geographic groups with regard to means for each variable (ANOVA and Multiple Range Test) and by providing a quantitative measure of the degree of resemblance among the groups (Generalized distances) (Pimentel 1979). We used UPGMA clustering to summarize the Generalized distances among all pairs of group centroids into a single phenogram.

To relate the floral measurements used in this analysis to anther and stigma exsertion characters used in previous treatments we calculated values of these characters for each of the nine groups defined for discriminant analysis. Anther exsertion was calculated by summing mean filament length and insertion distance and subtracting mean corolla tube length. Stigma exsertion was calculated by mean style length from mean corolla tube length. Calculations were made from means calculated as part of the ANOVA mentioned above, and were not subject to statistical analysis.

We calculated similarity matrices, principal coordinates analyses and MDS using the NTSYS 1.8 software package (Rohlf 1993). We calculated discriminant analyses using the BioΣtat II (Pimentel 1986) and CSS Statistica 3.1 packages.

RESULTS

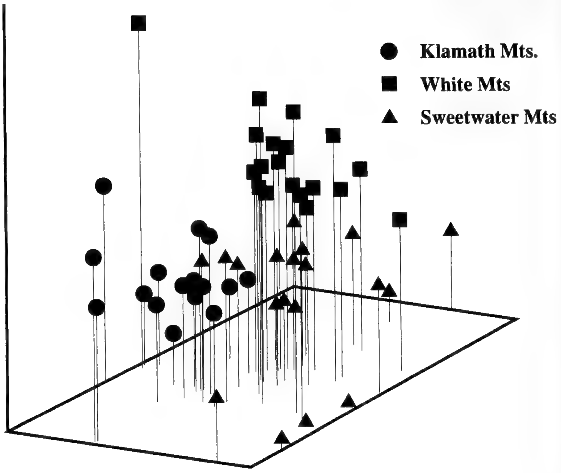

FIG. 2. Multidimensional Scaling of *P. chartaceum* From Three Mountain Ranges. Symbols represent individual plants. Lines extending down from each symbol allow the position of the symbol to be interpreted with regard to all three axes.

Reductions of the 16-dimensional relationships in the original data set to three dimensions by means of MDS are shown in Figures 2–4. In Figure 2 plants from the Klamath Mountains and the White Mountains occupy different areas of the plot, while plants from the Sweetwater Mountains are scattered in between. Plants from the Sonora Pass (Sierra Nevada) are separated from those of other Sierran populations in Figure 3. In Figure 4 Sonora Pass plants are separated from conspecific ones elsewhere in the Sierra Nevada (as in Fig. 3), although Figure 4 depicts the result of an MDS of *P. chartaceum* and *P. eximium* together.

ANOVA's show significant ($P < 0.05$) differences among means of all 16 characters (Table 2) among the nine geographic groups defined for discriminant analysis. Patterns of differences among means were resolved by the Student-Newman-Keuls Multiple Range test (Table 2) for 11 of the 16 variables. The synthetic character "anther exsertion" (Table 2) separates populations currently assigned to *P. chartaceum* from those assigned to *P. eximium* with the exception of Sonora Pass populations (Table 2, Geographic Code "L"). Geisser classification results (Table 3) show that the only misclassifications involve the Sweetwater Mountains—1 plant from the Sweetwater Mountains erroneously assigned to the Klamath Mountains, 4 plants from the Sweetwater Mountains erroneously assigned to the Sonora Pass Sierra Nevada, and 1 plant from the Sonora Pass Sierra Nevada erroneously assigned to the Sweetwater Mountains. The first three canonical variates axes (Fig. 5) account for 91% of the total variance among all eight axes. On the horizontal axis the Sonora Pass group as well as populations assigned to *P. chartaceum* are separated from populations assigned to *P. eximium.* On the vertical axis the Sonora Pass group is separated from both *P. chartaceum* groups and southern Sierra *P. eximium* groups. The centroid representing *P. elegans* is close to centroids assigned to *P. chartaceum* on both horizontal and vertical axes,

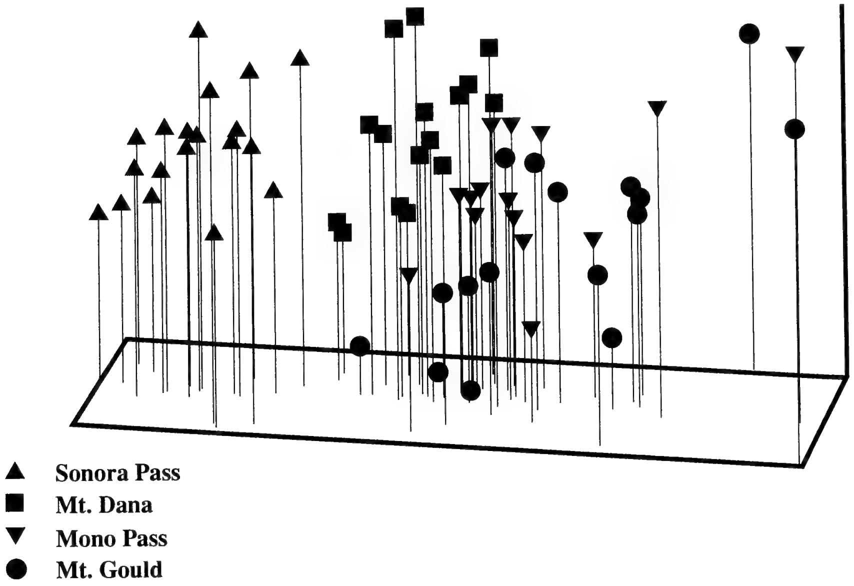

FIG. 3. Multidimensional Scaling of *P. eximium* from Four Regions in the Sierra Nevada. Symbols represent individual plants. Lines extending down from each symbol allow the position of the symbol to be interpreted with regard to all three axes.

while the *P. viscosum* centroid is close only on the horizontal axis. Generalized distances among all nine group centroids on all eight canonical axes as summarized by UPGMA clustering (Fig. 6) are consistent with pattern of centroids on the first three canonical axes in Figure 5.

DISCUSSION

These results reveal a level of resolution of morphological variation finer than any previously attained. Patterns are observed with regard to floral and foliar architecture as well as overall similarity among populations.

Previous workers have described floral morphology of California alpine polemoniums in terms of discrete forms with regard to anther exsertion. Flowers of *P. chartaceum* are regarded as having exserted anthers, while those of *P. eximium* have included anthers (Davidson 1950; Munz 1973; Grant 1989; Wilken 1993). Results in Table 2 show

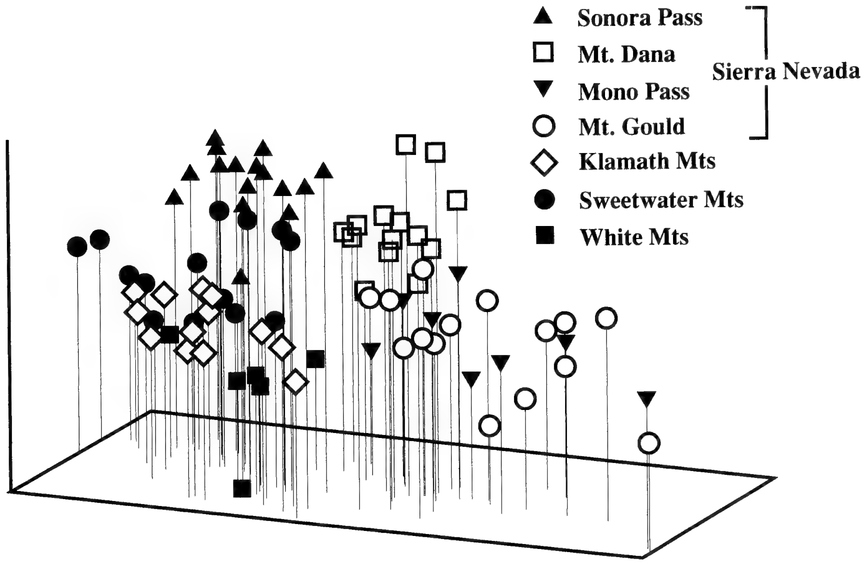

FIG. 4. Multidimensional Scaling of *P. chartaceum* (from three mountain ranges) and *P. eximium* (from four regions in the Sierra Nevada). Symbols represent individual plants. Lines extending down from each symbol allow the position of the symbol to be interpreted with regard to all three axes.

TABLE 3. RESULTS OF GEISSER CLASSIFICATION. Numbers are numbers of plants. Rows are *a priori* group assignments and columns are predictions (6 misses/153 hits = 96% classification rate). Any numbers not on the diagonal represent misclassifications. See Table 2 for interpretation of geographic codes.

Geographic code	R	K	L	D	G	C	S	T	W
R	16	0	0	0	0	0	0	0	0
K	0	19	0	0	0	0	0	0	0
L	0	0	18	0	0	0	1	0	0
D	0	0	0	16	0	0	0	0	0
G	0	0	0	0	16	0	0	0	0
C	0	0	0	0	0	16	0	0	0
S	0	1	4	0	0	0	14	0	0
T	0	0	0	0	0	0	0	19	0
W	0	0	0	0	0	0	0	0	19

that stigma exsertion also distinguishes these two floral forms, and more importantly, that there is a third floral form not previously recognized. This form is largely restricted to Sonora Pass plants, and is characterized by flowers with significantly ($P < 0.05$) greater insertion distances and significantly shorter filaments than those of flowers from any other areas. In terms of anther exsertion, Sonora Pass flowers (Table 2 Geographic code "L") are intermediate between those of *P. chartaceum* and those of *P. eximium* from the central and southern Sierra Nevada. In terms of the components of anther exsertion, however, "L" flowers have extreme values, thus possess a unique floral form. Whether or not this form is recognized, future treatments will have to put in an exception clause for Sonora Pass plants if the customary two-state anther exsertion character is used.

Variation in foliar architecture reveals a different pattern. Rather than being interpretable in terms of several discrete forms, there is only one relatively stable form of leaflet morphology in California. This form is characterized by a predominantly two-part leaflet dissection and is restricted to plants in the Klamath Mountains.

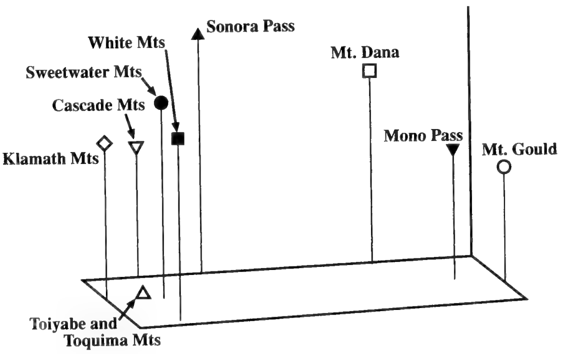

FIG. 5. Canonical variates analysis of alpine *Polemonium* populations. Symbols indicate centroids along canonical variates axes of plants assigned to nine geographic groups defined for discriminant analysis.

Leaflet dissection among plants of other regions is significantly greater than that of Klamath Mountain plants, and is best interpreted in terms of a cline rather than discrete forms. There is a significant increase in degree of dissection (Table 2) among California populations from north to south. This pattern is especially clear among *P. eximium* populations in the Sierra Nevada, but also holds for *P. chartaceum*. Given the importance of foliar morphology in regulation of CO_2 and H_2O balances, this latitudinal increase in leaflet dissection might offer a fruitful subject of investigation for physiological ecologists.

When leaflet and floral characters are considered together to assess overall similarity, geographic variation is apparent in both intra- and inter-specific MDS results (Figs. 2–4), and on a finer scale, in successful Geisser classification of almost every plant sampled from all nine geographic areas (Table 3). The six Geisser misclassifications are the only data that suggest any patterns of similarity that cross (rather than coincide with) geographic boundaries.

While populations in all nine geographic areas may be separable via discriminant analysis, not all areas have equally stable and distinct morphological forms. Data in Figures 2 and 4, and Geisser misclassifications (Table 3) suggest that populations in the Sweetwater Mountains may be more variable than populations in other areas. While we cannot rule out the possibility that this variation may be an artifact of unequal and generally small sample sizes, there are several biological hypotheses worthy of consideration. One hypothesis is that the variability may be evidence of sympatry between *P. chartaceum* and *P. eximium.* All Sweetwater Mountain plants have been assigned to *P. chartaceum* by previous workers. The four Sweetwater Mountain plants misclassified as Sonora Pass plants (Table 3), however, have the short-filament floral morphology characteristic of Sonora Pass plants, which have been assigned to *P. eximium.*

No field observations have been made of sympatric populations of *P. chartaceum* and *P. eximium.* Rather, observations have been made in the Sweetwater Mountains that the same plant may have some flowers with the exserted (*P. chartaceum*) design and other flowers with the short-filament Sonora Pass design. This suggests that introgression and/or hybridization with plants from Sonora Pass may be a better interpretation than sympatry. A final hypothesis is that this floral variation could be evidence that populations in the Sweetwater Mountains are composed of a form ancestral to the (florally) more uniform forms which now occur elsewhere (Morefield personal communication).

All hypotheses are consistent with the geography of the area. The terrain between the Sonora Pass populations and the Sweetwater Mountains (about

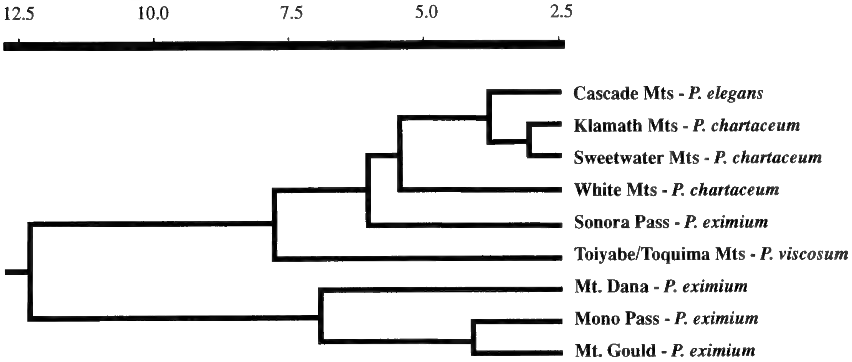

FIG. 6. Phenogram based on UPGMA clustering of generalized (Mahalanobis') distances among centroids of geographic groups defined for discriminant analysis. Numbers on the scale above the phenogram represent standard deviations. The greater the number at which a group is joined to a cluster, the less the similarity.

30 km apart) is high enough so it would have had a habitat suitable for alpine *Polemonium* colonization as recently as the end of the last glacial period. Further investigation is needed to properly interpret the significance of morphological variation in Sweetwater Mountain plants.

The southern Sierra Nevada is another area where populations which can be separated by means of discriminant analysis (Geographic Codes D, C, and G in Table 2; Mt. Dana, Mono Pass, and Mt. Gould in Fig. 5) should not necessarily be treated as separate morphological entities. Patterns in Figures 3 and 4 show that, while there is considerable variation among plants in the Sierra Nevada (*P. eximium*), there is one principal morphological discontinuity that separates Sonora Pass populations from those to the south. The intermediate position of the Mt. Dana population, both morphologically (Figs. 4 and 5) and geographically (Fig. 1), suggests a latitudinal cline may exist in the Sierra Nevada from populations near Sonora Pass south at least as far as to those around Mono Pass.

We observed two additional characters (inflorescence congestion and anther color) that display this pattern. While these characters were not quantified for use in multivariate analysis, repeated field observations have shown Sonora Pass plants to have noticeably less congested inflorescences and a much greater abundance of yellow pollen (as opposed to cream-colored pollen) than do plants from farther south in the Sierra Nevada.

If variation in the Sierra Nevada is interpreted to represent two forms, and variation in the Sweetwater Mountains is hypothesized to result from introgression, four areas (of the seven areas in California defined for discriminant analysis) are left in which discrete morphological forms occur—the Klamath Range, the White Mountains, Sonora Pass, and the southern Sierra Nevada.

The fact that the morphological forms identified above do not co-occur is consistent with theories of *Polemonium* evolution by previous workers. Grant (1989) hypothesized an allopatric mode of speciation. He wrote that the common ancestor of *P. eximium* and *P. chartaceum* "had a semicontinuous distribution in the far west at a cool stage of the Pleistocene. Character divergence among these taxa developed along with geographic isolation."

Davidson (1950) wrote "if cognizance were taken of the minute differences between populations on different mountains one might eventually delimit as many subspecies as there are populations on isolated mountains." In this statement Davidson implied allopatric speciation and anticipated the recognition of geographic-morphological entities such as those discussed above. He did not, however, consider the possibility that taxonomic treatment of these entities might require substantial revisions (as opposed to simply splitting species into subspecies).

The phenogram in Figure 6 infers the taxonomic complexity of this group of populations. It suggests that Klamath Mountain populations have a greater affinity with Cascade Mountains populations of *P. elegans* and Sweetwater Mountain populations than with the White Mountain populations with which they are included in the current circumscription of *P. chartaceum.* The White Mountains group are sister to the Cascade-Klamath-Sweetwater group, forming an *elegans-chartaceum* group. This treatment is consistent with Davidson's and Wilken's suggestions, but inconsistent with Murray's reduction of *P. chartaceum* to *P. viscosum* ssp. *chartaceum.*

Curiously, the Sonora Pass populations of *P. eximium* are sister to the *elegans-chartaceum* group rather than with other Sierra Nevada populations (Mt. Dana, Mt. Gould and Mono Pass) with which they are included in *P. eximium.* No previous treatments have placed any Sierra Nevada populations in the same taxon with those occurring in the Klamath, Sweetwater, or White Mountains.

Populations of *P. viscosum* from the Toiyabe and Toquima Mountains are sister to the group consisting of *P. elegans, P. chartaceum,* and one population of *P. eximium.* This treatment is not consistent with any published or proposed taxonomic treatment. The three remaining populations of *P. eximium* (groups Mt. Dana, Mt. Gould, and Mono Pass in Fig. 6) constitute a lineage clearly distinct from and sister to the rest of the alpine species of *Polemonium.* Thus, with the use of explicit, quantitative analytical techniques, taxonomic grouping in this complex is even more difficult. One resolution of the question of rank would be the creation of a single western North American alpine *Polemonium* species, with all four California morphological entities, as well as *P. elegans* and *P. viscosum,* treated as subspecies (Stebbins personal communication). In this treatment the apparent arbitrariness of current circumscriptions and ranks regarding floral and foliar characters would be eliminated. This treatment, however, would not give sufficient attention to obvious morphological differences among populations from different regions. It may also obscure evolutionary relationships in its oversimplification.

Nevertheless, current circumscriptions of *P. chartaceum* and *P. eximium* are inconsistent with patterns of floral and leaflet variation. These two taxa might just as easily be treated as four or five species, depending on the taxonomic interpretation of populations in the Sweetwater Mountains. Patently the Sierran *P. eximium* is more taxonomically complex than has been thought. Three of these entities show greater similarity to *P. elegans* of the Cascade Range than to *P. viscosum* of the Rocky Mountains and Great Basin. This suggests that, in addition to revisions of circumscriptions of California species, relationships with regional congeners must be reconsidered as well.

It is premature to make further inferences regarding the relationships between California alpine *Polemonium* species and *P. viscosum,* due to the wide distribution and minimal sampling of *P. viscosum* in this examination. According to Grant (1989), however, there is an east-west clinal decrease in floral size from Rocky Mountains populations of *P. viscosum* to those in the Great Basin. The two populations sampled in this examination are the western-most in the Great Basin, and presumably represent the small end of this cline. Since they are still larger in almost all measurements than most California populations (except southern Sierran), differences between *P. viscosum* and California forms may be underestimated in this examination. Further sampling of *P. viscosum* might reinforce, rather than change, the basic pattern of relative similarities described above.

One taxonomic conclusion supported by the current morphometric analysis is that the Klamath Mountain population is readily distinct from those from the White Mountains; based on these data, *P. chartaceum* should not refer to both entities. Additional support of the distinction between Klamath and White Mountain taxa is afforded by ITS sequence data (de Geofroy et al. 1996), which show that White Mountain populations are more closely related to *P. eximium* from the northern Sierra Nevada than they are to the Klamath Mountain population on Mt. Eddy. Taxonomic recognition of the Klamath material as a distinct species is being undertaken (Pritchett and de Geofroy unpublished).

Our primary goal in this study was to decipher the systematic complexity of the California alpine polemoniums and delineate the taxa that are recognizable based on morphology. The next logical goal is to reconstruct the evolutionary history of the alpine polemoniums; however, the morphological characters that can be used for recognition of taxa are likely too few to allow a rigorous phylogenetic reconstruction. Recently de Geofroy (1998) undertook a molecular phylogeny of the alpine polemoniums. Her results based on sequences of the ITS region of nuclear ribosomal DNA, are in general accord with our phenetic analysis of morphological data. In particular her results support our conclusion that intra-specific variation within *P. chartaceum* and *P. eximium* require revision of these species. Final evaluation of all data, molecular and morphological, will generate a phylogenetic model of the complex that can be used to test future hypotheses on the evolution of this genus.

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ADULT SEX RATIO OF *ARCEUTHOBIUM TSUGENSE* IN SIX SEVERELY INFECTED *TSUGA HETEROPHYLLA*

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ABSTRACT

The adult sex ratio of *Arceuthobium tsugense* (C. Rosend.) G. N. Jones ssp. *tsugense* (western hemlock dwarf mistletoe) was 1:1 (n = 1608 plants) in the crowns of six large, *A. tsugense*-infected *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) at the Wind River Canopy Crane Research Facility in south-central Washington. One tree, however, had a female-biased adult sex ratio and another had a male-biased adult sex ratio. Plants in the lower crowns (less than 20 m in height) exhibited a female-biased adult sex ratio. Our results suggest that an earlier study, which sampled plants near the ground and reported a female-biased sex ratio for *A. tsugense,* may have been biased because of the sampling method used.

Dwarf mistletoes *Arceuthobium* spp. (dwarf mistletoes) are obligate, dioecious flowering plants that are parasitic on conifers. The ratio of male to female adult plants is typically 1:1 (Hawksworth and Wiens 1972, 1996). However, many adult populations of *Arceuthobium tsugense* (C. Rosend.) G. N. Jones ssp. *tsugense* (western hemlock dwarf mistletoes) are reported to exhibit female-biased adult sex ratios of approximately 3:2, even though the embryonic sex ratio for this species is 1:1 (Wiens et al. 1996). Many of the adult sex ratio determinations for *A. tsugense* reported by Wiens et al. (1996) were based on samples of less than 100 plants (10 of 16 populations), but some of their adult sex ratio determinations (3 populations) used more than 400 plants. Each of the three populations that sampled >400 plants had significantly female-biased adult sex ratios, as did their entire sample population of 3057 plants (59 percent females).

The Wind River Canopy Crane Research Facility is located in the Wind River Experimental Forest of the Gifford Pinchot National Forest in southern Washington. The facility uses a construction tower crane (Liebherr 550 HC) 75 m in height with a jib arm 85 m long that is capable of accessing 2.3 ha of an old-growth *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest (Parker 1997, http://depts.washington.edu/wrccrf. Accessed on February 3, 1999). Approximately one third of the over- and under-story *T. heterophylla* within the crane-accessible area are infected with *A. tsugense. Arceuthobium tsugense* counted in the populations examined by Wiens et al. (1996) were growing within approximately 4 m of the ground. Because the Wind River Canopy Crane (WRCC) provides access to the upper and middle crowns of large, severely infected *T. heterophylla*, the adult sex ratio of this population of *A. tsugense* could be determined using several hundred plants examined at heights much greater than 4 m. The objectives of this study were to determine if the adult sex ratio of *A. tsugense* has a sex-bias when several hundred plants within the crowns of large, severely infected *T. heterophylla* are sampled and if sex ratio varies on individual trees or by height of infection.

METHODS

Six individuals of *T. heterophylla* severely infected with *A. tsugense* were sampled using the WRCC in 1996. Selected trees were greater than 40 m in height, infected in most, if not all, of their crown, and were accessible by the crane (most of their outer and upper crowns could be accessed). Trees had been assigned identification numbers when the crane site was stem mapped in 1995. Each tree was sampled from the bottom of the crown on the north side, gradually working up that side to the tree top. *Arceuthobium tsugense* was sampled on crane-accessible branches which were attached to the north side of the trunk. Each crane-accessible infection on a sample branch was examined for infections by *A. tsugense* and adult plants (plants with flowers). The approximate height of each branch sampled was recorded, based on the vertical distance between the crane gondola and the load jib. Individual infections were detected by the spindle-shaped swellings induced by *A. tsugense* and/or the presence of *A. tsugense* on branches. When *A. tsugense* shoots were absent on an obvious single infection, the infection was recorded as nonreproductive. Where adult plants were observed a small section of a plant was removed and examined to determine its sex (Hawksworth and Wiens 1996). When necessary, shoots and their attached flowers were examined with a 10× hand lens to aid sex determination. *Arceuthobium tsugense* on witches' brooms that could not be distinguished as arising from separate infections were not sampled. In many cases separate infections that were close to each other on a branch or witches' broom could be distinguished because the adult plants they produced were of a different sex. When adjacent infections on the same branch were the same sex, the infection was treated as the same infection.

After sampling the north side of a tree, the procedure was repeated on its west, south and east side. The north and south sides of the six trees were sampled in late April. In mid September, the east and west sides of the trees were sampled using the above methods in order to increase the sample size of reproductive infections. The east side of one tree (# 1134) and the west side of one tree (# 2119) could not be accessed by the crane. Thus, four trees (#'s 1129, 2002, 2054 and 2131) were sampled on four sides and two on only three sides (#'s 1134 and 2119).

Data were tallied by branch and tree for male and female plants and for nonreproductive infections. Male and female plants also were tallied by height classes (<20, 20.0–24.9, 25.0–29.9, 30.0–34.9, 35.0–39.9, 40.0–45.0 and >45 m). These height classes were selected to provide a uniform representation of the number of branches sampled in each height class.

Frequencies of male and female adult *A. tsugense* (sex ratios) were compared for individual trees and height classes using chi-square tests. Differences were judged to be significant at $P \leq 0.05$. Based on previous reports of sex ratios for *A. tsugense* (Wiens et al. 1996) we hypothesized that the sex ratio of *A. tsugense* in the trees we sampled would be female-biased at a ratio of approximately 3:2.

RESULTS

The crane survey sampled 239 branches and 1980 dwarf mistletoe infections. Of these 1980 infections, 1608 had flowering plants, 805 male and 803 female, and 372 were nonreproductive. Thus, the adult sex ratio for this population of *A. tsugense* based on a sample of 1608 plants was essentially 1:1. There was variation in the sex ratio between the six trees sampled (Table 1). One tree (# 2119) had a significantly female-biased sex ratio (60 percent female) and one tree (# 2131) had a significantly male-biased sex ratio (44 percent female).

Nonreproductive infections varied from 10 to 26 percent of the total number of infections sampled per tree (Table 1). More than 20 percent of the infections were recorded as nonreproductive on four of the trees. However, we did not sample every infection on each tree because many of the infections close to the main bole of the trees were inaccessible by the crane. In addition, we have no estimate of how many infections were missed on accessible branches because we could not distinguish the infections.

TABLE 1. ADULT SEX RATIO OF REPRODUCTIVE INFECTIONS AND PERCENTAGE OF NONREPRODUCTIVE INFECTIONS OBSERVED ON SIX *TSUGA HETEROPHYLLA* AT THE WIND RIVER CANOPY CRANE RESEARCH FACILITY. [1]Significant deviation in the adult sex ratio from 1:1. Chi-square statistics ($P \leq 0.05$).

Tree number	Branches sampled	Total infections	Reproductive infections	Adult sex ratio (% females)	P	Nonreproductive infections (%)
1129	40	348	315	50	0.956	10
1134	50	254	197	52	0.618	23
2002	36	441	373	50	0.877	16
2054	44	261	193	53	0.428	26
2119	21	194	154	60[1]	0.010	21
2131	48	482	376	44[1]	0.013	22
Total/Mean	239	1980	1608	50	0.960	19

TABLE 2. ADULT SEX RATIO OF REPRODUCTIVE INFECTIONS AND PERCENTAGE OF NONREPRODUCTIVE INFECTIONS ON SIX *TSUGA HETEROPHYLLA* BY HEIGHT CLASS, WIND RIVER CANOPY CRANE RESEARCH FACILITY. [1]Significant deviation in the adult sex ratio from 1:1. Chi-square statistics ($P \leq 0.05$).

Height class (m)	Number branches sampled	Number reproductive infections	Adult sex ratio (% females)	Non-reproductive infections (%)
<20	26	82	61[1]	53
20.0–24.9	23	89	47	49
25.0–29.9	19	113	43	32
30.0–34.9	45	351	53	17
35.0–39.9	41	201	47	15
40.0–45.0	44	398	50	7
>45	41	375	50	3
Total/Mean	239	1608	50	19

The sex ratio and percentage of nonreproductive infections by height classes are presented in Table 2. The number of infections with plants increased as height class increased. There was little variation in the 1:1 sex ratio for height classes >30 m. The <20 m height class had a significantly female-biased sex ratio of approximately 3:2 (P = 0.047). The majority of observable nonreproductive infections (61 percent) were in the lower part of the crowns (<30 m).

The sex ratio and percentage of nonreproductive infections for the tree with the largest sample of plants (# 2131) is summarized by height classes in Table 3. This tree had a significantly male-biased sex ratio (Table 1). The distribution of sex ratio by height class for this tree was female-biased in the lower crown (<20 m), but the sex ratio was consistently male-biased as height class increased. However, the sample size in the lower crown was small (only 14 plants), but plant counts increased dramatically as height class increased in all of the trees sampled (Table 3). The tree with the next greatest plant count (# 2002) had a similar distribution of plant numbers and non-reproductive infections were predominantly in the lower crown as well. It also had a female-biased sex ratio in the lower crown (<20 m), but had a consistent 1:1 sex ratio as height class increased, which resulted in an approximate 1:1 adult sex ratio for all *A. tsugense* sampled on that tree (Table 1). Other trees with a 1:1 sex ratio (#'s 1129, 1134 and 2054) had similar distributions of male and female adult plants within their crowns. Tree # 2119 had a female-biased sex ratio because it had a predominance of female plants in its lower and middle crowns, but approximately equal numbers of male and female plants in its upper crown. However, only 154 plants were sampled on tree # 2119, the lowest sample size for an individual tree.

DISCUSSION

Based on the 1608 *A. tsugense* we sampled, the adult sex ratio for this population of *A. tsugense* is approximately 1:1. This ratio differed from that (3:2) reported for many other populations of *A. tsugense* (Wiens et al. 1996). The differences in adult sex ratios between these studies may be related to sample sizes and sampling methods. For example, 10 of the 16 populations sampled by Wiens et al.

TABLE 3. ADULT SEX RATIO OF REPRODUCTIVE INFECTIONS AND PERCENTAGE OF NONREPRODUCTIVE INFECTIONS ON TREE # 2131 BY HEIGHT CLASS, WIND RIVER CANOPY CRANE RESEARCH FACILITY. [1]Significant deviation in the adult sex ratio from 1:1. Chi-square statistics ($P \leq 0.05$). Chi-square analysis was not performed on this data set for individual height classes because of the small sample sizes.

Height class (m)	Number branches sampled	Number reproductive infections	Adult sex ratio (% females)	Non-reproductive infections (%)
<20	4	14	79	75
20.0–24.9	4	8	50	64
25.0–29.9	5	29	35	41
30.0–34.9	8	45	44	24
35.0–39.9	8	71	44	15
40.0–45.0	10	118	39	14
>45	9	91	45	1
Total/Mean	48	376	44[1]	22

(1996) had less than 100 plants and they sampled within 4 m of the ground. Wiens et al. (1996) pointed out that in their study, deviations from a female predominant 3:2 sex ratio were primarily related to small sample sizes or to host species. Their data also indicated that not all populations of *A. tsugense* display a female-biased sex ratio. One of the populations they sampled had a 1:1 sex ratio (Lake Cowichan, British Columbia) and was based on a relatively large sample size (257 plants). Therefore, if the populations of *A. tsugense* with female-biased adult sex ratios reported by Wiens et al. (1996) were resampled to obtain larger sample sizes from the entire crowns of infected trees, it is possible that adult sex ratios for those populations may show trends towards the 1:1 sex ratio reported here for the WRCC population of *A. tsugense* and reported for other species (Hawksworth and Wiens 1972, 1996).

Wiens et al. (1996) inferred that the most likely reason for female-biased sex ratios in populations of *A. tsugense* is a greater longevity of female plants. Differential mortality of male and female plants also was hypothesized as a probable reason for the female-biased sex ratio of another obligately dioecious mistletoe, *Phoradendron tomentosum* (DC.) Gray, in central Texas (Nixon and Todzia 1985). Female plants of juniper mistletoe *Phoradendron juniperinum* A. Gray (juniper mistletoe) are also reported to have greater longevity than males (Dawson et al. 1990). Smith (1971) reported that the life span of *A. tsugense* shoots was at least five years and although he did not discuss that female plants live longer than males, his Tables 2 and 3 indicate that on young infections, female plants live longer than males. Therefore, the idea that greater longevity of female plants may account for the female-biased adult sex ratios reported for several populations of *A. tsugense* is plausible. Whether or not female *A. tsugense* live longer than male plants throughout the crowns of severely infected trees remains unknown. But our data from the lower crowns of *T. heteropyhlla* we sampled at the WRCC site demonstrated a definite female-biased sex ratio (Table 1). In addition, we conducted a preliminary survey of infections by *A. tsugense* in an attempt to determine an adult sex ratio for the *A. tsugense* population growing within 4 m of the ground in the WRCC site (unpublished). Of the nearly 300 infections we observed near the ground, only three percent had plants that could be sexed and nearly all of these were females. These preliminary data and the crane survey data from the lower crowns of the large *T. heterophylla* sampled (Tables 1 and 2) support the idea that female plants may be surviving longer than males in the lower crowns of *T. heterophylla* infected by *A. tsugense*. Therefore, sex ratio determinations based on samples from the lower crowns of *T. heterophylla* infected by *A. tsugense* will be consistently female-biased.

Our data (Table 2) demonstrate that *A. tsugense* is more abundant in the middle and tops of large, severely infected *T. heterophylla*. Smith (1969) also reported that *A. tsugense* shoot production was more abundant in the middle and upper crowns of severely infected *T. heterophylla*. Less shoot production in the lower crowns of *A. tsugense*-infected trees may be related to the age of infections, as older infections often produce fewer shoots (Smith 1971). Because initial infection of trees occurs in the lower crown and moves upward in individual trees (Richardson and van der Kamp 1971; Parmeter 1978; Shaw 1982), infections in the lower crowns are generally older than infections in the upper crowns. However, many investigators have associated poor shoot production of *A. tsugense* with low light intensity in the lower crowns of infected trees or within dense forests (Weir 1916; Korstian and Long 1922; Gill 1935; Wagener 1961; Smith 1969; Richardson and van der Kamp 1971; Smith 1971) and Baranyay (1962) provided data to support this relationship.

Whatever the reason for the large number of nonreproductive infections in the lower crown (age of infections, shading or other factors), sampling infected hemlock near the ground will mean that many infections of *A. tsugense* can not be used for adult sex ratio determinations. If the malate dehydrogenase method of sex determination reported by Wiens et al. (1996) could be applied to *A. tsugense* tissue extracted from infected branches (endophytic system tissue), then the sex of nonreproductive infections could be determined. If the sex of all infections could thus be determined, then perhaps, the sex ratio for all infections sampled would be 1:1 since the embryonic sex ratio is 1:1 for *A. tsugense* (Wiens et al. 1996).

Because of the variation in sex ratio by crown position and individual trees in the *A. tsugense* population at the WRCC site, adult sex ratios should be determined for additional *A. tsugense* populations using methods that minimize the bias we feel is associated with sampling a few trees from near the ground. Adult sex ratio determinations should be made by sampling several trees from throughout their crowns and plant counts should consist of at least 1000 individuals for each *A. tsugense* population sampled. Therefore, we recommend that *A. tsugense* adult sex ratio determinations be made by destructively sampling several trees per population. Destructive sampling allows access to branches in the middle and upper crowns where many more *A. tsugense* plants can be sexed. This will increase plant counts and should eliminate the bias that our data indicates is probably associated with sampling from the lower crowns of infected *T. heterophylla*. The senior author has used this technique for *Arceuthobium laricis* (Piper) St. John (larch dwarf mistletoe) in northeastern Washington (results reported in Table 3 of Wiens et al. 1996) and found destructively sampling several *A. laricis*-infected western larch *Larix occidentalis* Nutt. (western larch) provided a large sample (over 1500 plants) with a reasonable expenditure of time and effort. It also eliminated the potential bias of arbitrarily selecting mistletoe plants on infections near the ground and the possibility of sexing the same plants more than once. Destructive sampling also allows the ages of individual infections to be determined (Scharpf and Parmeter 1966; Smith 1971; Shaw 1982), thus making it possible to correlate adult sex ratio with age structure of the population. If female plants possess greater longevity than male plants, then older infections should be comprised of a higher proportion of females.

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POPULATION ECOLOGY OF *DUDLEYA MULTICAULIS* (CRASSULACEAE); A RARE NARROW ENDEMIC

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ABSTRACT

Dudleya multicaulis (Rose) Moran is a rare geophyte, endemic to the coastal plain of southern California. This species has a patchy distribution associated with the imperiled coastal sage scrub community. We investigate the population size, gene flow, and genetic structure at two different geographical scales; discrete colonies within the University of California, Irvine Ecological Reserve and from eight populations sampled across the range of this species. The objective of this protocol was first to determine what constituted a *D. multicaulis* population as interpreted from protein electrophoretic data, and second to estimate the population genetic structure and amount of gene flow among populations throughout the geographical range. This kind of information is important for rare species and should be used with any plan designed to protect them from further decline. Our data indicate that all individuals within the University of California, Irvine campus now, or in the past, functioned as one population and it is estimated to be in the order of 1200 individual adult plants distributed over approximately 63 acres. The low population genetic structure and high gene flow found at this scale may be explained by pollen transport between colonies. At the regional level we found there is little gene flow among populations across the range of the species, that there is a high level of intrapopulation genetic variation, but more importantly, that there is significant genetic differentiation among populations. We discuss the implications of our results for the conservation of genetic diversity in *D. multicaulis*.

Dudleya (Crassulaceae, Rosales), a New World genus, consists mostly of perennial succulent herbs adapted to arid environments, many of which have restricted geographical distributions and specific habitat requirements (Moran 1951; Mulroy 1976). *Dudleya* species usually occur along the coastal plain of southern California and northern Baja California with the highest number of species centered around San Diego (Mulroy 1976). Moran (1951) revised the genus and recognized fifty-five taxa grouped into the two subgenera: *Dudleya* and *Hasseanthus* (see also Uhl and Moran 1953). Most of the literature on this genus has dealt with the classification and distribution of the different species (e.g., Bartel 1992; Bartel and Shevock 1983, 1990; Boyd et al. 1995; Moran 1951; McCabe 1997; Nakai 1987; Uhl and Moran 1953). However, our knowledge of its ecology, genetics and habitat requirements remains poor (but see Clark 1989; Mulroy 1979; Thomson 1993). This is particularly important because of two factors that make many species within *Dudleya* prone to extinction: narrow endemism with low population numbers and the increasing destruction and fragmentation of, and invasion by non-native species, into Southern California's natural landscape (Keeley 1995; Painter 1995; Schierenbeck 1995).

Our work focuses on the population ecology of *Dudleya multicaulis,* (Rose) Moran a rare, narrow endemic of southern California. The California Native Plant Society (CNPS) recognizes it as rare and endangered in California (List 1B, Elias 1986). The CNPS also notes that the major threats to this species are from development, road construction, grazing, and recreation (Elias 1986), all of which have increased dramatically in southern California. It is then reasonable to expect that populations of *D. multicaulis* will continue to be destroyed, and with them the genetic diversity of the species representing perhaps adaptations to local environments.

Dudleya multicaulis is a small, succulent geophyte endemic to the coastal plains of southern California and is usually found growing on rocky outcrops (Dice 1990, personal observation). Its range extends from northern San Diego County to southern Los Angeles County and east to Riverside County. *Dudleya multicaulis* remains dormant during the dry months (usually June–November) as an underground corm. Rainfall coupled with cold nights triggers the start of plant growth (personal observation). Depending on the timing and amount of rain, plants may emerge starting in mid-November or as late as mid-January. The cymose inflorescence usually appears in March and is fully developed by April or early May. Plants flower for about forty days. A plant may have two to several inflorescences, each bearing three to many flowers. The small seeds are primarily gravity-dispersed, generally traveling no more than 25 cm (Harker and DeViso unpublished). The mean number of seeds

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TABLE 1. LOCATION, POPULATION REFERENCE CODES USED IN THE PAPER, NUMBER OF INDIVIDUAL PLANTS SAMPLED FROM EACH LOCATION AND SITE DESCRIPTION FOR THE LOCAL SCALE ANALYSIS.

Population name and location	Reference code	Sample size	Micro-habitat description
UCI Ecological Preserve			
Twin Peaks	TP	40	Rocky Outcrop
Whoeler's Folley	WF	40	Rocky Outcrop & Soil
Campus View	CV	40	Rocky Outcrop
Chancellor's Hill	CH	28	Rocky Outcrop
UCI Environmental Hazard Site	EH	38	Rocky Outcrop
Crystal Cove, Corona del Mar	CC	24	Sandy Soil & Grasses

per fruit is 26.2 ($N_{fruits} = 200$, SE = 11.4, $N_{plants} = 60$, Orjuela and Marchant unpublished). It has been suggested that lichens from the genus *Niebla* (Ramalinaceae) serve as a nutrient-rich seed trap for the propagation of *Dudleya* species on sheer rock (Reifner and Bowler 1995). A *Dialictus* (Apidae) species successfully pollinates plants of *D. multicaulis,* but may not be the sole pollinator (Casares personal observation). Our preliminary data indicates that this species can self, but we have not investigated if this results in lower fitness of such progeny.

Any attempt to design a management plan to protect a particular species should be based on an understanding of its genetic structure (Franklin 1980), as well as its demographic characteristics and natural history. Therefore we investigated the level of genetic diversity and gene flow of *D. multicaulis* at two different scales: 1) within and among colonies at the University of California, Irvine. 2) Within and among populations throughout the range of this species. We provide estimated plant densities for each population and we further discuss the implications of these findings for the conservation and protection of extant *D. multicaulis* populations.

MATERIALS AND METHODS

Plant sampling protocol: colony scale. We collected leaf material of individual plants from three areas; 1) the Environmental Hazard (EH) site located on the University of California, Irvine (UCI) main campus, which is about one km from the UCI Ecological Reserve (this population has been isolated from contiguous populations of *D. multicaulis* by roads, parking lots, and construction developments at the University), 2) the UCI Ecological Preserve (UCIEP) which is adjacent to the campus, and 3) Crystal Cove State Park about seven km distant (Table 1). We had previously surveyed the Ecological Preserve and recorded all known *D. multicaulis* populations on a vegetation map and used the natural topography of the area to define discrete colonies; Twin Peaks (TP), Chancellor's Hill (CH), Woehler's Folley (WF), and Campus View (CV). These colonies are mostly on rocky outcrops between twenty-five and 100 meters distant from each other. We collected leaf samples from 24–40 individuals within these colonies during the winters of 1994 and 1995. At each plot we set up a transect and collected leaves from plants that were at least 50 cm apart. From each adult plant we removed one healthy leaf (about 5 cm long) which was transported on ice back to the laboratory to be homogenized using a phosphate grinding buffer (Soltis et al. 1983), and stored at −80°C for subsequent electrophoresis. This sampling protocol imposed no apparent damage to plants.

Plant sampling protocol: regional scale. We collected leaf material from 8 distinct Orange County populations; Laguna Niguel, Orange, El Toro, Ortega, San Clemente, Coastal, Laguna Beach, and UC, Irvine (Table 2, Fig. 1). The populations were separated from the UC Irvine population by 7 to

TABLE 2. LOCATION, REFERENCE CODES USED IN THE PAPER, NUMBER OF INDIVIDUAL PLANTS SAMPLED FROM EACH LOCATION, ESTIMATE OF POPULATION SIZE, SITE DESCRIPTION AND DISTANCE (km) FROM THE UCIEP POPULATIONS.

Population name and location	Reference code	Sample size	Population size estimate	Micro-habitat description	Distance (km) from UCI
Coastal	CO	40	300	Sandy Soil and Grasses	7
Laguna Niguel	LN	40	300	Rocky Outcrop	15
El Toro	ET	40	500	Sandy Soil and Grasses	14
Ortega Highway	OH	40	200	Sandy Soil and Grasses	29
San Clemente	SC	40	1000	Sandy Soil and Grasses	32
Laguna Beach	LB	40	1200	Rocky Outcrop	10
Orange	OC	40	300	Sandy Soil and Grasses	19
UCI Irvine	UC	40	1200	Rocky Outcrop	0

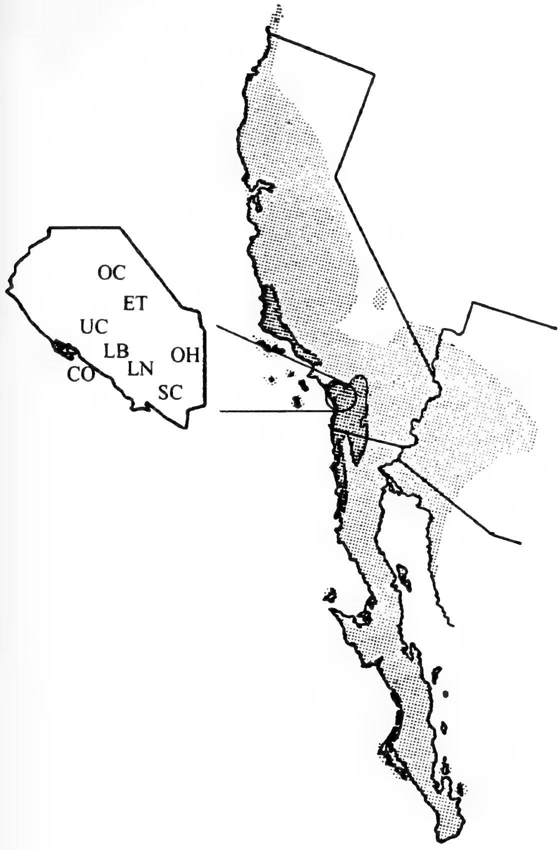

FIG. 1. The shaded area represents the distribution of the *Dudleya* genus. The darker area shows the region of higher species diversity. The inset shows the distribution of Orange County populations of *Dudleya multicaulis* sampled for this study. (Modified from Mulroy 1976).

32 km (Table 2). The main criteria for selecting the populations were their representative distribution of the species in Orange County and population size of about 500–1000 individuals. At each location leaf samples were collected as before.

Electrophoretic analysis. Protein electrophoresis procedures followed Soltis et al. (1983). We prepared leaf material in 0.1 M phosphate grinding buffer (Ranker et al. 1989; Acquaah 1992) and placed the extract in microcentrifuge tubes. Whatmann #3 filter paper strips were soaked in the supernatant and placed into wells in a gel of 11.7% starch concentration. Using the staining protocol of Ranker et al. (1983), and buffers and recipes from Soltis et al. (1983) and Acquaah (1992), we screened the following enzymes: Aldolase (ALD), Fructose-1,6-Diphosphate (FBP), and Menadinone Reductase (MNR), resolved in system 9; Malic Enzyme (ME), Phosphoglucomutase (PGM), Phosphoglucoisomerase (PGI), and Diaphorase (DIA) resolved on system 6; Acid Phosphatase (ACP), Esterase (EST), Glucose-6-phosphate Dehydrogenase (G6P), and Glutamate Oxaloacetate Transaminase (GOT) resolved on system 8; Hexokinase (HXK), Shikimate Dehydrogenase (SKD) and Isocitrate Dehydrogenase (IDH) resolved on system TC-8; and Alcohol Dehydrogenase (ADH), Glyceraldehyde 3-phosphate Dehydrogenase (G3P), 6-phosphogluconate Dehydrogenase (6PG), and Malate Dehydrogenase (MDH) were resolved on a morpholine-citrate pH 6.1 from Wendel and Weeden (1989a). For the regional scale we utilized a digital camera (Alpha Imager 2000, Alpha Innotech Corp.) to obtain a computer image of each gel and photo imaging software (Adobe Photoshop 4.0) to assist in analyzing the banding patterns produced by the allozymes.

We inferred the genetic banding pattern based on the subunit structure and subcellular compartmentalization of the enzymes (Gottlieb 1981). We denoted allozymes alphabetically with the farthest moving allozyme designated as "*a.*"

Statistical analysis. We estimated the following parameters using the computer software BIOSYS-1 Release 1.7 (Swofford and Selander 1989): (1) the percentage of polymorphic loci using the 99% criterion; (2) the mean number of alleles; (3) the observed and expected heterozygosity; (4) the population genetic structure using F statistics (Nei 1977; Wright 1951); (5) Nei's 1972 measures of genetic distance and similarity; (6) deviations from Hardy-Weinberg equilibrium using chi-squared goodness of fit test; and (7) generated a cluster analysis using the unweighted pair group method (UPGMA) based on Nei's (1972) genetic similarity, and the modified Roger's genetic distance. We estimated Nm values for the interpopulation gene flow from the equation $F_{ST} = 1/(1 + 4Nm)$ following Wright (1951). Since we do not have estimates of the effective population number (N) we cannot infer the migration rate. In this study we use Nm values only for comparisons of gene flow between the populations sampled at the local and regional scales. The use of F_{ST} to estimate gene flow is based in several assumptions, including neutrality of alleles and genetic equilibrium, which may not hold in the case of recently fragmented populations such as for *D. multicaulis.* However, it can nevertheless be used as a parameter of comparison between the two scales of analysis used herein. Moreover, we have monitored individual plants for several years and we estimate a lifespan of about 15 years. Thus we feel that the recent human-induced fragmentation has not yet produced significant effects on allele frequencies.

RESULTS

Genetic variation at the colony scale. For the detailed analysis of the UCI population we used more enzymes that for the geographical range. Of the original eighteen enzymes screened we were able to interpret fourteen putative loci from ten en-

TABLE 3. PARAMETERS OF GENETIC VARIATION AND POPULATION GENETIC STRUCTURE AT THE LOCAL AND REGIONAL SCALE. P = proportion polymorphic loci at the 99% criteria; A = mean number of alleles per locus; H = mean expected heterozygosity; F_{ST} = the genetic correlation of individuals among sub-populations; F_{IS} = the genetic correlation of individuals within each sub-population; and F_{IT} = genes within individuals in the entire population.

Scale	P	A	H	F_{IS}	F_{IT}	F_{ST}	N_m
Local	0.238	1.23	0.82	0.391	0.408	0.028	8.7
Regional	0.582	1.73	0.42	0.196	0.367	0.213	0.9

zymes systems: ALD, DIA-1, DIA-2, SKD, IDH, G6P, EST, PGI-1, PGI-2, G3P-1, G3P-2, PGM, 6PG-1, and 6PG-2. Of the fourteen loci examined, four were polymorphic in at least one of the colonies (28.6% at the 99% criterion). DIA-2 and EST were polymorphic in all populations, while PGI-1, PGI-2, G3P-1, G3P-2, PGM, 6PG-1, ALD, SKD, IDH, and G6P were monomorphic in all colonies. The mean number of alleles per locus was 1.3 (SE = 0.1) and the mean genetic diversity (unbiased H_e) was 0.085 (SE = 0.046). The observed mean genetic diversity, when all the colonies were treated as one population, was not significantly different than the expected (H_o = 0.062, SE = 0.036). Two loci deviated significantly from Hardy-Weinberg equilibrium (DIA-1 and EST), and they both showed positive fixation index values suggesting a lack of heterozygosity.

The mean percentage of polymorphic loci for all colonies was 23.8% (SE = 3.7) and the mean number of alleles per locus was 1.23 (SE = 0.1). All colonies had an observed level of heterozygosity less than the expected value and a population mean of 0.082 (SE = 0.046).

We estimated three F-statistic parameters for the analysis of population structure at the UCIEP: F_{ST}, which represents the genetic correlation of individuals among sub-populations, was 0.028; F_{IS}, which shows the genetic correlation of individuals within each sub-population, was 0.391; and F_{IT}, which correlates the genes within individuals in the entire population, which was 0.408 (Table 3). The estimated amount of gene flow (*Nm*) was ~8.7. Because of the low number of polymorphic loci and overall low genetic variation, the coefficients for genetic distance and similarity showed little differentiation.

Genetic variation at the regional scale. At the regional level we had fewer consistently resolvable loci for all populations and could only assay individuals for the following enzymes: PGI, EST, ALD, 6PG, DIA, G3P, FBP, IDH, and MDH. Of all the loci examined 69.2% were polymorphic in at least one population (EST-1, EST-2, 6PG-2, DIA-2, G3P-1, IDH-1, IDH-2, FBP, and MDH). The proportion of polymorphic loci present in each population ranged from 0.4615–0.6154 with a mean of 0.5824, while the number of alleles and expected heterozygosity ranged from 1.69–1.85 and a mean of 1.73 and 0.130–0.208 with a mean of 0.424 respectively (Table 3).

The calculated F statistic were as follow: F_{IS} = 0.196, F_{IT} = 0.367, F_{ST} = 0.213 (Table 3). The amount of gene flow calculated from the F_{ST} value was 0.92. The clade showing the relationships among the populations revealed that the genetic distance between them ranged from 13% to 28% (Fig. 2).

DISCUSSION

Although one of the goals of many conservation programs is to maintain genetic diversity in species that are rare, threatened, and/or have small population sizes (Frankel and Soulé 1981; Simberloff 1988), researchers have usually neglected genetic considerations when generating plans for rare plant conservation (Barrett and Kohn 1991). We argue that information on the ecology, natural history, demographics, and also the genetic structure of rare and threatened plants is important and necessary for conservation plans. Information that includes all these parameters can increase the probability of

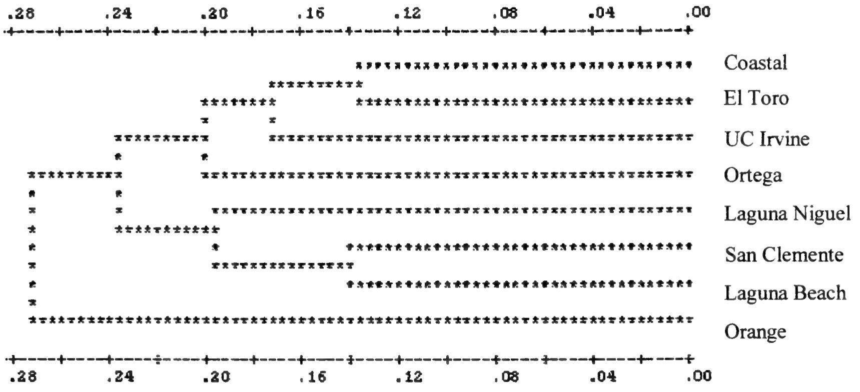

FIG. 2. UPGMA cluster analysis of the *Dudleya multicaulis* populations using modified Rogers' genetic distance.

success for restoration and re-introduction, or even seed-banking strategies.

Local scale analysis. The major component of F_{IT} was F_{IS} indicating that the genetic variation found by this data set was due mainly to differences among individuals, not between colonies (Table 3). The high estimated gene flow (*Nm* = 8.7) which resulted from the limited genetic structure among colonies in the UCI population (F_{ST} = 0.028) is indicative of a large panmictic population. Our results indicate little genetic variation among colonies at UCI and accordingly the UPGMA cluster analysis groups all individual plants at UCI as one population. This includes the colonies found at the UCIEP and the now disjoined EH site on the main campus. Significant deviations from Hardy-Weinberg equilibrium at each variable locus show that 87.5% of them were in heterozygote deficit. We interpret this deficit as a consequence of a high degree of relatedness among individuals possibly resulting from founder effects and subsequent mating among relatives.

Regional scale analysis. One of the objectives of this study was to estimate historical or long term rates of gene flow (*Nm*) between populations sampled based on the genetic structure (F_{ST}) among populations. We estimated *Nm* to be 0.92. According to Wright's island model (Wright 1951). *Nm* values much greater than 1 result in gene flow overcoming the effects of drift, and thus preventing local differentiation. On the other hand, values much less than 1 indicate that drift plays a dominant role. F_{ST} values in the range of 0.15 to 0.25 indicate great genetic differentiation (Wright 1978). Therefore, our data suggest that overall there is only a small amount of gene flow between populations across the range of the species and that there is a high level of intrapopulation genetic variation. More importantly, the data indicate that there is significant genetic differentiation among populations (Fig. 2).

Since gene flow may determine the extent to which local populations function as an independent evolutionary unit, low gene flow among populations may produce functionally unique populations which are evolving under different selection regimes (Slatkin 1994). Since *D. multicaulis* is characterized by geographically isolated populations, across its entire range, each population of *D. multicaulis* may foster unique genotypic characteristics that could have evolved and adapted to microhabitats. Moreover, when species are characterized by small and fragmented populations, genetic drift will dominate population genetic structure and presumably increase a population's vulneribility to extinction (Barrett and Kohn 1991). Concomitant reduction in the genetic variation of a species may hinder its ability to adapt to changes in the environment and augment its susceptibility to disease (Fisher 1930; Hamilton 1982; Beardmore 1983). One of the primary goals of many conservation plans is to retain present genetic variation but, in species that are rare, and possibly endangered, present levels of genetic variation among extant populations may already be lower than historical levels.

Previous studies conducted by the authors indicate that the distribution of *D. multicaulis* appears to be constricting throughout its range. Approximately 30% of the populations known from Orange County in 1981 were extripated by 1988 (Casares and Marchant personal observation) and possibly up to 50% may now be extinct (Webb and Marchant personal observation). An increasing number of species in California are becoming endangered as habitat loss and other threats continue affecting those species that are naturally rare (Skinner and Pavlik 1994; Skinner et al. 1995). Fiedler (1995) suggests that we should focus our conservation efforts on the protection of the rarest of species. Conservation strategies for rare species with populations threatened by anthropogenic activities should include estimations of genetic and demographic characteristics before population fragmentation and habitat conversion significantly affect them.

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SEQUOIADENDRON GIGANTEUM-MIXED CONIFER FOREST STRUCTURE IN 1900–1901 FROM THE SOUTHERN SIERRA NEVADA, CA

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ABSTRACT

Historical data collected from eight mixed conifer and four giant sequoia *Sequoiadendron giganteum* (Lindley) Buchholz (giant sequoia)-mixed conifer plots in the southern Sierra Nevada by George Sudworth in 1900–1901 were analyzed to determine historic forest structure. Although it is not possible to document details of the sampling methodology used by this early forest inventory, the plots were dominated by large trees of several species. Average diameter at breast height (DBH) was 110 cm (43 inches) in the mixed conifer plots and 145 cm (57 inches) in *S. giganteum*-mixed conifer plots for trees greater than 30.5 cm DBH. Results indicate that both shade intolerant and shade tolerant species were abundant. Average tree density was low at 278 trees/ha (111 trees/acre) in mixed conifer plots and 272 trees/ha (109 trees/acre) in *S. giganteum*-mixed conifer plots for trees greater than 30.5 cm DBH. The most common size classes are in the medium to large size classes for all *S. giganteum*-mixed conifer species. This is in contrast to published studies of current stands that have determined small size classes of shade tolerant species are occurring at higher frequencies. Early land uses such as logging and grazing at the turn of the 20th century impacted mixed conifer and *S. giganteum*-mixed conifer forests of the southern Sierra Nevada. Information from this study can assist in the characterization of the "natural range of variability" of these forests which could be used in their restoration and management.

The United States Forest Service (USFS) has changed its philosophy of land management. Ecosystem management has been selected and in California it has been defined as the skillful, integrated use of ecological knowledge at various scales to produce desired resource values, products, services, and conditions in ways that also sustain the diversity and productivity of ecosystems (Manley et al. 1995).

Determining which ecosystem structures are sustainable is a complex problem. The USFS has chosen pre-historical (the period before the influence of European settlement) ecosystem structure as the desired future condition but there is presently very little quantitative information in this area for the diverse ecosystems found in California.

Historical and prehistoric information on the structure of mixed conifer and *S. giganteum*-mixed conifer forests is also limited. Information of this type is useful in characterizing the "natural range of variability" that the ecosystems historically operated in and can assist in specifying desirable future conditions in the restoration and management of these forests. Sources of this type of information include early photographs, personal journals, books, forest stand reconstruction from contemporary plot data, fire histories, and analysis of early forest inventories.

Several investigators have examined past forest structure in the southern Sierra Nevada, including sizes of forest aggregations based on tree diameter (Bonnicksen and Stone 1982) and forest structure as determined from tree age (Stephenson et al. 1991). Historic inventory data primarily from the northern Sierra Nevada and the Transverse Ranges of southern California have also been analyzed (McKelvey and Johnston 1992). Results indicate that shade tolerant species such as *Abies concolor* (Gordon & Glend.) Lindl. and *Calocedrus decurrens* (Torrey) Florin have increased in abundance since fire suppression was initiated early in the 20th century (Parsons and DeBendeetti 1979).

Each type of historic or prehistoric data has advantages and disadvantages. Photographs can give excellent visual representations of past landscapes and can assist in the determination of species composition, relative tree size, and density; but it is not possible to derive quantitative inventory data from them for analysis (Vankat and Major 1978). Books and early journals can give descriptions of the past landscapes, but in most cases, lack quantitative information.

Forest stand reconstruction based on sampling the diameter of current *S. giganteum*-mixed conifer forest trees (Bonnicksen and Stone 1982) can

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give information on past and current forest structure but also has limitations. This type of analysis attempts to recreate past landscapes based on tree aggregations and stand structure comparisons. In many cases, diameter at breast height (DBH) is used as a surrogate for tree age which can be inaccurate (Oliver and Larson, 1995). Problems with analysis and interpretation from forest aggregations studies have been reviewed elsewhere (Stephenson 1987).

Fire history investigations can give information on the past fire regime of an ecosystem if appropriate trees are available for sampling (e.g., old, fire scarred trees that are resistant to decay). These histories can give accurate and precise information of the temporal and spatial distribution of the past fire regime, but use of this information to reconstruct past forest structure is difficult because of our limited understanding of the effects of prehistoric fires.

Prediction of the effects and behavior of past fires is difficult when the fuel complexes and forest structures they operated within are fundamentally different than the present. The spatial distribution of prehistoric fires has not been investigated thoroughly making it impossible to estimate how extensive prehistoric fires were. Limited information on the spatial extent of prehistoric fires is available in the southern Sierra Nevada (Kilgore and Taylor 1979; Swetnam et al. 1990; Swetnam et al. 1992; Caprio and Swetnam 1995).

Early forest inventories can provide quantitative information on historic forest structure, however, the results from the analyses of these data can be biased. In most cases, the methods used in the inventory were not carefully recorded and it is not possible to determine how the samples were selected. Reconstruction from early forest inventory data are also limited because so few inventories were conducted.

The objective of this paper is to analyze mixed conifer and *S. giganteum*-mixed conifer forest inventory data acquired in 1900–1901 from the southern Sierra Nevada to further our understanding of forest conditions and their management at the turn of the 20th century.

STUDY SITE AND METHODS

Forest survey area. The historic data were obtained from the area of the southern Sierra Nevada that is now Sequoia-Kings Canyon National Parks, the southern portion of Sierra National Forest and the northern portion of Sequoia National Forest (Fig. 1).

The mixed conifer forest in this area is composed of *S. giganteum, Pinus lambertiana* Douglas, *Pinus ponderosa* Laws., *A. concolor,* and *C. decurrens.* The inventory also recorded *Abies magnifica* Andr. Murray and *Pinus jeffreyi* Grev. and Balf., but they were relatively rare.

Forest survey. Information on species composition and diameter at breast height (DBH) of the mixed conifer and *S. giganteum*-mixed conifer forests was provided from an early forest inventory (Sudworth 1900a). George B. Sudworth, head of the dendrology project in Washington D.C., collected timber inventory data while employed by the United States Geological Survey (USGS). The purpose of this survey was to inventory the forest reserves of the Sierra Nevada. The original unpublished field notebooks were the source of the inventory data analyzed in this paper.

The field notebooks contain information from many different vegetation types in the southern Sierra Nevada but only plots with *S. giganteum*-mixed conifer or mixed conifer data were used in this analysis. Exact plot locations are not given in the field notebooks but references to rivers, dominant mountains, and landmarks are included. Sudworth may have carried an early USGS map with him during the inventory, but the location of this map is unknown. An incomplete set of photographs associated with Sudworth's forest inventory are also available at the University of California, Berkeley, Bioscience and Natural Resources Library.

Eight mixed conifer plots and four *S. giganteum*-mixed conifer plots were recorded in the 1900–1901 field notebooks (Sudworth 1900a). Locations of plots that were recorded in mixed conifer forests include:

1) Westside of north fork of Kings river, one half way up slope.
2) Bubbs creek near Charlotte creek mouth (tributary Kings river).
3) Near sugar pine mill.
4) One mile west of sugar pine sawmill.
5) Sample area near fish camp. Headwaters of Big creek (tributary Merced river) and near head of Fresno river (Lewis fork).
6) Sample area near fish camp. Headwaters of Big creek (tributary Merced river) and near head of Fresno river (Lewis fork) (similar description used in plot 5).
7) Headwater of Chiquito creek; typical of this area down to the middle fork of the San Jouquin river.
8) Middle east slope, middle fork of San Jouquin river.

Plot locations that were recorded in *S. giganteum*-mixed conifer forests include (only 3 plots had the locations recorded in the field notebooks):

1) North end of giant forest.
2) Near round meadow giant forest.
3) Round meadow giant forest.

Sudworth recorded the species, DBH, and number of 4.9 m (16 ft) logs for each tree greater than 30.5 cm (12 inches) DBH. Plot size was typically 0.1 ha (0.25 acres) with one *S. giganteum*-mixed conifer

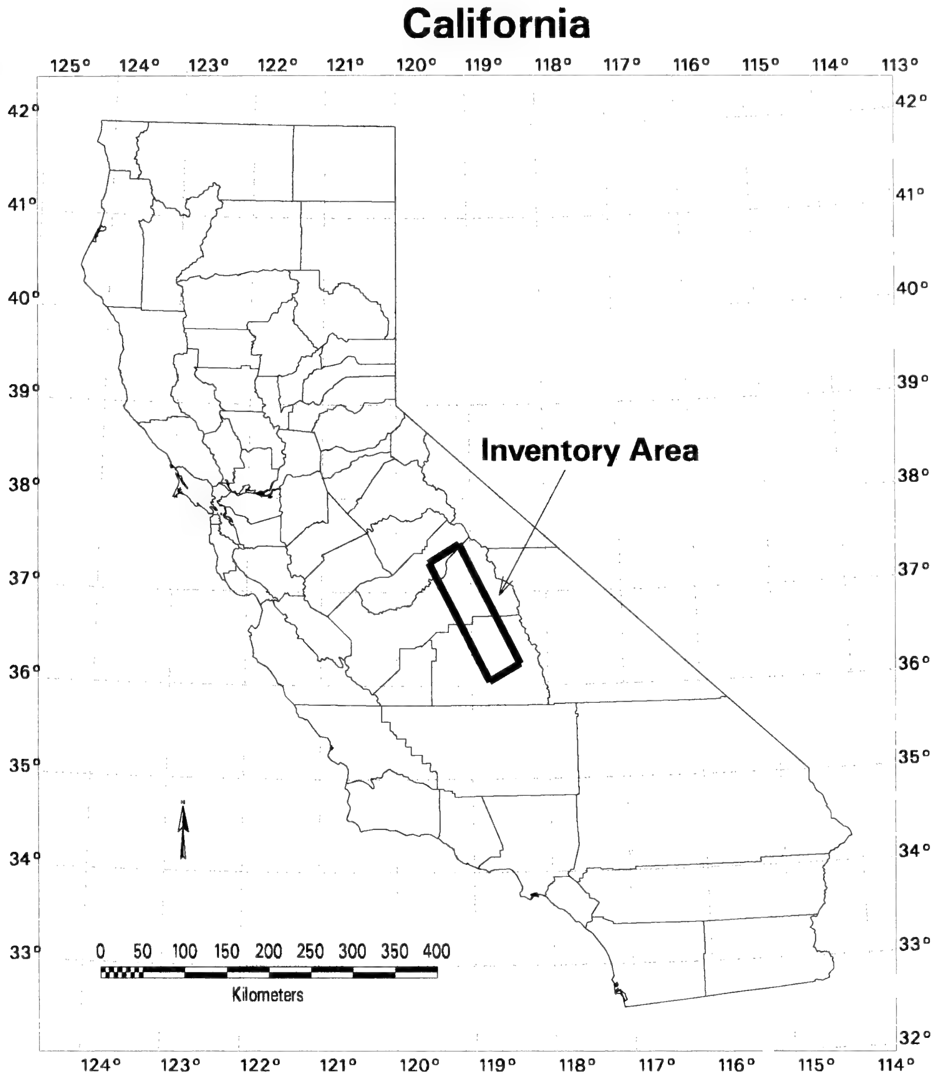

FIG. 1. George Sudworth's Southern Sierra Nevada forest inventory area.

plot of 0.2 ha (0.5 acres) recorded. Only plots with specified sample areas were used in this analysis. Many other much larger plots were recorded in Sudworth's field notebooks in *S. giganteum*-mixed conifer forests, but the area sampled was roughly estimated and were therefore not conducive to quantification.

The following plot values were calculated: average basal area per hectare by species, average number of trees per hectare by species, average quadratic mean diameter by species, average percent plot basal area by species, and average percent plot stocking by species. Histograms of DBH for each species were also produced.

Plot data are summarized and discussed, but a statistical analysis was not performed. Selection of an appropriate analysis method requires information on sampling procedures which are unknown for this early forest inventory.

RESULTS

The smallest tree inventoried in most plots had a DBH of 30.5 cm. No comprehensive inventory data exists for trees below 30.5 cm DBH but the field notebooks had written descriptive observations on regeneration and the impacts from early land uses which are summarized below.

Mixed conifer plots. The eight mixed conifer plots were dominated by large trees of several species. The average quadratic mean diameter at breast height was 110 cm (43 in.) for all trees inventoried. Average tree density was 278 trees/ha or ranged 180–400 tree/ha (111 trees/acre, range 72–160

TABLE 1. SUMMARY OF AVERAGE STAND CALCULATIONS OF GEORGE SUDWORTH'S 8 MIXED CONIFER PLOTS OF THE SOUTHERN SIERRA NEVADA IN 1900–1901. (STANDARD ERROR)

Tree	Basal area (m^2/ha)	Trees/ha	DBH (cm)	Percent basal area	Percent trees/ha
A. concolor	75	113	91	28	40
	(13.5)	(20.7)	(3.5)		
C. decurrens	48	55	114	18	20
	(11.9)	(19.8)	(15.7)		
P. lambertiana	97	53	152	36	19
	(25.3)	(10.7)	(10.5)		
P. ponderosa	33	33	117	12	12
	(16.7)	(15.3)	(21.4)		
P. jeffreyi	14	18	112	5	6
	(8.9)	(10.3)	(20.7)		
A. magnifica	3	8	74	1	3
	(0)	(0)	(0)		

trees/acre) for trees greater than 30.5 cm DBH. Average basal area was 271 m^2/ha (1166 ft^2 /acre). Table 1 summarizes all stand calculations for the mixed conifer plots.

The largest trees in the mixed conifer plots were *P. lambertiana* with an average DBH of 152 cm (60 in.). The largest *P. lambertiana* recorded in the inventory had a DBH of 305 cm (120 in.). *P. lambertiana* made up only 19% of the trees/ha but contributed 36% of the basal area of the plots because of their large size.

Abies concolor was the most common tree found in the plots contributing 41% of the individuals inventoried. *Abies concolor* accounted for 28% of the basal area of the plots, second to *P. lambertiana.* The average DBH of the *A. concolor* trees was the smallest of the species found in the mixed conifer forests.

Pinus ponderosa and *C. decurrens* both have similar average DBH values. *Calocedrus decurrens* was more common contributing 20% of plot stocking compared to 12% for *P. ponderosa. Pinus jeffreyi* also had a similar DBH of 112 cm (44 in.) but was uncommon in the plots contributing 6% of plot stocking. Histograms of DBH by species are given in Figure 2.

The following comments were written by Sudworth in the original field notebooks and include information about regeneration and impacts from early European settlers in the mixed conifer plots (Sudworth 1900a).

September, 1900. Westside of north fork of Kings river, one half way up slope. No reproduction, sheep grazed till 2 years ago and burned over.

September, 1900. Bubbs creek near Charlotte creek mouth (tributary of Kings river), an exceptionally dense stand. No reproduction, complete shade, fire marks.

September, 1900. Near sugar pine mill. Area cut, no reproduction, all timber sound but fire marked.

September, 1900. 1 mile west of sugar pine sawmill. In rich sandy loam, abundant reproduction, 0.5–4 ft of all species. All timber severely fire marked at collar.

October, 1900. Headwater of Chiquito creek; typical of this area down to the middle fork of the San Joaquin river. 60 concolor seedlings 3–6 ft high. No humans, sheep and cattle grazing of long standing.

October, 1901. Heavy shade, no reproduction, humans, 8–10, steep, rocky loam soil, east slope.

Sudworth's notes indicate there were significant human settlement impacts to these ecosystems by the turn of the century. He noted recent evidence of fire in the majority of the plots, and he believed the fires were probably ignited by sheep herders in the area to increase forage production for livestock. In one plot, he noted regeneration of all species was present and in another that only white fir regeneration was found, indicating regeneration was not uniform in the plots. Forests were relatively open during Sudworth's inventory (Fig. 3). Repeat photography has not been attempted because photo points were not permanently marked.

Sequoiadendron giganteum-*mixed conifer plots.* The four *S. giganteum*-mixed conifer plots were dominated by large trees of several species and the average quadratic mean diameter at breast height was 145 cm (57 inches) for all trees inventoried. Omitting *S. giganteum* data, the average DBH of the remaining trees was 111 cm (44 inches) which is similar to the eight mixed conifer plots (110 cm). *Sequoiadendron giganteum* groves were also relatively open during the inventory (Fig. 4).

Average tree density was 272 trees/ha (range 220–290 trees/ha) [109 trees/acre (range 88–116 trees/acre)] for trees greater that 30.5 cm DBH. Average basal area was 2381 m^2/ha (2307 ft^2 /acre). Omitting *S. giganteum* data, average basal area of the remaining trees was 121 m^2/ha (520 ft^2 /acre) which is less than 50% of the average basal area of the eight mixed conifer plots. Table 2 summa-

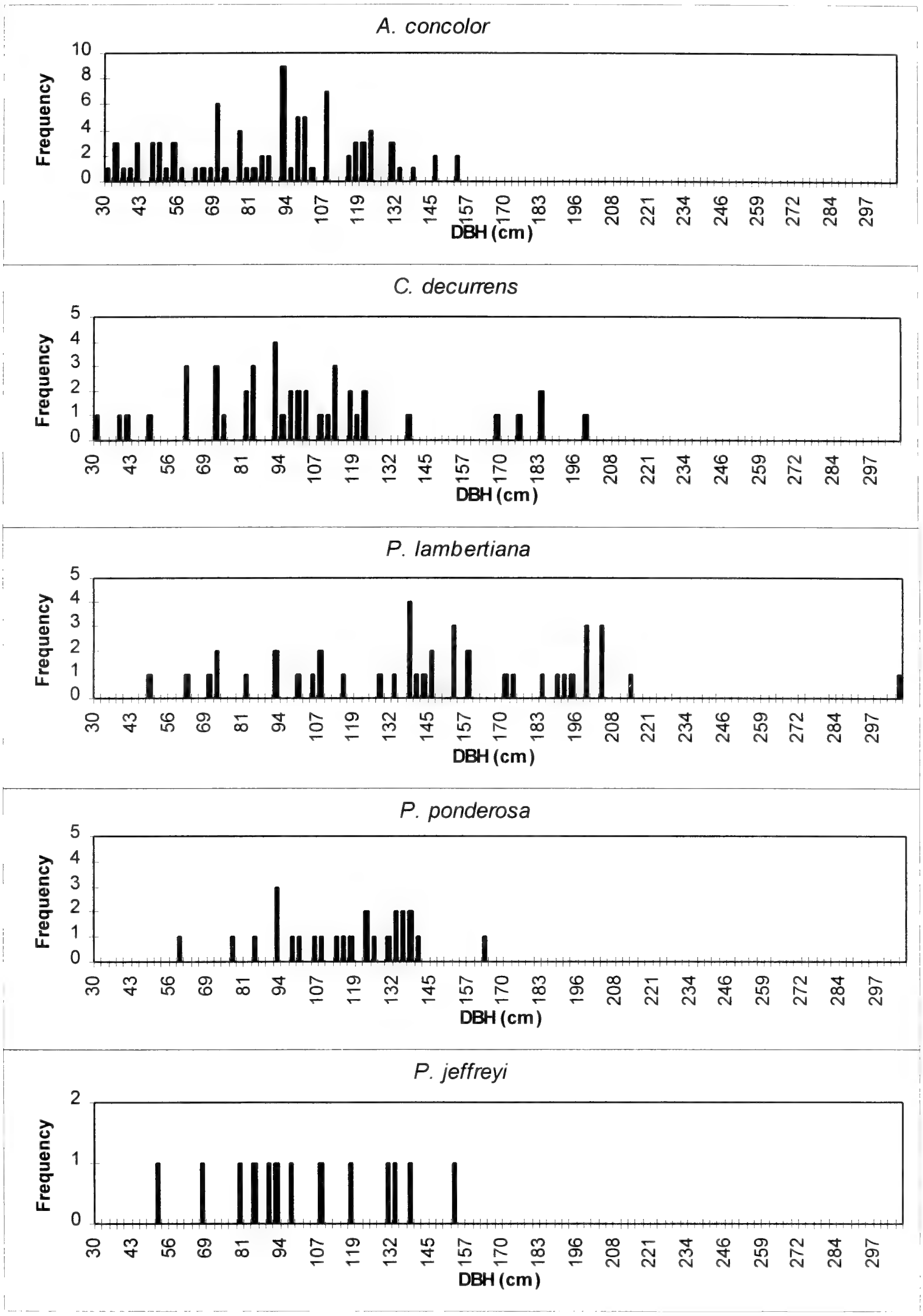

FIG. 2. Histograms of George Sudworth's eight mixed conifer plots of the southern Sierra Nevada in 1900–1901.

rizes all stand calculations for the *S. giganteum*-mixed conifer plots.

Sequoiadendron giganteum were the largest trees in the twelve plots. The largest *S. giganteum* recorded in the inventory had a DBH of 536 cm (211 in.). *S. giganteum* made up only 32% of the trees/ha but contributed 77% of the basal area of the plots because of their large size. Compared to the mixed conifer plots, *P. lambertiana* was a much smaller component in the *S. giganteum*-mixed conifer plots. *Abies magnifica* and *P. jeffreyi* were rare in the *S. giganteum*-mixed conifer

FIG. 3. Tulare county. Interior of forest on bench of Peppermint Meadow, characteristic of east slope of the Kern river at the head of Dry Creek. *Pinus ponderosa, P. jeffreyi, P. lambertiana, Calocedrus decurrens, Abies concolor,* 1901.

plots. Histograms of DBH by species are given in Figure 5.

DISCUSSION

Early land uses have impacted *S. giganteum*-mixed conifer forests of the Sierra Nevada (Stephenson 1996; Elliott-Fisk et al. 1997). Livestock grazing and logging were common in many areas of the Sierra Nevada in the late 1800's (McKelvey and Johnston 1992). In 1900, few *S. giganteum* groves were in government ownership and logging was thought to be a major concern (Perkins 1900). A total of 470 ha (1173 acres) was privately held inside Sequoia and General Grant National Parks (later to become Grant Grove section of Kings Canyon National Park) and the majority of the other groves were in private ownership by people who had every right, and in many cases every intention, to cut them into lumber (Perkins 1900).

Sudworth's field notes recorded that the majority of plots had no regeneration. Regeneration probably occurred pre-historically in these forests with the creation of small canopy gaps. Sudworth verified this by recording that very little reproduction

FIG. 4. Tulare county. Freeman Creek canyon with *S. giganteum* forest on north slope of basin. *Sequoiadendron giganteum* 1.75–2.5 meters in diameter and associated species of *P. ponderosa, P. jeffreyi, P. lambertiana, A. concolor, C. decurrens,* and occasional *A. magnifica,* 1901.

occurred in mixed conifer forests except for occasional patches in open spaces (Sudworth 1900a). Patchy, high intensity fires may have created the openings varying in size between 0.1–0.4 ha. in the *S. giganteum*-mixed conifer forests of the southern Sierra Nevada (Stephenson et al. 1991). Areas that had recently burned with a patchy high intensity fire could have abundant regeneration because duff and surface fuels would have been consumed producing a mineral soil seedbed, and resources such as light and water were available because of reduced competition. Since Sudworth apparently did not sample areas that had recently experienced a localized high intensity fire, regeneration was sparse in the sampled plots. The plots, therefore, cannot be assumed to be an unbiased sample of the forest structure of mixed conifer and *S. giganteum*-mixed conifer forests in 1900–1901.

The plots were dominated by large trees of several species. Both shade intolerant and shade tolerant species were abundant in the plots. Age distributions can vary dramatically in stands, often

TABLE 2. SUMMARY OF AVERAGE STAND CALCULATIONS OF GEORGE SUDWORTH'S 4 *S. GIGANTEUM*-MIXED CONIFER PLOTS OF THE SOUTHERN SIERRA NEVADA IN 1900–1901. (STANDARD ERROR)

Tree	Basal area (m^2/ha)	Trees/ha	DBH (cm)	Percent basal area	Percent trees/ha
A. concolor	84	151	81	16	55
	(29.9)	(44.7)	(5.5)		
P. lambertiana	32	29	127	6	11
	(29.3)	(27.1)	(37.1)		
P. jeffreyi	3	2	114	0.3	1
	(0)	(0)	(0)		
S. giganteum	415	88	282	77	32
	(163.9)	(40.3)	(41.3)		
A. magnifica	3	2	122	0.7	1
	(0)	(0)	(0)		

with no relation to diameter distributions (Oliver and Larson 1995) making it impossible to make conclusions on the age structure of the plots.

The most common size classes are in the medium to large size classes for all mixed conifer and *S. giganteum*-mixed conifer species. This is in contrast to published studies of current stands in Sequoia National Park that have determined small size classes of shade tolerant species (*A. concolor* and *C. decurrens*) are occurring at higher frequencies relative to larger size classes (Parsons and DeBendeetti 1979). If all trees less than 30.5 cm DBH are removed from the Parsons and DeBendeetti study, the remaining smaller shade tolerant size classes still have much higher frequencies than those Sudworth recorded.

Sudworth's notes indicate there were significant land use impacts on these forests by the turn of the 20th century. He noted recent evidence of fire in the majority of the plots, and believed most of the fires were ignited by sheep herders. Sheep herders burned to increase forage production and to remove

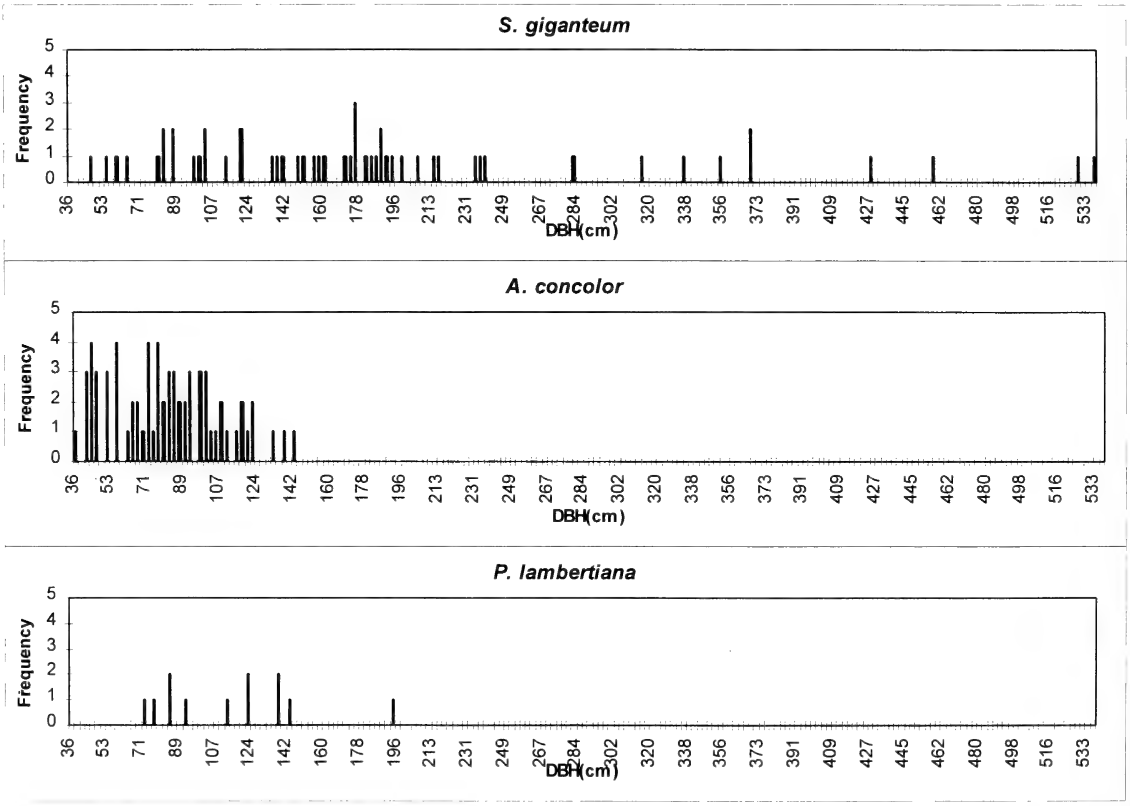

FIG. 5. Histograms of George Sudworth's four *S. giganteum*-mixed conifer plots of the southern Sierra Nevada in 1900–1901.

obstacles from the forest floor which impeded the movement of their livestock (Sudworth 1900b; McKelvey and Johnston 1992).

Sudworth also believed livestock grazing in riparian areas was affecting the hydrology of some *S. giganteum* groves. In a previous inventory, Sudworth believed springs and perennial streams were being effected by excessive sheep browsing which reduced *S. giganteum* regeneration at the "Calaveras" Giant Sequoia grove in the central Sierra Nevada (now part of Calaveras State Park in Calaveras and Tuolumne counties) (Sudworth 1900b).

Some of Sudworth's inventory plots were recently harvested or in the process of being harvested during the survey. He also witnessed the impacts of early logging in *S. giganteum* groves when he camped at the Enterprise Mill in 1901 (Sudworth 1900a). This mill operated two years and harvested many large *S. giganteum* within the present boundaries of Mountain Home Demonstration State Forest, Tulare County.

Most early logging operations in *S. giganteum* groves wasted a great deal of wood. When the trees were felled, the trunk and upper extremities frequently broke into almost useless fragments (Perkins 1900). Additional waste that also occurred at the sawmill resulted in less than half of the standing volume of each harvested *S. giganteum* being converted into wood products (Perkins 1900).

Slash produced by early logging operations in the *S. giganteum*-mixed conifer ecosystems was enormous. It was frequently 2 meters thick and was thought to be a certain source of future fires (Perkins 1900). Early logging operations probably contributed to large, intense wildfires because of increases in surface fuel loads and increased ignitions from field crews.

The absence of trees less than 30.5 cm DBH in Sudworth's plots most likely occurred because they were relatively rare in the sampled plots. The objective of the survey was to assess the timber resources in the Sierra Nevada, and therefore, areas with large dense stands were probably favored. Sudworth sampled areas dominated by large trees and regeneration in these areas would be low since the majority of site resources (light and water) were already being used by the existing mature trees.

The plots sampled by Sudworth represent historic conditions for areas dominated by very large trees in mixed conifer and *S. giganteum*-mixed conifer forests of the southern Sierra Nevada. However, this analysis does not provide information on areas that were dominated by regeneration of trees of smaller size classes. Information from all forest mosaics is needed to completely describe the natural range of variability that occurred in these ecosystems. This analysis gives information only on areas dominated by large trees, and therefore, is incomplete in describing the historic forest structure.

CONCLUSION

Although it is not possible to document the sampling methods used by this early forest inventory, the mixed conifer and *S. giganteum*-mixed conifer plots sampled by George Sudworth in the southern Sierra Nevada were dominated by large trees of several species. Shade intolerant and shade tolerant species were both abundant in the plots. This contrasts to present forests where small shade tolerant species are more common and represents a structural and compositional shift of forest condition.

Mixed conifer forests were impacted by livestock grazing, fire, and logging at the turn of the 20th century. Some *S. giganteum* groves such as the Converse Basin Grove, now part of Sequoia National Forest in Fresno county, were almost completely clear-cut at this time (Elliott-Fisk et al. 1997). Sheep grazing was intense and fires were frequently ignited by sheep herders to increase forage production and to remove obstacles. Thus, even 100 years ago, these forests were subjected to significant European settlement alteration and do not reflect prehistoric conditions.

Trees less than 30.5 cm DBH were probably rare in Sudworth's plots. This analysis does not provide information on areas that were dominated by regeneration or by trees of smaller size classes. Information from all forest mosaics is needed to completely describe the natural range of variability that occurred in these forests.

Early land use decisions have impacted the present mixed conifer and *S. giganteum*-mixed conifer ecosystems of the southern Sierra Nevada. Knowledge of these practices and their ecological effects is useful in interpreting and understanding current forest structure.

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DISTRIBUTION OF WINTER ANNUAL VEGETATION ACROSS ENVIRONMENTAL GRADIENTS WITHIN A MOJAVE DESERT PLAYA

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ABSTRACT

Discovery of distinct bands of winter annual vegetation on dry playas in the Mojave Desert caused us to investigate the relationships between edaphic factors and plant distribution. We established three transects across the band of vegetation in Deadman Dry Lake and measured soil and plant characteristics. *Monolepis nuttalliana,* (Schultes) E. Greene *Oligomeris linifolia,* (M. Vahl) J. F. Macbr. and *Schismus barbatus,* (L.) Thell., all psuedohalophytic winter annuals, were encountered within the band. Soil texture and salinity appeared to be the primary determinants of the presence of vegetation. Distribution of winter annual vegetation within Deadman Playa appeared to be constrained by low soil moisture towards the outer edge, and high soil salinity towards the inner edge of the vegetation band.

Dry lakes and playas have primarily been classified according to soil chemistry, groundwater, surface features, and vegetation (Forshag 1926; Thompson 1929). Motts (1965) described six different playa types according to surface and hydrogeomorphic conditions. Stone (1956) also developed a classification scheme which divides playas into three categories: wet, dry, and mixed. Wet playas, which have groundwater within 10 m of the surface throughout most of the year, are further grouped into either clay-encrusted, salt-encrusted, or crystal body. Dry playas are divided into two main groups: clay pan or lime pan. Mixed playas have an occurrence of both dry and wet features distributed across the playa. Seasonal ponded water is mostly associated with dry playas due to the hard and impenetrable surface while wet playas pond water less frequently because on gentle slopes and hummocky surfaces resulting from ground water influences.

Phreatophytic species, those possessing extremely long roots to reach the water table, are most often associated with wet playas (Hunt 1966). Likewise, bands of halophytic plants, associated with areas with high salt concentrations, and xerophytic shrubs are often found adjacent to dry clay pan playas (Shreve 1925). Halophytic shrubs, which create centimeter high and higher soil mounds, have also been observed on one centimeter high and higher soil mounds located near the edges on dry, clay pan playas (Vasek 1983; Barbour et al. 1990). Similarly, Dahlgren et al. (1997) noted plant communities established on small dust dunes on the playas at Owens Lake, California. Indeed, these dust dunes offer plants an area of decreased salinity and increased rooting zone. Nevertheless, both dry and wet playas within the Mojave Desert are usually devoid of any vegetation (Stone 1956). While delineating the boundaries of several playas during the winter of 1992, we observed the remnants of vegetation in a band along one particular dry clay pan playa (Deadman Dry Lake) (Lichvar and Pringle 1993). During February 1993, winter annual vegetation was again observed growing in a distinct band on Deadman Dry Lake. This playa lacked both soil mounds and phreatophytic species within the band of vegetation. While vegetation literature from other parts of the country and the world described different types of vegetation patterns ranging from playas that are entirely vegetated to dominated by shrub communities along the edges (Wondzell et al. 1990; Smettan et al. 1993; Hoagland and Collins 1997), this particular distribution pattern of vegetation in relation to environmental gradients within playas of the Mojave Desert has not been well described. The objective of this research was to investigate edaphic factors that may influence the distribution of winter annual vegetation within Deadman Dry Lake, San Bernardino County, CA.

MATERIALS AND METHODS

Study site. The study area (Deadman Dry Lake or Playa) is located within the Marine Corps Air-Ground Combat Center (MCAGCC) at 34°18′36″ latitude and 116°08′06″ longitude, 12 miles north of the town of Twentynine Palms, San Bernardino County, CA (Fig. 1). Deadman Playa results from local fault block activity and is located near the bottom of a 56,860 ha watershed (Londquist and Martin 1991). The playa itself is 6300 m long along its greatest axis, has an average width of 960 m, and is approximately 361 ha in size (Lichvar and Pringle 1993). Deadman Playa has an active wash that enters from the northwest and diffuses at the

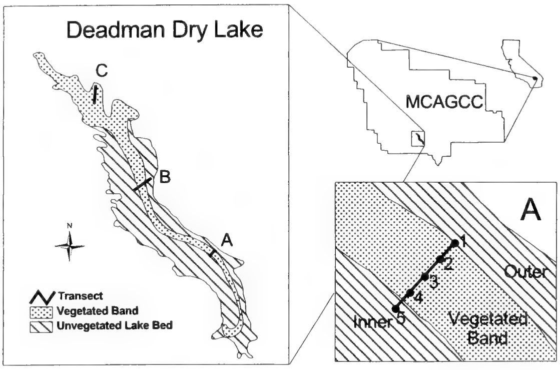

FIG. 1. Location of vegetation band within Deadman Dry Lake, San Bernardino County, CA, and locations of Transects A, B, and C. Also shown is the location of sampling points in relation to the vegetation band of Transect A. Vegetation band is not drawn to scale (MCAGCC = Marine Corps Air–Ground Combat Center).

northern part of the playa where the water remains until it evaporates. Deadman Playa is connected to Mesquite Dry Lake to the east by an inactive dry wash located at the southeast corner. Therefore, there is no evidence that surface water currently flows out of the southeast side of the playa. Thus, the association of plant occurrence with allochothonous soil material from the active wash is uncertain.

The elevation at Deadman Playa is 554 m. Adjacent areas reach elevations of 1062 m and are gently sloping on all sides except to the north, where the playa abuts a bajada. This bajada is dominated by Creosote series (*Larrea tridentata* [DC.] Cov.), while the remaining areas are dominated by the halophytic saltbushes (*Atriplex canescens* [Pursh] Nutt. and *A. polycarpa* [Torrey] S. Watson). The playa itself is unvegetated except for the here-described annual plant community and is classified as a dry, hard, clay-type playa by Stone (1956).

Deadman Playa is located in a region characterized by a warm, hyperarid climate with hot summers and mild winters (Minnich 1991). Freezing temperatures occasionally occur at Deadman Playa during December and January; summer temperatures often exceed 35°C. The temperature between January and March 1993 ranged from 25 to 33°C, while annual precipitation averages from 50 to 150 mm each year. A total of 89 mm of precipitation was received between January and March 1993.

Plant and soil sampling. Three transects were established during March 1993 across the winter annual vegetation band within Deadman Playa, CA (Fig. 1). Transects were located by selecting representative locations within the vegetated band. Transects A and B contained five sampling locations, while Transect C contained three sampling locations. Three replicate 1 m^2 quadrats, spaced 1 m apart, were placed at each sampling location along the three transects (Fig. 1). The length of each transect was 160 m, 280 m, and 200 m, respectively. Density, richness, and percent cover of all species were recorded and surface soil samples (0–10 cm deep) were taken within each quadrat. Plant densities were recorded for each species as the number of individuals per m^2, while species richness was recorded as number of species per m^2. Percent cover values were estimated for each species in each m^2. Voucher specimens were verified by and deposited at UCR. Soil samples collected from each of the three replicate quadrats at all sampling locations were pooled and subsequently analyzed for texture, electrical conductivity (EC), Water Content (WC), Ca^{+2}, Mg^{+2}, Na^{+1}, and Sodium Absorption Ratio (SAR) by the U.S. Department of Agriculture, Natural Resources Conservation Service, National Soil Laboratory, Lincoln, NE (Soil Survey Laboratory Staff 1992). Water content was obtained by analyzing double bagged soil samples measured at 15 bars. In addition, SAR, a derived salinity measure using a sodium paste extract soil solution, was calculated following direct soil analysis. Salinity and sodic status of the soils were classified using criteria established by the Soil Science Society of America (Terminology Committee 1979).

Data analysis. Pearson Product-Moment Correlation coefficients were calculated to assess the relationships among the ten environmental variables and the three vegetation variables (species richness, density, and percent cover). In addition, Canonical Correspondence Analysis (CCA: ter Braak 1988) was used to determine the relationship between the species density values, composition, and environmental variable values. Only identified species were input into this analysis. CCA is a direct gradient analysis technique that relies on the assumption of unimodal relationships between species and environmental variables. To determine the components that explained the greatest proportion of variance in the species data, stepwise forward selection of environmental variables was employed. Finally, Monte Carlo permutation analysis was performed on the first ordination axis to determine its' significance (Manly 1990). Subsequent to CCA, species density data for the 39 sampling locations were classified using TWINSPAN (Hill 1979). TWINSPAN is a polythetic, divisive classification technique which bases groupings on percent similarity. To facilitate interpretation of the dendrogram, species data in the three replicate quadrats in each of the 13 sampling locations were averaged.

RESULTS

Soils parameters. Particle size distribution of soils within Deadman Playa varied within transects (Table 1). Clay and silt content was lower at the outer edge and increased toward the inner edge of the band within each transect, while sand content

TABLE 1. MEANS (±1 SD) FOR CLAY, SILT, SAND, AND COARSE MATERIAL (>2m) CONTENT AND WATER CONTENT OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION WITHIN DEADMAN PLAYA, CA.

Sampling location	% clay	% silt	% sand	% coarse	WC (%)
Transect A					
1	33.6	14.3	52.1	2.33	15.73
	(0.44)	(0.6)	(0.7)	(0.58)	(0.63)
2	40.9	16.4	42.7	0.83	19.40
	(2.0)	(1.1)	(3.1)	(0.29)	(0.94)
3	39.2	15.8	45.3	0.50	19.00
	(0.7)	(0)	(0.4)	(0.9)	(1.02)
4	41.7	17.1	41.2	0.50	20.07
	(3.4)	(1.2)	(4.1)	(0)	(1.05)
5	43.6	16.2	40.2	0	20.37
	(2.7)	(0.7)	(2.8)	(0)	(0.25)
Transect B					
1	17.3	10.2	72.5	25.7	7.90
	(3.50)	(1.10)	(4.50)	(3.78)	(1.50)
2	35.3	14.4	50.2	3.7	16.10
	(0.7)	(1.1)	(0.5)	(2.08)	(0.60)
3	42.5	14.2	43.0	0	18.70
	(2.8)	(1.4)	(4.2)	(0)	(3.4)
4	43.6	14.7	41.0	0	20.60
	(1.6)	(1.3)	(2.4)	(0)	(1.5)
5	50.4	20.9	28.7	0	24.2
	(1.7)	(1.0)	(2.7)	(0)	(1.1)
Transect C					
1	12.6	7.1	80.3	7.3	5.37
	(1.3)	(1.3)	(1.9)	(0.6)	(0.31)
2	28.3	32.0	30.0	0.7	15.23
	(1.9)	(5.2)	(5.3)	(1.0)	(1.82)
3	37.3	32.0	30.7	0.7	19.40
	(3.1)	(3.4)	(5.7)	(0.6)	(0.56)

was higher at the outer edge and decreased toward the inner edge. The percent coarse material, although generally low, was highest at the outer edge of the vegetation band, particularly in Transect B. EC and SAR varied widely within each of the transects (0.7 to 10.2 mmhos cm^{-1} and 8.3 to 67.5, respectively). Both EC and SAR were higher near the outer and inner edge of the vegetation band, and lower in the center of the vegetation band along Transect A (Table 2). In Transect B and C, both EC and SAR were lower along the outer edge and center of the band and increased toward the inner edge.

The salinity and sodic status of soils within Deadman Playa varied between normal (non-saline, non-sodic) and saline-sodic (Table 2). Soils were generally sodic to normal at the center of the vegetation band and saline-sodic at the inner and outer edges of the band. Soil moisture content (WC) in Deadman Playa ranged from 5.4% to 24.2%, and exhibited similar trends in each of the transects. Soil moisture was lowest at the outer edge of the vegetation band and increased towards the inner edge of the band.

Plant parameters. Six winter annual species were encountered within the vegetation band of Deadman Playa. *Monolepis nuttalliana* (Schultes) E. Greene, native species considered as a facultative wetland species (FACW) (Reed 1988) that occurs primarily in alkaline areas with clay soils, was dominant and occurred in each of the three transects. *Oligomeris linifolia* (M. Vahl) J. F. Machr. and *Schismus barbatus* (L.) Thell. also occurred, but less frequently. *Oligomeris linifolia,* a native facultative wetland species (FACW), is normally found in areas ranging from creosote scrub to alkaline sinks, while *S. barbatus,* an upland species (UPL), is an alien grass occurring primarily in dry areas associated with sandy soils. *Nama demissum* A. Gray var. *demissum* was observed on the vegetated band but was not present in any quadrat. Two additional species were observed within the quadrats, but could not be identified because the material was immature.

Subsequent to averaging the replicates within each sampling locations, species richness of winter annuals observed in Deadman Playa was greatest

TABLE 2. MEANS (±1 SD) FOR ELECTRICAL CONDUCTIVITY (EC), SODIUM ABSORBANCE RATIO (SAR), CA:MG RATIO, AND SALINITY TYPE MEASURED AT 15 BARS FROM SOILS OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION WITHIN DEADMAN PLAYA, CA. [a] Terminology Committee (1979).

Sampling location	EC (mmhos/cm)	SAR (mol/mol)	Ca:Mg	Salinity type[a]
Transect A				
1	10.15 (2.91)	54.33 (8.99)	8.18	saline-sodic
2	2.40 (0.88)	24.33 (6.85)	3.32	sodic
3	1.16 (0.87)	21.33 (1.25)	3.35	sodic
4	1.50 (0.14)	20.00 (3.27)	4.35	sodic
5	5.99 (4.69)	37.33 (9.84)	7.68	saline-sodic
Transect B				
1	0.74 (0.092)	12.22 (4.22)	2.09	normal
2	1.10 (0)	16.00 (2.65)	3.33	sodic
3	0.98 (0.33)	14.67 (5.13)	3.35	sodic
4	1.18 (0.40)	18.00 (9.64)	3.35	sodic
5	6.15 (0.08)	67.50 (10.61)	5.00	saline-sodic
Transect C				
1	0.84 (0.19)	12.00 (4.58)	4.00	normal
2	0.95 (0.13)	8.33 (2.08)	4.65	normal
3	2.59 (1.15)	18.93 (8.05)	6.76	sodic

at the outer edge of the vegetation band in Transects A and B and lowest at the inner edge (Table 3). Richness along Transect C was greater than the richness observed along all sampling locations of Transects A and B. Average plant density was lowest at the outer and inner edges and greatest at the center of the vegetation band in Transects A and B. Transect C maintained disproportionately higher density values at all sampling locations. The average percent area covered by vegetation was lowest at the outer and inner edges of the vegetation band in Transects A and B. While, average vegetation cover was low at the inner edge of Transect C along the vegetation band and increased toward the outer edge, percent cover was greater in all zones of Transect C than in Transects A and B.

Correlations among soil and plant parameters. Pearson Product Moment Correlation coefficients suggested species density and percent cover exhibited a negative relationship with the salinity parameters of the soil (Table 4). In addition, species richness was correlated with soil texture and soil moisture parameters.

Canonical Correspondence Analysis (CCA) indicated the overall amount of variation in the species matrix accounted for by the environmental variables was 61.1% on the first axis and 10.5% on the second axis. However, initial CCA results suggested high multicollinearity existed between environmental variables. Indeed, Variable Inflation Factors were greater than the threshold amount of 20 for most variables (ter Braak 1988). A stepwise forward selection of environmental variables reported that two variables (percent clay and EC) accounted for over 90% of the variance explained on the first ordination axis (Fig. 2). In addition, Monte Carlo permutation analysis indicated that the first axis of the ordination was significant when only percent clay and EC were used ($P < 0.01$). The first ordination axis was negatively correlated with both soil texture (percent clay) and salinity parameters (EC) (Table 5). The second ordination axis, while similarly negatively correlated with percent clay was positively correlated with EC.

TWINSPAN classified the 13 pooled sampling locations into three groups which were biologically

TABLE 3. MEANS (± 1 SD) FOR THE PLANT PARAMETERS OF THE THREE POOLED REPLICATE QUADRATS FOR EACH SAMPLING LOCATION ON DEADMAN PLAYA, CA.

Transect distance (m)	Richness (No./m²)	Density (No./m²)	Cover (%)
Transect A			
1	2.3 (0.6)	25.7 (18.5)	3.7 (2.1)
2	1.7 (0.6)	267.3 (76.8)	55.7 (5.5)
3	1.0 (0)	233.3 (28.9)	50.0 (8.7)
4	1.0 (0)	58.3 (16.1)	10.0 (2.0)
5	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Transect B			
1	2.33 (1.53)	75.67 (25.5)	5.67 (2.52)
2	1.00 (0)	283.33 (14.43)	18.33 (2.89)
3	1.67 (0.58)	142.67 (62.53)	43.33 (12.58)
4	1.00 (0)	141.67 (52.04)	27.67 (11.24)
5	0 (0)	0 (0)	0 (0)
Transect C			
1	4.67 (0.58)	301.67 (114.73)	59.67 (9.29)
2	4.33 (1.16)	290.00 (101.89)	82.33 (4.51)
3	3.67 (1.16)	181.00 (36.37)	82.00 (5.57)

meaningful (Fig. 3). Initially, the two innermost sampling locations (sampling location 5) on Transects A and B were excluded from the analysis as they were unvegetated. TWINSPAN then calculated the first major division in the remaining sampling locations based on spatial orientation. The three sampling locations at Transect C were separated from Transects A and B. *Schismus barbatus,* found primarily along Transect C, was an indicator of sandy conditions at those sampling locations. The second major division extracted by TWINSPAN indicates differences in soil texture and salinity. The outer sampling locations were recognized as having either lower WC or higher percent clay values than those seen in the center of the vegetation band. Such conditions may allow *M. nuttalliana* to be more prevalent at the central sampling locations while the upland species, *O. linifolia,* was found exclusively in the outer sampling locations.

DISCUSSION

Distinct horizontal gradients in EC, SAR, and other salinity factors were observed within transects across the vegetation band within Deadman Playa. Vegetation was largely restricted to normal or sodic (non-saline) sites that generally exhibited higher soil moisture. Three saline-sodic sites were observed in this study. Of those three sites, one was sparsely vegetated and the other two were unvegetated.

Among the salinity parameters examined in this study, EC was described by CCA to be the factor related to salinity that explains the greatest amount of variation in the species richness, density and percent cover. EC was negatively correlated with total species density. Plant distribution seems to be restricted to sites with an EC of less than 5 mmhos/cm. Normally, plant distribution decreases toward the center of the playa due to increasing salt concentrations (Egbahl et al. 1989). Indeed, the average EC value on the unvegetated inner sampling locations was 6.07 mmhos cm^{-1}. While one vegetated site did exceed an EC of 5 mmhos cm^{-1}, this site also had a relatively high percent sand content and WC. The occurrence of low EC at the outer edge of Transect B may be related to the extremely high sand content of this sampling location. It is

TABLE 4. PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS AMONG SOIL AND PLANT PARAMETERS OF POOLED REPLICATE QUADRATS WITHIN DEADMAN PLAYA, CA. Levels of significance are indicated by * P = 0.05 and P = 0.001, all other correlations are insignificant (% coarse percent of coarse fragments, EC = Electrical Conductivity, SAR = Sodium Absorbance Ratio, WC = Water Content in Soil, Ca:Mg = ratio of Calcium to Magnesium).

	% clay	% silt	% sand	% coarse	EC	SAR	WC	Ca : Mg	Richness	Density	% cover
% clay	—	0.30	−0.81**	−0.71*	0.35	0.50	0.98**	0.22	−0.76*	−0.41	−0.28
% silt		—	−0.78*	−0.42	0.07	0.02	0.44	0.35	0.24	0.09	0.53
% sand			—	0.72*	−0.25	−0.31	−0.88**	−0.33	0.34	0.18	−0.14
% coarse				—	−0.24	−0.27	−0.73*	−0.40	0.23	−0.06	−0.21
EC					—	0.88**	0.38	0.80**	−0.28	−0.67*	−0.48
SAR						—	0.48	0.57*	−0.49	−0.68*	−0.55*
WC							—	0.27	−0.68*	−0.38	−0.18
Ca : Mg								—	0.27	−0.46	−0.11
Richness									—	0.54*	0.72*
Density										—	0.78*
% cover											—

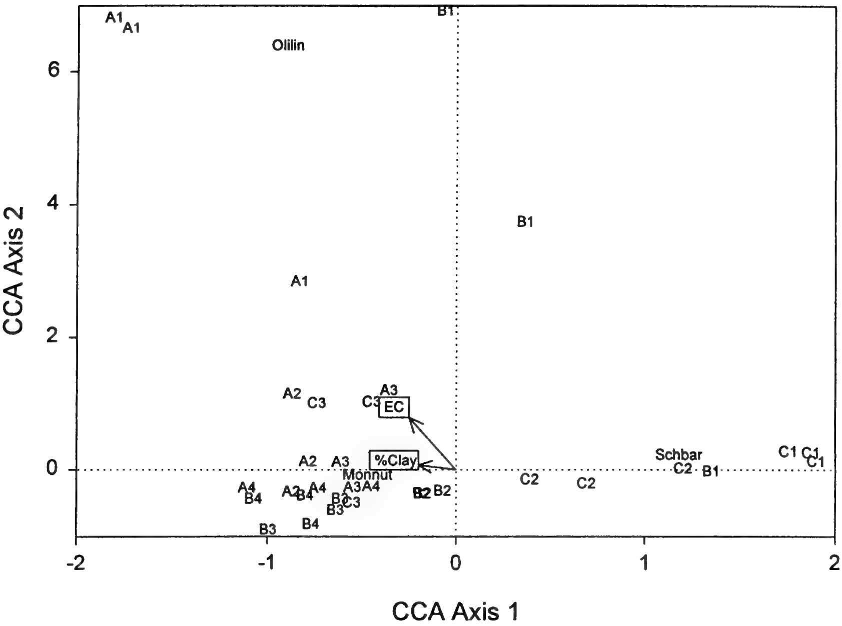

FIG. 2. CCA triplot of samples, species, and environmental variables (extracted via stepwise forward selection). Monnut = *Monolepis nuttalliana,* Olilin = *Oligomeris linifolia* and Schbar = *Schismus barbatus.*

possible that percolation of surface water through the soil profile in the outer edge of Transect B is great enough to prevent the accumulation of salts at the surface. Additional hydrologic and soil porosity studies are needed to quantify the movement of water through the soil profile.

The distribution of winter annual vegetation in Deadman Playa was also constrained by percent clay and soil moisture. Percent clay was extracted by CCA as the environmental variable which explained the most variance in the species data. As one might expect, percent clay was highly correlated with WC (Table 4). Both percent clay and WC were negatively correlated with species richness. *Monolepis nuttalliana* was clearly the most common species in the vegetated sites (>90% relative density), so variation in plant density primarily represents variation in the distribution of *M. nuttalliana.* The relationship of *M. nuttalliana* cover to salinity parameters suggests that this species is a pseudohalophyte (a species present at moist. non-saline sites within larger saline locations) rather than a true halophyte (Waisel 1972).

The xerophytic grass, *Schismus barbatus,* was found primarily on Transect C. Transect C, had lower average values for all salinity parameters than Transects A and B. These relatively normal soils may have allowed *S. barbatus* to outcompete the more halophytic species, *M. nuttalliana* and *O. linifolia* in many sampling locations. Finally, *O. linifolia* was uncommon in most of the sampling locations. However, it was found in four of the six quadrats in the outer sampling locations. Although there are no clear indicators which explain *O. linifolia* association with the outer quadrats, it does appear to be found in areas with relatively high EC and percent sand.

In summary, the winter annual taxa encountered within Deadman Playa during the winter of 1993 appear to be pseudohalophytes distributed largely within a non-saline area within a larger saline location. The distribution of these annual taxa appears to be limited by salinity near the inner edge of the band and low water availability at the outer edge of the band. The vegetation band represents a window of suitable conditions for growth in an otherwise stressful location. It appears that, given sufficient precipitation during the winter, soil conditions are suitable for the germination and establishment of winter annual vegetation within non-saline locations of Deadman Playa.

TABLE 5. INTRA-SET CORRELATIONS OF ALL ENVIRONMENTAL VARIABLES WITH CCA ORDINATION AXES.

Variable	Axis 1	Axis 2
% clay	−0.92	−0.15
% silt	0.04	−0.10
% sand	0.44	0.16
% coarse	0.38	0.39
Electrical Conductivity (EC)	−0.42	0.57
Sodium Absorption Ratio (SAR)	−0.59	0.41
Water Content (WC)	−0.85	−0.16
Species Richness	0.91	0.04
Density	0.53	−0.33
% cover	0.56	−0.22

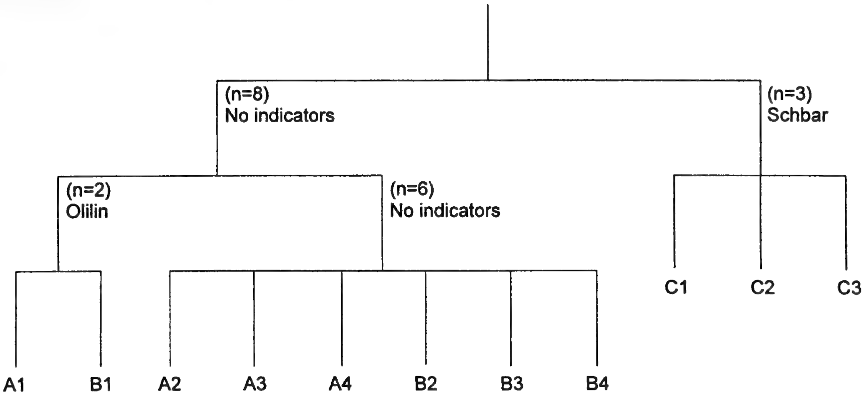

FIG. 3. Results of TWINSPAN analysis of sampling locations expressed as pooled averages of replicate quadrats. Groups distinguished at each level are shown (n = number of sampling locations per group) with indicator species. Olilin = *Oligomeris linifolia* and Schbar = *Schismus barbatus.*

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FLOWERING PHENOLOGY AND SEX EXPRESSION OF *CROTON CALIFORNICUS* (EUPHORBIACEAE) IN COASTAL SAGE SCRUB OF SOUTHERN CALIFORNIA

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ABSTRACT

Croton californicus is reportedly a dioecious plant species. In the present study, monoecious morphs were observed in four populations of southern California. The prevalence of monoecious individuals was moderately low with relative abundance ranging from 2.5–18.0%. Female plants were more numerous than male plants in two of the four populations with male : female sex ratios ranging from 0.76–1.22. Individual plants were monitored monthly for flowering during the 1994 season. Though flowers were present throughout the year, their abundance varied widely. Flowering of male and female plants started to increase in January, with rapid increases in the production of flowers and fruits during April. Peak flowering and fruiting for female plants occurred in April and May respectively, while for male plants peak flowering occurred in May. A small, second peak flowering and fruiting appeared in October followed by a drop with almost no flowers produced during December Monoecious plants had a similar seasonal flowering pattern and were on average simultaneously bisexual for 59.6% of the flowering periods. Monoecious morphs also exhibited various degrees of sex expression from almost total maleness to total femaleness in a bimodal distribution pattern skewed towards maleness. This pattern indicates that *C. californicus* might be dimorphic with phase choices.

Flower lifespan differed with gender. Staminate flowers lasted 4.5 d, whereas pistillate flowers lasted 13.2 d and fruits dehisced at 42.3 d. Pistillate flowers and fruits were significantly greater in biomass than staminate flowers. Male plants were significantly larger than female plants for crown diameter, while monoecious morphs were usually significantly larger than either female or male plants. Female plants exhibited higher floral biomass production and reproductive effort than male plants despite their smaller size. Monoecious plants produced more floral biomass than either female or male plants. Spatial segregation of male and female plants was also observed in one population.

The idea that the sex of an individual of a dioecious plant species is genetically determined and fixed throughout life was prevalent in past literature (Freeman et al. 1980). However, recent studies indicate a significant environmental influence on sex determination and gender modification in "dioecious plants" (Freeman et al. 1980; Freeman et al. 1984; Lloyd and Bawa 1984; Sakai and Weller 1991; McArthur et al. 1992; Wheelwright and Bruneau 1992). Many species described as dioecious, subdioecious, or sequential hermaphrodites contain individuals that are sexually labile or inconstant for sex expression (Freeman et al. 1980; Lloyd and Bawa 1984). Among these are several species listed as having well-differentiated sex chromosomes (Freeman et al. 1980).

Many dioecious species are known to have populations with monoecious or hermaphrodite individuals at low to moderate frequencies (Freeman et al. 1980; Willson 1983; Lloyd and Bawa 1984; Bullock 1985; Sakai and Weller 1991) and there exist many intergrades between the various sexual systems of plants (Willson 1983; Lloyd and Bawa 1984; Bullock 1985; Thomson et al. 1989). The presence of bisexual individuals in diclinous species often indicates the occurrence of sex lability and sex change (Freeman and McArthur 1984; Freeman et al. 1984). Most botanical studies on gender modifications have focused on the proximate causes of modification such as the mechanistic effect of hormones, photoperiod, temperature, and nitrogen levels (Lloyd and Bawa 1984). The adaptive value of sex modifications received little attention until the early 1980's (Freeman et al. 1980; Freeman et al. 1984; Lloyd and Bawa 1984; McArthur et al. 1992; Ramadan et al. 1994) and to date is still not well understood.

Euphorbiaceae exhibit diverse and unusual breeding systems with evidence of considerable gender modification. Bullock (1985) noted variable sex expression in some dioecious species of a tropical deciduous forest in Jalisco, Mexico, particularly in *Jatropha* and *Bernardia* of the Euphorbiaceae. For example, males vary in the tendency to produce single female flowers at the base of the inflorescence. *Croton* is interesting for its diversity at this same locality: monoecy typifies most species, but the ratio of male to female flowers varies widely; two species consist of monoecious and female individuals; and two species are dioecious (Bullock 1985; Tejada and Bullock 1988). Sex expression is determined by a genetic system in two species of the Euphorbiaceae (Shifriss 1956; Dellaporta and Calderon-Urrea 1993). However, some Euphorbiaceae exhibit sex lability due to environmental influence. Pruning, gibberellin, and potassium are known to induce femaleness in a few euphorbs (Heslop-Harrison 1957; Shifriss 1961). Although

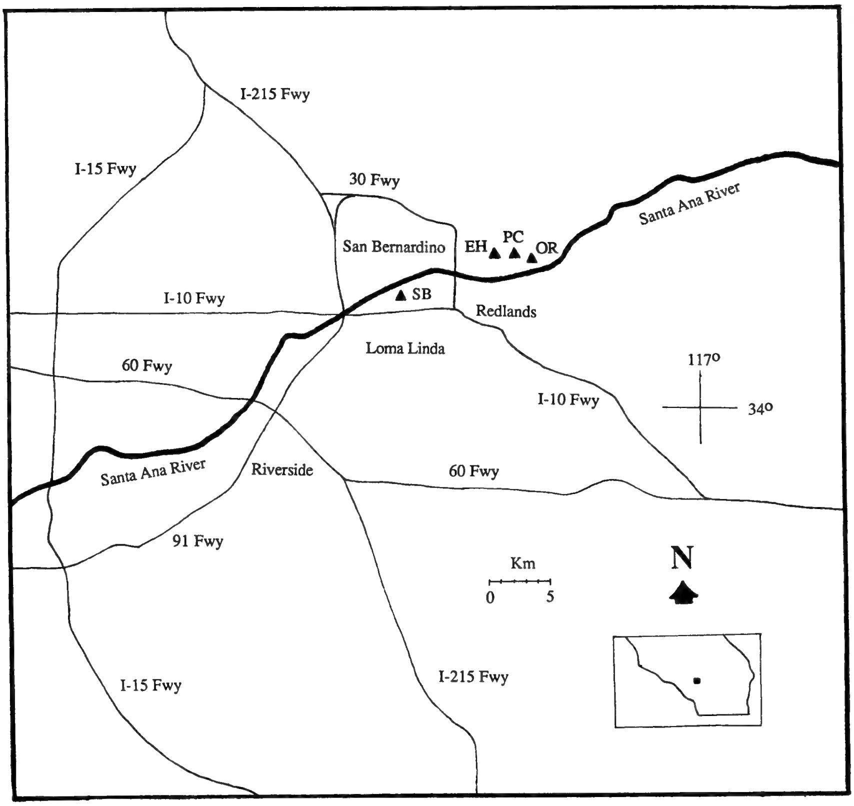

FIG. 1. Map of study area. Study populations of *Croton californicus* are indicated by triangles. OR = Orchard; PC = Plunge Creek; EH = East Highlands; and SB = San Bernardino.

proximate causes have been studied for some euphorbs, little is known on the adaptive significance of gender modification.

Croton californicus Muell. Arg. is reported to be a dioecious plant (Webster 1993). The presence of monoecious morphs in several populations of southern California (Martin 1995a, b) indicates that *C. californicus* is in a diclinous condition other than dioecy proper. Although some authors (Lloyd and Bawa 1984; Schlessman 1986) reject the common practice of separating bisexual individuals of dimorphic populations into a separate class such as monoecious, others have shown the importance of monitoring such morphs in order to understand the adaptive significance of sex lability and sex change (Freeman et al. 1984; McArthur et al. 1992; Ramadan et al. 1994). However, it is critical that quantitative data on gender expression and gender dynamics of monoecious individuals be measured (Schlessman 1986). This study quantifies the monthly flowering and sex expression of male, female, and monoecious plants of *C. californicus* for one season and documents the prevalence, characteristics, and phenotypic gender of monoecious individuals. Data are presented that indicate plants of *C. californicus* change sex and that the species might be "dimorphic with phase choices" (Lloyd and Bawa 1984). Results contribute to a better understanding of diclinous breeding systems and the adaptive significance of gender modification and sex lability.

METHODS

Species and study sites. Croton californicus is a subshrub inhabiting sandy soils, dunes, and washes below 900 m in various plant communities of California, Arizona, and Baja California. The small (ca. 5 mm in diameter; Webster 1993), greenish-white flowers are unisexual (or occasionally morphologically bisexual; see Results), with five sepals and no petals. The pistillate flowers have twice forked styles that resemble the numerous stamens of the staminate flowers. Flowers appear to be visited by small bees and other small generalist insects (Martin unpublished).

Four populations of *C. californicus* were studied in the Santa Ana River floodplain of the Highland and San Bernardino areas of southern California (Fig. 1). The Orchard, Plunge Creek, and East Highlands populations were components of Riversidian coastal sage scrub association 2 (Kirkpatrick and Hutchinson 1977). The San Bernardino population had a unique floodplain association and was previously studied (Martin 1995a). The East Highlands population burned approximately one year prior to the present study (Martin 1995b).

Flowering phenology and sex expression. Monthly measurements of *C. californicus* were performed in the four study populations between January and December 1994. Plot sampling, using 25 m^2 quadrats, was performed to record the flowering and sexual condition for *C. californicus* as well as to determine population density, cover, and frequency. Four to six quadrats were randomly sampled in approximately 1 ha of each study location and all plants were tagged and numbered for monthly monitoring. Plants were monitored at approximately 4 wk intervals (mean time between censuses = 30.4 ± 3.2 d) for the duration of the flowering season. Sexual condition was determined by counting all of the flowers and/or fruits on a plant. During the peak flowering months of April through July, counts were determined by utilizing a 0.25 m^2 quadrat frame that was centered on the crown of each plant. The quadrat was subdivided with string into four 625 cm^2 subquadrats. The northwest subquadrat or quadrant (if crown was larger than the 0.25 m^2 quadrat frame) was counted and multiplied by four to determine an extrapolated flower and fruit count. It was necessary to make extrapolated counts due to some female plants producing more than 500 flowers and fruits and some male plants producing more than 700 flowers. Full floral counts were compared to extrapolated counts and found to be virtually identical. Cover was calculated from plant crown diameters which were measured during January 1994.

Monoecious morphs. Monoecious morphs were determined to be plants that bore both staminate and pistillate flowers and/or fruits simultaneously or temporally during the 1994 season. Extrapolated counts could not usually be made for monoecious individuals due to an uneven spatial expression of sexuality. Plant structure of *C. californicus* was very complex so trying to count the number of male or female stems and branches was practically impossible to do. The number of bisexual racemes (male and female flowers adjacent to each other) and bisexual flowers on monoecious morphs was recorded in order to give some estimate of sexual uniformity or segregation within a plant.

An estimated floral gender (EFG) was used to determine the maleness or femaleness of monoecious morphs (Thomson et al. 1989). This was quantified by the number of male and female flowers produced during the 1994 flowering season calculated from monthly mean floral count data adjusted by the longevity of male and female flowers. The EFG was calculated as the number of pistillate flowers divided by all flowers. Thus, EFG describes phenotypic gender or morphological femaleness (Delesalle 1989) as a continuous variable potentially ranging from 0 (complete maleness) to 1.0 (complete femaleness). The proportion of the year that monoecious morphs simultaneously bore staminate and pistillate flowers and/or fruits was also determined. In order to increase the sample size for monoecious plants, a stratified random sample was tagged outside the quadrats during December 1993 to include in the analysis with quadrat data.

Floral morphology, development, and biomass. Floral morphology and development was measured during May and June 1995 in the East Highlands population. Two staminate flowers on ten different male plants (n = 20) and two pistillate flowers on ten different female plants (n = 20) were tagged in mature budding stages and monitored daily starting 1 May 1995 to determine floral longevity. Stages for male flowers were classified as follows: bud opening, anthesis, stamens withering (appressing), and flower abscission. Stages for female flowers and fruits were classified as follows: bud opening, anthesis, styles withering, small fruit, immature fruit, mature fruit, and abortion or dehiscence. The number of sepals and stamens on male flowers and the number of sepals, style branches, and carpels on female flowers were also counted.

Flower and fruit biomass was measured on 17 April 1995 and 20 April 1995 in the East Highlands and Plunge Creek populations respectively. In each population, ten floral structures were measured on ten different plants (n = 100) each for staminate flowers, pistillate flowers, and fruits to determine a mean biomass for the different floral structures. Floral biomass was measured fresh due to the extreme fragility and small size of flowers. A total fresh and dry floral biomass was also measured to determine the amount of moisture in the fresh floral biomass for a more accurate estimate of floral biomass and reproductive effort. An estimate for yearly mean floral biomass production for male, female, and monoecious plants was calculated from monthly mean flower count, floral longevity (adjusting for sex differences in flower and fruit production and abortion rate), and mean dry floral biomass data.

Climatic data and statistics. Monthly rainfall and mean high temperature data for 1994 was obtained for the San Bernardino area from the Western Regional Climate Center in Reno, Nevada. This information was analyzed with monthly flowering data to observe any relationship between climatic and flowering patterns.

One-way ANOVA followed by Tukey's HSD test was utilized to statistically compare gender differences in floral parts, flower and fruit biomass, and crown diameter. Linear correlation was used to explore the relationship between EFG and plant crown diameter and the relationships of flowering with monthly rainfall and mean high temperature. Chi-square contingency analysis was used to test for spatial segregation and frequency of the *C. californicus* sexual morphs.

Table 1. Relative Abundance (%) for Sexual Morphs of *Croton califorinicus* in Four Populations of Southern California during the 1994 Flowering Season.

Population	Relative abundance						Male : female ratio
	Female		Male		Monoecious		
	n	%	n	%	n	%	
Orchard	15	38.5	17	43.6	7	18.0	1.13
Plunge Creek	38	47.5	35	43.8	7	8.8	0.92
East Highlands	45	55.6	34	42.0	2	2.5	0.76
San Bernardino	36	39.6	44	48.4	11	12.1	1.22
Total =	134	46.1	130	44.7	27	9.3	0.97

RESULTS

Frequency of sexual morphs. Monoecious morphs of *Croton californicus* were present in all four of the study populations (Table 1). Relative abundance of monoecious morphs was moderately low with a total relative abundance of 9.3% and values ranging from 2.5–18.0% for the different populations. Overall, females were more numerous than males. Male : female sex ratios ranged from 0.76–1.22 in the various populations with the total male : female ratio being 0.97. There were no significant differences in the frequency of sexual morphs or male : female sex ratios within or among populations. The Orchard and San Bernardino populations with male dominant sex ratios exhibited considerably higher numbers of monoecious morphs.

Flowering phenology. Flowering of male and female plants started to increase in January, with rapid increases in the production of flowers and fruits during April (Fig. 2). Peak flowering for female plants occurred in April with peak fruiting in May, whereas for male plants peak flowering occurred during May. Both sexes displayed a sharp decline in flowering through August, with fruits exhibiting a similar pattern lagging until September. A small, second peak flowering and fruiting period appeared in October followed by a drop with almost no flowers produced during December. Monoecious plants had a similar seasonal flowering pattern (Fig. 3), but exhibited lower peak flowering periods with a larger discrepancy between the floral sexes at the peak and had more sustained flowering levels through the season. Also, the small, second peak

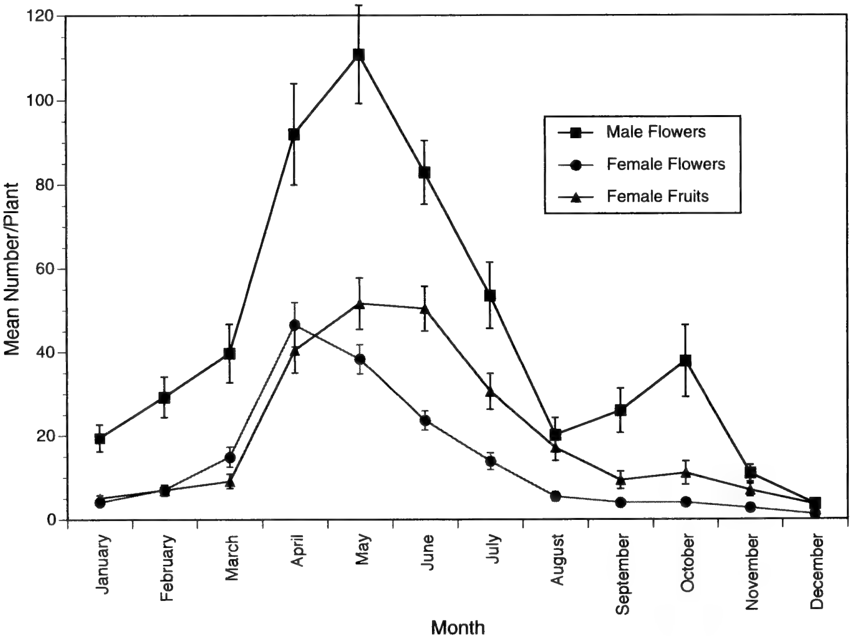

Fig. 2. Mean number of staminate and pistillate flowers and fruits for male and female plants of *Croton californicus* in four populations of southern California during the 1994 flowering season. Plant sample sizes: January, male n = 130, female n = 134; December, male n = 121, female n = 122.

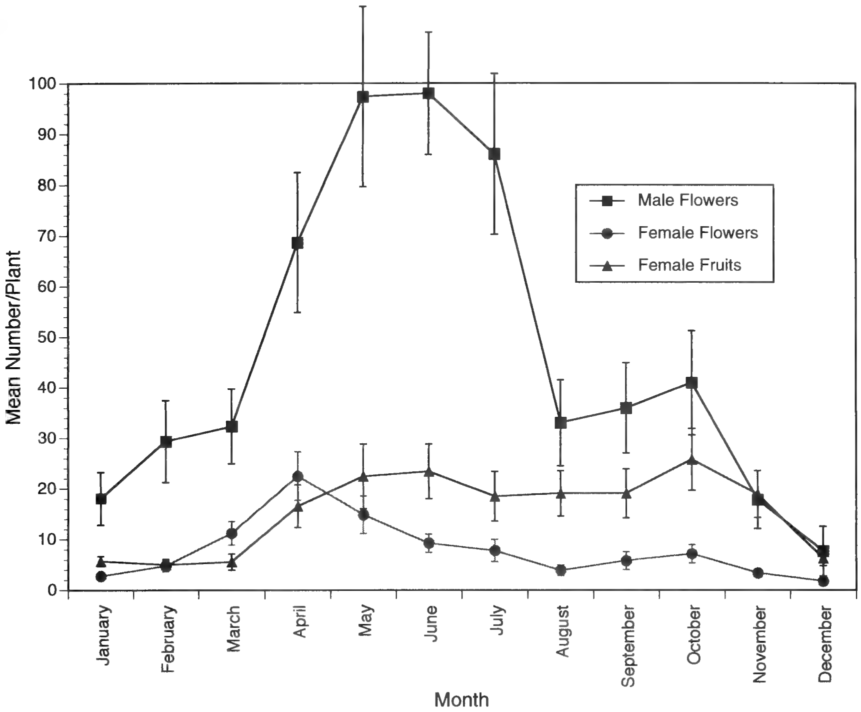

FIG. 3. Mean number of staminate and pistillate flowers and fruits for monoecious plants of *Croton californicus* in four populations of southern California during the 1994 flowering season. Plant sample sizes: January, n = 62; December, n = 59.

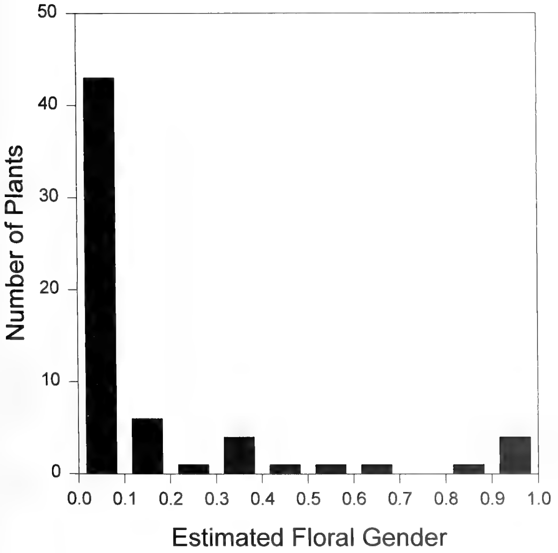

FIG. 4. Frequency distribution of estimated floral gender (EFG) for 62 monoecious plants of *Croton californicus* in four populations of southern California during the 1994 flowering season. EFG describes phenotypic gender or morphological femaleness (Delesalle 1989) as a continuous variable potentially ranging from 0 (complete maleness) to 1.0 (complete femaleness).

flowering and fruiting period was more pronounced for female flowers and fruits.

For both unisexual and monoecious plants, a positive correlation ($r = +0.81$; $P < 0.01$) was observed between monthly rainfall and mean number of floral structures/plant when a two month lag period was applied (each month's flower data was compared to rainfall two months prior). Although no correlation was observed between monthly mean high temperature and mean number of floral structures/plant (regardless of a lag period), monthly rainfall and mean high temperature were negatively correlated (-0.74; $P < 0.01$).

Sex expression of monoecious morphs. Monoecious morphs of *C. californicus* exhibited a wide array of sex expression. Values of EFG ranged from nearly 0.00 to 1.00 in a bimodal distribution for the various ranges of EFG (Fig. 4). This bimodal distribution was skewed towards the male side with 69.4% of monoecious plants having highly male dominant EFGs of <0.10. On the other end of the spectrum 6.5% of monoecious plants exhibited EFGs of >0.90 and only 4.8% of monoecious individuals had EFGs ranging from 0.40–0.80. One monoecious morph from the stratified sample of the San Bernardino population that was monoecious during December 1993 became totally female during the 1994 season. Also, only one monoecious morph temporally separated its bisexuality during

TABLE 2. PERCENT OF FLOWERING PERIOD (%) OBSERVED IN SIMULTANEOUS BISEXUALITY FOR MONOECIOUS PLANTS OF *CROTON CALIFORNICUS* IN FOUR POPULATIONS OF SOUTHERN CALIFORNIA DURING THE 1994 FLOWERING SEASON.

		Length of simultaneous bisexuality		Length of flowering period		Percent of flowering period in bisexuality
Population	n	Range (months)	Mean ± SD (months)	Range (months)	Mean ± SD (months)	(%)
Orchard	7	1–9	5.3 ± 3.4	6–12	9.6 ± 2.5	55.2
Plunge Creek	8	1–12	3.5 ± 4.0	6–12	8.4 ± 2.4	41.7
East Highlands	19	2–12	7.7 ± 3.4	7–12	10.5 ± 1.9	73.3
San Bernardino	28	1–11	4.8 ± 2.8	4–12	8.9 ± 2.3	53.9
Total =	62	1–12	5.6 ± 3.5	4–12	9.4 ± 2.3	59.6

the 1994 season and was also from the San Bernardino population. All other monoecious morphs produced male and female flowers and/or fruits simultaneously. Monoecious plants were simultaneously bisexual for 5.6 mo of a mean flowering period of 9.4 mo reflecting that 59.6% of the flowering period was spent in the bisexual condition (Table 2).

Three main temporal floral progressions were observed in monoecious morphs for flowering periods: 1) simultaneous bisexuality for the whole flowering period; 2) male expression initially followed by simultaneous bisexuality for the majority of the flowering period; and 3) male expression initially followed by simultaneous bisexuality followed by male expression towards the end of the flowering period. These three patterns occurred with a frequency of 25.8%, 17.7%, and 16.1% for the 62 monoecious plants respectively. The other 40.4% of the plants exhibited ten other floral progressions including sex change within the year. Seven plants (11.3%) alternately expressed one sex with simultaneous bisexuality two or more times during the flowering period. Another seven plants (11.3%) expressed one sex initially and eventually expressed the opposite sex exclusively during the middle or end of the flowering period. One of these seven plants changed from female to male without exhibiting a period of simultaneous bisexuality.

The spatial expression of sex on monoecious plants of *C. californicus* was quite variable. Many monoecious morphs predominantly expressed one sex with a minority of branches or portions of the plant expressing the opposite sex while some individuals appeared to have a relatively even or equal dispersion and expression of male and female flowers. At a finer level of sexual segregation, bisexual racemes and bisexual flowers were also observed on 54.8% and 12.9% monoecious plants respectively (Table 3). Bisexual flowers were relatively uncommon and often malformed with fewer stamens and/or abnormally shaped pistils. One unusual monoecious plant in the East Highlands population produced 12 bisexual flowers and 40 bisexual racemes during April 1994.

Floral morphology, development, and biomass. Flowers of *C. californicus* showed variation in number of floral parts. Male and female flowers usually had 5 sepals per flower but some flowers developed only 4; mean number of sepals per staminate or pistillate flower of 4.9 ± 0.3 and 5.0 ± 0.2 respectively. Male flowers averaged 12.2 ± 1.5 stamens per flower with a range of 9–15. Female flowers averaged 3.3 ± 0.5 carpels per flower with a range of 3–4, and averaged 13.4 ± 2.4 style branches per flower with a range of 8–18. The mode for style branches was 12 which is equivalent to four style branches (twice bicleft) per carpel. There was no significant difference between male and female flowers for the number of sepals or for stamens versus style branches.

Staminate flowers matured quickly relative to pistillate flowers (Table 4). Male flower buds reached anthesis in 3 d and abscised in 4–5 d. Female flower buds reached anthesis in 5 d and fruits dehisced by 42 d. Spontaneous abortion of fruits occurred on average at 25 d with an abortion rate of 35%. Stamens of male flowers became appressed to each other after shedding pollen just before abscission.

Staminate and pistillate flowers were very small with fresh biomass of female flowers weighing twice as much as male flowers (Table 5). Female fruit biomass was almost ten times more than female flowers and almost 20 times more than male flowers. Both female flowers and fruits were significantly greater ($P < 0.001$) in biomass than male flowers. Dry floral biomass was 28.0%, 30.3%, and 28.5% of the fresh floral biomass for male flowers, female flowers, and female fruits respectively. These differences are small enough that either fresh or dry floral biomass should approximate reproductive effort equally well.

Plant size and reproductive effort. Male plants of *C. californicus* were found to be larger when com-

TABLE 3. NUMBER OF BISEXUAL RACEMES AND BISEXUAL FLOWERS OBSERVED ON MONOECIOUS PLANTS OF *CROTON CALIFORNICUS* IN FOUR POPULATIONS OF SOUTHERN CALIFORNIA DURING THE 1994 FLOWERING SEASON.

		Bisexual racemes			Bisexual flowers		
Population	n	Number of racemes	Number of plants with racemes	Percent of plants with racemes (%)	Number of flowers	Number of plants with flowers	Percent of plants with flowers (%)
Orchard	7	10	4	57.1	0	0	0.0
Plunge Creek	8	12	5	62.5	1	1	12.5
East Highlands	19	95	15	79.0	28	7	36.5
San Bernardino	28	22	10	35.7	0	0	0.0
Total =	62	139	34	54.8	29	8	12.9

pared to female plants (Table 6). Male crown diameter was larger in all populations and significantly larger ($P < 0.001$) when totals were analyzed for the four populations. Monoecious morphs were significantly larger ($P < 0.001$) than males or females in two populations as well as for totals of the four populations, and then only with stratified random samples, which have much larger mean diameters than the monoecious plants in the quadrats. The mean crown diameters for monoecious plants with male dominant EFGs (<0.50) and female dominant EFGs (>0.50) was 56.6 ± 26.0 cm and 47.7 ± 10.9 cm respectively. These mean crown diameters were not significantly different and crown diameter was not correlated with EFG.

Floral biomass estimates indicate that females allocated more energy into reproduction than males. Female plants produced a mean dry floral biomass of 7.60 $g\cdot plant^{-1}\cdot yr^{-1}$ while males produced 7.11 $g\cdot plant^{-1}\cdot yr^{-1}$. This difference becomes more pronounced when considering that females were smaller plants (60.1% of the mean crown area of male plants) and produced a proportionally higher amount of floral biomass than male plants. Utilizing mean crown area, females produced 90.0 $g\cdot m^{2-1}\cdot yr^{-1}$ while males produced 50.6 $g\cdot m^{2-1}\cdot yr^{-1}$. Monoecious plants produced a mean dry floral biomass of 7.65 $g\cdot plant^{-1}\cdot yr^{-1}$ for male flowers and 4.36 $g\cdot plant^{-1}\cdot yr^{-1}$ for female flowers and fruits for a total mean dry floral biomass of 12.01 $g\cdot plant^{-1}\cdot yr^{-1}$. These plants produced 49.5 $g\cdot m^{2}$ $^{-1}\cdot yr^{-1}$ when utilizing mean crown area to calculate floral biomass production.

Population spatial patterns. Plant densities for *C. californicus* were relatively high in three of the four populations (Table 7). Cover values were also highest in these three populations. However, the cover in the recently burned East Highlands population was considerably lower. Frequency values were all 100% due to the large quadrat size used in sampling.

Spatial segregation of the sexes was observed only in the East Highlands population. There was a significant difference ($P < 0.001$) in the segregation of male and female plants in the four quadrats. Two quadrats were male dominant, with 72.2% of 18 plants and 77.8% of 9 plants being male, whereas the other two quadrats were female dominant, with 93.8% of 16 plants and 63.9% of 36 plants being female. This spatial segregation is even more notable when considering the large quadrat size (25 m^2) used.

DISCUSSION

Flowering phenology. Flowering of *Croton californicus* occurs to some degree throughout the whole calendar year. Male and female plants exhibited similar seasonal patterns with synchronous periods of maximal flowering, as found in other dioecious species (Lloyd and Webb 1977; Bullock

TABLE 4. NUMBER OF DAYS (MEAN ± SD) FOR FLORAL DEVELOPMENT OF STAMINATE AND PISTILLATE FLOWERS ON MALE AND FEMALE PLANTS OF *CROTON CALIFORNICUS.* Values are from the East Highlands population during May 1995. Bud opening refers to the uncurling of stamens or styles in flower buds. Small fruits were <3 mm diameter; immature fruits 3–5 mm diameter; mature fruits >5 mm diameter.

	Floral development			
Floral stage	n	Male (days)	n	Female (days)
Bud opening	20	1.0 ± 0.0	20	2.1 ± 2.0
Anthesis	20	2.0 ± 0.0	20	5.0 ± 2.8
Stamen or style withering	20	3.0 ± 0.8	20	8.1 ± 2.8
Small fruit	—	—	20	13.2 ± 1.6
Immature fruit	—	—	18	18.6 ± 1.1
Mature fruit	—	—	13	22.4 ± 2.4
Abortion	—	—	7	24.6 ± 4.3
Abscission or dehiscence	20	4.5 ± 0.9	13	42.3 ± 3.1

and Bawa 1981; Armstrong and Irvine 1989; Carr 1991; Aronne et al. 1993). The correlation between rainfall and flowering indicates that flowering is primarily related to soil moisture. Flowering patterns for monoecious plants were very similar to male and female plants. The larger discrepancies between male and female flower production reflects the higher number of monoecious morphs with male dominant EFGs. The more sustained flowering patterns appeared related to the larger plant size of monoecious individuals compared to male and female plants. Larger plants possess very deep taproots (Martin unpublished) which allow monoecious plants to access moisture better and longer during the hot, dry summer months.

Sex expression. Over 90% of *C. californicus* plants were constant in sex expression as male or female plants during the 1994 flowering season. The frequency of monoecious morphs observed in this study was considerable in some populations (18%) and many times higher than previously reported (Martin 1995a, b). This discrepancy is due to previous study sampling performed only once during a flowering season versus the 12 monthly samples measured in this study. Not all monoecious plants are simultaneously bisexual at any given time of the year. The one monoecious plant that changed sex between the 1993–1994 flowering season and the 14 others that changed sex during the 1994 flowering season indicate that many monoecious plants and possibly some male and female plants are sexually labile and capable of sex change. Additional sex changes have been observed in *C. californicus* to support this hypothesis (Martin unpublished).

Although monoecious plants reflect a complete array of sex expression with various degrees of maleness and femaleness, the bimodal distribution pattern for EFGs appears to indicate that *C. californicus* exhibits some stability to be either male or female. Bimodal gender distributions are indicative of plant species that are either diphasic or dimorphic with phase choices (Lloyd and Bawa 1984). However, one could interpret this bimodality as dimorphism with male and female inconstancy exhibiting long tails of gender adjustment that merge into one another (Lloyd and Bawa 1984). The skew towards maleness in this bimodal distribution may reflect that male plants more often than female plants become monoecious or spend a longer period of time with a male dominant EFG if plants of *C. californicus* are changing sex. Similar bimodal distribution patterns for EFGs or phenotypic genders have been observed in sex changing or sex labile plant species (Condon and Gilbert 1988; Delesalle 1989; Allison 1991).

TABLE 5. FLORAL BIOMASS (MEAN ± SD) FOR STAMINATE AND PISTILLATE FLOWERS ON MALE AND FEMALE PLANTS OF *CROTON CALIFORNICUS.* Values are from two populations during April 1995. All flowers and fruits were weighed fresh. Sample sizes are numbers in parentheses (n). All values differed significantly (P < 0.001) from ANOVA comparing different floral conditions.

	Floral biomass (g)		
Population	Male flower	Female flower	Female fruit
Plunge Creek	0.008 ± 0.002 (100)	0.013 ± 0.003 (100)	0.125 ± 0.023 (100)
East Highlands	0.007 ± 0.001 (100)	0.014 ± 0.004 (100)	0.147 ± 0.027 (100)
Total	0.007 ± 0.002 (200)	0.014 ± 0.004 (200)	0.136 ± 0.027 (200)

TABLE 6. CROWN DIAMETERS (MEAN ± SD) FOR SEXUAL MORPHS OF *CROTON CALIFORNICUS* IN FOUR POPULATIONS OF SOUTHERN CALIFORNIA. Sample sizes are numbers in parentheses (n). K = number of 25 m^2 quadrats measured. a = monoecious morphs in quadrats. b = monoecious morphs in quadrats and from stratified random sample. F = female, M = male, Mon = monoecious^b. Underlining between sexual morphs for Tukey's pairwise comparisons designates nonsignificant differences.

Population	K	Crown diameter (cm) Female	Male	Monoecious^a	Monoecious^b	P	Tukey's pairwise comparisons
Orchard	6	25.0 ± 11.7 (15)	30.0 ± 19.9 (17)	40.6 ± 21.0 (7)	— —	0.16	F M Mon
Plunge Creek	4	38.1 ± 15.9 (38)	50.7 ± 23.3 (35)	42.1 ± 22.5 (7)	45.1 ± 22.5 (8)	<0.05	F Mon M
East Highlands	4	29.7 ± 17.5 (45)	38.2 ± 23.4 (34)	45.5 ± 29.0 (2)	57.4 ± 15.9 (19)	<0.001	F M Mon
San Bernardino	4	34.2 ± 16.4 (36)	43.5 ± 21.8 (44)	37.3 ± 14.8 (11)	61.0 ± 29.7 (28)	<0.001	F M Mon
Total	18	32.8 ± 16.6 (134)	42.3 ± 23.1 (130)	40.0 ± 18.5 (27)	55.6 ± 24.9 (62)	<0.001	F M Mon

TABLE 7. DENSITY, COVER, AND FREQUENCY OF *CROTON CALIFORNICUS* IN FOUR POPULATIONS OF SOUTHERN CALIFORNIA. Cover was calculated from plant crown diameters. K = number of 25 m^2 quadrats sampled.

Population	K	Density (no./ha)	Cover (%)	Frequency (%)
Orchard	6	2600	13	100.0
Plunge Creek	4	8000	14.8	100.0
East Highlands	4	8100	9.9	100.0
San Bernardino	4	9900	14.5	100.0
Total =	18	6644	9.5	100.0

When a plant is monoecious, its bisexual expression is observed for a majority (59.6%) of the flowering period and 25.8% of the plants exhibited simultaneous bisexuality for the whole period. This indicates the possibility of geitonogamous self-fertilization if *C. californicus* is self-compatible. *Croton californicus* exhibited bisexuality at a local level within an individual with a majority of monoecious individuals expressing bisexual racemes and very few individuals expressing bisexual flowers. Bisexual flowers were often malformed and may not be functional.

Sex characters. Staminate flowers of *C. californicus* were morphologically similar to the pistillate flowers. They were also short-lived and more numerous compared to the pistillate flowers. Similar floral characteristics have been observed in a monoecious species of the Euphorbiaceae (Bawa et al. 1982).

Size appears to be a secondary sex character of *C. californicus* in which males are larger than females, as has been previously reported (Martin 1995a, b). Most secondary sex characters of plants are subtle and usually are expressed in terms of growth, resource allocation, and timing or longevity (Lloyd and Webb 1977; Richards 1986). Energy expenditure into vegetative growth per plant structure may likely have been comparable for male and female plants since there is no significant difference in leaf size (Martin 1995a) and overall leaf density appeared similar.

Estimates of floral biomass production for the year may reflect greater reproductive effort for females when compared to males. The smaller female plant size may be a result of this higher expenditure of energy for reproduction (Lloyd and Webb 1977; Shea et al. 1993; Allen and Antos 1993; Cipollini et al. 1994). Higher reproductive effort of females has been observed in many studies (Wallace and Rundel 1979; Allen and Antos 1993; Armstrong and Irvine 1989; Dawson et al. 1990; Vasiliauskas and Aarssen 1992; Shea et al. 1993) which often results in a shorter lifespan or higher mortality rate for females (Lloyd and Webb 1977; Allen and Antos 1993; Cipollini et al. 1994). Although not significantly different, more females than males died in the present study.

Monoecious plants were larger than male and female plants with 1.78 and 2.88 times more mean crown area respectively. Understandably, these plants have the potential of producing more floral biomass. Estimates of total mean dry floral biomass indicate that monoecious morphs produce 1.69 times and 1.58 times more floral biomass than male and female plants respectively. It is also interesting to note that monoecious individuals also produce 7.6% more male floral biomass than male plants and only 57% of the female floral biomass of female plants. This 1.76 male : female floral sex ratio in part reflects the higher proportion of male dominant EFGs. It may also reflect that male plants become monoecious more often than female plants.

Population spatial patterns. Density and cover data for populations of *C. californicus* were considerably higher than previously reported (Zembal and Kramer 1984; Martin 1995a, b) in all populations except Orchard. Total density and cover were also higher. Female biased sex ratios, as observed in this study and previously (Martin 1995a, b), are rarer in nature than male biased sex ratios (Willson 1983; Richards 1986). The sex ratio in plant populations may not be equal due to microhabitat segregation by the different sexes (Handel 1983; Waser 1984; Bierzychudek and Eckhart 1988; Dawson and Bliss 1989; Sakai and Weller 1991; Shea et al. 1993). Gross spatial segregation of the sexes was observed in the East Highlands population. However, environmental factors (e.g., soil moisture, soil fertility, etc.) were not measured in this study. It should be noted that this population was a young, fire-disturbed population. Although the overall sex ratio observed in this study was female dominant, the high number of male dominant monoecious plants would functionally create an overall male dominant sex ratio of 1.14. In most subdioecious species, one sex (male or female) is relatively constant in sex expression while the opposite sex is labile (McArthur and Freeman 1982; Freeman and McArthur 1984). The high proportion of male dominant monoecious individuals observed in this study may indicate that males of *C. californicus* are the more labile sex.

Dimorphism with phase choices versus diphasy. Dimorphic species with phase choices contain two genetic morphs that are predisposed but not irrevocably committed toward male and female modes, respectively, and in certain conditions are induced to switch to the other mode (Lloyd and Bawa 1984). The two morphs switch at different thresholds of cueing factors so the sex ratio varies according to conditions. It is quite possible that *C. californicus* is a dimorphic species with phase choices. There are several observations that support this hypothesis. First, sex change has been observed in *C. californicus* within and between flowering seasons. Second, the frequency of monoecious morphs was relatively high (up to 18%), considering the data represents one season only. Studies conducted over several seasons typically reveal higher numbers of labile or monoecious individuals (McArthur and Freeman 1982). Third, sex ratios varied from 0.76–1.22 among populations suggesting that sex ratios are not stable and may be changing with phase choices. Also, the San Bernardino population sex ratio in 1991 was 0.78 (female dominant; Martin 1995a, and in 1994 was 1.22 (male dominant). When monoecious morphs are added into "male" or "female" categories the sex ratio for San Bernardino becomes 1.46. Fourth, monoecious EFGs exhibited bimodal gender distribution. The skew towards maleness might be explained by a lower threshold value for phase choice in males than for females (Lloyd and Bawa 1984).

Diphasy seems unlikely in *C. californicus* for two reasons. First, it appears that there are two genetic morphs (male and female) which would indicate dimorphism with phase choices. Diphasic species contain individuals belonging to one genetic class but choose their sexual mode in a given season according to circumstances (Lloyd and Bawa 1984). Second, small, young sapling plants have been observed to be male or female in approximately equal frequency and the mean plant size for females of all ages is smaller than for males. Most diphasic species choose male expression early in life and become female as they increase in size (Lloyd and Bawa 1984). Further studies are being conducted to follow *C. californicus* through several seasons to conclusively determine the breeding system.

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LIMACINIASETA GEN. NOV. A CALIFORNIA SOOTY MOLD

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Abstract

Limaciniaseta californica is described as a sexually monomorphic species, developing on living plant surfaces. The distinguishing characters are dark cell-wall pigmentation, a stalked and setose ascocarp, a centrum with periphysoids, and an extenditunicate ascus that produces pigmented, traversely-septate ascospores.

Foliicolous ascomycete species adapted to the utilization of insect mediated plant exudates have been noted on the surface of living California plants by Millspaugh and Nuttal (1923), Miller and Bonar (1941), Farr et al. (1989) and Reynolds (1989c). These fungi have a dark, melanoid pigment in the cell walls of ascocarps and hyphae, and often form a mycelial mat of varying thickness on the living surfaces of leaves and nearby stems. A new species has been observed from among the foliicolous fungal assemblages associated with *Baccharis pilularis* D. C. in California.

Materials and Methods

Observations were made from materials collected in California since 1983. Representative collections have been preserved as curated specimens in Herbarium LAM. Light microscopic observations were made with a Zeiss light microscope and a Nikon compound microscope utilizing squash mounts and hand-cut sections of whole ascocarps. Scanning electron micrographs were made with a Cambridge Electron Microscope at the University of Southern California Center for Electron Microscopy.

TAXONOMY

Limaciniaseta D. R. Reynolds, gen. nov.

Mycelium in superficiebus plantarum vivarum. Hyphae ramosae, septatae, partietibus profunde pigmentiferis. Ascocarpus profunde pigmentifer, stipitatus, globosus et ostiolatus. Setis in supero hemisphaero. Hyalnis periphysoidibus apice loculi ascocarpi. Ascus extenditunicatus. Ascosporae brunneae, transseptatae.

The mycelium is superficial on living plant surfaces. The hyphae are branched, septate and darkly pigmented. The ascocarp is pigmented, stipitate, globose and ostiolate. The setae are formed in the upper hemisphere of the ascocarp. Hyaline periphysoids occur in the ascus locule. The ascus is an extendetunicate type, with brown transseptate ascospores.

Etymology. The name of the genus refers to a setose ascocarp similar to that of *Limacinia* Neger (Reynolds 1985).

The mycelium is formed on living plant surfaces. The hyphae are branched, septate, with walls that are darkly pigmented. The ascocarp is darkly pigmented, short-stalked, globose, and ostiolate; several setae form on its upper hemisphere. Multicellular, hyaline periphysoids are present in the ascocarp centrum originating from the inner surface at the apex of the ascal locule. The asci are arranged in a basal hymenium. The ascus wall is extenditunicate. The eight, passively released ascospores are darkly pigmented and transversely septate at maturity.

Limaciniaseta californica D. R. Reynolds, sp. nov. (Figs. 1–2)

Ascocarpus usque ad 120 μm diametero, stipitatus, stipe ad 40 μm alto, subiculo, subtento hypharum profunde pigmentarum, plerumque oriundarum a aliquot distinctis speciebus. Setae acuminatae, Ostiolum setis profunde pigmentiferis, septatis, 162 ad 180 μm longis, hyalinis. Periphysoidibus multiseptatis, apice loculi ascocarpi, 2 × 25 μm. Hymenium maturione centrifugo intraliquidam hygroscopicam matricem. Maturus ascus ad 45 μm longus. Ascosporae octavae, fusiforme, triseptatae, profunde brunneae, 13–22 × 6–9 μm.

Etymology. The species name indicates an occurrence in California. The ascocarp has a diameter up to 120 μm. Its stipe measures up to 40 μm in height, formed from darkly pigmented subtending hyphae. The darkly pigmented setae are acuminate, 12–85 × 5–6 μm and surround an ostiole. The apical periphysoids are multiseptate and measure 2 × 25 μm. The mature hymenium forms centrifically in a hygroscopic matrix. The mature ascus measures up to 45 μm in length and the 8, fusiform ascospores are three-septate and brown, measuring 13–22 × 6–9 μm.

Limaciniaseta californica is sexually monomor-

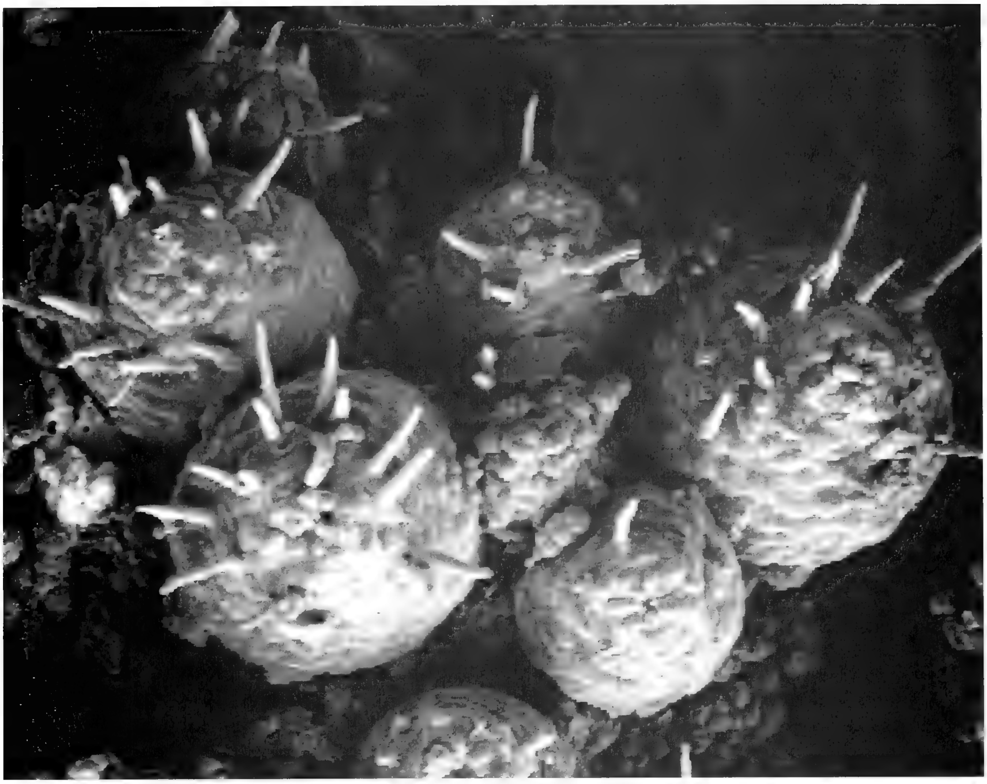

FIG. 1. *Lamaciniaseta californica* Apical view of setose ascocarps formed on a mycelial subiculum. SEM. Magnification = 300×.

phic because it is known to exhibit only a sexual reproductive stage. The term "teleomorph" is understood to apply only to the sexual stage in a pleomorphic species, in the sense of Reynolds (1993), and should be used in opposition to an asexual or "anamorph" reproduction stage occurring in the same life cycle. There is no evidence of pleomorphy in *L. californica.* Thus, the species is termed monomorphic.

Holotype. USA, California, Santa Barbara County, Highway 101, south of El Capitan State Park, on living surfaces of *Baccharis pilularis* DC, 17 April 1996, Don R. Reynolds and D. Minor, DRR136496 (holotype), on living surfaces of *Baccharis pilularis.*

Additional specimens examined. USA, California, Contra Costa County, north end of Wildcat Canyon, 21 April 1931, L. Bonar, UC 966391, det. *Morfea hendrickxii* (Hansford) Batista & Ciferri. USA, California, Santa Barbara County, Highway 101, south of Santa Maria, on living surfaces of *Baccharis pilularis,* 17 April 1996, Don R. Reynolds and D. Minor. USA, California, Santa Barbara County, 17 April 1996, Don R. Reynolds and D. Minor, DRR136564. USA, California, Contra Costa State Park, Tilden State Park, on living surfaces of *B. pilularis,* 31 July 1983, Don R. Reynolds, DRR136024, USA, Oregon, Cannon Beach, on living surfaces of *Umbellifera californica,* 31 October 1935, J. P. Thom (=Oregon State University 9280), BPI, det. *Capnodium tuba* Cooke & Harkness, (=IMUR 5247, det. *Morfea tuba* (Cooke & Harkness) Batista & Ciferri). Australia, Queensland, Tambourine Mountain, May 1934, A. Burge, BPI (det. *Capnodium fuliginoides* Rehm), type of *Morfea helianthemi* (Maire) Batista & Ciferri var. *major.* USA, Florida, Indian Town, 11 December 1919, C. V. Piper, IMUR 5520, det. *Capnodium tuba* (Cooke & Harkness) Ciferri & Batista. Costa Rica, San Jose, La Palma, P. C. Stanley 38094 (Plants of Costa Rica) BPI, type of *Morfea miconia* Batista & Ciferri—This is *Trichomerium grandisporum* (Reynolds 1979) with hyaline ascospores rather than "fuscoideae" as characterized in the type description (Batista and Ciferri 1963). DRR138563, on living surfaces of *Baccharis pilularis.*

The origin of hyphae giving rise to the ascocarps of *L. californica* and their possible connection to mitosporic fruit bodies is obscured in the collections examined because of their formation in association with a plant surface mycelial layer of variable thickness to 3 mm. The layer is comprised of darkly pigmented hyphae similar to *L. californica* and derives from several fungal species, including the mitospore and ascospore stages of the

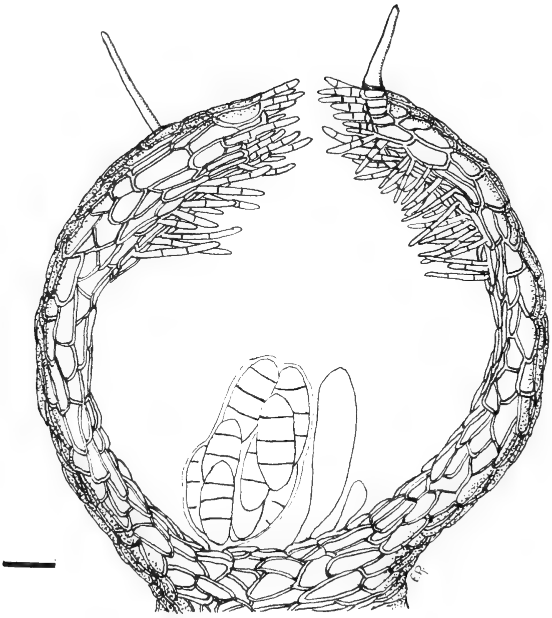

FIG. 2. *Lamaciniaseta californica* Composite drawing representing longitudinal, median view of ascocarp. A short stalk subtends the fruitbody; two setae extend from their orgin near the ostiole; sterile hairs line the apical ostiole; periphysoids line the upper portion of the ascal chamber; the hymenium is depicted with two young asci in a stage prior to ascospore and wall development and as a mature ascus with a cluster of 8 ascospores surrounded by a thinly stretched wall. Scale = approx. 10 μm.

pleomorphic sooty mold, *Capnodium salicinum.* The hyphal strands immediately subtending the ascocarp are comprised of darkly pigmented, rectangular shaped cells. The ascocarp forms on a columinate stalk that is comprised of firmly adhering, hyphal-like strands. The length of the stalk is variable; its width is 60–70% of the width of the ascocarp, although, sometimes it is minimally present, especially where an underlying mycelial layer is substantially thickened. The acuminate setae form in the upper hemisphere surrounding the ostiole (Fig. 1), which is lined with darkly pigmented, septate, pendulate but sometimes upwardly curving hairs. The multicellular, subulate, hyaline periphysoids form a layer, originating from the cells of the interior, upper wall of the hymenial locule and extending into the space between the ascocarp wall and the ascal layer (Fig. 2). The basal hymenium undergoes centrifugal maturation within a clear hygroscopic matrix that fills the ascocarp cavity. The young, clavate ascus measures 16–18 μm before the ascospore initials are internally delimited by a refractive wall. The ascus apical wall is thickened and has a rudimentary *nasse apicale* at an early stage of ascospore formation similar to that of the fissitunicate type (Reynolds 1989a). The ascus increases approximately twice in volume during ascospore formation, corresponding with a diminished apical wall thickness. The cylindrical ascus containing mature ascospores measures 36 μm in length. This fully developed ascus has the appearance of an extenditunicate ascus type (Reynolds 1989b) with the wall thinly stretched around the ascospores. The delineated ascospore wall is at first hyaline. After the formation of the first, centrally positioned cross septum, a brown pigmentation begins to intensify in the wall. A second cross septum subsequently divides each of the first two ascospore cells and the exterior spore surface ephemerially takes on an faintly echinulate appearance. The eight, fully formed ascospores are fusiform, three-septate, and golden brown in color in transmitted light. A passive release of the ascus and ascospores as a unit is suggested by their regular occurance on the surface of the ascocarp, particularly near the ostiole and in its immediate vicinity.

The ascocarp of *Limaciniaseta* is similar to that of *Scorias* Fries (Reynolds 1979) but with less stalk. The setae are similar to those characteristic of species of *Trichomerium* Spegazzini (Reynolds 1982). The ascospores are comparable in shape and septation to those of *Limacinia* Neger (Reynolds 1985) and *Trichomerium,* and in pigmentation to those of *Capnodium* Montagne (Reynolds 1978) and *Limacinia.* The periphysoids are like those found in the centrum (Luttrell 1965) of the type species of *Capnodium, Scorias,* and *Trichomerium.*

Two specimens cited under *Morfea* in Batista and Ciferri (1963) were found to be representative of *Limaciniaseta californica.* Batista and Ciferri (1963) utilized *Limacinia* Neger subgenus *Morfea* Arnaud as the basis of their genus *Morfea.* They designated *M. spongiosa* Arnaud as the generic type species because it was the first taxon listed by Arnaud (1911). No specimens were cited as having been examined in support of this decision. The authors characterized their listed fungi with a "2-tunicate" ascus and "brown, transversely pluriseptate" ascospores. The ascocarp was characterized as globose to cylindric, pseudo-ostiolate, setose, sessile, and formed from superficial, darkly pigmented hyphae. Most of the nine species included in this curious generic revision have been reassigned to other taxa (Barr 1955; Hughes 1976). One of the two *L. californica* specimens determined as a *Morfea* species (UC 966391) was listed as *Morfea hendrickxii* (Hansford) Batista & Ciferri.

Specimen OSU 9280 was cited by Batista and Ciferri (1963) as *M. tuba* Batista & Ciferri, a species transferred to *Capnodium* without these authors having seen type material. A Thom collection from Washington State (rather than California as stated) was indicated as the basis of an emendation of *M. tuba.* The authors stated, "it is possible that this material [the Thom specimen used as the basis of the redescription and nov. comb. in *Morfea*] . . . would be referable to *Capnodium tuba,* agreeing with the description of Cooke and Harkness for perithecia, since the ascospore were not described [by them]." "In our taxonomy, this specimen . . . does not belong to the genus *Capnodium.*"

The Thom specimen (BPI) was found to be somewhat accurately depicted by Batista and Ciferri (1963) with the ascus and ascospores differing in size from that given in their emendation of the description. Using the Thom material, Batista and Ciferri (1963) interpreted the ascocarp as "harboring at the top by short continuous setae . . . ." Figure 53 (Batista and Ciferri 1963) shows three setae positioned near the ostiole of an upright, elongate fruit body. This perception of the ascocarp is made apparently in deference to the Cooke and Harkness (1884) reference to the position as "perithecium" hairs on *C. tuba.*

The name *Morfea tuba* with the authorship (Cooke & Harkness) Batista and Ciferri (Batista and Ciferri 1963) is discounted for two reasons. First, the Thom specimen is inappropriate as an implied or undesignated lectotype. The Batista and Ciferri redescription is regarded as in serious conflict with the Cooke and Harkness protologue (Greuter et al. 1994: ICBN Article 9.13). Cooke and Harkness (1884) reported no ascus from the California material that was the basis of the name *Capnodium tuba* ("*ascis nondum visis*"). No specimen has been found that would properly serve as the type specimen for *C. tuba.* Further, the description of *C. tuba* by Cooke and Harkness (1884), repeated by Ellis and Everhart (1892), is likely that of a *Leptoxyphium* species. A mitosporic fungus is clearly described by Cooke and Harkness (1884) as having an erect, branched, infundibuliform column that is "*sursum ciliate.*" The mitosporic *Leptoxyphium* fruit body is accurately depicted by Hughes (1976) as "simple and variously proliferated." This same depiction also accounts for the position of cilia mentioned by Cooke and Harkness that occurred on a "perithecium." "Toward the apex [of the *Leptoxyphium* fruit body], component hyphae" form a funnel-shaped head comprised of hyphae that "terminate in a long . . . hyaline cell and together they form a fringe of sterile hairs." The Cook and Harkness (1884) citation antedates the 1897 type description for *Leptoxyphium* by Spegazzini (1918) and Hughes (1976).

The second reason for ignoring the nomenclature of Batista and Ciferri (1963) is that their emendation results in the name *Morfea tuba* Batista & Ciferri. This authorship constitutes a nomen nudum for lack of a Latin description or diagnosis (Greuter et al. 1994).

CONCLUSIONS

Several groups of sooty mold fungi species have been proposed as families (Hughes 1976). The taxon concepts were based on the perception of a common hyphal morphology type that provided a putative morphological link of unique sexual and asexual reproductive structures with pleomorphic implications at life cycle and phylogenetic levels. These delineated groups comprised of pleomorphic and mitosproric and ascosporic monomorphic species can be regarded as hypothetical monophyletic clades.

Limaciniaseta californica has morphological characters derived from the hyphae and the ascocarp that suggest a sister relation to *Capnodium, Trichomerium,* and *Scorias* in one of the Hughes groups, the Capnodiaceae. An exception is the ascus type; the capnodiaceous species have a fissitunicate ascus. The extenditunicate ascus of *L. californica* was first described for *Meliolina sydowiana* Stevens (Reynolds 1989b). *Meliolina* has been shown on the basis of 18s rDNA data to have a basal rather than a derived position on a filamentous ascomycete clade (Saenz 1997) and thus has no close relation to *Meliola* as predicted (Hughes 1993).

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LIGNOTUBERS IN *SEQUOIA SEMPERVIRENS*: DEVELOPMENT AND ECOLOGICAL SIGNIFICANCE

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ABSTRACT

Seedlings of *Sequoia sempervirens* (D. Don) Endl. develop lignotubers as part of their normal ontogeny from detached meristems located in the axils of the two cotyledons. Within four months of germination, each axillary cotyledonary meristem gives rise to a large central bud with two or more collateral accessory buds. As seedlings age, bud and cortex proliferation phenomena associated with lignotuber formation spreads distally to include axillary meristems located immediately above the cotyledonary node. Lignotubers continue to expand throughout the life of a *Sequoia,* eventually forming massive, basal swellings that are covered with leafy shoots and/or suppressed shoot buds. The *Sequoia* lignotuber is a specialized organ of regeneration and carbohydrate storage that contributes to the long-term survival of the tree by producing buds that can develop into shoots following traumatic injury to the primary trunk and by generating new roots that increase the stability and the vigor of both young and old trees. In response to a variety of exogenous factors, *Sequoia* will also produce induced lignotubers, or burls, on the trunks of mature trees as well as on the "layered" lateral branches of young trees, where they come in contact with the soil.

The California coast redwood, *Sequoia sempervirens* (D. Don) Endl. (Taxodiaceae (henceforth referred to as *Sequoia*)), is famous not only for being one of the tallest trees in the world but also for its ability, unusual among conifers, to resprout vigorously after being cut down. While much has been written about the commercial and ecological importance of resprouting in redwood (Olson et al. 1990), little is known about the precise origin of these sprouts, which arise from a large "burl" located at the base of the tree (Becking 1968; Stone and Vasey 1968; Simmons 1973; Groff and Kaplan 1988).

There are numerous reports in the literature of woody plants that can resprout from underground burls, technically known as lignotubers, following traumatic injury to the primary trunk. Anatomical studies on several arborescent taxa, including *Eucalyptus* spp. (Carr et al. 1984), *Arbutus unedo* (Sealy 1949), *Quercus suber* (Molinas and Verdaguer 1993), and *Ginkgo biloba* (Del Tredici 1992, 1997), have shown that lignotubers are genetically determined structures that develop from buds located in the axils of both cotyledons and a few of the leaves immediately above them. Over time, lignotubers can become quite large and contribute to the survival of plants in three ways: 1) they are a site for the production and storage of suppressed shoot buds that can sprout following injury to the primary stem; 2) they are a site for the storage of carbohydrates and mineral nutrients, which may allow for the rapid growth of these suppressed buds following stress or damage; and 3) for plants growing on steep slopes, they can function as a kind of clasping organ that anchors the tree to the rocky substrate (Sealy 1949; James 1984; Del Tredici et al. 1992).

Lignotuber-producing species are most commonly found in Mediterranean-type ecosystems that are characterized by hot, dry summers and periodic fires (James 1984; Mesleard and Lepart 1989; Canadell and Zedler 1994). The purpose of the present study is twofold: first, to determine whether or not the basal swellings produced by *Sequoia* fit the definition of an ontogenetic lignotuber (Carr et al. 1984; James 1984; Canadell and Zedler 1994), and second, to examine the ecological role that these structures play in the tree's native habitat in the coastal forests of northern California.

MATERIALS AND METHODS

Seeds of *Sequoia sempervirens* were extracted from green cones collected from the ground in Richardson Grove State Park, Humboldt County, California, on 28 October 1993. The cones had been dislodged from trees by squirrels feeding in the tree crowns. Cones were taken to the Arnold Arboretum in Boston, Massachusetts, where they were allowed to air dry until they shed their seeds. These were sown in a warm greenhouse (heated to a minimum temperature of 17°C) on 29 November 1993 and 13 April 1994. For both dates, germination commensed about two weeks later. A minimum of ten undamaged seedlings were sampled at each of four time periods: 15, 37, 59, and 133 days after germination. At the time of sampling, two to three mm long segments of the primary axis, including tissue above and below the point of attachment of the cotyledons, were collected from the plants, fixed in FAA, dehydrated in a t-butyl alcohol series, and embedded in paraplast. Serial transections, 10 microns thick, were cut on a rotary microtome and stained with Heidenhain's hematoxylin and safranin (Johansen 1940). For the purpose of studying the later stages of lignotuber development, a dozen three-year-old redwood seedlings were purchased from a California nursery and cultivated in containers in the greenhouse for three years.

Observations on mature *Sequoias,* both logged and unlogged, were made during October 1993, at four sites in northern California: Redwood National Park and Humboldt Redwoods State Park in Humboldt County, Big Basin Redwoods State Park in Santa Cruz County, and Samuel P. Taylor State Park in Marin County. Seedlings of *Sequoia,* mostly one to four years old, were collected on 26 October 1993, along with a few small layered branches from older *Sequoia* saplings. Both the seedlings and the layers were brought back to the Arnold Arboretum for further study and documentation. At the same time, numerous "live burls" were purchased from tourist shops located near Redwood National Park. These were placed in shallow dishes of water in a warm greenhouse heated to a minimum temperature of 10°C.

RESULTS

Lignotuber development on seedlings: 15 to 180 days. Observations on greenhouse-grown seedlings indicate that lignotubers in *S. sempervirens* originate from exogenous meristems located in the axils of the two cotyledons. On 15-day-old seedlings, the axillary cotyledonary meristems are poorly differentiated, being little more than a single, superficial layer of meristematic cells approximately 0.3 mm across, with no vascular connection to the stele (Fig. 1). By 37 days, structures identifiable as meristems develop in the axils of the cotyledons, but their vascular connection to the stele is only partially complete. By 59 days, the axillary cotyledonary meristems produce foliar primordia and establish a complete vascular connection to the stele (Fig. 2). By 133 days, the axillary cotyledonary meristems develop into distinct buds that protrude from the stem by as much as 0.5 mm, and collateral accessory buds develop adjacent to the primary cotyledonary bud (Fig. 3). By the time seedlings are six months old, clusters of buds are readily visible at both cotyledonary nodes, with some of them producing vegetative shoots.

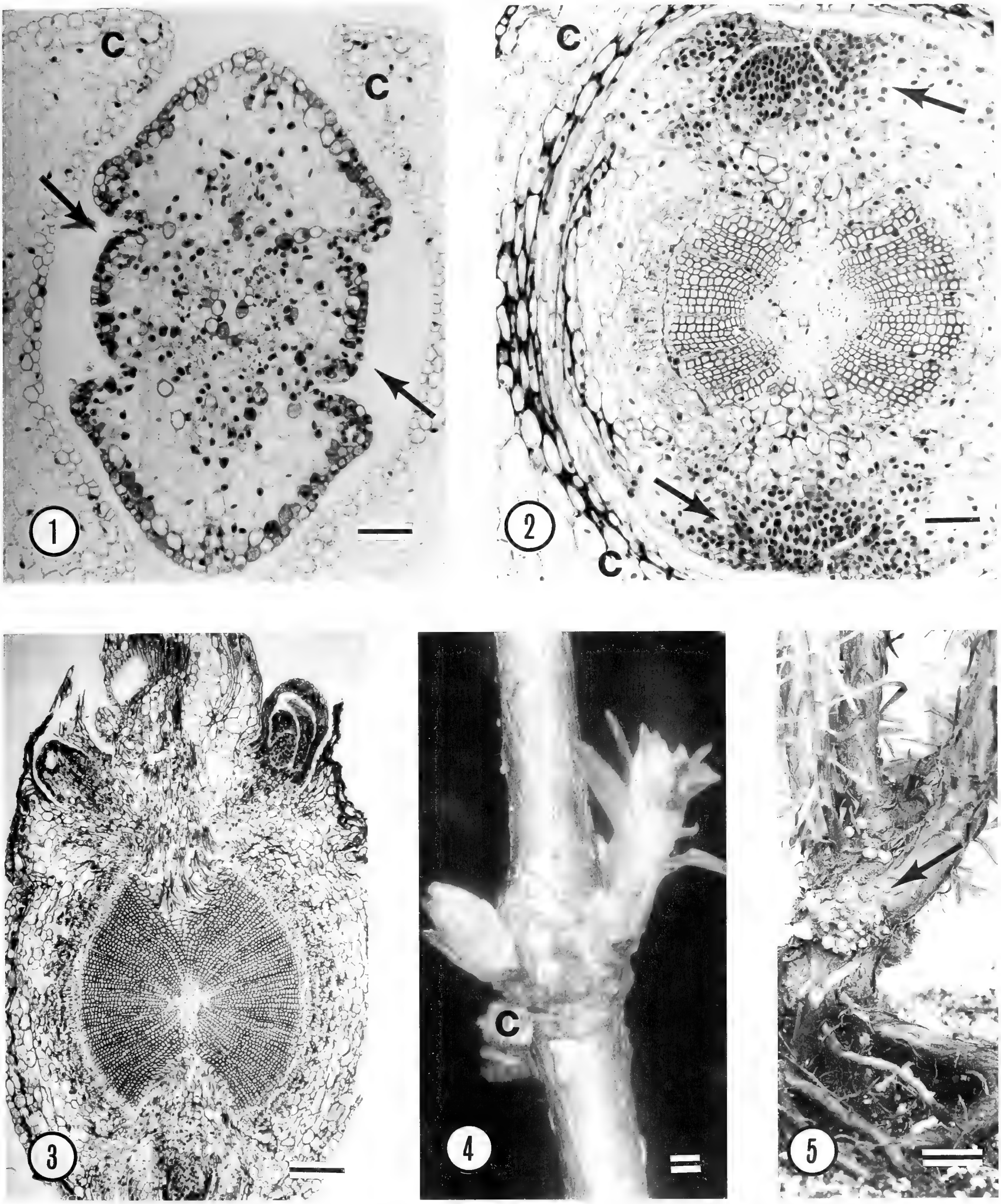
Lignotuber development on older seedlings: one to five years. On 3 to 5-year-old collected seedlings, the cotyledonary node is readily identifiable by the oppositely arranged pair of protruding bud-clusters at the base of the stem. Depending on the vigor of the seedling and the amount of damage it has sustained, one, both, or neither of the cotyledonary bud-clusters were producing leafy shoots, 0.5 to 4.0 cm long (Fig. 4). While sprouting is common in seedlings that have experienced damage to the primary stem, it also occurs in seedlings that showed no signs of injury. In addition to shoot production, the cotyledonary node region of the collected seedlings often produce adventitious roots in response to partial burial.

Typically, wild-grown *Sequoia* seedlings do not develop visible bud swellings at the cotyledonary node until they are between three and six-years-old (Becking 1968; Simmons 1973). In contrast, lignotubers of greenhouse-grown seedlings produce abundant bud clutsters and/or sprouts by the time they reach one and a half years old. After four or five years of cultivation, the cortical swelling and bud proliferation associated with lignotuber formation spreads distally to engulf many of the nodes produced during the first growing season (Fig. 5).

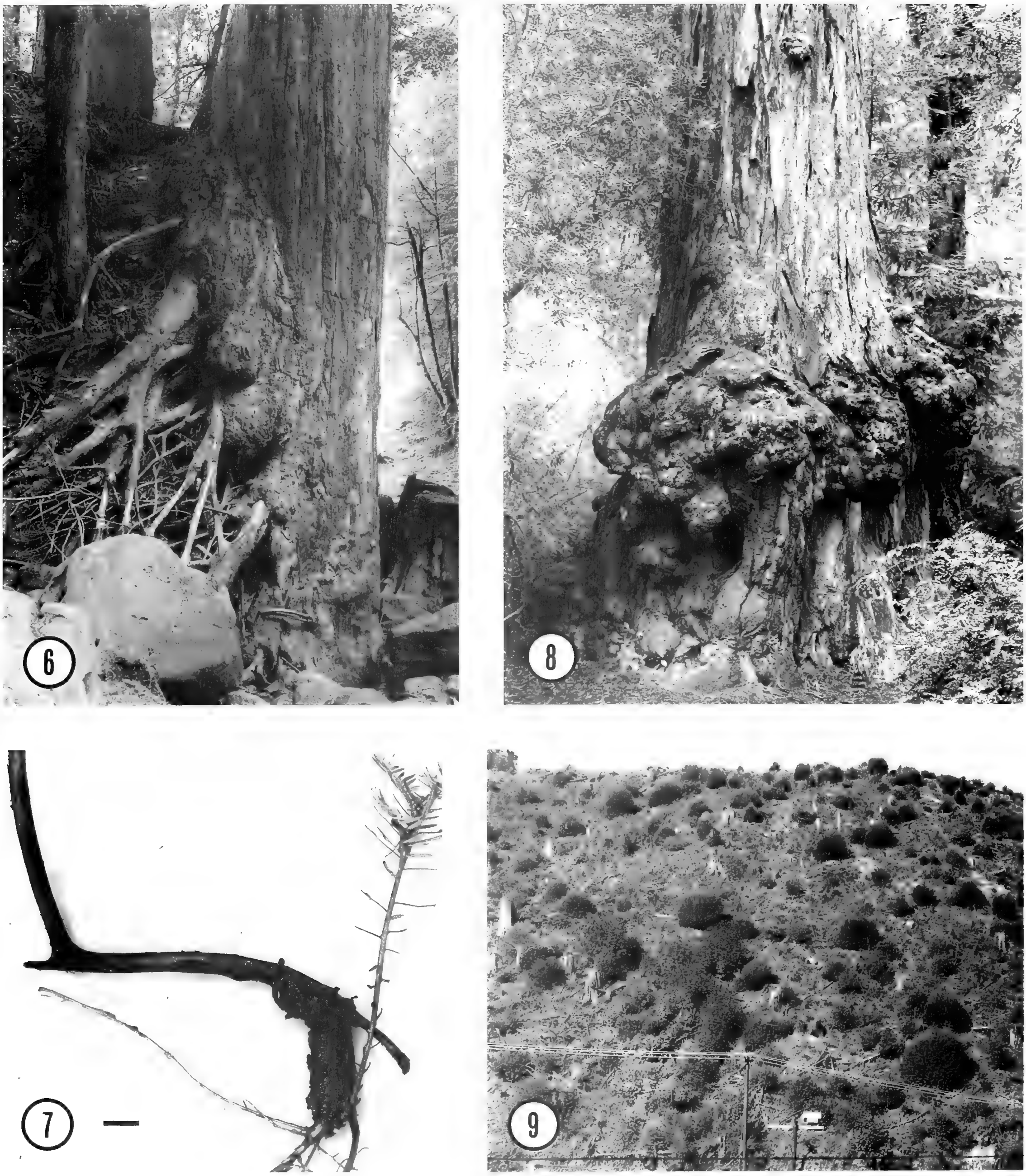
Lignotuber development on mature trees. Lignotubers expand throughout the life of a *Sequoia,* eventually forming a massive, woody swelling at or just below ground level. The outer surface of this swelling is generally covered with shoot buds. On undamaged trees, lignotubers typically give rise to clusters of small leafy shoots encircling the base of the trunk. On trees damaged by logging or erosion, lignotubers give rise to large secondary trunks that equal or exceed the primary trunk. Mature trees that had been logged 90 to 100 years ago have now developed lignotuber sprouts well over a meter in diameter. When second-generation trees are found growing on a steep slope near a stream or a road cut, the woody lignotuber is readily observable as a massive "plate" of downward-growing tissue that follows the contours of the ground and extends two to three m out from the nearest trunk. As well as giving rise to new shoots, such exposed lignotubers are also the source of roots that help to anchor trees to eroding slopes (Fig. 6). On rocky sites, the lignotuber has a tendency to form a kind of clasping organ that envelops the adjacent substrate, further stabilizing the tree.

Induced lignotuber development on layered branches. Induced lignotubers were observed to develop on the layered branches of 29-year-old *Sequoia* saplings, the growth of which was limited by low light levels that prevail beneath a mature redwood forest canopy. The stems of these plants are typically weak and spindly, and, when pinned down by a fallen limb or tree, they take root and turn upwards to reestablish a vertical orientation. Typically a single, downward-growing lignotuber develops along the side of the stem in contact with the soil, although in a few cases more than one had formed along a single stem. On such layered branches, the original connection to its parent trunk typically withers away, leaving only the bowed shape of the stem and the off-center lignotuber as evidence of it origin from a branch (Fig. 7).

As is the case with lignotubers derived from axillary buds at the cotyledonary node, those formed by layered branches possess the ability to generate



FIGS. 1–5. 1–3. Transverse sections of the cotyledonary node region of 15- to 133-day-old seedlings of *Sequoia sempervirens*. (1) A 15-day-old seedling showing the relationship of the superficial meristems (arrows) to the cotyledons (c). Bar = 0.1 mm. (2) A 59-day-old seedling showing fully developed cotyledonary meristems (arrows), foliar primordia, and the vascular connection to the stele. Bar = 0.1 mm. (3) A 133-day-old seedling showing fully developed cotyledonary bud (bottom) and two accessory collateral buds (top). Bar = 0.3 mm. FIG. 4. A three to four-year-old *Sequoia* seedling, collected from the wild, showing sprouting cotyledonay buds, accessory collateral buds, and the remnants of a cotyledon (c). Bar = 1.0 mm. FIG. 5. A five-year-old greenhouse grown seedling showing the proliferation of suppressed buds (arrow) at and above the cotyledonay node. Bar = 1.0 cm.



FIGS. 6–9. 6. A large *Sequoia* growing along a stream bank in the Humboldt Redwoods State Park showing extensive root and trunk development from its exposed, downward-growing lignotuber. Photo by R. Becking. FIG. 7. A layered lateral branch of *Sequoia*. Note that the downward-growing induced lignotuber has produced both roots and a vegetative shoot. Bar = 1.0 cm. FIG. 8. An ancient *Sequoia* in Big Basin Redwoods State Park showing massive burl development. FIG. 9. A forest of *Sequoias* in Korbel, California, resprouting from their lignotubers three years after clear-cutting.

both shoot buds and roots. How long it takes for a branch to develop a visible lignotuber after it has been pinned to the ground is unknown, but is probably at least two years.

Induced lignotuber development on the trunk of mature trees. Large, lignotuber-like structures often develop on the lower portions of the trunk of mature redwood trees in response to traumatic injury from fire, wind, or floods. Typically lignotubers are initiated above the point of injury, eventually growing down over the wound to cover it. On very old trees, extensive growths of contorted callus tissue can project out from the trunk 50 cm or more (Fig. 8). If these burls come in contact with the ground, which they often do, they will develop both roots and shoots. When cut off and placed upside down in a dish of water in a warm greenhouse, they will produce numerous leafy shoots within two weeks, and roots after six months to one year.

Observations suggest that burls on the trunks of old redwood trees originate as wound-induced callus tissue which, as it proliferates, incorporates nearby shoot buds into its structure. There appear to be two distinct types of lignotubers on *Sequoia,* the contorted type, located mainly on the lower portions of the trunk, which is irregular in shape, downward-growing in orientation, and covered with sprouts and/or shoot buds. The second type, which occurs higher on the trunk, is nearly hemispherical in shape, lacks the downward orientation, and produces comparatively few sprouts or shoot buds.

Trunk-burls are probably best interpreted as a case of uncontrolled bud and cortex proliferation induced by old age, traumatic injury, or environmental stress. They serve as sites for the production of new shoots and adventitious roots on trees that have been partially buried with silt from flooding or on leaning trees whose trunks have come into contact with the soil.

DISCUSSION

According to Strauss and Ledig (1985): "Architectural patterns established during the first few months of life are indicative of development decades to centuries later, when the plant has increased a millionfold in size." The lignotuber of *S. sempervirens,* which can be fully functional in four-month-old seedlings and remain functional on trees that are at least 1100 years old, clearly illustrates the truth of this observation. Regardless of the age or size of the tree, the redwood lignotubers often resprout within two to three weeks of logging. While most of these sprouts do not survive to maturity, enough of them do to effectively regenerate a new forest (Olson et al. 1990). One study done with an old-growth forest that had been clear-cut showed that the ability of redwoods to resprout (i.e., the number of sprouts per meter circumference) is greatest in trees that were between 200 and 400 years of age, and decreases rapidly thereafter. Trees more than one thousand years old are able to resprout at only 20 to 25% of the peak rate (Powers and Wiant 1970). The authors also reported that 92% of all surviving sprouts grow out from the lignotuber, 6% from the bole proper, and 2% from the cut surface of the stump. When a tree was growing on a slope greater than 20%, the sprouts are more numerous on the downhill side of the trunk.

The remarkable ability of redwood trees to resprout from its basal lignotuber, regardless of age, is clearly the basis of the redwood's persistence in the face of extensive clear-cutting (Fig. 9). Throughout its natural range, logging has served to transform *S. sempervirens* into a clonally reproducing species that spreads by means of its underground lignotuber. Jepson (1910) described one colony of 45 large redwoods that formed a third-generation "fairy ring," 17 m by 15 m across. As significant as lignotuber sprouting is for mature trees, however, the process is probably of greater importance to seedlings and saplings that are struggling to survive in dense shade or on exposed slopes (Becking 1968; Canadell and Zedler 1994).

Despite the abundant documentation on the importance of *Sequoia* lignotuber sprouting to forestry, there is very little information available on its significance in the absence of logging-related disturbance. One study on an uncut *Sequoia* forest in Humboldt County found that basal sprouting in redwood was closely associated with the occurrence of fire (Stuart 1987). By correlating fire scars on the primary trunk of the tree with basal sprouts from its lignotuber, the author determined that during the "pre-settlement period" (between 1775 and 1875) fires occurred regularly in the forest, at an average interval of 24.6 ± 2.8 years. Other studies, which analyzed fire scars on the cut stumps of old-growth redwoods, support the idea that fires were common in the redwood region prior to European settlement (Fritz 1931; Jacobs et al. 1985; Finney and Martin 1992). These findings are consistent with studies in other Mediterranean climates which report the occurrence of lignotuber-producing angiosperms in habitats where fire, or other types of recurring disturbance, is common (James 1984; Mesleard and Lepart 1989).

The trunk of a redwood tree, above the lignotuber, also shows a strong ability to resprout following traumatic injury. In the older forestry literature, there are numerous reports of large trees, entirely defoliated by fire, that sprout vigorously to form lush "fire columns" (Jepson 1910; Fritz 1931). Similarly, the author has observed recently blown down trees that sprouted new growth along the entire length of the horizontal trunk. Fink (1984) studied the ability of *Sequoia* stems to resprout following injury and found that clusters of replacement buds developed exogenously in the needle axils of young branches over a one to two year period. Except for the length of time involved, the process he described for the development of preventitious shoot buds is very similar to that of the cotyledonary buds described in this paper. One must keep in mind, however, that the lignotuber formed at the cotyledonary node is under strict genetic control while those that develop elsewhere on the trunk are under environmental control. In this regard, *Sequoia* is similar to *Ginkgo biloba* which produces positively geotropic lignotubers from axillary cotyledonary buds (basal chichi), as well as induced lignotubers (aerial chichi) on its trunk and branches

(Del Tredici 1992, 1997). As is the case with *Sequoia,* shoot and root regeneration by the *Ginkgo biloba* lignotuber play an important role in the persistence of the species in its native habitat in the temperate forests of eastern China (Del Tredici et al. 1992).

From both the morphological and physiological perspectives, lignotuber-generated shoots can be considered "juvenile" relative to the rest of the tree (Greenwood 1995). This conclusion is supported by *in vitro* studies which found that tissue cultures started with lignotuber shoots from the base of a 90-year-old *Sequoia* were more vigorous and rooted more readily than those started with shoots from the crown of the same tree (Bon et al. 1994). The authors also identified numerous membrane-associated proteins that were synthesized in greater abundance in cultures derived from lignotuber shoots that those derived from the upper portions of the tree. Certainly it is not by chance that *Sequoia* was the first conifer to be successfully cultured using in vitro techniques, and that the cultures were derived from lignotuber sprouts (Ball 1950).

ACKNOWLEDGMENTS

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CAREX SERPENTICOLA (CYPERACEAE), A NEW SPECIES FROM THE KLAMATH MOUNTAINS OF OREGON AND CALIFORNIA

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Carex serpenticola P. F. Zika (*Carex* section *Acrocystis*) is described from ultramafic deposits in the Klamath Mountains of southwestern Oregon and northwestern California. It appears most similar to *C. globosa* Boott, from which it is distinguished by frequently unisexual culms and dark purple pistillate scales. *C. serpenticola* perigynia are shorter, and differ in the length of stipe and nerving on the faces. Bisexual culms closely resemble *C. concinnoides* Mackenzie, from which it is separable by its three subplumose styles.

Lilla Leach was an early botanical explorer in the remote regions of the Klamath Mountains. On 1 May 1931, while collecting on serpentine bedrock deposits in the mountains east of Game Lake, Curry Co., OR (Leach and Leach 1938; Love 1991, and personal communication), she gathered the earliest known specimens of an unknown *Carex*. For decades Leach's serpentine sedge was overlooked, until the *Carex* Working Group began work on an atlas of Oregon *Carex* in 1993. Reviewing the collections of Leach and subsequent botanists, we were puzzled by plants labeled "*C. globosa*?" and disjunct from its known range in California (Fig. 1). Further field and herbarium investigations disclosed that this sedge was a distinctive undescribed species. As most or all collections of this new *Carex* were from ultramafic bedrock zones, we chose a name to reflect its preference for serpentine soils.

Carex serpenticola P. F. Zika, sp. nov. (section *Acrocystis*). (Fig. 2)—TYPE: USA, California, Del Norte Co., sunny moist slope, SW aspect, serpentine soil, with *Libocedrus, Umbellularia, Rhamnus californica* Eschsch., *Quercus vaccinifolia* Kellogg, *Carex mendocinensis* Olney, *Mimulus guttatus* DC., *Danthonia californica* Bolander, SE of Azalea Lane, N of Middle Fork Smith River, ca. 0.8 km SE of bridge in the town of Gasquet, 41°51′N, 123°57.5′W (T17N R2E sect. 21 SW¼; Humboldt Meridian), elev. 120 m, 29 April 1997, *P. F. Zika and K. Kuykendall 13062* (holotype, OSC; isotypes, HSC, MICH, NY, UC, US).

Differt a *Carex globosa* Boott culmis staminatis aut pistillatis interdum moneociis; perigyniis 3.1–3.6 mm longis, enervibus, stipitibus 0.4–0.8 mm longis; squamis pistillatis atropurpureis sine nervis secundariis ad nervum medium parallelis.

Perennial, rhizomatous between small tufts of shoots; capable of forming mats 2 m in diameter; *rhizomes* 2.5–7.5 (−10) cm long, 1.2–2.2 (−3.4) mm thick; young rhizomes clad in purple-black scales 5–7 mm long, the largest with fibrillose sheaths. Base of erect shoot scaly with bladeless *sheaths,* dark red-purple; ventral face of bladeless sheaths deteriorating with age and leaving a pinnate-reticulate network of persistent veins. *Leaves* mostly basal, margins scabrous; leaf blades variable depending upon exposure, long, straight and nearly flat when in favorable sites, folded, short, and falcate in harsh sites; all leaves somewhat V-shaped in cross section, widest leaves (1.5−) 2.2–3.5 (−5.0) mm wide when spread flat, longest basal leaves 8–28 (−35) cm long, semi-evergreen, never glaucous; sheath mouth and *ligule* minutely scabrous (at 40×). Ligule wider than tall, obtuse, membranous, discolored, 0.2 mm thick. Only shoots of the previous season producing flowering culms. *Culms* 8–38 cm tall, bearing 2–5 highly reduced green or purple-margined leaves, culms erect in flower, pistillate and bisexual culms arching to the ground in fruit (Fig. 2F). Culms usually either pistillate (Fig. 2D, E, F) or staminate, thus the species superficially appearing dioecious. Bisexual culms rarely with terminal spike gynecandrous (Fig. 2C). Most bisexual culms with a solitary terminal staminate spike and sessile 4–9-flowered pistillate spikes (Fig. 2B). Staminate culms with 1–3 lateral aborted spikes marked by short inflorescence bracts (Fig. 2A). Some rhizomes bearing shoots with both bisexual and unisexual culms. *Bracteal sheaths* essentially absent, 0–2 mm long, dark purple-margined when present. *Inflorescence bract* minute, purple, shorter than lateral spike, to green and leafy, equaling or exceeding inflorescence, 0.1–9.2 cm long; bracts minutely scabrous-ciliate at tip; blades of larger inflorescence bracts dark purple-margined at base, with green midrib varying in width, sometimes with purple stripes flanking green midrib, sometimes with slender white-hyaline margin (this, if present, 0.1–0.2 mm wide). *Staminate inflorescence* 13–24 mm long, (1.4−) 2.0–4.1 mm diameter; *stamens* 3 per scale, dried *anthers* 2.1–4.0 mm long, *staminate scales* oblanceolate, 4.6–5.6 mm long, 1.1–1.6 mm wide, purple-black, fading to reddish, minutely erose-margined. *Pistillate inflorescence* with terminal spike up to 65 flowered and 8–47 mm long, 6–9 mm wide. *Bisexual inflorescence* 15–28 mm long, 4–9 mm wide; subter-

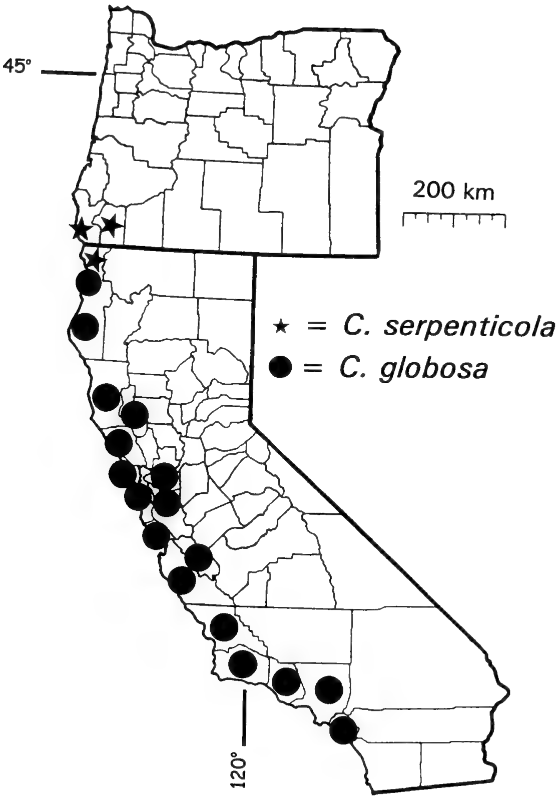

FIG. 1. Distributions of *Carex serpenticola* and *C. globosa*. Mexican populations of *C. globosa* are not mapped.

minal pistillate spikes 5–8 mm long, sessile or rarely on erect peduncles 5–10 mm long, lateral spikes 4–9 flowered. Axillary basal or near-basal pistillate spikes rarely present (*Zika and Kuykendall 13062* UC) on some pistillate or bisexual culms, on peduncles 1–11 cm long. *Pistillate scales* lanceolate, glabrous or scabrous-tipped, longer and narrower than perigynia, acuminate, 3.8–4.6 mm long, 1.3–1.8 mm wide, widely spreading as perigynia mature, dark purple. Pistillate scale midrib green or yellow-brown, flat or slightly keeled, glabrous or slightly scabrous; rarely 1–2 pistillate scales on plant with 1–2 faint lateral nerves (*Rolle 327* ID). Pistillate scale margins with hyaline-border 0.1–0.4 mm wide. *Stigmas* ca. 3 mm long above orifice of perigynium, stigmas 3, subplumose. *Perigynium* obovate, gradually tapered to a cuneate base, 3.1–3.6 × 1.5–1.8 mm, short hairy, green, some ripening to a dark purple, plump, trigonous, wingless, with marginal ribs, the faces nerveless (rarely 5 nerves up to mid-length), facial nerves hard to see on fresh material. Perigynia abruptly short beaked, *beak* 0.5–1.0 mm long, dark purple except for hyaline margin of shallowly toothed orifice, teeth 0.2 mm long. Dried *stipe* shriveled and discolored, 0.4–0.8 mm long below achene, plump and pale when fresh. *Achene* globose-trigonous, faces convex, tightly filling the central perigynium body, 1.9–2.2 × 1.4–1.8 mm, medium to light brown, finely papillate (at 40×) in longitudinal rows; style base 0.1 mm long, cleanly articulated.

Paratypes. USA, Oregon, Curry Co.: Berry Cabin, between Game Lake and Horse Sign Butte, ca. 13 km S of Agness, 1 May 1931, *Leach 3325* (ORE); Pistol River Hill Rd., E of Ismert Ln., 8 May 1988, *Stansell s.n., 3114* (WS), 3 May 1995, *Stansell 3041* (WS); 8 km S of Gold Beach, 23 Jul 1945, *Peck 23951* (WILLU); Lemmingsworth Gulch, 17 Apr 1984, *Stansell s.n.* (OSC); 2.4 km W of Doe Gap, 26 Jun 1993, *Rolle 608* (OSC); ca. 1.6 km SW of Signal Butte, May 1990, *Stansell s.n.* (OSC, RSA, UC, WTU); ca. 3.8 air km NE of Signal Butte, 1 May 1989, *Stansell s.n.* (OSC), 6 May 1995, *Wilson et al. 7630* (WS); Dry Butte Trail, Kalmiopsis Wilderness, 4 Jun 1994, *Stansell 3023* (IDS); near Hunter Cr. Bog, 19 Jun 1997, *Zika et al. 13167* (OSC); Josephine Co.: S of Mikes Gulch, 4.3 air km ENE of Fiddler Mt., 20 Apr 1993, *Zika 11972* (WTU); road to Day's Gulch, Josephine Cr., 15 Apr 1984, *Greenleaf 1473* (ORE); ca. 0.4 air km NW of Eight Dollar Mt., 30 May 1988, *Zika 10485* (OSC); 2.1 air km SSW of Eight Dollar Mt., 21 Apr 1993, *Zika 11975* (MICH, OSC, WTU); 2.4 air km SSW of Eight Dollar Mt., 21 Apr 1993, *Zika 11976* (WS); ca. 1.2 road km SW of Illinois River bridge, FS Rd. 4201, 28 May 1994, *Wilson et al. 6790 and 6791* (OSC), 23 Mar 1996, *Clery et al. 57* (OSC); near small roadside pool, 1.3 road km E of Illinois River bridge on FS Rd. 4201, 22 April 1995, *Zika 12297* (UBC, UC), 14 May 1994 *Wilson et al. 6793* (GH, ID, MICH, OSC, RSA, WTU); slope above and N of Illinois River bridge on FS Rd. 4201, 24 May 1996, *Zika 12865* (WTU); BLM fen, S of Eight Dollar Mt., 18 April 1984, *Stansell s.n.* (OSC), 23 March 1996, *Clery 55 et al.* (OSC, WS, WTU); Star Flat Rd., NNW of Eight Dollar Mt., 17 May 1990, *Rolle 329* (WTU); NE of Woodcock Mt., 23 May 1995, *Perkins 950523* (IDS), 24 May 1995, *Newhouse 95001b* (WTU); near N ridgeline of Woodcock Mt., 15 Jun 1995, *Perkins 950615* (UBC, WS), 23 May 1995, *Newhouse 95002c* (OSC); Oak Flat Rd., 21 km W of Selma, 18 Apr 1969, *White and Lillico 148* (OSC), Pearsoll Peak Rd., ca. 32 road km W of Selma, 13 May 1962, *Addor 1425* (ORE); Chrome Ridge, 29 May 1995, *Rolle 893* (US). California, Del Norte Co.: N side of Middle Fork of Smith River, on Old Gasquet Toll Rd., near Gasquet, 1 Jun 1935, *Parks and Tracy 11200* (HSC), 14 May 1994, *Wilson 6803* (RSA); Gasquet Mountain, close to town of Gasquet, 18 Jun 1979, *Clifton and Griswold 5379* (HSC); Humboldt Flat, 5.6 km S on French Hill Rd. from Rte. 199, 14 May 1983, *Janeway 292 and 293* (HSC); Old Gasquet Toll Rd., 0.2 km N of southern entrance, 12 Apr 1975, *Barker 247* (HSC); French Hill Rd., 0.6 km above Rte. 199, Gasquet, 3 May 1995, *Zika 12322* (OSC); Old Gasquet Toll

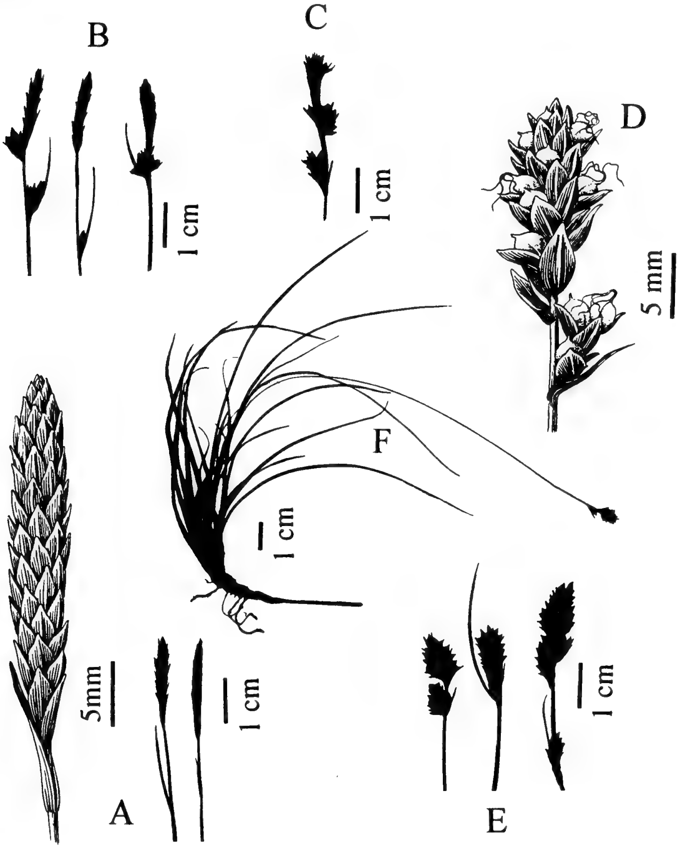

FIG. 2. *Carex serpenticola* P. F. Zika. A) *Carex serpenticola* ♂ spikes, note bracts marking aborted lateral spikes (*Rolle 608* OSC; Curry Co., Oreg.); B–E) infructescences (*Zika 12322* OSC; Del Norte Co., Cal.); B) terminal spike ♂, lateral spike(s) ♀; C) terminal spike ♀/♂, lateral spikes ♀; D, E) all spikes ♀; F) lax habit when fruiting (*Newhouse 95001B* WTU; Josephine Co., Oreg.).

Rd., 1.1 km above river bridge, 3 May 1995, *Zika 12323* (IDS, MICH, OSC, WTU); Old Gasquet Toll Rd., 2.3 km N of southern entrance, 7 Mar 1979, *Barker 211* (HSC); Old Gasquet Toll Rd., 4.3 km N of southern entrance, 15 May 1974, *Barker 261* (HSC); N entrance to Old Gasquet Toll Rd., confluence of E and W Forks of Patrick Cr., 19 May 1997, *Zika 13082* (OSC); near Stony Cr., ca. 2 km W of Cold Spring Mt., 1 Jun 1980, *Baker 1667* (HSC); Stony Cr. Bog, 13 May 1973, *Smith 6712* (HSC); near Browns Mine, 1 Jun 1980, *York 899* (HSC); near Cold Spring Mt., 1 June 1980, *Baker 1650* (HSC); near Diamond Cr., North Fork, 2 Jun 1980, *York 944* (HSC); along Elk Camp Ridge NE of Gasquet, 7 Mar 1975 and 12 Apr 1975, *Klipfel 358 and 359* (HSC); near Wimer Rd., close to town of Smith River, 21 May 1979, *Clifton and Overton 2706, 2976, and 3372* (HSC), 6 May 1994, *Stansell 3117* (WTU); Low Divide Rd., 2300 feet, 6 May 1994, *Stansell 3115* (WS); near junction of Wimer and Low Divide Rds., 29 Apr 1997, *Zika and Kuykendall 13068* (OSC); Low Divide, Wimer Rd., 29 Apr 1997, *Zika and Kuykendall 13075, 13076* (OSC); ridge S of Black Butte, 18 Jun 1994, *Stansell 3060* (WS).

Distribution. *Carex serpenticola* appears to be restricted to the Klamath Mountains of California and Oregon, west of the Cascade Mountain highlands. We documented populations in three counties: Del Norte Co., CA, and Curry and Josephine Cos., OR. *Carex serpenticola* ranges as far southwest as the xeric serpentine plant communities in the Smith River drainage, in the Gasquet region of Del Norte Co. *Carex globosa* ranges north to within 8 km of *C. serpenticola,* in the wet maritime redwood forest zone on the lower reach of the Smith River in Del Norte Co. (*Zika 13087* WTU). From there *C. globosa* ranges south and east on the coast and in the coastal mountains. We mapped the distribution of the two species based on our collections and herbarium materials (Fig. 1).

Affinities. Based on morphology, we considered placement of *Carex serpenticola* in the three (rather loosely defined) subgeneric sections discussed below.

Sectional placement. Although similar to *Carex* section *Scirpinae* in gross morphology, *C. serpenticola* fails to fit there because its pistillate and bisexual culms are multispicate. Culms in *C.* sect. *Scirpinae* are generally unispicate, but when multispicate and bisexual (e.g., *C. scabriuscula* Mack.), the perigynial architecture is quite different. A better fit is in the circumboreal *C.* sect. *Acrocystis.* Members of the section are generally plants of upland habitats characterized by plump, pubescent, tristigmatic perigynia in short, subterminal spikes, subtending a staminate spike, with essentially sheathless inflorescence bracts and basal foliage that is glabrous in the region described in this study *Carex serpenticola* shares the growth habit, upland ecology and general morphology of species in section *Acrocystis.* We note that recent unpublished molecular investigations (Roalson personal communication.) support our morphological data, and place *C. serpenticola* among the western members of *C.* sect. *Acrocystis.*

The weak boundary between *Carex* section *Acrocystis* and *C.* sect. *Digitatae* led Koyama (1962) to synonymize them. North American authors still segregate them, although traditional key characters such as achene shape (Mackenzie 1931–1935; Hermann 1970) fail to separate the sections. *Carex serpenticola* does not share characters now used for defining *C.* sect. *Digitatae:* well-developed bracteal sheaths, insignificant bracteal blades, and poorly developed perigynial beaks that are essentially toothless and ≤0.5 mm long. *Carex concinna* R. Br. and *C. concinnoides* Mackenzie are anomalies in *C.* sect. *Digitatae,* with unusual warty and non-plumose styles. *Carex concinnoides* is also exceptional with its highly reduced bracteal sheath, and relatively elongate beak, and closely resembles *C. serpenticola.* These species could be viewed as transitional between the sections *Acrocystis* and *Digitatae,* and molecular studies are recommended for a fresh definition of the sectional boundaries.

Similar species. *Carex* section *Acrocystis* is found in the Old and New World, however no Eurasian taxa occur in North America (Hultén 1968; Fernald 1950). None of the Eurasian species are a close match to the unusual key characters of *C. serpenticola,* which combines long rhizome internodes, unisexual culms and a dark (almost black) scale color. Eastern North American taxa in the section are not similar to *C. serpenticola.* Although *C. umbellata* Schk. ex Willd. does show a tendency to produce unisexual culms, it differs substantially in other characters. Based on morphology, geography, and ecology, *Carex serpenticola* is most similar to *C. globosa* among western members of *C.* sect. *Acrocystis.* Collections of the two species have confused more than one respected caricologist. Both plants share features such as stem height, leaf length, leaf width, loosely spreading habit, wide obovoid perigynia with pronounced swollen stipes and distinct, abruptly tapered beaks, and sharp-tipped pistillate scales that are widely spreading in the mature infructescence. Unisexual culms are common on *C. serpenticola,* but rare among similar taxa in western North America. *Carex globosa* culms can be unisexual (Howell 1949), further suggesting it is related to *C. serpenticola.* Geographically the two taxa are adjacent to each other along the Pacific coast (Fig. 1). And ecologically, both species occur on ultramafics, an unusual edaphic tolerance in the section.

Important morphological distinctions between *Carex globosa* and *C. serpenticola* follow. Ordinarily *C. globosa* does not produce unisexual stems. The perigynia of *C. globosa* are longer, 3.9–5.1 mm, including prominent discolored stipes. Measured from the base of the swollen achene to the base of the perigynium, stipes are 1.2–2.3 mm long. The perigynial faces of *C. globosa* have 2–5 thick longitudinal nerves (Fig. 3G). Pistillate scales are predominantly green with 2–4 nerves paralleling the midvein (Fig. 3G). By comparison, most *C. serpenticola* culms are unisexual. This species has perigynia 3.1–3.6 mm long, with stipes 0.4–0.8 mm long. *Carex serpenticola* perigynia have thick marginal ribs, but usually lack nerves on the faces. If facial nerves are present, they are generally thin and short. The perigynia of the two taxa look different because of the relatively long stipes characteristic of *C. globosa* (Fig. 3G, S). Finally, pistillate scales in *C. serpenticola* are predominantly dark purple-black with a single midvein, and lack parallel nerves. On rare occasions a few scales or perigynia on a culm have some nerves suggesting *C. globosa,* but the majority of scales and perigynia are not nerved. In summary, the two taxa can be separated reliably by perigynium dimensions and nerving, scale color and nerving, and presence or absence of unisexual culms within populations. In addition, the two have different habits in nature. *Carex globosa* is a loosely clumped species, with more vertical than horizontal rhizome development. *Carex serpenticola* tends to spread, forming diffuse mats or turfs, or producing small clumps of vertical shoots on elongate horizontal rhizomes. Habit differences are not easily assessed on most herbarium sheets.

Perigynium length is a reliable discriminator between *Carex globosa* and *C. serpenticola,* with a clear hiatus. *Carex serpenticola* perigynia are 3.1–3.6 mm long. Munz and Keck (1965) reported *C. globosa* perigynia were 4–5 mm long and Jepson (1925) reported they were 5 mm long. Although Mastrogiuseppe (1993) reported *C. globosa* perigynia at 3.3–5.0 mm long, we found a range of 3.9–5.1 mm for *C. globosa* perigynia from Marin Co., CA, and north and could not find mature specimens in the lower range reported by her. The *C. globosa* holotype has perigynia 4.0–4.7 mm long.

In the herbarium, *Carex serpenticola* collections commonly have been mistaken for *C. concinnoides.*

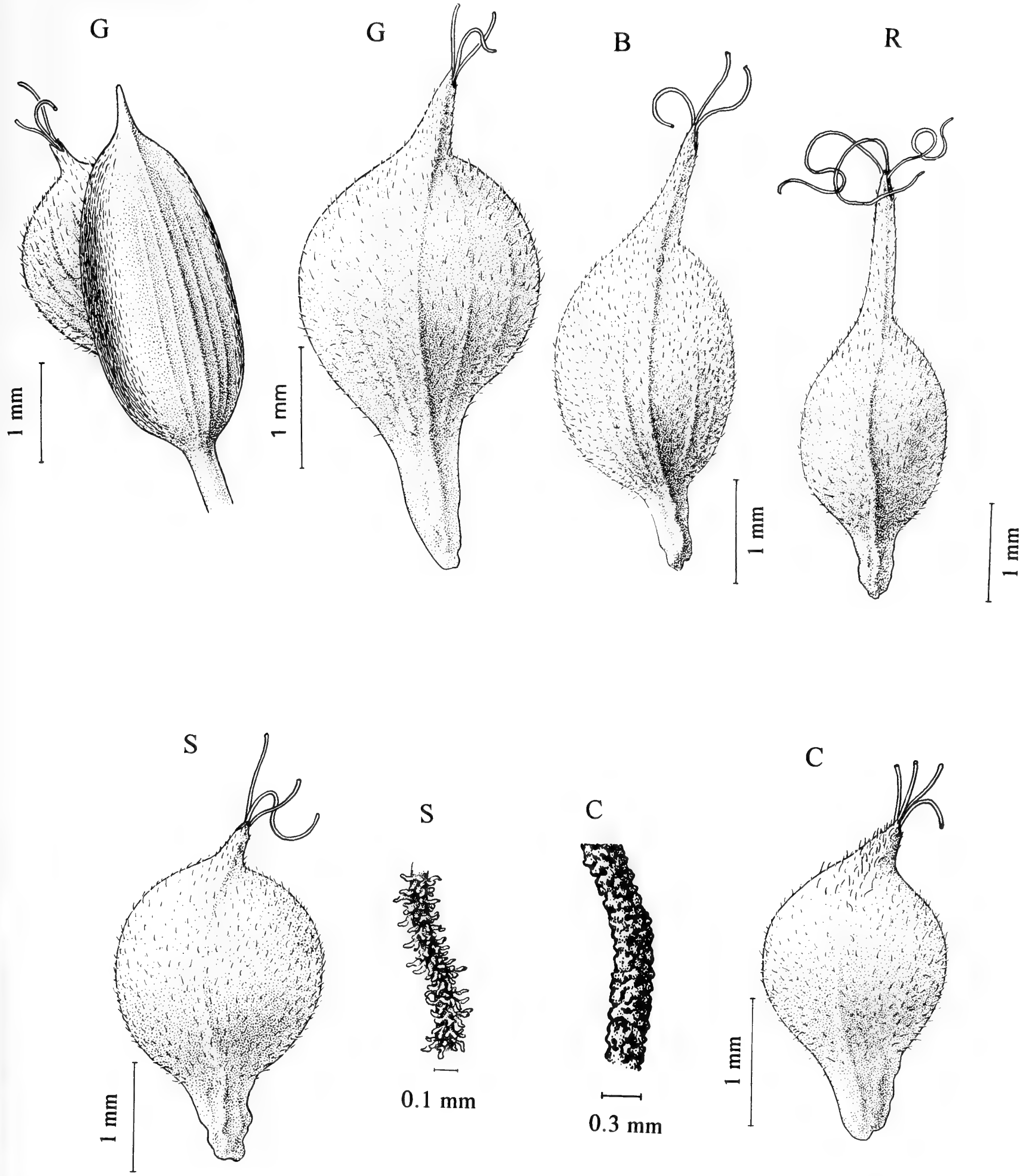

FIG. 3. Perigynia, scale and stigmas. All drawings prepared from dried herbarium materials. B) *Carex brainerdii* perigynium (*Zika 12372* OSC; Klamath Co., Oreg.); C) *C. concinnoides* stigma and perigynium (*Miller 56* OSC; Grant Co., Oreg.); G) *C. globosa* scale and perigynia (*Zika 12316* OSC; Marin Co., Cal.); R) *C. rossii* perigynium (*Zika 12300* OSC; Josephine Co., Oreg.); S) *C. serpenticola* stigma (*Zika 11972* WTU) and perigynium (*Zika 12297* UBC; both from Josephine Co., Oreg.).

The latter has a much wider range, across much of western North America. Where sympatric, the two have a similar habit and habitat, although *C. concinnoides* is less tolerant of wetland soils. Mixed collections and our observations show they sometimes grow intermingled. Their perigynia (Fig. 3C, S), dark scales, and arching bisexual culms (Fig. 2F) are strikingly similar, suggesting a close relationship. However, the subtle but profound differences between the species suggests to us convergent evolution (presumably for seed dispersal), rather than recent divergence from common ancestry. Only *C. serpenticola* generates unisexual culms. Furthermore, they are quickly and reliably separated by the thick warty stigmas typical of *C. concinnoides* (Fig. 3C) which contrast with the slender, subplumose stigmas in *C. serpenticola* (Fig. 3S). *Carex concinnoides* also has 4 styles and quadrangular-based globose achenes. *Carex serpenticola* has 3 styles and trigonous-based globose achenes.

Although Peck (1961), Hitchcock et al. (1969), and others have suggested *Carex concinnoides* can have three stigmas, our study revealed only 4-stigmatic flowers, echoing the results of St. John and Parker (1925). We speculate that Hermann (1970) may have perpetuated reports of three stigmas in *C. concinnoides* based on his examination of unrecognized *C. serpenticola* from northern California. As recently as 1977, Hermann annotated 3-styled *C. serpenticola* as *C. concinnoides* (e.g., *Parks and Tracy 11200* HSC, *Barker 261* HSC).

Synonymy. We found no available synonyms of California and Oregon species of section *Acrocystis* that might apply to *C. serpenticola,* nor has A. A. Reznicek (personal communication). The holotype of *Carex globosa* (*Nuttall s.n.,* K!) is merely labeled "California" and lacks a specific locality or date (Boott 1845). It was most likely collected along the coastline, at a point accessible to ships of the day, no further north than Monterey, in California *Alta,* in spring of the year 1836, according to historical summaries of Nuttall's travels in the American west (e.g., McKelvey 1955). This places the *C. globosa* holotype well south of the known range of *C. serpenticola.* We have also examined the holotype of *C. concinnoides* (*Williams s.n.,* NY!) from "Columbia Falls, MT," far to the northeast of the known range of *C. serpenticola* (Mackenzie 1906).

Taxonomic rank. We rejected placement of the new taxon as a subspecies of *Carex globosa.* More than two consistent morphological features differentiate them. They are entirely allopatric. Both can occur on low-elevation serpentine meadows along the coast (*C. globosa* in California, *C. serpenticola* in Oregon), but in these similar ecological conditions they maintain their morphological differences. We found no intermediate plants to suggest widespread introgression or hybridization in populations we studied in the field. We believe these differences are best summarized by assigning the rank of full species to *C. serpenticola.*

Dichotomous identification key. Our key is for identification of all pubescent-fruited *Carex* from the Klamath Mountains, west of the Cascade Mountains. The key is actually composed of 3 keys, one for staminate culms, one for pistillate culms, and one for bisexual culms. We excluded species such as *C. mendocinensis* and *C. scopulorum* Holm, as their perigynia have only sparse apical bristles and are not densely or uniformly pubescent. Our key includes all six *C.* sect. *Acrocystis* taxa known from in or near the Klamath region (*C. brainerdii* Mackenzie, *C. brevicaulis* Mackenzie, *C. globosa, C. inops* L. Bailey ssp. *inops, C. rossii* Boott and *C. serpenticola*). Like Hitchcock et al. (1969), we elected to treat *C. rossii* in the broad sense, including *C. brevipes* W. Boott and *C. diversistylis* Roach. We followed Dunlop (1997) and submerged *C. gigas* (Holm) Mackenzie in *C. scabriuscula* Mack.

A KEY TO PUBESCENT-FRUITED *CAREX* in the Klamath Mountains

1\. Culms all unisexual 2

  2. Culms staminate 3

    3. Base of flowering culms scaly, lacking fibers; spikes 2–4 . . . . **C. scabriuscula**

    3′ Base of flowering culms lacking scales, fibrous; spikes solitary 4

      4. Ventral surface of sheath glabrous; ligules wider than tall . . . . **C. serpenticola** (Fig. 2A)

      4′ Ventral surface of sheath pubescent; ligules taller than wide . . . . **C. scirpoidea** Michaux var. **pseudoscirpoidea** (Rydb.) Cronq.

  2′ Culms pistillate 5

    5. Perigynia flat except over relatively small achenes, sessile, bases truncate . . . . **C. scabriuscula**

    5′ Perigynia plump, filled by achenes, with distinct stipes or tapered to cuneate bases 6

      6. Spikes 2–4, lowest well-separated or obvious, elliptic-ovate to subglobose (Fig. 2D, E); perigynia beaks bidentate . . . . **C. serpenticola**

      6′ Spikes usually solitary, rarely with 2 spikes, these overlapping; oblong-cylindrical; perigynia beak tips essentially entire, toothless . . . . **C. scirpoidea** var. **pseudoscirpoidea**

1′ Some or all culms bisexual 7

  7. Stigmas 4, (Fig. 3C); stigmatic surface warty, non-plumose at 15× (Fig. 3C); achenes quadrangular-based . . . . **C. concinnoides**

  7′ Stigmas 3 (Fig. 3B, G, R, S); stigmatic surface finely plumose at 15× (Fig. 3S); achenes trigonous-based 8

    8. Foliage pubescent; perigynia with 3 flat faces, obviously trigonous . . . . **C. gynodynama** Olney

    8′ Foliage glabrous; perigynia with 2 flat faces or plump-globose, never obviously trigonous 9

9. Perigynia body flattened except over the relatively small achene; perigynia shiny, purplish-black . . . . **C. scabriuscula**

9′ Perigynia body plump, filled by the relatively large achene; perigynia dull, green to brown or purple 10

10. Numerous short-peduncled basal spikes hidden among the rosettes 11

11. Pistillate scales with 1 prominent midvein, perigynia lacking nerves 12

12. Perigynia > 1.7 mm wide, body subspherical; staminate scales scabrous near tip of midrib; coastal dunes and headlands . . . . **C. brevicaulis**

12′ Perigynia < 1.6 mm wide, body elliptic; staminate scales not scabrous; Coast Range and inland . . . . **C. rossii** (Fig. 3R)

11′ Pistillate scales with 3–5 prominent nerves; perigynia strongly nerved 13

13. Foliage pale or glaucous; perigynia with beaks ca. equal stipes; perigynia bodies barrel-shaped, broadest near middle; leaves generally papillate on underside at 40×; all basal spikes erect on short peduncles . . . . **C. brainerdii** (Fig. 3B)

13′ Foliage green, not glaucous; perigynia with stipes ca. 1.5–2 times as long as beaks, perigynia bodies obovoid, broadest near beaks; leaves papillate only on veins or epapillate at 40×; some basal spikes arched on long peduncles . . . . . . **C. globosa** (Fig. 3G)

10′ Lacking short-peduncled basal spikes 14

14. Staminate spikes 2–3, the terminal spike > 30 mm long; culms 60–100 cm tall; emergent in shallow marshes . . . . **C. pellita** Muhl.

14′ Staminate spikes solitary and < 30 mm long; culms < 50 cm tall; upland mesic or xeric sites 15

15. Scales and base of inflorescence bract green to red (like apples); pistillate scales and lower staminate scales with conspicuous white margins 0.4–0.8 mm wide; populations lacking unisexual culms; approaching our area on volcanic substrates in the Cascade Mountains . . . . **C. inops** ssp. **inops**

15′ Scales and base of inflorescence bract dark purple or black (like beets); pistillate scales and lower staminate scales with thin white margin 0.1–0.2 mm wide; populations primarily unisexual culms; ultramafic substrates in the Klamath Mountains . . . . **C. serpenticola** (Fig. 2)

Sexual expression. The facultative production of unisexual culms is unusual in *Carex* section *Acrocystis.* Asian and eastern North American taxa with sporadic unisexual culms are otherwise not very similar to *Carex serpenticola.* Howell (1949) noted that some *Carex globosa,* when on serpentine, can produce a "terminal inflorescence . . . either entirely staminate or . . . [with] 1 (or rarely 2) pistillate flowers." His voucher (*Howell 19368A* RSA!) approaches *C. serpenticola,* with some culms that apparently aborted most or rarely all lateral pistillate flowers. These plants, however, maintained the diagnostic heavily nerved perigynia and 3–5-nerved pistillate scales (Fig. 3G) of *C. globosa.* Fewer than 1% of the *C. globosa* stems we examined in the field and herbarium exhibited unisexual culms (by reduction). Culms of *C. globosa* (commonly) and *C. serpenticola* (rarely) produce essentially basal long-peduncled pistillate spikes, which might be confused with unisexual culms.

Carex serpenticola produces two culm types, bisexual and unisexual. We sampled 179 stems from 15 populations, and found 92% of the culms were unisexual (Fig. 2A, D). Unisexual culms were staminate (74 stems, 41% of sample) or pistillate (90 stems, 50%). One rhizome can form both truly staminate culms and functionally staminate culms. The latter exhibit a terminal staminate spike and one (or more) aborted lateral pistillate spikes. Aborted spikes are marked by a bract (Fig. 2A). Some culms in most populations develop 1–2 lateral pistillate spikes near the terminal staminate spike (Fig. 2B). One rhizome can bear both unisexual and bisexual culms. Thus *C. serpenticola,* like most members of the genus, is not dioecious. Standley (1985) found dioecy in fewer than 10 of the ca. 1500 *Carex* species worldwide. Bisexual culms of *C. serpenticola* have staminate (Fig. 2B) or rarely gynecandrous (Fig. 2C) terminal spikes. Our field observations raise questions about the influence of age, site conditions, and vagaries of climate on the sex of inflorescences. More research is needed to explain sexual expression in *C. serpenticola.*

Ecology. Carex serpenticola is associated with the largest ultramafic exposures in North America. The soils derived from ultramafic bedrock are generally referred to as serpentine by biologists. In a region otherwise heavily forested, serpentine soils support sparse, low-productivity plant communities like *Darlingtonia* fens, *Umbellularia-Rhododendron occidentale* (Torrey & A. Gray) A. Gray riparian strips, *Pinus jeffreyi* Grev. & Balf. savannas, and transitional or successional scrublands dominated by *Quercus vaccinifolia, Rhamnus californica,* and *Lithocarpus densiflorus* (Hook. & Arn.) Rehder var. *echinoides* (R. Br. Campst.) Abrams (Jimmerson et al. 1995). We located populations of *C. serpenticola* in or at the margins of each of these serpentine vegetation assemblages. Habitats supporting the most robust individuals of *C. serpenticola* were vernally moist to mesic meadows and

TABLE 1. ULTRAMAFIC ENDEMICS (*SENSU* KRUCKEBERG 1984; SMITH AND SAWYER 1988) FOUND AT *CAREX SERPENTICOLA* SITES.

Arnica cernua Howell
Calochortus howellii S. Wats.
Cardamine nuttallii E. Greene var. *gemmata* (E. Greene) Rollins
Erythronium citrinum S. Watson
Hastingsia bracteosa S. Wats.
Lomatium howellii (S. Watson) Jepson
Poa piperi A. Hitchc.
Salix delnortensis C. Schneider
Sanicula peckiana J. F. Macbr.
Senecio hesperius Greene
Viola cuneata S. Watson

riparian strips, at or near the upland-wetland boundary. Populations were observed between 60 and 1200 m elevation on slopes of all aspects. Slopes were flat or gentle at those sites with the largest plants. Compact plants with short culms and falcate leaves were found on steeper, well-drained slopes. The forests were usually serpentine savannas or riparian strips, dominated by *Pinus jeffreyi, Calocedrus decurrens* (Torrey) Florin, *Arctostaphylos nevadensis* A. Gray, *A. patula* E. Greene, *A. viscida* C. Parry, *Ceanothus cuneatus* (Hook.) Nutt., *C. pumilis* E. Greene, and *Juniperus communis* L. Some associated non-endemic taxa, typical of serpentine soils, were *Aspidotis densa* (Brackenr.) Lellinger, *Carex mendocinensis* Olney, *Cerastium arvense* L., *Deschampsia cespitosa* (L.) Beauv., *Erythronium citrinum* S. Watson, *Festuca idahoensis* Elmer, *Hastingsia alba* (Durand) S. Watson, *Microseris howellii* Gray, *Poa secunda* J. S. Presl, *Ranunculus californicus* Benth., *R. occidentalis* Nutt., *Scirpus criniger* Gray, *Trillium rivale* S. Watson, and *Viola lobata* Benth.

Carex serpenticola appears to be a narrowly distributed edaphic endemic. Many of its associates are also endemic to the ultramafic exposures in the area (Table 1). Unlike *C. serpenticola, C. globosa* is a *bodenvag* species, abundantly documented from both ultramafic and other bedrock exposures, at least from Marin Co., California and south. Curiously, we have not seen evidence that *C. globosa* grows on serpentine soils north of Marin County.

Individuals of *C. serpenticola* from wetland margins are often large and easy to locate, at least prior to the summer drought. Small individuals with a compact growth form, widely scattered across drier serpentine slopes, are harder to find.

We have noted that *C. globosa* occupies different habitat than *C. serpenticola* where their ranges converge in northern California. The former is found in partial to full shade, under or at the edge of dense forests with sparse understory, close to the coast and at low elevations (<300 m). *Carex globosa* is on well-drained non-serpentine soils in this wet climatic region. Dominant woody plants are often *Sequoia, sempervirens,* (D. Don) Endl. *Quercus chrysolepis* Leibm., *Lithocarpus densiflorus,* or *Pseudotsuga menziesii* (Mirbel) Franco, over *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene and *Vaccinium ovatum.* From Marin Co., California, and south, however, *Carex globosa* is well documented in a variety of different plant communities and on serpentine or non-serpentine soils (e.g., Hardham 1962; Howell 1949).

Carex serpenticola individuals flower and fruit earlier than most *Carex* in the region, which may help explain the paucity of specimens found in herbaria. Flowering occurs from the first week of March to early May. Mature fruiting plants were collected between late April and June, depending on elevation and exposure.

Pollination ecology might explain why the stigmatic surfaces differ in *C. serpenticola* and *C. concinnoides. Carex serpenticola* and *C.* sect. *Acrocystis* display inconspicuously colored, slender subplumose stigmas (Fig. 3S). They are typical wind-pollinated sedges, and we never observed insects visiting their flowers. Leppik (1955) reported insect-pollinated *Carex* spp. with bright white floral displays composed of showy bracts, and bright white anthers and stigmas. *Carex concinnoides* may be evolving towards entomophily. We observed Hymenoptera occasionally visiting the striking white clustered presentation of stigmas on *C. concinnoides,* topped with showy pale yellow to whitish anthers. The broad, conspicuous warty stigmas of *C. concinnoides* (Fig. 3C) might attract pollinators and enhance pollen capture from non-aerial sources.

We are not aware of seed dispersal investigations among the representatives of *Carex* sect. *Acrocystis* in the Klamath region. Some taxa (e.g., *C. brainerdii, C. brevicaulis,* and *C. rossii*) present their mature fruits close to ground level on abbreviated culms. Other members of the section position some of their fruit output on the ground with long, weak, basal peduncles (e.g., *C. globosa*). *Carex concinncides* (sect. *Digitatae*) and *C. serpenticola* have erect flowering culms that arc to place infructescences on the soil surface (Fig. 2F). All these growth habits suggest adaptations facilitating diaspore collection by ants in upland habitats (Handel 1976, 1978). Seed dispersal by ants is well documented in a variety of plants and habitats (e.g., Beattie 1985; Bossard 1991; Boyd 1996). The plump, pale fresh stipes in *C. globosa* and *C. serpenticola* resemble structures described or illustrated as ant lures in sedges such as *C. communis* Bailey, *C. jamesii* Schwein., *C. laxiculmis* Schwein., *C. pedunculata* Muhl., *C. pilulifera* L. and C. *umbellata* Schkuhr (Kjellsson 1985a, b; Beattie and Culver 1981). Dried herbarium material (Fig. 3) does not reveal how expanded the stipe is in nature. We observed the velvety tree ant (*Liometopum occidentale,* Formicidae, Dolichoderinae) carrying off mature perigynia we scattered on the ground near fruiting *C. serpenticola.* We suspect myrmecochory in *C. serpenticola,* which differs from most *Carex* in its upland habitat, its "weeping" stems, and peculiar perigynial bases.

Conservation status. Carex serpenticola appears to be a narrow endemic (Fig. 1), but its status, distribution and abundance are still poorly documented. We discovered populations inland on extensive serpentine areas, as well as coastal colonies on small, isolated serpentine knobs. *C. serpenticola* may be a widespread and characteristic member of the regional ultramafic flora, on what geologists refer to as the Josephine ophiolite.

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NOTES

ANTENNARIA DIOICA (ASTERACEAE: INULEAE): ADDITION TO THE VASCULAR FLORA OF CALIFORNIA.—Jerry G. Chmielewski, Department of Biology, Slippery Rock University, Slippery Rock, PA 16057, USA.

The California flora includes about one-third of the North American *Antennaria* species (Bayer 1984; Bayer and Stebbins 1993; Chmielewski 1997; Chmielewski and Chinnappa 1988; Chmielewski et al. 1990). Specifically, Jepson (1925) included eight species, Munz (1959) included 10 species, Ferris (1960) included 13 species, and Stebbins and Bayer (1993) included 14 species. Only four species, *A. argentea* Benth., *A. dimorpha* (Nutt.) Torrey & A. Gray, *A. geyeri* A. Gray, and *A. luzuloides* Torrey & A. Gray were consistently included among the species by these respective authors.

Here I report the occurrence of *Antennaria dioica* (L.) Gaertner in the California flora. Although Jepson (1925) included *A. dioica,* the varieties *congesta* DC., *corymbosa* Jepson, *kernensis* Jepson, *marginata* Jepson, and *rosea* Eat. were not consistently considered to be part of the species, but rather distinct species or synonyms of others, in subsequent treatments of either the flora (Munz 1959; Ferris 1960; Stebbins and Bayer 1993) or genus (Bayer 1984; Bayer and Stebbins 1993; Chmielewski 1997; 1998; Chmielewski and Chinnappa 1988; Chmielewski et al. 1990).

Antennaria dioica, the mountain or dioecious cat's-paw, is a diploid (Fedorov 1969, Bayer 1984), dioecious, mat-forming species that was described from Europe. The species is characterized by green, glabrous, occasionally tomentose adaxial leaf surfaces and white or pink, broadly obovate (staminate plants) or oblong-obovate (pistillate plants) involucral bracts. It previously was reported to be distributed across northeastern Europe from Scandinavia and the British Isles, eastward into Asia as far as Japan, northward to the Kamchatka Peninsula, eastward to Bering Island and western Aleutian Islands (Hultén 1949; 1968; Anderson 1959; Polunin 1959; Welsh 1974). The species typically inhabits heaths, dry grasslands, sandy or stoney slopes, and gravelly soil in the alpine zone (Polunin 1959; Tutin et al. 1976).

The single collection of *Antennaria dioica* that is the basis of this report consists of three staminate shoots bearing immature, pink-bracted involucres. These specimens are morphologically similar to hundreds of collections of *A. dioica* that I have observed from the Aleutian Islands and Europe. Hultén (1949) indicated that Aleutian Island material did not appear to be closely related to any American species of *Antennaria* known to him. Circumscription of the species by Jepson (1925), however, indicated similar features to *A. marginata* E. L. Greene [syn. = *A. dioica* var. *marginata* (E. L. Greene) Jepson] from southwestern North America (Bayer and Stebbins 1987; Chmielewski et al. 1990). The two taxa differ in that the flowering stems and leaves of *A. marginata* bear distinctive, purple, glandular hairs, whereas those of *A. dioica* do not. Further, the stolon surface in *A. marginata* is densely woolly, but only pubescent in *A. dioica* (Bayer and Stebbins 1993).

The several thousand kilometer range extension (Aleutian Islands to California) is unusual, although not without precedent in the genus. It was not until the morphological limits were clarified for species of *Antennaria* from the arctic and Cordilleran regions that several species, including *A. alborosea* A. E. Porsild, *A. alpina* (L.) Gaertner, *A. aromatic* Evert, and *A. densifolia* A. E. Porsild, were shown to have large range extensions (Malte 1934; Porsild 1950; Porsild and Cody 1980; Evert 1984; Bayer 1989; Chmielewski and Chinnappa 1988; Chmielewski et al. 1990; Chmielewski 1993, 1996, 1998). The occurrence of *A. dioica* in the California mountains is suggestive of a more continuous, northward, preglacial distribution. The lack of previous reports from continental North America may be the result of factors working independently or in concert. First, the species may be restricted to the Sierra Nevada and represents either a disjunct population due to recent colonization, or alternatively is a remnant of a once more extensive distribution. Second, inaccessibility to much of the subalpine and alpine habitat in western North America at a reasonable cost has concurrently limited botanical exploration and collection. Because this part of the subalpine and alpine California flora is remote, it is among some of the least collected and explored. Third, to the uninitiated, *Antennaria* species are oftentimes difficult to determine, especially when the quality of the specimen is poor, that is, when not in good flowering or fruiting stages. Since neither the first nor second scenarios may be reasonably tested, the third may be at least partially dismissed based on my past experience with the genus. Admittedly, I have not seen all western North American collections however. It is my belief that in its entirety the second scenario is the most likely.

Antennaria dioica (L.) Gaertner, De Fruct. Sem. Pl. 2: 410. 1791. Basionym: *Gnaphalium dioicum* L. Sp. Pl. 850. 1753. Type locality: Habitat in Europae apricis aridis. Range extension: California, Inyo Co., Sierra Nevada, near Margaret Lakes, east of Bishop Pass, among granite fell fields and scattered *Pinus albicaulis,* elev. 10,800 ft, 19 Jul, 1962, *Betty H. Johnson 692,* CAS 898202.

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REVIEW

THE ONCE AND FUTURE FOREST: A GUIDE TO FOREST RESTORATION STRATEGIES. By L. J. Sauer. 1998. Island Press, Covelo, CA. 350 p. Hardcover, $50.00. ISBN 155963555255.

This book focuses on the restoration of urban forests and parks in the northeastern United States, although concepts covered can be transported to other areas, particularly those related to the social aspects of restoration. The book begins by reviewing important ecological concepts such as succession, fragmentation, and disturbance. Other issues discussed include how wildlife, the hydrologic cycle, and landforms/soils have been affected by urbanization, the section on changes in hydrology is particularly interesting.

Issues surrounding the restoration of areas dominated by non-native and opportunistic native species are extensively covered. Restoration is presented as a combination of art and science, and community involvement is paramount. One central idea present throughout the book is the necessity of local community involvement in restoration projects. I have personally witnessed many restoration projects that have failed because the people involved never sought local involvement, particularly in urban areas. The book advocates the need for monitoring to accompany all restoration projects and tells us that this is often neglected. I also believe monitoring is critically needed if the science of restoration is to move forward.

Watershed or large spatial scales is advocated in restoration projects. It is certainly not possible to include all such lands in all projects but people should consider how lands beyond their local sites could effect the project. The book tells us that there is no "step-by-step" method in restoration, rather a long-term effort is necessary requiring a high degree of expertise and commitment. The book also challenges the idea of "wilderness" and I believe correctly states that many landscapes have been affected by the practices of indigenous peoples for long periods.

The book states that the most important conditions for a successful restoration project are for it to be community- and science-based. To be community-based, it must represent a consensus, which in turn requires that it be participatory. Science-based restoration projects must be documented and monitored. The book advocates the best way to convey real information to a community is to have them gather the information themselves, through monitoring both before and during restoration.

The later chapters provide specific techniques that can be used in restoration projects. This section of the book can be thought of as a practical restoration guide, the sections on building soil systems and restoring natural water systems are very good. Specific field examples are primarily given from the northeastern United States, particularly Central Park in New York. This section could have been improved by including more examples from other areas in the United States (southeast, midwest, west) but compromises must be made to keep a book manageable, the author also writes from her strengths in the northeastern United States. This book could be improved by including additional references; in some cases, only one view is presented on topics that currently have diverse interpretations.

I recommend this book to people interested in developing community-based restoration projects. As populations grow the ecosystem effects of urbanization will increase and this book gives information on how to manage and restore these areas.

—Scott Stephens, Natural Resources Management Department, Cal Poly State University, San Luis Obispo, CA 93407.

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QUERCUS GARRYANA HOOK. (FAGACEAE) STAND STRUCTURE IN AREAS WITH DIFFERENT GRAZING HISTORIES

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ABSTRACT

We estimated seedling, sapling, and mature tree densities for two historically defined grazed-classes (LOW and HI) of the Mad River Ranger District, Six Rivers National Forest, CA. Using *Quercus garryana* Hook. vegetation coverages on a geographic information system and a variable probability sampling scheme, 9 oak stands were randomly selected from each grazed-class. We employed a second sampling stage by selecting 3 simple random samples of 100-m^2 quadrants from each of the 18 oak stands selected in the first sampling stage. We found greater seedling and mature tree densities for the HI grazed-class and greater sapling densities for the LOW grazed-class. Sapling densities were roughly double and seedling densities about 5 times mature tree densities regardless of grazed-class. We suggest that increased grazing intensity creates favorable environments for seedling survival, but may ultimately reduce the number of seedlings transitioning to the sapling size-class. Our results showing roughly 2:1 sapling to mature tree ratios indicate that *Q. garryana* regeneration is occurring on these rangelands.

The historical clearing of oak woodlands to maximize forage yield for livestock grazing or to convert to agricultural production has been well documented (Allen-Diaz and Holzman 1991; Bartolome et al. 1986; Bartolome and Standiford 1992; Muick and Bartolome 1987). Along with suburban encroachment, these land-use practices have been implicated as factors in the postulated decline of *Quercus douglasii* Hook. & Arn (blue oak), *Q. lobata* Nee (valley oak), and *Q. engelmannii* E. Greene Engelmann oak regeneration (Griffin et al. 1987; Muick and Bartolome 1985; Pavlik et al. 1991). Regeneration problems manifested as bimodal age structure biased towards seedlings and mature trees with a lack of sapling age-classes have been cited for each of the above species (Bartolome et al. 1986; Griffin 1971; Griffin 1976; Lathrop et al. 1990).

Quercus garryana Hook. has the longest north-south distribution among western *Quercus* spp. The northern range of *Q. garryana* extends onto Vancouver Island in Canada at 50°N latitude and the southern range runs into Los Angeles County at 34°N latitude (Stein 1990). The coastal range of *Q. garryana* terminates in Marin County, but it is found further south along the western slope of the Sierra Nevada in a limited and disjunct distribution.

The relationships between Northcoast *Q. garryana* populations and livestock grazing, land-use practices, and suburban encroachment have received limited attention (Griffin et al. 1987; Muick and Bartolome 1985; Reed and Sugihara 1986). Sugihara et al. (1987) defined plant community types for Northcoast *Q. garryana*-dominated landscapes and Saenz and Sawyer (1986) studied grazing effects on *Q. garryana* understory composition. Literature treating potential domestic livestock grazing effects on *Q. garryana* is limited to a statewide survey conducted by Muick and Bartolome (1987) and modeling efforts by Anderson and Pasquinelli (1984). Muick and Bartolome (1987) found no significant *Q. garryana* distribution patterns related to livestock grazing on the Northcoast. They assessed the adequacy of the existing *Q. garryana* sapling populations to replace trees lost through mortality by examining sapling to mature tree ratios on 13 Northcoast plots. Sapling to adult tree ratios were less than 1:1 for *Q. garryana* in their study, yet 75% of all individuals sampled were seedlings indicating no lack of seedling establishment, but a failure of seedlings to survive the transition to sapling size-classes.

Bolsinger (1988) assessed the age structure of *Q. garryana* by drawing inferences from seedling and

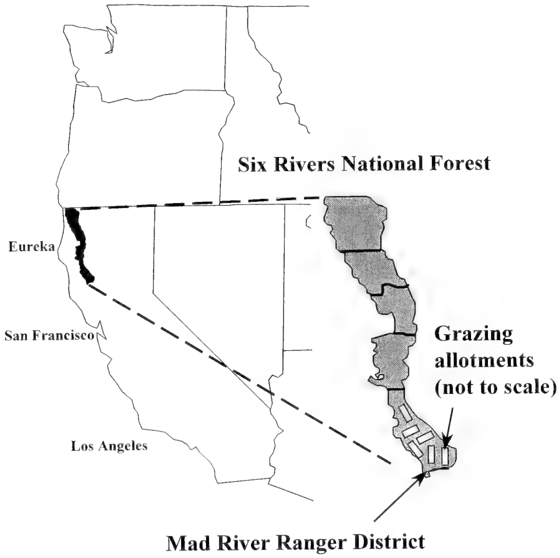

FIG. 1. Study sites located within Mad River Ranger District, Six Rivers National Forest, Humboldt County, CA.

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sapling counts from systematic plots established across California. He found 45% of *Q. garryana*-type plots contained no seedlings and 38% contained no saplings suggesting the potential for insufficient replacement populations or that present spatial distributions may be shifting. Anderson and Pasquinelli (1984) predicted declining *Q. garryana* distribution under "present trend" conditions. Their model parameterized livestock grazing, wildlife pressure, fire frequency, and weather conditions specific to the Northcoast's Sonoma and Mendocino Counties.

We designed this study to describe *Q. garryana* stand structure and to examine livestock grazing intensity effects on this structure. Specifically, we sought to determine whether differentially grazed stands contained significantly different densities of seedlings, saplings and/or mature trees. This information should provide insight about the regeneration status of *Q. garryana* on California's Northcoast.

METHODS

Study site. We conducted this study June and July 1995 on the Mad River Ranger District (MRRD), Six Rivers National Forest (SRNF), and Humboldt County, CA (Fig. 1). SRNF lies within sections of Humboldt, Del Norte, Siskiyou, and Trinity Counties in the northern California coast range. MRRD is typified by a Mediterranean climate of cool, moist winters and warm, dry summers. Average January temperatures range from −2 to 4°C (28 to 40°F) and average July temperatures range from 17 to 27°C (64 to 80°F) (Oakeshott 1978). Annual precipitation ranges from 127 to 152 cm (50 to 60 in). Eighty percent of this precipitation occurs between November and April. Miles (1993) described MRRD soils as derived from the Franciscan Melange Complex with *Quercus garryana* stands occurring predominantly on the Oxalis-Hecker-Doty association. These are well-drained, pale brown loams with moderate to strong blocky structure and a slightly acidic nature.

TABLE 1. SUMMARY OF HISTORICAL GRAZING ALLOTMENT DATA USED FOR ASSIGNING SIX GRAZING ALLOTMENTS TO ONE OF TWO GRAZED-CLASSES. [1] AU = Animal unit = 1 individual.

Allotment	Mean annual [1]AU	Oak ha	Oak ha·AU^{-1}	Grazed-class
Long Ridge	88	1859	21	LOW
Norris-Green	108	1839	17	LOW
Barry Creek	109	1484	14	LOW
Soldier Creek	66	616	9	HI
Buck Mountain	91	766	8	HI
Van Duzen	166	1166	7	HI

Grazed-classes. As an initial grazing allotment screening, we asked MRRD range personnel to identify 3 MRRD grazing allotments with high historical grazing intensity and 3 with relatively low historical grazing intensity. These allotments were to represent each of two grazed-classes (LOW or HI; Table 1). MRRD range personnel stated that each of the 3 LOW grazed-class allotments were historically grazed very lightly, and had no permitted grazing activity for 5 to 10 years prior to this study. MRRD range personnel also confirmed that historical permitted use (1950 to 1981) continued on the 3 HI grazed-class allotments after 1981.

We derived our grazed-classes by defining grazing intensities that were based on allotment-wise *Q. garryana* hectares (estimated using 1990's GIS technology) because we believed that the majority of available forage, hence grazing pressure, occurred on the oak woodland/savanna vegetation type. We used annual animal units records (1950 to 1981) and total *Q. garryana* hectare estimates for each allotment to quantify historical grazing intensities. Actual allotment-wise stocking rates were set by MRRD range managers using their assessments of suitable grazing hectares. Suitable hectares were comprised of oak savanna; coniferous forest; and small, open grassland areas known as "glades". However, Sawyer et al. (1977) described the understory layer of the Northcoast Douglas-fir—tanoak type (*Pseudotsuga menziesii* (Mirbel) Franco—*Lithocarpus densiflorus* (Hook. & Arn.) Rehder) as sparse, less developed, and dominated by shrubby *L. densiflorus* while others have confirmed this type of coniferous forest provides much less herbaceous productivity and available forage than oak woodlands (Sharrow and Leininger 1982). While glades provide excellent forage, the fraction of the allotments in this type is very small. Therefore, we assumed that oak woodlands provide the bulk of forage for grazing animals and only used *Q. garryana* hectares in grazing intensity quantification.

Sampling. Assuming that the total number of seedlings, saplings, and mature trees were a function of the area of any oak stand, we employed a 2-stage sampling design consisting of a variable probability selection scheme as the 1st-stage and simple random sampling (SRS) as the 2nd-stage. Nine *Q. garryana* stands were selected from each of 2 grazed-class subsets with probability proportional to the area of the remaining *Q. garryana* stands within that particular grazed-class. Hence, larger *Q. garryana* stands had higher selection probabilities. We incorporated these probabilities, known as 1st-order inclusion probabilities (Overton and Stehman 1995), into Horvitz-Thompson (HT) estimation of the size-class densities for each grazed-class (Horvitz and Thompson 1952). We calculated sample-based sampling variance estimates for the two-stage HT estimator using the Sen-Yates-Grundy (SYG) method (Yates and Grundy 1953). This method requires that the 2nd-order inclusion probabilities for the selected 1st-stage units (*Q. garryana* stands) be known. Second-order inclusion probabilities are the probabilities that any 2 particular *Q. garryana* stands were both chosen during the selection process. We estimated 2nd-order inclusion probabilities using the list sequential method outlined by Sunter (1977). The 2nd sampling stage entailed SRS of three 100-m^2 quadrats from each unit (18 oak polygons) selected in the 1st stage. We then scaled seedling, sapling, and mature tree estimates from each grazed-class, deriving mean values (per 100 m^2) for standardization and comparison ease. Ninety-five percent confidence intervals were constructed around each size-class density estimate for statistical comparisons.

We obtained Universal Transverse Mercator (UTM) coordinates for each point selected during the 2nd-stage of sampling from a geographic information system database. We arbitrarily decided that these UTM coordinates would serve as the southeastern corner of each 100-m^2 sampling quadrat. Quadrats were located in the field with a handheld geographic positioning system. We delineated boundaries of each quadrat with a handheld compass and cloth tape. Seedlings (<1 cm basal diameter), saplings (<10 cm and >1 cm basal diameter), and mature trees (>10 cm basal diameter) were enumerated for each quadrat. Definition of size-classes followed Muick and Bartolome (1987). We did not age individual seedlings, saplings, or mature trees.

We estimated several site variables at each quadrat to determine potential environmental disparities among the two grazed-classes. These variables included 1) slope, 2) azimuth, 3) canopy cover, and, 4) dominant herbaceous understory type. The sine of slope in degrees and the cosine of azimuth in degrees from N were multiplied to create a solar insolation indicator variable *northness* (*sensu* Borchert et al. 1989) which potentially varied from $+100$ to -100. Greater positive values of this variable indicate a N-facing steep slope while higher negative values indicate a S-facing steep slope. We ocularly estimated canopy cover at each site. We characterized the herbaceous understory type at each quadrat by making 6 randomly located herbaceous species cover estimates within the quadrat. Each estimate was made with a 10-point frame using the first foliar intercept criterion for each pin placement (Heady and Rader 1958). We then classified species into one of the following functional groups: 1) annual grass, 2) annual forb, 3) perennial grass, 4) perennial forb, or 5) woody perennial. Bare ground and dry organic matter 10-point frame hits were also recorded and categorized.

We estimated edaphic characteristics at a randomly chosen 1 of 3 quadrats at each of the 18 *Q. garryana* stands. Soil pits were excavated for estimation of the following variables: 1) solum depth, 2) rooting depth, 3) clay percent (by feel), 4) rock fragment percent (2-mm mesh sieve), 5) pH (LaMotte colorimetric method), 6) moist Munsell color value, 7) textural-class (by feel), and 8) available water-holding capacity (USDA 1993). Parametric tests were not performed to assess significant differences for these variables between grazed-classes, nor to correlate them to *Q. garryana* size-class estimates because they were collected with the variable probability sampling scheme described above. By definition, unequal probability samples do not meet the parametric test requirement of independent, identical distributions between groups (Sarndal et al. 1992). Therefore, we present continuous data in tabular form (Table 2) and discrete data in graphical (Fig. 2) form for grazed-class comparisons. Where tabular and graphical examination suggested differences between the grazed-classes in a given variable, we tested joint bivariate distributions with a two-dimensional Kolmogorov-Smirnov (2DKS) nonparametric procedure (Garvey et al. 1998). Two-DKS uses a bootstrapping technique (500 Monte Carlo simulations) to iteratively compare randomly derived expectation matrices with an observed joint-distribution matrix. This technique is effective at assessing both linear and non-linear relationships among bivariate distributions and makes no assumptions about functional responses.

RESULTS

Comparison of 95% confidence intervals showed that seedling and mature tree densities were greater in the HI grazed-class while sapling densities were greater in the LOW grazed-class (Fig. 3). Mean estimates are reported ± the 95% confidence interval and statistical significance determined by overlap or

Table 2. Sample Size (n), Means, and Standard Errors (SE) of Continuous Environmental Variables for Each Grazed-Class. [1] Units defined in text.

		HI		LOW	
Variable	n	Mean	SE	Mean	SE
Canopy cover (%)	27	54.3	4.5	63.7	4.4
Slope (degrees)	27	17.5	1.4	26.9	1.4
[1]Northness	27	2.6	4.9	−5.7	4.6
AWC	9	4.0	0.5	4.3	0.3
pH	9	6.2	0.1	6.2	0.1
Solum depth (cm)	9	115.7	4.1	118.4	3.1
Rooting depth (cm)	9	76.2	2.0	76.2	0.7
Clay (%)	9	15.4	1.1	17.4	0.5
Rock fragment (%)	9	46.0	3.6	42.7	1.1
Moist Munsell color value*	9	3.3	0.1	3.5	0.1

not. The seedling density estimate for the HI grazed-class was 33.5 ± 3.3 seedlings per 100 m^2 compared to 19.1 ± 1.2 seedlings per 100 m^2 for the LOW grazed-class. The mature size-class followed the same trend in that the HI mature tree estimate was greater than the LOW mature tree estimate (HI = 5.0 ± 0.5, LOW = 3.9 ± 0.4). Sapling size-class density estimates were the opposite. There were on average more saplings per 100 m^2 in the LOW grazed-class (10.8 ± 0.3) than in the HI grazed-class (9.3 ± 1.1; Fig. 3).

The greatest disparity in environmental variables between the two grazed-classes was average slope (HI = 17.5 ± 1.4, LOW = 26.9 ± 1.4; Table 2). Other continuous variables appeared quite similar so were not analyzed further than reporting means and standard errors. Examination of the dominant herbaceous understory type standard errors (Fig. 2) indicated similar distributions of this categorical variable between grazed-classes. Soil textural-class differences were evident; all 9 LOW grazed-class sites were classified as loams while 5 of 9 HI grazed-class soils were determined to be loams with 1 clay loam and 3 sandy loams. Only 1 soil pit per site was dug, therefore no dispersion statistics were estimable from these data.

Two-DKS results indicated that the joint distributions between slope and seedling density, slope and sapling density, and slope and mature tree density (Fig. 4) were not significantly different from random (P = 0.60, 0.53, and 0.50; respectively).

Discussion

Greater seedling densities coupled with lower sapling densities in areas with greater grazing intensities suggest that herbivory of surrounding vegetation may positively influence *Q. garryana* seedling survival and recruitment, but that incidental trampling and herbivory of the seedlings may discourage transition to the sapling stage. While this needs experimentation, there are experimental results for *Q. douglasii* which corroborate our inferences and may help to explain our observations. *Quercus douglasii* and *Q. garryana* are taxonomically and ecologically similar species. Both belong

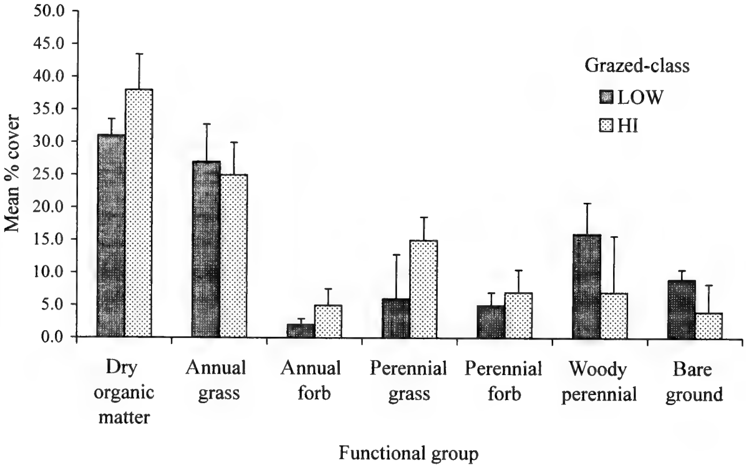
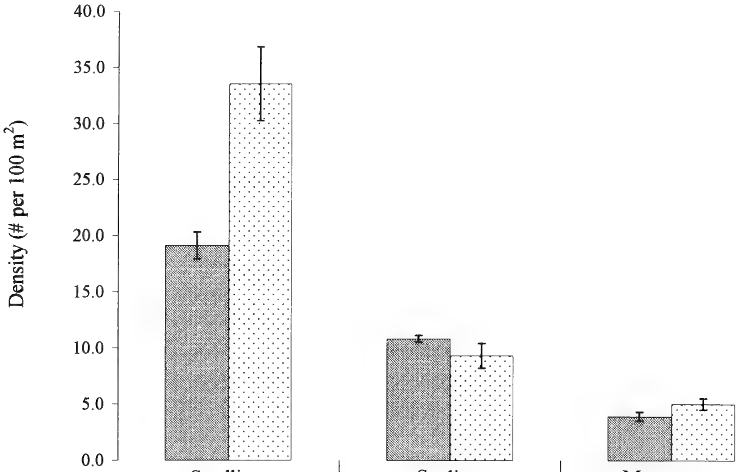


Fig. 2. Functional group cover means and standard errors (n = 9 for each grazed-class) as determined by 10-point frame estimates.



	Seedling	Sapling	Mature tree
▨ LOW-grazed	19.1	10.8	3.9
■ HI-grazed	33.5	9.3	5.0

FIG. 3. Seedling, sapling, and mature tree density means and 95% confidence intervals for each grazed-class.

to the white oak subgenus *Lepidobalanus* and occupy apparently similar ecological sites—shallow, rocky hill slopes—in distinctive Californian climatic regions (Rundel 1979; Rundel 1986; Stein 1990). Additionally, these species freely hybridize along climatic transition zones (Tucker 1979).

In greenhouse experiments, Gordon et al. (1989) found greater *Q. douglasii* seedling emergence and growth responses in annual forb (*Erodium* spp.) seeded plots compared to annual grass (*Bromus diandrus* L.) seeded plots. They attributed this to increased rates of water stress in the annual grass plots. This illustrates that competition between *Q. douglasii* seedlings and neighboring herbaceous vegetation does occur, however, Gordon et al. (1989) obtained their results absent defoliation. Welker and Menke (1990) reported that defoliation of annual vegetation surrounding growing *Q. douglasii* seedlings was beneficial in reducing evapotranspiration of competing vegetation, thereby reducing the rate at which the *Q. douglasii* seedlings encountered water stress. These results offer potential explanations for our findings, whereby herbivory is releasing *Q. douglasii* seedlings from resource competition with surrounding vegetation. Resources being competed for are probably water, nutrients, and space. However, this phenomenon is likely overwhelmed at higher grazing intensities where grazing selectivity lessens and seedlings are depredated more or less incidentally.

Hall et al. (1990) showed that at very high stocking rates, where animals are actually competing for space as well as forage, increased seedling depredation rates occurred. However, with reduced stocking rates, Hall et al. (1990) found little to no livestock preference for *Q. douglasii* seedlings. Given their similarities, these results likely hold for *Q. garryana*. Seedling depredation is probably a function of forage production and availability, rodent populations (Davis et al. 1990), and stocking rate. Experimental evidence for *Q. garryana* is needed.

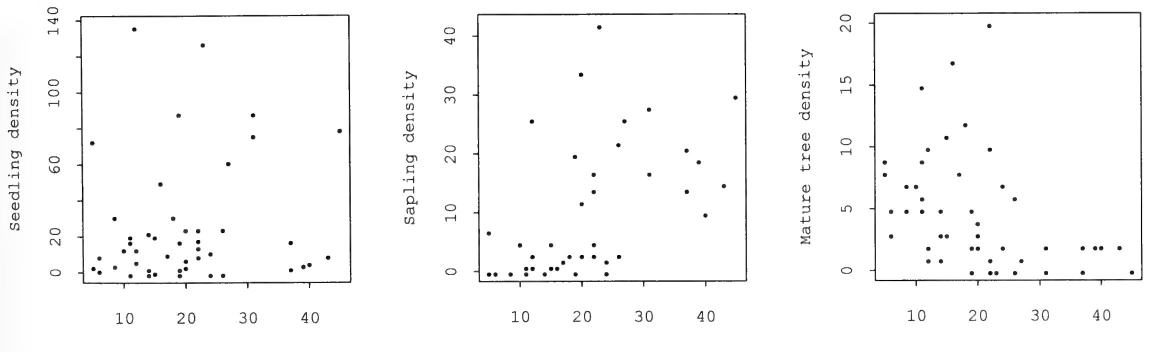


FIG. 4. Joint bivariate distributions of slope and seedling density, sapling density, and mature tree density.

We did not measure microtopographic relief or estimate soil disturbance, but these factors may be important reasons for higher seedling densities. Because livestock grazing creates soil disturbance (Kauffman and Krueger 1984), areas of higher grazing intensity tend to have greater micro-relief and therefore a higher probability of radicle interception and penetration with the soil (Watt 1919).

During autumn months, *Q. garryana* dormancy decreases interspecific competition for light and water between annual grasses and *Q. garryana* seedlings (Hibbs and Yoder 1993). This reduction in photosynthesis and growth allows seedling underground biomass persistence and promotes carbohydrate storage in root systems (Hibbs and Yoder 1993) while the annual grasses dominate available resources. Domestic stock grazing in the spring results in annual grass defoliation as well as the incidental *Q. garryana* seedling defoliation and trampling. However, Hibbs, and Yoder (1993) have shown that *Q. garryana* is a prolific and adventitious sprouter. They found 20-year-old *Q. garryana* seedling roots with aboveground shoots less than 3 years in age. Hence, should the *Q. garryana* seedling survive defoliation and water stress until annual grasses have been grazed or completed their life cycle, the *Q. garryana* seedling taproot and fine root system can eventually access resources at lower soil depths where annual grasses are not competing. Indeed, we usually found a dense network of fine *Q. garryana* roots dispersed throughout the solum to a depth of 75+ cm (Table 2), while annual grass roots were not observed below the surface 10-cm. Seedlings able to establish these deeper roots should increase their survival chances via resource partitioning (*sensu* Brown 1998). However, resource partitioning is likely not achieved until *Quercus* seedlings have successfully negotiated interspecific resource competition mediated by cattle dietary preferences for herbaceous grasses and forbs. Coupled with an ability to survive many seasons of foliage removal via sprouting, resource partitioning may account for greater *Quercus* seedling densities in areas with higher grazing intensities.

Litter decomposition rate is another potentially important factor that may be differentially treated across grazing regimes. Desiccation is a major cause of germination failure in California's predominantly dry oak woodlands (Borchert et al. 1989). However, the consistently moist, but cool Northcoast environs are more likely to result in low decomposition rates leading to higher litter accumulation with a concomitant increase in acorn rot. Opening of the herbaceous layer to increased solar insolation via phytomass removal by livestock may reduce the potential for acorn rot, thereby increasing germination and seedling success. These hypotheses all need *in situ* experimental testing in *Q. garryana* stands.

Significantly greater mature tree densities in the HI grazed-class may be the best explanation for both greater seedling densities and lesser sapling densities in this group. It follows that more trees lead to more acorns leading to more seedlings. Transition from seedling to sapling is probably inhibited by lack of sufficient light and other resources due to crowding by mature trees combined with seedling defoliation and depredation by livestock. Allen-Diaz and Bartolome (1990) concluded that while recruitment of *Q. douglasii* seedlings was frequent, none of their seedlings made the transition into sapling size-classes.

Why was mature tree density greater in the HI grazed-class? The HI-grazed allotment group was generally found on gentler slopes that may have had some indirect effects on sapling to mature tree transition. For example, fires are known to burn less intensively on gentler slopes (Albini 1976) which might have provided a more favorable environment for tree development. Alternatively, deeper soils on sites with gentler slopes may have provided a microclimate more conducive to sapling to tree transition. However, our soil data revealed no evidence for this. Examination of maps and field observation revealed no obvious geomorphological or topographical patterns that might account for these differences.

Aside from the grazed-class comparisons of size-class densities, our results indicate that natural *Q. garryana* regeneration on these MRRD sites is not at risk. Representing roughly double the mature tree stock, densities of about 10 saplings per 100 m^2 seems a surplus. Should one tree from a well-stocked stand die at any given time, several saplings should be available for replacement. To truly assess regeneration status, mortality and survival rates between each size-class must be known. Our single season study did not permit estimation of mortality rates even for seedlings. Our point-in-time estimates of age structure do provide compelling evidence that regeneration of this species is occurring. Annual assessment of seedling mortality rates coupled with creative techniques for estimating sapling to tree transition probabilities and tree mortality rates are needed to verify our results and quantify the regeneration status of this resource.

CONCLUSIONS

Higher seedling but lower sapling densities with increased grazing intensity indicates that grazing at higher stocking rates does not affect *Q. garryana* seedling recruitment. There seems to be plenty of seedlings beneath and around tree canopies, but seedlings in the higher grazed areas are making the transition to the sapling size-class in lesser numbers than those in the more lightly grazed areas. However, our results indicate that *Q. garryana* regeneration is potentially occurring regardless of grazing pressures as evidenced by the roughly 2:1 sapling to tree ratio estimates found for both grazed classes.

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RELATIVE CONTRIBUTION OF BREEDING SYSTEM AND ENDEMISM TO GENOTYPIC DIVERSITY: THE OUTCROSSING ENDEMIC *TARAXACUM CALIFORNICUM* VS. THE WIDESPREAD APOMICT *T. OFFICINALE* (*SENSU LATO*)

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ABSTRACT

We used allozymes to compare the population genetic structure of *Taraxacum californicum* Munz & I. M. Johnston, an outcrossing endemic of the San Bernardino Mountains of California, to that of its widespread weedy relative, *T. officinale* Wigg. (*sensu lato*), an obligate apomict. The average number of allozyme phenotypes per population of the endemic was six times that of the widespread species. The endemic had about twice as much genotypic diversity (estimated by *D*) per population than the widespread species, and that diversity was distributed much more evenly per population than in the widespread species. Both species had about the same level of average interpopulation differentiation. For this pair of related species, breeding system apparently plays a more important role than endemism in determining population genetic structure.

Restricted geographical distribution and small population size are characteristics of endemic plant species. Population genetic theory predicts that these conditions should influence population genetic structure, and, as a consequence, endemic species are expected to lack or to have reduced genetic polymorphism (reviewed by Ellstrand and Elam 1993). Empirical evidence that supports those theoretical expectations is accumulating; and genetic diversity tends to increase with species range size (e.g., Hamrick and Godt 1990; Karron 1991).

Breeding systems are also known to influence population genetic structure. Theory predicts that predominantly selfing and asexual species should exhibit lower variation within populations and greater interpopulation differentiation than outcrossers (Jain 1976; Baker 1959; Levin and Kerster 1971). Again, empirical data support these expected trends (e.g., Ellstrand and Roose 1987; Hamrick and Godt 1990).

It is not clear which factor, breeding system or endemism, should have a greater influence on population genetic structure. The answer to this question will be an important one for plant conservation managers who are rarely able to assess the genetic diversity of every species put in their charge. Such information will help managers judge under what circumstances loss of genetic variation might be most severe. For example, all other things being equal, if breeding system is more important than endemism, then outcrossing species will have more genetic variation to lose as their populations become increasingly fragmented under disturbance whereas clonal or selfing populations will tend to start with relatively low variation.

Population genetic comparisons of predominantly outcrossing endemic species and related selfing or asexual widespread species would reveal valuable information about the relative contributions of breeding system and endemism to population structure. If endemism is the more important factor, then genetic analyses should reveal a paucity of genetic polymorphism within populations of the endemic species compared to a widespread selfing or asexual congener. Alternatively, if breeding system influences population structure more than endemism, then within-population genotypic diversity of an outcrossing species with a restricted distribution should be greater than that of a selfing or asexual widespread species. And because interpopulation gene flow is typically higher in outcrossing species than a selfing or asexual species (Hamrick and Godt 1990), then we would expect that an outcrossing endemic should exhibit less interpopulation differentiation than a widespread selfing or asexual species.

A genus well suited for comparative study of the effects of endemism and breeding system on population genetic structure is *Taraxacum.* The great majority of species in this large genus are asexual, producing seeds that are genetically identical to the maternal parent through apomixis (agamospermy); and most of the remainder are predominantly or obligately outcrossing species (Grant 1981). The species we chose for study are the *T. californicum* Munz & I. M. Johnston (California dandelion) and

T. officinale Wigg. (common dandelion). Although *T. californicum* is in the section *Ceratophora* and *T. officinale* is in *Ruderalia*, the two species are so closely related that they occasionally spontaneously hybridize when they come in contact (Skinner and Pavlik 1994).

Taraxacum californicum is a predominantly outcrossing perennial herb endemic to moist, subalpine (1950–2400 m) meadows of the eastern San Bernardino Mountains of southern California (Munz 1974; Krantz 1980; Hickman 1993). The species was recently listed as endangered by the U.S. Fish and Wildlife Service (Federal Register 1998).

Taraxacum officinale, also a perennial herb native to Europe, is a pantemperate weed of lawns, meadows, and disturbed places (in California, from 0–3300 m); and, it occurs throughout North America (Munz 1974; Hickman 1993). The taxon is obligately apomictic. While treated as a single species by most North American researchers, *T. officinale* probably represents what many European experts judge to be a complex of agamospecies (Grant 1981; Richards personal communication). Like other North American researchers (Taylor 1987; King 1993), we were unable to identify any character that allowed for the easy assignment of separate taxa. Therefore, we consider the species to be "*sensu lato*".

The purpose of this study was to survey the genotypic diverity within and among populations of *T. califiornicum*, an outcrossing endemic, and *T. officinale*, its widespread apomictic congener. We compared their patterns of genetic diversity to distinguish the relative contributions of breeding system and endemism on their population genetic structure. Additionally, we add some baseline information on the genetic biology of *T. californicum* with bagging experiments and chromosome counts.

METHODS AND MATERIALS

Collection of material. We used unopened flower buds for our genetic analysis. In the case of *T. californicum*, in June 1982 we collected one unopened flower bud from each of 30 randomly selected plants in each of 5 representative populations from its range in the eastern San Bernardino Mountains of California (Fig. 1). The buds were stored in plastic bags and kept cool until they could be extracted for allozyme study in Riverside. We also collected achenes to be germinated for chromosomal analysis from 3 individuals located in the population near Bluff Lake.

In the case of *T. officinale*, flower buds were obtained from plants grown from seed. During June and July 1980 we collected a mature infructescence (head) from each of 30 randomly selected plants in each of 22 *T. officinale* populations across the United States, detailed in Lyman and Ellstrand (1984). Heads were considered to be mature when they were fully opened, with achenes exposed to the wind. The heads were transported to Riverside for germination as described below.

In collecting both species, plants sampled were separated spatially ($\gg$1 m) to insure that rosettes were not attached to the same taproot (Naylor 1941). All collection sites were isolated from each other by at least 4 kilometers.

Germination. Achenes were germinated in 4-inch styrofoam cups in a greenhouse at the University of California at Riverside and later transferred to clay pots in the lathhouse. Germination occurred readily within 3–7 days. One seedling per maternal parent was grown to maturity for electrophoretic analysis. Additional seedlings were used for chromosome counts.

Chromosome counts. Chromosome numbers were counted for the offspring of five individuals from the Bluff Lake population of *T. californicum* and from two individuals from each population of *T. officinale*. We germinated seeds from these populations on moist filter paper in petri dishes under lab conditions. Four- to six-day-old root tips were placed in vials with 0.2% colchicine solution for 2 h and then fixed in 1:3 aceto-alcohol (Richards 1972a). The root tips were hydrolyzed in 0.1 N HCl for 11 minutes at 60°C and then stained in Feulgen solution for at least 1 h before the squashes were prepared (Löve and Löve 1975). We squashed 2-mm lengths of root tips on microscope slides in 1% aceto-propionic acid before viewing root tip meiotic cells under the microscope. A minimum of three metaphase plates per plant were examined and counted.

Testing for apomixis and autogamy in California dandelion. We bagged flowers of *T. californicum* to test whether it can set seed without the assistance of animal vectors (i.e., by apomixis or autogamy). In June 1982 at Wildhorse Meadows, the least disturbed site, small-mesh net bags were placed over one unopened capitulum on each of five plants of *T. californicum*. The bags were secured tightly to the ground with metal spikes to prevent insect movement in and out of the bags. In July the bags were removed, and each head was placed in a separate plastic bag so that seed set, as judged by whether achenes were fully developed and filled, could be determined in the laboratory.

Electrophoretic analysis. Unopened flower buds from up to 30 plants per population of *T. californicum* collected from the field were subjected to isozyme analysis by starch gel electrophoresis. For *T. officinale*, we analyzed unopened buds from up to 20 plants per population of plants grown from field-collected seed. Individuals buds were homogenized in two drops of extraction buffer (0.01 M DTT buffered with 0.1 M Tris-HCl, pH 7.0). Homogenates were adsorbed to paper wicks which were inserted vertically into 12% electrostarch gels. We used the Tris-EDTA-borate continuous gel and

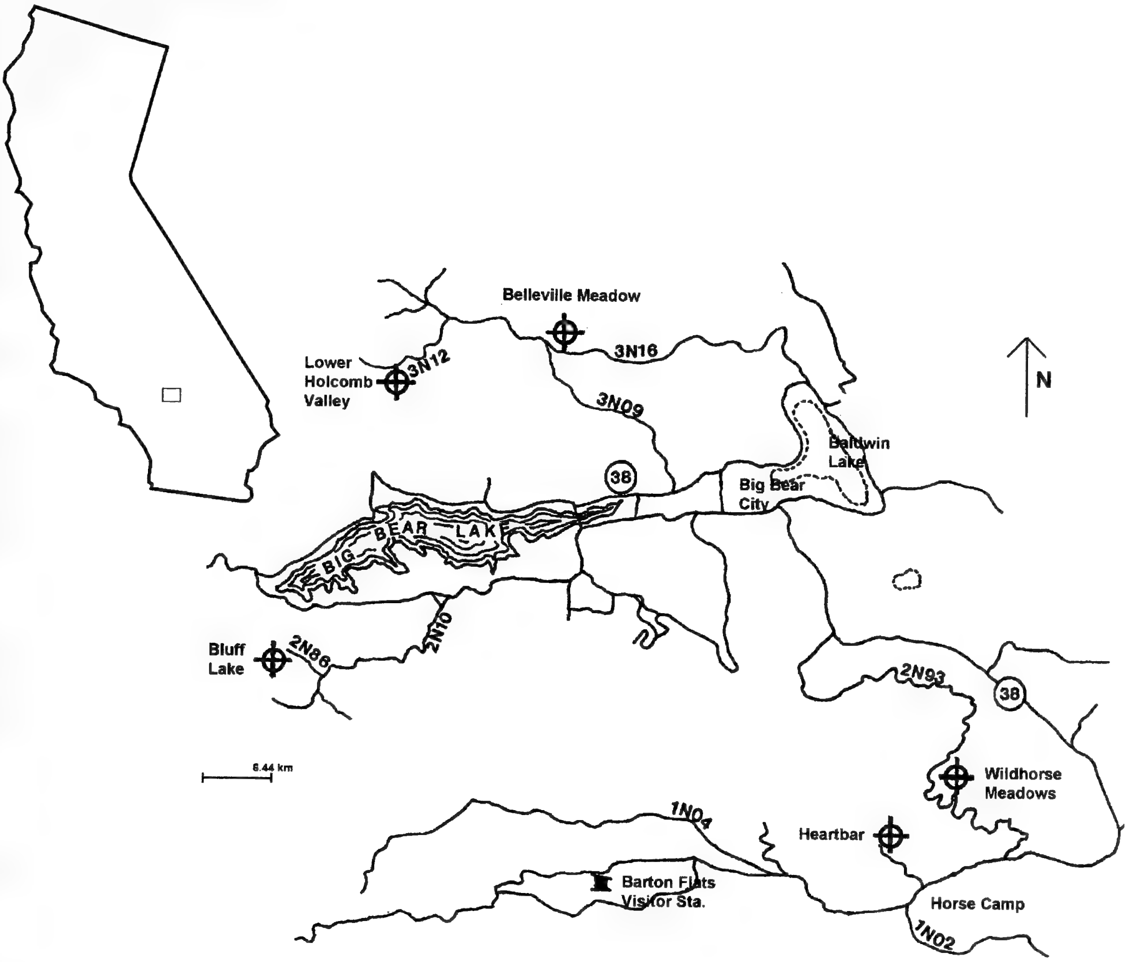

FIG. 1. Collection sites of 5 populations of *Taraxacum californicum*, San Bernardino Mountains, CA (inset area enlarged).

electrode buffer system of Heywood (1980). Electrophoresis was conducted for 4 h at 50 milliamps. Plastic containers of ice were placed on the gels during the run to prevent overheating. Internal standards were run on each gel to determine the electrophoretic equivalence of bands from different populations. We assayed for three enzymes—alcohol dehydrogenase (ADH), phosphoglucoisomerase (PGI), and phosphoglucomutase (PGM)—using the staining procedures described by Heywood (1980). Genetic analysis of isozyme patterns in related species (e.g., Roose and Gottlieb 1976) suggest that electrophoresis resolves five loci (one for ADH, two for PGI and PGM). Despite the polyploidy of these species (see Results), banding patterns were simple, and alleles were easily assigned.

RESULTS

Chromosome studies revealed a tetraploid chromosome complement in the nucleus of all individuals of *T. californicum* surveyed. In all counts, the number of chromosomes was 31 ($2n = 31$). Similar levels of unusual aneuploid tetraploidy have been reported in some sexual European species of *Taraxacum* (Richards 1972a, b, 1973). *Taraxacum officinale*, however, has been shown to be a triploid, $X = 8$, $2n = 24$ (Munz 1974). Our analysis of two individuals from each of 22 populations of this species showed the same chromosome number and ploidy level. Chromosome size was distinctly different in the two species. *Taraxacum californicum* chromosomes were observed to be more than twice the size of those of *T. officinale*.

Three of five bagged capitula produced no seed at all. The number of unfertilized ovules per head was 53, 73, and 76. Two remaining capitula produced a few filled achenes, 8 of 78 in one, and 2 of 67 in another. Overall, 2.9% of the ovules produced seed when foreign pollen was excluded. Unbagged inflorescences on the same plants had full seed set (100%). These data support the hypothesis that *T. californicum* is a self-incompatible outcrossing species.

TABLE 1. ALLELES IN *T. CALIFORNICUM* AND *T. OFFICINALE.*

		Taxon	
Locus	Allele	*T. californicum*	*T. officinale*
PGI-1	a	x	x
	b	x	x
	c	x	x
	d	x	x
	e	x	
	f	x	
PGM-1	a	x	x
	b		x
	c	x	x
	d	x	x
	e		x
	f	x	
ADH	a	x	x
	b	x	x
	c	x	x
	d		x
	e	x	

Genotypic variation was present within and among the populations of *T. californicum* and *T. officinale* investigated. We report genotypic rather than allele frequency data throughout this study because dosage effects due to polyploidy in both species were not clearly discernible on the starch gels, making it impossible to determine allele frequencies. Levels of variation were different for the two species. Of the five loci considered, two were monomorphic for both *T. officinale* and *T. californicum*. The polymorphic loci were shared by both species. Some alleles were common to both species, whereas others were species-specific (Table 1). We found 56 unique genotypes (allozyme phenotypes) among 147 individuals of *T. californicum* surveyed. The range of genotypes per population was 17–19 ($\bar{x}$ = 18.2; Fig. 2). No population contained more than six individuals of the same genotype. In contrast, only 21 genotypes were found among the 518 individuals surveyed, ranging from 1–9 ($\bar{x}$ = 3.2) genotypes per population (Fig. 2).

Pielou's correction version of the Gini Index (*D*) describes the degree of diversity within a population (cf. Ellstrand and Roose 1987). This index emphasizes changes in common rather than rare classes. *D* can be as little as 0 (a uniform sample) or as large as 1 (every individual different). The corrected values for the five populations of *T. californicum* ranged from 0.94–0.97 ($\bar{x}$ = 0.96). Values for *T. officinale* ranged from 0.00–0.89 ($\bar{x}$ = 0.50). Evenness values (*E*), which reflect how evenly the genotypes within a population are distributed among individuals, were also calculated (Fig. 3) (cf. Ellstrand and Roose 1987). This value also ranges from zero (extreme skewness) to 1.0 (complete equitability). The striking bimodal distribution of *E* for *T. officinale* showed that in some populations one or a few dominant clones predominated but that in the others, the clones were equitably distributed among the individuals of the population. All five *T. californicum* populations, however, had evenness values close to 1.0 (Fig. 3). Both evenness and diversity differed significantly between these species ($P < 0.01$; Mann-Whitney U test).

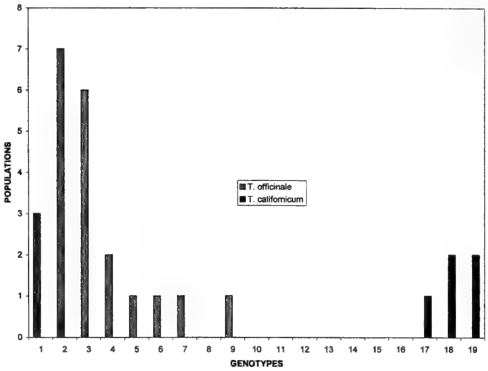

FIG. 2. Number of allozyme phenotypes per population for *T. californicum* and *T. officinale*.

Interpopulational differentiation within each species was measured using Hedrick's (1971) formula for genotypic similarity. This index is as follows:

$$I_{xy} = \frac{\sum_{j=1}^{n} P_{jx}P_{jy}}{\frac{1}{2}\left(\sum_{j=1}^{n} P_{jx}^{2} + \sum_{j=1}^{n} P_{jy}^{2}\right)}.$$

The values for this formula range from 0 (no similarity among populations) to 1 (complete genotypic identity among populations). The values of the five populations of *T. californicum* were uniformly high, from 0.70–0.96 ($\bar{x}$ = 0.83). The values for the 22 populations of *T. officinale* ranged from 0.35–1.0 ($\bar{x}$ = 0.81).

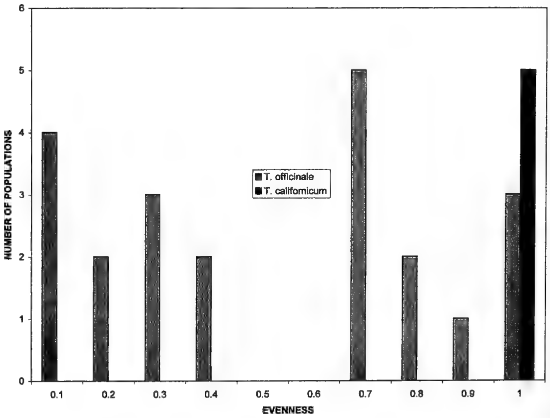

FIG. 3. Evenness values per populations for *T. officinale* and *T. californicum*.

DISCUSSION

In our comparison of two congeners having different recombination systems and range sizes, we found that the predominantly outcrossing endemic species *T. californicum* had substantially more genotypic diversity than the apomictic and widespread species *T. officinale* (*sensu lato*). The average number of allozyme phenotypes per population of the endemic was six times that of the widespread species. Likewise, the endemic had about twice as much genotypic diversity per population as the widespread species, and that diversity was distributed much more evenly per population than in the widespread species.

Both species had about the same level of average interpopulation differentiation as estimated by Hedrick's *I*. The similarity is curious, given that the two species were sampled over such different scales (*T. californicum* over a scale of tens of kilometers; *T. officinale* over hundreds of kilometers). We would expect much more interpopulation differentiation in *T. officinale* for two reasons. First, we would expect more isolation (and consequently more differentiation) among distantly sampled populations compared to those sampled at a finer scale. Second, as noted above, all other things being equal, we would expect an apomictic species to have reduced gene flow relative to a sexual species (and consequently more differentiation). Gene flow by seed is the only means available to those species that reproduce without fertilization, whereas sexual species can disperse their genes by both seed and pollen. The best interpretation we can make is that the level of isolation among the meadows that make the home of the California dandelion are roughly the same as the level of isolation among our widely sampled common dandelion populations.

Results from our bagging experiment are compatible with an outcrossing breeding system for *T. californicum* based on self-incompatibility. Bagged capitula set few or no seed; unbagged capitula on the same plants had full seed set. Although this species may be pseudogamous or semigamous, requiring pollination to stimulate apomictic seed production (Richards 1986), such syndromes are unknown for *Taraxacum* (Grant 1981). Also, net bags might have raised the temperature of the capitula to the point that apomictic seed production was disrupted (Stebbins personal communication). However, as noted above, self-incompatible, endemic montane *Taraxacum* are known in Europe (Richards 1973), and apomixis requiring pollination has never been reported for the genus (Grant 1981). Finally, the high genotypic diversity we discovered in *T. californicum* argues against high levels of apomictic seed production. Prior genetic surveys of agamospermous species typically show much lower genotypic diversity (e.g., Ellstrand and Roose 1987; Diggle et al. 1998). We acknowledge that demonstrating sexuality conclusively requires further experimentation, but, presently, all of the evidence supports outcrossing as *T. californicum*'s breeding system.

We recognize that using a small number of marker loci can underestimate genotypic diversity. Adding more characters may identify more genotypes (Ellstrand and Roose 1987). Nonetheless, it is clear that the two species have different population genetic structures for the same set of genetically based markers. Genotypic diversity in *T. officinale* is low, but virtually every individual of *T. californicum* was found to be genotypically distinct. Indeed, we are confident that if we were able to add a few more markers, we would be able to distinguish among those few individuals of *T. californicum* that shared a genotype in this study.

For this pair of species, the difference in breeding system is apparently more important in determining population genetic structure than the difference in range size. The relatively high levels of genotypic diversity persist in the apparently outcrossing *T. californicum* despite its limited geographic range. We are aware of only one other study that compares an endemic, outcrossing species with a widespread species that has an alternative breeding system. The self-incompatible endemic of New Mexico's Organ Mountains, *Oenothera organensis* Munz, is nearly monomorphic at several allozyme loci despite high polymorphism at self-incompatibility locus (Levin et al. 1979). Most of its congeners that have been studied have more genetic diversity (Levin et al. 1979), and almost all of these have an essentially clonal reproductive system (permanent translocation heterozygosity; Grant 1981). Thus, the trend in *Oenothera* is opposite that found here for *Taraxacum*.

Taraxacum californicum is believed to be a relict of the section *Ceratophora* (Jepson 1925) that is thought to have spread through the northern hemisphere during an interglacial period (Richards 1973). Fossil records of the section date to 1×10^5 years B.P. (Chearney and Mason 1936). Subsequently *T. californicum* is presumed to have become isolated from the many other species of the section, which occur in a circumpolar distribution (Richard 1973). Given its long isolation, the fact that its total population size may be less than 6×10^3 plants, and its restricted habitat, the polymorphism of *T. californicum* is surprisingly high.

The remarkable genetic diversity that *T. californicum* exhibits despite its endemism suggests that breeding system plays a greater role in maintenance of genetic variation than the constraints of endemism do to limit it. But there is another possibility to account for the origin and maintenance of genetic variation. The ploidy difference between *T. californicum* and *T. officinale* may explain at least some of the greater genotypic variation displayed in *T. californicum*. If this species does, in fact, belong to the section *Ceratophora*, then, like the tetraploid European members of this section, it is probably an allotetraploid derived from two diploid sexual species (Richard 1973). The resulting sexual amphiploid will initially breed true for a highly heterozygous genotype but will release that variation slowly over generations through rare tetrasomic recombination (Grant 1981; Roose and Gottlieb 1976).

Another possibility is that *T. californicum* is not yet in evolutionary equilibrium. If fragmentation and endemism are relatively recent in terms of the mean generation time of the species, the patterns we observed better represent historic inertia than the factors that are currently molding patterns of diversity (Ellstrand and Elam 1993). Because the species was only described in this century, we know little of its history. If *T. californicum* population genetic structure is not in equilibrium, we might expect to see the effects of isolation and endemism eventually work to erode the current levels of genetic diversity, but such changes could take decades.

A puzzling feature of the chromosome studies is the aneuploid condition found in the individuals of *T. californicum* at Bluff Lake. Investigators have noted the same phenomenon in a number of European *Taraxacum* species (Malecka 1962, 1967a, b, 1969; Sorensen and Gudjonsson 1946; Richards 1970, 1972a, b, 1973), including many sexual species (e.g., Sorensen and Gudjonsson 1946). The extent of the aneuploid condition and its role in reproductive events in *T. californicum* are presently unknown.

This research has uncovered relatively high levels of genotypic variation in an endemic species in comparison with its widespread apomictic congener. We conclude that endemics need not necessarily be genotypically depauperate species relative to widespread congeners. Instead, it is clear that the organization of genetic variation may be subject to other constraints such as breeding system and history. Further descriptive and experimental population genetics studies are needed for this and other species pairs to determine the nature of these constraints.

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EFFECTS OF SIMULATED OIL FIELD DISTURBANCE AND TOPSOIL SALVAGE ON *ERIASTRUM HOOVERI* (POLEMONIACEAE)

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ABSTRACT

The effects of simulated oil field disturbance and topsoil (i.e. *E. hooveri* seed bank) salvage on *E. hooveri* reestablishment were evaluated to develop effective strategies for conserving *Eriastrum hooveri* (Jeps.) Mason, a federally threatened plant. The study was conducted at two experimental sites at the former Naval Petroleum Reserve No. 1 (NPR-1), Kern County, CA. This species was initially present at Site 1 and nearly absent at Site 2. Six replications of five treatments were established simulating salvage and non-salvage of *E. hooveri* seed-laden soil before and after seed maturation and dispersion. *Eriastrum hooveri* densities were estimated in 1993 (pre-disturbance) and 1995 (post-disturbance). In this study we found that 1) surface disturbance negatively affected *E. hooveri* density for at least two growing seasons, 2) *E. hooveri* recolonized disturbed plots in two growing seasons from seed naturally dispersed from adjacent habitat, 3) topsoil salvage and respreading did not significantly affect the recolonization of *E. hooveri* on disturbed plots, 4) the timing of topsoil salvage had no effect, 5) *E. hooveri* was established at very low densities on several plots with no previous *E. hooveri* using topsoil from occupied habitat as a seed source, and 6) *E. hooveri* cover was inversely related to total vegetation cover but not to exotic grass cover.

Eriastrum hooveri (Jepson) H. Mason, is a small annual herb endemic to the southern San Joaquin Valley and southern Coast Range regions of California (Munz 1973; Patterson 1993; Moe 1995). Plants exhibit wiry stems, alternate thread-like leaves, and small white flowers arranged in dense bracteate heads (Patterson 1993; Moe 1995). The species occurs in annual grassland and chenopod scrub habitats in portions of seven California counties at elevations ranging from 50 to 910 m (Stebbins et al. 1992; Lewis 1992; CDFG 1993; Patterson 1993; Danielsen et al. 1994; Skinner and Pavlik 1994). *Eriastrum hooveri* often occurs in sandy loam soils derived from alluvial and colluvial parent material and underlying sedimentary rocks.

Habitats occupied by *E. hooveri* commonly overlie extensive hydrocarbon deposits; thus, oil and gas development and production activities have historically resulted in impacts to habitat suitable for this species. Such impacts primarily comprise soil disturbance from grading and facility and infrastructure construction activities. Although effects of oil and gas field related disturbances on *E. hooveri* were the focus of this study, the U.S. Fish and Wildlife Service (USFWS) cited impacts from agricultural development, urbanization, and water projects as the primary threats to the species' existence (USFWS 1990).

Eriastrum hooveri was listed as threatened by the USFWS in 1990 (USFWS 1990), largely in response to Taylor and Davilla's (1986) findings and the paucity of field observations during the three-year period of drought preceding federal listing. However, the results of more recent botanical surveys conducted during non-drought years showed that this species was more common and widespread than originally believed (Lyman et al. 1991; Stebbins et al. 1992; Lewis 1992, 1994). The need for its continued listing as threatened has been questioned (Lewis 1992, 1994; Willoughby 1995). Lewis (1994) suggested that the protection of large tracts of *E. hooveri* habitat on federally managed lands would ensure survival of the species. The Bureau of Land Management has submitted a proposal to the USFWS recommending the species be delisted and the USFWS has indicated that it may follow that recommendation. Currently, federal agencies continue to manage *E. hooveri* populations on federally administered lands in accordance with Section 2(c)(1) of the Endangered Species Act of 1973.

The conservation of *E. hooveri* within its range in petroleum producing areas such as the former NPR-1 (now referred to as the Elk Hills Oil Field), necessitates the understanding of the effects of oil and gas developmental activities on the species. Primary strategies recommended by the USFWS and used by the U.S. Department of Energy (DOE) to mitigate impacts to *E. hooveri* populations at the Elk Hills Oil Field included population avoidance, or, if unavoidable, salvage and replacement of *E.*

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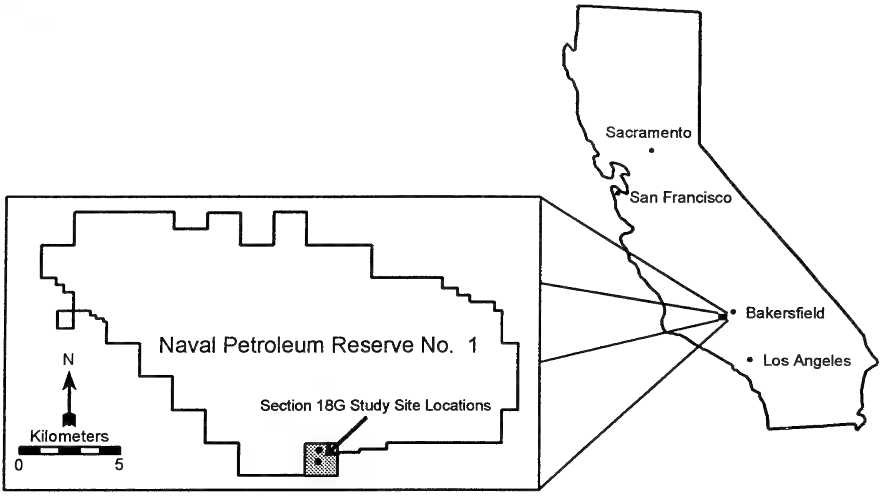

FIG. 1. Map of Naval Petroleum Reserve No. 1. Two *Eriastrum hooveri* study site locations are shown within Section 18G of the Reserve. Cartography by Mark R. M. Otten.

hooveri seed-laden topsoil. Subsequent to completion of oil field projects seed collection and reseeding was often not possible due to project timing and annual variation in *E. hooveri* seed production. Therefore, topsoil salvage and respreading following completion of the project or on nearby areas in need of habitat restoration typifies impact mitigations to this species. However, the effects of disturbance on *E. hooveri*, the effectiveness of topsoil salvage, and the effects of topsoil salvage timing were unknown. This study investigated the effects of simulated oil field disturbance on, and the efficacy of topsoil salvage for, *E. hooveri* prior to and following seed maturation and dispersion.

Entire journals are devoted to the topic of natural lands restoration and management (e.g., *Restoration Ecology, Restoration & Management Notes*) and the scientific literature has a profusion of books and articles describing the effects of various kinds of habitat manipulation on unwanted alien and desirable native and naturalized plants. Methods and results of transplanting, reseeding, and introduction of sensitive or endangered plants have been studied (Hiatt et al. 1995), especially those susceptible to poaching such as rare cacti and orchids (Lyons 1987; Allen 1994). However, except for research conducted by Holmstead and Anderson (1998) and reported in this issue, we are unaware of field trials involving experimental use of topsoil as a seed source at study sites occupied by threatened or endangered annual plants.

METHODS

The DOE conducted a manipulative field study (with USFWS approval) from April 1993 to July 1995 at the former NPR-1, 40 km southwest of Bakersfield, Kern County, CA (Fig. 1). Two *E. hooveri* study sites were located in Section 18G (Section 18, Township 31 South, Range 24 East, Mount Diablo Base & Meridian). Site 1 was about 170 m above sea level; and Site 2, located 850 m north of Site 1, was about 190 m above sea level (Fig. 2). Vegetation at both sites is characteristic of the Valley Saltbush Scrub community as described by Holland (1986). Prior to the study, *E. hooveri* was known to occur in relatively high densities at Site 1 and was believed absent at Site 2.

The regional climate is hot and dry in summer, and is cool and wet in winter with periodic fog. Annual ambient air temperatures generally range from 0–38°C (National Weather Service, no date). Annual precipitation averaged 156 mm between 1975 and 1994, occurring mostly as rain from November–April (National Climatic Data Center 1975–1995). Precipitation contributing to the growing season for annual plants (October–March precipitation) was 225 mm in 1993, 113 mm in 1994, and 227 mm in 1995 (National Climatic Data Center 1992–1995).

In the spring of 1993, thirty 6 × 30 m plots spaced 6 m apart were established at each study site. Six replications of five treatments were randomly assigned to the plots. Between April 15 and 30, the upper 5 cm of topsoil were removed from twelve Site 1 plots and saved. Using a tractor with a chisel-tooth plow and disk implements to simulate habitat disturbance from oil field-related activity, these plots and twelve Site 2 plots were ripped to a depth of 45 cm, and then disked to a depth of 15 cm. Following disking, topsoil containing *E. hooveri* was salvaged from Site 1, and then evenly spread on six plots at each site. The entire process was repeated on 12 different plots at each site in July 1993, following *E. hooveri* seed maturation and dispersion (when the topsoil presumably contained more *E. hooveri* seed). The remaining six

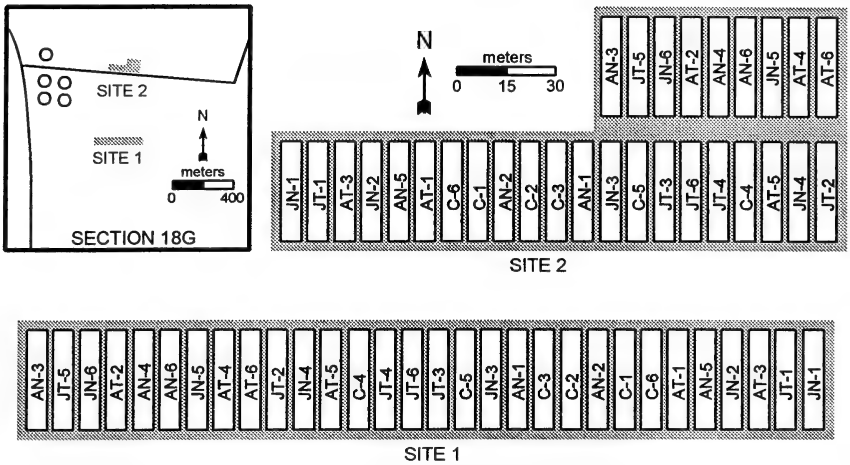

FIG. 2. *Eriastrum hooveri* study site map and experimental scheme. AN = April, no topsoil imported; AT = April, with topsoil; JN = July, no topsoil imported; JT = July, with topsoil; C = control; numbers 1–6 = replication number. Plots are 6 m × 30 m. Illustration by Mark R. M. Otten.

plots at each site were not treated, and served as controls. In summary, the treatments at Sites 1 and 2 were as follows: plots disked in April (before seed maturation) with no topsoil replacement (AN), plots disked in April and covered with topsoil containing *E. hooveri* seed (AT), plots disked in July (after seed maturation) with no topsoil replacement (JN), plots disked in July and covered with topsoil containing *E. hooveri* seed (JT), and undisturbed control plots (C).

Pre-disturbance baseline data from Sites 1 and 2 were collected in April 1993, prior to habitat manipulation. Total cover of detritus, bare ground, cryptogamic soil crust, and (vascular) vegetation cover (as defined by Bonham [1989]) by species was estimated on the plots using a tripod-mounted 10× ocular point projection device or "cover scope" (ESCO Associates Inc., Boulder, CO). *Eriastrum hooveri* density was estimated by recording the number of individuals observed in ten 0.25-m^2 quadrats sampled at 2.5-m intervals along a 25-m transect in each plot. In 1995, post-disturbance sampling was conducted during the peak of the growing season using the same methodology.

Mean pre-disturbance and post-disturbance *E. hooveri* densities among treatments on Sites 1 and 2 were analyzed using one-way ANOVA and Tukey's Studentized Range Test. Mean 1993 and 1995 *E. hooveri* densities at Site 1 were compared using two sample t-tests. Mean pre-disturbance and post-disturbance *E. hooveri* densities on Site 1 and 2 were correlated with total vegetation cover, dominant shrub cover (*Atriplex polycarpa* (Torrey) S. Watson), and dominant grass cover (*Bromus madritensis* L. ssp. *rubens* (L.) Husnot). Statistical analyses were performed using SAS/STAT v.6 software (SAS Institute Inc. 1990).

RESULTS

Pre-disturbance. Eriastrum hooveri was present on 28 of the 30 Site 1 plots prior to habitat manipulation. On a Site 2 JN plot transect, one *E. hooveri* plant was found in 1993. This plot was subsequently eliminated from the analysis to remove sample bias. Mean *E. hooveri* density was more than four times higher on the Site 1 JN plot transects before disturbance than other treatments (Table 1); however, when tested, this difference was found to be not significant because of highly variable data. *Eriastrum hooveri* density was negatively correlated with total vegetation cover, although the relationship was weak ($R^2 = 0.0964$; $P = 0.0950$). *Eriastrum hooveri* density was not related to *B. madritensis* ssp. *rubens* or *A. polycarpa* cover.

Post-disturbance. In 1995, *E. hooveri* densities were significantly lower ($F = 6.91$, df = 4, 29; $P = 0.0007$) on Site 1 disturbed plot (AN, AT, JN, JT) transects than control plot transects (Table 1). Mean *E. hooveri* densities in 1995 were higher on Site 2 JT plot transects than other treatments, but the differences were not statistically significant. One *E. hooveri* plant was present on a Site 2 control plot transect. No *E. hooveri* plants were observed on Site 2 AN and JN plot transects except on the JN plot which had been eliminated from the analysis. *Eriastrum hooveri* density was negatively correlated with total vegetative cover, but not related to *B. madritensis* ssp. *rubens*, or *A. polycarpa* cover.

Mean *E. hooveri* densities on Site 1 disturbed plot (AN, AT, JN, JT) transects were lower in 1995 compared to pre-disturbance densities, but the differences were not statistically significant. During the same period, mean *E. hooveri* density increased

TABLE 1. MEAN *ERIASTRUM HOOVERI* PRE-DISTURBANCE AND POST-DISTURBANCE DENSITIES AT SITES 1 AND 2. Density values shown are mean number of individual plants rooted within 0.25-m^2 frames sampled at 2.5-m intervals along 25-m transects. Standard errors are shown in parentheses. [1] Experimental site located within known *E. hooveri* population area. [2] Experimental site located in area with near absence of *E. hooveri* (in 1993). [3] AN = April, no topsoil imported; AT = April, with topsoil; JN = July, no topsoil imported; JT = July, with topsoil; C = control. [4] Pre-disturbance measurements. [5] Means within a column with different letters are significantly different at $\alpha = 0.05$.

	Site 1[1]		Site 2[2]	
Treatment[3]	1993[4]	1995	1993[4]	1995
AN	1.82 A[5] (0.7436)	0.85 A (0.5051)	0	0 A
AT	2.32 A (1.5372)	0.52 A (0.1956)	0	0.02 A (0.0167)
JN	11.8 A (7.7719)	1.75 A (0.8265)	0	0 A
JT	2.47 A (1.2785)	0.85 A (0.2377)	0	0.18 A (0.1641)
C	2.30 A (1.0139)	4.37 B (0.8758)	0	0.02 A (0.0167)

from 2.30 to 4.37 plants per 0.5 m^2 on Site 1 control plot transects, but again, this increase was not statistically significant.

DISCUSSION

The effects of surface disturbance on *E. hooveri* are poorly understood. A common perception held by the authors of this paper and other botanists who have studied *E. hooveri* is that colonies of this species appear to be tolerant of some undetermined level of disturbance and that the species is adapted to generally open microhabitats (e.g., Lewis 1992, 1994; Holmstead and Anderson 1998). *Eriastrum hooveri* plants are often present on previously disturbed areas (Taylor et al. 1988; Lyman et al. 1991; Lewis 1992; Holmstead and Anderson 1998), sometimes with the disturbance apparently defining *E. hooveri* colony boundaries (Lewis 1994). Lewis (1994) found that 49 of 53 *E. hooveri* sites threatened by off-highway vehicle usage were situated on previously disturbed sites. Cypher (1994) observed higher *E. hooveri* survival rates on grazed than ungrazed areas, and no difference in *E. hooveri* fecundity between grazed and ungrazed areas. Holmstead and Anderson (1998) suggested that some level of habitat disturbance is compatible with *E. hooveri* conservation. In our study, *E. hooveri* density was negatively correlated with total vegetation cover, although the relationship was admittedly weak. This is consistent with our general field observations. Many *E. hooveri* locations on and adjacent to NPR-1 are 1) naturally or artificially disturbed sites supporting early successional species, and 2) relatively open microhabitats at sites dominated by later successional species. We found no correlation between *B. madritensis* ssp. *rubens* cover and *E. hooveri* cover, so the amount of overall vegetation cover, rather than exotic grass cover, seems to limit *E. hooveri* growth.

Our results support the hypothesis that this species readily recolonizes relatively small sites subjected to simulated oil field disturbance. During the study, *E. hooveri* recolonized disturbed Site 1 plots two growing seasons after disturbance. If precipitation prior to the 1994 growing season had not been below average (113 mm versus 143 mm normal), *E. hooveri* recolonization might conceivably have occurred by the first growing season, as observed by Holmstead and Anderson (1998).

In our study, respreading of seed-laden topsoil led to the growth of *E. hooveri* at very low densities on several previously unoccupied Site 2 plots; however, *E. hooveri* densities were lower than on Site 1, probably due to the lack of seed dispersal from adjacent occupied habitat. Because of the extremely low densities that resulted, it appears that topsoil importation for the purpose of establishing *E. hooveri* on unoccupied habitat may not be an effective conservation measure.

Although *E. hooveri* reestablishment was achieved on Site 1, *E. hooveri* density was significantly lower on disturbed plots than control plots. This lower density is probably temporary because *E. hooveri* density on disturbed plots studied by Holmstead and Anderson (1998) was similar to or higher than on control plots after five growing seasons (Hinshaw unpublished). In our study, further monitoring will be needed to determine the recovery period for *E. hooveri* at Sites 1 and 2.

Eriastrum hooveri densities on Site 2 plots that received topsoil collected in July were higher than on plots receiving topsoil collected in April, but the difference was not statistically significant. This slight difference may have resulted from initially higher *E. hooveri* densities on Site 1 JN plots from which the topsoil was collected (Table 1). These data support the conclusion that timing of topsoil salvage did not affect post-disturbance *E. hooveri* densities. Apparently, seed dispersal from adjacent habitat and seeds contained in the soil seed bank contributed more to recovery than did the 1993 seed crop. Therefore, a mitigation requirement to delay oil field activities until after *E. hooveri* seed set would appear to be both ineffective and unnecessary for *E. hooveri* conservation.

Eriastrum hooveri densities on Site 1 were similar to or lower on disturbed plots receiving topsoil than disturbed plots with no topsoil. This result was unexpected because topsoil removal was equivalent to soil seed bank removal. *Eriastrum hooveri* plants on the plots with no topsoil probably resulted from seeds naturally dispersed from adjacent occupied habitat. On these plots, topsoil salvage did not appear to be an effective strategy for enhancing the recolonization of this species on relatively small disturbances. Seeds from adjacent habitat apparently dispersed onto disturbed sites, producing plants after 1–2 growing seasons. Therefore, topsoil salvage and respreading on relatively small disturbances within areas occupied by *E. hooveri* would seem unnecessary for purposes of species conservation.

Funding for future studies of *E. hooveri* is uncertain because this species apparently is slated for delisting (Warren personal communication). Should further research occur, however, we recommend that germination studies be conducted under controlled conditions to learn more about seed bank dynamics of this species. Habitat manipulation studies of the effects of flooding, fire, herbivory, and anthropogenic surface disturbance on *E. hooveri* would certainly add further insights useful in developing management strategies for conserving this species. In addition, we strongly support Lewis' (1992, 1994) contention that further field inventories are needed for this cryptic herb.

In conclusion, *E. hooveri* density was negatively affected by simulated oil field disturbance for at least two growing seasons, simulated topsoil salvage did not enhance *E. hooveri* reestablishment on disturbed plots, the timing of topsoil salvage did not affect the density of subsequent *E. hooveri* plants, and *E. hooveri* cover was not related to exotic grass (*B. madritensis* ssp. *rubens*) cover, but was inversely related to total vegetation cover.

Acknowledgments

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REESTABLISHMENT OF *ERIASTRUM HOOVERI* (POLEMONIACEAE) FOLLOWING OIL FIELD DISTURBANCE ACTIVITIES

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ABSTRACT

Little is known about the ecology of *Eriastrum hooveri* (Jepson) H. Mason or about its tolerance to oil field related habitat disturbance. Taylor and Davilla (1986) suggested the species was closely associated with dense cryptogamic soil crust, characteristic of undisturbed sites. We monitored reestablishment of *E. hooveri* on two sites disturbed by construction activities (a pipeline and a well pad) at the U.S. Department of Energy's Naval Petroleum Reserve No. 1, Kern County, CA. Before construction, topsoil from the sites was stockpiled. After construction, the topsoil was replaced, and the pipeline site and a portion of the well pad site were seeded with a mix of native shrub, grass, and forb species. Part of the well pad site was left unseeded so that reestablishment of *E. hooveri* could be compared between seeded and unseeded plots. Sites were monitored during the first two growing seasons following disturbance (1991 and 1992). Vegetation characteristics of the disturbed sites were compared with adjacent undisturbed habitat. *Eriastrum hooveri* recolonized both disturbed sites in the first growing season. Generally, the density and frequency of occurrence of *E. hooveri* on our transects increased from the first to the second growing season. Cryptogamic crust cover was low (≤4.6%) on both the disturbed and undisturbed sites in both years. Our observations suggest that 1) *E. hooveri* is able to quickly recolonize heavily disturbed sites, at least if topsoil is conserved and weather conditions are favorable; and that 2) cryptogamic crust cover may not be as important a correlate with the occurrence of *E. hooveri* as previously thought.

Eriastrum hooveri (Jepson) H. Mason (Hoover's woolly-star) is a small annual herb of the Polemoniaceae and endemic to the San Joaquin Valley, California. It was federally listed as threatened in July 1990, due to threats of agricultural land conversion, urbanization, reservoir construction, and oil and gas development (U.S. Fish and Wildlife Service 1990). Little is known about the ecology of *E. hooveri*. Taylor and Davilla (1986) provided some general observations on germination, soil seed reserves, growth phenology, and reproduction of the species.

Early observations by Taylor and Davilla (1986) typically associated *E. hooveri* populations on sites without dense annual plant cover and with dense cryptogamic soil crusts (eucaryotic algae, lichens, bryophytes, cyanobacteria, and fungi), which normally take several years to develop (Anderson et al. 1982a). A 1988 reconnaissance survey of NPR-1 (EG&G Energy Measurements 1988) and on-going surveys of NPR-1 (EG&G Energy Measurement 1992) have identified several *E. hooveri* populations in formerly disturbed sites. Most of these sites are on or near abandoned or infrequently-used roadways, suggesting that the species can respond favorably to disturbance. *Eriastrum hooveri* response to disturbance has not been experimentally investigated.

In this paper, we evaluate the reestablishment of *E. hooveri* on two oil field construction projects, an underground pipeline and a well pad, during the first two growing seasons following disturbance. We describe the chronology of each disturbance and subsequent restoration activities; and we compare the density and frequency of occurrence of *E. hooveri*, and other characteristics of associated vegetation, between the disturbed sites and adjacent undisturbed habitat.

On the well pad site, experimental plots were used to compare reestablishment of *E. hooveri* between plots of seeded topsoil (i.e., replaced topsoil seeded with a mix of shrub, grass, and forb species) and unseeded topsoil. We hypothesized that by not seeding the conserved topsoil, plant competition would be reduced and *E. hooveri* reestablishment would be enhanced.

Study area. The majority of the San Joaquin Valley is cultivated and very few remnants of native plant communities remain (Preston 1981). Although NPR-1 is an active oil and gas producing facility, it encompasses large tracts of native and naturalized vegetation in the San Joaquin Valley. It is located approximately 40 km southwest of Bakersfield, Kern County, CA, and consists of 19,120 ha. NPR-1 is located on the Elk Hills formation, which is in the most arid portion of cismontane California (Major 1977). Geomorphologically, the Elk Hills constitute a subsidiary upland of the Inner South Coast Ranges. The main ridge, oriented in a

TABLE 1. LIST OF SPECIES AND SEEDING RATES USED TO SEED REDISTRIBUTED TOPSOIL ON THE PIPELINE STUDY SITE (DECEMBER 1990) AND THE WELL PAD STUDY SITE (JANUARY 1991), NAVAL PETROLEUM RESERVE NO. 1, KERN COUNTY, CA. [a] PLS = Pure Live Seed, which equals (purity × germination)/100.

Study site	Life-form	Scientific binomial	kg PLS[a]/ha	PLS[a] /m^2
a. Pipeline	Shrub	*Atriplex polycarpa* (Torrey) S. Watson	1.1	16
		Atriplex lentiformis (Torrey) S. Watson	0.6	5
		Eriogonum fasiculatum (Benth.) Torrey & A. Gray	4.5	344
		Isomeris arborea Nutt.	3.4	5
	Grass	*Vulpia myuros* (L.) C. Gmelin	1.1	198
	Forb	*Lupinus densiflorus* Benth.	0.5	3
		Phacelia tanacetifolia Benth.	0.5	107
b. Well Pad	Shrub	*Atriplex polycarpa* (Torrey) S. Watson	2.3	32
		Eriogonum fasiculatum (Benth.) Torrey & A. Gray	4.5	344
		Isomeris arborea Nutt.	3.4	5
	Grass	*Vulpia myuros* (L.) C. Gmelin	1.1	198
	Forb	*Trifolium hirtum* All.	1.1	34
		Lupinus densiflorus Benth.	0.5	3
		Phacelia tanacetifolia Benth.	0.5	107

northwest-southeast direction, is flanked by deeply incised canyons and subsidiary ridges. The ridges and drainages extend into gently sloping, alluvial plains along the outer boundaries. Elevations range from 93 to 473 m above sea level.

NPR-1 lies within the Valley Grassland vegetation type (Heady 1977). Dominant shrubs include *Atriplex polycarpa* (Torrey) S. Watson, *Hymenoclea salsola* A. Gray, and *Isomeris arborea* Nutt. Herbaceous cover is dominated by *Bromus madritensis* L. and *Erodium cicutarium* (L.) L'Hér.

The climate in this region is hot and dry in summer, and cool and wet in winter with frequent fog. Temperatures in summer often exceed 38°C, and seldom go below 0°C in winter. Precipitation occurs primarily as rain falling between November and April (O'Farrell et al. 1987). Since 1981, when weather data collection began on NPR-1, annual precipitation has averaged 124 mm and ranged between 51 and 226 mm.

METHODS

Pipeline study site. In 1990, a gas company completed construction along two underground natural gas pipelines that crossed NPR-1. A large diameter pipeline was installed to replace a small pipeline constructed in 1930. A small pipeline, located approximately 1 km away, was also removed. The construction corridor along the pipelines ranged between 15–20 m wide, and was approximately 38 km long. Approximately 7 ha of habitat containing *E. hooveri* populations were disturbed within the pipeline corridors. Construction activities were delayed until August, several months after the typical flowering season for *E. hooveri* (April–May), to allow existing *E. hooveri* plants to set seed.

Prior to pipeline trenching operations, a road grader was used to scrape 7–8 cm of topsoil to the edge of the construction corridor in all *E. hooveri* habitat. A road grader was then used to replace the topsoil following construction. Due to the deep, powdery nature of the disturbed soil, straw mulch was applied at a rate of about 9,000 kg/ha to improve soil structure. Straw was crimped into the soil using a sheep's foot-type roller-crimper. All *E. hooveri* habitat was drill seeded with a mix of shrubs, forbs, and grasses at a rate of 11.2 kg of pure live seed (PLS) per hectare (Table 1a). Seeding was completed in December 1990.

In spring 1991, the length of the pipeline corridor in *E. hooveri* habit was divided into 0.1 km segments and ten segments were randomly selected. In each segment a random starting point was selected. At each starting point, two parallel 25-m line transects were established to monitor vegetation. One transect was located outside of the pipeline corridor in undisturbed habitat, and the other transect was located down the centerline of the reclaimed pipeline corridor. Vegetation was sampled along each transect in the spring of 1991 and 1992. An ocular point projection device (ESCO Associates Inc., Boulder, CO) was used to estimate ground cover. A total of 100 points or "hits" (a dimensionless plot such as a point frame-type sample) were sampled along each transect; 10 points at 2.5 m intervals. Points were recorded as bare ground, litter, cryptogamic crust, or live vascular plant material, by species. The elements classified as litter included both dead standing and detached biomass. Cryptogamic crust included just those elements that are identifiable in the field, without magnification. The density of *E. hooveri* was determined by recording the number of plants that occurred within a 2 × 25 m belt transect. The densities of grasses and forbs were determined by counting the number of individual plants within five 1 × 1 m quadrats placed at 5 m intervals along the transect. *Eriastrum hooveri* frequency was estimated by using five 1 × 1 m quadrats placed at 5 m intervals along each transect, and counting the number of quadrats containing *E. hooveri*. Frequency of occurrence was expressed as the percentage of quadrats containing *E. hooveri*.

Well pad study site. A second study site was established near a new water well. In July 1990, construction began on the well before a biological survey was conducted. About half of the area proposed for the well pad (0.4 ha) was scraped and 8–10 cm of topsoil was stockpiled. A survey of the site identified several small stands (5–50 plants each) of *E. hooveri* in the surrounding undisturbed areas of the well pad site. To avoid further disturbance to this *E. hooveri* population, the new well was relocated to a nearby existing well pad. After consultation with the U.S. Fish and Wildlife Service, the U.S. Department of Energy established vegetation monitoring transects at the original well site to document reestablishment of *E. hooveri*.

In August 1990, the stockpiled topsoil was spread back over the disturbed area, and the site was divided into nine study plots, about 10 × 50 m each. Three disturbed plots were drill seeded in January 1991 with a mix of shrubs, forbs, and grasses at a rate of 13 kg of PLS/ha (Table 1b), straw mulched at a rate of about 3,400 kg/ha, and crimped. Three disturbed plots were not seeded, and three plots were selected in adjacent undisturbed *E. hooveri* habitat. Due to the pattern of disturbance created by construction equipment, plots were arranged side by side starting with a seeded topsoil plot adjacent to unseeded topsoil plot, which was then adjacent to undisturbed habitat. This order of treatments was replicated three times.

A permanent 25-m line transect was established down the centerline of each plot to monitor vegetation. A random starting location was selected for the first transect and all additional transects were aligned parallel to the first. Vegetation was monitored in the spring of 1991 and 1992 using the methods previously described for the pipeline study site.

Precipitation data. Monthly precipitation was recorded with an All Weather Rain Gauge (Productive Alternatives, Inc., Fergus Falls, MN) at eight stations on NPR-1. Total annual precipitation is expressed on a water-year (WY) basis (e.g., WY91 = 1 July 1990 to 30 June 1991).

Data analysis. On the pipeline site, the density and frequency of *E. hooveri*, and other vegetative characteristics (e.g., total plant cover, cryptogamic cover, density of grasses and forbs) were compared between undisturbed habitat and seeded topsoil plots. On the well pad site, the density and frequency of *E. hooveri*, and vegetative characteristics were compared between undisturbed habitat, seeded topsoil, and unseeded topsoil plots. On each study site, and for each plot type, the effects of year (1991 and 1992) and treatment were evaluated using repeated measures analysis of variance. On the well pad site, linear contrasts between treatments were used to separate mean values. Means were considered significantly different at alpha ≤ 0.05. SAS/STAT v.6 software (SAS Institute Inc. 1990) was used to perform statistical computations.

RESULTS

Annual precipitation was 137 mm in WY91 (10% above average) and 155 mm in WY92 (25% above average).

Pipeline study site. Eriastrum hooveri was present on all transects on the seeded topsoil plots and undisturbed habitat in 1991 and 1992. The density and frequency of *E. hooveri* plants increased significantly from 1991 to 1992 and were significantly higher on the undisturbed habitat (Table 2a). From 1991 to 1992, density of *E. hooveri* on the undisturbed habitat increased from 2.1 to 5.3 plants/m^2, and on the seeded topsoil plots it increased from 0.1 to 0.9 plants/m^2 (Fig. 1a). Between 1991 and 1992, the frequency of *E. hooveri* increased from 38 to 68% on the undisturbed habitat, and from 18 to 26% on the seeded topsoil plots (Fig. 1a).

Total plant cover and density of grasses and forbs increased significantly from 1991 to 1992 and were higher on the undisturbed habitat (Table 2a). From 1991 to 1992, total plant cover, and the density of grasses and forbs generally increased significantly in both treatments (Table 3a).

In 1991, cryptogam cover was 4.6% on the undisturbed habitat, and absent on the seeded topsoil plots. In 1992, cryptogam cover was 1.3% on the undisturbed habitat and 0.5% on the seeded topsoil plots (Table 3a).

Well pad study site. As on the pipeline site, *E. hooveri* was present on all transects in both disturbed and undisturbed habitat in 1991 and 1992. The density of *E. hooveri* increased significantly from 1991 to 1992, but frequency of *E. hooveri* was not significantly different between years (Table 2b). The density and frequency of *E. hooveri* plants were not significantly different between treatments (Table 2b). From 1991 to 1992, density of *E. hooveri* increased from 0.8 to 1.9 plants/m^2 on the undisturbed habitat, increased from 0.4 to 2.3 plants/m^2 on the seeded topsoil plots, and increased from 0.4 to 4.0 plants/m^2 on the unseeded topsoil plots (Fig. 1b). From 1991 to 1992, the frequency of *E. hooveri* increased from 46.7 to 53.3% on the undisturbed habitat, decreased from 46.7 to 6.7% on the seeded topsoil plots, and increased from 26.7 to 33.3% on the unseeded topsoil plots (Fig. 1b).

Total plant cover and density of grasses and forbs increased significantly from 1991 to 1992 and were highest on the undisturbed habitat (Table 2b). From 1991 to 1992, total plant cover and density of grasses and forbs increased significantly in all treatments (Table 3b).

Total plant cover and density of grasses and forbs were higher on the seeded topsoil plots compared to the unseeded topsoil plots, but only total plant

TABLE 2. SUMMARY OF REPEATED MEASURES ANALYSIS OF VARIANCE ON THE EFFECTS OF YEAR AND TREATMENT ON *ERIASTRUM HOOVERI* DENSITY AND FREQUENCY, AND KEY VEGETATION CHARACTERISTICS ON THE PIPELINE AND WELL PAD STUDY SITES, NAVAL PETROLEUM RESERVE NO. 1, KERN COUNTY, CA. [a] Factors are listed in decreasing order of mean values where UND = undisturbed habitat, ST = seeded topsoil, and UST = unseeded topsoil. Factors differing significantly (P < 0.05, linear contrasts) are indicated by ">".

Study site	Characteristic	Factor	P value	Mean difference[a]
a. Pipeline	*E. hooveri* Density	Year	<0.001	1992 > 1991
		Treatment	0.006	UND > ST
		Year × Treatment	0.012	
	E. hooveri Frequency	Year	0.007	1992 > 1991
		Treatment	0.003	UND > ST
		Year × Treatment	0.094	
	Total Plant Cover	Year	<0.001	1992 > 1991
		Treatment	0.346	UND = ST
		Year × Treatment	0.053	
	Grass Density	Year	0.013	1992 > 1991
		Treatment	0.221	UND = ST
		Year × Treatment	0.011	
	Forb Density	Year	<0.001	1992 > 1991
		Treatment	0.001	UND > ST
		Year × Treatment	0.933	
b. Well Pad	*E. hooveri* Density	Year	0.008	1992 > 1991
		Treatment	0.538	UST = UND = ST
		Year × Treatment	0.249	
	E. hooveri Frequency	Year	0.436	1992 = 1991
		Treatment	0.374	UND = UST = ST
		Year × Treatment	0.199	
	Total Plant Cover	Year	<0.001	1992 > 1991
		Treatment	0.002	UND > ST > UST
		Year × Treatment	0.003	
	Grass Density	Year	<0.001	1992 > 1991
		Treatment	0.006	UND > ST = UST
		Year × Treatment	0.024	
	Forb Density	Year	0.008	1992 > 1991
		Treatment	0.538	UND = ST = UST
		Year × Treatment	0.249	

cover was significantly higher (Table 2b). Density and frequency of *E. hooveri* were higher on the unseeded topsoil plots compared to the seeded topsoil plots, but these differences were not significant (Table 2b).

No cryptogamic soil crust was observed on any of the plots in 1991. In 1992, cover of cryptogams was 2.0% on the seeded topsoil plots, 1.0% on the unseeded topsoil plots, and 0.7% on the undisturbed habitat (Table 3b).

DISCUSSION

Although these investigations are opportunistic in nature in that they were conducted without the opportunity to set up ideal experimental conditions, some observations can be made. These observations should be substantiated with appropriate experimental studies.

The results of this investigation demonstrate that *E. hooveri* can quickly colonize disturbed sites, at least when topsoil is conserved and returned, and adequate rainfall is received. At both study sites, *E. hooveri* occupied all disturbed plots after one growing season, and its density increased on the disturbed plots, at both study sites, from the first to the second growing season (Fig. 1). The frequency of *E. hooveri* increased on all disturbed plots except the seeded topsoil plots on the well pad study site, from the first to the second growing season (Fig. 1).

During the first few growing seasons following disturbance, we expected that the density and frequency of *E. hooveri* on the disturbed plots would not be as high as on undisturbed habitat. This expectation was confirmed at the pipeline study site (Table 2a). However, on the well pad site, neither the density nor the frequency of *E. hooveri* were significantly different between disturbed plots and undisturbed habitat (Table 2b). The small sample sizes (n = 3) for each treatment on the well pad site probably reduced the ability to detect significant differences.

We hypothesized that by not seeding the conserved topsoil at the well pad site, plant competition would be reduced and *E. hooveri* reestablishment would be enhanced. Unseeded plots had lower plant cover and lower densities of grasses and forbs than seeded topsoil plots in both 1991 and 1992 (Table 3b). However, *E. hooveri* density and frequency were not significantly higher on the unseeded plots than on the seeded plots (Table 2b).

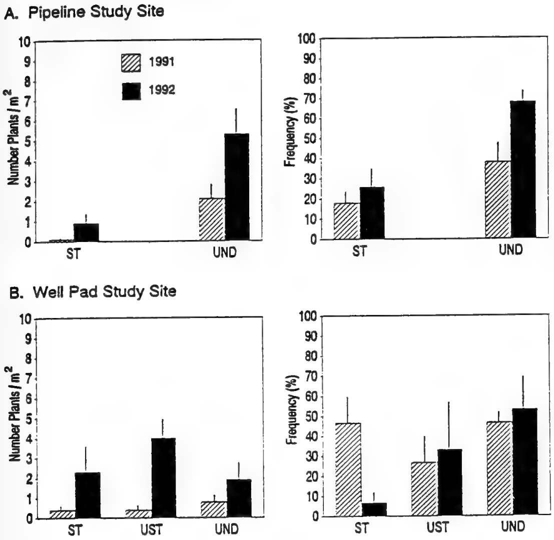

FIG. 1. Summary of *Eriastrum hooveri* density and frequency on the pipeline and well pad study sites where ST = seeded topsoil, UST = unseeded topsoil, and UND = undisturbed habitat, U.S. Naval Petroleum Reserve No. 1, Kern County, CA. Vertical bars indicate each standard error of the mean.

The capacity for *E. hooveri* to quickly invade disturbed sites is supported by other observations on NPR-1. In spring 1992 we observed seven populations of *E. hooveri* within a firebreak corridor that is maintained around the perimeter of NPR-1 (Holmstead and Anderson unpublished). Various sections of the firebreak have been annually disked for many years depending on the amount of vegetative cover present on the firebreak. Since 1990, all known *E. hooveri* populations have been avoided by disking operations. However, two of the populations we observed in spring 1992 were in sections of the firebreak that had been disked in 1991 and five populations were in areas disked in 1989.

The degree of reestablishment of *E. hooveri* in this study may partially be attributable to favorable growing conditions during WY91 and WY92. Annual plant population sizes vary widely from year to year (Holland 1987), and this variation is traditionally attributed to the vagaries of annual weather. A low rainfall year may result in very low numbers of a species, or even years when no plants are observed, while a higher rainfall year may result in large numbers of a species. Taylor and Davilla (1986) observed that *E. hooveri* germinated relatively late (January–February) as opposed to after the first rainfall (October–November). In WY91, rainfall was 10% above average, and 91% (124 of 137 mm) occurred from January–March. In WY92, rainfall was 25% above average, and 80% (124 of 155 mm) occurred from January–March. Abundant rainfall in both WY91 and WY92, and concentration of this rain between January–March may have promoted high germination and establishment of *E. hooveri*.

None of the disturbed or undisturbed plots at either study site had "dense patches of abundant soil cryptogams" that Taylor and Davilla (1986) reported were a principal correlate with the presence of *E. hooveri*. Cryptogamic cover was absent on most of the plots in 1991 (Table 3). The highest percent cover of cryptogams was 4.6%, which occurred on the undisturbed plots at the pipeline study site in 1991. In 1992, average cryptogam cover was ≤2.0% on all plots. These amounts of cryptogamic cover are well below what would be considered dense cover. Mean cover of cryptogams in nongrazed areas in Utah deserts was estimated at 53.6% (Brotherson et al. 1983). Average cover of

TABLE 3. VEGETATION CHARACTERISTICS ON THE PIPELINE AND WELL PAD STUDY SITES DURING THE FIRST AND SECOND GROWING SEASONS (1991 AND 1992) FOLLOWING CONSTRUCTION ACTIVITIES, NAVAL PETROLEUM RESERVE NO. 1, KERN COUNTY, CA. Standard errors of the mean are in parentheses.

		1991			1992		
Study site	Factor	Seeded topsoil	Unseeded topsoil	Undisturbed habitat	Seeded topsoil	Unseeded topsoil	Undisturbed habitat
a. Pipeline	Sample Size	10	—	10	10	—	10
	Cover (%)						
	Total Plant	31.3 (4.6)	—	41.8 (1.9)	67.6 (3.1)	—	65.8 (4.9)
	Cryptogams	0.0	—	4.6 (1.4)	0.5 (0.3)	—	1.3 (0.3)
	Density (no./m^2)						
	Grass	24.2 (6.8)	—	95.5 (9.6)	124.4 (31.1)	—	94.4 (8.6)
	Forb	13.8 (2.5)	—	61.8 (9.4)	49.8 (9.3)	—	98.9 (14.9)
b. Well Pad	Sample Size	3	3	3	3	3	3
	Cover (%)						
	Total Plant	26.7 (4.5)	12.0 (1.7)	55.0 (4.5)	62.7 (3.6)	55.3 (1.8)	69.7 (3.9)
	Cryptogams	0.0	0.0	0.0	2.0 (1.0)	1.0 (1.0)	0.7 (0.3)
	Density (no./m^2)						
	Grass	21.3 (4.3)	1.7 (0.5)	34.5 (8.8)	130.5 (8.5)	85.4 (10.3)	216.7 (31.6)
	Forb	15.1 (2.2)	7.0 (0.6)	36.7 (5.9)	36.7 (15.8)	31.7 (2.8)	61.3 (12.5)

cryptogams on grazed sites in Utah deserts was 6.3% on light developed crusts and 20.9% on moderate-heavy developed crusts (Anderson et al. 1982b). Our observations suggest that *E. hooveri* is not restricted to dense cryptogamic soil crusts. Quantification of site characteristics associated with *E. hooveri* populations are needed.

Some explanation for the low cryptogamic cover observed in this study compared to observations by Taylor and Davilla (1986), and for cover estimates reported for other investigations of cryptogamic crusts may be explained by 1) observer variability in cover estimates, 2) differences in antecedent precipitation that might have made the crust more apparent in one sample year than another, or 3) the components of cryptogamic crusts that are included in the cover estimates. Algal cover estimates can be quite subjective since algae are less obvious than lichens and mosses and their cover estimates are dependant upon experienced observers (Anderson et al. 1982a). Cryptogamic crust is known to consist of eucaryotic algae, lichens, bryophytes, cyanobacteria, and fungi that live on and just below the soil surface (Belnap 1994). Most general field inventory investigations focus on just those crust components that are visible without magnification, while more specific research on cryptogamic crust utilize laboratory detection procedures and estimate total cover of all components. The total cover estimates referenced in this paper used similar field methods.

The occurrence of *E. hooveri* on disturbed areas, and its apparent capacity to quickly occupy disturbed sites indicate that it may not be dependent on pristine habitats or dense cryptogamic cover. Some level of disturbance may be compatible with *E. hooveri* conservation. However, long term monitoring studies of disturbed *E. hooveri* populations and recently colonized disturbed sites are warranted. Such studies should investigate the persistence and vigor (size, flowering, and fruiting) of the plants over time.

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COAST LIVE OAK REVEGETATION ON THE CENTRAL COAST OF CALIFORNIA

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ABSTRACT

As part of a revegetation program for *Quercus agrifolia* Nee, we examined the reported effect of nurse plant facilitation on seedling establishment and growth. To investigate this location effect, acorns were planted directly in the ground in 100 positions under shrubs, and in 100 positions in the open. In addition, we tested for the effect of protection by covering half the planting positions with cages. In the first year, acorns planted in the open had higher germination but lower survival than acorns planted under shrubs, resulting in no significant location effect on the success of seedling establishment. The protection effect was significant, with the success of caged seedlings almost double that of uncaged seedlings. After two years, no location effect on seedling survival or growth was found. Cages continued to have a significant positive effect on seedling survival, but they tended to retard their growth. Over five years of monitoring, no significant effect of nurse plant facilitation on seedling survival or growth was found, although the number of seedlings that survived under shrubs was greater than that in the open. We also explored potential relationships of associated vegetation type and crowding on acorn seedling development. Seedling establishment, survival, and growth were associated with differences in vegetation type, and were higher in planting sites with more mesic vegetation. Crowding due to multiple seedlings growing in one planting position versus single seedlings did not negatively affect the growth of seedlings. Of 100 nursery-grown seedlings transplanted in the field in the first year, 99 were surviving at the end of the five-year monitoring period, and on average, they were much larger than the direct acorn plantings. As with the acorn seedlings, no significant nurse plant location effect was found for seedlings transplanted in the open or under shrubs.

Interest in the ecology, recruitment, and revegetation success of *Quercus agrifolia* Nee var. *agrifolia* (coast live oak) in California has heightened in recent years. A primary issue of ecological and conservation concern is that the extent of oak woodland and savanna habitats has decreased due to causes that are not well understood, but may include herbivory, competition, drought stress, cattle grazing, and development. The effects of these factors have been examined for California oaks, particularly *Quercus douglasii* Hook. & Arn. (blue oak) (Griffin 1971, 1976; Muick and Bartolome 1987; Borchert et al. 1989; Davis et al. 1991), but considerably fewer studies have concentrated on *Q. agrifolia.* Since there appears to be a net loss of oak populations statewide, the replacement of oak seedlings has been required as mitigation for development projects that result in the removal of adult oak trees. In many of these projects, the revegetation success with oaks has been poor. To understand fully the reasons for the lack of natural oak recruitment and the limited success of revegetation efforts, long-term studies of 10 or more years would be required; realistically, such long-term studies are seldom possible and systematic data beyond two years are rare.

In a two-year study on coast live oak establishment in Central California, Callaway and D'Antonio (1991) addressed the question of "nurse plant" interactions with *Q. agrifolia* seedling survivorship and found that seedlings grown under shrubs had higher survival rates than seedlings growing in open areas. They suggested that shrubs may reduce environmental stresses on young oak seedlings and provide protection from herbivory. Other researchers found that *Q. agrifolia* seedling survival was facilitated by shade and protection by caging (Muick 1991; Plumb and Hannah 1991).

As part of an environmental mitigation program, the U.S. Air Force was required to compensate for the loss of mature oaks that occurred during the construction of new facilities, roads, and railroads on San Antonio Terrace at Vandenberg Air Force Base (AFB). The project goal was to establish a total of 70 viable *Q. agrifolia* seedlings by the end of the five-year mitigation and monitoring program in 1995. Revegetation was carried out by growing oak seedlings from acorns planted directly in the ground (acorn seedlings), and by transplanting nursery-grown seedlings at the field site (transplant seedlings). We collected survival and growth data consistently over five years for both acorn and transplant seedlings, allowing us to quantify losses that took place during seedling germination and establishment phases. In this paper, we examine the location effect of nurse plant treatments on the survival and growth of the acorn and transplant seedlings. In addition, we investigate the protection effect of caging to explore the role of seed predation/herbivory in the early phases of acorn seedling establishment. Finally, we summarize and compare the survival and growth patterns of all seedlings over five years.

Study site. Vandenberg AFB occupies almost 40,000 ha north of Point Conception on the Central Coast of California. The San Antonio Terrace (34°49′N, 120°35′W) is located in the northern part of the base, between San Antonio Creek to the south and Shuman Creek to the north. The Terrace is ecologically important since much of its area comprises a unique ecosystem of stabilized sand dunes. Dune slopes and ridges are covered by coastal dune scrub vegetation dominated by *Ericameria ericoides* (Less.) Jepson (goldenbush) and *Artemisia californica* Less. (California sagebrush). Many interdune swales contain wetlands that support a number of different plant communities, including a variety of marsh and woodland vegetation types. The woodlands are dominated primarily by *Salix lasiolepis* Benth. (arroyo willow), but in several of the dune swales, *Q. agrifolia* is the dominant canopy species.

The area chosen for the oak revegetation project was located west of Live Oak Springs, a wetland of approximately 2 ha that was created on San Antonio Terrace as part of the environmental mitigation program. The site is within a swale near established oaks. Soils supporting the oaks are sandy, well drained, and have an ample supply of subsurface water. The presence of mature *Q. agrifolia* indicated environmental conditions favorable for the growth of this species; additionally, the shrubby habitat in the area provided some protection for seedlings from browsing animals. No cattle grazing occurs at the site, but *Odocoileus hemionus* (mule deer) and *Sylvilagus bachmani* (brush rabbits) are common in the area, and *Sus scrofa* (feral pigs) are known to be found nearby. Small mammals that prey on acorns, such as *Neotoma fuscipes* (wood rats), *Thomomys bottae* (pocket gophers) and *Spermophilus beecheyi* (ground squirrels), are present at the site, although not in large numbers.

METHODS

Planting and field methods. Oak acorns were collected from *Q. agrifolia* on San Antonio Terrace in November and December 1990. To ensure genetic diversity among acorns, several different collection locations were selected. Since live oak acorns require a 30–90 day cold stratification period before they germinate (Schopmeyer 1974), the acorns were stored in a refrigerator until direct planting was carried out in February 1991, during the winter rainy season. Although only 70 seedlings were required for mitigation, many more acorns and seedlings were planted to compensate for: 1) potentially low viability of collected acorns; 2) mortality of seedlings resulting from drought; and 3) potential losses of acorns and seedlings due to herbivory.

Locations for planting were chosen within the elevational zone of occurrence of neighboring mature oaks. For the acorn plantings, 100 locations were chosen under separate shrubs, and 100 locations were chosen about 1 m away from each shrub in open areas. The shrub species used as nurse plants were *E. ericoides, A. californica, Baccharis pilularis* DC. (coyote brush), and *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene (western poison oak). A total of 800 acorns were planted, four in a hole at each location, placed sideways just below the surface of the soil. Fifty randomly selected positions from each treatment (shrub/open) were covered with protective cages constructed of hardware cloth (mesh size about 1 cm^2) and shaded with 50 percent shadecloth. Cages were approximately 30 cm in diameter and 45 cm in height. To assure germination and to maintain emerging seedlings, all positions were hand-watered once a week in the initial months after planting, but less frequently thereafter.

Six hundred acorns were sent to a nursery to grow into seedlings. The nursery used a soil mix that included 40 percent sand, 3 percent redwood bark, and peat moss. A slow release fertilizer (19-6-12 nitrogen-potassium-phosphorus) was added, along with small amounts of other nutrients. In addition, a pH buffer of dolomitic lime maintained the mix at a pH of approximately 6 to 6.2 (sandy soils on the Central Coast are generally acidic). The acorns initially were planted in flats. When tap roots of seedlings reached the bottom of the flats, the seedlings were transplanted into 1-gallon containers, where lateral root systems could develop. Transplanting to the 1-gallon containers occurred in April 1991, approximately 60 to 90 days after germination. In November 1991, 100 of 401 available nursery-grown seedlings were transplanted in the field (hereafter referred to as transplant seedlings) at the same site as the acorn seedlings. Approximately half the transplants, chosen randomly, were located under shrubs, and half in open areas (an exact 50-50 split was not possible due to site constraints). Half were protected by cages similar to the acorn plantings, but these transplants were not selected completely at random because some seedlings already were too large to be caged. Due to this size bias, the protection treatment for the transplant seedlings was not analyzed statistically.

As seedlings outgrew the cages, they were removed or replaced by larger cages starting in Summer 1992, and continuing each year. All cages were removed in Fall 1995 at the end of the mitigation program. A drip irrigation system was installed in Fall 1991, with water emitters located at sites where seedlings survived from acorn plantings, and at all transplant locations. The seedlings were watered once per month in drier seasons (June–November). Irrigation ended in fall/winter each year, as soon as normal precipitation began, and was discontinued altogether in Fall 1995 at the end of the mitigation program. Neither the acorn nor the transplant seedlings received any artificial fertilization treatments after planting on San Antonio Terrace. The lack of long-term supplemental water and nutrients was designed to encourage seedlings to adapt to prevailing rainfall conditions and nutrient sources in their natural environment.

Data collection and analysis. Seedling survival was monitored approximately every two weeks in the first four months after acorn seedlings germinated in April 1991, then monthly through August 1992, and then annually through 1995. Transplants were monitored after November 1991 at the same time as the acorn seedlings. Survival data included counting seedlings and documenting their condition. Measurements of height, stem diameter, and leaf number were taken in the summers of 1991, 1992, and 1993 as indicators of growth of surviving acorn seedlings. Only height and stem diameter measurements were taken for transplant seedlings, since measuring leaf number would not have been time-effective. In 1994 and 1995, only height and stem diameter measurements were taken for all seedlings.

Survival and growth data were analyzed using contingency table analysis and two-way analysis of variance (ANOVA) respectively, testing for the effects of location (plantings under nurse shrubs or in the open) and protection (cages present or absent) on the acorn seedlings. Additional factors examined included associated plant species or vegetation type, and the potential effects of crowding due to multiple seedlings growing in a single position. For the transplant seedlings, only the effect of location was examined using ANOVA. Statistical analyses were carried out using CSS:STATISTICA (StatSoft, Inc. 1991).

RESULTS

Acorn seedling germination and survival—Year 1. Using data collected to 18 October 1991, percent germination, seedling survival, and seedling success were assessed for the location and protection treatments. Percent germination refers to the maximum number of acorns (out of the four planted) that germinated at any time. Percent survival is the proportion surviving after germination to a particular time. Percent success is the proportion of planted acorns that germinated and survived (germination multiplied by survival).

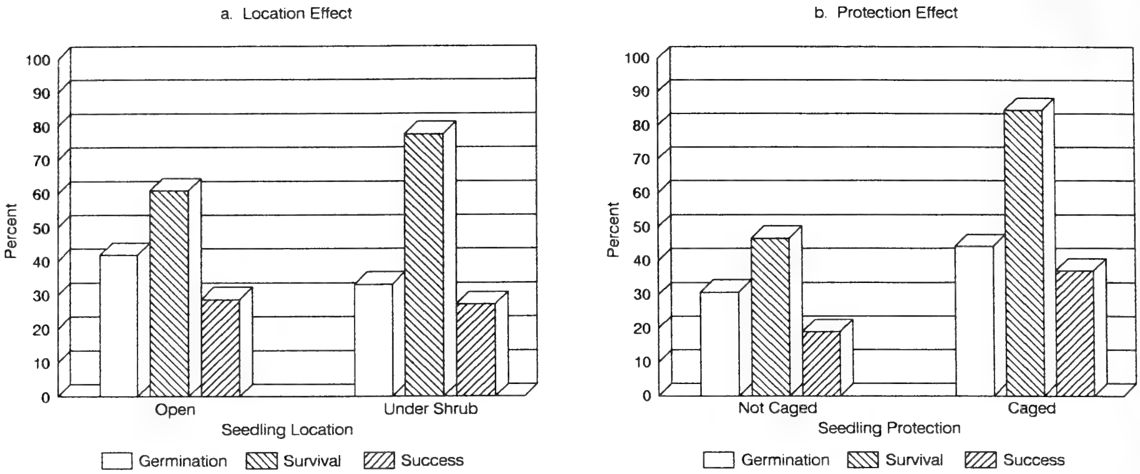
The germination, survival, and success data were examined using contingency table analysis. For germination, the effect of location was not statistically significant ($P > 0.05$); the overall mean was 41.8 percent for locations in the open and 33.3 percent for locations under shrubs (Fig. 1a). However, a significant effect of protection was found ($\chi^2 = 16.85$, $P < 0.01$), with a mean germination for caged acorns of 44.3 percent, and a mean of 30.8 percent for acorns without cages (Fig. 1b). Acorn germination stabilized at about the 60th day after first germination; the highest germination occurred for open and caged acorns, the lowest for unprotected acorns planted under shrubs (Fig. 2a).

The survival of acorn seedlings through this period was higher for seedlings that germinated under shrubs than those in the open, but this difference was not significant, with 77.5 percent surviving under shrubs, and 60.9 percent in open areas (Fig. 1a). Caged acorn seedlings survived at a rate almost double that of uncaged acorns; a significant difference, with means of 84.6 percent versus 46.5 percent ($\chi^2 = 26.61$, $P < 0.001$; Fig. 1b).

With respect to the success of acorn plantings, there was no significant effect of location (Fig. 1a), but again, a significant effect for protection was found ($\chi^2 = 39.95$, $P < 0.001$). Mean seedling success was 37.0 percent for caged seedlings and 19.0 percent for uncaged seedlings (Fig. 1b). The higher germination rate for acorns planted in the open was offset by a lower survival rate; and conversely, the lower germination for acorns under shrubs was compensated for by a higher survival rate over time (Fig. 2b). Therefore, overall success was not significantly different between acorn seedlings under shrubs and those in the open. This difference is most apparent when comparing the success of caged seedlings under shrubs and those in the open (Fig. 2c).

In addition to the effects of location and protection, we also examined the potential effect of species of nurse plant on percent germination, survival, and success. The species factor could not be controlled equally due to physical constraints of the planting area, however, the dominant shrub species at each planting location was recorded. Four major shrubs were present: *A. californica, E. ericoides, T. diversilobum,* and *B. pilularis* associated with an understory of *Carex praegracilis* W. Boott (clustered field sedge). Although beneath-shrub sample sizes were not appropriate for robust statistical analysis, a consistent seedling germination-survival-success pattern was observed, with *Baccharis/Carex* sites being followed by planting sites dominated by *Toxicodendron, Ericameria,* and *Artemisia* (Fig. 1c).

To summarize Year 1 results, germination was maximum for caged acorns, particularly in the open, suggesting that these acorns were protected from herbivory and may have received extra soil moisture due to the shadecloth covering the cages; moreover, increased sunlight in open conditions may have facilitated seedling germination. After germination rates leveled off, survival was better for protected seedlings and those under shrubs; protection from above-ground herbivory and good soil moisture retention apparently was provided both by cages and by shrubs. Acorns germinated and seedlings survived better in the *Baccharis/Carex* sites than in sites dominated by other shrub species. The higher success of seedlings in *Baccharis/Carex* sites may reflect higher soil moisture conditions, since these species occupy mesic environments such as wetland swales on the San Antonio Terrace.



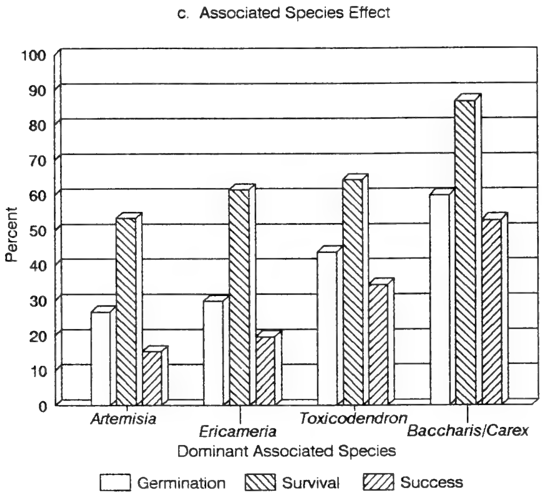


FIG. 1. Percent germination, survival, and success of acorn seedlings from data collected 18 October 1991: the effects of location, protection, and associated species.

Acorn seedling survival and growth—Year 2. At the end of Summer 1992, the effects of location and protection on the number of surviving acorn seedlings and their growth were examined. After this time, the removal of cages from seedlings that outgrew them precluded further experimental testing and analysis of the cage protection effect. The acorn seedlings had been sown in February and germinated by April 1991; therefore, they were approximately 6 months old during first measurements in 1991, and 15 months old during the next period of measurements in 1992, having progressed by then through two growing seasons in the field.

As in Year 1, the effect of the location treatment on seedling success in Year 2 was not found to be significant. With respect to the survival of acorn plantings, 45 positions in the open had live seedlings in 1991, decreasing to 40 in 1992. Under shrubs, 49 positions with live seedlings in 1991 decreased to 43 in 1992. A greater difference in individual seedling mortality was observed, with seedling losses between 1991 and 1992 in the open being three times that under shrubs: 24 of 113 seedlings observed in 1991 were lost in the open, but only 8 of 106 seedlings under shrubs.

The effect of the protection treatment in Year 2 continued to be significant ($\chi^2 = 14.66, P < 0.01$). High germination and survival rates for caged positions through 1991 resulted in 146 acorn seedlings, while only 73 survived in uncaged positions. By 1992, seedling survival remained better in caged positions compared to uncaged positions, with 121 seedlings in 54 caged positions versus 66 seedlings in 29 uncaged positions.

ANOVA was used to examine growth measurements taken of acorn seedlings in the first two years. Height and stem diameter of seedlings planted in the open or under shrubs did not show a significant location effect. Likewise, the effect of protection by caging on the growth of acorn seedlings

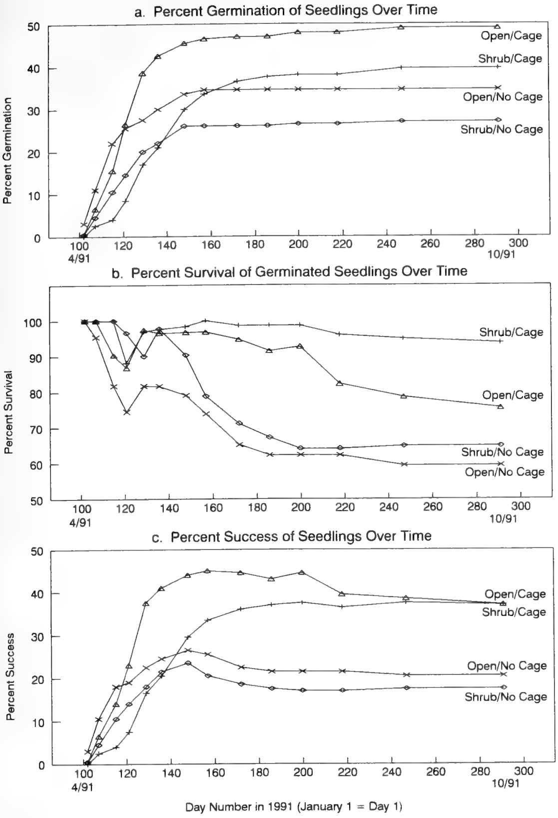


FIG. 2. Percent germination, survival, and success of acorn seedlings with respect to location and protection, April to October 1991.

was not apparent after the first growing season (Figs. 3a and 3b). Subsequently, absolute changes in height and stem diameter were substantially greater for the non-caged seedlings, which doubled in size by 1992. In contrast, the caged seedlings lagged in growth, resulting in a significant difference in both growth parameters for the cage protection effect in 1992 (height: $F_{1,185} = 17.93$, $P < 0.0001$; stem diameter: $F_{1,185} = 23.55$, $P < 0.0001$). The cages apparently tended to retard the growth of seedlings.

For the live acorn seedlings in 1991 and 1992, data were collected on leaf number of seedlings at the same time that the other two growth parameters were measured. In 1991, mean leaf number was 7.34, and by 1992 it was 17.24—an increase of about 135 percent. In both years, the effects of location and protection were significant: leaf number was higher for seedlings located in the open and not caged. For seedlings growing under shrubs or caged, leaf number was lower in both years, likely due to the effect of shading by shrubs or the shadecloth around the cages.

Acorn seedling survival and growth over five years. In early 1991, the mean germination for acorns planted in the field was about 38 percent, yielding 249 seedlings in June, a seedling establishment success of 31 percent. The initial mortality of acorn seedlings was 12.0 percent between June and October 1991. Mortality rates were 14.6 percent between 1991 and 1992; 12.3 percent between 1992 and 1993; 9.8 percent between 1993 and 1994; and 6.8 percent between 1994 and 1995. There were 32, 23, 16, and 10 seedlings lost in these four periods, respectively. By July 1995, 138 live acorn seedlings were recorded (Fig. 4a), a five-year seedling success of 17 percent. Of the 200 planting positions, 72 had at least one live seedling, a success by position of 36 percent.

At various times over the course of the project, the oak seedlings were subject to browsing, mold attacks, woolly oak aphids, leaf mining, and drought stress. These factors apparently resulted in the mortality of acorn seedlings. We also noted in

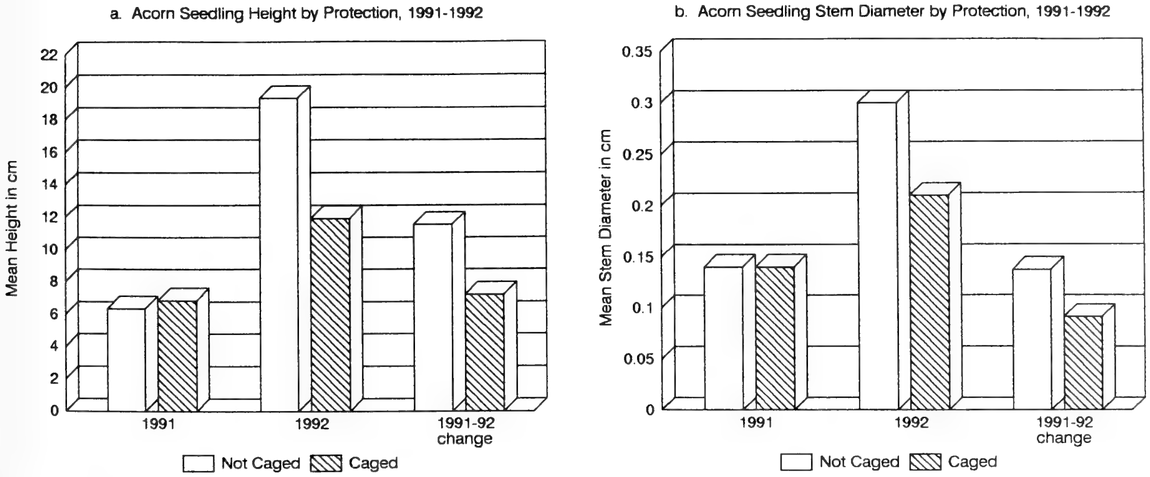


FIG. 3. Growth of acorn seedlings for the protection effect, 1991 to 1992.

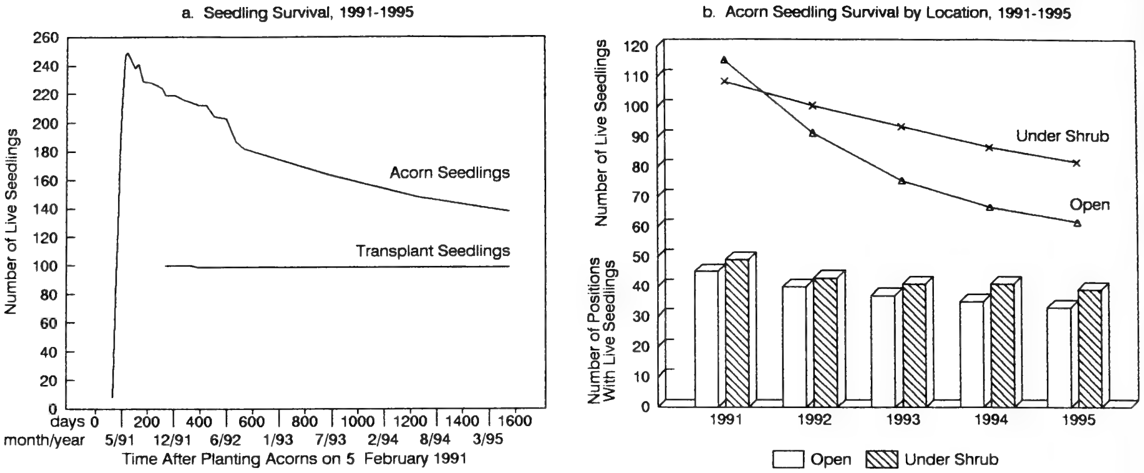


FIG. 4. Seedling survival, and acorn seedling survival by location, 1991 to 1995.

the field that heavy understory cover in the planting positions, both of native and non-native species, tended to have a negative effect on the survival and growth of seedlings in initial years. The understory species probably grew rapidly in response to irrigation of the planting positions in dry months; we observed that clearing the planting positions did appear to facilitate seedling growth, although this factor was not tested experimentally.

With respect to the effect of location on acorn seedling survival, the number of planting positions under shrubs with live seedlings only slightly exceeded the number in the open during the five years of the project. Initially, higher germination led to a greater number of individual seedlings in the open in 1991, but these seedlings suffered higher mortality in later years (Fig. 4b). By 1995, therefore, the absolute number of seedlings surviving under shrubs was greater than that in the open (79 versus 59). This difference, however, was not found to be statistically significant ($\chi^2 = 5.23$, $P > 0.10$).

As discussed previously for the first two years, patterns of acorn seedling growth, analyzed separately each year for years 3 through 5, showed no significant effects of location, with mean height and stem diameter measures being comparable for seedlings growing in the open and under shrubs.

In contrast to the lack of an effect of nurse plant location on the growth of oak seedlings, we observed in the field that acorn seedlings growing in the *Baccharis/Carex* sites were considerably larger than those elsewhere. We therefore combined growth and survival data for the planting sites associated with the shrub species *Artemisia, Ericameria*, and *Toxicodendron*, and compared them to data from the *Baccharis/Carex* sites. We found that from 1992 onwards, both height and stem diameter were significantly greater for acorn seedlings in the *Baccharis/Carex* sites (Figs. 5a and 5b). By 1995, means for height were 33.8 cm versus 55.5 cm for the two vegetation types; and stem diameter means were 0.6 cm versus 1.1 cm (height: $F_{1,136} = 13.42$, $P < 0.001$; stem diameter: $F_{1,136} = 21.80$, $P < 0.0001$).

A further examination of survival of acorn seedlings in the *Baccharis/Carex* vegetation type showed that although the number of planting positions and absolute number of live seedlings were smaller in the first two years, these seedlings survived considerably better over the longer term than those planted in the other sites (Fig. 5c). By 1995, the number of positions in each type was similar, but 82 live seedlings survived in the *Baccharis/Carex* sites, compared to 56 in the *Artemisia/Ericameria/Toxicodendron* sites. This finding indicated that more multiple seedlings were present by 1995 in the *Baccharis/Carex* sites, while more self-thinning occurred at the other sites.

Acorn seedling self-thinning. The issue of thinning the oak acorn seedlings in reference to positions with multiple seedlings arose while evaluating the revegetation program in later years. To assess for possible crowding effects, survival and growth data were analyzed for the years 1991 to 1995. The number of positions with multiple seedlings decreased over the years, indicating that self-thinning had occurred, particularly where 3 or 4 seedlings were present (Fig. 5d). Analysis of the growth data revealed no significant crowding effects on height or stem diameter over each of the five years, and multiple seedlings (2 to 4) growing in a single position were not significantly different in size than single seedlings. Moreover, no observable differences in health of the single versus multiple seedlings were noted in the field. Therefore, we decided not to thin the seedlings at the end of the monitoring period, and to allow natural mortality to continue.

Transplant seedling survival and growth over five years. Oak seedlings grown in the nursery ger-

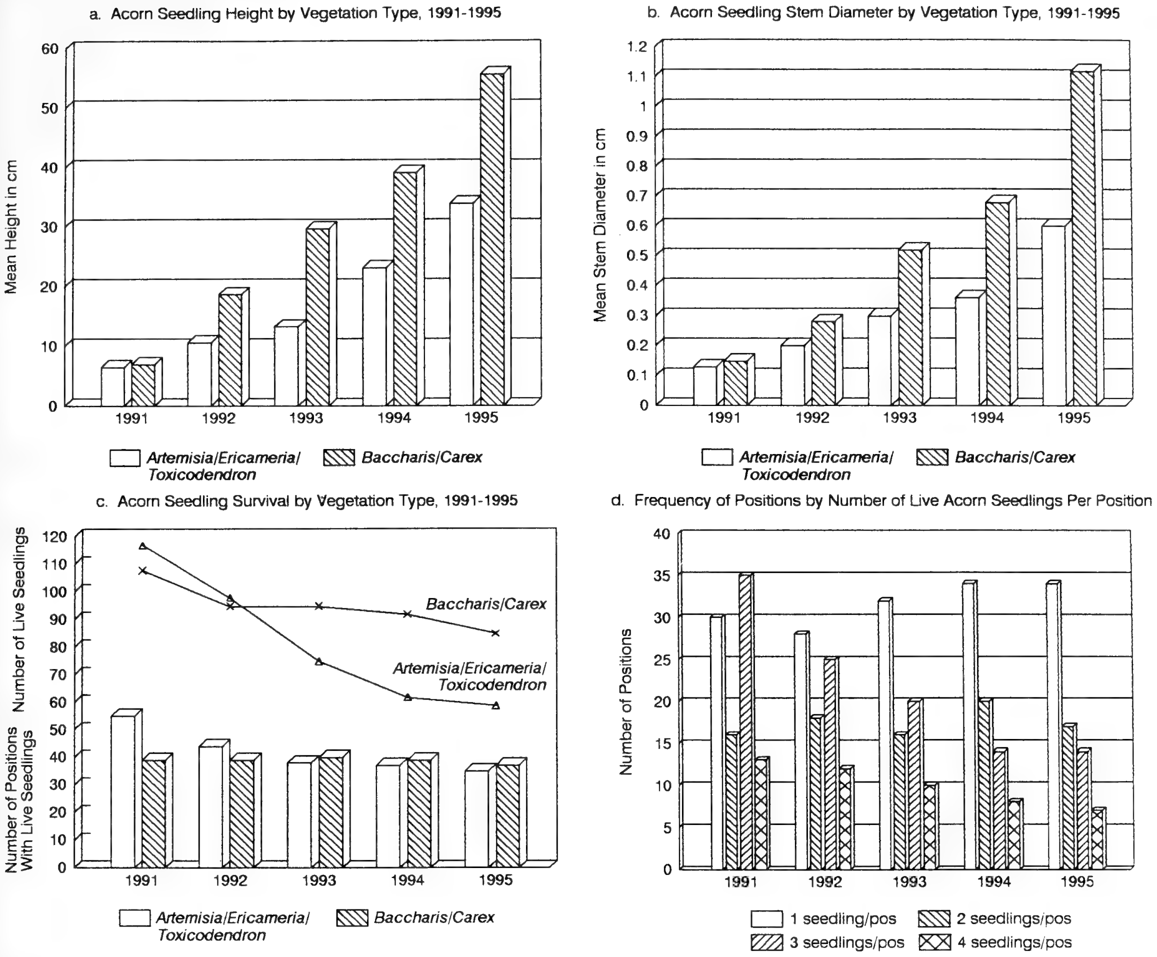


FIG. 5. Acorn seedling growth and survival by vegetation type, and number of acorn seedlings per position, 1991 to 1995.

minated by April 1991, and thus were approximately the same age as the acorn seedlings. One hundred of these seedlings were transplanted in the field in November 1991, after having progressed through one growing season in the nursery. Of the 100 transplants, only one seedling (planted in the open and uncaged) died (in March 1992) throughout the five-year monitoring period (Fig. 4a). Since seedling mortality was negligible, there clearly was no evident effect of location or protection on the survival of transplant seedlings.

By the time the nursery-grown seedlings were transplanted in the field in 1991, they already were much larger than the acorn seedlings. In fact, some of the transplants were too large to be caged, and the protection treatment could not be applied at random, therefore, the effect of caging on growth was not examined. Height and stem diameter measurements were taken at the time of transplanting to provide baseline growth data. In 1991, mean height of transplant seedlings was 45.6 cm and mean stem diameter was 0.81 cm, compared to a mean height of 6.7 cm and a mean stem diameter of 0.14 cm for the acorn seedlings. These two growth parameters were monitored for the transplants and analyzed each year using ANOVA to test for the location treatment, but the results did not show a significant effect for seedlings planted in the open or under shrubs.

Transplant seedlings grew more rapidly and remained much larger than acorn seedlings for all five years. Both height and stem diameter for acorn and transplant seedlings increased dramatically from 1994 to 1995, coinciding with a particularly high rainfall year, when precipitation was almost double the average of the previous four rain years. By the end of the five-year monitoring period in 1995, the mean height of transplant seedlings was 108.8 cm and mean stem diameter was 2.93 cm, compared to a mean height of 46.7 cm and a mean stem diameter of 0.91 cm for the acorn seedlings.

In summary, although it is suggested often that revegetation may be more successful by mimicking natural processes, i.e., favoring the direct planting of acorns in the ground allowing natural root systems to establish, we found that nursery-grown transplants were more successful in the field. They survived at 99 percent and grew on average to more than double the size of directly planted acorn seedlings over five years.

DISCUSSION

The results of this coast live oak revegetation project should be interpreted within the context of the local environmental conditions on the San Antonio Terrace at Vandenberg AFB; the applicability of this study elsewhere would have to be assessed at other sites and in other habitats. Nevertheless, this study raises a number of issues relevant to oak restoration programs in California, and also has implications for future ecological research on the mechanisms of recruitment of this species.

We observed three aspects related to the location effect examining nurse plant facilitation of oak seedlings. 1) Initially, relatively low germination rates but higher survival rates for acorns planted under shrubs led to a similar level of success as that of acorns planted in the open, which germinated at a higher rate but did not survive as well. 2) Over the five years of the project, acorn seedling survival was considerably higher under shrubs, although the difference was not statistically significant. This finding suggests, but does not confirm, that a longer term nurse plant facilitation effect may exist that might not be apparent in early years. 3) With respect to the growth of both acorn and transplant seedlings, their height and stem diameter was not affected by planting positions being located in the open or under shrubs. It appears, rather, that local site factors such as soil moisture, texture, and associated vegetation may have a greater effect on the success and growth of the seedlings. Planting acorns in mesic sites, dominated on the Terrace by *Baccharis/Carex* vegetation was more successful with significantly greater growth than planting in drier sites, even though large healthy oak trees were present very close to the planting positions in the drier sites and all sites were irrigated equally. This finding may partially explain the remarkable success of nursery-grown seedlings which were transplanted primarily to the *Baccharis/Carex* area.

Regarding the protection of acorns planted directly in the ground, caging in the initial months appears to facilitate both germination and survival of seedlings, therefore leading to higher initial success. However, in the second year of the program, the cages tended to retard the growth of the seedlings, indicating that they should be constructed to be larger in size from the beginning, or that they should be removed as soon as seedlings begin to outgrow the cages.

We also found that crowding of seedlings due to germination of multiple acorns planted in one position did not affect the growth of seedlings, and that self-thinning did occur at the scale of individual planting positions. Longer-term monitoring would help to assess the progress of multiple seedlings at this scale, as well as to examine the density and distribution of revegetated oaks at the larger site scale as seedlings grow into the sapling and tree stages. Such monitoring would enable the investigation of larger scale growth and thinning processes and the evaluation of optimum spacing between surviving healthy plants.

Our findings are consistent with field observations (Griffin 1973) as well as experimental results (Callaway 1990), which indicate that *Q. agrifolia* tends to be scarce in drier habitats, due in part to its dependence on lateral root systems that acquire moisture from the upper layers of the soil. In addition to its relatively short roots, Matsuda and McBride (1986, 1987) suggest that the distribution of *Q. agrifolia* in mesic sites is related to its slower germination and a larger leaf area to root weight ratio than other California oaks. In general, we found that although there appears to be some nurse plant facilitation of oak seedling survival, if not growth, other key factors related to microsite variations, particularly soil moisture, may be more important in affecting both seedling survival and growth. The effect of associated vegetation type that we observed may reflect a complex of ecological variables including those related to topography, geology, and hydrology, such as slope, aspect, elevation, soil texture, chemistry, nutrients, and moisture. More research and experimental investigation over greater periods of time than five years is needed to evaluate these factors.

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ALPINE VASCULAR FLORA OF HASLEY BASIN, ELK MOUNTAINS, COLORADO, USA

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ABSTRACT

The alpine habitat of Hasley Basin in the Elk Mountains of central Colorado was surveyed for its vascular flora in the summers of 1994, 1995, and 1996. A total of 209 species from 35 families and 109 genera were collected, including ten Colorado endemics and one species endemic to the Southern Rocky Mountains.

Vascular plant diversity surveys of specific geographic areas are an important prerequisite for a variety of systematic and ecological research activities. Such surveys aid ecological researchers in understanding the basic natural history of those areas (Kass 1988). The resulting documentation of the geographic distributions of particular plant species is necessary for monographic research in plant systematics. These surveys are also the basis for research in phytogeography, from the initial definition of floristic regions (Takhtajan 1986; McLaughlin 1989) to biogeographic studies that analyze the historical and evolutionary basis for present plant distributions (Weber 1965; Raven and Axelrod 1974; Taylor 1977; Billings 1978; Harper et al. 1978; Crovello 1981; Humphries and Parenti 1986; Hadley 1987). Floristic surveys are also vital for the location of populations of rare and endangered species (O'Kane 1988) and can function as baseline data to monitor both the disappearance of native plants and the encroachment of alien species (Snow 1995).

Many regions of Colorado and the United States have never been systematically surveyed for their plant diversity (Weber 1990; Hartman 1992). Whenever an area is systematically surveyed for the first time, botanical knowledge usually increases significantly. As an example, surveys by the Rocky Mountain Herbarium from 1974 to 1989 discovered 306 species new to the state of Wyoming and 51 taxa new to science (Hartman 1992). Similar surveys in Colorado from 1979 to 1989 found 179 plant species new to the state (Weber 1979, 1981, 1982, 1983, 1984, 1985, 1989).

This research surveyed the alpine vascular flora of Hasley Basin, a high basin in the Elk Mountains of central Colorado. Although nearby areas such as the Crested Butte Quadrangle (Langenheim 1955), the Gunnison Basin (Barrell 1969), the Ruby Range (Hartman and Rottman 1987), and the Gothic area (Buck and Frase 1993) have been previously studied, Hasley Basin itself has never been systematically surveyed. The primary objective of this research was to document the occurrence, distribution, and relative abundance of vascular plant species found in this relatively isolated alpine basin.

Study area. Hasley Basin is a high alpine basin located west of the Continental Divide in the Elk Mountains of central Colorado. The Elk Mountains are located in Gunnison County west of the Sawatch Range, south of the Colorado River, and north of both the Gunnison River and the San Juan Mountains. The Elks contain six peaks over 4268 m and are one of the more topographically rugged ranges in the Southern Rocky Mountains. Hasley Basin itself is located at 39 degrees 3 minutes 30 seconds North latitude and 107 degrees 2 minutes 30 seconds West longitude (Sections 24, 25, and 26, Township 11 South, Range 87 West, and Sections 19, 30, and 31, Township 11 South, Range 86 West). Located 20.9 km north and 4.8 km west of Crested Butte, CO, Hasley Basin lies in the Maroon Bells-Snowmass Wilderness Area, White River National Forest.

The basin is a glaciated valley drained by Hasley Creek and is geographically defined by ridges to the west, south, and east that are consistently over 3689 m in elevation. These ridges form a basin that is also U-shaped in areal view and is open towards the north. Six unnamed peaks on these ridges reach over 3808 m. Hasley Creek cuts through the center of the basin; to either side are located broad shelves that range in elevation from 3537 m to 3569 m. The shelves contain at least six glacially-derived kettle ponds (Prather 1982), some permanent and some ephemeral. Elevations in the basin range from 3232 m in the north near the confluence of Hasley Creek with the North Fork of the Crystal River to the basin's high point, an unnamed 3861 m peak on the western ridge. Geographically, Hasley Basin is adjacent in all directions to high basins and peaks, specifically Fravert Basin and Maroon Peak (4316 m) to the east, Lead King Basin and Snowmass Mountain (4296 m) to the north, Schofield Park and Treasure Mountain (4124 m) to the west, and Mt. Bellview (3817 m) to the south. The basin covers approximately 26 km^2.

The western ridge and basin are coterminous with the Elk Mountain Structure Zone, an area of steeply tilted rock strata at the edge of the block uplifts which produced the Elk Mountains (Prather 1982). The western ridge consists of strata which have been tilted to a near vertical position, while the strata of the eastern ridge are nearly horizontal, similar to those found in the Maroon Bells to the east.

Hasley Basin contains several rock types (Mutschler 1970). The Snowmass Stock (of Oligocene age in origin) is a light gray granodiorite found in the northeast portion of the Basin. Sedimentary formations include the Mancos Shale (Cretaceous), a dark gray-black calcareous shale found on the western ridge; the Dakota Sandstone (Cretaceous), a white-gray orthoquartzite located on the western ridge; the Morrison Formation (Jurassic), also found on the western ridge and consisting of greenish to dark gray shale, siltstone, sandstone, limestone, and dolomite; the Maroon Formation (Pennsylvanian-Permian), a gray brown to dusky red arkosic, micaceous, calcareous siltstone and conglomerate, found throughout most of Hasley Basin and on all its ridges; and the Gothic Formation (Pennsylvanian), a brownish gray to pale reddish brown shale, siltstone, sandstone, conglomerate, and limestone, located on the western and southern ridges and within the basin itself. Hasley Basin also contains various talus and scree slopes, several rock glaciers, and recent stream and pond deposits.

Climatic data are lacking for the study site itself. However, some data exist from the Rocky Mountain Biological Laboratory, located 12.9 km south and 3.2 km east at an elevation of 2887 m. Here mean snowfall for the 23 years of the data is 1121 cm, with a maximum of 1641 cm during 1994–1995 and a minimum of 474 cm in 1976–1977 (Barr personal communication). The mean January temperature is −11°C. At RMBL, the maximum temperature ever recorded is 29°C, while the coldest is −40°C. More complete data exists from Crested Butte; however, this town is located 20.9 km south and 4.8 km east of Hasley Basin and at the lower elevation of 2703 m. Mean annual snowfall here is 424 cm, while mean annual precipitation is 71 cm, with two maxima occurring, one in January and the other during the period from July to September (Langenheim 1962). Mean January temperature is −10.2°C, while mean July temperature is 39.0°C (Langenheim 1962).

Based upon both the above data and the personal experience of the authors, the climate at Hasley Basin can be characterized as being cold in the winters with a large accumulation of snow and cool but dry in the summers. Most precipitation falls as winter snow; summer rains generally fall during violent but brief thunderstorms. At RMBL, the access road is generally closed from November to mid-May due to snow. Hasley Basin, at a much higher elevation, is snow-free for only two or at most three months of the year. Estimates for mean snowfall range as high as 1.5 times greater than at RMBL (Barr personal communication).

The two primary years of the study were, in fact, noteworthy for their climatic extremes. The winter of 1993–1994 had a relatively low snowfall of only 954 cm (Barr personal communication). Consequently, Hasley Basin was largely snow-free by early June (Seagrist personal observation). This drought persisted throughout the summer. By mid-August 1994, most plants in the tundra had senesced and many late season species failed to flower at all (Seagrist personal observation). The winter of 1994–1995, however, had the heaviest snowfall of any year since 1973 (when RMBL's weather data begins), a total of 1641 cm. Hasley Basin was almost completely covered by snow as late as 15 July, with only a few south- and west-facing ridge crests beginning to melt free of snow (Seagrist and Taylor personal observation). However, by mid-August the Basin had become largely free of snow. It is possible that the weather extremes during the period of our study may have affected those plant species flowering and hence collected during the research.

METHODS

Collections of vascular plant species were made during June, July, and August in 1994, July, August, and September in 1995, and June, July, and August in 1996. Collections were confined to the alpine zone, defined here to mean all areas of the basin and its surrounding ridges located at and above the krummholz habitat (found in Hasley Basin at about 3354 m). Specimens were collected, placed within plastic bags to prevent drying, and carried back to the Rocky Mountain Biological Laboratory in nearby Gothic, CO. Here they were identified, pressed, dried, and mounted using standard herbarium techniques (Liesner n.d.). Identifications were done by the authors using Harrington (1954), Weber (1987), Weber and Wittmann (1996), and Welsh et al (1993). Nomenclature follows Weber and Wittmann (1996). Specimens were deposited at RMBL.

PLANT COMMUNITIES

Krummholz. The krummholz community is defined by the presence of wind-stunted *Picea engelmannii* Parry *ex* Engelmann and *Abies bifolia* A. Murray. It is located at elevations ranging from 3354 m to 3476 m, both in the central interior of the basin and on all slopes of the basin's surrounding ridges. Other common species found here include *Heracleum sphondylium* L. ssp. *montanum* (Schleicher *ex* Gaudin), *Ligusticum porteri* Coulter & Rose, *Lomatium dissectum* (Nuttall) Mathias & Constance, *Pseudocymopterus montanus* (A. Gray) Coulter, *Mertensia ciliata* (James *ex* Torrey) G. Don, *Geranium richardsonii* Fischer & Troutuettler, *Veratrum tenuipetalum* Heller, *Poa cusickii* vasey ssp. *edilis* (Scribner) Co. A., *Trisetum spicatum* L., and *Aconitum columbianum* Nuttal *ex* Torrey & Gray.

Riparian. Riparian habitat is found along Hasley Creek and its tributaries in the center of Hasley Basin. Elevations range from 3573 m at the base of the South Ridge to 3354 m on the north where Hasley Creek enters subalpine spruce-fir forest. Characteristic plant species include *Ligusticum filicinum* S. Watson, *Pseudocymopteris montanus, Arnica rydbergii* Greene, *Dugaldia hoopesii* (A. Gray) Rydberg, *Mertensia ciliata, Cardamine cordifolia* A. Gray, *Noccaea montana* (L.) F. R. Meyer, *Rhodiola integrifolia* Rafinesque, *Chamerion subdentatum* (Rydberg) Löve & Löve, *Aquilegia coerulea* James *ex* Torrey, *Phleum commutatum* Gaudin, *Trisetum spicatum, Psychrophila leptosepala* (De Candolle) W. A. Weber, *Delphinium barbeyi* (Huth) Huth, *Ranunculus adoneus* A. Gray, *Ranunculus alismifolius* Geyer *ex* Bentham, *Trollius albiflorus* (A. Gray) Rydberg, *Salix drummondiana* Barratt, *Castilleja rhexifolia* Rydberg, and *Pedicularis groenlandica* Retzius.

Ponds. At least six glacially-derived ponds are located within Hasley Basin, five on the Western Shelf and one on the Eastern Shelf. The Western Shelf ponds sit at elevations of 3315 m, 3543 m, 3573 m, 3659 m, and 3713 m, while the Eastern Shelf pond (really a set of small adjacent ponds) is located at 3598 m. Common plant species located within or immediately adjacent to these ponds include *Noccaea montana, Rhodiola integrifolia, Carex aquatilis* Wahlenberg, *Juncus drummondii* E. Meyer, *Erythronium grandiflorum* Pursh, *Oreobroma pygmaea* (A. Gray) T. J. Howell, *Psychrophila leptosepala, Ranunculus adoneus, Ranunculus alismifolius, Ranunculus inamoenus* Greene, *Salix geyeriana* Anderson, *Castilleja rhexifolia, Pedicularis bracteosa* Bentham in Hooker ssp. *paysoniana* (Pennell) W. A., *Pedicularis groenlandica*, and *Pedicularis parryi* A. Gray.

Wet meadows. Wet meadows are located along Hasley Creek in the center of the basin and also adjacent to the scattered glacial ponds. These relatively lush meadows range in elevation from 3415 m to 3713 m. Characteristic plants include *Pseudocymopteris montanus, Boechera drummondii* (A. Gray) Löve & Löve, *Erysimum capitatum* (Douglas) Greene, *Noccaea montana, Campanula parryi* A. Gray, *Rhodiola integrifolia, Clementsia rhodantha* (A. Gray) Rose, *Carex illota* L. H. Bailey, *Lupinus bakeri* Greene ssp. *amplus* (Greene) Fleak & Dunn, *Phacelia sericea* (R. Graham) A. Gray, *Juncus drummondii, Erythronium grandiflorum, Phleum alpinum* L., *Poa cusickii* ssp *edilis, Bistorta bistortoides* (Pursh) Small, *Primula parryi* A. Gray, *Anemonastrum narcissiflorum* L., *Aquilegia coerulea, Psychrophila leptosepala, Ranunculus adoneus, Ranunculus inamoenus, Trollius albiflorus* (A. Gray) Rydberg, *Acomastylis rossii* (R. Brown) Greene ssp. *turbinata* (Rydberg) W. A. Weber, *Salix drummondiana, Besseya alpina* (A. Gray) Rydberg, *Castilleja occidentalis* Torrey, *Castilleja rhexifolia*, and *Pedicularis groenlandica*.

Dry meadows. Dry meadows are the most widespread habitat found within Hasley Basin. They are ubiquitous above the krummholz zone (above 3354 m), within the basin, along the slopes of the surrounding ridges, and on the highest ridge crests up to 3861 m. Characteristic plant species include *Pseudocymopteris montanus, Antennaria media* Greene, *Antennaria rosea* Greene, *Cirsium hesperium* (Eastwood) Petrak, *Heterotheca villosa* (Pursh) Shinners, *Rydbergia grandiflora* (Torrey & Gray) Greene, *Eritrichum aretoides* (Chamisso) De Candolle, *Boechera drummondii, Erysimum capitatum, Smelowskia calycina* (Stephan *ex* Willdenow) C. A., *Noccaea montana, Silene acaulis* L. ssp. *subacaulescens* (F. N. Williams) Hitchcock & Maguino, *Frasera speciosa* Douglas *ex* Grisebach, *Hydrophyllum capitatum* Douglas *ex* Bentham, *Festuca brachyphylla* Schultes ssp. *coloradensis* Fredricksen, *Trisetum spicatum, Polemonium viscosum* Nuttall, *Bistorta bistortoides, Claytonia megarhiza* (Parry *ex* A. Gray), *Anemone multifida* Poiret var. *globosa* (Nuttall) Torrey & Gray, *Acomastyllis rossii* (R. Brown) Greene, ssp. *turbinata* (Rydberg) W. A. Weber, *Dryas octopetala* L. ssp. *hookeriana* (Juzepczok) Holten, *Ivesia gordonii* (Hooker) Torrey & Gray, *Pentaphylloides floribunda* (Pursh) Löve, *Salix arctica* Pallas, *Salix brachycarpa* Nuttall, *Castilleja occidentalis*, and *Penstemon whippleanus* A. Gray.

Results

The alpine vascular flora of Hasley Basin consists of 209 species, including 34 families, 107 genera, and 207 species of angiosperms, and 1 family, 2 genera, and 2 species of gymnosperms. The largest family is Asteraceae with 45 species, followed by Scrophulareaceae with 16 species, Poaceae with 14 species, Cyperaceae with 13 species, and Brassicaceae and Rosaceae with 12 species. Ten species are woody, the rest are herbaceous.

Eight species endemic to Colorado were found in Hasley Basin: *Ligularia amplectens* (A. Gray) W. A. Weber, *Ligularia holmii* (Greene) W. A. Weber, *Ligularia porteri* (Greene) W. A. Weber, *Ligularia soldanella* (A. Gray) W. A. Weber, *Townsendia rothrockii* A. Gray *ex* Rothrock and *Townsendia leptotes* (A. Gray) Osterhout (all in Asteraceae), plus *Polemonium confertum* A. Gray (Polemoniaceae) and *Castilleja puberula* Rydberg (Scrophulariaceae) (Weber and Wittmann 1992, 1996). *Clementsia rhodantha* (A. Gray) Rose (Crassulaceae) is endemic to the Southern Rocky Mountains (Weber and Wittmann 1996).

Polemonium confertum A. Gray is a Colorado endemic species which has been located at only a few scattered locations in the central ranges of the state. Prior to this study, it had previously been found at Rollins Pass, Buchanan Pass, Gray's Peak, Hoosier Ridge, and on Avery Peak (12.9 km south and 3.2 km east of Hasley Basin and adjacent to RMBL) (Grant 1989); the authors' work has extended the plant's range to include North Italian Mountain, West Hasley Ridge, Frigid Air Pass, Maroon Peak, and Pyramid Peak within the Elk Range and on the summit of East Buffalo Peak within the Mosquito Range (Seagrist and Taylor in press; Taylor personal observation). *Polemonium confertum* was always found by the authors in fellfields and along rocky alpine streams. It appears that this species may not be as rare as previously thought; it just grows in high elevation, hard-to-access habitats.

DISCUSSION

Hasley Basin seems to have a relatively diverse alpine flora when compared to similar areas in Colorado. Floristic data from comparable studies indicate that 289 species were collected from sixteen sites in the Sawatch Range (Hartman and Rottman 1988), 220 species from eight basins in the Ruby Range (Hartman and Rottman 1987), 197 species from three basins in the San Juan Mountains (Hartman and Rottman 1985b), and 167 species from the Mt. Bross massif in the Mosquito Range (Hartman and Rottman 1985a). Our total of 209 species compares favorably to previous research, especially when it is taken into account that most of the above studies collected from multiple basins or sites.

It is possible that we have undercollected the Cyperaceae and the Poaceae. Our collections indicate totals of 13 sedges and 14 grasses from Hasley Basin, as compared to 23 sedges and 19 grasses from the nearby Ruby Range (Hartman and Rottman 1987). However, two additional factors must be considered. The Ruby Range study collected from eight scattered locations within the range; we collected from only one basin. Consequently, the greater numbers of sedges and grasses could be due to greater geographic diversity within the Ruby Range study rather than undercollection on our part. It is also possible that the variable weather conditions found during the summers of 1994 and 1995 affected the results. The summer of 1994 was exceptionally dry, due to both low snowfall in the previous winter and to low rainfall during June and July. It was observed that vegetation in Hasley Basin had senesced due to drought by mid-August (Seagrist personal observation). Since many sedges and grasses flower in late summer (Weber 1987, 1996), this could have skewed our samples. In addition, the summer of 1995 was affected by exceptionally heavy snowfall during the previous winter. Hasley Basin still lay under deep snow as late as July 20 (Seagrist and Taylor personal observation) and isolated snow patches persisted into late August. This could also have affected the flowering of sedges and grasses and could have negatively impacted our collection samples.

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Nomenclature follows Weber and Wittmann (1992, 1996).

Alsinaceae

Cerastium beeringianum Chamisso & Schlechtendal ssp *earlei* (Rydberg) Hulten; dry meadow.

Cerastium strictum L. emend Haenke; dry meadow.

Eremogone congesta (Nuttall *ex* Torrey & Gray) Ikonnikov; dry meadow.

Eremogone fendleri (A. Gray) Ikonnikov; dry meadow.

Apiaceae

Angelica grayi (Coulter & Rose) Coulter & Rose; dry meadow.

Heracleum sphondylium L. ssp. *montanum* (Schleicher *ex* Gaudin) Briquet in Schinz & Thellung; krummholz.

Ligusticum tenuifolium Watson; riparian, wet meadow, pond.

Ligusticum porteri Coulter & Rose; pond, krummholz, wet meadow.

Lomatium dissectum (Nuttall) Mathias & Constance; dry meadow.

Oreoxis alpina (A. Gray) Coulter & Rose; dry meadow.

Oxypolis fendleri (A. Gray) Heller; wet meadow, riparian.

Pseudocymopterus montanus (A. Gray) Coulter & Rose; dry meadow, wet meadow, krummholz, riparian.

Asteraceae

Agoseris aurantiaca (Hooker) Greene; dry meadow.

Agoseris glauca (Pursh) Rafinesque; dry meadow.

Antennaria media Greene; dry meadow.

Antennaria rosea Greene; dry meadow.

Antennaria umbrinella Rydberg; dry meadow.

Arnica cordifolia Hooker; dry meadow.

Arnica mollis Hooker; pond, wet meadow.

Arnica parryi A. Gray; dry meadow.

Arnica rydbergii Greene; dry meadow, pond, krummholz, riparian.

Artemisia scopulorum A. Gray; dry meadow.

Chaenactis alpina (A. Gray) Jones; dry meadow.

Cirsium hesperium (Eastwood) Petrak; dry meadow.

Dugaldia hoopesii (A. Gray) Rydberg; krummholz, riparian, wet meadow, pond, dry meadow.

Erigeron compositus Pursh; dry meadow.

Erigeron coulteri T.C. Porter; dry meadow.

Erigeron elatior (A. Gray) Greene; riparian, krummholz.

Erigeron formosissimus Greene; krummholz, riparian, dry meadow.
Erigeron leiomerus A. Gray; dry meadow.
Erigeron melanocephalus A. Nelson; dry meadow, riparian, wet meadow.
Erigeron pinnatisectus (A. Gray) A. Nelson; dry meadow.
Erigeron simplex Greene; dry meadow.
Erigeron speciosus (Lindley) De Candolle; krummholz, riparian, dry meadow.
Erigeron vagus Payson; dry meadow.
Helianthella quinquenervis (Hooker) A. Gray; krummholz, riparian.
Heterotheca villosa (Pursh) Shinners; dry meadow.
Ligularia amplectens (A. Gray) W.A. Weber; dry meadow; **endemic in Colorado.**
Ligularia holmii (Greene) W.A. Weber; dry meadow; **endemic in Colorado.**
Ligularia porteri (Greene) W.A. Weber; dry meadow; **endemic in Colorado.**
Ligularia soldanella (A. Gray) W.A. Weber; dry meadow; **endemic in Colorado.**
Packera cana (Hooker) Weber & Löve; krummholz, riparian.
Packera dimorphophylla (Greene) Weber & Löve; wet meadow, ponds, dry meadow.
Packera streptanthifolia (Greene) Weber & Löve; dry meadow.
Packera werneriifolia (A. Gray) Weber & Löve; dry meadow.
Pyrrocoma clementis Rydberg; dry meadow, krummholz, riparian.
Rydbergia grandiflora (Torrey & Gray) Greene; dry meadow.
Senecio crassulus A. Gray; wet meadow, dry meadow, pond, krummholz, riparian.
Senecio fremontii Toerrey & Gray ssp. *blitoides* (Greene) W.A. Weber; wet meadows, ponds.
Senecio triangularis Hooker; wet meadow, dry meadow.
Solidago simplex Humboldt, Bonpland, & Kunth var *nana*; dry meadow.
Taraxacum eriophorum Rydberg; dry meadow.
Taraxacum officinale G. H. Weber *ex* Wiggers, riparian.
Tonestus lyallii (A. Gray) A. Nelson; dry meadow.
Townsendia leptotes (A. Gray) Osterhout; dry meadow; **endemic in Colorado.**
Townsendia rothrockii A. Gray *ex* Rothrock; dry meadow; **endemic in Colorado.**
Wyethia amplexicaulis (Nuttall) Nuttall X *Wyethia arizonica* A. Gray; dry meadow.

Boraginaceae

Eritrichum aretioides (Chamisso) De Candolle; dry meadow.
Hackelia floribunda (Lehmann) I. M. Johnston; dry meadow.
Mertensia ciliata (James *ex* Torrey) G. Don; dry meadow, wet tundra, riparian.
Mertensia lanceolata (Pursh) A. De Candolle; krummholz, riparian.

Brassicaceae

Boechera drummondii (A. Gray) Löve & Löve; dry meadow, wet meadow, riparian.
Cardamine cordifolia A. Gray; krummholz, pond, wet meadow, riparian.
Draba aurea M. Vahl *ex* Hornemann; dry meadow.
Draba breweri S. Watson var *cana* (Rydberg); dry meadow.
Draba crassa Rydberg; dry meadow.
Draba crassifolia R. Graham; dry meadow.
Draba fladnizensis Wulfen var. *pattersonii* (Schulz) Rollins; dry meadow.
Draba oligosperma Hooker; dry meadow.
Draba spectabilis Greene; dry meadow, wet meadow, pond.
Erysimum capitatum (Douglas) Greene; dry meadow, wet meadow.
Noccaea montana (L.) F.K. Meyer; dry meadow, wet meadow, riparian, pond.
Smelowskia calycina (Stephan *ex* Willdenow) C.A. Meyer; dry meadow.

Campanulaceae

Campanula parryi A. Gray; wet meadow.
Campanula rotundifolia L.; dry meadow.

Caprifoliaceae

Distegia involucrata (Banks *ex* Sprengel) Cockerell; dry meadow.
Symphoricarpos rotundifolius A. Gray; dry meadow, krummholz.

Caryophyllaceae

Gastrolychnis kingii (S. Watson) W.A. Weber; dry meadow, wet meadow.
Silene acaulis (L.) ssp. *subacaulescens* (F.N. Williams) Hitchcock & Maguire; dry meadow.

Crassulaceae

Clementsia rhodantha (A. Gray) Rose; wet meadow; **endemic in southern Rocky Mountains.**
Rhodiola integrifolia Rafinesque; riparian, wet meadow, dry meadow.

Cyperaceae

Carex albo-nigra Mackenzie in Rydberg; wet meadow, pond, dry meadow.
Carex aquatilis Wahlenberg; pond.
Carex athrostachya Olney; wet meadow, pond.
Carex chalciolepsis Holm; wet meadow, pond, dry meadow.
Carex crandallii Gandoger; wet meadow, pond.
Carex ebenea Rydberg; dry meadow.
Carex egglestonii Mackenzie; riparian, wet meadow.

Carex elynoides Holm; wet meadow, pond, dry meadow.
Carex foenea Willdenow; wet meadow, pond.
Carex illota L.H. Bailey; wet meadow.
Carex lachenalii Schkuhr; dry meadow, riparian, pond, wet meadow.
Carex nigricans C.A. Meyer; wet meadow, pond.
Carex vernacula L.H. Bailey; wet meadow, pond.

Fabaceae

Astragalus alpinus L.; dry meadow.
Astragalus molybdenus Barneby; dry meadow, wet meadow.
Astragulus robbinsii (Oakes) A. Gray var. *minor* (Hooker) Barneby; dry meadow.
Hedysarum occidentale Greene; dry meadow.
Lupinus argenteus Pursh; riparian, pond, wet meadow, dry meadow.
Lupinus bakeri Greene ssp. *amplus* (Greene) Fleak & Dunn; dry meadow, wet meadow.
Oxytropis deflexa (Pallas) De Candolle ssp. *deflexa*; dry meadow.
Oxytropis podocarpa A. Gray; dry meadow.
Oxytropis viscida Nuttall *ex* Torrey & Gray; dry meadow.

Gentianaceae

Frasera speciosa Douglas *ex* Grisebach; dry meadow.
Gentianopsis barbellata (Engelmann) Iltis; dry meadow.
Gentianopsis thermalis (Kuntze) Iltis; pond, wet meadow.
Pneumonathe parryi (Engelmann) Greene; dry meadow.
Swertia perennis L.; pond, wet meadow.

Geraniaceae

Geranium richardsonii Fischer & Trautvetter; pond, wet meadow, krummholz.
Geranium viscosissimum Fischer & Meyer ssp. *nervosum* (Rydberg) W.A. Weber; dry meadow.

Grossulariaceae

Ribes montigenum McClatchie; dry meadow.

Helleboraceae

Aconitum columbianum Nuttall *ex* Torrey & Gray; krummholz.
Aquilegia coerulea James *ex* Torrey; dry meadow, riparian, wet meadow.
Delphinium barbeyi (Huth) Huth; wet meadow, riparian, pond.
Psychrophila leptosepala (De Candolle) W.A. Weber; wet meadow, riparian.
Trollius albiflorus (A. Gray) Rydberg; wet meadow, riparian.

Hydrophyllaceae

Hydrophyllum capitatum Douglas *ex* Bentham; dry meadow.
Phacelia sericea (R. Graham) A. Gray; dry meadow, wet meadow.

Juncaceae

Juncus drummondii E. Meyer; wet meadow, pond, dry meadow.
Luzula parvifola (Ehrhart) Desvaux; dry meadow.

Lamiaceae

Agastache urticifolia (Bentham) Kurtze; dry meadow.

Liliaceae

Erythronium grandiflorum Pursh; wet meadow, riparian, krummholz.
Lloydia serotina (L.) Salisbury *ex* Reichenbach; dry meadow, wet meadow.

Linaceae

Adenolinum lewisii (Pursh) Löve & Löve, krummholz.

Melanthaceae

Anticlea elegans (Pursh) Rydberg; krummholz, dry meadow.
Veratrum tenuipetalum Heller; krummholz.

Onagraceae

Chamerion subdentatum (Rydberg) Löve & Löve; riparian.
Epilobium clavatum Trelease; wet meadows, ponds.
Epilobium saximontanum Haussknecht; krummholz, riparian.

Pinaceae

Abies bifolia A. Murray; krummholz.
Picea engelmannii Parry *ex* Engelmann; krummholz.

Poaceae

Deschampsia cespitosa (L.) P. Beauvois; wet meadow, pond, dry meadow.
Elymus lanceolatus (Scribner & Smith) Gould; krummholz, riparian, wet meadow.
Elymus scribneri (Vasey) Jones; dry meadow.
Elymus trachycaulus (Link) Gould *ex* Shinners ssp. *andinus* (Scribner & Smith) Löve & Löve; wet meadow, pond, dry meadow.
Festuca brachyphylla Schultes ssp. *coloradensis* Fredricksen; dry meadow.
Phleum commutatum Gaudin; dry meadow, riparian, pond, wet meadow.
Poa alpina L; dry meadow.

Poa cusickii Vasey ssp. *epilis* (Scribner) W.A. Weber; dry meadow, wet meadow, pond, krummholz.

Poa fendleriana (Steudel) Vasey; wet meadow, dry meadow, riparian.

Poa glauca M. Vahl ssp. *rupicola* (Nash) W.A. Weber; dry meadow.

Poa juncifolia Scribner; dry meadow.

Poa nemoralis L. ssp. *interior* (Rydberg) W.A. Weber; dry meadow.

Poa tracyi Vasey; dry meadow.

Trisetum spicatum (L.) Richter ssp. *congdonii* (Scribner & Merrill) Hultén; dry meadow, wet meadow, riparian, pond.

Polemoniaceae

Polemonium confertum A. Gray; **endemic in Colorado.**

Polemonium pulcherrimum Hooker ssp. *delicatum* (Rydberg) Brand; dry meadow, wet meadow, riparian.

Polemonium viscosum Nuttall; dry meadow.

Polygonaceae

Bistorta bistortoides (Pursh) Small; dry meadow, wet meadow, pond.

Eriogonum coloradense Small; dry meadow; **endemic in Colorado.**

Eriogonum umbellatum Torrey var. *aureum* (Gandoger) Reveal; dry meadow.

Oxyria digyna (L.) J. Hill; dry meadow.

Rumex densiflorus Osterhout; krummholz, pond.

Portulacaceae

Claytonia lanceolata Pursh; dry meadow, riparian.

Claytonia megarhiza Parry *ex* (A. Gray) dry meadow.

Oreobroma pygmaea (A. Gray) T.J. Howell; pond, dry meadow.

Primulaceae

Androsace chamaejasme Host ssp. *carinata* (Torrey) Hultén; dry meadow.

Androsace septentrionalis L.; dry meadow, wet meadow.

Primula parryi A. Gray; wet meadow.

Ranunculaceae

Anemonastrum narcissiflorum (L.) Holub ssp. *zephyrum* (A. Nelson) W.A. Weber; dry meadow, wet meadow.

Anemone multifida Poiret var. *globosa* (Nuttall) Torrey & Gray; dry meadow.

Anemone parviflora Michaux; dry meadow.

Ranunculus adoneus A. Gray; dry meadow, wet meadow, riparian.

Ranunculus alismifolius Geyer *ex* Bentham var. *montanus* S. Watson; wet meadow, riparian, pond.

Ranunculus eschscholtzii Schlechtendal; dry meadow, wet meadow, riparian.

Ranunculus inamoenus Greene; dry meadow, wet meadow, riparian.

Ranunculus uncinatus D. Don; wet meadow, ponds.

Rosaceae

Acomastylis rossii (R. Brown) Greene ssp. *turbinata* (Rydberg) W.A. Weber; dry meadow, wet meadow.

Dryas octopetala L. ssp. *hookeriana* (Juzepczuk) Hultén; dry meadow.

Fragaria vesca L. ssp. *bracteata* (Heller) Staudt; dry meadow, wet meadow, pond.

Ivesia gordonii (Hooker) Torrey & Gray; dry meadow.

Pentaphylloides floribunda (Pursh) Löve; dry meadow.

Potentilla concinna Richardson; dry meadow.

Potentilla diversifolia Lehmann; dry meadow, wet meadow, krummholz, pond, riparian.

Potentilla nivea L.; dry meadow.

Potentilla pulcherrima Lehmann; dry meadow.

Potentilla rubicaulus Lehmann; dry meadow.

Potentilla subjuga Rydberg; riparian.

Sibbaldia procumbens L.; dry meadow.

Salicaceae

Salix arctica Pallas ssp. *petraea* (Andersson) Löve *et al.*; dry meadow.

Salix brachycarpa Nuttall; dry meadow, wet meadow, pond, riparian.

Salix drummondiana Barratt; riparian, wet meadow, dry meadow.

Salix geyeriana Andersson; dry meadow, pond, wet meadow.

Saxifragaceae

Ciliaria austromontana (Wiegand) W.A. Weber; dry meadow.

Micranthes odontoloma (Piper) Heller; dry meadow.

Micranthes oregana (T.J. Howell) Small; wet meadow.

Micranthes rhomboidea (Greene) Small; dry meadow, wet meadow, riparian.

Scrophulariaceae

Besseya alpina (A. Gray) Rydberg; dry meadow, wet meadow.

Castilleja linariifolia Bentham in De Candolle; dry meadow, wet meadow.

Castilleja miniata Douglas *ex* Hooker; dry meadow, riparian, wet meadow.

Castilleja occidentalis Torrey; dry meadow, wet meadow.

Castilleja puberula Rydberg; dry meadow.

Castilleja rhexifolia Rydberg; riparian, pond, dry meadow.

Castilleja sulphurea Rydberg; wet meadow, riparian.

Mimulus guttatus De Candolle; krummholz, riparian.

Pedicularis bracteosa Bentham in Hooker ssp. *paysoniana* (Pennell) W.A. Weber; wet meadow, pond, krummholz.

Pedicularis groenlandica Retzius; riparian, pond.

Pedicularis parryi A. Gray; dry meadow, pond.

Pedicularis procera A. Gray; dry meadow.

Penstemon mensarum Pennell; krummholz; **endemic.**

Penstemon strictus Bentham in De Candolle; dry meadow.

Penstemon whippleanus A. Gray; dry meadow, wet meadow, pond.

Veronica nutans Bongard; riparian, pond, wet meadow, dry meadow.

Valerianaceae

Valeriana capitata Pallas *ex* Link ssp. *acutiloba* (Rydberg) F.G. Meyer; dry meadow, wet meadow.

Valeriana edulis Nuttall; wet meadow.

Valeriana occidentalis Heller; wet meadow.

Violaceae

Viola labradorica Schrank; dry meadow, wet meadow, pond.

Viola nuttallii Pursh; pond, dry meadow.

Viola praemorsa Douglas *ex* Lindley ssp. *major* (Hooker) M.S. Baker; wet meadow.

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ALPINE VASCULAR FLORA OF BUFFALO PEAKS, MOSQUITO RANGE, COLORADO, USA

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ABSTRACT

The alpine flora of the Buffalo Peaks, twin volcanic mountains in the Mosquito Range of central Colorado, was surveyed during the summers of 1994 and 1995. A total of 173 species from 32 families and 99 genera were collected, including two species endemic to Colorado and one not native to North America.

Vascular plant diversity surveys are an important prelude to many types of ecological and systematic research, including basic natural history knowledge (Kass 1988), flora preparation (Stuessy 1990), monographic revision (Stuessey 1990), and phytogeographic analysis (Weber 1965; Raven and Axelrod 1974; Taylor 1977; Billings 1978; Harper et al. 1978; Hadley 1987). Floristic surveys are also vital for the location of rare species (O'Kane 1988) and serve as baseline data for monitoring the disappearance of native plants and the encroachment of exotics (Snow 1995).

This research surveyed the alpine vascular flora of the Buffalo Peaks, twin mountains within central Colorado's Mosquito Range. Although nearby areas such as the Sawatch Range (Hartman and Rottman 1988) and the Mt. Bross massif (Hartman and Rottman 1985) have been previously studied, the Buffalo Peaks themselves have never been systematically surveyed (Weber 1990). The Mosquito Range is known for its high alpine plant diversity (Weber 1990), yet the Buffalo Peaks are volcanic in origin in a range otherwise consisting of sedimentary and intrusive igneous rocks (Chronic and Chronic 1972). Consequently, this area may contain a unique flora of high floristic significance.

Study area. The Buffalo Peaks are high, rounded summits located east of the Continental Divide within the Mosquito Range of central Colorado. Lying within the Buffalo Peaks Wilderness Area (San Isabel and Pike National Forests), the twin peaks are located 16.1 km north and 1.6 km east of Buena Vista (Chaffee County), at a latitude of 38 degrees 59 minutes 0 seconds North and a longitude of 106 degrees 7 minutes 25 seconds West (Sections 21 and 22, Township 12 South, Range 78 West). The twin peaks are rounded in profile, have relatively high elevations (West Buffalo Peak is 4066 m, East Buffalo Peak is 4055 m), and consequently have extensive areas of alpine tundra. Lying to the east of the Sawatch Range (the highest range in the Central Rocky Mountains) and hence in its rain shadow, the Buffalo Peaks are probably dryer than would be expected given their fairly lofty elevations.

Topographically, the Buffalo Peaks region consists of a broad rounded ridge with two major and three minor summits. From west to east these summits are "Mt. Columbine" (an unnamed 3699 m peak on the U.S.G.S. topographic maps), "Mt. Bluebird" (unnamed 3694 m peak), "Pika Peak" (unnamed 3938 m summit), West Buffalo Peak (4066 m), and East Buffalo Peak (4055 m). Extending to the northeast from East Buffalo Peak is the "Great Plateau", an unnamed plateau largely above treeline whose summits range from 3846 m to 3855 m.

The south- and west-facing slopes lose their winter snow relatively early (late June in 1995) and have a fairly gentle topography. Conversely, the north- and east-facing slopes retain snow much longer (into late July in 1995) and have been glacially eroded into much steeper topography.

Structurally, the Mosquito Range is a highly asymmetrical anticline, sloping gently on the east and sharply on the west (Chronic and Chronic 1972). The range crest, which includes four 4,268 m peaks, is primarily capped with fossiliferous Paleozoic sedimentary rocks. However, a few of the higher peaks consist of quite different rock types, including Mt. Bross and Mt. Lincoln (Lincoln Porphyry, a Tertiary intrusive) and Quandary Peak (Precambrian granite) (Chronic and Chronic 1972).

The Buffalo Peaks themselves are two highly eroded volcanoes (Chronic and Chronic 1972) primarily composed of Tertiary andesitic lava and ash flows (Chronic 1980). The upper portions of both West and East Buffalo Peaks consist of the Buffalo Peak Andesite, an Oligocene brownish-gray augite-hornblende andesite (Scott 1975). The lower portions are mainly composed of a white, pinkish-gray, gray, or reddish-brown nonwelded to densely welded pumiceous ash-flow, air-fall, or water-laid tuff (Scott 1975). This formation is covered in many places, however, by thick talus consisting primarily of large angular blocks of Buffalo Peak Andesite (Scott 1975). In addition, the north-facing col between the West and East Peak is covered by a rock glacier dating from the Pinedale Glaciation which may contain an icy center (Scott 1975).

No weather data exist for the Buffalo Peaks region itself. However, there are weather stations at Buena Vista (2418 m), located 17.7 km south of West Buffalo Peak, and at Climax (3454 m), located 41.9 km north and 6.4 km west of West Buffalo. The latter station lies in the northern Mosquito Range and is probably closer in climate to the study site.

The most concentrated collecting activity at Buffalo Peaks was during the period of June, July, August, and September in 1995. Data from Climax indicate that the mean temperatures during these months were 41.1°, 48.3°, 52.5°, and 42.6°F, respectively (NOAA 1995). Temperatures fell below freezing 27 days in June, 16 days in July, zero days in August, and 23 days in September. Total precipitation during this four month period was 5.22 inches, 1.52 below normal. This was partially compensated by heavy winter snowfall which lingered late into June (Seagrist and Taylor personal observation).

At Buena Vista, closer geographically but at a much lower elevation, no data existed for June 1995. However, mean temperatures for July, August, and September were 61.1°, 64.2°, and 53.8°F (NOAA 1995). There were zero days below freezing in July and August and only 8 in September. Total precipitation during the three-month period was 4.22 inches, 0.67 inches below normal.

METHODS

Collections of vascular plants were made during June, July, and August in 1994 and during June, July, August, and September in 1995. Collections were made within the alpine zone only, defined here as including the krummholz and all habitats located at higher elevations. Specimens were collected, placed inside plastic bags to prevent drying, and transported back to the Rocky Mountain Biological Laboratory in Gothic, CO. They were then identified, pressed, dried, and mounted using accepted herbarium techniques (Liesner n.d.). Identifications were done by the authors using Harrington (1954), Weber (1990), Weber and Wittman (1996), and Welsh et al. (1993). Nomenclature follows Weber and Wittman (1996). Specimens were deposited at RMBL.

PLANT COMMUNITIES

Krummholz. Krummholz is located at elevations ranging from 3,537 m to 3,720 m on all slopes of the Buffalo Peaks region. This habitat is defined by the presence of wind- and cold-stunted *Picea engelmannii* Parry *ex* Engelmann and *Abies bifolia* A. Murray. At Buffalo Peaks, dwarfed *Populus tremuloides* Michaux are also present in large numbers, as are *Pinus aristata* Engelmann, *Pinus flexilis* James, and *Pinus contorta* Douglas. The major groves of *Pinus aristata* are located on the east-facing slopes of the Great Plateau at elevations of about 3700 m and on the southeast-facing slopes of East Buffalo Peak at about 3600 m. Characteristic plant species include *Pseudocymopterus montanus* (A. Gray) Coulter & Rose, *Mertensia ciliata* (James *ex* Torrey) G. Don, *Erysimum capitatum* (Douglas) Greene, *Noccaea montana* (L.) F.K. Meyer, *Juniperus communis* L., *Frasera speciosa* Douglas *ex* Grisebach, *Ribes montigenum* McClatchie, *Delphinium barbeyi* (Huth) Huth, *Polemonium pulcherrimum* Hooker ssp. *delicatum* (Rydberg) Brand, *Ranunculus inamoenus* Greene, *Salix glauca* L., *Salix geyeriana* Andersson, *Salix planifolia* Pursh, *Micranthes rhomboidea* (Greene) Small, *Castilleja occidentalis* Torrey, and *Penstemon whippleanus* A. Gray.

Shrub tundra. Shrub tundra is defined by the presence of various *Salix* species, including *Salix geyeriana, S. glauca,* and *S. planifolia.* At Buffalo Peaks, this habitat is primarily located in the col between Mt. Bluebird and Pika Peak at an elevation of approximately 3,689 m. Other common plant species include *Pseudocymopteris montanus, Mertensia ciliata, Erysimum capitatum, Noccaea montana, Ribes montigenum, Psychrophila leptosepala* (De Candolle) W. A. Weber, *Lloydia serotina* (L.) Salisbury *ex* Reichenbach, *Bistorta bistortoides* (Pursh) Small, *Pulsatilla patens* (L.) P. Miller, *Ranunculus eschscholtzii* Schlechtendal, and *Micranthes rhomboidea* (Greene) Small.

Fellfield. Fellfield is a habitat consisting of large, fairly solid rock fragments interspersed with dry tundra vegetation. It is located on the summits of Mt. Columbine (3699 m), Mt. Bluebird (3694 m), Pika Peak (3938 m), West Buffalo Peak (4066 m), East Buffalo Peak (4055 m), and the Great Plateau (3846 m to 3855 m). Characteristic plant species include *Oreoxis alpina* (A. Gray) Coulter & Rose, *Artemisia scopulorum* A. Gray, *Erigeron compositus* Pursh, *Rydbergia grandiflora* (Torrey & Gray) Greene, *Taraxacum ovinum* Greene, *Cystopteris fragilis* (L.) Bernhardi, *Eritrichum aretoides* (Chamisso), *Erysimum capitatum, Noccaea montana, Sambucus microbotrys* Rydberg, *Ribes montigenum, Phlox condensata* (A. Gray) E. Nelson, *Polemonium confertum* A. Gray, *Claytonia megarhiza* (Parry *ex* A. Gray), *Androsace septentrionalis* L., *Primula angustifolia* Torrey, *Ranunculus macauleyi, Acomastylis rossii* (R. Brown) Greene, and *Pentaphylloides floribunda* (Pursh) Löve.

Wet meadows. Wet meadows, defined by the presence of standing water or boggy soil during most of the growing season, are rare at Buffalo Peaks. They are located at only a few scattered locations, usually on north- and east-facing slopes near patches of melting or recently melted snow fields. Characteristic species include *Clementsia rhodantha* (A. Gray) Rose, *Rhodiola integrifolia* Rafinesque, *Gentianella acuta* (Michaux) Hiitonen, *Psychrophila leptosepala, Trollius albiflorus* (A. Gray) Rydberg, *Polemonium confertum, Potentilla* *rubricaulis* Lehmann, *Heuchera parvifolia* Nuttall *ex* Torrey & Gray var. *nivalis* (Rosendahl) Löve *et al.*, *Castilleja occidentalis*, and *Pedicularis groenlandica* Retzius.

Dry meadows. Dry meadows are ubiquitous at the Buffalo Peaks, being found on most areas above treeline at elevations ranging from 3,659 m to 4,066 m. Common plants species found in this habitat include *Cerastium beeringianum* Chamisso & Schlechtendol, *Cerastium strictum* L. *emend* Haenke, *Oreoxis alpina, Pseudocymopteris montanus, Cirsium scopulorum* (Greene) Cockeral, *Rydbergia grandiflora, Eritrichum aretoides, Boechera drummondii* (A. Gray) Löve & Löve, *Erysimum capitatum, Noccaea montana Astragalus alpinus* L., *Ribes montigenum, Aquilegia coerulea* James *ex* Torrey, *Aquilegia saximontana* Rydberg *ex* B. L. Robinson in A. Gray, *Phlox condensata* (A. Gray) E. Nelson, *Polemonium viscosum* Nuttall, *Oreobroma pygmaea* (A. Gray) T. J. Howell, *Androsace septentrionalis* L., *Primula angustifolia, Pulsatilla patens, Acomastylis rossii, Dryas octopetala* L. ssp. *hookeriana* (Jozepczuk) Hultén, *Ivesia gordonii* (Hooker) Torrey & Gray, *Ciliaria austromontana* (Wiegand) W. A. Weber, *Heuchera parvifolia* var *nivalis, Micranthes rhomboidea, Besseya alpina* (A. Gray) Rydberg, *Castilleja occidentalis, Pedicularis parryi* A. Gray, *Penstemon hallii* A. Gray, *Penstemon harbourii* A. Gray, *Penstemon whippleanus*, and *Valeriana capitata* Pallas *ex* Link ssp. *acutiloba* (Rydberg) F. G. Meyer.

RESULTS

The alpine flora of the Buffalo Peaks consists of 173 species distributed across 32 families, including 1 family, 1 genus, and 1 species of pteridophytes, 2 families, 4 genera, and 6 species of gymnosperms, and 29 families, 94 genera, and 166 species of angiosperms. The largest families include the Asteraceae with 39 species, the Poaceae (21 species), the Rosaceae (12 species), and the Brassicaceae (10 species).

Two species endemic to Colorado were found at Buffalo Peaks, *Ligularia amplectens* (A. Gray) W. A. Weber (Asteraceae) and *Polemonium confertum* (Scrophulariaceae) (Weber and Wittmann 1992, 1996). One exotic species, *Artemisia biennis* Willdenow (Asteraceae), was also collected (Weber and Wittmann 1996).

Polemonium confertum is a species endemic to Colorado that had been located at only a few scattered locations prior to our study (Grant 1989). The authors' work has extended the range of this species to include North Italian Mountain, West Hasley Ridge, Frigid Air Pass, Maroon Peak, and Pyramid Peak in the Elk Range and East Buffalo Peak and the Great Plateau in the Buffalo Peaks region of the Mosquito Range (Seagrist and Taylor 1996, Taylor personal observation).

Bristlecone pines (*Pinus aristata*) were common at scattered locations within the Buffalo Peaks, with the heaviest concentrations lying on the southern slopes of East Buffalo Peak and on the northeast slopes of the Great Plateau. Brunstein (1993) reports that 14 individual bristlecone pines have been located on National Forest land near South Park (just east of Buffalo Peaks) that have been dated to greater than 1600 years of age; the oldest is at least 2436 years old. The Buffalo Peaks' bristlecones may or may not be this ancient, but these groves are nonetheless worthy of high conservation priority and protection.

DISCUSSION

The total of 173 species collected at Buffalo Peaks compares well with studies from comparable alpine sites in Colorado. A total of 289 species have been reported from sixteen sites in the Sawatch Range (Hartman and Rottman 1988), 220 species from eight basins in the Ruby Range (Hartman and Rottman 1987), 197 species from three basins in the San Juan Mountains (Hartman and Rottman 1985b), and 167 species from the Mt. Bross massif in the northern Mosquito Range (Hartman and Rottman 1985a). It is noteworthy that our total of 173 species compares best with the 167 species collected from Mt. Bross. Not only are both Mt. Bross and the Buffalo Peaks located in the Mosquito Range, but both studies collected at only one site; the other cited studies collected from multiple sites within a single range.

It must be noted that the two years of our study were exceptional in terms of weather. The summer of 1994 was quite dry, due both to low snowfall the previous winter and to low rainfall in June and July. The flowering season in 1995 began late due to a very heavy snowfall the previous winter. Much of the alpine zone at Buffalo Peaks was under heavy snow as late as July 1 and most areas didn't become snow-free until a few weeks later (Seagrist and Taylor personal observation). The stresses related to these shortened growing seasons may have negatively impacted the flowering of certain species and consequently we may have undercollected certain plant groups.

ANNOTATED CATALOG OF VASCULAR TAXA

Nomenclature follows Weber and Wittmann (1996).

Alsinaceae

Cerastium beeringianum Chamisso & Schlechtendal ssp. *earlei* (Rydberg) Hulten; dry meadow, krummholz.

Cerastium strictum L. *emend.* Haenke; krummholz, dry meadow.

Eremogone fendleri (A. Gray) Ikonnikov; krummholz, dry meadow, shrub tundra.

Lidia obtusiloba (Rydberg) Löve & Löve; dry meadow.

Paronychia pulvinata A. Gray; dry meadow.

Apiaceae

Angelica grayi (Coulter & Rose) Coulter & Rose; dry meadow, krummoholz.
Oreoxis alpina (A. Gray) Coulter & Rose; fellfield, dry meadow.
Pseudocymopterus montanus (A. Gray) Coulter & Rose; krummholz, shrub tundra, dry meadow.

Asteraceae

Achillea lanulosa Nuttall var. *alpicola* Rydberg; krummholz, dry meadow.
Agoseris glauca (Pursh) Rafinesque; krummholz.
Antennaria media Greene; krummholz.
Antennaria pulcherrima (Hooker) Greene ssp. *anaphaloides* (Rydberg) W. A. Weber; krummholz.
Antennaria rosea Greene; krummholz, dry meadow.
Antennaria umbrinella Rydberg; dry meadow.
Arnica cordifolia Hooker; krummholz.
Arnica mollis Hooker; shrub tundra.
Artemisia biennis Willdenow; krummholz; (non-native).
Artemisia frigida Willdenow; dry meadow.
Artemisia scopulorum A. Gray; fellfield, krummholz.
Chrysothamnus parryi (A. Gray) Greene ssp. *parryi*; krummholz.
Cirsium hesperium (Eastwood) Petrak; krummholz.
Cirsium scopulorum (Greene) Cockerell; dry meadow, fellfield.
Erigeron compositus Pursh; fellfield, dry meadow, krummholz.
Erigeron elatior (A. Gray) Greene; krummholz.
Erigeron leiomerus A. Gray; dry meadow.
Erigeron peregrinus (Banks *ex* Pursh) Greene spp. *callianthemus* (Greene) Cronquist; shrub tundra.
Erigeron pinnatisectus (A. Gray) A. Nelson; dry meadow.
Erigeron simplex Greene; krummholz, dry meadow.
Erigeron speciosus (Lindley) De Candolle; krummholz.
Erigeron ursinus D. C. Eaton; krummholz.
Heterotheca villosa (Pursh) Shinners; krummholz.
Ligularia amplectens (A. Gray) W.A. Weber, krummholz, dry tundra; endemic in Colorado.
Ligularia pudica (Greene) W.A. Weber; wet tundra.
Oreochrysum parryi (A. Gray) Rydberg; krummholz, dry tundra.
Packera cana (Hooker) Weber & Löve; krummholz, dry meadow.
Packera werneriifolia (A. Gray) Weber & Löve; dry meadow.
Pyrrocoma clementis Rydberg; dry tundra.
Rydbergia grandiflora (Torrey & Gray) Greene; fellfield, dry meadow.
Senecio atratus Greene; krummholz, wet tundra.
Senecio crassulus A. Gray; krummholz.
Senecio fremontii Torrey & A. Gray ssp. *blitoides* (Greene) W.A. Weber; dry meadow.
Senecio integerrimus Nuttall; dry meadow, krummholz, wet tundra.
Solidago simplex Humboldt, Bonpland, & Kunth var. *nana* (A. Gray) Ringins; dry tundra.
Taraxacum officinale G.H. Weber *ex* Wiggers; dry meadow.
Taraxacum ovinum Greene; fellfield.
Tetraneuris brevifolia Greene; dry meadow.
Tonestus pygmaeus (Torrey & Gray) A. Nelson; krummholz, dry meadow.

Athyriaceae

Cystopteris fragilis (L.) Bernhardi; fellfield, dry meadow.

Boraginaceae

Eritrichum aretioides (Chamisso) De Candolle; dry meadow, fellfield.
Mertensia ciliata (James *ex* Torrey) G. Don; krummholz, shrub tundra, dry meadow.
Mertensia lanceolata (Pursh) A. De Candolle; fellfield, krummholz, dry meadow.

Brassicaceae

Boechera divaricarpa (A. Nelson) Löve & Löve; krummholz.
Boechera drummondii (A. Gray) Löve & Löve; dry meadow, krummholz, shrub tundra.
Cardamine cordifolia A. Gray; krummholz.
Descurainia incana (Bernhardii) Dorn; krummholz.
Draba albertina Greene; fellfield.
Draba aurea M. Vahl *ex* Hornemann; dry meadow, fellfield.
Draba crassifolia R. Graham; krummholz, shrub tundra.
Draba spectabilis Greene; fellfield, dry meadow, krummholz.
Erysimum capitatum (Douglas) Greene; dry meadow, fellfield, krummholz, shrub tundra.
Noccaea montana (L.) F.K. Meyer; krummholz, wet meadow, shrub tundra, fellfield, dry meadow.

Campanulaceae

Campanula parryi A. Gray; krummholz.
Campanula rotundifolia L.; wet meadow, krummholz.
Campanula uniflora L.; dry meadow.

Caprifoliaceae

Sambucus microbotrys Rydberg; fellfield.

Caryophyllaceae

Gastrolychnis drummondii (Hooker) Löve & Löve; krummholz.

Crassulaceae

Amerosedum lanceolatum (Torrey) Löve & Löve; dry meadow, krummholz.

Clementsia rhodantha (A. Gray) Rose; wet meadow.

Rhodiola integrifolia Rafinesque; dry meadow, wet meadow, krummholz.

Cupressaceae

Juniper communis L. ssp. *alpina* (J.E. Smith) Celakovsky; krummholz.

Cyperaceae

Carex albo-nigra Mackenzie in Rydberg, dry meadow.

Carex aquatilis Wahlenberg; ponds.

Carex arapahoensis Clokey; krummholz.

Carex chalciolepsis Holm; shrub tundra, fellfield, krummholz.

Carex egglestonii Mackenzie; shrub tundra, krummholz.

Carex elynoides Holm; dry meadow, krummholz, fellfield.

Carex foenea Willdenow; dry meadow, krummholz.

Carex stenophylla Wahlenberg ssp. *eleocharis* (L.H. Bailey) Hultén; dry meadow.

Fabaceae

Astragalus alpinus L.; dry meadow, krummholz.

Oxytropis splendens Douglas *ex* Hooker; dry tundra.

Trifolium dasyphyllum Torrey & Gray; krummholz, dry meadow, wet meadow, fellfield.

Trifolium nanum Torrey; dry meadow, fellfield.

Trifolium parryi A. Gray; dry meadow.

Trifolium salictorum Greene *ex* Rydberg; krummholz, dry meadow.

Gentianaceae

Frasera speciosa Douglas *ex* Giseback, krummholz, dry meadow.

Gentianella acuta (Michaux) Hiitonen; wet meadow.

Gentianodes algida (Pallas) Löve & Löve; shrub tundra, wet tundra.

Pneumonanthe parryi (Engelmann) Greene; shrub tundra.

Grossulariaceae

Ribes montigenum McClatchie; dry meadow, fellfield, krummholz, shrub tundra.

Helleboraceae

Aconitum columbianum Nuttall *ex* Torrey & Gray; shrub tundra.

Aquilegia coerulae James *ex* Torrey; dry meadow, krummholz.

Aquilegia saximontana Rydberg *ex* B. L. Robinson in A. Gray; dry meadow.

Delphinium barbeyi (Huth) Huth; krummholz.

Delphinium ramosum Rydberg; dry meadow.

Psychrophila leptosepala (De Candolle) W. A. Weber; shrub tundra, wet meadow.

Trollius albiflorus (A. Gray) Rydberg; shrub tundra, wet meadow.

Hydrophyllaceae

Phacelia sericea (R. Graham) A. Gray; dry meadow.

Liliaceae

Lloydia serotina (L.) Salisbury *ex* Reichenbach; dry meadow, krummholz, shrub tundra.

Melanthiaceae

Anticlea elegans (Pursh) Rydberg; krummholz.

Onagraceae

Chamerion danielsii D. Löve; dry meadow.

Chamerion subdentatum (Rydberg) Löve & Löve; krummholz, dry meadow.

Pinaceae

Abies bifolia A. Murray; krummholz.

Picea engelmannii Parry *ex* Engelmann; krummholz.

Pinus aristata Engelmann; krummholz.

Pinus contorta Douglas Var. *latifolia* Engelmann; krummholz.

Pinus flexilis James *ex* London; krummholz.

Poaceae

Calamagrostis canadensis (Michaux) P. Beauvois; dry meadow.

Calamagrostis purpurascens R. Brown in Richardson; krummholz.

Deschampsia cespitosa (L.) P. Beauvois; shrub tundra, krummholz, dry meadow.

Elymus scribneri (Vasey) Jones; dry meadow.

Elymus trachycaulus (Link) Gould *ex* Shinners ssp. *andinus* (Scribner & Smith) Löve & Löve; dry meadow, krummholz, wet meadow.

Festuca arundinacea Schreber; krummholz.

Festuca brachyphylla Schultes spp. *coloradensis* Frederiksen; dry meadow.

Festuca idahoensis Elmer; krummholz, shrub tundra, dry meadow.

Helictotrichon mortonianum (Scribner) Henrard; dry meadow.

Hierochloë hirta (Schrank) Borbas ssp. *arctica* (J. Presl in K. Aesl) G. Weimarck; krummholz, shrub tundra.

Poa abbreviata R. Brown ssp. *pattersonii* (Vasey) Löve *et al*; krummholz, shrub tundra.

Poa alpina L.; krummholz.

Poa arctica R. Brown; dry meadow.
Poa cusickii Vasey ssp. *epilis* (Scribner) W.A. Weber; dry meadow, krummholz.
Poa fendleriana (Steudel) Vasey; krummholz.
Poa glauca M. Vahl ssp. *rupicola* (Nash) W.A. Weber; dry meadow, shrub tundra, krummholz.
Poa leptocoma Trinius; krummholz.
Poa nemoralis L. ssp. *interior* (Rydberg) W.A. Weber; krummholz, dry meadow.
Poa palustris L.; dry meadow.
Poa reflexa Vasey & Scribner; dry meadow.
Trisetum spicatum (L.) Richter ssp. *congdonii* (Scribner & Merrill) Hultén; krummholz, dry meadow.

Polemoniaceae

Phlox condensata (A. Gray) E. Nelson; dry meadow, fellfield.
Polemonium confertum A. Gray; wet meadow, fellfield, dry meadow, endemic.
Polemonium pulcherrimum Hooker ssp. *delicatum* (Rydberg) Brand; krummholz.
Polemonium viscosum Nuttall; dry meadow, krummholz.

Polygonaceae

Bistorta bistortoides (Pursh) Small; krummholz, shrub tundra, fellfield.
Eriogonum jamesii Bentham in A. De Candolle; dry meadow.

Portulacaceae

Claytonia megarhiza (Parry *ex* A. Gray); fellfield.
Oreobroma pygmaea (A. Gray) T.J. Howell; dry meadow.

Primulaceae

Androsace septentrionalis L.; dry meadow, fellfield.
Primula angustifolia Torrey; dry meadow, fellfield.
Primula parryi A. Gray; krummholz.

Ranunculaceae

Anemonastrum narcissiflorum (L.) Holub ssp. *zephyrum* (A. Nelson) W.A. Weber; fellfield, krummholz.
Pulsatilla patens (L.) P. Miller ssp. *multifida* (Pritzel) Zamels; krummholz, dry meadow, shrub tundra.
Ranunculus eschscholtzii Schlechtendal; shrub tundra, dry meadow.
Ranunculus inamoenus Greene; krummholz.
Ranunculus macauleyi A. Gray; dry meadow, fellfield.

Rosaceae

Acomastylis rossii (R. Brown) Greene ssp. *turbinata* (Rydberg) W.A. Weber; dry meadow, fellfield.
Dryas octopetala L. ssp. *hookeriana* (Juzepczuk) Hultén; dry meadow.
Fragaria vesca L. ssp. *bracteata* (Heller) Staudt; fellfield, dry meadow, krummholz.
Ivesia gordonii (Hooker) Torrey & Gray; dry meadow.
Pentaphylloides floribunda (Pursh) Löve; fellfield, dry meadow, wet meadow.
Potentilla concinna Richardson; krummholz, dry meadow, fellfield.
Potentilla diversifolia Lehmann; fellfield, dry meadow, krummholz, shrub tundra.
Potentilla nivea L.; dry meadow.
Potentilla pensylvanica L. var. *paucijuga* (Rydberg) Welsh & Johnston; dry meadow.
Potentilla pulcherrima Lehmann; fellfield, krummholz.
Potentilla rubricaulis Lehmann; krummholz, shrub tundra, wet meadow, dry meadow.
Potentilla subjuga Rydberg; fellfield, dry meadow, krummholz.

Salicaceae

Populus tremuloides Michaux; krummholz.
Salix brachycarpa Nuttall; dry meadow.
Salix drummondiana Barratt; shrub tundra.
Salix geyeriana Andersson; krummholz, shrub tundra.
Salix glauca L.; krummholz, shrub tundra.
Salix planifolia Pursh; krummholz, shrub tundra.

Saxifragaceae

Ciliaria austromontana (Wiegand) W.A. Weber; dry meadow.
Heuchera parvifolia Nuttall *ex* Torrey & Gray var. *nivalis* (Rosendahl) Löve *et al.*; wet meadow, dry meadow, krummholz.
Micranthes rhomboidea (Greene) Small; shrub tundra, dry meadow, fellfield, krummholz.

Scrophulariaceae

Besseya alpina (A. Gray) Rydberg; dry meadow.
Castilleja occidentalis Torrey; wet meadow, dry meadow, krummholz.
Pedicularis groenlandica Retzius; krummholz, wet meadow.
Pedicularis parryi A. Gray; dry meadow.
Penstemon hallii A. Gray; krummholz, dry meadow.
Penstemon harbourii A. Gray; dry meadow.
Penstemon whippleanus A. Gray; dry meadow, krummholz.
Veronica nutans Bongard; krummholz.

Valerianaceae

Valeriana capitata Pallas *ex* Link ssp. *acutiloba* (Rydberg) F. G. Meyer; dry meadow.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

QUERCUS CEDROSENSIS C. H. Muller (FAGACEAE).—San Diego Co., San Ysidro Mts.: southwest slope of Otay Mtn. in unnamed canyon along U.S.—Mexican border, 0.7 km ENE border monument number 251, 4.2 km SSW Otay Mtn. summit, UTM 11S-513, 200E, 3,602, 100N (T18S, R1E; 32°32′N, 116°51′45″W); local and occasional on dry northeast-facing canyon slope in chaparral, 335 m elevation, *Fred M. Roberts, D. Ann Kreager, and Gail Kobetich 4972*, August 15, 1996 (RSA, SD). San Ysidro Mtns.: southeastern slope along western edge of Marron Valley above Tijuana River, 0.2 km NNE border monument number 250, (T18S, R2E, S32; 32°32′N, 116°48′W); infrequent in north-facing canyon at margin of chaparral and Diegan coastal sage scrub in rocky soil, 274 m elevation, *Fred M. Roberts and Jim Dice 4975*, September 5, 1996 (RSA, SD).

Previous knowledge. Disjunct and scattered in coastal hills and mountains in association with coastal sage scrub, chaparral, and closed cone pine forest from just east of Tijuana, Baja California, Mexico, south to the Sierra San Borja west of Bahia de Los Angeles, and on Cedros Island.

Significance. First records for the United States and San Diego County. Previously considered endemic to northwestern Baja California, Mexico. Nearest collection about 16 km to the south in La Presa Canyon, Baja California, Mexico. The population west of Otay Mountain was burned in October 1996 and possibly damaged as a result of road construction by BLM for border patrol activities.

—FRED M. ROBERTS, JR. P.O. Box 231176, Encinitas, CA 92023.

CALIFORNIA

CASTILLEJA AMBIGUA Hook. & Arn. ssp. *humboldtiensis* (Keck) Chuang & Heckard (SCROPHULARIACEAE).—Marin Co.: Tomales Bay, Shields Marsh. 122°50.3′W, 38°05′N, Inverness Quad., in salt marsh, with *Distichlis spicata, Jaumea carnosa* and *Triglochin concinna*, 17 June 1992, *T. I. Chuang s.n.* (JEPS!); 3 April 1993, *M. Wetherwax 2436 & G. Fletcher* (JEPS!); Tomales Bay, Willow Point, 122°50.5′W, 38°05.2′N, Inverness Quad, in salt marsh, with *Distichlis spicata, Jaumea carnosa*, and *Triglochin concinna*. Site is in separate drainage system, 250 meters north of Shields marsh site, 11 April 1995, *G. Fletcher 951* (JEPS!); Tomales Bay, Toms Point, 122°56.8′W, 38°13.2′N, Tomales Quad., in salt marsh with *Distichlis spicata, Jaumea carnosa, Triglochin concinna*, 18 April 1995, *G. Fletcher 952* (JEPS!); 29 April 1996, *G. Fletcher 961* (CAS!); 3 May 1997, *G. Fletcher 972* (JEPS!); Tomales Bay, Millerton Point north salt marsh, 122°51′W, 38°06.7′N, Inverness Quad, in salt marsh adjacent to small slough emptying into Bay with *Distichlis spicata, Jaumea carnosa* and *Triglochin concinna*, 29 April 1997, *G. Fletcher 971* (JEPS!). Mendocino Co.: Big River Estuary 123°46.7′W, 43°50.7′N, 1.5 km from mouth of river in salt marsh with *Distichlis spicata, Triglochin maritima* and *Grindelia sp.*, May 12 1997, *M. Wetherwax 2658* (JEPS!); Big River Estuary 123°45.8′W, 43°50.3′N, 2.8 km from mouth of river in salt marsh with *Distichlis spicata* and *Jaumea carnosa*, 12 May 1997, *M. Wetherwax 2660* (JEPS!).

Previous knowledge. TYPE: Humboldt Co., Eureka. Partly dry saline flats, 20 June 1925, *P. A. Munz 9890* (POM!) All collections prior to the present report were from Humboldt County. The earliest record was Humboldt Bay, 1868, *Kellogg A. & G. W. hartford 701* (CAS!), the most recent was Humboldt Bay, S side of Eureka Slough, 8 August 1993, *M. Wetherwax and K. Downing 2455* (JEPS!). 42 collections from the Humboldt Bay area were examined, of which 28 provided sufficient detail to permit estimation of the geographic coordinates. The remainder provided only general information *i.e.* "Humboldt County"(2), "Humboldt Bay"(4), "Eureka"(5), and "Samoa"(3). The occurrences with geographic detail encompass an area of about 20 square miles of the Humboldt Bay region. The most northerly identified site was at Lanphere-Christensen Dunes Preserve, 124°8.1′W, 40°56′N, 11 June 1989, *Leonel Arguello s.n.* (HSC!) and the most southerly at mouth of Eel River, 124°19.3′W, 40°37.8′N, 19 May 1979, *T. Nelson & D. Niles 4694* (HSC!).

Significance. Extends distribution from near mouth of Eel River in Humboldt Co., 285 km south to Marin Co., Shields Marsh on Tomales Bay with intervening populations in Mendocino Co. at Big River and Marin Co. on Tomales Bay at Toms Point, Millerton Point and Willow Point. The Willow Point population has declined in distribution and number (120 and 6 plants 1995 and 1998 respectively) as result of silt run-off and gravel deposits that occurred following the 1996 Mt. Vision fire and the 1997/98 winter storms. The occurrence in the north salt marsh at Millerton Point is apparently of recent origin, as the taxon was not found in surveys of this site prior to 1997.

—GRANT FLETCHER, Audubon Canyon Ranch, Cypress Grove Research Center, P.O. Box 808, Marshall, CA 94940 and MARGRIET WETHERWAX, Jepson Herbarium, University of California, Berkeley, CA 94720.

CALIFORNIA

ASCLEPIAS SUBULATA Dcne. (ASCLEPIADACEAE).—Riverside Co., Vail Lake area, upper benches and adjacent slopes of the E flank of "Big" Oak Mtn., just S of the E summit, T8S R1W N½ sec. 3, 610–701 m, clay soil on gabbro, colony of about 100 plants, steep, xeric slope, NE corner sec. 3, 3 Apr 1990, *Steve Boyd et al. 4072* (RSA).

Previous knowledge. Known from arroyos and washes, mostly below 700 m, Colorado and eastern Mojave deserts of California to Arizona, Nevada, and northwestern Mexico (J. C. Hickman [ed.], The Jepson Manual: Higher Plants of California, 1993).

Significance. First report for the cismontane slope of southern California. In Baja California, Mexico, the species extends to the coastal slope of the Peninsular Ranges from the vicinity of Ensenada, southward. The area about Vail Lake, east of Temecula in Riverside County, hosts a variety of principally desert taxa in addition to *Asclepias* *subulata*, including *Asclepias erosa, Encelia actoni, Malacothrix glabrata, Chilopsis linearis, Cryptantha maritima, Pectocarya recurvata, Pectocarya setosa, Prosopis glandulosa* var. *torreyana, Stanleya pinnata, Echinocereus engelmannii, Quercus cornelius-mulleri, Pholistoma membranaceum, Loeseliastrum matthewsii, Langloisia setosissima, Simmondsia chinensis, Calycoseris parryi*, and *Mentzelia involucrata* ssp. *megalantha* (see below).

Calycoseris parryi Gray (ASTERACEAE).—Riverside Co., Bundy canyon, ca. 3.5 km SE of Lake Elsinore and 1 km N of Bundy Canyon Rd., off Raciti Rd., T6S R4W SE/4 S24, coastal sage scrub on fairly steep slopes with *Salvia mellifera, Adenostoma fasciculatum, Artemisia californica*, and *Ceanothus crassifolius*, scarce in open disturbed areas, alt 700 m, 2 Mar 1987, *B. Pitzer* and *L. LaPré 436* (UCR); North Domenigoni Hills, ca. 1 km SE of end of Warren Road, just NE of large prominent peak in NW corner of sec. 31 and within old quarry area, T5S R1W NW/4 S31, disturbed Riversidian sage scrub with *Bebbia juncea, Senecio californicus, Stipa coronata, Poa scabrella*, etc., soil rocky fine sandy loam, alt. 660 m, 9 May 1991, *D. Bramlet 2134* (UCR); Domenigoni Hills, N side of Domenigoni-Diamond Valleys ESE of Winchester, vicinity of ultramafic outcrop on ridge top S of S-end of Warren Rd, T5S R1W N/2 S31, burned coastal sage scrub, locally common on magnesite? deposits in and around old open-pit mine, alt. 550–670 m, 13 May 1991, *S. Boyd & D. Bramlet 6243* (RSA, UCR); Hwy 79, immediately W of U.S. Forest Service Campground at Dripping Springs, near 33°27′N, 116°58′W, Vail USGS quad, T8S R1W sec. 22, elev ca. 550 m, 13 May 1991, *Scott White 91-89* (SD).

Previous knowledge. Widespread on the deserts of southern California (P. A. Munz, A Flora of Southern California, 1974). This plant's distribution on the deserts is actually centered on the Mojave Desert, but it extends south along the western edge of the Colorado Desert on the eastern slope of the Peninsular Range. Across the Colorado Desert lowlands this species is largely (not completely) replaced by *Calycoseris wrightii* Gray. Several authors can be read to suggest cismontane occurrences for the species (e.g., R. M. Beauchamp, A Flora of San Diego County, 1986; J. C. Hickman, *loc. cit.*; H. M. Hall, Compositae of Southern California, Univ. California Publ. in Botany 3:1–302, 1907), but the published documentation of *Calycoseris parryi* from the coastal slope of southern California has been ambiguous. While Beauchamp (*loc. cit.*) indicates a "cismontane and desert" distribution for the taxon within San Diego County, all localities cited are from the desert slope of the Peninsular Range (although from floristically transitional areas). Hickman (*loc. cit.*) indicates *Calycoseris parryi* is reported from the Peninsular Range, but no distinction is made between cismontane and transmontane slopes. Hall (*loc. cit.*) notes that the species is known from "Palomar Mt., in the southern part of Riverside Co.," citing Jepson and Hall [s.n.] as the voucher. Undoubtedly, this refers to UC 63095, collected by W. L. Jepson and H. M. Hall between 17 May and June 1 1901. The locality given on that specimen is vague. The pre-printed portion of the label reads "Journey of W. L. Jepson and H. M. Hall from Riverside to Santa Rosa Peak and Palomar, May 17–June 1, 1901." Additional handwritten data specific to the specimen reads "Palomar, over 5000 feet". Although the lower northern flanks of Palomar Mountain are in Riverside County, areas of the range with elevations above 5000 feet are all within San Diego County. It is doubtful that *Calycoseris parryi*, a desert annual, would be found growing in the mesic pine forests atop Palomar Mountain. Given Hall's (*loc. cit.*) specific mention of Riverside County, it is more likely that the specimen was actually taken in the arid Santa Rosa Mountains.

Significance. First unambiguous records from the coastal slope of southern California for this desert species. We are also aware of the (former?) existence of a specimen (F. M. Reed 10073) from the "hills south of Perris, 2000 ft." but are unable to locate it. This collection was made prior to 1939 (possibly May 7, 1926) and is recorded in the database derived from the F. M. Reed herbarium cardfile (maintained at UCR). Reed's duplicates are widely distributed (BUT, RM, RSA, UC, UCR, US, etc.), but most of his 10,000 specimen personal herbarium was accidentally destroyed (remnants at UCR). Pending the discovery of a duplicate, this is just a sight record, but is of interest in that it corresponds with the distribution based on recent collections.

Interestingly, the type of *C. parryi*, a portion of a single plant, is reported to have been taken by C. C. Parry in the "mountains east of Monterey, California" (A. Gray, Bot. Mex. Bound. pg. 106, 1859). Hall (*loc. cit.*) discounted the type locality as being "certainly erroneous". Given the now well documented presence of *C. parryi* in cismontane western Riverside county, it is not unreasonable to believe that it may have been present in the Inner Coast Ranges during the late 1850's prior to the extensive invasion of exotic Eurasian grasses and forbs.

Mentzelia involucrata S. Watson ssp. Megalantha I. M. Johnston (Loasaceae).—Riverside Co., Vail Lake Area, steep SE flank of Oak Mtn. above NE end of lake, T8S R1W NE¼ SW¼ sec. 2, 550 m elev., white volcanic ash deposit with gabbro scree, 3 May 1990, *Steve Boyd et al. 4567* (RSA).

Previous knowledge. Known from the Colorado and Mojave deserts of California, east into southern Arizona, and south into northwestern Mexico. Generally found in washes, alluvial fans, and steep slopes at elevations below 900 m (P. A. Munz & D. D. Keck, *loc. cit.*; P. A. Munz, *loc. cit.*; J. C. Hickman, *loc. cit.*).

Significance. First report for the cismontane slope of southern California. See discussion of *Asclepias subulata* above for information on desert taxa in the Vail Lake region.

Navarettia fossalis Moran (POLEMONIACEAE).—Los Angeles Co., ca. 3.25 km N of Solemint, just off Arline Rd., ca. 3.25 km from intersection with Sierra Hwy., 34°27′02″N, 118°27′21″W, in vernal pool on shelf above Plum Canyon and Arline Rd., elevation ca. 610 m, 5 Jun 1996, *J. Mark Porter, et al. 10912* (RSA); Sink near Inglewood, 19 Jul 1906, *F. W. Peirson 950* (RSA) det. by S. Spencer, 1996.

Previous knowledge. Known from cismontane vernal pool habitats in northwestern Baja California, northward through western San Diego and western Riverside counties at elevations below 1300 m, with a single historical occurrence in San Luis Obispo County (J. C. Hickman, *loc. cit.*).

Significance. First reports for Los Angeles County. The Plum Canyon population, in the Santa Clarita Valley area, represents a disjunction of ca. 145 km from the northernmost Riverside County populations in the San Jacinto Valley. The Peirson collection from Inglewood, a disjunction of ca. 75 km west of the nearest Riverside County populations. The Inglewood station clearly represents an extirpated population, but suggests this taxon once had a broader distribution in the coastal lowlands of Los Angeles, and probably Orange counties. The San Luis Obispo County record is based on a collection by R. Hoover

8322 (CAS) collected in a dry pool bed, 1.5 km east of Creston, 17 May 1953. That specimen has been most recently annotated by Alva Day in 1987 and Stanley Spencer in 1996. Day's annotation contains a note that there were about 9 seeds in an immature capsule and that the calyx lobes are mostly entire. This suggests the San Luis Obispo material may be somewhat anamalous relative to the core populations in southern California and northern Baja California, Mexico. It is separated from the Plum Canyon station by ca. 210 km.

ORCUTTIA CALIFORNICA Vasey (POACEAE).—Los Angeles Co., ca. 2 mi. N of Solemint, just off Arline Rd. 3.25 km W from jct. with Sierra Hwy., in vernal pool basin (not evident from rd.) on shelf just N of and above Plum Canyon bottom . . . , in NE of 3 small depressions within basin, 34°27′02″N, 118°27′21″W, elev. ca. 610 m, 5 Jun 1996, *J. Travis Columbus et al. 2687* (RSA).

Previous knowledge. Known from cismontane vernal pool habitats in northwestern Baja California, northward through the Los Angeles basin into the Simi Valley (Ventura County) at elevations below 625 m (P. A. Munz, *loc. cit*; P. A. Munz & D. D. Keck, A California Flora, 1959; J. C. Hickman, *loc. cit.*).

Significance. First report for this taxon within the Santa Clara River drainage. *Orcuttia californica* occurs with *Navarettia fossalis* at Plum Canyon. The Plum Canyon populations of these two taxa represent small outliers from a larger vernal pool complex on Cruzan Mesa, approximately 1.5 km to the north. The Cruzan Mesa site has been subjected to very heavy disturbance in recent years, associated with land "development", and may now be extirpated.

SIBARA FILIFOLIA (E. Greene) E. Greene (BRASSICACEAE).—Los Angeles Co., Santa Catalina Island, Cape Canyon, rocky dry slope, east exposure, 305 m alt., 5 Jun 1973 [n.b.: date on original field collection label (in fragment packet on sheet) reads "6-5-73", an ambiguous style of date notation that should never be used with scientific specimens], *Doug Probst & Mark Hoefs 350* (RSA) det. by Steve Boyd, 1996.

Previous knowledge. Known from historic collections on Santa Cruz (latest 1932) and Santa Catalina (latest 1901) islands, and more recently, San Clemente Island (R. F. Thorne, 1967, Aliso 6:1–77; T. S. Ross, *et al.*, 1997, Aliso 15:27–40; S. Junak, *et al.*, A Flora of Santa Cruz Island, 1995; J. C. Hickman, *loc. cit.*).

Significance. First documentation of the taxon on Santa Catalina Island in 72 years. Botanists searched potential habitat within Cape Canyon in March 1997, but were unable to locate any extant populations (Mark Elvin, pers. comm., 1997). Future surveys of Santa Catalina Island for populations of *Sibara filifolia*, especially during years of favorable rainfall, are crutial to ensuring long-term survival of this extremely rare taxon. Otherwise known extant from a single, small population at the southern tip of San Clemente Island (T. S. Ross, *et al., loc. cit*).

SIBARA VIRGINICA (L.) Rollins (BRASSICACEAE).—Riverside Co., Skunk Hollow, ca. 10 km E of Murrieta, on W side of Pouroy Rd., elev. ca. 460 m, vernal pool, 10 Apr 1996, *G. R. Ballmer s.n.* (UCR, RSA) det. by A. C. Sanders, 1996; Orange Co., Fairview Park, City of Costa Mesa, 366 m N of the intersection of Wilson and Canyon Dr., 152 m W of the Canyon School, on a mesa overlooking the Santa Ana River, Newport Beach 7.5′ USGS Quad., UTM: 4 12 360mE × 37 24 490mN, elevation 24 m, 29 Apr 1995, *D. Bramlet 2405* (RSA); Costa Mesa, Fairview Park, just west of end of Canyon Drive, 0.1 km W of Canyon School, UTM 11[S] 4 12 700mE 37 24 600mN, alt. 24 m, 25 May 1995, *F. M. Roberts, Jr. & N. Hancock 4949* (RSA).

Previous knowledge. Known in southern California from mostly historic collections about vernal pools in Los Angeles and San Diego counties, ranging northward in California to the Central Valley, and southward into northwestern Baja California, Mexico, then disjunct to southeastern and central United States and northeastern Mexico (R. C. Rollins, Cruciferae of Continental North America, 1993; P. A. Munz, *loc. cit.*; J. C. Hickman, *loc. cit.*).

Significance. First documentation of the taxon in Riverside and Orange counties. As in the other California stations, this plant is associated with desiccating vernal pool habitats in Riverside and Orange counties. Rollins (*loc. cit.*) noted that *Sibara virginica* has become a weed in the principal part of its range in eastern North America. It is apparently capable of utilizing fallow agricultural fields by germinating in the fall and flowering early in the spring, thus completing its life cycle by the time field cultivation begins in the later spring. He also noted that the weediness is expressed in areas where the species occurred naturally, and evidence for dispersal into new areas is lacking. The taxon has apparently been extirpated in Los Angeles County and is very rare in Orange, Riverside, and San Diego counties, where vernal pool habitats have been largely eliminated. *Sibara virginica* is apparently native in the California floristic province, and the possibility that California populations represent a distinct variety, due to probable long isolation, should be investigated.

—STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711 and ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124.

MONTANA

ARABIS DEMISSA Greene var. *languida* Rollins (BRASSICACEAE).—Carbon Co., Pryor Mtns. Desert, bottom of Gypsum Creek Canyon, uncommon in juniper woodland with *Agropyron spicatum* and *Ribes cereum*, T9S R27E Sec7, 1735 m, 21 May 1991, *P. Lesica 5312* (MONTU); outwash plains 1 km S of the mouth of Big Coulee, common in stony soil of a small drainage with *Juniperus osteosperma* and *Agropyron spicatum*, T9S R28E S32, 1265 m, 13 Jun 1993, *P. Lesica 6003* (MONTU, GH). *Lesica 6003* determined by R. C. Rollins (GH).

Significance. First report for MT, a range extension ca. 280 km N from c. WY.

ASTER GLAUCODES Blake (ASTERACEAE).—Carbon Co., Pryor Mtns., on ridge just e of Tony Island, common in shallow limestone-derived soil with *Penstemon caryi* and *Achillea millefolium*, T8S R27E S11, 2345 m, 13 Aug 1995, *Lesica 7021* (MONTU, RM); common around limestone outcrops on narrow ridge just e. of Big Coulee with Penstemon caryi and Galium boreale, T8S R28E S20, 2315 m, 14 Aug 1995, *Lesica 7022* (MONTU); *Lesica 7021* verified by Robert Dorn (RM).

Significance. First report for MT although known from adjacent Big Horn Co., WY.

BALSAMORHIZA HISPIDULA W. M. Sharp [=*B. hookeri* var. *hispidula* (Sharp) Cronq.] (ASTERACEAE).—Beaverhead Co., Centennial Valley, hills s. of Lima Reservoir, common in sagebrush steppe with *Artemisia tridentata*, *A. tripartita* and *Festuca idahoensis*, 2105 m, T14S R6W

S21 SE¼, 31 Jul 1997, *P. Lesica 7487* (CO, MONTU). Determined by W. A. Weber COLO.

Significance. First report for MT, ca. 150 km north of nearest location in Snake River Plains of ID.

BOTRYCHIUM PALLIDUM Wagner (OPHIOGLOSSACEAE).—Flathead Co., Glacier National Park, south end of Big Prairie, scattered colonies in grasslands in an area of sagebrush that burned in 1988 with *B. paradoxum, B. simplex, Festuca idahoensis* and *F. scabrella*, 1095 m, T35N R21W S16, 7 Jul 1997, *P. Lesica 7453 with J. Asebrook, S. Erdt, T. Luna, T. Williams* (MICH); nw edge of Round Prairie, scattered colonies in grasslands in an area of sagebrush that burned in 1992, 1160 m, T36N R21W S19, 7 Jul 1997, *P. Lesica 7455 with J. Asebrook, S. Erdt, T. Luna, T. Williams*. Both specimens determined by W. H. Wagner (MICH).

Significance. First report for MT, ca. 400 km sw. of sw. Sask.

CAREX DILUTA M. Bieb. (CYPERACEAE).—Madison Co., south margin of Piedmont Swamp just south of Whitehall, locally common in a saline meadow near the old railroad grade with *Scirpus nevadensis* and *Carex nebrascensis*, 1325 m, T1N R4W S17, 5 Sept 1995, *P. Lesica and P. Husby 7173* (MICH, MONTU); same location, 8 Aug 1996, *P. Lesica 7353* (MICH, MONTU). Determined by A. Reznicek (MICH).

Significance. First record for N. America. Widespread in Eurasia; the presence of other Eurasian saline steppe plants such as *Oxytropis riparia* at this site suggests that it was introduced. After examining Asian material, A. Reznicek concluded that specimens were most similar to *C. karelinii* Meinsh., but this taxon is included under *C. diluta sensu lato* in Flora Europaea.

CAREX NORVEGICA Retz. ssp. *norvegica* [=ssp. *inserrulata* Kalela] (CYPERACEAE).—Stillwater Co., Beartooth Mtns., head of a small cirque on the n. side of Froze-to-Death Mtn., uncommon in moist turf along a small creek with *Carex nelsonii* and *C. misandra*, 3320 m, T7S R16E S21, 15 Aug 1984, *P. Lesica 3253* (MONTU); Carbon Co., Beartooth Mtns., along the stream above Crescent Lake on Hellroaring Plateau, uncommon in wet or inundated soil of a small fen with *Carex paysonis* and *Koenigia islandica*, 3110 m, T9S R18E S15, 8 August 1993, *P. Lesica 6191* (MONTU); Park Co., Crazy Mtns., ca. 2 km w. of Crazy Pk, locally common in gravelly, open soil of a dried vernal seep area in tundra with *Carex capitata* and *Polygonum viviparum*, 2865 m, T3N R11E S12, 11 Aug 1996, *P. Lesica 7365* (MICH, MONTU). Determined by T. Spribille; *Lesica 7365* verified by A. Reznicek (MICH).

Significance. First report for MT and continental U.S.; low arctic, disjunct 1700 km sw from Man.

ERIGERON TENER Gray (ASTERACEAE).—Beaverhead Co., Beaverhead Range, along Coyote Creek, common in stony, limestone-derived soil on the lower slopes of morraine with *Astragalus miser* and *Geum triflorum*, 2620 m, T15S R12W S12, 6 Sep 1997, *P. Lesica 7535* (BRY, MONTU). Verified by N. D. Atwood (BRY).

Significance. First report for MT; previously known from just w. in ID.

JUNCUS GERARDII Loisel (JUNCACEAE).—Madison Co., on the s. margin of Piedmont Swamp near old railroad grade, locally common in a saline meadow with *Scirpus nevadensis* and *Carex nebrascensis*, 1325 m, T1N R4W S17, 5 Sept 1995, *P. Lesica & P. Husby 7175* (MONTU, KANU); verified by Ralph Brooks (KANU).

Significance. First report for MT. This species is native to coastal Atlantic N.A. and is sporadically introduced inland (R. Brooks, pers. comm.).

LOMATIUM NUTTALLII (A. Gray) F. Macbr. (APIACEAE).—Big Horn Co., Squirrel Creek drainage ca. 5 km N of Decker, uncommon in shallow, rocky soil of a sandstone cliff with *Agropyron spicatum, Pinus ponderosa* and *Juniperus scopulorum*, ca. 915 m, 18 Jul 1980, *P. Husby s.n.* (MONTU, UC). Determined by L. Constance (UC).

Significance. First report for MT, a range extension of ca. 250 km NW from the Black Hills of South Dakota.

LOMATOGONIUM ROTATUM (L.) Fries. (GENTIANACEAE).—Beaverhead Co., Tendoy Mtns., along Deadman Creek just above Pine Creek, common in wet organic soil of a spring fen With *Juncus balticus* and *Carex simulata*, T15S R10W S22, 2135 m, 16 Aug. 1994, *P. Lesica and S. V. Cooper 6523* (MONTU, RM); just north of Simpson Creek ca. 3 km above Cabin Creek, common in a moist alkaline meadow with *Potentilla fruticosa* and *Juncus balticus*, T14S R11W S27, 2185 m, 17 Aug. 1994, *P. Lesica and S. V. Cooper 6528* (MONTU, MONT). *Lesica and Cooper 6523* verified by R. Dorn (RM).

Significance. First report for Montana.

LYCOPODIUM LAGOPUS (Laestadius ex Hartman) Zinserling ex Kuzeneva-Prochorova (LYCOPODIACEAE).—Glacier Co., Glacier National Park, Logan Pass, common in alpine turf along drainages or on edges of breaks with *Sphagnum*, 2275 m, 12 July 1964, *Harvey & Pemble 7081* (MONTU); ca. ½ km nw. of Mt. Reynolds, locally common at treeline with *Kalmia microphylla* and *Salix arctica*, 2285 m, 18 Aug 1985, *P. Lesica 3654* (MONTU). Determined by T. Spribille; verified by W. H. Wagner (MICH).

Significance. First report for MT ca. 350 km s. of nearest station in Canadian Rocky Mtns.

OXYTROPIS PARRYI Gray (FABACEAE).—Beaverhead Co., Beaverhead Range, on the ridge running ne from unnamed peak 4 km e of Red Conglomerate Peak, common in stony, calcareous soil with *Haplopappus acaulis* and *Erigeron caespitosus*, T15S R8W S36, 2745 m, 8 July 1986, *P. Lesica 3945* (MONTU); on a windswept ridgetop on w side of Little Beaver Creek, locally common in stony calcareous soil with *Selaginella densa* and *Erigeron caespitosus*, T15S R8W S36, 2865 m, 15 Aug 1992, *P. Lesica 5859* (MONTU, BYU); determined by Stanley Welsh (BYU).

Significance. First correct report for MT. Previous report for Glacier Co. was based on a misidentified specimen of *O. campestris* var. *cusickii* (R. Barneby, pers. comm.).

POTENTILLA HYPARCTICA Malte (ROSACEAE).—Carbon Co., Beartooth Mtns., on the e side of Mt Rearguard, common in moist turf along streams below snowfields with *Geum rossii* and *Sedum rosea*, T9S R18E S16, 3535 m, 8 Aug 1993, *P. Lesica 6195* (MONTU, UC); on a gentle nw-facing slope of the Beartooth Plateau w of Jasper Lake, common in turf between stone stripes with *Geum rossii* and *Carex scirpoidea*, T9S R17E S24, 3475 m, 8 Aug 1994, *P. Lesica 6520* (MONTU, UC); determined by Barbara Ertter (UC).

Significance. First report for Montana and the U.S. cordillera, a range extension of ca. 700 km se from Alberta.

PUCCINELLIA LEMMONII (Vasey) Scribn. (POACEAE).—Beaverhead Co., Centennial Valley, 1 km n. of Red Rock River, abundant in open soil of frost-churned hummock in a moist meadow with *Poa juncifolia* and *Solidago nemorosa*, 2040 km, T13S R3W S26 NW¼, 1 Aug 1997, *P. Lesica 7494* (BRY, MONTU); n. of Lima Reservoir, common on broad hummocks in an alkaline meadow with *Poa juncifolia* and *Haplopappus uniflorus*, 2010 m, T13S

R3W S26 NW¼, 1 Aug 1997, *P. Lesica 7557* (MONTU). *Lesica 7494* verified by N. D. Atwood (BRY).

Significance. First report for MT; ca. 200 km n. of closest station in Snake River Plains of s. ID.

RIBES VELUTINUM Greene (GROSSULARIACEAE).—Beaverhead Co., Beaverhead Range, along Coyote Creek above the lake, common in open spruce forest with *Shepherdia canadensis* and *Festuca idahoensis*, 2650 m, T15S R12W S12 SW¼, 6 Sep 1997, *P. Lesica 7532* (BRY, MONTU). Verified by N. D. Atwood (BRY).

Significance. First report for MT; previously known from just w. in ID.

SISYRINCHIUM SEPTENTRIONALE Bicknell (IRIDACEAE).—Sheridan Co., 2 km e. of Comertown, local in moist soil around a prairie pothole with *Anemone canadensis* and *Crepis runcinata*, 685 m, T36N R57E S25, Jun 1997, *P. Lesica 7428 & B. Martin* (MONTU). Determined by A. Cholewa (MIN).

Significance. First report for MT, known from just n. in Sask.

THESIUM ARVENSE Horva'tovsky. (SANTALACEAE).—Madison Co., S side of Ruby River just E of Ledford Creek Road, locally common on hummocks in calcareous wet meadows with *Juncus balticus* and *Potentilla fruticosa*, T9S R4W S3, 1715 m, 28 Jul 1992, *P. Lesica 5806* (CO, MONTU); head of Spring Creek on S side of Ruby River, common in moist grasslands with *Elymus cinereus* and *Agropyron smithii*, T9S R4W S34, 2040 m, 28 Jul 1992, *P. Lesica 5808* (MONTU). *Lesica 5806* determined by W.A. Weber (COLO).

Significance. First report of this introduced hemiparasite for MT and North America. *Thesium linophyllon* has been reported for one site in nc. ND (*Great Plains Flora*, 1986, University Press of Kansas); however, it may be based on a misidentification of *T. arvense*. Nomenclature in this group is confused and has been discussed by Hendrych (1961, Taxon 10:20–23).

TRISETUM ORTHOCHAETUM A. S. Hitchc. (POACEAE).—Glacier Co., Glacier National Park, along the SW side of Swiftcurrent Lake, locally common in moist areas of open spruce-fir forest with *Calamagrostis canadensis, Senecio triangularis* and *Trisetum wolfii*, 1495 m, 24 Jul 1994, *P. Lesica 6411B* (MONTU, MONT). Verified by J. H. Rumely (MONT).

Significance. This putative hybrid of *T. wolfii* and *T. canescens* was previously known from a small area 240 km to the SW near the MT-ID border.

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BRITISH COLUMBIA

MAIANTHEMUM CANADENSE Desf. West Fernie: trail starting up Mt. Fernie from near corner of Stewart Ave. 28 May 1998. Kuijt 9034 (UVIC).

Previous knowledge. Common in the deciduous forests of the northeastern United States, and in woods across Canada into northern and central British Columbia, as far south as Boat Encampment on the Big Bend of the Columbia River (T. M. C. Taylor. 1966. The Lily Family (Liliaceae) of British Columbia. B. C. Prov. Mus. Handb. 25).

Significance. Small perennial, spreading by means of slender rhizomes. The collection represents a single patch of 2 m in diameter, about 400 km south of the nearest known locality.

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PRESIDENT'S REPORT FOR VOLUME 45

Normally, the President's Report precedes the program year. However, due to the challenges the Council faced this year in getting *Madroño* onto a normal publishing schedule following the resignation of the previous editor, this report comes at the end of the program year. Nevertheless, welcome to the California Botanical Society's 1998–1999 program year. New and returning Council Members for the program year include myself, Past President, Wayne Ferren; First Vice-President, Susan D'Alcamo; Second Vice-President, Dave Keil; Recording Secretary, Roxanne Bittman; Corresponding Secretary, Sue Bainbridge; Treasurer, Mary Butterwick; Council Members, Jim Shevock, Margriet Wetherwax, and Diane Elam; Graduate Student Representative, Dennis Wall; and the new Editor of *Madroño*, Kristina Schierenbeck. The Society thanks each of you! New Council Members for this program year included Dave Keil and Diane Elam.

Susan D'Alcamo, in her second year as First Vice-President, organized an excellent slate of six speakers for the 1998–1999 Lecture Series. The lectures are held on the third Thursday of each month from October through May, in the Valley Life Sciences Building at the University of California, Berkeley Campus. The lectures have been very well attended this year by members as well as many non-members. The Council appreciates the efforts of Dennis Wall in helping with room reservations, projection equipment, and the reception. An informal reception follows each presentation which allows an opportunity to mingle with the speaker, other botanists, and guests. Refreshments are furnished by the Jepson and University Herbaria. All members are invited and encouraged to attend the talks and receptions. We thank Brent Mishler and the Jepson and University herbaria for providing space for the Council meetings, Lecture Series, and receptions.

Dave Keil organized an outstanding Annual Banquet which was held on 20 February 1999, at the California Polytechnic University, San Luis Obispo. President Little presented "Outstanding Service Awards" to Board Members in recognition of their contributions to the organization. Recipients included Wayne Ferren, Diane Ikeda, Dave Keil, Mary Butterwick, Roxanne Bittman, Susan Bainbridge, Margriet Wetherwax, Staci Markos, and Tony Morosco. Our guest speaker was Dr. Sherwin Carlquist, Research Associate at Santa Barbara Botanic Garden, who spoke on "Three Discoveries."

Graduate Student Meetings are normally sponsored by the California Botanical Society every other year, and were last held at U.C. Berkeley in 1998. However, due to the high level of interest expressed by Cal Poly students, a decision was made by the Society to sponsor Graduate Student Meetings at Cal Poly on the same day as the Annual Banquet. Graduate Student Representative Dennis Wall coordinated with David Keil's students to make it happen. Together, the graduate students made all arrangements for the meetings. Many thanks to all the Council members who assisted with these meetings.

I wish to acknowledge the contributions of Mary Butterwick. This is her third and final year as Treasurer for the Society. Her replacement has not been found. Please contact any Council Member if you, or someone you know, would be interested in volunteering for this position. This is also the final year for Roxanne Bittman as Recording Secretary, a position she has held for 7 years. She has been very faithful in attending virtually all Council meetings during this period. Her replacement for the 1999–2000 program year will be Dean Kelch. Susan Bainbridge has done an outstanding job as Corresponding Secretary and has been very diligent in responding to requests for information from members and non-members. Sue has volunteered to remain as Corresponding Secretary for one more year. The Society also appreciates the contributions of Council Members Jim Shevock, Margriet Wetherwax, and Diane Elam. This is Margriet's last year as Council Member. She will be replaced by Bien Tan. The Society is fortunate that Kristina Schierenbeck volunteered to be Editor of *Madroño*. She has done an outstanding job of working through a backlog of manuscripts and is proceeding to get *Madroño* back on schedule. Dr. Fosiee Tahbaz, at the U.C. Herbarium Berkeley, will replace Dave Keil as Second Vice-President for the 1999–2000 program year.

—R. JOHN LITTLE, PH.D.
17 May 1999

MADROÑO, Vol. 45, No. 4, p. 332, 1998

EDITOR'S REPORT FOR VOLUME 45

This report serves to inform members of the California Botanical Society the status of *Madroño* from manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 44[4]), the journal received 73 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 64 of these have been accepted for publication. Average turn-around time for articles from submission to publication was initially 20 months due to logistical difficulties with the editorial transition. However, the time from article submission to publication has been reduced to six months and it is my full expectation that this will remain the standard. Very few manuscripts were rejected after review. Authors of *Madroño* articles are generally quite responsive to reviewer and editorial suggestions.

The new format was in progress and all of the hard work completed when I came aboard. Linda Ann Vorobik, Elizabeth Painter and the CBS Council are responsible for the beautiful and more botanically correct art work and cover layouts. We all thank them for their hard effort and beautiful results, particularly Linda Ann Vorobik for the art work. The larger format provides *Madroño* with a more standard size for shelf storage and allows for the accommodation of more manuscripts.

There are many individuals who contribute to the editorial process; Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who continues to assemble the Index and Table of Contents; Dieter Wilken and Margriet Wetherwax, who edit the Noteworthy Collections; David Parks, my editorial assistant extraordinaire; Michael Abruzzo, Chair of the Department of Biological Sciences at California State University Chico, who provides the funds to support David; Annielaurie Seifert and Karen Ridgway at Allen Press who eased the editorial transition and continue to ease the ongoing process; and members of the CBS executive council who enthusiastically support *Madroño* in every aspect. I continue to rely on the council of Robert Patterson, Wayne Ferren, Jon Keeley, John Strother, and Beth Painter for guidance about the editorial process. On behalf of the society, I thank the volunteer reviewers and the Board of Editors on whom we all depend to make the peer review process work for this valuable regional journal.

As I complete my first and admittedly difficult year, I look forward to smooth sailing for volumes 46 and 47.

Madroño, Vol. 45, No. 4, p. 333, 1998

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INDEX TO VOLUME 45

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

DATES OF PUBLICATION OF MADROÑO, VOLUME 45

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Number 2, pages 93–185, published 5 May 1999
Number 3, pages 187–274, published 22 June 1999
Number 4, pages 275–336, published 17 September 1999

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($27 per year; family $30 per year; emeritus $17 per year; students $17 per year for a maximum of 7 years). Late fees may be assessed. Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available ($60). Membership is based on a calendar year only. Life memberships are $540. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

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Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE-SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, 5 key words or phrases, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or 'erasable' paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units, except specimen citations, which may include English or metric measurements.

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CALIFORNIA BOTANICAL SOCIETY, INC.

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MADROÑO, Vol. 46, No. 1, pp. 1–6, 1999

UNDERSTORY LIGHT AND GAP DYNAMICS IN AN OLD-GROWTH FORESTED WATERSHED IN COASTAL CALIFORNIA

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ABSTRACT

This paper describes the understory light environments and gap dynamics of forests in the watershed of Maddock Creek, Big Basin Redwoods State Park, Santa Cruz County, CA. Most of this 230 ha watershed is covered by old-growth forests representative of upland redwood forests and the *Pseudotsuga*-hardwood forests which intergrade with them. Species of canopy trees include *Sequoia sempervirens* (D. Don) Endl., *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, *Pseudotsuga menziesii* (Mirbel) Franco, *Arbutus menziesii* Pursh, and *Quercus chrysolepis* Liebm., in descending order of cover. In the understory of these forests, total light was about 12% of that incident upon the canopy. Understory light levels differed between aspects and were influenced by canopy species composition and gaps. Except for *Lithocarpus*, regeneration of canopy species was associated with higher understory light levels and the species less tolerant of shade (*Arbutus, Pseudotsuga,* and *Quercus*) filled more gaps on the south-facing slopes, where light levels were higher. In contrast, *Lithocarpus* was abundant throughout the understory, present in most gaps at a high cover, and filling twice as many canopy gaps as it had formed. In the presence of surface fires, we suggest that *Lithocarpus* would not increase in dominance. However, in the absence of fire, our results indicate an increasing dominance by *Lithocarpus*, and suggest that interspecific differences in shade cast and shade tolerated are contributing to the dynamics of forests in central coastal California.

In north coastal California, upland redwood and *Pseudotsuga*-hardwood forests are the predominant forest types (Barbour and Major 1988). These forests have a two-layered canopy: an upper layer (to 70 m high) dominated by gymnosperms, and a lower layer (to 40 m) dominated by angiosperms (Whittaker 1960; Sawyer et al. 1988; Zinke 1988). The most important gymnosperms are *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir, Pinaceae) and *Sequoia sempervirens* (D. Don) Endl. (redwood, Taxodiaceae), and the most important angiosperms are *Arbutus menziesii* Pursh (madrone, Ericaceae) and *Lithocarpus densiflorus* (Hook. & Arn.) Rehder (tanoak, Fagaceae).

The dynamics of these forests involve both fire and tree falls. Prior to the twentieth century, fires typically burned through these forests at intervals of 5–50 yr (Greenlee 1983; Jacobs et al. 1985; Rice 1985; Agee 1991; Finney and Martin 1992). For most of this century, however, fires have been suppressed, and tree falls have dominated the dynamics of older stands. Because the dominant species differ in longevity and shade tolerance (Burns and Honkala 1990), species composition and structure could be changing substantially. If so, these on-going changes generally have not been documented, and are not well understood (but see Sugihara 1992; Hunter 1997a).

This paper contains two components of an investigation into the dynamics of an old-growth forested valley which has not experienced fire for 60–80 years. The first examines understory light as a potentially significant factor affecting recruitment of saplings. The second examines canopy gaps from throughout the watershed, and for each gap documents the species of the canopy tree(s) that formed the gap and of the understory tree(s) filling it.

The study area is Maddock Creek Watershed in the Santa Cruz Mountains of California's central coast (37°10′N, 122°15′W). This watershed is 13 km from the coast, 230 ha in size, and at 340–535 m in elevation. Ridgelines run northwest to southeast, and have steep slopes of 11–52°.

Most of this watershed is covered by old-growth forest, portions of which last burned in 1904 and 1936 (Greenlee 1983). These forest stands are representative of upland redwood forests and the *Pseudotsuga*-hardwood forests that intergrade with them (Hunter 1989). They have a two-tiered canopy: the conifers *Pseudotsuga menziesii* and *Sequoia sempervirens* form an upper tier, while the angiosperms

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Arbutus menziesii, Lithocarpus densiflorus, Quercus chrysolepis Liebm., and *Quercus wislizeni* A. DC. form a lower layer dominated by *Lithocarpus.* (Nomenclature follows Hickman 1993.) Neither tier forms a complete layer: each covers about two-thirds of the forest floor. Canopy gaps (breaks in both canopy layers) occupy approximately 11% of the land area with an average size of 91 m^2 (Hunter and Parker 1993). In species composition and structure, the understory vegetation beneath canopy gaps is similar to that at canopied locations (Hunter 1989). The shrub layer (0.5–3 m) typically has 25–50% cover and is dominated by *Vaccinium ovatum* Pursh and juvenile *Lithocarpus.* The herb layer (<0.5 m) typically has <1% cover.

METHODS

Understory light environments. We used computer analysis of hemispherical photographs to estimate light levels at the forest floor relative to light levels above the forest canopy (Pearcy 1989). This technique allows a reasonably precise comparison of the light environments at different locations (Chazdon and Field 1987; Becker et al. 1989). It is outlined below and described in more detail by Anderson (1964), Becker et al. (1989), Pearcy (1989), and Rich (1989).

In hemispherical photographs, the distance from the image's center is proportional to the angle from the zenith of the hemisphere which was above the camera. Therefore, the photograph can be divided into regions corresponding to ranges of zenith and azimuth angles, and the sun's path can be plotted across these regions. Each region can be weighted by the proportion of total irradiance coming from that section of sky. This procedure is done separately for direct and indirect components of light. Direct light is received only from those regions of sky along the sun's path, whereas indirect light (diffuse light which has been scattered by the atmosphere) is received from all regions of the sky but is more intense towards the zenith. For each region of sky, the fraction of light reaching the understory is assumed to equal the fraction of sky unobscured by foliage.

We used the "Canopy" computer program to analyze the photographs (Rich 1989). For calculating the percentage of indirect light, the program divides the image into 160 regions, and weights these assuming a standard overcast sky. For calculating the percentage of direct light, it divides the sun's annual path across the sky into monthly paths, each of which gets sub-divided into half-hour intervals.

We took photographs of the canopy at 80 points randomly located throughout the watershed. A Telesar hemispherical lens on a Pentax K1000 body was used with ASA-64 slide film. (The slide images had very sharp contrasts between sky and foliage, partially due to ideal weather.) The camera was positioned on a level surface 1 m above the forest floor and a white pole used to mark true north in the photograph. We took photographs only when the sky was uniformly overcast and no wind was blowing.

At each point, we recorded slope aspect, understory species, and canopy characteristics. Within a radius of 2 m from the camera, all species in the herb and shrub layers (0–0.5 m and 0.5–3 m high, respectively) were recorded and total cover visually estimated. All canopy species within approximately 30 m of the camera were listed in order of estimated cover. We also noted if the camera was below a gap.

Gap dynamics. To obtain a random sample of 80 canopy gaps, we randomly located 20 points within the watershed. From these points, the nearest gap within each compass quadrant (N, E, S, W) was located. We defined a gap as any break in both canopy tiers due to tree or limb mortality and below which vegetation was less than two thirds the height of the adjacent lower canopy tier (minimum diameter 4 m). The edge of the adjacent crowns of canopy trees was considered the gap edge, and was determined with a canopy densitometer. The canopy densitometer has a mirror, level and cross-hairs allowing the user to determine the point directly overhead (GRS 1992).

For each gap, we recorded slope aspect, area, understory vegetation, gap-forming species, and gap-filling species. Within the gaps, species cover was visually estimated for herb, shrub and sapling layers (0–0.5, 0.5–3 and >3 m respectively).

We used position of logs and their state of decay to determine the species present in the canopy before the gap was created (the gap-forming species). Ten of the sampled gaps had been formed by more than one canopy species. In all cases, the removal of one species created most of the gap's area, and this species was considered the gap-forming species.

We considered the tree species present in a gap's uppermost vegetation layer to be the species filling that gap. (For 78 of the 80 gaps, the sapling or shrub layer was uppermost.) Twenty gaps had more than one tree species in the uppermost layer. In these gaps, the species with the greatest cover in the upper layer, we identified as the species filling the gap. Where an angiosperm and a conifer species were both in the uppermost layer, the conifer could have been considered the gap-filling species, even if at a lower cover, because of its greater maximum size and potentially faster growth (McArdle et al. 1949; Porter 1965). However, in no gap was *Sequoia* both in the uppermost layer and at a lower cover than an angiosperm in that layer, and in only three gaps was *Pseudotsuga* both in the uppermost layer and at a lower cover than an angiosperm species. If *Pseudotsuga* had been considered the species filling those three gaps, the results would have

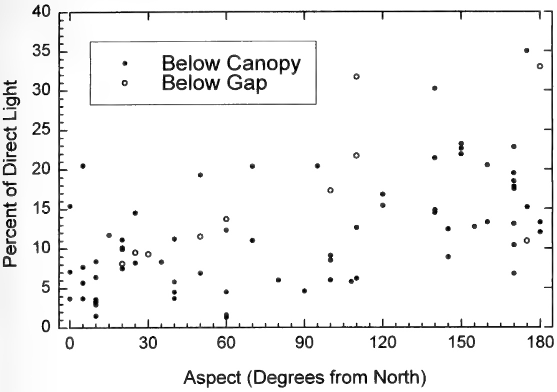

FIG. 1. Aspect and direct light reaching the understory for 80 locations in the watershed of Maddock Creek, Santa Cruz Co., CA. Percent direct light is percent of light incident upon canopy that reaches understory.

remained similar, and their interpretation would not have been altered.

RESULTS

Understory light environments. For the year and the watershed as a whole, total light reaching the understory was about 12% of that incident upon the canopy. Direct light averaged 12.5 ± 7.3% and ranged from 0.1 to 35%. Indirect light had a comparable average (11.8%), but less variation (1 SD = 3.6, range 4.8–21.0%).

More light reached points beneath canopy gaps (n = 10, direct light mean 16.7 ± 9.2%, indirect light mean 13.7 ± 3.6) than beneath the canopy (n = 70, direct light mean 11.9 ± 6.9%, indirect light mean 11.6 ± 3.6%; Mann-Whitney U, P = 0.03 and 0.02, respectively). However, light levels at gap locations were not disjunctly higher than light levels at canopied locations. The range of light levels within gaps fell within the range of light levels at canopied locations (8.1–33% and 0.1–35% direct light, respectively).

Understory light environments also differed between aspects (Fig. 1). Twice as much direct light reached the understory of south-facing slopes (90–270°, n = 38, mean = 16.9 ± 7.1%) than of north-facing slopes (270–0–90°, n = 42, mean = 8.4 ± 5.3%; Mann-Whitney U, P < 0.001). Twenty-two percent more indirect light reached the understory of south-facing slopes (13.8 ± 3.4%) than of north-facing slopes (10.8 ± 2.9%; Mann-Whitney U, P < 0.001). The higher indirect light levels on south-facing slopes indicate a more open canopy.

Interestingly, species composition of the canopy also influenced understory light levels. On south-facing slopes, canopy species composition was patchier and separated into two distinct canopy types: (1) a *Pseudotsuga*-hardwood type with emergent *Pseudotsuga* above a layer of angiosperms dominated by *Arbutus* and the *Quercus* species, and (2) an upland redwood type with emergent *Sequoia* above a layer of *Lithocarpus.* Light levels beneath the *Pseudotsuga*-hardwood canopy (22.4 ± 8.4%, n = 7) were substantially higher than beneath the *Sequoia-Lithocarpus* canopy (12.6 ± 6.4%, n = 7; Mann-Whitney U, P = 0.05). This difference between canopy types was comparable to that between canopied and gap locations, and indicates that local variation in canopy composition can affect understory light environments significantly. These two canopy types covered 37% of south-facing locations, and the remaining locations were intermediate in canopy structure and light environment.

There was a correspondence between light levels and distribution of tree species in the understory. For *Arbutus, Pseudotsuga,* and *Quercus,* understory saplings in the shrub layer occurred at significantly high light levels (Table 1). *Sequoia* saplings in the shrub layer were not found at high light levels, but established seedlings in the herbaceous layer were found at significantly high light levels (mean = 20.5 ± 7.0% direct light). This result is consistent with the species' biology: saplings of *Sequoia* are

TABLE 1. MEAN LIGHT ENVIRONMENTS FOR UNDERSTORY INDIVIDUALS OF CANOPY TREE SPECIES. N is the number of locations (out of 80) at which species were present in a given vegetation layer. Means (±1 SD) are of percent of light incident upon the canopy that reaches the understory. Asterisks denote an average significantly higher than locations without the species; * P < 0.05, ** P < 0.01 (Mann-Whitney U test).

Species	N	Direct light ave.	Indirect light ave.
Shrub layer			
Arbutus menziesii	2	25.6 ± 8.6*	17.4 ± 1.2*
Quercus chrysolepis	4	22.3 ± 9.1**	16.0 ± 2.9*
Pseudotsuga menziesii	6	19.6 ± 7.6**	14.5 ± 3.6*
Lithocarpus densiflorus	69	11.7 ± 7.3	11.7 ± 3.7
Sequoia sempervirens	22	10.9 ± 7.0	10.0 ± 3.4
Herbaceous layer			
Sequoia sempervirens	5	20.5 ± 7.0*	17.0 ± 14.7
Quercus chrysolepis	9	19.1 ± 11.3*	14.2 ± 4.5
Pseudotsuga menziesii	5	14.5 ± 7.5	12.6 ± 2.4
Lithocarpus densiflorus	24	12.0 ± 8.1	11.6 ± 3.5

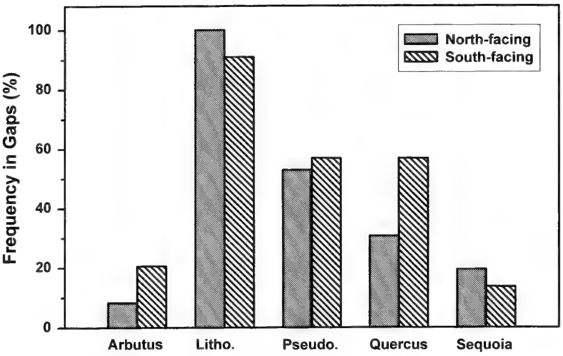

FIG. 2. Frequency of tree species beneath canopy gaps on north-facing (n = 36) and south-facing (n = 44) aspects of Maddock Creek's watershed, Santa Cruz Co., CA. Arbutus = *Arbutus menziesii,* Litho. = *Lithocarpus densiflorus,* Pseudo. = *Pseudotsuga menziesii,* Quercus = *Quercus chrysolepis* and Sequoia = *Sequoia sempervirens.*

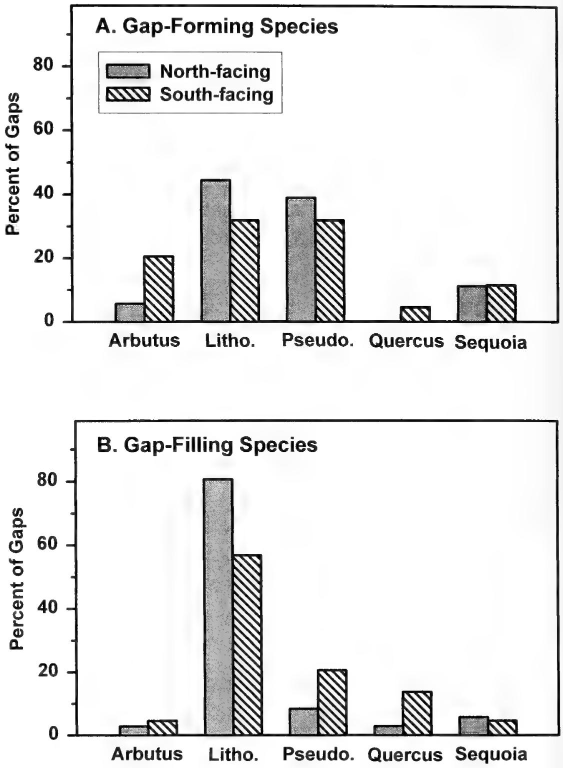

FIG. 3. Species forming and filling gaps on north-facing (n = 36) and south-facing (n = 44) aspects of Maddock Creek's watershed, Santa Cruz Co., CA. Species abbreviations as in Figure 2.

shade-tolerant and persist in the understory for decades, but establishment of seedlings is strongly affected by light levels (Jacobs 1987). Only *Lithocarpus,* by far the most abundant and widespread tree in the understory, had no correspondence between light levels and seedling or sapling distribution.

Gap dynamics. Most tree species were absent from a large portion of gaps (Fig. 2). Only *Lithocarpus* was present in almost all gaps (95%), and at a high cover (mean = 36.4 ± 27.4%). *Pseudotsuga* and *Quercus* were in a large portion of gaps (49 and 45% respectively) but when present were at a low cover (5.5 ± 9.4 and 6.1 ± 11.6%), while *Arbutus* and *Sequoia* were rarely present (15 and 16% respectively) and were at a low cover (mean = 7.5 ± 11.2 and 12.3 ± 19.5%).

Lithocarpus also was filling the most gaps (Fig. 3). Of 80 gaps, *Lithocarpus* was filling 68%, *Pseudotsuga* 15%, *Quercus chrysolepis* 9%, *Sequoia* 5%, and *Arbutus* 4%. Because *Lithocarpus* had formed significantly less of the gaps (38%) than it was filling, it was increasing in importance within the canopy (χ^2 test, df = 1, P = 0.0001). *Pseudotsuga* and *Arbutus* had formed significantly more of the gaps (35 and 14% of gaps, respectively) than they were filling, and thus were declining in importance within the canopy (χ^2 test, df = 1, P = 0.004 and 0.025 respectively). *Sequoia* and *Quercus* did not have significant differences between the number of gaps formed and the number filled, though an increase in *Quercus* is suggested (P = 0.086).

There was also a relationship between gap-forming and gap-filling species. Of gaps formed by *Lithocarpus* (n = 30), *Lithocarpus* filled 90%, significantly more than expected (χ^2 test, df = 1, P = 0.001). This result may be due in part to a significantly lower presence of other species in gaps formed by *Lithocarpus* (χ^2 test, df = 1, P = 0.002). Gaps formed by *Lithocarpus* (n = 30) averaged 1.8 ± 0.8 tree species versus 2.4 ± 0.9 present below gaps formed by other species (Mann-Whitney U, P = 0.003). Also, *Lithocarpus* was the only tree species present below 43% of gaps formed by *Lithocarpus,* while just 10% of gaps formed by other species had only *Lithocarpus* present beneath them (χ^2 test, df = 1, P < 0.001). The data also suggest self-replacement by *Sequoia.* Three of four gaps formed by *Sequoia* were being filled by basal sprouts of the same tree(s) that had formed the gap.

Although there was no relationship between gap area and species filling the gap, there was a relationship between slope aspect and gap-filling species (Fig. 3). Species less tolerant of shade (*Arbutus, Quercus chrysolepis,* and *Pseudotsuga*) filled significantly more south-facing gaps (39%) than north-facing gaps (14%; χ^2 test, df = 1, P = 0.014). As a consequence, succession differed between north and south-facing slopes. On north-facing slopes, *Pseudotsuga* formed significantly more gaps than it filled (χ^2 test, df = 1, P = 0.002) and therefore declined in importance, while on south-facing slopes there was no significant difference in the number of gaps formed and filled by *Pseudotsuga* (P = 0.23). The data also suggested differences between aspects in the dynamics of *Lithocarpus* and *Quercus*.

DISCUSSION

In upland redwood and *Pseudotsuga*-hardwood forests, tree species differ in shade-tolerance. For example, *Quercus* species, *Arbutus* and *Pseudotsuga* are clearly less tolerant than *Lithocarpus, Sequoia* and *Umbellularia californica* (Hook. & Arn.) Nutt. (Waring and Major 1964; Unsicker 1974; Tappiener et al. 1986; Burns and Honkala 1990; Sugihara 1992; Hunter 1997a and 1997b). Together with the influence of fire, these interspecific differences in shade-tolerance probably determine most patterns of sapling recruitment into the canopy.

Prior to fire suppression, surface fires would have removed most understory regeneration, including *Lithocarpus* saplings (Kauffman 1986). This effect would have limited the successful recruitment of understory *Lithocarpus* into the canopy, while creating seedbed and understory conditions favorable for the other canopy species (Jacobs 1987; Hermann and Lavender 1990; Hunter 1994). Currently, however, *Lithocarpus* saplings accumulate in forest understories (Tappeiner and McDonald 1984; Hunter 1997a).

By affecting sapling establishment prior to gap formation, the transmission of light through canopies can influence substantially the species composition of regeneration (Canham et al. 1994). This was the case in this watershed's forests. Here, most gaps were filled by saplings that had established prior to the gap's formation. As a consequence, the most abundant species throughout the understory, the shade-tolerant *Lithocarpus,* was also the species filling the majority of canopy gaps.

Because forest canopies vary on a fine scale in species composition, leaf area and height, light reaching the understory is also variable (Baldocchi and Collineau 1994). In this study, canopied locations received from 0.1 to 35% of the direct light incident upon the canopy. This range of light levels had ecological significance because four of the five canopy species had understory regeneration associated with higher understory light levels, and because the less shade tolerant species were filling more gaps on south-aspects, where light levels were higher.

Interestingly, much of the variation in understory light seems to be due to interspecific differences in shade cast. In this study, on south-facing slopes, light levels beneath a *Pseudotsuga*-mixed hardwood canopy were nearly twice those beneath a *Sequoia-Lithocarpus* canopy (ave. 20.7% vs. 12.6%), a difference comparable to that between gaps and canopied locations (16.7% vs. 11.9%). In other studies, there is also evidence that the more shade-tolerant species can develop a denser crown and therefore allow less light to pass through to the understory (Waring & Major 1964; Unsicker 1974; Minore 1986; Harrington et al. 1984).

If much of the variation in understory light is due to interspecific differences in transmission of light through the crown, then this attribute could be an important cause of observed patterns in the stand dynamics in California's coastal forests. For example, the self-replacement of *Lithocarpus* (observed in this study) may be promoted by low levels of light passing through the crowns of canopy-sized *Lithocarpus,* allowing advance regeneration of the shade-tolerant *Lithocarpus* but not of less tolerant species. Similarly, relatively high levels of light passing through the crowns of *Quercus* species and *Arbutus* may contribute to their replacement by *Pseudotsuga* and *Umbellularia,* which occurs in several types of forest and woodland vegetation (McBride 1974; McDonald and Littrell 1976; Hunter 1995; Safford 1995; Barnhart et al. 1996).

For the dominant trees of California's coastal forests, the magnitude of interspecific differences in shade cast, and the influence of these differences upon succession both deserve further investigation.

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THE REPRODUCTIVE BIOLOGY AND HOST SPECIFICITY OF *OROBANCHE PINORUM* GEYER (OROBANCHACEAE)

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ABSTRACT

This study is the first examination of the reproductive biology of *Orobanche pinorum* Hook., a rare, parasitic flowering plant of western North America. Plants from six separate populations were treated to test reproductive strategies, including xenogamy, autogamy, and agamospermy. Seeds that developed from the flowers of treated plants were counted to determine the reproductive success of each strategy. The results showed *O. pinorum* to be predominantly autogamous, producing a mean of nearly 700 seeds per capsule and over 70,000 seeds per plant. There was some evidence for xenogamy, but potential pollinators were seen only on six occasions in three years. Two were collected—solitary bees *Osmia exigua* and *Ashmeadiella cactorum.* No evidence was found for agamospermy. *Orobanche pinorum* appeared to parasitize only one host—the shrub *Holodiscus discolor* (Pursh) Maxim.

INTRODUCTION

Orobanche pinorum Hook. (pine broomrape, Fig. 1a–d) is in the Orobanchaceae, a family of achlorophyllous, obligate root parasites (Kuijt 1969). An endemic of western North America, this uncommon species has been found from northern California through Oregon, and north to central Washington and Idaho (Munz 1930; Hitchcock et al. 1959; Abrams and Ferris 1960; Heckard 1993). In Washington state, *O. pinorum* is listed as a "monitor" species due to its relative rarity (Washington Natural Heritage Program 1997). A literature search provided no published studies on this species other than descriptive reports and a single chromosomal count in one specimen (Heckard and Chuang 1975).

The flowers of Orobanchaceae are apparently adapted for cross-pollination, displaying traits typically associated with bee pollination—tubular corolla complete with landing platform, nectar guides, contrasting colors around the floral entry, and nectar rewards (Kuijt 1969). The campanulate corolla of the zygomorphic flowers is yellowish with purple exterior veins which probably serve as nectar guides. The two broad, deltoid lobes of the upper lip form a hood over the stamens and stigma while the three lanceolate lobes of the lower lip provide a potential insect landing platform (Fig. 1a–c).

Reproductive strategies besides xenogamy have also evolved within Orobanchaceae. While the flowers of most species are chasmogamous, cleistogamy has been reported in *Epifagus, Cistanche,* and *Boschniakia* (Thieret 1971; Musselman 1980; Olsen and Olsen 1980). Although Kuijt (1969) argues that insects play the most important role in pollination, the work of Musselman (1980) and Musselman et al. (1981) show autogamy to be commonly employed in varying degrees. Jenson (1951) found that populations of *Orobanche uniflora* L. in New England were obligately agamospermous, and Reuter (1986) found that populations of *Orobanche fasciculata* Nutt. in Wisconsin produced similar numbers of seeds via agamospermy, autogamy, and xenogamy.

Species within Orobanchaceae parasitize a variety of herbaceous and woody host species (Musselman 1980). The majority of broomrapes appear to have broad host ranges, with more narrow host-specificity found occasionally among physiological races (Musselman 1980). Although most references suggest *O. pinorum* is hosted by coniferous species (Geyer 1851; Hitchcock et al. 1959; Munz and Keck 1968; Peck 1961), the most recent accounts (Heckard 1993; Smith-Kuebel and Lillybridge 1993) suggest instead the shrub *Holodiscus discolor* (Pursh) Maxim.

The purpose of this study was to examine the reproductive strategy of *O. pinorum,* collect and identify any potential pollinators, and examine host specificity.

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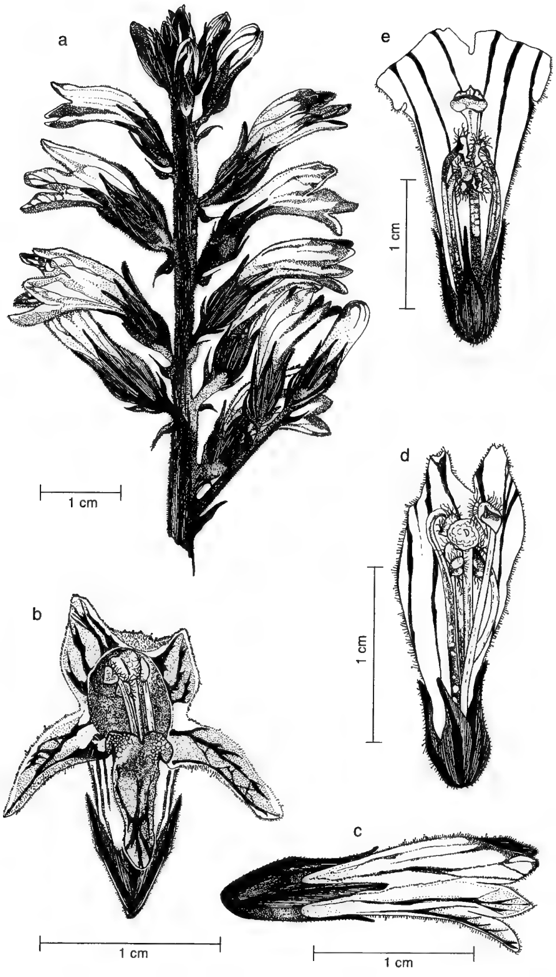

FIG. 1. a. upper ⅓ of *Orobanche pinorum* stalk with flowers and terminal buds. b. frontal view of *O. pinorum* flower. c. lateral view of *O. pinorum* flower. d. *O. pinorum* flower with ventral half of corolla tube excised. e. *O. uniflora* flower with ventral half of corolla excised. Drawings by Eve Ponder.

METHODS

Study area. All field research sites were located in Washington state, within the Leavenworth Ranger District of the Wenatchee National Forest. The sites were on moderate to steep slopes, in lithosolic substrates with gravitational instability and poor horizontal development. The forest communities were generally mixed-coniferous, dominated by *Pseudotsuga menziesii* (Mirbel) Franco, *Pinus ponderosa* Laws., and *Abies grandis* (Douglas) Lindley with less than 50% canopy cover. The area is underlain by the Chumstick Formation, a bedrock composed of middle Eocene materials including micaceous feldspathic sandstone, interbedded pebbly sandstone, conglomerate, and shale (Tabor et al. 1987). The great soil groups in this region include cryorthods, haplorthods, and xerochrepts (Franklin and Dyrness 1973). The climate is characterized by warm to hot summers (maximum temperatures approaching 38°C) and cold winters (minimum temperatures below −18°C) (Donaldson and Ruscha 1975). Mean annual precipitation at the study sites ranges from 64–89 cm with two thirds falling between October and March. The summers are characterized by drought, with less than 2.5 cm of rain falling from July through August. Table 1 provides summary descriptions of the study sites.

Individuals of *O. pinorum* from six populations were selected and treated in two reproductive experiments. Data from two additional populations were used to estimate the mean number of flowers per plant. In this study, populations of *O. pinorum* were considered distinct if they were separated by at least a half mile with no individuals found between populations. Data were collected during the growing seasons of 1993, 1994, and 1995.

First reproduction experiment. Six treatments were applied to test reproductive strategies of *O. pinorum* (Table 2). The criteria for selecting plants were health and phenology. In each population, plants were selected if they appeared healthy and showed no visible signs of insect infestation (i.e., caterpillar silk, feces, or herbivory). To ensure that all reproductive structures would be well developed, buds just prior to anthesis were treated. Treatments were assigned randomly to each suitable plant, using a calculator's random function. For each treatment, eight plants from five different populations (Sites 1–5) were selected with two flower buds treated per plant.

In Treatment 1 (T1), autogamous seed production

TABLE 1. APPROXIMATE LOCATION, ASPECT, POPULATION SIZE, SLOPE AND ELEVATION OF *O. PINORUM* STUDY SITES. All sites were located in Washington state, within the Leavenworth Ranger District of the Wenatchee National Forest.

Site #	Elev. (m)	Slope (°)	Aspect	Pop. size	Location
1	720–1100	30–45	w	>100	Negro Creek
2	880	20–30	e	16–34	North Ruby Creek
3	830	30	e	2–5	South Ruby Creek
4	610	10	sw	3–9	Lower Camas
5	990	<10	e	9–22	Upper Camas
6	1170	30	se	2–3	King Creek
7	520–670	40	n	>100	W. Spromberg Canyon
8	500–575	40	n	41	E. Spromberg Canyon

TABLE 2. TREATMENT DESCRIPTIONS FOR THE FIRST REPRODUCTION EXPERIMENT.

Treatment #	Treatment test	Treatment procedure
T1	Autogamy	Flowers bagged to exclude pollinators
T2	Control	Flowers not bagged or modified
T3	Potential Xenogamy	Flowers emasculated and hand-crossed
T4	Vectoral Xenogamy	Flowers emasculated, open to pollination
T5	Agamospermy-1	Flowers emasculated, bagged to exclude pollinators
T6	Agamospermy-2	Flowers emasculated, stigmas excised, bagged to exclude pollinators

was tested by bagging the selected buds in a tight-weave cotton cloth to exclude pollinators and wind-borne pollen. In T2 (Control), selected plants and buds were left unmodified. In T3 (Potential Xenogamy), buds selected were emasculated and hand-crossed with pollen from other plants to test the potential for seed production via vectoral cross-pollination (insects, wind, etc.). In T4 (Vectoral Xenogamy), buds selected were emasculated and left open to pollination to test directly for xenogamous seed production. In T5 (Agamospermy-1), buds selected were emasculated and then bagged to exclude pollinators and wind-borne pollen to test for agamospermy. In T6 (Agamospermy-2), both anthers and stigmas were excised from the selected buds, and the buds were then bagged to exclude pollinators and wind-borne pollen. This treatment provided a more thorough test of agamospermy, since no stigmatic surface was available for the germination of pollen that the experimental design might fail to exclude from the flower.

Once the capsules of the treated buds matured, they were collected prior to dehiscence and stored to dry. Once dry, the capsules were opened and the seeds removed and spread evenly on a grid and counted under 15× magnification.

Second reproduction experiment. Four treatments were applied to test for the relative success of four potential pollination strategies in *O. pinorum* (Table 3). Again, healthy and phenologically suitable plants were selected for treatment, and the treatments were applied randomly for each plant, using a calculator's random function. Nine plants were selected for each treatment from sites 1–6. As in the first pollination experiment, flower buds that appeared ready to open were selected for treatment. For each treatment, the entire plant was bagged to exclude potential pollinators and wind-borne pollen. Capsules were collected and seeds removed and counted as in the first reproductive experiment.

In T1 (Xenogamy/Vicinism), selected buds were emasculated and hand-crossed with pollen from flowers on nearby plants in the same population to test the potential reproductive success of vicinism. In T2 (Xenogamy/Non-Vicinism), buds selected were emasculated and hand-crossed with pollen from different populations to test the potential reproductive success of xenogamy between plants less likely to be related. All cross-pollinations in T2 were made between plants from populations separated by at least one mile. In T3 (Potential Geitonogamy), buds selected were emasculated and hand-pollinated with pollen from flowers on the same plant to test the potential reproductive success of geitonogamy. In T4 (Geitonogamy), buds from the middle or lower portions of the plant were emasculated and left available for pollination via pollen falling from flowers above them.

Although the bag would help prevent wind from blowing pollen from one flower to another, pollen that did exit a flower might fall onto flowers below. For that reason, buds tested in treatments T1–T3 were all located at the tops of plants so that no flowers were directly above them.

Unlike the first reproduction experiment, hand-crossing was employed as the pollination method in the treatments T1–T3. In this way, potential variations in results due to the different success rates between hand-pollination and natural self-pollination were averted.

Statistics. The research was designed for the two reproductive experiments so that all data could be analyzed by Analysis of Variance (ANOVA) using a completely randomized design with subsampling. The alpha level of significance was preset at 0.05.

The mean number of seeds per capsule for *O.*

TABLE 3. TREATMENT DESCRIPTIONS FOR THE SECOND REPRODUCTION EXPERIMENT. All plants bagged to exclude pollinators. All flowers emasculated.

Treatment #	Treatment test	Treatment procedure
T1	Xenogamy/Vicinism	Flowers hand-crossed with pollen from plants in the same population
T2	Xenogamy/Non-Vicinism	Flowers hand-crossed with pollen from plants in different populations
T3	Potential Geitonogamy	Flowers hand-crossed with pollen from other flowers on the same plant
T4	Geitonogamy	Flowers selected from the middle or lower region of the inflorescence

TABLE 4. MEAN SEED COUNTS PER CAPSULE FOR THE FIRST REPRODUCTION EXPERIMENT. * Treatments significantly different at the 0.05 level.

Mean	Treatment #	T1	T2	T3	T4	T5	T6	Treatment test
868	T1		*	*	*	*	*	Autogamy
689	T2	*		*	*	*	*	Control (unmodified)
248	T3	*	*		*	*	*	Potential Xenogamy
13	T4	*	*	*				Vectoral Pollination
0	T5	*	*	*				Agamospermy-1 (emasculated only)
0	T6	*	*	*				Agamospermy-2 (emasculated and stigma excised)

pinorum was calculated from the data in T2 (Control) of the first reproduction experiment. The mean number of flowers per plant was calculated from 33 plants over a two-year period. An estimated mean number of seeds per plant was then derived by multiplying the mean number of flowers per plant by the mean number of seeds per capsule.

Potential pollinators. Over 100 hours were spent observing plants for insect pollination activities. These observations were made during visits to the sites for data collection, applications of experimental treatments, and fruit collections. Since preliminary observations suggested that there were few if any insect pollinators, no systematic method of observation was employed. The importance of flower visitors was inferred by a combination of factors: the number of observed visitations, pollen load ratios, insect behavior, and the results of treatments that tested for xenogamy. Pollen load ratios of insect specimens were determined using a dissecting microscope and pollen was identified by comparing the grains with those taken from *O. pinorum* anthers.

Host specificity. Four specimens of *O. pinorum* were excavated (including one in Oregon) to identify the host species. Host roots were located and traced back to their sources. Since *O. pinorum* is rare in Washington, Oregon, and California (Jepson 1970; Heckard 1973; Heckard and Chuang 1975; Heckard 1993), the number of excavations were intentionally limited in number.

RESULTS

First reproduction experiment. The mean numbers of seeds per capsule for each of the six treatments are given in Table 4. The treatment testing for autogamy showed the highest production of seeds, with the control a close second. The hand-crossed treatment testing for potential Xenogamy produced less than half as many seeds as the control and autogamy treatments, but nearly 20 times more than the test for naturally occurring vectoral pollination. Neither treatment for agamospermy produced any seeds at all.

TABLE 5. MEAN SEED COUNTS FOR THE SECOND REPRODUCTION EXPERIMENT. * Treatments significantly different at the 0.05 level.

Mean	Treatment #	T1	T2	T3	T4	Treatment test
319	T1				*	Xenogamy/Vicinism
264	T2				*	Xenogamy/Non-Vicinism
194	T3				*	Potential Geitonogamy
16	T4	*	*	*		Geitonogamy

Second reproduction experiment. The mean numbers of seeds per capsule for the four treatments are given in Table 5. The capsules in Treatments T1 (Xenogamy/Vicinism), T2 (Xenogamy/Non-Vicinism), and T3 (Potential Geitonogamy) did not produce significantly different numbers of seeds from each other, but produced significantly more seeds than capsules in T4 (Geitonogamy).

Seed production. The mean number of flowers per plant was 96 (95% Confidence Interval {CI} ± 14) and the mean number of seeds per capsule was 689 (95% CI ± 126). The estimated mean number of seeds per plant is 71,656.

Potential pollinators. During the summers of 1993, 1994, and 1995, insects were seen entering *O. pinorum* flowers on only six different occasions. All were small hymenopterans. Two were collected and identified as solitary leafcutting bees in the superfamily Apoidea, family Megachilidae (Dr. Terry Griswold, bee taxonomist, Utah State University, Logan, UT, personal communication). *Ashmeadiella cactorum* is a small, long-tongued, dark brown bee with light stripes derived from densely packed white hairs at the sulci separating the abdominal tergites. The second species was *Osmia exigua,* a slightly larger, long-tongued green bee. Just before capture, both bees had been actively and systematically entering flowers, crawling completely into the corolla tube, then backing out, flying to another flower, and repeating the process. *Osmia exigua* could be heard apparently buzz-pollinating the flowers it entered, suggesting that it was actively collecting pollen.

Both bees had a ventrally located abdominal scopa where the majority of pollen grains were collected. Pollen examined on the body of *A. cactorum* was exclusively that of *O. pinorum.* The body of *O. exigua* held two types of pollen, approximately

75% of which was from *O. pinorum* (the other pollen type was not identified).

Host specificity. In all four excavations of *O. pinorum,* the host root was traced back to *H. discolor.* Although species composition varied at *O. pinorum* sites, all *O. pinorum* individuals seen in this study were found within five meters of one or more *H. discolor* plants.

DISCUSSION

Reproductive strategy. The results suggest predominant autogamy is the reproductive method employed by *O. pinorum* (although pseudogamy has not been ruled out). Facultative autogamy is a common reproductive strategy for annuals and parasites, and for species within Orobanchaceae in particular (Holzner 1982; Musselman et al. 1981). Open habitats select for colonizing species, and successful colonizers tend to have restricted recombination systems (Grant 1981; Begon and Mortimer 1986). Such colonizers can rapidly multiply and occupy a site.

Although the flowers of *O. pinorum* show most of the hallmarks of bee pollination, the positioning of their stamens promotes selfing. In *O. uniflora,* the predictable arrangement of the androecium relative to the stigma would tend to discourage self-pollination and facilitate crossing (Fig. 1e). The short filaments prevent the anthers from reaching the stigma, and the anthers are located beneath the more or less horizontal style. In this way the stigma is positioned to receive pollen carried from other flowers by the intruding insect pollinator. As the vector continues further, the anthers are positioned to dust it with pollen. In contrast, the maturing anthers of *O. pinorum* flowers examined in this study grew toward the stigma, with one or more contacting it directly (Fig. 1b, d). Hairs on the pollen sacs became entangled in the sticky fluid of the stigmatic surface, so that when the anthers dehisced, self-pollination was assured. As a result, the majority of ovules were self-fertilized, producing hundreds of seeds per capsule without relying on the vagaries of insect vectors. In this study, insect pollination accounted for an average of less than 20 mature seeds per capsule while self-pollination produced an average of nearly 700 (Table 4).

The parasitic habit of this species is highly specialized, and *O. pinorum* appears to occupy a niche with few if any direct competitors. One may predict that inbreeding would tend to maintain genetic stability in this parasite, and that predominant autogamy would in turn be reinforced by the stabilizing selection of its parasitic niche (Grant 1981). Thus predominant autogamy provides a stabilizing mechanism for this parasite as well as a means of dependably high seed production necessary to assure continued contacts with its host.

No evidence was found for pollen selection other than first-come-first-served, since pollen from the same plants, neighboring plants, and plants in distant populations all produced seeds with equal success. The apparently homogamous flowers of *O. pinorum* ensure selfing, which occurs approximately at (and on rare occasion before) the onset of anthesis. With no physiological barrier to xenogamy, *O. pinorum* retains the potential for cross-pollination and the subsequent infusion of new genetic variation.

Apparent pollinators. The recovery of two flower-visiting hymenopterans lends support to the potential for occasional out-crossing. That the pollen loads of both bees were composed primarily of *O. pinorum* pollen (entirely on *A. cactorum*) suggests a specificity that could be the result of a long-term relationship between pollinator and plant. Although the average vectoral seed production shown in this study was very low (13/flower, Table 4), its occurrence establishes out-crossing as a clear possibility.

Still, the evolutionary direction may be toward increasingly restricted recombination. The findings here document that insect visitation is infrequent and likely to be preceded by self-pollination when it occurs. Furthermore, many if not most visits by hymenopteran vectors may result in geitonogamous pollination, as they systematically probe successive flowers on the same plant.

The occasional dehiscence of *O. pinorum* anthers before anthesis noted in this study suggests the possibility of a trend toward cleistogamy. Olsen and Olsen (1980) found that a population of *Boschniakia hookeri* Walp., a related species within Orobanchaceae, had achieved obligate autogamy via cleistogamy.

Host specificity. The type specimen of *O. pinorum* was collected by Andreas Geyer nearly 150 years ago (Geyer 1851). In his notes he wrote that it was "growing on the roots of *Abies balsaminea.*" It seems evident that Geyer coined the epithet *pinorum* based on what he assumed was the host family. Most of the regional floras and identification books that followed mention coniferous hosts for *O. pinorum* (Munz 1930; Hitchcock et al. 1959; Abrams and Ferris 1960; Munz and Keck 1968; Peck 1961), but most fail to mention the host species, and the reliability of these accounts is doubtful. Musselman (1980) questioned the biological veracity of many reported hosts of species in Orobanchaceae. There appears to be no mention in the literature of gymnosperm hosts for any of the Orobanchaceae other than *O. pinorum.* Confirmation of such a finding would be an important contribution.

Abrams and Ferris (1960) mention anecdotal reports of *O. pinorum* parasitizing *H. discolor,* which may be the earliest published suggestion of this association. Major and Taylor (1977) list "*Holodiscus microphyllus* (with *Orobanche pinorum*)" among alpine vegetation habitats in California's Cascades. Two recent works also name *Holodiscus* as the host. Heckard (1993) mentions "*Holodiscus* spp."

which suggests the possibility that *H. discolor, H. microphyllus,* and *H. boursiéri* might all be hosts. He goes on to state emphatically that *O. pinorum* is "not known on conifers." Finally, Smith-Kuebel and Lillybridge (1993) specifically mention *H. discolor* as the host, and include the comment that *O. pinorum* was "originally thought to be parasitic on conifers." The findings of this study on host specificity, although limited, support these last two reports.

A species limited to a single host appears unusual in Orobanchaceae. The range of host families is very diverse, including herbs, shrubs, and trees. Monocot hosts are rare, and gymnosperm hosts may not exist. Musselman (1980) argues that most species in Orobanchaceae are very promiscuous, with broad host ranges, and that only physiological races are restricted to narrow host ranges. Furthermore, he claims that *O. crenata* may have the most narrow host range, restricted to legumes. Thus *O. pinorum* may be unusual in having a narrow host range—possibly the most narrow within Orobanchaceae—if it is truly restricted to three or fewer *Holodiscus* species.

Acknowledgments

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ALIEN ANNUAL GRASSES AND FIRE IN THE MOJAVE DESERT

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ABSTRACT

Fires have become more frequent in the Mojave Desert since the 1970's, threatening native plants and animals. This study describes how different annual plants facilitate the spread of fire during summer when weather conditions are optimal for fire. Eight annual plant taxa were evaluated: the alien grasses *Bromus* (*B. madritensis* L. subsp. *rubens* (L.) Husnot, *B. tectorum* L., *B. trinii* Desv.) and *Schismus* (*S. arabicus* Nees, *S. barbatus* (L.) Thell.), the alien forb *Erodium cicutarium* (L.) L'Hér, the native grass *Vulpia* (*V. microstachys* (Nutt.) Munro, *V. octoflora* (Walter) Rydb.), the native forbs *Amsinckia tessellata* A. Gray, *Descurainia pinnata* (Walter) Britton, and *Phacelia tanacetifolia* Benth., and other native forbs (119 species combined). Frequency and cover of dead annual plants were measured to describe the composition of fine fuels in summer (7 to 14 July), and compared to measurements of live annual plants in spring (12 April to 11 May) to determine their persistence as fuels after they senesced (summer : spring ratio). These data were collected during 1995 at 34 sites in the central, southern, and western Mojave Desert. Also described were the effects of each annual plant group in facilitating the spread of three 2.25 ha experimental fires conducted in August, 1995.

Absolute frequency and cover and summer : spring ratios were highest for *Bromus* and *Schismus*, and lowest for native forbs. Alien annual grasses contributed most to the continuity and amount of dead annual plants and to the spread of summer fires. Fire spread rapidly (12 m/min) and continuously across interspaces with *Bromus* and slowly (1 m/min) and discontinuously with *Schismus*. No other annual plant group produced sufficient continuous biomass to carry fire across interspaces. Fire management must include the control of alien annual grasses in the Mojave Desert.

The frequency of fire, the number of fires caused by humans (Fish and Wildlife Service 1994; Brooks 1998a), and the dominance of alien annual grasses (Hunter 1991; Brooks 1998b; Kemp and Brooks 1998) all increased between the 1970's and 1990's in the Mojave Desert. Fires caused by humans are most common near urban developments, major roads, and where off-highway vehicle use is unlimited (United States Department of the Interior records), whereas fires caused by lightening are typical of more remote wilderness areas. Alien annual grasses dominate all of these areas, and biomass of one species in particular, *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, is strongly correlated with size and frequency of fire (Brooks 1998b). Abundance of alien annual grasses is also positively correlated with the frequency of fire in the Sonoran Desert (Brown and Minnich 1986; Schmid and Rogers 1988). Thus, dominance of alien annual grasses appears to be a primary environmental correlate of fire in the Mojave Desert.

Areas dominated by alien annual grasses often have lower biomass and diversity of native forbs (Brooks 1998b; Brooks and Berry 1999), but it is unclear why landscapes dominated by them are more flammable than those dominated by native forbs in the Mojave Desert. Possible reasons include the higher surface to volume ratio of grasses compared to forbs that makes them easier to ignite (Kauffman and Uhl 1990), the more continuous cover of fuel that annual grasses often create on the landscape (Pyne et al. 1996), and the apparent ability of alien annual grasses to remain rooted and upright longer than native forbs allowing them to persist as flammable fuels into the summer when the threat of fire is highest (Brooks and Berry 1999).

Widely spaced shrubs and bunchgrasses with relatively bare interspaces between them characterize native Mojave Desert plant communities (Rundel and Gibson 1996). Frequent breaks in the continuity of fine fuels hinder the spread of fire, which is a primary reason fire is considered to be historically uncommon in this region (Humphrey 1974; O'Leary and Minnich 1981; Brown and Minnich 1986). The ability of alien annual grasses to produce high amounts of persistent flammable fuels in perennial plant interspaces seems to promote Mojave Desert fires (Brooks 1998b).

The purpose of this study was to compare the roles of alien annual grasses and other annual plants in facilitating the spread of fire in the Mojave Desert. This was accomplished by measuring the frequency and cover of fine fuels produced by different annual plant species and describing how flames spread through these fuels during experimental summer fires. Frequency was measured to evaluate the continuity and cover was measured to evaluate the amount of annual plant fuels. The summer : spring ratios of frequency and cover were calculat-

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ed to determine the amount that each decreased between spring and summer. Absolute frequency and cover during summer were measured to compare the characteristics of annual plant fuels during the time of year when high temperatures, low relative humidity, and low fuel moisture levels create conditions that are ideal for fire.

METHODS

Eight annual plant taxa were analyzed: *Bromus* [*B. madritensis* subsp. *rubens, B. tectorum* L., *B. trinii* Desv.], *Schismus* (*S. arabicus* Ness, *S. barbatus* [L.] Thell.), *Erodium cicutarium* (L.) L'Hér, *Vulpia* (*V. microstachys* [Nutt.] Munro, *V. octoflora* [Walter] Rydb.), *Amsinckia tessellata* A. Gray, *Descurainia pinnata* (Walter) Britton, *Phacelia tanacetifolia* Benth., and other natives (119 forb species, Brooks 1998b Appendix 3.1). The first two are alien grasses, the third is an alien forb, the fourth is a native grass, and the remaining species are native forbs. These taxa are among the most widespread and abundant annual plants in the central, southern, and western Mojave Desert (Brooks 1998b). The one exception is *Vulpia,* which was included because of its possible ecological similarities with the alien annual grasses. Some species were grouped and analyzed as genera because they could not be reliably distinguished during the summer. Plant nomenclature followed Hickman (1993).

Frequency and cover of annual plants. Frequency and cover of annual plants were measured at each of 34 sites located in the central (n = 16), southern (n = 8), and western (n = 10) Mojave Desert (Fig. 1). Sites were chosen by randomly selecting half the townships located within each of the three regions and randomly selecting one of the 1 mi^2 sections within each township from those that did not contain playas, mountaintops, or private lands. Final sites were located within each section adjacent to but greater than 50 m from dirt roads and greater than 2 km from paved roads and human habitations.

A single 360 m transect with twenty-five sampling points placed 15 m apart was established at each of the study sites. The transect was oriented parallel to the elevational contour to sample alternating run-off and run-on microtopographic positions. At each site twenty-five replicate measurements were made within two microhabitats, beneath the north side of perennial plant canopies (>50 cm dia.) and in the interspace between them (>1 m from perennial plant canopies). Within each microhabitat cover and frequency were estimated using a 22 cm long point-frame of ten equally spaced 1.5 mm diameter pins (Greig-Smith 1964). The frame was oriented perpendicular to the ground, each pin was lowered to the surface of the soil, and the number of times each pin touched above-ground parts of annual plant species was recorded. Frequency was estimated as the proportion of the pins in each frame that touched at least one plant part and cover was estimated as the total number of pin touches per 10-pin frame. More detailed site and sampling design descriptions were presented by Brooks (1998b).

Data were obtained during spring and summer 1995 following a winter with 200% of average rainfall (National Oceanographic and Atmospheric Administration 1995). Measurements were first made from 12 April through 11 May when most species had reached peak biomass and just before they began to senesce. Only living plant material was measured. The second measurements were made from 7 through 14 July, when all germinated annual plants were dead. Because spring measurements were followed by biomass clipping (Brooks 1998b), summer measurements were recorded 20 cm from the spring measurements. Dead annual plant material included some senescent biomass from previous years in addition to plants that grew during the spring. Only material that was alive in spring 1995 was used to calculate the summer: spring ratios. Annuals that were alive in spring could be identified in summer because they were golden brown and often contained inflorescences and leaves. Annuals still standing after one year typically acquire a gray hue and lose their inflorescences and leaves.

Average frequency and cover of the eight annual plant taxa from each site were used as replicates to calculate average values across the entire study region (n = 34 replicates). Sites that did not possess at least one point-frame hit for a given plant taxa during the spring were not used in the estimate of summer: spring ratios. Some of the less common species (e.g., *P. tanacetifolia*) were not detected at some sites, reducing the number of replicates for this group. Hence, sample sizes varied among groups and differences among them were tested using Tukey's studentized range test that is robust for unequal sample sizes ($P \leq 0.05$) (Sokal and Rohlf 1995). Arcsine transformations were performed on ratios and square root transformations were performed on absolute counts prior to testing.

Experimental fires. To evaluate the role of different annual plants in facilitating the spread of fire, detailed observations were made during three experimental fires in the western (35°14′30″N, 117°51′15″W), central (35°07′30″N, 117°07′45″W), and southern (34°41′30″N, 117°57′30″W) Mojave Desert (Fig. 1). These fires were conducted on 16, 22, and 24 August 1995 respectively. Each site was 150 × 150 m (2.25 ha) and dominated by *Bromus* spp. and/or *Schismus* spp. Dead annual plants were ignited using a continuous flame line applied with a drip-torch (diesel/unleaded gas mix) along the upwind border of each site.

The total amount of annual plant fuels (nearest dry 25 kg/ha) and the dominant annual plant species in the beneath-canopy and interspace micro-

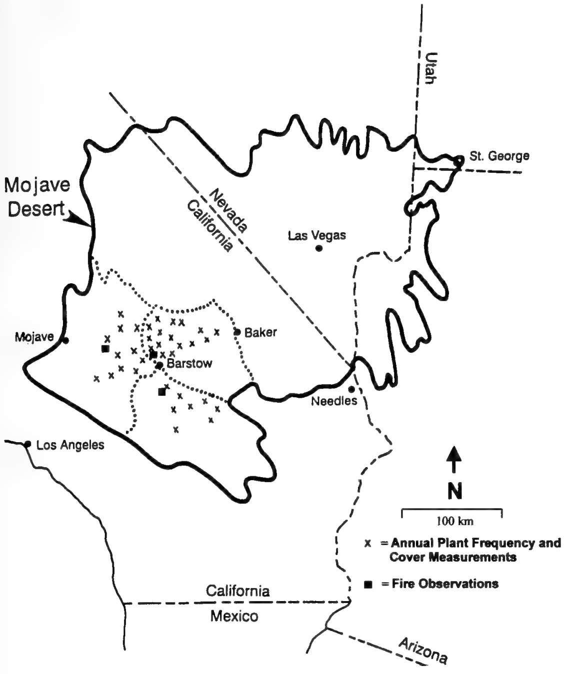

FIG. 1. Locations of the 34 study sites in the central, southern, and western regions of the Mojave Desert.

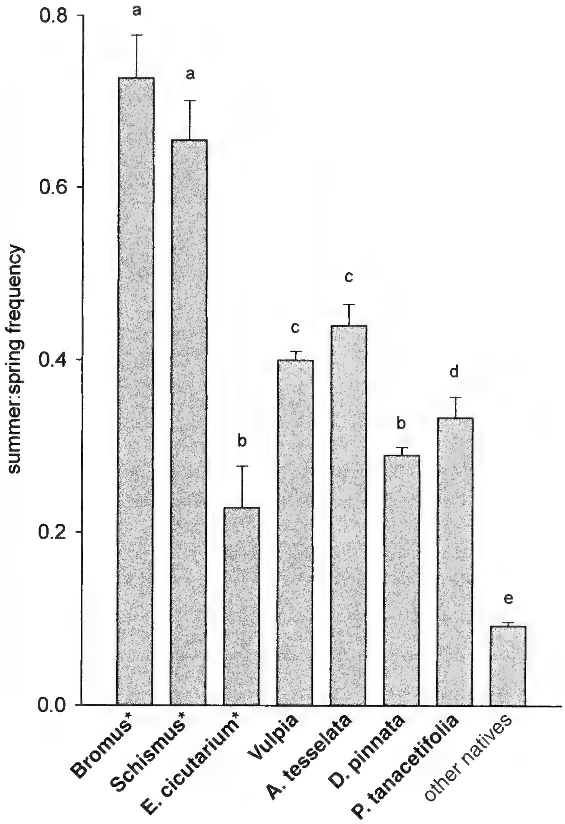

FIG. 2. Summer : spring frequency of annual plants averaged over 34 sites in 1995 (+1 SE). Dissimilar letters indicate significant differences using Tukey's studentized range test ($P < 0.05$). * alien species.

habitats were determined using visual estimation. These estimates were based on the author's experience physically sampling annual plant biomass and visually estimating cover in the Mojave Desert. Rates of fire spread and flame lengths were recorded at 15 random interspace points during each fire. The total amount of burned area (nearest 25%) and continuity of burning were visually estimated after each fire. Air temperature, relative humidity, cloud cover, wind speed and direction, at the beginning and end of each fire were recorded, because weather conditions can affect fire behavior.

RESULTS

Frequency and cover of annual plants. The proportion of point frame hits for *Bromus* spp. was 90% *B. madritensis* subsp. *rubens* and 10% *B. tectorum* and *B. trinii* combined during spring 1995. The proportion of *Schismus* spp. species were not estimated because *S. arabicus* and *S. barbatus* could not be reliably distinguished in the field. The proportion of *Vulpia* species was 60% *V. octoflora* and 40% *V. microstachys.* Estimates of total annual plant cover were highly correlated with concurrent measurements of above-ground live biomass during spring 1995 (Brooks 1998b, $r = 0.64$).

Summer : spring frequency was highest for *Bromus* spp. and *Schismus* spp. and lowest for the other natives category (Fig. 2). *Vulpia* spp., *A. tessellata, D. pinnata,* and *P. tanacetifolia* had intermediate frequency ratios, but very low absolute frequencies (Fig. 3). *Erodium cicutarium* had an intermediate frequency ratio and absolute frequency. The combination of high summer : spring frequencies and high absolute frequencies during summer indicate that *Bromus* spp. and *Schismus* spp. contributed most to the frequency of dead annual plants in the summer.

Summer : spring cover was highest for *Bromus* spp. and lowest for the other natives category (Fig. 4). *Schismus* spp., *A. tessellata, D. pinnata,* and *P. tanacetifolia* had intermediate ratios, but absolute cover of *Schismus* was significantly higher than all groups except *Bromus* spp. ($P < 0.05$, Fig. 5). Summer : spring and absolute cover were relatively low for *E. cicutarium.* Similar to the frequency results, the combination of high summer : spring cover ratios and high absolute cover during summer indicate that *Bromus* spp. and *Schismus* spp. contributed most to the cover of dead annual plants in the summer.

Experimental fires. The central Mojave site had the lowest amount of fine fuels (Table 1) and the lowest wind speed and highest relative humidity during the fire (Table 2). As a result, fire did not spread beyond ignition points.

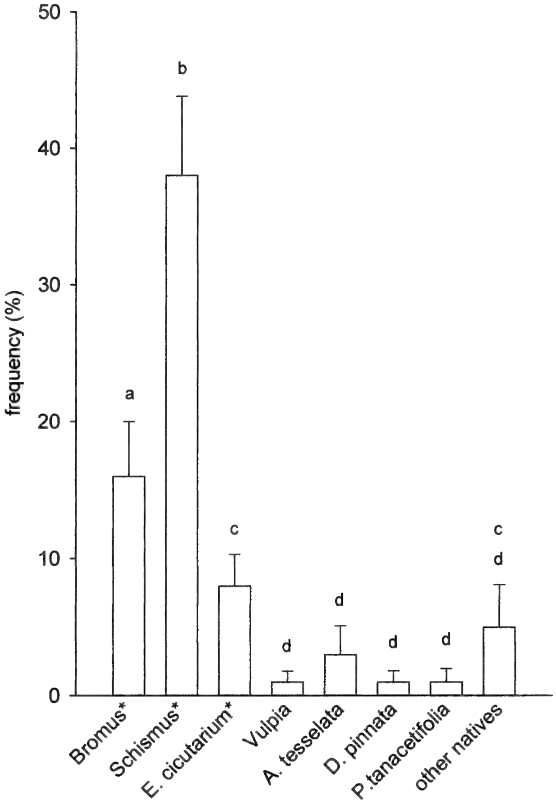

FIG. 3. Absolute frequency of annual plants averaged over 34 sites in 1995 (+1 SE). Dissimilar letters indicate significant differences using Tukey's studentized range test (P < 0.05). * alien species.

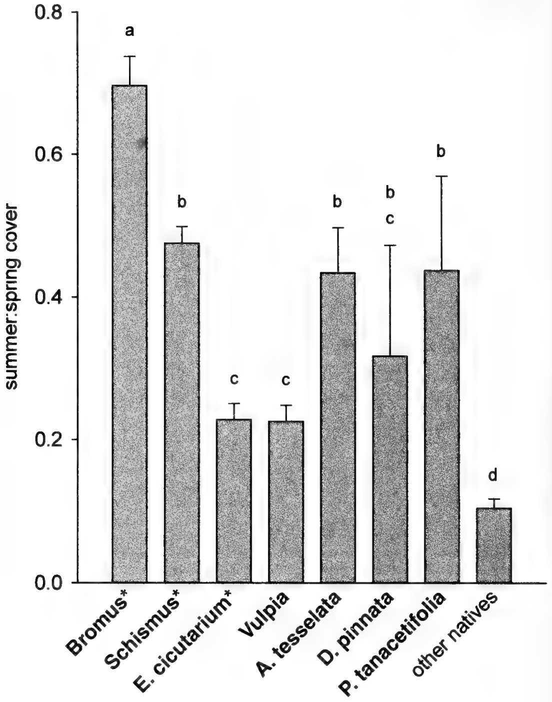

FIG. 4. Summer:spring cover of annual plants averaged over 34 sites in 1995 (+1 SE). Dissimilar letters indicate significant differences using Tukey's studentized range test (P < 0.05). * alien species.

The southern Mojave site had relatively high amounts of fine fuels in the beneath-canopy and interspace microhabitats (Table 1). Relative humidity was relatively low and wind speeds were moderate, so fire spread relatively fast across interspaces and 50% of the site burned over large continuous areas (Table 2).

The western Mojave site had high amounts of fine fuels in the beneath-canopy microhabitat, but only moderate amounts in the interspaces (Table 1). Relative humidity was relatively low and wind speeds were high (Table 2), but fire spread relatively slow and 50% of the total site burned in many small patches.

Low humidity, moderate to high wind speeds, and substantial interspace biomass of fine fuels comprised mostly of alien annual grasses were associated with high rates and continuities of fire spread. In contrast, relatively high humidity, low wind speeds, and virtually no fine fuels between shrubs were associated with no fire spread. Differences in fire behavior were not attributed exclusively to weather or fuel composition, because these variables were confounded. However, fires were always fueled by the dead stems of alien annual grasses.

Fire spread was extensive and rapid where *Bromus* spp. was codominant with *Schismus* spp. in interspaces (southern Mojave site; Table 1). Fire spread was patchy and slow where only *Schismus* spp. was dominant in interspaces (western Mojave site). Average wind speed during the fire at the western Mojave site was twice that at the southern Mojave site (Table 2), yet fire spread faster and more continuously across the latter site (Table 1). Thus, high interspace biomass of *Bromus* spp. and *Schismus* spp. resulted in greater fire danger at the southern Mojave site, even though wind speeds were much higher at the western Mojave site.

Where *Bromus* spp. was abundant in interspaces fire spread approximately 12 m/min with flame lengths up to 30 cm. The heat generated by *Bromus* spp. was sufficient to ignite and consume dead stems of native forbs and plant litter. *Schismus* spp. was also effective at carrying fire across interspaces, but only at 1 m/min with flame lengths 5–10 cm. Flame lengths from *Schismus* spp. could not easily be seen and often only burned the top 25% of *Schismus* spp. stems, indicating that temperatures were relatively low. Most dead native forb stems and litter material were unburned. Although *Bromus* spp. and *Schismus* spp. both facilitated the spread of fire, only *Bromus* spp. produced long

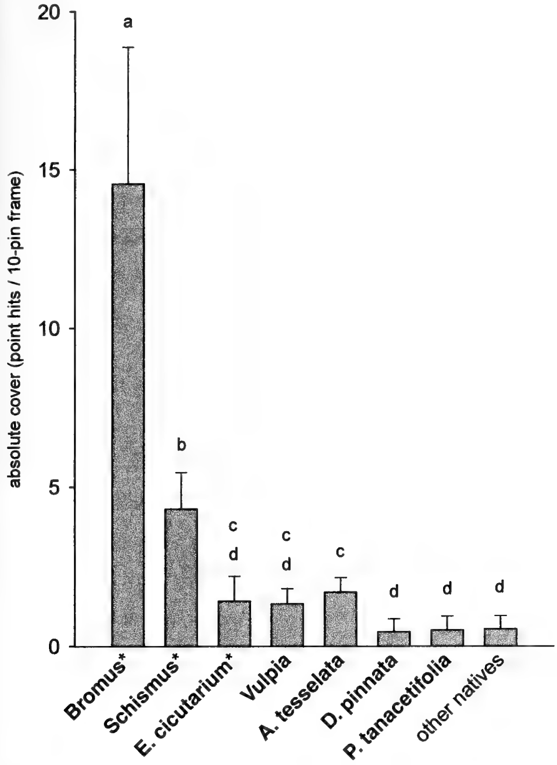

FIG. 5. Absolute cover of annual plants averaged over 34 sites in 1995 (+1 SE). Dissimilar letters indicate significant differences using Tukey's studentized range test ($P < 0.05$). * alien species.

flame lengths that consumed considerable amounts of annual plant biomass. *Erodium cicutarium* and native annuals did not contribute significantly to the spread of fire, because of low frequency and cover.

Flames fueled by *Bromus* spp. were sufficient to consume small shrubs such as *Ambrosia dumosa* (A. Gray) Payne, *Krascheninnikovia lanata* (Pursh) A. D. J. Meeuse & Smit, *Hymenoclea salsola* A. Gray, and *Lycium andersonii* A. Gray, whereas flames fueled by *Schismus* spp. were rarely hot enough to ignite these shrubs. Fire intensity in *Bromus* spp. was usually insufficient to ignite large shrubs such as *Larrea tridentata* (DC.) Cov. However, *Larrea tridentata* containing large accumulations of *Bromus* spp. stems and dead shrub stems in the sub-canopy were highly susceptible to burning. In these cases fire carried from *Bromus* spp. stems, to dead shrub stems, to live shrub stems, and typically resulted in the entire shrub being consumed by flames.

DISCUSSION

The alien annual grasses *Bromus* spp. and *Schismus* spp. appear to be necessary for fire to spread across the Mojave Desert landscape. These were the only annual plant taxa that produced abundant and continuous cover of fine fuels that persisted into the summer fire season.

Intermediate fuels produced by large forbs can add to the continuity and amount of flammable biomass, although fine fuels produced by alien annual grasses are generally required to sustain a fire (Brooks personal observation). These large forbs include the alien mustards *Brassica tournefortii* Gouan, *Hirschfeldia incana* (L.) Lagr.-Fossat, *Sisymbrium altissimum* L., *Sisymbrium irio* L., and *Descurainia sophia* (L.) Webb, and the weedy native *A. tessellata.* They are especially common along roads where fires frequently start and some of the alien species are rapidly expanding their range and becoming established away from roads in the Mojave and Colorado deserts (Kemp and Brooks 1998; Brooks and Berry 1999). Hence, large weedy forbs may present a more widespread fire hazard in the future.

Thick layers of annual plant litter often develop where alien annual grasses are abundant (Brooks and Berry 1999). Accumulations of litter led to particularly hot temperatures, long flame residency times, and continuous burn patterns in experimental fires conducted during summer 1995 and 1996 in the Mojave Desert (Brooks unpublished). Plant litter decomposes slowly in desert regions and grasses can be among the slowest (Facelli and Pickett 1991). Thus, litter accumulation may be another mechanism by which alien annual grasses facilitate the spread of Mojave Desert fires.

The current study suggests that *Bromus* spp. fuel fast moving hot fires whereas *Schismus* spp. fuel slower moving cooler fires. This pattern is gener-

TABLE 1. SITE DATA FOR EXPERIMENTAL FIRES CONDUCTED IN AUGUST 1995.

Site	Fine fuels (kg/ha)		Dominant annuals (spp. >25% relative cover)		Interspace fire spread (m/min) (1 SE)	Area burned (% of 2.25 ha)
	Beneath-canopy	Inter-space	Beneath-canopy	Interspace		
Central Mojave	300	25	*Bromus/Schismus*	*Schismus*	0 (0)	0
Southern Mojave	700	200	*Bromus*	*Bromus/Schismus*	12 (8)	50 (continuous)
Western Mojave	800	100	*Bromus/Schismus*	*Schismus*	1 (1)	50 (patchy)

TABLE 2. WEATHER DATA FOR EXPERIMENTAL FIRES CONDUCTED IN AUGUST 1995.

Site		Time (PST)	Air temperature (°C)	Rel. humidity (%)	Cloud cover (%)	Wind direction	Wind speed (km/h) (gusts)
Central Mojave	begin	1030	35	32	0	SSW	0 (8)
	end	1115	41	25	0	SSW	0 (8)
Southern Mojave	begin	1020	33	17	0	SSE	5 (5)
	end	1130	35	15	0	SSE	8 (13)
Western Mojave	begin	1130	37	19	0	NNE	16 (18–32)
	end	1215	38	10	0	NNE	16 (18–32)

ally consistent among seasons and years (Brooks personal observation). The immediate ecological effects of *Bromus* spp. fires are probably more significant, because they are more intense and often consume perennial shrubs. However, *Schismus* spp. can facilitate the spread of fire between patches of *Bromus* spp., and promote fires at arid low elevation sites where *Bromus* spp. are less abundant (Brooks 1998b). During the 1990's in the Mojave Desert some fires fueled mostly by *Schismus* spp. exceeded 40 ha (100 acres) before they were extinguished by fire crews (United States Department of the Interior records).

High postfire dominance of alien annual grasses can promote subsequent fires in the Great Basin desert (Whisenant 1990; Peters and Bunting 1994; Billings 1994) and other ecosystems (D'Antonio and Vitousek 1992). Post-fire plant communities in the Mojave and Sonoran deserts are also typically dominated by alien annual grasses (O'Leary and Minnich 1981; Brown and Minnich 1986; Brooks unpublished), so previously burned areas appear to be more susceptible to fire than unburned areas. This grass/fire cycle is a significant ecological threat because most native plant species are poorly adapted to survive fire in the deserts of southwestern North America (Tratz 1978; O'Leary and Minnich 1981; Wright and Bailey 1982; Brown and Minnich 1986; Billings 1994; Lovich and Bainbridge 1999).

Drought years may reduce the dominance of *Bromus* spp. in both recently burned and unburned areas decreasing the chance of fire (Minnich personal communication), but these effects vary among sites. For example, the winter of 1998–1999 was very dry in the Mojave Desert and most *Bromus* spp. seedlings did not survive to maturity on low elevation bajadas, whereas many survived and reproduced on high elevation hills and mountains (Brooks personal observation). High elevation sites may provide more mesic conditions that allow *Bromus* spp. to survive drought better than at lower elevations. Recurrent fire is most prevalent at these high elevation sites (Brooks unpublished) where high biomass of alien annual grasses and the physical effects of steep slopes promote fire. Establishment of the grass/fire cycle appears to be more likely on high elevation slopes than on low elevation bajadas.

Management of fire in the Mojave Desert should focus on minimizing the dominance of alien annual grasses and preventing the establishment of new plant species that can increase landscape flammability (Brooks and Berry 1999). Such species include large forbs and the perennial bufflegrass (*Pennisetum ciliare,* Brooks et al. 1999). Sources of ignition from human activities should also be minimized, especially where alien annual grasses are abundant and topography is conducive to the spread of fire.

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SYNCHRONY AND ASYNCHRONY OF ACORN PRODUCTION AT TWO COASTAL CALIFORNIA SITES

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ABSTRACT

We measured annual acorn production of oaks *Quercus* spp. at Hastings Reservation and at Hopland Research and Extension Center, located 320 km apart in the outer coast ranges of California, for 16 years between 1982 and 1997. Of the three species measured at both sites, acorn production by *Quercus lobata* Nee (valley oak) and *Quercus douglasii* Hook. & Arn. (blue oak) was significantly correlated between sites, whereas acorn production by *Quercus kelloggii* Newb. (California black oak) was not. Both *Q. lobata* and *Q. douglasii* acorn production was significantly correlated with mean April temperatures and rainfall at their respective localities, but more closely with April temperatures at Hastings and with rainfall at Hopland. Synchrony in acorn production between *Quercus* spp. requiring one year to mature acorns was significantly greater than among those requiring two years to mature acorns. The geographic extent of the populations producing acorn crops synchronously differs between species, but in some cases may extend over distances of at least several hundred kilometers.

Mast-fruiting, or masting, is a population phenomenon (Kelly 1994). That is, a single tree may produce highly variable numbers of seeds from year to year, but it is only when a population of trees produce seeds synchronously from one year to the next that masting can be considered to occur. Recent studies in New Zealand (Norton and Kelly 1988), the midwestern United States (Sork et al. 1993) and California (Koenig et al. 1994a, 1996) have begun to elucidate the patterns and causes of masting behavior in forest trees. However, work has only recently begun to address the question: what is the geographic extent of the 'population' producing seeds synchronously?

Here we analyze data relevant to this question using data on three species of *Quercus*. Specifically, we independently collected data on acorn production by *Q. lobata* (valley oak), *Q. douglasii* (blue oak), and *Q. kelloggii* (California black oak) oaks at two sites in coastal California 320 km apart: Hopland Research and Extension Center in Mendocino County (38°58.5′N, 123°07′W; hereafter "Hopland") and Hastings Natural History Reservation in Monterey County (36°23′N, 121°33′W; hereafter "Hastings"), over a 16 year period from 1982 to 1997 (Fig. 1). We ask: 1) does the population of masting oaks extend over this distance in California? and 2) is acorn production correlated with similar environmental factors at the two sites?

METHODS

At Hopland, acorn production by each species was censused using 10 traps consisting of plastic garbage bags 0.46 m in diameter, each placed at a random location under a tree of the appropriate species. Traps were checked in December at the end of the season and the total number of sound acorns trapped log-transformed ($ln[N+1]$). Species censused included *Q. lobata, Q. douglasii, Q. kelloggii,* and interior live oak *Q. wislizenii* A. DC. (interior live oak).

At Hastings, acorn censuses were done visually between mid-September and early October just prior to acorn fall (Koenig et al. 1994b). For each tree two observers scanned different areas of the tree's canopy and counted as many acorns as possible in 15 sec. Counts were added to yield the number of acorns counted in 30 sec (N30). Values for each

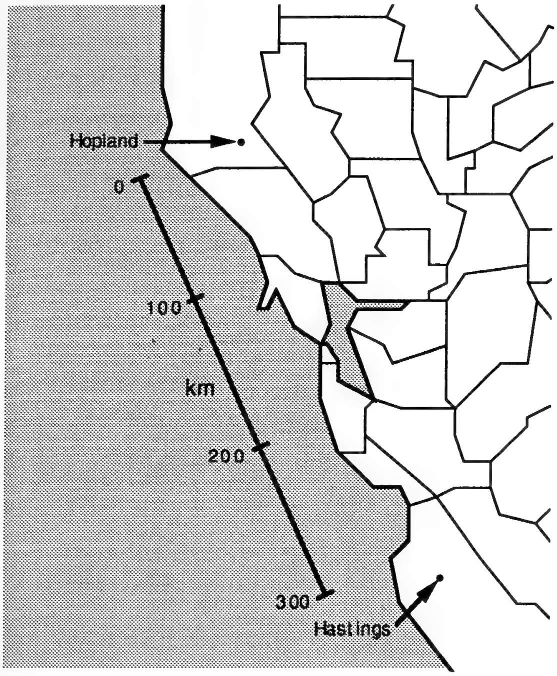

FIG. 1. A map of central coastal California showing the locations of Hopland Research and Extension Center and Hastings Natural History Reservation relative to the San Francisco Bay area (center). Lines are county boundaries; Hopland is in Mendocino County while Hastings is in Monterey County.

tree were log-transformed (ln[N30+1]) and averaged to yield the mean log-transformed number of acorns counted per tree of each species. The relative merits of visual surveys versus traps for censusing acorns in California oak woodland habitat are discussed in Koenig et al. (1994b), who also provide data demonstrating that values derived from visual counts are significantly correlated with numbers of acorns obtained by trapping for *Q. lobata* at Hastings.

Species included and the number of trees censused per species were *Q. lobata* (87), *Q. douglasii* (57), *Q. kelloggii* (21), *Q. agrifolia* Nee (coast live oak; 63), and (*Q. chrysolepis* Liebm. canyon live oak; 21). Thus, three species (*Q. lobata, Q. douglasii,* and *Q. kelloggii*) were surveyed at both localities. These species differ in that both *Q. lobata* and *Q. douglasii* are "1-year species" requiring a single year to mature acorns, whereas *Q. kelloggii* is a "2-year species" requiring two years to mature acorns. Of the three live oak species censused at one or the other site, *Q. agrifolia* (at Hastings) is a one-year species while *Q. wislizenii* (at Hopland) and *Q. chrysolepis* (at Hastings) are two-year species.

Weather data came from stations located near headquarters at both sites. Variables analyzed included seasonal rainfall (1 Sept. of year x-1 to 31 August of year x) and mean April temperature (mean of the daily averages of the maxima and minima). Statistical analyses were made using nonparametric Spearman rank correlations and Mann-Whitney U tests. P-values are two-tailed; values listed are means ± SD.

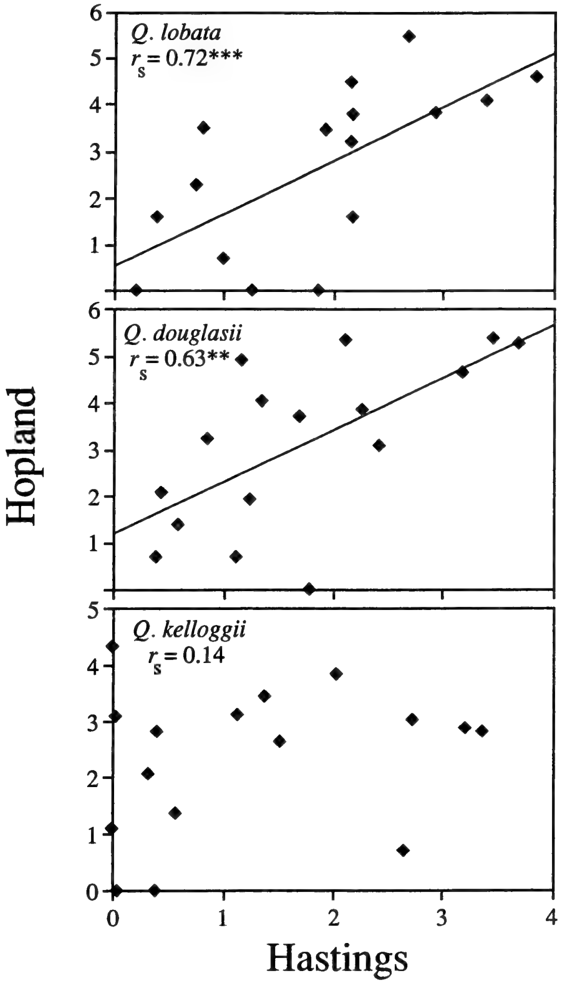

FIG. 2. Correlations between the log-transformed mean acorn crops of *Q. lobata, Q. douglasii* and *Q. kelloggii* at Hopland and Hastings between 1982 and 1997 (N = 16 years). Spearman rank correlations and their significance values (** = $P < 0.01$; *** = $P < 0.001$) are listed.

RESULTS

Annual acorn production at the two sites was highly correlated for *Q. lobata* and *Q. douglasii,* but not for *Q. kelloggii* (Fig. 2). Prior studies of *Q. lobata* and *Q. douglasii* at Hastings have demonstrated significant correlations between acorn production by these two species and mean April temperatures during the peak of flowering and pollination (Koenig et al. 1996), whereas no environmental variable has as yet been identified to correlate with acorn production by *Q. kelloggii.* Correlations between acorn production of these

TABLE 1. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION AT HASTINGS AND HOPLAND AND ENVIRONMENTAL VARIABLES MEASURED AT THE SAME SITES BETWEEN 1982 AND 1997 (N = 16 YEARS). * = P ≤ 0.05; ** = P < 0.01; *** = P < 0.001.

	Mean April temp.	Mean April temp. (year *x* − 1)	Seasonal rainfall	Seasonal rainfall (year *x* − 1)
Hastings				
Q. lobata	0.82***	−0.10	−0.65**	0.04
Q. douglasii	0.73***	−0.25	−0.48	0.26
Q. kelloggii	0.04	0.59*	−0.09	0.01
Hopland				
Q. lobata	0.63**	−0.32	−0.77***	0.35
Q. douglasii	0.50*	−0.35	−0.72**	0.57*
Q. kelloggii	0.12	0.42	−0.19	−0.28

three species at both Hastings and Hopland over the 16 years analyzed here and both mean April temperature and seasonal rainfall are summarized in Table 1.

Correlations between the environmental variables at the two sites over the 1982–1997 period were high (rainfall: $r_s = 0.79$, $n = 16$, $P < 0.001$; mean April temperature: $r_s = 0.94$, $n = 16$, $P < 0.001$). However, the relationships between these environmental factors and acorn production were not identical at the sites. Acorn production by *Q. lobata* and *Q. douglasii* were positively correlated with mean April temperature at both sites; however, the correlations were much higher at Hastings than at Hopland. Interestingly, the reverse pattern holds for the relationship between acorn production by these two species and seasonal rainfall: all correlations were negative, but they were considerably stronger at Hopland than at Hastings. Multiple regression analyses with these two variables yielded identical results. Acorn production by *Q. douglasii* at Hopland was also significantly positively correlated with seasonal rainfall lagged one year while *Q. kelloggii* at Hastings was positively correlated with mean April temperature lagged one year; both these correlations were low and not statistically significant at the other site.

We also compared interspecific correlations between one-year (Table 2) and between two-year (Table 3) species of oaks, both within and between sites. For the one-year species, 9 of 10 interspecific correlations were significant, including all six of the cross-site comparisons. Overall, the mean interspecific correlation coefficient was 0.64 ± 0.16 and did not differ significantly between cross-site (mean = 0.62 ± 0.10) and within-site comparisons (mean = 0.68 ± 0.24; Mann-Whitney *U*-test, $z = 0.6$, $P = 0.52$). For the two-year species, none of the six pairwise correlation coefficients was significantly different from zero and the mean interspecific correlation coefficient was 0.11 ± 0.21, significantly less than the interspecific correlations between one-year species (Mann-Whitney *U*-test, $z = 3.2$, $P < 0.002$). Among the two-year species, only the correlation between *Q. kelloggii* and *Q. chrysolepis* at Hastings came close to being significant ($P = 0.06$).

DISCUSSION

These results demonstrate that for *Q. lobata* and *Q. douglasii* annual acorn crops are highly synchronous between two sites in coastal California 320 km apart. Furthermore, acorn crops of these species at the two sites are both correlated with mean April temperatures. This is consistent with the hypothesis that masting occurs over large geographic areas in these two species, and furthermore suggests that the proximate cues used by trees to synchronize reproductive effort are also similar over large distances (Koenig et al. 1996). However, patterns were not identical at the sites. At Hastings, both species were positively and strongly correlated with mean April temperature and negatively, but less strongly, correlated with seasonal rainfall, whereas at Hopland the pattern was reversed. This suggests that the precise mix of environmental fac-

TABLE 2. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION OF ONE-YEAR *QUERCUS* SPECIES, BOTH WITHIN AND BETWEEN HASTINGS AND HOPLAND, BETWEEN 1982 AND 1997 (N = 16 YEARS). * = P ≤ 0.05; ** = P < 0.01; *** = P < 0.001.

	Q. agrifolia (Hastings)	*Q. lobata* (Hastings)	*Q. douglasii* (Hastings)	*Q. lobata* (Hopland)
Q. lobata (Hastings)	0.38	—	—	—
Q. douglasii (Hastings)	0.59*	0.85***	—	—
Q. lobata (Hopland)	0.53*	0.72***	0.75***	—
Q. douglasii (Hopland)	0.53*	0.57*	0.63**	0.89***

TABLE 3. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION OF TWO-YEAR *QUERCUS* SPECIES, BOTH WITHIN AND BETWEEN HASTINGS AND HOPLAND, BETWEEN 1982 AND 1997 (N = 16 YEARS). All P > 0.05.

	Q. kelloggii (Hastings)	*Q. chrysolepis* (Hastings)	*Q. wislizenii* (Hopland)
Q. chrysolepis (Hastings)	0.48	—	—
Q. wislizenii (Hopland)	0.05	0.16	—
Q. kelloggii (Hopland)	0.14	−0.05	−0.10

tors influencing acorn production may differ at different localities, potentially explaining the lower correlation between acorn production at the sites (r_s = 0.82 for *Q. lobata* and 0.73 for *Q. douglasii*) compared to that for the critical environmental factor (r_s = 0.94 for mean April temperatures).

In contrast, we found no evidence of synchrony between acorn production by *Q. kelloggii* surveyed at the two sites. Because *Q. kelloggii* requires two years to mature acorns, it is possible that the environmental factors synchronizing reproduction are more complicated, and thus less likely to be geographically synchronous, than those used by the one-year species. Consistent with this hypothesis, analyses at Hastings Reservation using the 16 years of data between 1980 and 1995 found no relationship between any plausible environmental variable and acorn production in *Q. kelloggii* (Koenig et al. 1996). However, with the 1982 to 1997 data used here, there is a statistically significant correlation between mean April temperature lagged one year and acorn production by *Q. kelloggii* at Hastings. This correlation is not significant in the Hopland data over the same time period. More data will be needed before we will be able to understand what environmental factors influence acorn production in this species.

We also performed pairwise interspecific comparisons of the acorn crops of the one-year and the two-year species both within and between sites. All interspecific comparisons between one-year species were positive and 9 of 10 were statistically significant (Table 2). Mean correlations were high and there was no difference between the within-site compared to the between-site cross-correlations. In contrast, only 4 of 6 comparisons between two-year species were positive and none was statistically significant (Table 3). These results support the hypothesis that acorn production of two-year *Quercus* species is geographically less synchronous than that of one-year *Quercus* species.

Analyses of acorn production from data reported in the literature similarly indicate that the geographic extent of synchrony in acorn production by two-year *Quercus* species is less than that of one-year species (Koenig and Knops 1997). At the proximate level, this could be because the two-year species are sensitive to more complicated environmental factors or because they are sensitive to different sets of environmental factors in different sites, as suggested by our results for *Q. lobata* and *Q. douglasii.* At a more ultimate level, it could be because the ecological factors selecting for mast-fruiting in two-year species differ from those important to one-year species, due for example to differences in the habitats they inhabit. Hypotheses suggested to favor masting include predator satiation (Silvertown 1980), wind pollination (Smith et al. 1990), and several other lesser ways by which efficiency may be increased by devoting more resources to reproduction in some years than others (Norton and Kelly 1988; Kelly 1994).

These results add to the small but growing amount of data available concerning the geographic scale of, and the proximate factors involved in, synchronizing acorn production by *Quercus* spp. Combined with prior analyses demonstrating significant synchrony between acorn production of *Q. lobata* and *Q. douglasii* at Hastings and at Jasper Ridge in San Mateo County 130 km away, and between acorn production of *Q. agrifolia* not only at Jasper Ridge and at Hastings but also at Pozo, 290 km south of Jasper Ridge (Koenig et al. 1996), these data extend synchrony in acorn production by *Quercus* spp. to a distance of over 300 km. The proximate cue used to synchronize acorn production by *Q. lobata* and *Q. douglasii* throughout this range appears to be either spring temperature or seasonal rainfall, which are themselves correlated over large distances. Whether these patterns extend throughout the state is currently under investigation.

In contrast, we found no statistical synchrony in acorn production by *Q. kelloggii* between Hopland and Hastings. This negative finding is consistent with prior analyses indicating that the environmental factors affecting synchrony in acorn production in oaks requiring two years to mature acorns are more difficult to discern than those used by one-year species of *Quercus*.

Also supporting the contention that synchrony is lower in oaks requiring two years to mature acorns are the results of interspecific correlations, both within and between sites, between one-year and between two-year *Quercus* species. Correlations between annual acorn production of one-year species were all positive and, with a single exception, statistically significant. In contrast, correlations between annual acorn production of two-year species were not consistently positive or negative and none was significantly different from zero. Geographic synchrony in acorn production appears to be greater both within and between one-year species than within or between two-year species of *Quercus*.

These results suggest a complex pattern of spatial autocorrelation in acorn production by *Quercus* spp. Within and even between one-year species, the extent of geographic synchrony in acorn production appears to be large, possibly encompassing the entire state. However, for two-year *Quercus* species, geographic synchrony appears neither to be as extensive nor to cross species boundaries.

What this means for a particular locality depends largely on the geographic scale being considered. On a local scale of a few square kilometers, many California sites contain only one-year *Quercus* species and thus may be subject to relatively frequent community-wide acorn crop failures due to the synchrony in acorn production across one-year *Quercus* species. Such synchrony is likely to extend over large geographic areas thousands or even tens of thousands of square kilometers in size. However, once the geographic scale over which one is concerned starts to encompass such larger areas, the topographic heterogeneity and complexity of the California landscape will generally ensure that sites containing both one-year and two-year *Quercus* species will be present somewhere within the area. Thus, despite large-scale geographic synchrony in at least several of the most widespread species of California oaks, the diversity of habitats occurring over moderately large geographic areas makes it unlikely that the acorn crop of all species will fail in any particular year (Koenig and Haydock 1999).

Masting by oaks has been shown to have cascading effects on communities in the eastern United States via its affect on mouse populations (Jones et al. 1998). Consequently, large-scale geographic synchrony in acorn production such as is suggested here could plausibly have major effects on communities over similarly large geographic areas, especially to the extent that the species involved are specialized on the acorns of one-year *Quercus*. No vertebrate acorn predator of which we are aware is specialized in this way. However, at least some of the many invertebrate species that depend on acorns are restricted to the acorns of particular *Quercus* subgenera, and sometimes usually a single *Quercus* species (Russo 1979; Cornell 1985). The effects of geographic synchrony in acorn production on populations of such taxa remain to be documented.

ACKNOWLEDGMENTS

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FIRE SEASON AND MULCH REDUCTION IN A CALIFORNIA GRASSLAND: A COMPARISON OF RESTORATION STRATEGIES

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ABSTRACT

Prescribed burning and mulch reduction via grazing are two restoration strategies employed for the enhancement of native flora in California grasslands. However, the effectiveness of these methods to restore native species and suppress alien species is poorly understood. In particular, the effectiveness of different seasons of burning to restore native vegetation has been attributed to several factors, including plant phenology patterns (phenology hypothesis), fire intensities (intensity hypothesis), and accumulated mulch biomass (mulch hypothesis). In order to test these hypotheses and compare the efficacy of burning and grazing as restoration tools, the short-term effects of fire season and mulch reduction on grassland vegetation were evaluated in the Carrizo Plain Natural Area (San Luis Obispo Co., CA). Warm-season (late-spring and fall) burning significantly increased the cover and diversity of native vegetation and decreased the cover and seed viability of alien grasses relative to control treatments. Winter burning and mulch reduction did not increase the cover or diversity of native plants and were only moderately effective at reducing alien plant cover. Seed germination data showed that the seeds of one common native plant species, *Phacelia ciliata* Benth, responded positively to fire. These results indicated that fire season is a significant factor in grassland restoration, and that the success of different fire seasons for restoration is determined by plant phenology patterns, season-specific fire intensities, and potentially the removal of all mulch biomass. Warm-season prescribed burning and not grazing or cool-season burning is the most effective strategy for restoring native annual vegetation to California grasslands.

Fire is an important restoration tool for ecologists, yet very few studies have examined the significance of fire season for the regeneration of plant communities. Controlled burning programs allow resource managers to simultaneously reduce undesirable species and enhance desirable species (Towne and Owensby 1984; Parsons and Stolhgren 1989; Whisenant and Ursek 1990; Howe 1995). Such a shift in community composition may be achieved by burning strategies that incorporate the effects of fire season. These management strategies have proven to be particularly effective in the restoration of a variety of native grassland communities, including California bunchgrass (Menke 1992), Texas wintergrass (Whisenant et al. 1984), North American fescue (Grilz and Romo 1994), Kansas tallgrass prairie (Towne and Owensby 1984), Wisconsin tallgrass prairie (Howe 1995), and California valley grassland (Parsons and Stohlgren 1989).

California's valley grassland is an example of an annual dominated community in which fire is a natural and regular phenomenon (Parsons 1981). Although historic accounts of species composition are sparse, it is believed that native winter annuals once dominated this community in the relatively arid central and southern part of the state (Wester 1981; Keeley 1990). Today, however, these grasslands are dominated by a variety of introduced annual grasses primarily of Mediterranean origin (Heady 1977; Heady et al. 1992; Keeley 1990). Most of these alien annuals are tolerant of grazing and drought, and are highly competitive (Heady 1977; Heady et al. 1992; Keeley 1990). Furthermore, they produce large amounts of mulch that suppress the growth of native plants (Heady 1956; Bartolome 1979). Most of these alien grass species in California are susceptible to fire and lack any adaptations to frequent burning (Evans and Young 1970; Smith 1970; Menke 1989). Burning reduces the aboveground biomass of alien grasses, and promotes growth of native and alien forbs (Hervey 1949; Larson and Duncan 1982; Menke 1989). However, most of these post-fire changes are transitory: Two years after a fire, alien grasses regain dominance, mulch biomass returns to pre-burn levels, and native forbs revert to a state of rarity (Hervey 1949; Bentley and Fenner 1958; Parsons and Stohlgren 1989).

Several controlled burning strategies have emerged within recent years for the enhancement of native plants in grasslands. One strategy focuses on plant phenology patterns to maximize the effects of burning. When undesirable species are more vulnerable and desirable species are less susceptible to the negative effects of fire, a controlled burn may enhance native plants or reduce exotics. Such a burning strategy has been effective in enhancing the biomass of native species in California (Parsons and Stohlgren 1989) and under-represented "phenological guilds" elsewhere (Howe 1994, 1995). In

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California grasslands, carefully-timed burns have been moderately successful in the restoration of native perennial bunchgrass communities (Ahmed 1983; Keeley 1990; Menke 1992), and may be a beneficial strategy for the enhancement of native annual communities. For instance, during the late spring, alien grass seeds in California grasslands are still contained in the inflorescence and have undeveloped seed coats, making them extremely vulnerable to fire (McKell et al. 1962; Menke 1992). Likewise, in the winter, alien grasses are in the seedling stage when they are highly susceptible to disturbance. A fire during either the late-spring or winter should be detrimental to alien grass survivorship. Unlike alien grasses, native forbs maintain a persistent soil seed bank that is relatively protected from severe environmental stresses throughout the year (Young et al. 1981; Rice 1989a). Consequently, a carefully-timed burn in the late-spring or winter could be used to facilitate the concurrent reduction of alien grasses that are in a vulnerable stage of development and enhancement of native forbs that persist as seeds in the protected soil environment.

A second burning strategy for the enhancement of native diversity focuses on the relationship between fire season and fire intensity. By employing a controlled burn of relatively high intensity, resource managers can achieve elevated levels of alien species mortality. Such high-intensity fires have been successful in reducing seed survivorship of alien grasses, such as *Taeniatherum caput-medusal* (McKell et al. 1962). Native grassland species that are adapted to intense fires, however, would likely benefit from the effects of a high temperature burn. Such is the case with California grassland forbs, which occur in high densities following intense, warm-season fires (Hervey 1949; Larson and Duncan 1982; Parsons and Stohlgren 1989). Consequently, the application of a high intensity fire may be suitable for California annual grassland restoration. Unfortunately, our understanding of the relationship between fire season and fire intensity does not extend beyond the conventional wisdom that fires during the moist winter season are of low intensity and those during the dry summer season are of high intensity.

A third burning strategy for the enhancement of native plants focuses on the removal of mulch. This approach considers the amount of mulch to be the principal factor determining changes in the floristic composition in California grasslands (Heady 1977; Heady et al. 1992). Mulch refers to all dead aboveground herbage, both that lying on the soil surface and that remaining in the canopy (Heady 1956; Heady et al. 1992). Mulch acts as an insulating layer that promotes the establishment of alien grasses and suppresses the growth of native seedlings (Evans and Young 1970; Smith 1970). In the absence of mulch, grassland composition changes to one dominated by native and alien forbs (Heady 1956, 1965). Based on these observations, previous authors have assumed that burning and grazing cause similar changes in grassland composition (Heady 1977; Heady et al. 1992). Furthermore, a burn that is timed to occur when it has the greatest capacity to reduce mulch should be the most effective for the restoration of native forbs (although such a burn would also be expected to enhance alien forbs; Hervey 1949; Heady 1972, 1977; Heady et al. 1992). However, to date, no study has directly compared the effects of fire and mulch reduction on a California annual plant community. Consequently, it is not clear to what extent the direct effects of fire (e.g., high temperatures during burning) and the indirect effects of fire (e.g., higher soil moisture depletion and soil surface temperature fluctuations following mulch reduction; Evans and Young 1970) influence composition changes in California grasslands.

The purpose of this study was to directly compare the effects of fire and grazing, and evaluate the effectiveness of different burning regimes for simultaneously reducing alien plant cover and enhancing native plant cover and diversity in a California annual grassland. Three hypotheses, each addressing a specific burning strategy, were tested. These hypotheses state that the optimal burn treatment for the restoration of native plants is (1) burning when alien grass seeds or seedlings are most susceptible to disturbance (the phenology hypothesis), (2) burning when fire temperatures attain their greatest annual intensity (the intensity hypothesis), or (3) burning when fire has the greatest capacity to remove mulch (the mulch hypothesis). The specific burn season conforming to the intensity and mulch hypotheses were determined from fire temperature and mulch biomass data, respectively. The most effective burn seasons according to the phenology hypothesis were determined from phenology patterns of California annual plants. It is important to note that these hypotheses are not mutually exclusive, and that the optimal burn season may encompass the expected predictions of two or even all three hypotheses.

METHODS

Experimental site. The study site was located at the Carrizo Plain Natural Area in San Luis Obispo County, CA, a 81,000 ha preserve in the southwest corner of the San Joaquin Valley region. It is the largest remaining fragment of valley grassland in the state. The site was on a flat part of the plain at an elevation of 595 m. The soil is clayey and seasonally dry (from April–May to October–December) and derived from Miocene marine sandstones, siltstones, and shales of the surrounding Caliente and Temblor Ranges (Reid et al. 1993). Maximum temperatures average 9°C in January and 29°C in July. Precipitation, which occurs almost exclusively as winter rain, averages about 14.5 cm annually and varied during this study from 31.1 cm/year (1994–1995) to 14.8 cm/year (1995–1996; Buttonwillow, CA; National Oceanic and Atmospheric Administration 1996). Vegetation at the site was dominated by fast-growing winter alien annuals. 97.2% and 1.5% of the total annual vegetation cover was comprised of alien and native plants, respectively. Grass cover at the site was 90.6%, forb cover was 8.1%, and bare ground was 1.3%. The site was dominated by four alien grass species: *Bromus madritensis L., Hordeum murinum L., Avena barbata Link,* and *Avena fatua L.* (in order of abundance; nomenclature follows Hickman 1993). Other less common plant species include the alien species *Erodium cicutarium (L.) L. Hér, Bromus diandrus Roth, B. hordeaceous L., B. tectorum L., Lactuca serriola L.,* and the native species *Amsinckia tessellata A. Gray, Monolopia lanceolata Nutt.,* and *Lotus humistratus E. Greene.* Mulch, which is characteristic of grass-dominated late-successional California grasslands, constituted an additional 99.3% cover in the experimental plots. Burrowing rodents, such as *Thomomys bottae* (gophers) and *Dipodomys* spp. (Kangaroo rats) were absent from the study plots but present in adjacent areas. Like grasslands throughout the region, the site had a long history of cattle and sheep grazing and periodic dryland farming (i.e., site has been plowed; Cronise 1868; Burcham 1957; Preston 1981; Stromberg and Griffin 1996). During but not prior to the period of this study, livestock were excluded from the research site by a barbed-wire fence.

Experimental design. Thirty 6 × 6 m plots were arranged in a rectangular grid and surrounded by a barbed-wire fence. Each individual experimental plot was surrounded by a 2 m buffer zone that was mowed for the duration of this study (June 1995 to May 1996). Six replicate plots were randomly subjected to each of the following experimental treatments: (1) unmanipulated (control), (2) mulch reduction, (3) late-spring burn (17 June 1995), (4) fall burn (24 Sept. 1995), or (5) winter burn (9 Feb. 1996). The amount of time it took to burn each plot increased from late-spring (15–30 seconds) to fall (30–60 seconds) to winter (60–120 seconds). Fires were ignited by starting a backing fire followed by a flanking fire and finally a head fire. This fire ignition sequence was used to ensure fire safety rather than for any specific experimental reason. Wind conditions during each burn were <5 mph, and each fire produced flames that were estimated to be 0.5 to 1.5 m in height. Soil surface burn temperatures were measured by placing a temperature sensitive indicator profile (Omega Engineering Inc.) on the soil surface in the center of each plot. Fall-burned plots also contained a temperature indicator profile at the plot periphery in order to evaluate the variability in fire temperature within plots. Each temperature profile contained sixteen waxes with a range of melting points (ranging from 107°C to 427°C) that were pasted on a 20 × 20 cm ceramic tile. Mulch reduction plots were mowed with an Echo weedeater and the mulch canopy was removed with a hand rake and by hand on 30 September 1995. This treatment was done to simulate the effects of grazing on mulch biomass. Care was taken not to rake the soil surface and the bottom several centimeters of the mulch canopy was left in place in order to avoid removing seeds from the soil surface seed bank. In addition, the basal 6 cm of the mulch canopy was not removed in order to minimize disturbance to this seed bank.

Vegetation Sampling. Vegetation in the experimental plots was sampled once in April 1995 for pre-treatment data and once in April 1996 for post-treatment data. A single post-treatment sampling period appeared sufficient to capture the short-term effects of each treatment on above ground vegetation, since: (1) previous authors have shown the effects of fire and mulch reduction to occur primarily in the first post-burn or post-mulch reduction year in California grassland (Heady 1956; Parsons and Stohlgren 1989), and (2) our visual survey of the treatment plots in the second post-treatment growing season (using a Daubenmire [1959] cover class system and pooling spieces according to the following groups: alien grasses, aliens forbs, native forbs), revealed that grasses had regained dominance and native forbs had become rare (<5% cover). The point-intercept method was used for both censuses, and estimates of percent cover for each plant species and species diversity of native plants were determined (Barbour et al. 1987; Schiffman 1994; Sawyer and Keeler-Wolf 1995). For the pre-treatment census, three 6 m long parallel transects were randomly positioned along an east-west axis within each plot. Pins were placed at 20 cm intervals along each transect (Schiffman 1994) and the plant species (or bare ground) encountered at each pin point were recorded (for a total of 90 sample points per plot). *Avena barbata* and *A. fatua* were lumped because of their delayed phenology and the difficulty in distinguishing them from one another given only vegetative characters. In the post-treatment census, eleven 6 m parallel transects were systematically placed along an east-west axis within each plot. Pins were placed at 50 cm intervals along this transect and data were recorded in the same manner as in the pre-treatment census (121 total sample points per plot). Analyses of variance of the pre-treatment data revealed that there were no significant differences among plots in terms of the percent cover of any plant species encountered ($F_{1,4} > 7.71$, $P > 0.05$ for each species), with the exception of *Amsinckia tessellata* ($F_{1,4} = 14.26$, $P = 0.002$), which was rarely encountered in either census. In order to estimate the relative biomass of mulch among treatments, the height of the mulch canopy was sampled in April 1996 in ten randomly selected locations within each plot.

Seed bank and seed viability tests. Ten soil samples were collected for seed bank assessment from randomly selected points within 5 control plots (collected on 30 September 1995), 6 late-spring burn plots (collected on 24 September 1995), and 6 fall burn plots (collected on 9 December 1995). Burned plot seed samples were collected following burn treatments, and all seed samples were collected prior to winter rainfall. Cores of dry soil (6 cm in diameter and 5 cm in depth) were extracted using a cylindrical bulb planter and transported to the laboratory where they were stored in plastic bags for 3–12 weeks at room temperature. The soil samples were then thoroughly mixed with vermiculite (1:1 soil-to-vermiculite ratio), placed in 5 cm diameter plastic pots in a greenhouse, and watered for a period of 4–6 weeks. All germinating forb seedlings were identified to species when possible. All germinating grasses were lumped into a single grass category.

Soil surface seed samples were collected from locations adjacent to each soil coring point within the control, late-spring, and fall burned plots. These samples were used to estimate seed viability of the soil surface seed bank following each treatment; samples were not used to estimate seed rain. Seed samples were gathered by hand at the same time that soil seed bank samples were collected, placed in plastic bags, and stored in the laboratory at room temperature for a period of 3–12 weeks. Seeds of *Bromus madritensis, Hordeum murinum, Avena barbata* and *Avena fatua.* (the four most abundant plant taxa in the Spring of 1995) were separated from the rest of the mulch material and placed on moist filter paper in petri dishes. *Avena* spp. were combined since identification to species was not possible. Each petri dish contained 10–20 seeds, and all dishes were kept moist for the duration of the seed viability study. The total number of tested seeds varied among the three grass species due to variability in sample seed densities. *Bromus madritensis* seed viability trials consisted of twenty seeds per plot, times six replicates. *Hordeum murinum* seed viability trials consisted of 100 seeds per plot, times six replicates. *Avena* seed viability trials consisted of 20 seeds per plot times three to five replicate plots. The petri dishes containing these seeds were placed in a growth chamber set at a constant 20°C and a 12-hour light/dark cycle. In addition, since *Avena* spp. are known to exhibit extended seed dormancy (Richardson 1979), petri dishes containing *Avena* seeds were treated with 5 ml of 10^{-3} M gibberellic acid (GA_3) solution to ensure radicle emergence of viable seeds (Richardson 1979). Seeds of all three taxa were scored as viable if they exhibited radicle emergence within a 20-day period.

Seed samples of the native forbs *Phacelia ciliata, Monolopia lanceolata,* and *Amsinckia tessellata* were also collected from experimental plots (June 1996), placed in plastic bags, and stored in the laboratory at room temperature for five months. One-hundred seeds of each native species collected were subjected either to an open flame from an alcohol lamp for approximately 0.5 seconds (flame treatment) or were unmanipulated (control treatment). Seeds were then put in petri dishes (10 seeds per dish) between two moist pieces of filter paper, placed in a growth chamber set at 20°C and a 12-hour light/dark cycle, and observed for radicle emergence for a 20 day period.

Data analysis. Cover percentages were calculated for all major species (frequency of each species in 121 sampling points) encountered in the 1996 vegetation census. In addition, percent cover data for grasses versus forbs and native versus alien plants were determined by pooling species belonging to each of these categories. Species diversity estimates were calculated using a modified Shannon index of diversity ($H' = -\Sigma P_i \ln(P_i + 0.0001)$; Magurran 1988). This index yielded nearly identical results as the standard Shannon index and was necessary to compensate for zero values of diversity encountered in samples lacking species in the native or alien plant guilds. Soil surface temperatures during burning were estimated using the median melting point temperature between the highest melted and lowest unmelted indicator values from each temperature profile. Percent cover, species diversity, litter height, seed viability, seed bank, and soil surface burn temperature data were analyzed with Model I one-way ANOVA. All multiple pairwise comparisons were analyzed using a Tukey's HSD test with a Bonferroni adjusted α (Rice 1989b). ANOVA assumptions of randomness, independence, and normality were generally shown to be met. The ANOVA assumption of equality of variances was assessed using the F_{max} test for homoscedasticity. In cases where this last assumption was not met, the nonparametric analog of ANOVA, the Kruskal-Wallis test, was used to compare experimental treatments. In the native seed flame-treatment experiments, a χ^2 test was used to test if seed germination was significantly enhanced by fire (for each species, samples were pooled among pretreatment plots). Differences were considered to be significant at $\alpha = 0.05$. All statistical tests were conducted using SYSTAT version 5.2.

RESULTS

Fire intensities. Fire intensities differed significantly among the three burn seasons ($F_{1,4} = 69.97$, $P < 0.001$) (Fig. 1). In particular, the winter burn was significantly lower in intensity than the late-spring or fall burns. Fall burning yielded the highest soil surface burn temperatures, but these temperatures were not significantly different than late-spring burned plots. In addition, coefficients of variation for soil surface burn temperatures within a burned plot and among burned plots were similar (CV = 9.9 and 12.2, respectively).

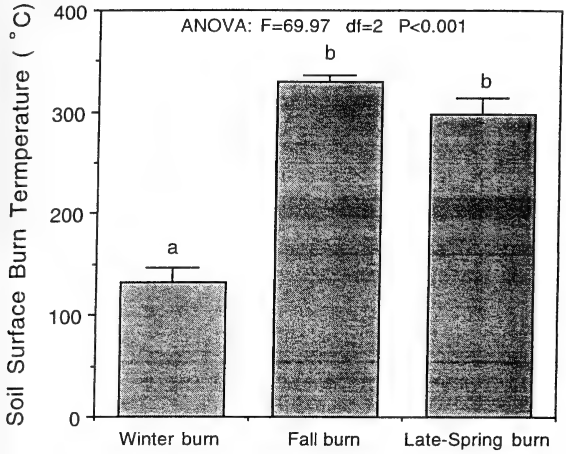


FIG. 1. Mean fire temperature (+SE) for winter, fall, and late-spring burns. Different lowercase letters indicate significant differences between treatments in this and following figures (n = 6 per treatment).

General patterns of post-fire vegetation cover. The percent cover of alien annual plants was significantly greater in the control plots than in the burned plots (Fig. 2a). Mulch reduction plots were intermediate with respect to alien plant cover. Among the three burn treatments, alien plant cover was highest in the winter burned plots and lowest in the late-spring and fall burned plots. In contrast to the alien cover data, the percent cover and diversity of native plants were significantly lower in the control, mulch reduction, and winter burn treatments ($H_{1,4}$ = 21.47, P < 0.001 for native cover; $H_{1,4}$ = 23.05, P < 0.001 for native diversity). Fall and late-spring burn treatments had the greatest cover and diversity of native plants, one order of magnitude greater than the control, mulch reduction, or winter burned plots (Fig. 2b and 3, for cover and diversity, respectively).

Both the grass and forb guilds responded strongly to the fire and mulch reduction treatments. Alien grass cover (Fig. 4a) was similar to the cover of all alien plants (Fig. 2a) in treatment plots. It was highest in the control plots, intermediate in the mulch reduction plots, and lowest in the burned plots. Moreover, among burn treatments, grass cover was lowest in the late-spring burn treatment, intermediate in the fall burn treatment, and greatest in the winter burned plots. Interestingly, patterns of forb cover (Fig. 4b) were not similar to the patterns of native plant cover (Fig. 2b) in these experimental plots. Instead, the cover of forbs was greatest in late-spring and control plots, and lowest in the mulch reduction, winter burned, and fall burned plots.

Species cover. The native annual forbs *Monolopia lanceolata* and *Phacelia ciliata* had significantly higher cover following the fall and late-spring burn treatments ($H_{1,4}$ = 21.36; P < 0.001 for *M.*

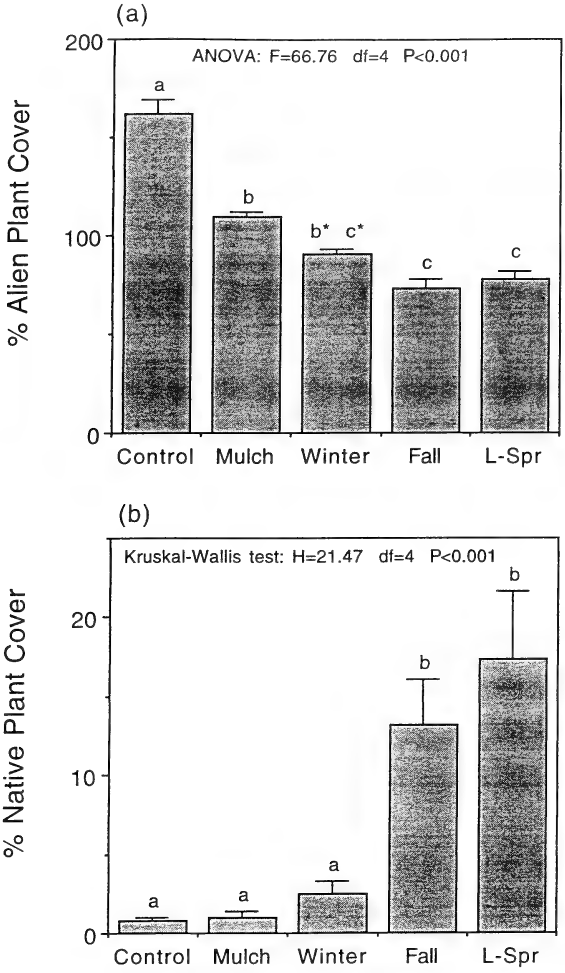


FIG. 2. Mean % alien (a) and native (b) plant cover (+SE) for the five treatments. Note that y-axis scales in these paired figures and the following paired figures are different.

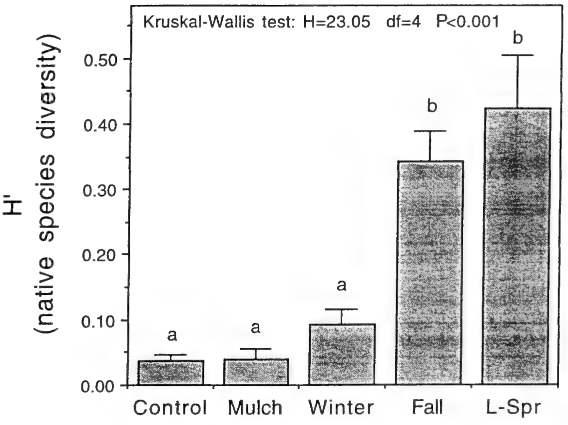


FIG. 3. Mean native plant species diversity (+SE) as indicated by a modified Shannon index of diversity (H′).

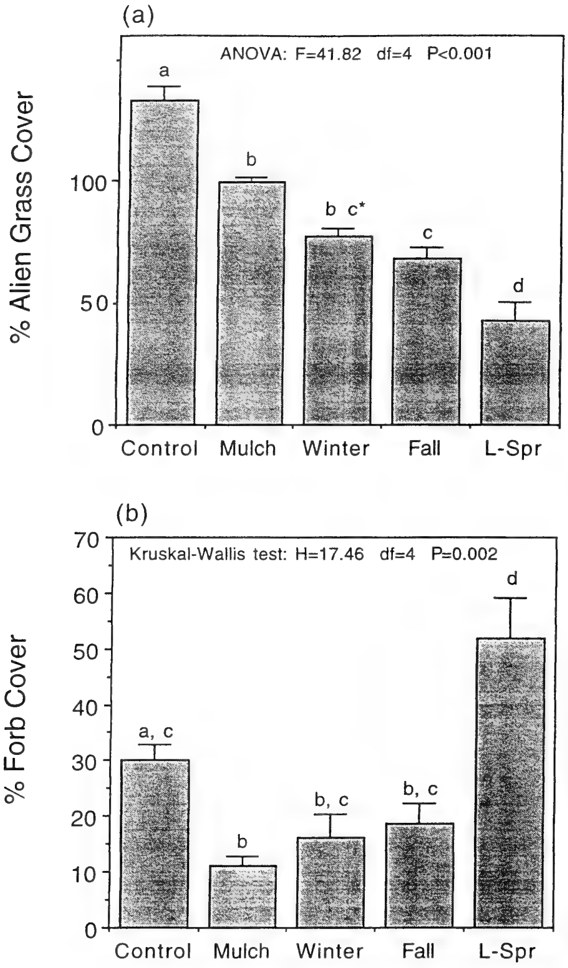
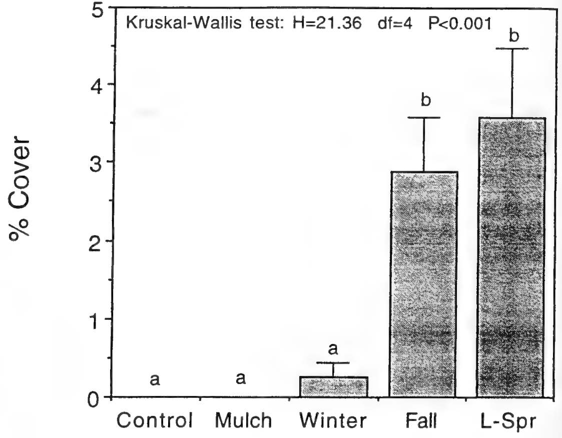


FIG. 4. Mean % alien grass (a) and forb (b) cover (+SE) for the five treatments.

(a) *Monolopia lanceolata*



(b) *Phacelia ciliata*

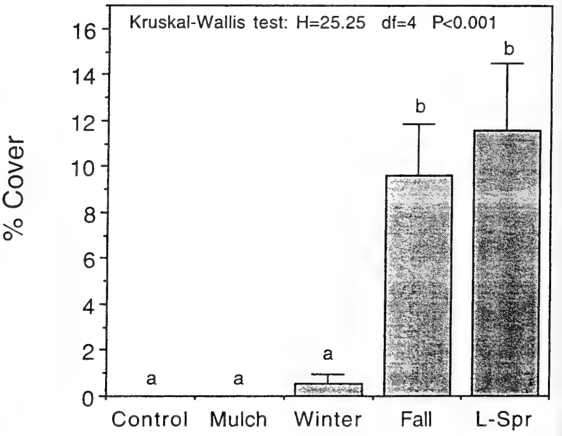


FIG. 5. Mean % cover (+SE) of the native forbs *Monolopia lanceolata* (a) and *Phacelia ciliata* (b).

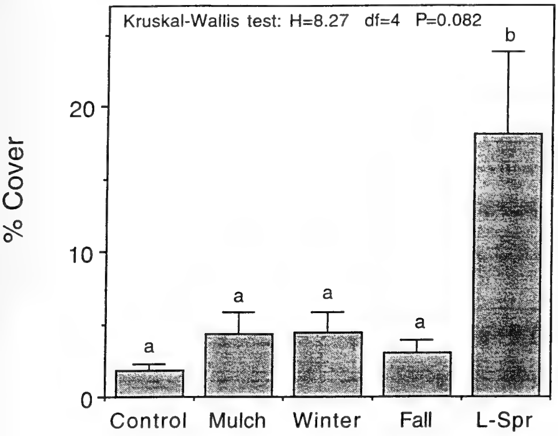
lanceolata; $H_{1,4}$ = 25.25, P < 0.001 for *P. ciliata*) (Fig. 5). These species were completely absent from the control and mulch reduction treatment plots and had <1% cover in the winter burned plots. Most of the native cover found in fall and late-spring burned plots (95.5% and 88.8%, respectively; Fig. 2b) was due to the combined presence of these two native forbs. Other native forbs, including *Amsinckia tessellata* and *Lotus humistratus,* had very little cover in any of the treatments. No significant treatment effect was detected for either of these uncommon native species ($H_{1,4}$ = 2.20, P = 0.699 for *A. tessellata*; $H_{1,4}$ = 5.78, P = 0.216 for *L. humistratus*).

Patterns of abundance of individual alien forb species were different from the trends detected for the native forb species. *Erodium cicutarium,* an alien grassland forb, had significantly greater cover in late-spring burned plots (Fig. 6a). All other treatments yielded relatively low amounts of cover for this alien forb. In contrast, the alien forb *Lactuca serriola* had the greatest cover in control plots, followed by the late-spring burned plots (Fig. 6b). Mulch reduction, winter burned, and fall burned plots contained relatively low cover of *L. serriola.*

Four abundant alien grass species, *Bromus madritensis, Hordeum murinum, Avena barbata,* and *Avena fatua,* collectively accounted for most of the grass cover in all treatment plots (Fig. 4a). These species tended to have their greatest cover in unburned plots, with the exception of the *Avena* spp. The cover of *B. madritensis* was lowest following winter, fall, and late-spring burn treatments (Fig. 7a). Late-spring and fall burning also significantly reduced the cover of *H. murinum* (Fig. 7b). Insignificant differences were found between experimental treatments for *Avena* spp. ($F_{1,4}$ = 2.57, P = 0.062). Similarly, Bonferroni analyses revealed no significant differences (P > 0.05) between all pairwise treatment comparisons of *Avena* spp. cover. Mulch reduction and late-spring burn treatments had the lowest cover of *Avena* spp. (Fig. 7c).

Patterns of post-fire mulch biomass. Burning and mulch reduction both significantly reduced the

(a) *Erodium cicutarium*



(b) *Lactuca serriola*

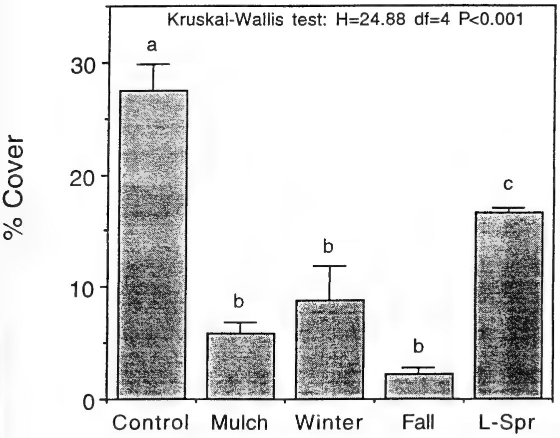
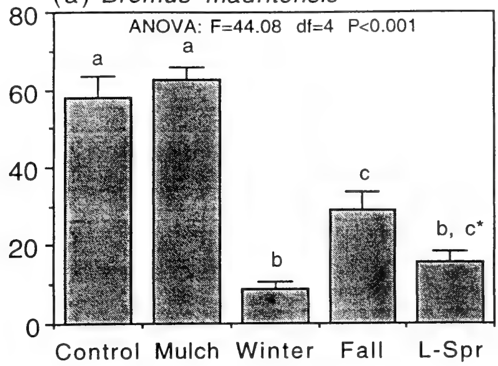


FIG. 6. Mean % cover (+SE) of the alien forbs *Erodium cicutarium* (a) and *Lactuca serriola* (b).

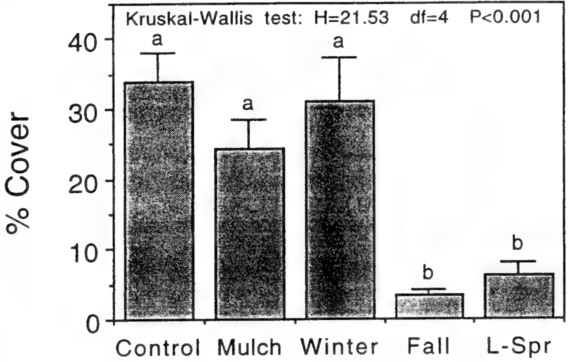
height of the mulch canopy ($H_{1,4}$ = 23.09, P < 0.001; Fig. 8a). As would be expected, the mulch canopy was highest in the control plots. It was significantly shorter in the winter burned and mulch reduction plots, and virtually non-existent in the fall and late-spring burned plots. Bare ground was substantially greater in fall and late-spring burned plots and lower in control, mulch reduction, and winter burned plots ($H_{1,4}$ = 23.14, P < 0.001; Fig. 8b).

Seed viability and seed bank estimates. Seed bank data complemented the vegetation data. The densities of germinating forb seeds were significantly greater in plots burned in the late-spring than those burned in the fall or left unburned (control; Fig. 9a). This high density of forb seeds in the late-spring can be attributed to the high density of *Erodium cicutarium* seeds that remained viable after the late-spring burn treatment (Fig. 9a). Germinating grass seed bank densities, on the other hand, were greatest in the control plots and lowest in the fall and late-spring burned plots (Fig. 9b).

(a) *Bromus madritensis*



(b) *Hordeum murinum*



(c) *Avena spp.*

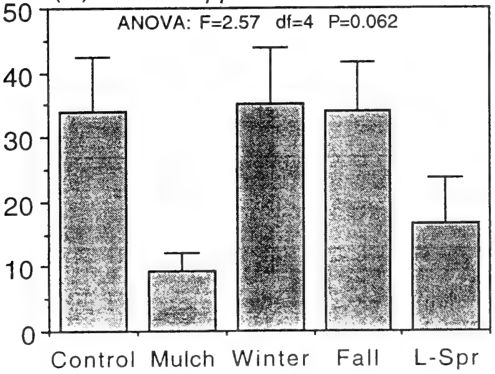


FIG. 7. Mean % cover (+SE) of the alien grasses *Bromus madritensis* (a), *Hordeum murinum* (b), and *Avena* spp. (c). For *Avena* spp., there are no significant pairwise differences between treatments.

Seed viabilities for the alien grass taxa (*B. madritensis, H. murinum,* and *Avena* spp.) were highest in control plots and lowest in late-spring burned plots (Fig. 10). Although, the differences in viability between late-spring and fall burn treatments were significant for *Avena* spp. seeds, these differences were not significant for the seeds of the other two alien grass species.

In the native seed viability tests, 32% of flame-treated *Phacelia ciliata* seeds and 1% of control seeds demonstrated radicle emergence, indicating

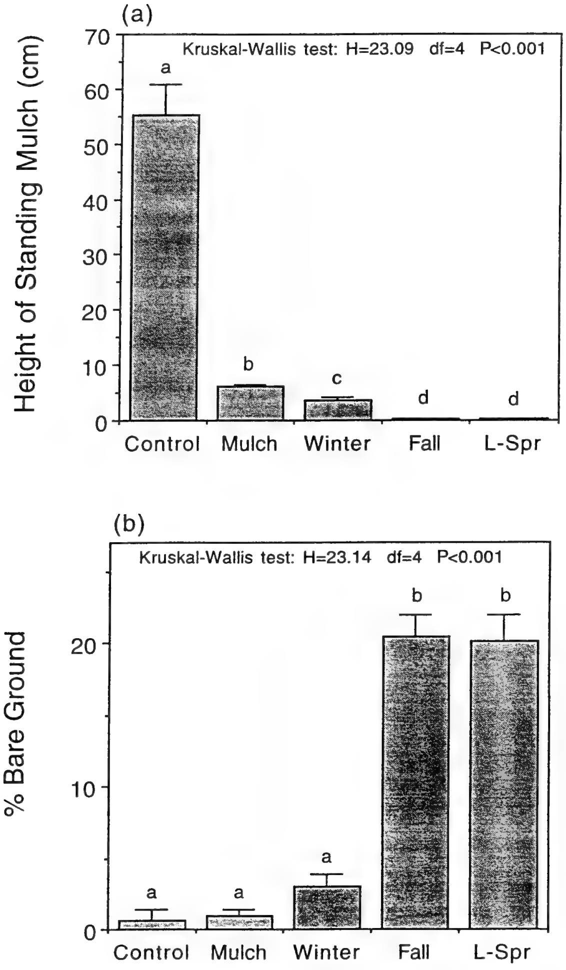


FIG. 8. Mean (+SE) height of the mulch canopy (a) and % bare ground (b) for the five treatments.

that *P. ciliata* seed germination was significantly enhanced by fire ($\chi^2 = 34.87$, df = 1, $P < 0.001$). No flame-treated or control seeds of *Monolopia lanceolata* and *Amsinckia tessellata* germinated.

DISCUSSION

Burn season restoration strategies. Fire season has a significant influence upon the regeneration patterns of a variety of terrestrial plant communities (Martin 1983; Towne and Owensby 1984; Whisenant et al. 1984; Menke 1992; Glitzenstein et al. 1995; Howe 1995). In this study, fire season influenced short-term vegetation cover and diversity, seed viability, and fire intensity in a California annual grassland. Burn treatments also varied in their effect on native annual vegetation: warm season burns (fall and late-spring) were far more effective at increasing native species cover and diversity and at reducing the cover of alien species than cool season burns (winter). In particular, late-spring burning was most effective at enhancing native cover and

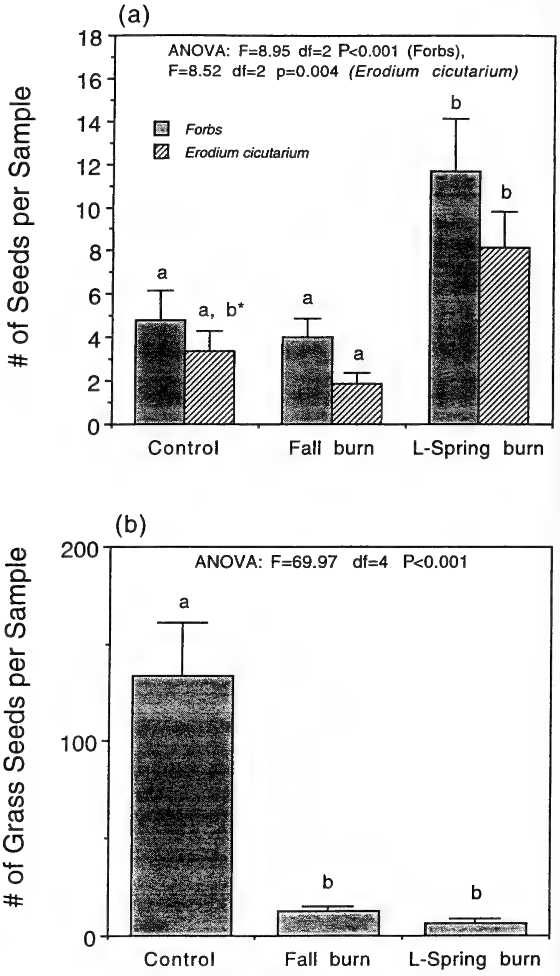


FIG. 9. Mean seed bank densities (+SE) of forbs and *Erodium cicutarium* (a) and alien grasses (b) for control, fall burn, and late-spring burn treatments.

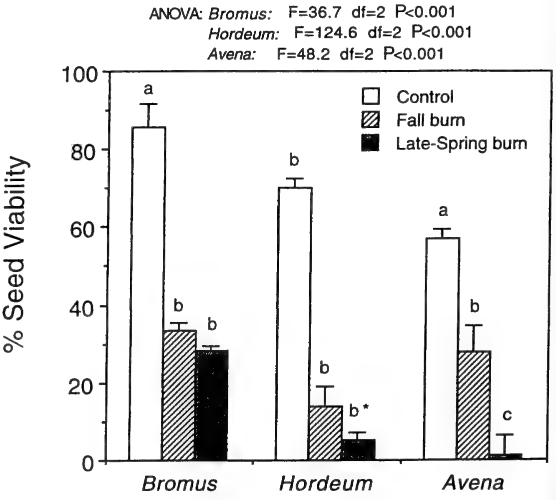


FIG. 10. Mean alien grass seed viability (+SE) for control, fall burn, and late-spring burn treatments.

reducing alien grass cover and seed viability (although it did increase the cover of *E. cicutarium*). These results indicate that fire season is an important factor for the restoration of native annuals in California. Yet, the underlying mechanism of the success of warm season burning (particularly late-spring burning) is unclear. Consequently, it is not known whether the success of warm season burning is a result of fire season and plant phenology patterns (phenology hypothesis), a fire season-intensity relationship (intensity hypothesis), or increased bare ground (mulch hypothesis). Each of these hypotheses are evaluated below.

The phenology hypothesis predicts that the most effective burn season for the restoration of native plants occurs when alien plants are most vulnerable to fire. During the winter in California grasslands, alien plants are in a vulnerable seedling stage (Chiariello 1989; Heady et al. 1992). Unlike alien grasses which lack inter-annual seed dormancy, native plants maintain a persistent seed bank in the protected soil environment (Young et al. 1981; Rice 1989a). Given these phenology patterns (particularly the greater vulnerability of alien species) it was predicted that the winter season would be an ideal time in which to burn grassland vegetation; this is assuming that substantial seed germination of alien grasses has already occurred and that fuel loads are of sufficient biomass to facilitate a fire. Native and alien plant cover data, however, did not support this prediction: winter burning was only partially effective at reducing alien cover. Moreover, it failed to increase native cover and diversity at least during the winter immediately following burning. There are three possible explanations for these results. The failure of winter burning to immediately restore native vegetation may be due to a delay in the response of native species to fire. For instance, in a previous experiment, native species such as *Monolopia lanceolata* did not show increased cover following a winter burn until the second post-fire year (P. M. Schiffman unpublished). However, based on visual surveys of all of the experimental plots (see Methods), we found no delayed effect of fire in the second year of this study. Alternatively, winter fires may not burn hot enough to induce native seed germination and cause sufficient alien plant mortality. Lastly, fire may kill germinating native seedlings along with alien seedlings, since the phenologies of these two groups are similar. Additional study of the effects of fire season will be needed to determine the plausibility these latter two possibilities.

The phenology hypothesis predicts that late-spring is also an optimal burn season for the restoration of native vegetation. In the late-spring, alien grass seeds have a high moisture content and incompletely developed seed coats and, hence, are more vulnerable to fire than later in the season when their seed coats are dry and hardened (McKell et al. 1962). Thus, based purely on plant phenology patterns, a fire in the late-spring would be expected to have a greater negative impact upon alien grass seeds than a fire in the fall. This prediction was supported by the data: alien grass cover and seed viability were lower in late-spring burned plots. In particular, the cover and seed viability of *Bromus madritensis* and *Avena* spp. decreased significantly after the late-spring burn. These results contrasted with the previous findings of Parsons and Stohlgren (1989) who found that fall burning was more effective at reducing *Avena* and *Bromus* biomass than late-spring burning. However, this incongruence may have been due to differences in the seasonal moisture content of grass seeds between the two studies. Parsons and Stohlgren (1989) observed that alien grass seeds had a higher moisture content and were more vulnerable to fire in the fall rather than in the late-spring. If we assume that the levels of seed moisture in this study were higher in the late-spring, then this result would explain the discrepancy between the results of Parsons and Stohlgren (1989) and this study. Moreover, it would lend support to both the phenology hypothesis and McKell et al.'s (1962) seed phenology post-fire succession hypothesis.

Evidence for the intensity hypothesis was conflicting. High temperature, warm-season fires generated the greatest native species cover and diversity and lowest alien species cover. This positive association between fire intensity and native cover and negative association between fire intensity and alien cover was consistent with the intensity hypothesis. However, given that burn temperatures were generally higher or the same on fall burned plots, fire intensity alone does not explain why late-spring burning was more effective than fall burning at reducing alien grass cover and seed viability. This finding may be the result of a threshold response of alien grass seeds to elevated burn temperatures. That is, as fire intensity increases beyond some critical temperature range, it becomes an insignificant factor influencing alien grass seed mortality. For instance, seed viability in dry seeds of the California alien grasses, *Bromus hordeaceus L.* and *Taeniatherum caput-medusae,* drops dramatically at 180 to 200°C, but above and below this critical temperature range, seed viability decreases at an extremely low rate (McKell et al. 1962). The same is true of moist seeds of these two species but at a range closer to 160 to 180°C (McKell et al. 1962).

Evidence for the mulch hypothesis was also conflicting. Heady (1956) and Heady et al.'s (1992) mulch hypothesis makes two predictions: (1) the complete removal of mulch (with only bare ground remaining) should mimic the effects of fire, and (2) there is a negative linear relationship between mulch biomass and the proportion of native and exotic forb species present. The results of this study lend some support the first prediction but do not support the second. Even though 89% of the mulch

TABLE 1. PREDICTIONS AND EVALUATION OF THE THREE BURN SEASON RESTORATION HYPOTHESES. The season to the left of the greater-than sign (>) indicates the more effective burn season for native species restoration. The equality sign (≈) is used to signify that both treatments are similar in effectiveness. Mulch reduction refers to a significant drop in the height of the mulch canopy, whereas mulch removal refers to the removal of all mulch biomass (both in the canopy and on the soil surface).

Hypothesis	Predicted optimal burn season or result	Prediction supported?
1. Phenology hypothesis	a) winter b) late-spring	a) no b) yes
2. Intensity hypothesis	fall > late-spring > winter	yes (fall & late-spring > winter) no (late-spring > fall)
3. Mulch hypothesis	a) mulch reduction ≈ fall burn b) mulch removal ≈ fall burn	a) no b) prediction not tested

canopy was removed in the mulch reduction treatment, this treatment did not enhance native cover or diversity and was significantly less effective at reducing alien cover than the fall and late-spring burn treatments. These results may have been due to the fact that compositional changes, particularly the increase in native and alien forbs, do not occur until all the mulch canopy is removed and the ground is exposed. Thus, the greater cover of native forbs in the burned plots may be a result of the increased amount of bare ground following burning and not changes in total mulch biomass. In particular, the positive association between bare ground and native cover that was observed in this study supports this conclusion. Furthermore, bare ground has been associated with specific environmental cues that enhance germination or seedling survivorship in several annual forb species (Rice 1989a). For instance, Rice (1985) found that *Erodium botrys* (Cav.) Bertol and *Erodium brachycarpum* (Godron) Thell. had significantly higher germination on bare ground than under litter. Similarly, in the absence of dead grass blades of *Poa annua* L., emergence and survivorship of *Capsella bursa-pastoris* (L.) Medikus and *Senecio vulgaris* L. seedlings increase significantly (Bergelson 1990). Therefore, the amount of bare ground, rather than the biomass of mulch, was the more likely factor causing changes in native species cover and diversity.

Of the three burn treatments evaluated in this study, the late-spring burn prediction of the phenology hypothesis received the most support from the experimental results (Table 1). The evidence also supported the prediction that warm-season burns were more effective than cool-season burns at restoring native vegetation (intensity hypothesis). The mulch hypothesis was partially rejected based on differences in the effectiveness of mulch reduction and fire treatments for enhancing native cover and reducing alien cover.

Responses of species and guilds. Individual species responded differently to fire and mulch reduction treatments. The native forbs *Phacelia ciliata* and *Monolopia lanceolata* were abundant only after a warm-season fire. Species such as these that respond positively to fire are often classified as "fire annuals" (Keeley et al. 1985). However, only *P. ciliata* appeared to be dependent on fire for significant germination: the seeds of *P. ciliata* showed a significant increase in radicle emergence following flame/heat/smoke treatment, a trait found in other species of the family Hydrophyllaceae (Keeley and Fotheringham 1998) and genus *Phacelia* (Keeley and Keeley 1982). The alien forb *Erodium cicutarium* was classified as an "opportunistic annual" (Keeley et al. 1985). Opportunistic annuals are abundant after fire but also occur in higher densities in areas where bare ground is common (i.e. canopy gaps). Moreover, unlike *P. ciliata* and *M. lanceolata, E. cicutarium* was common only on late-spring burn plots. The germination of *E. cicutarium* seeds was also greatest for seed bank samples collected from late-spring burned plots. Parsons and Stohlgren (1989) noted a similar increase in *Erodium botrys* density following late-spring burning, but not fall burning. Similarly, York (1997) found a decline in *Erodium brachycarpum* following a late September fire. Such a pattern may be the result of enhanced germination following exposure to the extreme temperature fluctuations of bare ground during the summer, a seed characteristic found in several species of *Erodium* (Rice 1985). *Erodium* seeds probably did not experience these wide fluctuations on fall burn plots since these plots were insulated with mulch throughout the summer. By the time of the fall burn, cooler, more moderate temperatures of the fall season predominated, and the conditions necessary for *Erodium* seed germination were lacking.

Species were also classified as mulch-dependent or fire-intolerant. The only mulch-dependent species was *Lactuca serriola. Lactuca serriola* cover was highest on control plots where mulch biomass was an order of magnitude or two greater than any of the treatment plots. In addition, *Bromus madritensis* and *Hordeum murinum* were considered fire-intolerant species. *Bromus madritensis* cover was significantly reduced in all burned plots, and *H. murinum* cover decreased significantly in warm-season burned plots. Plants that exhibited none of the above patterns included *Avena* spp. and two native herbs that were uncommon in this study (*Lotus humistratus* and *Amsinckia tessellata*).

Plant guilds also varied in their response to fire and mulch reduction. Grasses were negatively affected by the removal of mulch but most significantly reduced in burned plots. Forbs, however, had greater cover in control and late-spring burned plots and lower cover in fall and winter burn plots. These post-fire patterns in forb cover contrasted with the results of Hervey (1949) and Parsons and Stohlgren (1989), who found forb cover to be consistently greater in burned plots, regardless of the season of burning. This inconsistency in forb cover can be attributed to the abundance of the alien forb, *Lactuca serriola,* in the control plots of this study. *Lactuca serriola* is common to areas of high mulch biomass in central California grasslands (M. Meyer, personal observation). However, this species was absent from the study plots of Hervey (1949) and Parsons and Stohlgren (1989). More importantly, the observation of decreased *L. serriola* cover following a fire demonstrated that not all species within the forb guild respond similarly to fire.

Implications for grassland management. The effects of fire on grassland composition have long been considered to be consistent with the effects of mulch reduction (Heady 1956, 1972; Heady et al. 1992). As a result, the influence of fire and livestock grazing on grassland vegetation have also been viewed as equivalent, since both methods facilitate a reduction in mulch biomass (Hervey 1949; Heady 1972). It is surprising, however, that virtually no studies directly comparing the effects of fire and mulch reduction or fire and grazing on California grassland composition have ever been conducted. Nevertheless, the direct comparison of burned and mulch reduction plots in this study strongly suggest that fire and grazing do not facilitate equivalent changes in community composition, particularly with respect to changes in native cover and diversity. This result is consistent with Stromberg and Griffin (1996) who found no increase in native species cover or diversity in grasslands recently grazed by cattle. The dissimilarity between burned and mulch reduction plots in this present study may have been the result of differences in the amount of bare ground, since warm-season burned plots had significantly more post-treatment bare ground than mulch reduction plots. Exposed bare ground following fire can cause changes in soil moisture and soil surface albedo, relative humidity, and temperature (Evans and Young 1970). Alternatively, enhanced native cover and diversity may be due to direct effects of fire. While neither of these two alternatives can be rejected with the results of this study, the latter possibility cannot be discounted for two reasons. First, alien grass seed viability was significantly reduced following fire (a result that cannot be attributed to mulch reduction since the fall-burned seed samples were covered by a layer of mulch until they were burned). Second, radicle emergence of *Phacelia ciliata,* a species endemic to California grasslands, increased significantly following flame treatment. These results not only indicate that the direct effects of fire do have a very significant impact upon the germination and survivorship of California grassland species, but also infer that fire may have been historically important within this plant community. These results indicate that the direct effects of fire do have a significant impact upon the germination and survivorship of California grassland species. Consequently, this evidence suggests that fire is a more effective method than grazing for native species restoration.

Successful fire management in California grasslands will also require an understanding of the variable nature of plant phenology patterns within these communities. High variability in the annual rainfall in California grasslands generates high variability in the phenology patterns of grassland plants. For instance, in a dry early-rainfall year, grassland plants set seed much earlier in the season (e.g., April) than in a year of abundant, late rainfall (seeds set in June). This change in the timing of seed set with rainfall should, in turn, influence the effectiveness of a particular fire season to kill alien grass seeds and increase native plant cover. Consequently, the success of the mid-June burn in this study should not be considered to be the only date for the restoration of native biological diversity to a California annual grassland. Instead, a successful burn should be timed just prior to when alien grasses set seed, whether this occurs later or earlier in the spring season.

Fire and grazing are the primary tools for grassland management. Yet, our understanding of the efficacy of each of these strategies to restore native vegetation still remains largely unexplored. California grassland restoration and management, in particular, have long rested upon the conclusions of only a few experiments and studies that have focused almost entirely on the effects of mulch reduction (e.g., Heady 1956; Heady et al. 1965). Moreover, virtually all previous studies of California grassland vegetation have focused on the restoration of a single perennial bunchgrass species, *Nassella pulchra* (A. Hitchc.) Barkworth (e.g., Ahmed 1983; Fossom 1990; Menke 1992; Dyer and Rice 1997). This study provides a new perspective on the use of fire and grazing in California grassland management and emphasizes the influence of these management strategies on the diverse annual component of grassland communities. The conflicting results of this study with previous ones underscores the need for more comparative studies of fire, grazing, and other management practices used to restore native annual vegetation to California grasslands.

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FLORA OF A VERNAL POOL COMPLEX IN THE MAYACMAS MOUNTAINS OF SOUTHEASTERN MENDOCINO COUNTY, CALIFORNIA

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ABSTRACT

Vernal pools in the Mayacmas Mountains of southeastern Mendocino County, CA typically occupy topographic depressions related to landslide dams and fissures. A group of pools within a 1290 ha study area range in size from 180 to 3069 m^2, and are located at elevations between 329 and 902 m on slopes of oak woodland and chaparral. *Eryngium aristulatum* Jepson var. *aristulatum* and *Isoetes howellii* Engelm. codominate shallow, wide-margined pools and are associated with vernal pool specialist taxa such as *Gratiola, Navarretia, Plagiobothrys,* and *Pogogyne.* Deep, narrow-margined pools are characterized by cosmopolitan wetland taxa such as *Callitriche, Carex, Eleocharis, Juncus,* and *Ranunculus.* Plant surveys conducted in 1996 and 1999 indicate no significant change in species abundance or composition between the two years.

The characteristic flora and fauna of California's vernal pools and their distribution is well documented (Jain 1976; Holland and Jain 1987; Zedler 1987; Keeler-Wolf et al. 1995; King et al. 1996; Bauder and McMillan 1998; Holland 1998). Of the16 vernal pool regions in the state described by Keeler-Wolf et al. (1995), the Mendocino Region, which lies entirely in Mendocino County, is one of the least known. The purpose of this study was to provide a description of the flora of a vernal pool complex in the arid, mountainous portion of southeastern Mendocino County based on observations from 2 years. These interior cismontane vernal pools occur on relatively unstable soils that are derived from marine sedimentary rocks. A number of floristic studies have been completed in the area and the occurrence of vernal pools has been mentioned (Neilson and McQuaid 1981; Murphy and Heady 1983; De Nevers 1985; Smith and Wheeler 1991, 1992; Baad 1998), but our knowledge of vernal pool floristics remains poorly understood.

Study area and methods. The 1290 ha study area is located in the interior north coast ranges of southeastern Mendocino County. Lying just east of the Russian River and 6 km northeast of U.S. Hwy 101 near Hopland, CA, the area includes portions of the University of California, Hopland Research and Extension Center (HREC) and adjacent public and private lands (Fig. 1). The area consists of moderately steep, predominately southwest-facing slopes in the Mayacmas Mountains, with elevations ranging from 183 to 914 m. Many high gradient ephemeral creeks bisect this terrain creating a series of parallel ridges and deep gullies. Lying approximately 65 km inland from the Pacific Ocean, the study area experiences a typical Mediterranean climate of hot-dry summers and cool-wet winters. Rainfall for the winters of 1995–1996 and 1998–1999 totaled 1074 mm and 880 mm respectively; the 35-year average is 947 mm (Table 1).

The 12 vernal pools in this study range in elevation from 329 m to 902 m and are situated on benches originating from old landslides and soil slips. The soils are predominately fractured sandstones and shales (Sutherlin Series) or glaucophane schist and related metamorphic rocks (Yorkville Series) of the Franciscan Formation (Gowans 1958), which are especially prone to landslipping. The pool basins are underlain with a moderately compact clay hardpan. Mixed oak woodland and savan-

TABLE 1. MONTHLY RAINFALL (mm) FOR WINTERS OF 1995–1996 AND 1998–1999 AT THE UNIVERSITY OF CALIFORNIA HOPLAND RESEARCH AND EXTENSION CENTER, MENDOCINO COUNTY, CA. Elevation = 244 m. 35 year average = 947 mm.

Year	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Tot
1995–1996					5	350	214	244	88	88	64	21	1074
1997–1998		22	17	41	215	92	325	502	150	71	111		1546
1998–1999				24	184	74	101	287	149	57	4		880

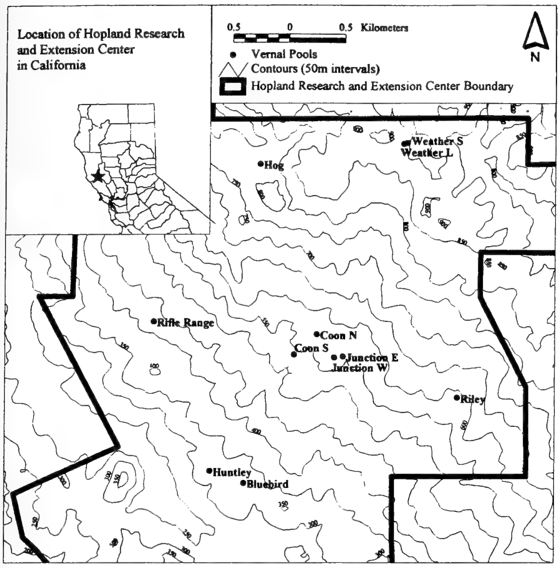

FIG. 1. Location of vernal pools at the Hopland Research and Extension Center, Mendocino County, CA. Twining pool is located 5 km northwest of Hog pool. Township 13 North, Range 11 West.

na dominate the lower elevations, whereas chaparral and patches of closed cone forest are common above 675 m (Murphy and Heady 1983). Some pools are shaded by mature *Quercus* spp. (*Quercus douglasii* Hook. & Arn., *Q. lobata* Nee, *Q. garrayana* Hook., *Q. agrifolia* Nee), but otherwise are surrounded by annual grassland or chamise chaparral. A group of sag ponds just outside of the study area support perennial wetland taxa such as *Scirpus, Typha,* and *Potamogeton,* which were absent from the larger vernal pools. Cattle were excluded from the Twining pool in 1996; all other pools, except Bluebird and Riley, are grazed by sheep.

We visited each pool in mid April, May and June of 1996 and 1999 to inventory the vascular plants. A species list was compiled for each pool, noting all species from pool center to upper strand line or interface where there was an obvious change in species composition from the adjacent upland vegetation. The DAFOR scale (Kent and Coker 1992): dominant (5), abundant (4), frequent (3), occasional (2), and rare (1) was used to obtain a subjective measure of species abundance for each pool. Tree canopy cover was determined from an ocular estimate of noon shade over the pools in June. Since all pools were round in shape the mean of 4 radii were used to determine pool area. Representative species new to the study site were collected and deposited into the HREC herbarium.

RESULTS AND DISCUSSION

Of the 90 vascular plants and one bryophyte found at the 12 vernal pools during the April–June, 1995–1996 and 1998–1999 sampling period, 63

TABLE 2. SUMMARY DATA FOR VERNAL POOLS AT THE HOPLAND RESEARCH AND EXTENSION CENTER AND ADJACENT PRIVATE LAND, MAYACMAS MOUNTAINS, MENDOCINO COUNTY, CA. Note: No grazing in Bluebird since 1989, Riley since 1956, and Twining since 1996.

	Huntley	Bluebird	Junction West	Junction East	Riley	Coon North	Coon South	Weather Small	Weather Large	Hog	Rifle Range	Twining
Elevation (m)	329	335	579	579	597	567	543	902	902	799	412	268
Grazing (Yes, No)	Y	N	Y	Y	N	Y	Y	Y	Y	Y	Y	N
Pool area (sq m)	2262	612	300	490	432	180	288	180	341	3069	215	1230
Maximum water depth (cm)	42	33	45	52	105	65	100	32	40	115	68	60
Water depth (cm) 30 May 1996	9	2	0	13	100	30	90	20	30	110	0	45
Water depth (cm) 18 Jun 1996	0	0	0	0	80	10	40	0	0	100	0	38
Water depth (cm) 26 May 1999	1	0	0	2	55	0	70	8	8	100	0	12
Water depth (cm) 21 Jun 1999	0	0	0	0	53	0	38	0	0	75	0	5
% tree canopy cover	20	0	5	1	35	40	0	0	0	0	0	5
Number of plant species	29	27	16	24	33	12	33	25	23	45	18	35

TABLE 3. ABUNDANCE DATA FOR VERNAL POOLS AT THE HOPLAND RESEARCH AND EXTENSION CENTER AND ADJACENT PRIVATE LAND, MENDOCINO COUNTY, CA. Data collected April–June, 1996 and 1999. 5 = Dominant, 4 = Abundant, 3 = Frequent, 2 = Occasional, 1 = Rare. Nomenclature follows Hickman (1993).

Species	Huntley-96	Huntley-99	Bluebird-96	Bluebird-99	Junction West-96	Junction West-99
Achyrachaena mollis Schauer						
Agrostis exarata Trin.						
Aira caryophyllea L.			3	2		1
Allium unifolium Kellogg						
Anagallis arvensis L.			2	1	1	1
Aristida oligantha Michaux						
Avena barbata Link					2	1
Briza maxima L.						
Briza minor L.	2	2	3	2		
Brodiaea elegans Hoover	1		2		1	1
Brodiaea stellaris S. Watson						
Bromus diandrus Roth			1	1		
Bromus hordeaceus L.	2	2	1	1		
Callitriche heterophylla Pursh var. *bolanderi* (Hegelm.) Fassett	2	2				
Carex athrostachya Olney						
Carex feta L. Bailey						
Carex subbracteata Mackenzie						
Castilleja attenuata (A. Gray) Chuang & Heckard						
Centunculus minimus L.						
Cerastium glomeratum Thuill.	3	2				
Ceratophyllum demersum L.						
Cicendia quadrangularis (Lam.) Griseb.						
Crassula aquatica L. Schönl.	2	2				
Cynodon dactylon (L.) Pers.			4	3		
Cynosurus echinatus L.						
Dactylis glomerata L.						
Danthonia californica Bolander						
Deschampsia danthonioides (Trin.) Munro	2	2	4	4	4	3
Deschampsia elongata (Hook.) Munro						
Downingia cuspidata (E. Greene) E. Greene						
Elatine californica A. Gray						
Eleocharis acicularis (L.) Roemer & Schultes	4	4	3	4		
Eleocharis macrostachya Britton	5	4	5	5	2	1
Elymus glaucus Buckley						
Eremocarpus setigerus (Hook.) Benth.	3	3				
Eryngium aristulatum Jepson var. *aristulatum*	2	5	5	5	5	5
Festuca rubra L.						
Galium aparine L.	2		2			
Geranium bicknellii Britton						
Geranium dissectum L.					1	
Glyceria leptostachya Buckley						
Gratiola ebracteata Benth.	3	4	4	4		
Heterocodon rariflorum Nutt.						
Hordeum marinum Hudson subsp. *gussoneanum* (Parl.) Thell.	3	3	2	2	2	4
Hypochaeris glabra L.						
Isoetes howellii Engelm.	5	5	2	2		
Juncus bufonius L.	2	2				
Juncus patens E. Meyer						
Juncus tenuis Willd.						
Juncus xiphioides E. Meyer				3		
Lasthenia californica Lindley						
Lasthenia glaberrima A.DC.						
Leptodictyon riparium (Hedw.) Warnst.						
Lilaea scilloides (Poiret) Hauman						
Lolium multiflorum Lam.			2	3	5	4
Lolium temulentum L.						
Lythrum hyssopifolium L.	2	2			3	2
Madia gracilis (Smith) Keck						
Mentha pulegium L.				2		
Microseris douglasii (DC.) Schultz-Bip.						

TABLE 3. EXTENDED

Junction East-99	Junction East-99	Riley-96	Riley-99	Coon North-96	Coon North-99	Coon South-96	Coon South-99	WS-96	WS-99	WL-96	WL-99	Hog-96	Hog-99	Rifle Range-96	Rifle Range-99	Twining-96	Twining-99
3	1							1	1								
		4	2									2	2				
						3	2	2	1		1	1	2	2	2	2	2
		1	2														
		1					2					1	1	1	1	1	1
						1								5	4		
											1					1	
																3	3
		1	2			3	2	2	2		2	2	2			2	2
														1	1		
		1									1					1	1
	2	1				3	1	2	1		1		1			1	1
		1	3	1	4	3	4	2	1			3	1			2	2
												2	2				
												2	4				
		5	5								1	2	4				
						1	1									1	1
							2			3	1	2					
		1	2			2	2		2		2						
						1	1										
												1					
	3					2	2			3	2	4	3	2	2	2	3
												2	1		2		
	2	1	2	1	1		2		1								
		2	2														
			1									1	2				
1	2					3	3	2	3			2	2	5	4		
		2	4														
												2	2			1	2
																1	
3	1			2	1	5	5	3	2	2		2	4			4	3
		4	5			5	5	4	5	3	4	5	5	3	2	5	5
		2	2														
												3	3		2		
5	5							5	5	5	5	5	5	4	4		
		2	2														
		1	2														
		1	3														
		1	2								1						
																3	3
3	3					3	3	3	1	4	2	4	4	3	2	3	3
			1				2										
2	4			2	2	3	2	3	4	3	4	2	2	3	3		
						2	1										
5	5							5	5	5	4	5	5			5	5
2	1					4	2	2	2			2	1				
		2	2									2	4			1	1
2	1	2	1			3	1	3	3	2	3	2	3			2	2
												5	5			4	4
4	4																
																2	2
						5	5										
					2												
4	4			2	2	3	2									2	2
		1															
	2							2	2	2	2	1	1	1	2	2	2
			2														
												1	2			5	5
	2																

TABLE 3. ABUNDANCE DATA FOR VERNAL POOLS AT THE HOPLAND RESEARCH AND EXTENSION CENTER AND ADJACENT PRIVATE LAND, MENDOCINO COUNTY, CA. Data collected April–June, 1996 and 1999. 5 = Dominant, 4 = Abundant, 3 = Frequent, 2 = Occasional, 1 = Rare. Nomenclature follows Hickman (1993).

TABLE 3. EXTENDED

Species	Huntley-96	Huntley-99	Bluebird-96	Bluebird-99	Junction West-96	Junction West-99	Junction East-99	Junction East-99	Riley-96	Riley-99	Coon North-96	Coon North-99	Coon South-96	Coon South-99	WS-96	WS-99	WL-96	WL-99	Hog-96	Hog-99	Rifle Range-96	Rifle Range-99	Twining-96	Twining-99
Achyrachaena mollis Schauer							3	1							1	1								
Agrostis exarata Trin.									4	2									2	2				
Aira caryophyllea L.			3	2		1							3	2	2	1		1	1	2	2	2	2	2
Allium unifolium Kellogg									1	2														
Anagallis arvensis L.			2	1	1	1			1					2					1	1	1	1	1	1
Aristida oligantha Michaux													1								5	4		
Avena barbata Link					2	1												1					1	
Briza maxima L.																							3	3
Briza minor L.	2	2	3	2					1	2			3	2	2	2		2	2	2			2	2
Brodiaea elegans Hoover	1		2		1	1																		
Brodiaea stellaris S. Watson																					1	1		
Bromus diandrus Roth			1	1					1									1					1	1
Bromus hordeaceus L.	2	2	1	1				2	1				3	1	2	1		1		1			1	1
Callitriche heterophylla Pursh var. *bolanderi* (Hegelm.) Fassett	2	2							1	3	1	4	3	4	2	1			3	1			2	2
Carex athrostachya Olney																			2	2				
Carex feta L. Bailey																			2	4				
Carex subbracteata Mackenzie									5	5								1	2	4				
Castilleja attenuata (A. Gray) Chuang & Heckard													1	1									1	1
Centunculus minimus L.														2			3	1	2					
Cerastium glomeratum Thuill.	3	2							1	2			2	2		2		2						
Ceratophyllum demersum L.													1	1										
Cicendia quadrangularis (Lam.) Griseb.																			1					
Crassula aquatica L. Schönl.	2	2						3					2	2			3	2	4	3	2	2	2	3
Cynodon dactylon (L.) Pers.			4	3															2	1		2		
Cynosurus echinatus L.								2	1	2	1	1		2		1								
Dactylis glomerata L.									2	2														
Danthonia californica Bolander										1									1	2				
Deschampsia danthonioides (Trin.) Munro	2	2	4	4	4	3	1	2					3	3	2	3			2	2	5	4		
Deschampsia elongata (Hook.) Munro									2	4														
Downingia cuspidata (E. Greene) E. Greene																			2	2			1	2
Elatine californica A. Gray																							1	
Eleocharis acicularis (L.) Roemer & Schultes	4	4	3	4			3	1			2	1	5	5	3	2	2		2	4			4	3
Eleocharis macrostachya Britton	5	4	5	5	2	1			4	5			5	5	4	5	3	4	5	5	3	2	5	5
Elymus glaucus Buckley									2	2														
Eremocarpus setigerus (Hook.) Benth.	3	3																	3	3		2		
Eryngium aristulatum Jepson var. *aristulatum*	2	5	5	5	5	5	5	5							5	5	5	5	5	5	4	4		
Festuca rubra L.									2	2														
Galium aparine L.	2		2						1	2														
Geranium bicknellii Britton									1	3														
Geranium dissectum L.					1				1	2								1						
Glyceria leptostachya Buckley																							3	3
Gratiola ebracteata Benth.	3	4	4	4			3	3					3	3	3	1	4	2	4	4	3	2	3	3
Heterocodon rariflorum Nutt.										1				2										
Hordeum marinum Hudson subsp. *gussoneanum* (Parl.) Thell.	3	3	2	2	2	4	2	4			2	2	3	2	3	4	3	4	2	2	3	3		
Hypochaeris glabra L.													2	1										
Isoetes howellii Engelm.	5	5	2	2			5	5							5	5	5	4	5	5			5	5
Juncus bufonius L.	2	2					2	1					4	2	2	2			2	1				
Juncus patens E. Meyer									2	2									2	4			1	1
Juncus tenuis Willd.							2	1	2	1			3	1	3	3	2	3	2	3			2	2
Juncus xiphioides E. Meyer				3															5	5			4	4
Lasthenia californica Lindley							4	4																
Lasthenia glaberrima A.DC.																							2	2
Leptodictyon riparium (Hedw.) Warnst.													5	5										
Lilaea scilloides (Poiret) Hauman												2												
Lolium multiflorum Lam.			2	3	5	4	4	4			2	2	3	2									2	2
Lolium temulentum L.									1															
Lythrum hyssopifolium L.	2	2			3	2		2							2	2	2	2	1	1	1	2	2	2
Madia gracilis (Smith) Keck										2														
Mentha pulegium L.				2															1	2			5	5
Microseris douglasii (DC.) Schultz-Bip.								2																

TABLE 3. CONTINUED

Species	Huntley-96	Huntley-99	Bluebird-96	Bluebird-99	Junction West-96	Junction West-99
Mimulus guttatus DC.	2	2	2	3		
Mimulus pilosus (Benth.) S. Watson						
Montia fontana L.						
Navarretia intertexta (Benth.) Hook.	3	3			2	1
Phalaris aquatica L.						
Plagiobothrys bracteatus (T. J. Howell) I. M. Johnston	3	2			3	5
Poa annua L.	2	1				
Poa secunda J. S. Presl						
Pogogyne zizyphoroides Benth.	2	1			2	1
Polypogon interruptus Kunth	1	1				
Polypogon monspeliensis (L.) Desf.	3	3	3	1		
Potamogeton foliosus Raf.						
Psilocarphus tenellus Nutt.						
Ranunculus aquatilus L.						
Ranunculus lobbii (Hiern) A. Gray	2	1				
Rumex crispus L.			2	2	1	2
Silene gallica L.						
Sisyrinchium bellum S. Watson						
Spiranthes pornifolia Lindley			1	3		
Spirodela polyrrhiza (L.) Schleiden	2	1				
Stellaria media (L.) Villars						
Taeniatherum caput-medusae (L.) Nevski				1		
Trichostema laxum A. Gray						
Trifolium dubium Sibth.						
Trifolium variegatum Nutt.	3	3	2	3		
Trisetum canescens Buckley						
Triteleia hyacinthina (Lindley) E. Greene			2			
Veronica peregrina L. subsp. *xalapensis* (Kunth) Pennell	2	1	2	3	1	1
Vulpia bromoides (L.) S. F. Gray	2	2	3	1		
Vulpia myuros (L.) C. Gmelin						
Zigandenus micranthus Eastw.						
Total number of species	29	27	24	24	15	15

(70%) were native species (Appendix 1). Species richness ranged from 12 at Coon North pool to 45 at Hog pool (Table 2). *Centunculus minimus* L., *Crassula aquatica* (L.) Schönl, *Deschampsia danthonioides* (Trin.) Munro, *Downingia cuspidata* (E. Greene) E. Greene, *Elatine californica* A. Gray, *Eryngium aristulatum* Jepson var. *aristulatum, Gratiola ebracteata* Benth., *Isoetes howellii* Engelm., *Plagiobothrys bracteatus* (T. J. Howell) I. M. Johnston, *Pogogyne zizyphoroides* Benth., and *Ranunculus lobbii* (Hiern) A. Gray, were restricted to vernal pools in the study area, but absent from other nearby wetland types. Of these species, Hog pool had the highest number (7) compared to Riley and Coon North pools, which had none. *Eleocharis acicularis* (L.) Roemer & Schultes, *E. macrostachya* Britton, *Eryngium aristulatum* var. *aristulatum, Gratiola ebracteata, Hordeum marinum* Hudson subsp. *gussoneanum* (Parl.) Thell., and *Plagiobothrys bracteatus* had the highest constancies, occurring in 8 out of 12 pools. Species richness was highest in a band approximately 1 meter below the high strand line where a mix of introduced annuals and native wetland species occurred. Below this band and extending toward the pool centers, *Eryngium aristulatum* var. *aristulatum, Eleocharis macrostachya, and Isoetes howellii* were common and usually the dominant species (Table 3). Of 27 exotic species, *Briza minor* L., *Hordeum marinum* ssp. *gussoneanum, Lolium multiflorum* Lam., and *Polypogon monspeliensis* (L.) Desf. were the most abundant, commonly encroaching into the pools from the outer margin. Exotic species were rare toward the pool centers.

There were no significant changes observed in species composition and abundance between the two sampling periods of 1995–1996 and 1998–1999 (Table 3). Although the two winters fell close to the 35 year rainfall average of 947 mm, a wet late spring and early summer in 1996 lengthened the period of inundation by several weeks over those in 1999. Surprisingly, the pool phase was shorter after the El Niño winter of 1997–1998, which produced 1546 mm of rainfall (Table 1). Results from cover estimates taken in September of 1997 are shown in Table 4 and reflect the summer pool vegetation.

The variables that seem to influence differences

TABLE 3. EXTENDED CONTINUED

Junction East-99	Junction East-99	Riley-96	Riley-99	Coon North-96	Coon North-99	Coon South-96	Coon South-99	WS-96	WS-99	WL-96	WL-99	Hog-96	Hog-99	Rifle Range-96	Rifle Range-99	Twining-96	Twining-99
		1	2					1	1			1	3				
		1	1														
						2	1	1	1							1	
4	4						1						2	4	3	2	2
												1	3				
3	3					3	4	2	2	4	4	1	2	3	3	1	2
				1	1				2	1		1					
				1	1												
4	4													3	2		
		1	2														
2	1		2			2	2			1		2	2	2	2	1	1
																3	3
2	1																
				2	3		5					3	4			2	2
		3	5			4	3	2	2			2	2			2	2
		1	4	1	1							1	1			1	1
						2										1	1
												2	1				
		1				1											
				2	1												
3	1																
1	3											2	2				
		1	2			4	4	3	2			2	2			2	3
		2		1	1												
						2	1					1	1				
1	2					2	2			1	2	1	2		1		
								2	2	1	2					3	3
								1				2					
			2									1					
19	24	29	28	11	12	27	30	22	24	15	20	43	40	15	18	35	32

between pools in this study are pool depth and profile, length of inundation phase, degree of shade, and management. Deep pools such as Riley, Coon South, Coon North, and Hog experience longer periods of inundation and often support taxa more typical of perennial wetlands such as *Juncus, Eleocharis,* and *Carex.* Riley and Coon South pools are also steep-profiled with narrow margins, a topography that did not support vernal pool specialist plants common on shallow-profiled pools with wide margins. Coon South was the only vernal pool underlain with a dense mat of the aquatic moss *Leptodictyon riparium.* Although Coon North and Riley pools are both deep, densely shaded, steep-profile pools, they had little in common floristically. Coon North, which receives heavy sheep use, was essentially devoid of herbaceous vegetation, while Riley, protected from livestock use since 1956, had a dense band of *Carex subbracteata* Mackenzie, *Eleocharis macrostachya, and Agrostis exarata* Trin around its upper perimeter. Both pools lack *Eryngium aristulatum* var. *aristulatum* and *Isoetes howellii* which were characteristic of many of the other vernal pools. Hog is the largest (3069 m^2) and deepest (115 cm) vernal pool but has a very shallow profile, thus supporting a diverse mix of perennial wetland and vernal pool specialist taxa.

Huntley, Bluebird, Junction West, Junction East, Weather Small, Weather Large, Rifle Range, and Twining pools are relatively shallow with wide margins and little or no tree canopy. *Eryngium aristulatum* var. *arisulatum* was a dominant species in both Junction West and Junction East, which lie adjacent to each other. Junction East was the deeper of the two with *I. howellii* as a codominant, whereas *Lolium multiflorum* codominated in Junction West. Weather Large and Weather Small, paired pools similar in many respects, were both codominated by *E. aristulatum* var. *aristulatum* and *I. howellii.* Huntley and Bluebird pools lie within 500 m of each other at similar elevations and are both codominated by *E. macrostachya* and *E. aristulatum* var. *aristulatum.* Rifle Range pool was originally a shallow profile vernal pool with an area of ca. 1200 m^2. Excavation of the fragmented shales that overlay the surface resulted in the creation of several small, deep pools, which are dominated by *E. aristulatum* var. *aristulatum* in the basins and

TABLE 3. CONTINUED

TABLE 3. EXTENDED CONTINUED

Species	Huntley-96	Huntley-99	Bluebird-96	Bluebird-99	Junction West-96	Junction West-99	Junction East-99	Junction East-99	Riley-96	Riley-99	Coon North-96	Coon North-99	Coon South-96	Coon South-99	WS-96	WS-99	WL-96	WL-99	Hog-96	Hog-99	Rifle Range-96	Rifle Range-99	Twining-96	Twining-99
Mimulus guttatus DC.	2	2	2	3					1	2					1	1			1	3				
Mimulus pilosus (Benth.) S. Watson									1	1														
Montia fontana L.													2	1	1	1							1	
Navarretia intertexta (Benth.) Hook.	3	3			2	1	4	4						1						2	4	3	2	2
Phalaris aquatica L.																			1	3				
Plagiobothrys bracteatus (T. J. Howell) I. M. Johnston	3	2			3	5	3	3					3	4	2	2	4	4	1	2	3	3	1	2
Poa annua L.	2	1									1	1				2	1		1					
Poa secunda J. S. Presl											1	1												
Pogogyne zizyphoroides Benth.	2	1			2	1	4	4													3	2		
Polypogon interruptus Kunth	1	1							1	2														
Polypogon monspeliensis (L.) Desf.	3	3	3	1			2	1		2			2	2			1		2	2	2	2	1	1
Potamogeton foliosus Raf.																							3	3
Psilocarphus tenellus Nutt.							2	1																
Ranunculus aquatilus L.											2	3		5					3	4			2	2
Ranunculus lobbii (Hiern) A. Gray	2	1							3	5			4	3	2	2			2	2			2	2
Rumex crispus L.			2	2	1	2			1	4	1	1							1	1			1	1
Silene gallica L.													2										1	1
Sisyrinchium bellum S. Watson																			2	1				
Spiranthes pornifolia Lindley			1	3					1				1											
Spirodela polyrrhiza (L.) Schleiden	2	1																						
Stellaria media (L.) Villars											2	1												
Taeniatherum caput-medusae (L.) Nevski				1																				
Trichostema laxum A. Gray							3	1																
Trifolium dubium Sibth.							1	3											2	2				
Trifolium variegatum Nutt.	3	3	2	3					1	2			4	4	3	2			2	2			2	3
Trisetum canescens Buckley									2		1	1												
Triteleia hyacinthina (Lindley) E. Greene			2										2	1					1	1				
Veronica peregrina L. subsp. *xalapensis* (Kunth) Pennell	2	1	2	3	1	1	1	2					2	2			1	2	1	2		1		
Vulpia bromoides (L.) S. F. Gray	2	2	3	1											2	2	1	2					3	3
Vulpia myuros (L.) C. Gmelin															1				2					
Zigandenus micranthus Eastw.										2									1					
Total number of species	29	27	24	24	15	15	19	24	29	28	11	12	27	30	22	24	15	20	43	40	15	18	35	32

(70%) were native species (Appendix 1). Species richness ranged from 12 at Coon North pool to 45 at Hog pool (Table 2). *Centunculus minimus* L., *Crassula aquatica* (L.) Schönl, *Deschampsia danthonioides* (Trin.) Munro, *Downingia cuspidata* (E. Greene) E. Greene, *Elatine californica* A. Gray, *Eryngium aristulatum* Jepson var. *aristulatum*, *Gratiola ebracteata* Benth., *Isoetes howellii* Engelm., *Plagiobothrys bracteatus* (T. J. Howell) I. M. Johnston, *Pogogyne zizyphoroides* Benth., and *Ranunculus lobbii* (Hiern) A. Gray, were restricted to vernal pools in the study area, but absent from other nearby wetland types. Of these species, Hog pool had the highest number (7) compared to Riley and Coon North pools, which had none. *Eleocharis acicularis* (L.) Roemer & Schultes, *E. macrostachya* Britton, *Eryngium aristulatum* var. *aristulatum*, *Gratiola ebracteata*, *Hordeum marinum* Hudson subsp. *gussoneanum* (Parl.) Thell., and *Plagiobothrys bracteatus* had the highest constancies, occurring in 8 out of 12 pools. Species richness was highest in a band approximately 1 meter below the high strand line where a mix of introduced annuals and native wetland species occurred. Below this band and extending toward the pool centers, *Eryngium aristulatum* var. *aristulatum*, *Eleocharis macrostachya, and Isoetes howellii* were common and usually the dominant species (Table 3). Of 27 exotic species, *Briza minor* L., *Hordeum marinum* ssp. *gussoneanum*, *Lolium multiflorum* Lam., and *Polypogon monspeliensis* (L.) Desf. were the most abundant, commonly encroaching into the pools from the outer margin. Exotic species were rare toward the pool centers.

There were no significant changes observed in species composition and abundance between the two sampling periods of 1995–1996 and 1998–1999 (Table 3). Although the two winters fell close to the 35 year rainfall average of 947 mm, a wet late spring and early summer in 1996 lengthened the period of inundation by several weeks over those in 1999. Surprisingly, the pool phase was shorter after the El Niño winter of 1997–1998, which produced 1546 mm of rainfall (Table 1). Results from cover estimates taken in September of 1997 are shown in Table 4 and reflect the summer pool vegetation.

The variables that seem to influence differences between pools in this study are pool depth and profile, length of inundation phase, degree of shade, and management. Deep pools such as Riley, Coon South, Coon North, and Hog experience longer periods of inundation and often support taxa more typical of perennial wetlands such as *Juncus, Eleocharis,* and *Carex.* Riley and Coon South pools are also steep-profiled with narrow margins, a topography that did not support vernal pool specialist plants common on shallow-profiled pools with wide margins. Coon South was the only vernal pool underlain with a dense mat of the aquatic moss *Leptodictyon riparium.* Although Coon North and Riley pools are both deep, densely shaded, steep-profile pools, they had little in common floristically. Coon North, which receives heavy sheep use, was essentially devoid of herbaceous vegetation, while Riley, protected from livestock use since 1956, had a dense band of *Carex subbracteata* Mackenzie, *Eleocharis macrostachya, and Agrostis exarata* Trin around its upper perimeter. Both pools lack *Eryngium aristulatum* var. *aristulatum* and *Isoetes howellii* which were characteristic of many of the other vernal pools. Hog is the largest (3069 m²) and deepest (115 cm) vernal pool but has a very shallow profile, thus supporting a diverse mix of perennial wetland and vernal pool specialist taxa.

Huntley, Bluebird, Junction West, Junction East, Weather Small, Weather Large, Rifle Range, and Twining pools are relatively shallow with wide margins and little or no tree canopy. *Eryngium aristulatum* var. *arisulatum* was a dominant species in both Junction West and Junction East, which lie adjacent to each other. Junction East was the deeper of the two with *I. howellii* as a codominant, whereas *Lolium multiflorum* codominated in Junction West. Weather Large and Weather Small, paired pools similar in many respects, were both codominated by *E. aristulatum* var. *aristulatum* and *I. howellii.* Huntley and Bluebird pools lie within 500 m of each other at similar elevations and are both codominated by *E. macrostachya* and *E. aristulatum* var. *aristulatum.* Rifle Range pool was originally a shallow profile vernal pool with an area of ca. 1200 m². Excavation of the fragmented shales that overlay the surface resulted in the creation of several small, deep pools, which are dominated by *E. aristulatum* var. *aristulatum* in the basins and

Table 4. Percent Cover of Dominant Species Below Lower Edge of Outside Vegetation Band, Hopland Research and Extension Center and Adjacent Private Land, Mendocino County, CA. Data collected on 23 Sept. 1997. The no grazing status of Junction West, Junction East, and Hog pools are for observations made inside 16 m^2 grazing exclosures placed inside pools.

Grazing	Y	N	N	Y	N	Y	N	Y	Y	Y	Y	N	Y	Y	N
Species	Huntley	Bluebird	Junction West	Junction West	Junction East	Junction East	Riley	Coon North	Coon South	Weather Small	Weather Large	Hog	Hog	Rifle Range	Twining
Leptodictyon riparium									80						
Aristida oligantha														25	
Cynodon dactylon		25													
Deschampsia danthonioides														25	
Eleocharis acicularis									15						
Eleocharis macrostachya							20			10		30	15	5	5
Eremocarpus setigerus	5											5	25		
Eryngium aristulatum	5	70	50	10	45	45				65	70	40			
Hordeum marinum														5	
Isoetes howellii															25
Lolium multiflorum			25	5											
Lythrum hyssopifolium															10
Mentha pulegium															50
Trichostema laxum					10	10									
Barren (Litter/Soil)	90	5	25	85	45	45	80	100	5	25	30	25	60	40	10

Deschampsia danthonioides around the rims. The Twining pool is located ca. 5 km to the northwest of HREC on private land; cattle were fenced out in 1996. Dominants include *I. howellii, E. macrostachya,* and *Mentha pulegium* L.

Narrow endemic or rare plants, so characteristic of geologically older vernal pool complexes in other parts of the state (Thorne 1984), are absent from the pools in the study area. Instead, many of the species restricted to vernal pool habitat here and nearby vernal pools (de Nevers 1985; Baad 1998) are widely distributed outside California, except *Eryngium aristulatum* var. *aristulatum,* which is found only in the San Francisco Bay Area and the North Coast Ranges of California.

These cismontane pools occur in a relatively wet part of the state, resulting in prolonged periods of inundation and the establishment of perennial wetland taxa. Keeley and Zedler (1998) note that such a habitat might be more aptly described as a vernal marsh rather than a vernal pool. In addition, their relatively recent origin and limited lifespan differentiate them from pools of older geomorphological origin such as those associated with southern California coastal terraces, Central Valley alluvial terraces, or more widespread lava flow landforms (Holland 1978; Keeler-Wolf et al. 1995).

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NOTES

IMPACT OF A NON-NATIVE PLANT ON SEED DISPERSAL OF A NATIVE.—*Salsola tragus* L. (Mosyakin 1996), or tumbleweed, was introduced to the United States from Eurasia in the late 1800's (Young 1991). It has subsequently invaded large portions of the arid western United States and Canada. The impact that *Salsola* spp. have upon neighboring native plant survival during succession has been the subject of a number of studies (e.g., Lodhi 1979; Allen and Allen 1988; Johnson 1998). However, the impact of the invader upon the seed dispersal of natives has not been quantified. Plants such as *Salsola* spp. that have a shrubby growth form act as barriers that slow wind currents and trap wind-dispersed seeds (Day and Wright 1989). *Salsola tragus* often reaches densities higher than native species on disturbed sites. As a result, *S. tragus* may impact the seed dispersal of other species to a greater extent than natives with a similar architecture. Thus, the presence of the non-native *S. tragus* has the potential to alter the ability of natives to colonize successfully by altering seed dispersion patterns and plant survival.

Castle Mountain Mine near Searchlight, NV, contains a large (ca. 50 ha) overburden area where unusable excavated material from deep within the mountain is piled. The surface consists of heavily compacted rock fragments with nutrient-poor (total Kjeldahl nitrogen <1.5 mg/g), alkaline (pH $= 8.0$) soils that have little organic matter ($<1.59\%$) and clay ($<1.0\%$) (Walker unpublished data). The most common colonizers include the non-native annual *S. tragus* and the more diffusely constructed native annual *Eriogonum deflexum* Torrey (Hickman 1993), or flat-topped buckwheat. Although both species have wind-dispersed seeds, the two plants differ in their specific mechanisms of seed dispersal. *Salsola tragus* disperses its seeds after the main stem abscises at the base. The wind subsequently pushes the elliptical plants, jarring seeds loose from leaf axils as the plants bounce on the ground over a considerable distance. Stallings et al. (1995) found that *Salsola tragus* seeds were evenly distributed across the landscape if they were dropped during the tumbling phase. Seeds were concentrated in areas below the plant before the stem abscised and where the plant came to rest for a time (i.e., obstructions). By contrast, *E. deflexum* have winged seeds carried from the maternal plant by wind currents. The dispersal of these seeds depends upon the speed and direction of the wind, which may be altered by plants in the area. *Salsola tragus* in southwestern Wyoming had wind speeds of 13 m/sec one meter above the plant, 11 m/sec 15 cm above the plant, 9 m/sec 10 cm in front (i.e., upwind) of the plant, and 2.5 m/sec 10 cm behind (i.e., downwind from) the plant (Allen & Allen 1988). We hypothesized that *S. tragus* plants provide a barrier to *E. deflexum* seed dispersal through slowed wind currents. *Eriogonum deflexum* plants may in turn affect *S. tragus* seed dispersal by furnishing a physical obstruction to movement during the tumbling phase.

On the overburden pile at Castle Mountain Mine, we selected a flat, 600 m^2 plot dominated by *S. tragus* and, to a lesser extent, *E. deflexum.* We haphazardly chose sixty plants representative of the entire 600 m^2 plot: fifteen each of live *S. tragus,* dead (but attached to the ground by the main stem) *S. tragus,* live *E. deflexum,* and dead *E. deflexum.* Most plants chosen were at least 50 cm from their nearest neighbor (dead *E. deflexum* were occasionally as close as 20 cm to their nearest neighbor). In September 1996 we collected seed and plant litter within a 10 cm × 15 cm quadrat under each plant and from the nearest plant-free clearing within 25 cm to 100 cm east of each focal plant's eastern canopy edge. We used the difference between each canopy sample and its adjacent open area for analysis. This approach adjusted for differences in species substrate preferences on a microsite scale (e.g., living *E. deflexum* were more common in seed-catching rocky areas while living *S. tragus* were more common on sandy substrates). Litter was separated from the inorganic soil by sieving each sample and floating the organic matter. Each litter sample was dried and weighed. Due to the time-consuming nature of seed counting, five random samples from each treatment were selected for seed counts. All seeds were identified for each sample,

TABLE 1. DESCRIPTIVE STATISTICS FOR ALL STATUS AND SPECIES COMBINATIONS ADJUSTED FOR MICROSITE (UNDER CANOPY—ADJACENT OPEN AREA) [MEAN (SE)]. Seed densities expressed as number of seeds per cm^2. Litter mass expressed as grams dry weight per cm^2.

	Dead *E. deflexum*	Live *E. deflexum*	Dead *S. tragus*	Live *S. tragus*
Seed densities				
E. deflexum	1.35 (1.20)	4.30 (1.93)	9.62 (4.31)	2.32 (1.24)
S. tragus	0.23 (0.19)	0.09 (0.09)	4.05 (2.78)	3.85 (1.30)
Litter mass	0.0010 (0.0005)	0.0139 (0.0024)	0.6720 (0.2390)	0.0315 (0.0053)

TABLE 2. SUMMARY FROM TWO-WAY ANOVA WITH STATUS OF PLANT (DEAD OR ALIVE) AND SPECIES (*E. DEFLEXUM* or *S. TRAGUS*). Seed densities and litter adjusted for microsite (under plant—adjoining open area) and natural log transformed prior to analysis. F ratios are reported, with asterisks denoting significance level (* = P < 0.050; ** = P < 0.010).

Source of variation	df	*E. deflexum* seed density	*S. tragus* seed density	df	Litter
Status	1	0.01	0.14	1	16.19**
Species	1	0.00	10.77**	1	50.95**
Status × Species	1	0.40	2.61	1	18.81**
Error	16			56	
Total	19			59	

but seeds other than *S. tragus* and *E. deflexum* were very rare and not included in the analysis. The data were analyzed with a two-way ANOVA (Minitab 1991) which included main effects of species and status (dead or alive) and the interaction between them.

RESULTS

Samples from open areas had less litter (mean ± SE; 0.003 ± 0.001 vs. 0.032 ± 0.007 g. dry wt./cm^2), fewer *E. deflexum* seeds (1.30 ± 0.54 vs. 5.69 ± 1.39 seeds/cm^2), and fewer *S. tragus* seeds (0.19 ± 0.08 vs. 2.25 ± 0.84 seeds/cm^2) than areas under plant canopies, as expected. After adjusting the under plant sample for microtopography using the open sample, the presence of *S. tragus* plants resulted in *E. deflexum* seed densities statistically equal to those under living *E. deflexum* plants, regardless of plant status (Tables 1 and 2; Fig. 1A). These results suggest that *S. tragus* plants served as an effective trap for *E. deflexum* seeds. However, *S. tragus* seed density was more than 16 fold greater under *S. tragus* than under *E. deflexum* (Tables 1 and 2; Fig. 1B), indicating that the native *E. deflexum* does not provide a major barrier to tumbling *S. tragus*. Plant status, species, and the interaction between them were all significant for litter data (Tables 1 and 2; Fig. 1C). Thus *S. tragus* plants were also more effective than *E. deflexum* in catching and/or retaining litter under the canopy.

The data suggest that *E. deflexum* seeds under *E. deflexum* fall from the plant and are blown away, while *E. deflexum* seeds under *S. tragus* have been captured by the slowed wind currents (Fig. 1A) and

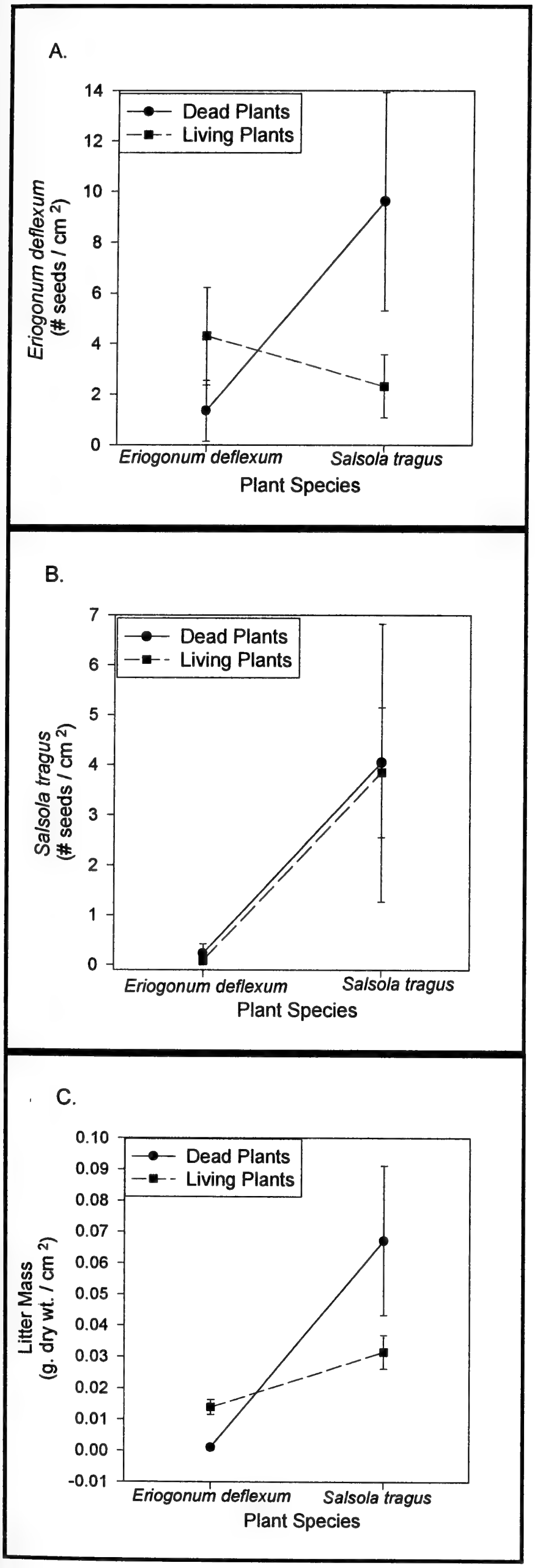

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FIG. 1. Interactions between plant status and species for a) *Eriogonum deflexum* seeds, b) *Salsola tragus* seeds, and c) litter [mean ± SE]. Means adjusted for microsite by subtracting adjacent open sample from canopy sample. Numbers shown in Table 1.

perhaps held by litter under dead *S. tragus* (Fig. 1C). Figure 1B indicates *S. tragus* seeds under *S. tragus* plants probably came from the plant above them, since *E. deflexum* had very few *S. tragus* seeds under their canopies (Table 1). We conclude that *S. tragus* has a significant effect upon the dispersion of *E. deflexum* seeds, but *E. deflexum* plants do not affect the dispersion of *S. tragus* seeds. However, the time period for which this pattern is obtainable may be strongly influenced by tumbleweed abscission later in the season, a possibility not addressed in this data set.

Further work is needed to identify the overall impact that the seed-catching function of the alien *S. tragus* has upon native seedling establishment and plant success. We showed that a native plant's seed distribution can be affected by *Salsola tragus*. Other work has indicated that *Salsola* spp. can positively or negatively interact with nearby natives throughout the plants' lives. Allen and Allen (1988) propose *Salsola kali* may facilitate native grass seed colonization and establishment but may later compete with adults for water and nutrients. *Salsola kali* has an extensive root system and efficient uptake of phosphorus (Itoh and Barber 1983). In addition, *S. kali* can significantly alter soil nutrient concentrations in mixed culture, perhaps due to its rapid growth rate (Allen 1982). *Salsola tragus* can even make phosphorus more available to neighboring plants through a high oxalate concentration in canopy leachates (Cannon et al. 1995; Hageman et al. 1988). Clearly, *Salsola* spp. affect neighboring natives, but the net effect of this interference is unknown. This study has shown that *Salsola* spp. can concentrate native plant seeds under the *Salsola* spp. canopies, where germination and growth may then be either facilitated or inhibited. Further understanding of the effects of *Salsola* spp. on native colonizers will enhance efforts to reintroduce native species to damaged ecosystems.

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NASCENT INFLORESCENCES IN *ARCTOSTAPHYLOS PRINGLEI*: RESPONSE TO KEELEY

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In an account of the absence of nascent inflorescences in *Arctostaphylos pringlei,* C. Parry Keeley (1997) pays lip service to the diversity of these developmental structures in the genus but illustrates only the expanded paniculate type of his own species, "*A. rainbowensis*". Unfortunately, he seems unaware that there is wide variation in stages of development of the nascent inflorescence in different species of *Arctostaphylos.* Whatever the failing may be, I cut to the point by illustrating the nascent inflorescence on one of my collections of *A. pringlei* (Fig. 1), dated November 6, 1986, from the San Bernardino Mountains, CA (typical of five or more on as many specimens).

FIG. 1. Life-size scan of branchlet of *Arctostaphylos pringlei,* as it was collected on November 6, 1986. The bracteose nascent inflorescence is at the upper left, where it terminates a 1986 shoot of the year. Note the distal position above the mature leaves of the year.

All species of *Arctostaphylos* have the inflorescences terminal at the ends of branchlets. Terminal meristems shift from a vegetative mode producing leaves to a flowering mode producing a dormant, embryonic (nascent) inflorescence at the tip of the branchlet. The nascent inflorescence terminates growth on that axis; it forms as the new leaves mature below it on the same shoot. Both nascents and new leaves are produced on shoots of the current year, following completion of flowering on separate shoots of the preceding year. Thus, in Figure 1, the new (1986) shoots have fully mature leaves, but the bracteose, distal nascent inflorescence is immature and dormant on November 6, 1986; the separate shoots bearing ripe fruits (the 1985 shoots) were collected but are not shown.

The period of dormancy of the nascent inflorescence varies from 5–10 months; in most species this prevents flowering in the summer and fall, when the drought of the Mediterranean isoclime is most intense. Most of the coastal manzanitas bloom in the dead of winter, peaking in January. Among the later species is *A. glandulosa,* which often flowers in March (the tetraploid crown-sprouters are late-bloomers). Latest of all to bloom are the montane species, notably *A. pringlei,* which flowers in April and May. Since the formation of nascent inflorescences on the new shoots may be much later in *A. pringlei* than in most other species, they may well be overlooked.

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NASCENT INFLORESCENCES IN *ARCTOSTAPHYLOS PRINGLEI*: RESPONSE TO KEELEY AND WELLS

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Character states involving nascent inflorescences in *Arctostaphylos* (Ericaceae) are of great taxonomic value. Accordingly, as Keeley (1997) observes, the general absence of a nascent inflorescence in the genus is worthy of notice. *Arctostaphylos pringlei* C. Parry is a species of arid montane environments in southern California, Arizona, and northern Baja California that consists of two subspecies, subsp. *pringlei* and subsp. *drupacea* (C. Parry) P. Wells that differ in the fusion of nutlets in the fruit. The former occurs in Arizona, the latter in southern Califonrnia, and both subspecies have been found in northern Baja. Like other montane species of *Arctostaphylos,* flowering occurs between mid-spring through early summer. Typically, *Arctostaphylos* spp. develop a dormant (nascent) inflorescence at the tips of their new stem growth during the time fruits mature and disperse in late spring and summer. Nascents can be observed from the end of stem growth until flowering the next year. In contrast, Keeley (1997) has observed that *A. pringlei* does not produce nascents after stem growth, but produces inflorescences as flowering begins. Hence, the controversy raised by Wells (Wells, 1999) concerns the developmental timing of the formation of an inflorescence with floral buds, rather than an all or nothing type of character state, as would be implied by "nascents present versus absent."

Wells implies that Keeley's (1997) general observation is incorrect. He cites five specimens that he collected in November 1986 to demonstrate that *A. pringlei* does indeed produce nascent inflorescences. One of us (MCV) has observed *A. pringlei* in the field in northern Baja California and in Arizona. Jon Keeley had mentioned the lack of inflorescences in *A. pringlei* before a trip to the Sierra San Pedro Martir Mountains in the fall of 1995, which made it a character of interest. On November 25, 1995, one individual (and only one) was found with a nascent inflorescence; other shrubs in the area appeared to lack this structure. Given this controversy, we decided to distinguish between the separate interpretations of Keeley and Wells by posing a pair of simple alternative hypotheses: 1) the development of nascents should occur just before and during flowering (flowering phase); versus 2) the development of nascents should occur during and following fruiting (fruiting phase). Confirming hypothesis 1 and rejecting hypothesis 2 would support Keeley (1997), while confirming hypothesis 2 and rejecting 1 would support Wells (this issue).

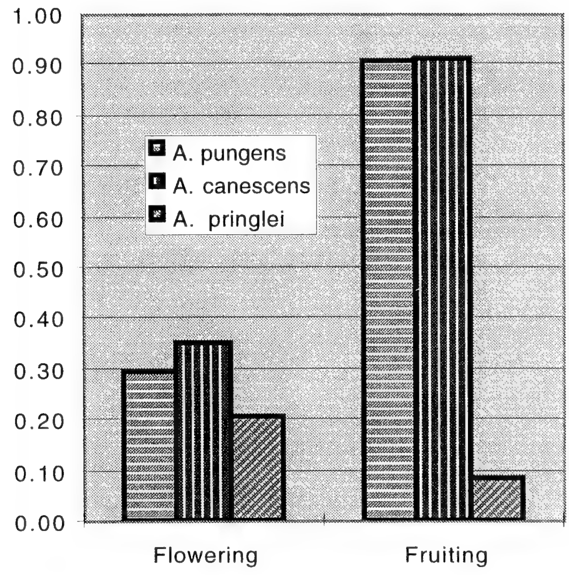

FIG. 1. Percentage of specimens examined that contained presumed nascent inflorescences for *A. pungens, A. canescens,* and *A. pringlei.* Data are presented for two phenological stages, if the specimen was in flower, and if the specimen was maturing fruit.

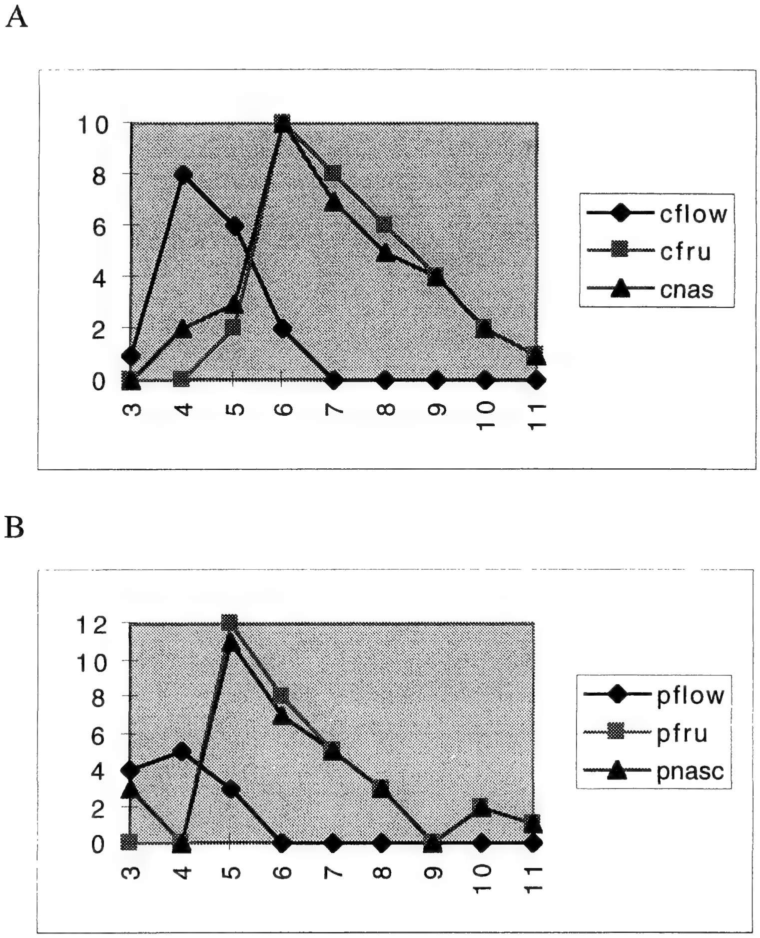

FIG. 2. Sequence of flowering, fruiting and nascent inflorescence production found in specimens housed at California Academy of Sciences. A) sequence for *A. canescens*; B) sequence for *A. pungens.*

TABLE 1. CHI-SQUARE ANALYSES OF PRESENCE OR ABSENCE OF NASCENT INFLORESCENCES AGAINST FLOWERING OR FRUITING AMONG COMBINATIONS OF *A. PRINGLEI, A. CANESCENS,* AND *A. PUNGENS.* Values in the right column include both Chi-square values and significance levels.

	Nascents	Flowering	Fruiting	Total	Chi-Square
A. pringlei	with	11	4	15	
	without	42	44	86	2.169 NS
A. pungens	with	5	29	34	
	without	12	3	15	22.572 p<<0.001
A. canescens	with	6	30	36	
	without	11	3	14	20.083 p<<0.001
A. pungens+ A. canescens	with	11	59	70	
	without	23	6	29	39.653 p <<0.001
	Species	W/nascents	W/o nascents		Chi-Square
Flowering	*A. pringlei*	11	42	53	
	A. pungens+	11	23	34	2.152
	A. canescens	22	65	87	NS
Fruiting	*A. pringlei*	4	44	48	
	A. pungens+	59	6	65	79.438
	A. canescens	63	50	113	p<<0.001

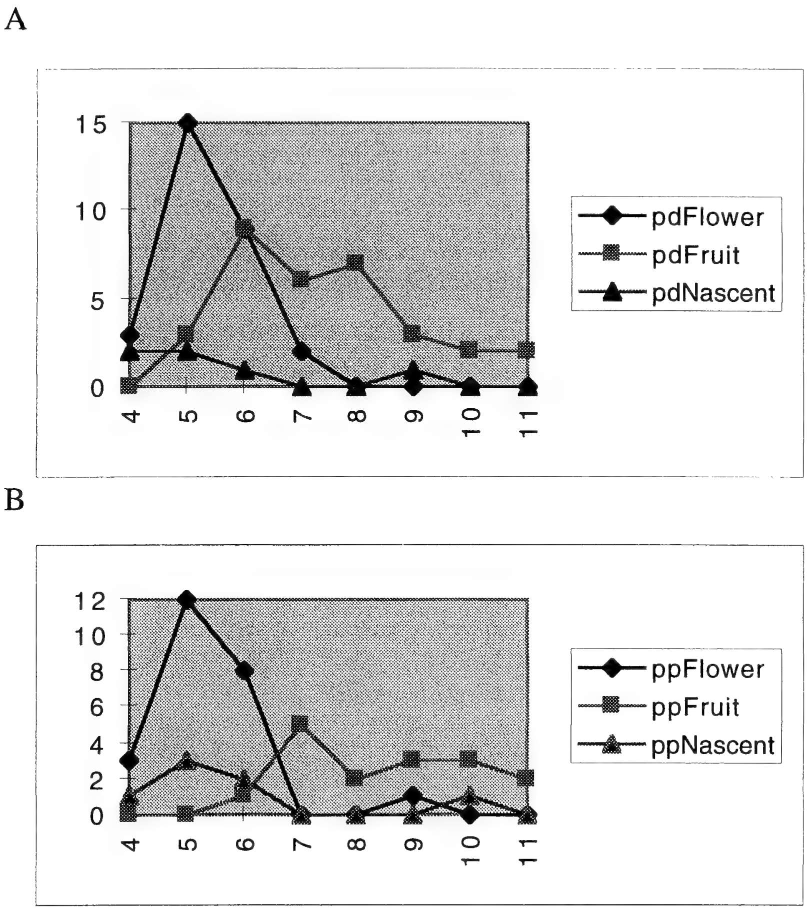

FIG. 3. Sequence of flowering, fruiting and nascent inflorescence production found in specimens housed at California Academy of Sciences. A) sequence for *A. pringlei* subsp. *drupacea*; B) sequence for *A. pringlei* subsp. *pringlei.*

METHODS

Initially, 101 sheets of specimens from the California Academy of Sciences (CAS) of both subspecies of *A. pringlei* collected throughout its range were examined for phenological stage and presence or absence of apparent nascent inflorescences (note: shortly prior to flowering, immature inflorescences appear similar to "nascents"). Collection numbers for each sheet were recorded as well as dates of collection, county, phenological stage (early flowering, flowering, early fruiting, fruiting, and past fruiting), and presence or absence of nascent inflorescences. For comparative purposes, two other mid-montane species, 49 sheets of *A. pungens* and 50 sheets of *A. canescens,* were examined in a similar way (a total of 99 sheets for the two species combined). Chi-square 2 × 2 contingency analysis was used to test for differences in nascents between flowering and fruiting stages (Zar 1984).

RESULTS

Arctostaphylos pungens Kunth and *A. canescens* Eastw. are typical of other species in the genus. The development of nascent inflorescences occurs at the time fruits are maturing on the tips of newly elongating stems (Fig. 1, 2). Approximately 90% of the specimens in the fruiting phase are developing nascent inflorescences. Note that this pattern holds true for both of these species and there is no significant difference between them (Table 1). *Arctostaphylos pringlei* is not substantially different from the other two species during the flowering phase (Fig. 1, 3), however, during the fruiting phase, less than 10% of the *A. pringlei* specimens possessed nascent inflorescence structures (Fig. 1, 3). This pattern held true equally for both subspecies suggesting that this unusual developmental character is a shared feature in the *A. pringlei* lineage. The stark contrast between *A. pringlei* and the other species during the fruiting phase (Fig. 1, Table 1) are consistent with our hypothesis 1, which supports the conclusions of Keeley (1997).

Granted, four out of 48 specimens of *A. pringlei* were found to present nascent inflorescences apparently established during the fruiting phase. We underscore "apparently" given the possibility that these individuals represent shrubs that may be flowering out of season. One CAS specimen (#563576), for example, was flowering in September, clearly an "exception from the rule" that may be associated with phenological opportunism on the part of this individual; such opportunism is common in the genus. In contrast, 59 out of 65 sheets of *A. pungens* and *A. canescens* had nascents during the fruiting phase (Fig. 1, 2). This difference in the pattern of nascent inflorescence establishment between *A. pringlei* and other species of *Arctostaphylos* during the fruiting phase is significant. These findings are very consistent with the observations of Keeley (1997).

DISCUSSION

Given its near universal occurrence in *Arctostaphylos,* the nascent inflorescence developmental character is logically ancestral in this genus. In that case, the general lack of nascent inflorescences in *A. pringlei* during the fruiting phase is likely a derived condition. With this feature combined with its unusual pink deciduous bract characters, characters that Wells (1992) interpreted as warranting subsectional status for this species, *A. pringlei* appears to be a distinctive lineage within the genus. Keeley (1997) introduces an important observation concerning the general lack of nascent inflorescences in *A. pringlei.* Our analysis of specimens from CAS confirms his observations with nascents rarely occuring during the fruiting phase in *A. pringlei* in decided contrast to other species in the genus in which a large majority of individuals establish nascents during this phenological stage (Fig. 1, 2, 3, Table 1).

Having observed numerous populations of *Arctostaphylos* in the field, we have come to the conclusion that few single characters are completely consistent in this genus. Instead, within *Arctostaphylos,* consistency is revealed in a suite of characters that distinguish species reliably. That rare exceptions occur to the "lack of nascent inflorescence" status of *A. pringlei* is hardly surprising. Taking the position that "exceptions must make the rule" in this instance and that Keeley's two years of population observations are somehow uninformed or incorrect seems unlikely to advance our understanding of this complex group.

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DEINANDRA BACIGALUPII (COMPOSITAE—MADIINAE), A NEW TARWEED FROM EASTERN ALAMEDA COUNTY, CALIFORNIA

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ABSTRACT

Deinandra bacigalupii is a new tarweed known from alkaline meadows in the vicinity of Livermore, Alameda County, California. The taxon has been treated as conspecific with *Deinandra* [*Hemizonia*] *increscens,* but represents a separate lineage that is morphologically, ecologically, and geographically distinct. Unlike other members of *Deinandra, D. bacigalupii* combines the following morphological characteristics: proximal primary-stem leaves mostly entire or irregularly lobed, distal cauline leaves mostly narrowly linear or lance-linear, ray florets mostly 8 per head, ray corolla limbs 2–4 mm long, anthers yellow, and disc pappi of highly irregular, erose scales <1 mm long or reduced to crowns of minute bristles.

Results of molecular phylogenetic and morphological studies of *Deinandra* Greene *sensu* Baldwin (1999) [=*Hemizonia* DC. sect. *Madiomeris* Nutt. sensu Tanowitz (1982) plus "Fruticosae" or "Zonamra" (see Clausen 1951; Keck 1959)] lead me to conclude that plants from eastern Alameda County, California, treated by Tanowitz (1982) as geographically disjunct members of *Hemizonia increscens* (H. M. Hall ex D. D. Keck) Tanowitz [=*Deinandra increscens* (H. M. Hall ex D. D. Keck) B. G. Baldwin] constitute a distinct lineage. Although morphologically similar to *D. increscens,* the Alameda County plants possess mostly entire or irregularly lobed (rather than pinnatifid) proximal primary-stem leaves, yellow (not dark-purple) anthers, and a shorter, more irregular pappus. Ecologically, the Alameda County plants are somewhat unusual in *Deinandra* for occurring in poorly drained, alkaline habitats more typical of the closely-related genus *Centromadia* Greene [=*Hemizonia* DC. sect. *Centromadia* (Greene) D. D. Keck]. Results of molecular phylogenetic analyses of nuclear rDNA spacer sequences place the Alameda County plants closer to *D. corymbosa* (DC.) B. G. Baldwin than to a lineage comprising representatives of *D. increscens* subsp. *increscens* and *D. increscens* subsp. *villosa* (Tanowitz) B. G. Baldwin (Baldwin unpublished). The chromosome number shared by *D. increscens* and the Alameda County plants ($2n=12$ II), but not shared with *D. corymbosa* ($2n=10$ II), is modal and putatively basal in *Deinandra.* Based on the foregoing morphological, ecological, and phylogenetic considerations, I propose a new species to accomodate the distinctive *Deinandra* populations from eastern Alameda County.

Deinandra bacigalupii B. G. Baldwin, sp. nov. (Fig. 1).—TYPE: USA, California, Alameda County, north of Livermore, junction of Ames Street and Raymond Road, in sandy alkaline soil, 31 Aug 1966, *R. F. Hoover 9954* (holotype, UC; isotypes, CAS, OBI, UC).

A ceteris speciebus *Deinandrae* differt characteribus conjuncte foliis proximalibus plerumque integris vel irregulariter lobatis; foliis caulinis distalibus plerumque anguste linearibus vel lanceolatis-linearibus; floribus radiorum (6–)8(–9), limbis corollarum 2–4 mm longis; antheris flavis; squamis papporum irregulariter erosis <1 mm longis vel pappis coroniformibus setis minutis.

Annual herbs, strongly odorous. *Stems* erect, branched in distal half or to near base (the branches ascending-virgate), tawny or whitish (or purplish), shiny near base, to 4 dm high, sparsely to densely hirsute, minutely stipitate-glandular distally, the glands yellowish or clear. *Leaves* sessile, mostly cauline, evenly distributed, alternate (except in basal rosette), ascending to appressed along stems, usually much longer than internodes; blades of primary-stem leaves narrowly oblanceolate (near base of stem) to linear or lance-linear, ≤1 dm long, gradually reduced distally, mostly entire or irregularly lobed, slightly revolute, sparsely hirsute and minutely stipitate-glandular, the glands yellow or clear; blades of branch-stem leaves linear to lance-linear, ≤1 cm long on distal branches, slightly revolute, uniformly hirsute and stipitate-glandular. *Capitulescences* loosely corymbiform, the side branches overtopping central branches. *Peduncles* inconspicuous (<length of phyllaries). *Involucres* often partially hidden by overlapping leaves, hemispheric or somewhat urn-shaped, ca. 5(–6) mm diam. *Phyllaries* usually 8, same number as ray florets, lance-attenuate, ca. 5(–6) mm long, herbaceous, each investing abaxial surface of a ray ovary (the free tips < half the length of the whole), weakly keeled, sparsely hirsute and densely glandular. *Ray florets* (6–)8(–9), pistillate, fertile, corollas bright yellow, the tube ca. 2 mm long and densely

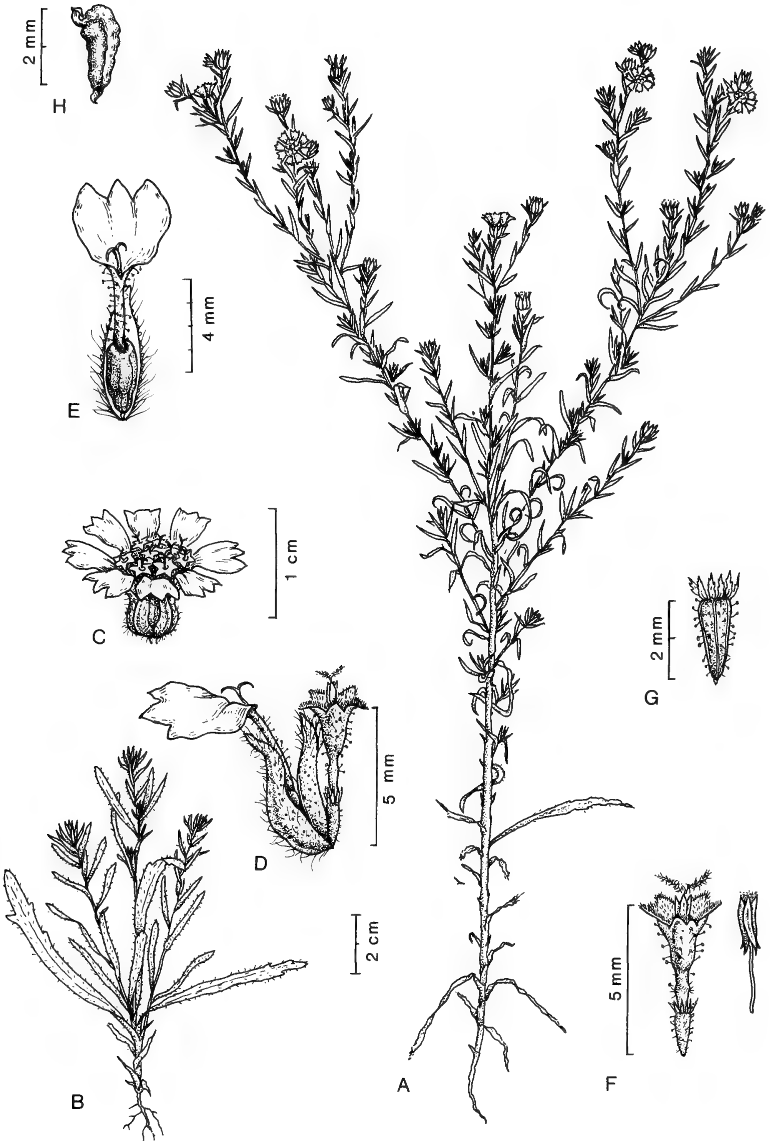

FIG. 1. *Deinandra bacigalupii.* (a) habit of mature plant; (b) habit of immature plant; (c) head; (d) phyllary, ray floret, palea, and disc floret (left to right); (e) adaxial view of ray floret and associated phyllary; (f) disc floret and stamens (left to right); (g) disc ovary and pappus; (h) ray cypsela.

stipitate-glandular, the lamina broadly obovate, 2–4 mm long, 2–3 mm wide, glandular abaxially, shallowly 3-lobed, the central lobe narrower than the lateral lobes. *Disc florets* (10–)15–18(–21), functionally staminate, ca. 5 mm long, corollas bright yellow, the tubes much shorter than the narrowly funnelform throats, glandular, 5-lobed, the lobes densely bristly along adaxial margins. *Anthers* yellow. *Style branches* hispidulous. *Disc ovaries* narrowly clavate, glandular. *Receptacles* flat or slightly convex, glabrous. *Paleae* ca. 8–11, in one peripheral series, connate in basal half, similar to phyllaries. *Cypselae* black, gibbous, obovoid, somewhat 4-angled, ca. 2–2.5 mm long, rugose, with prominent beaks and short basal stipes, glabrous. *Ray pappi* none. *Disc pappi* of basally connate, whitish to tawny, highly irregular, quadrate to subulate, shallowly to deeply erose scales, <1 mm long, or reduced to crowns of minute bristles. *Chromosome number* $2n=12$ II (reported here from *B. G. Baldwin 1053* [JEPS] and [fide annotation by Dale E. Johnson] from *D. E. Johnson 231* with *J. E. Eckenwalder* [UCSB]).

Paratypes. USA, California: Alameda County, Livermore Valley, Raymond Road and Ames Street, 29 Aug 1969, *R. F. Hoover 11564* (CAS, OBI, UC); just SW of intersection of Raymond

Road and Ames Street, 19 Aug 1976, *D. E. Johnson 231* with *J. E. Eckenwalder* (UC, UCSB); *loc. cit.*, 2 Jun 1999, *B. G. Baldwin 1078* (JEPS); 0.1 to 0.15 miles south of junction with Las Positas Road along the east edge of N. Greenville Road, 30 Jul 1996, *R. E. Preston 989* (DAV); *loc. cit.*, 5 Aug 1997, *R. E. Preston 1047* (JEPS); *loc. cit.*, 8 Oct 1998, *B. G. Baldwin 1053* (JEPS); *loc. cit.*, 2 Jun 1999, *B. G. Baldwin 1077* (JEPS); *loc. cit.*, 14 Jul 1999, *B. G. Baldwin 1082* (JEPS).

Distribution, habitat, and phenology. Deinandra bacigalupii appears to be narrowly endemic to the eastern San Francisco Bay region, near the northern distributional limit of *Deinandra.* The two populations known to me are the type and another (discovered by Robert E. Preston) along N. Greenville Road, Livermore. Both populations occur in poorly-drained, seasonally dry, alkaline meadows, in the vicinity of barren, alkali scalds. Associated species of *D. bacigalupii* include *Allenrolfia occidentalis* (S. Watson) Kuntze, *Atriplex depressa* Jeps. (in adjacent, alkali-scald habitat), *Bromus hordaceus* L., *Centromadia pungens* (Hook. & Arn.) Greene, *Cuscuta salina* Engelm. (on *Deinandra bacigalupii*), *Deschampsia danthonioides* (Trin.) Munro, *Distichlis spicata* (L.) Greene, *Frankenia salina* (Molina) I. M. Johnst., *Holocarpha virgata* (A. Gray) D. D. Keck, *Hordeum depressum* (Scribn. & J. G. Sm.) Rydb., *Hordeum marinum* Huds. subsp. *gussoneanum* (Parl.) Anghel & Velican, *Juncus bufonius* L. var. *bufonius, Lasthenia californica* DC. ex Lindl., *Linanthus liniflorus* Greene, *Parapholis incurva* (L.) C. E. Hubb., *Spergularia macrotheca* Heynh. var. *longistyla* R. Rossbach, *Trifolium microcephalum* Pursh, *Vulpia bromoides* Gray, *V. microstachys* (Nutt.) Benth. var. *pauciflora* (Beal) Lonard & Gould, and *V. myuros* (L.) C. C. Gmel. *Deinandra bacigalupii* flowers from late spring through early fall (ca. June–October).

No other species that can be easily mistaken for *D. bacigalupii* is known from the East Bay region. The paucity of herbarium records of *D. bacigalupii* from an area frequented by generations of plant collectors, including the tarweed specialists Clausen, Keck, and Hiesey, may reflect extreme rarity of the plant. Field work is needed to locate any other populations that may exist. Rapid urban development of the Livermore Valley and surrounding areas may pose a significant threat to continued existence of the species.

Deinandra bacigalupii is named for the late Rimo Bacigalupi, first Curator of the Jepson Herbarium, who annotated the holotype on 26 April 1967 with the following statement: "Does not seem to match any thus far published species of *Hemizonia*".

ACKNOWLEDGMENTS

I am especially grateful to Dean G. Kelch, who first alerted me to the existence of the new tarweed, and Robert E. Preston, who informed me about the Greenville Road population. I also thank Susan J. Bainbridge for field and herbaria assistance; Gerald D. Carr, David J. Keil, Robert E. Preston, and John L. Strother for reviewing the manuscript; Lesley B. Randall for preparing the illustrations; Kristina A. Schierenbeck for expeditious editing of the manuscript; Alan R. Smith and John L. Strother for assistance with the Latin diagnosis; Bridget L. Wessa for laboratory assistance; and Margriet Wetherwax for greenhouse assistance.

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A NEW SPECIES OF *STEPHANOMERIA* (ASTERACEAE) FROM NORTHWESTERN WYOMING

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ABSTRACT

Stephanomeria fluminea, a new species known only from northwestern Wyoming, is similar to the widespread *S. tenuifolia* (Torrey) H. M. Hall in characteristics of its heads, cypselae and pappus bristles, but has a distinct vegetative appearance because of its large cauline leaves that remain green at flowering. The new species grows only on raised, cobble benches in the shifting gravel beds of creeks and rivers, a habitat that is unique among all species of *Stephanomeria.*

Within *Stephanomeria* Nuttall, a widespread western North American genus of six annual and ten herbaceous perennial species, the reproductive structures, particularly the cypselae and pappus bristles, have provided the most useful characters to distinguish species. This is particularly so with the two perennial species *S. tenuifolia* (Torrey) H. M. Hall and *S. pauciflora* (Torrey) Nelson; for example, Cronquist (1994) states, "The only consistently dependable difference between the two lies in the pappus." Another notable example is the presence versus absence of a narrow, longitudinal groove or shallow channel on each face of the seeds that distinguishes *S. virgata* Benth. from all other annual stephanomerias (Gottlieb 1972). Emphasis on reproductive structures, though extremely valuable in this genus, has lessened attention to various vegetative traits.

Here, I describe a new species of *Stephanomeria* that closely resembles *S. tenuifolia* in characters of its heads, cypselae and pappus bristles. The new species has been collected since 1894, and generally was referred to this congener, but it differs markedly in vegetative appearance and, importantly, in its unusual and specialized habitat. The new species, known only from northwestern Wyoming, has large leaves all along its stems and branches that remain green at flowering whereas the cauline leaves of *S. tenuifolia* are very reduced and bract-like, rarely measuring as much as 15 × 1 mm. The new species grows only on impermanent, slightly raised, cobble benches in the flat, gravelly beds of creeks that flood and churn after spring snow melt, a habitat that is unique among all species of *Stephanomeria.* The habitats of *S. tenuifolia* are described as crevices in volcanic, granite and sandstone outcrops, open rocky ridges and slopes, and the bases of cliffs.

Stephanomeria fluminea Gottlieb sp. nov. (Fig. 1).—TYPE: USA, Wyoming, Teton Co., gravel bars in Pilgrim Creek, north of trailhead in Bridger-Teton National Forest, north of boundary with Grand Teton National Park, T46N R114W sect. 20 E½, 7200 ft (2200 m), 15 Aug 1998, ***Gottlieb and Ford 9807*** (Holotype: DAV; Isotypes: COLO, MO, MONT, NY, RM, UC). $2n=16$ (from chromosome counts of root tip cells of two seedlings grown from seed collected at the type locality).

Ab *S. tenuifolia* (Torrey) H. M. Hall foliis caulinis magnis, viridibus sub anthesi, foliis ad ½ altitudines caulium (32–)35–46(–60) × 3–5 mm, foliis ad ⅔ altitudines caulium (28–)30–40(–50) × 2–3.5 mm, et habitatione distincta in lectis fluviorum differt.

It differs from *S. tenuifolia* in that the cauline leaves are large and green at anthesis, the leaves at half stem height are (32–)35–46(–60) × 3–5 mm, the leaves at ⅔ stem height are (28–)30–40(–50) × 2–3.5 mm, and its habitat in the beds of streams is distinctive.

Herbaceous perennials from creeping rhizomes; stems, branches and leaves densely short-tomentose throughout; stems 1–8, 15–40 cm. Basal leaves in a rosette, oblong-oblanceolate, entire or very sparsely toothed; cauline leaves persistent along entire stem, (32–)35–46(–60) × 3–5 mm at ½ stem height, (28–)30–40(–50) × 2–3.5 mm at ⅔ stem height, green at flowering, oblong-oblanceolate, margins entire. Heads terminal and axillary on peduncles 2–10 mm long. Involucres with 5 equal phyllaries, 8–10 mm long, subtended by a calyculus of bractlets 2–4 mm long. Receptacles epaleate. Florets 5(6). Cypselae tan, 4–4.4 mm, each face with a central, narrow, longitudinal groove, the faces smooth (not bumpy or rugulose) but with a scaberulous vesture of minute upward pointing hairs, generally not ribbed between adjacent faces. Bristles of the pappus white, 30–40, plumose throughout, not widened at bases, occasionally connate in pairs at basal 0.1–0.2 mm, otherwise free, persistent.

Representative specimens. Wyoming. Park Co. ***Hartman 19617*** (RM), 27 Aug 1984, S. Fk. Shoshone R. between Robinson and Younts Crs.; Sub-

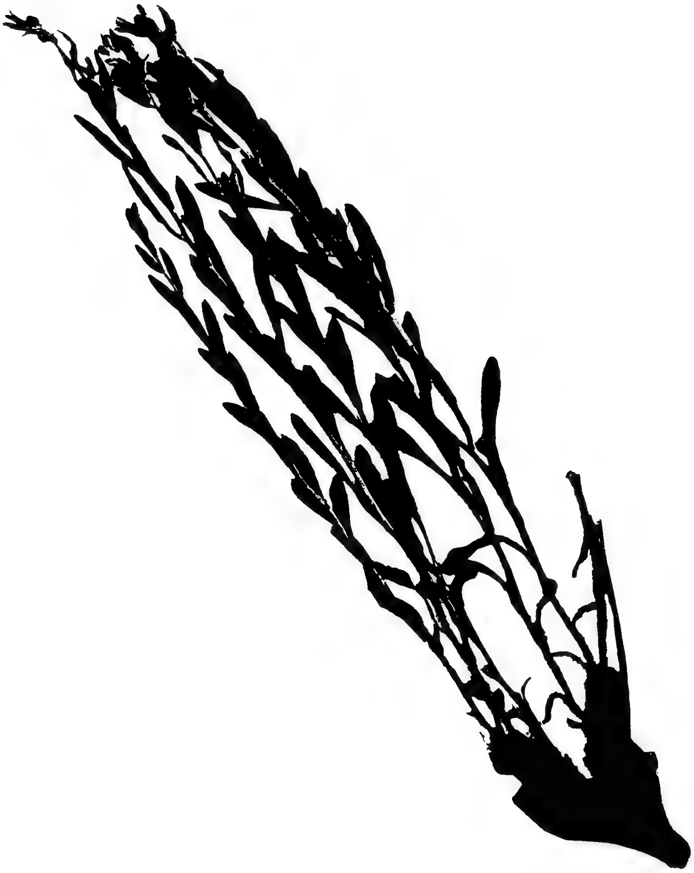

FIG. 1. Silhouette of *Stephanomeria fluminea.*

lette Co. ***Payson and Payson 3076*** (RM), 19 Aug 1922, Hoback R. Canyon near Cliff Cr.; Teton Co. ***Beetle 5062*** (WSC, WTU), 11 Aug 1947, 5 mi N of Moran; ***Dorn 4726*** (COLO, NY, RM), 28 July 1987, Pacific Cr.; ***Evert 32257*** (RM), 25 July 1996, Pilgrim Cr.; ***Fertig 16286*** (RM), 13 Aug 1995, Cottonwood Cr., Fish Cr. drainage; ***Gottlieb and Ford 9803*** (DAV, GH, MO, NY, RM, UC), 13 Aug 1998, Pacific Cr.; ***Hartman 28285*** (RM), 25 Aug 1990, S. Fk. Fish Cr. between Purdy and Hackamore Crs.; ***A. Nelson 925*** (RM, UTC), 15 Aug 1894, Bacon Cr., Fish Cr. drainage; ***B. E. Nelson 20332*** (RM), 25 Aug 1990, S. Fk. Fish Cr.; ***Reed 1065*** (RM), 10 Aug 1947, Pacific Cr.; ***N. Snow 1386*** (RM), 23 July 1987, Pacific Cr.; ***Venrick 366*** (MO), 13 Aug 1960, Pacific Cr.; ***L. Williams 320*** (RM), 3 Aug 1931, Snake River bottom, Jackson Hole; ***L. Williams 976*** (GH, MO, NY, RM, UTC), 31 July 1932, Snake River bottom gravel.

All but one of the known populations of *S. fluminea* are located in channels of creeks and rivers that flow westerly into the Snake River in the general region of Jackson Hole, Wyoming. A single collection is from a different drainage: ***Hartman 19617*** from east of the continental divide in the channel of the South Fork of the Shoshone River. In the summer of 1998, the population in the Pilgrim Creek type locality included between 1000 and 2000 plants, and the one at the collection site in Pacific Creek numbered between 250 and 500 plants. All individuals examined in these populations had large cauline leaves.

Other populations, however, growing in creek beds to the south, had numerous individuals with shorter, more narrow leaves that appear to be intermediate in size between those of *S. fluminea* and the very reduced bractlike leaves of *S. tenuifolia.* For example, plants with intermediate leaf sizes were collected at Spread Creek near Hwy. 26/89/191 (***Gottlieb and Ford 9810,*** DAV), the Gros Ventre River near Hwy. 26/89/191 (***Gottlieb and Ford 9806,*** DAV), and Fish Creek (***Gottlieb and Ford 9805,*** DAV), in the upper Gros Ventre drainage, 34 miles east of Hwy. 26/89/191. At Fish Creek, cauline leaves on seven plants averaged 28.1 × 1.9 mm at ½ stem height and 19.7 × 1.1 mm at ⅔ stem height. On the Gros Ventre River, just east of the highway bridge on Hwy. 26/89/191, cauline leaves on seven plants averaged 36.0 × 1.4 mm at ½ stem height and 23.4 × 0.9 mm at ⅔ stem height. Specimens probably collected from the same Gros Ventre site in 1933 (***L. Williams 1321,*** MO and

UTC) had cauline leaves less than 20 × 1.5 mm. Intermediate dimensions were also evident on the cauline leaves on some specimens in another collection of Williams from the Snake River bottom in Jackson Hole (***976,*** acc. 161207, RM), but other specimens from the same collection (***Williams 976,*** GH, NY, RM, and UTC) show large cauline leaves, typical of *S. fluminea* as well as several with leaves having intermediate sizes. The shorter and narrower leaves on plants from these localities and their greater variability suggest they might be a consequence of interspecific hybridization between *S. fluminea* and *S. tenuifolia.*

Stephanomeria tenuifolia, though apparently not common in the region, has been collected (***Wehmeyer, Martin, and Loveland 5414,*** GH, MO, NY) from near Red Hill Bridge over the Gros Ventre River, about 15 miles east of Hwy. 26/89/191. Many other collections of *S. tenuifolia* have been made along both the North Fork and the South Fork of the Shoshone River in adjacent Park County, to the north and east of Jackson Hole (for example, ***Hartman 59574, 54931*** and ***60004***; ***Rosenthal 2221***; ***Evert 8796, 9504*** and ***9423***; all RM). The two species can be expected to make contact at numerous places in the region where creeks flow beneath rocky cliffs and other outcrops.

Individual genotypes of *S. fluminea* are probably often multiplied when their rhizomes are broken apart as the cobbles beneath them shift and grind during spring floods. These fragments can be moved to new sites where they may reroot. Indeed, rhizomes that reroot would seem to be particularly adaptive in the rocky creek bed habitat of this species. At Pacific Creek, we found plants with shoots that emerged from large, multi-year root crowns and that had at least one previous year's dried stems still attached as well as plants with shoots growing from slender rhizomes with no evidence of previous shoot growth. In addition, we found several plants as much as 15 cm apart above ground that arose from a common rhizome.

All of the creek bed habitats where *S. fluminea* is now found were covered 18,000 to 20,000 years ago by the massive Pinedale glacier (Good and Pierce 1996), suggesting the possibility that the species evolved relatively recently after the glacier retreated.

ACKNOWLEDGMENTS

I thank Ellen Dean, director of the University of California, Davis, herbarium, for her helpfulness and the many courtesies she extended to me while I was preparing the taxonomic treatment of *Stephanomeria* for the Flora of North America. I thank John L. Strother for many helpful comments on the original manuscript, and both him and Alan R. Smith for translating the species diagnosis into Latin. I thank the curators of the following herbaria for loans of specimens: COLO, GH, IDS, MO, MONT, MONTU, NY, RM, UTC.

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MADROÑO, Vol. 46, No. 1, pp. 61–64, 1999

ERYNGIUM PENDLETONENSIS (APIACEAE), A NEW SPECIES FROM SOUTHERN CALIFORNIA

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ABSTRACT

Eryngium pendletonensis (Apiaceae) is a new species from Camp Pendleton Marine Corps Base, San Diego County, CA. It occurs in seasonally moist grasslands, swales, and vernal pools on coastal slopes and mesas and is distinguished from other species of *Eryngium* sect. *Armata* in having a combination of flower bracts with thickened margins, pinnately divided leaves, and short, central primary stem axes.

Eryngium L. sect. *Armata* Sheikh contains 12 species (14 infraspecific taxa) of perennial plants distributed in California, western Oregon, southeastern Washington, southwestern Idaho, and northern Baja California, Mexico (Sheikh 1978, 1983). Ecological studies conducted at Camp Pendleton Marine Corps Base, San Diego County, CA (Bliss and Zedler 1993) resulted in the discovery of a new taxon referable to this section (Hickman 1993, 1996; Munz 1959, 1968).

Eryngium pendletonensis K. L. Marsden & M. G. Simpson, sp. nov.—TYPE: USA, California, San Diego Co., Camp Pendleton Special 1-DMATC series V795S ± 10", Camp Pendleton Marine Corps Base, bluffs just south of Las Pulgas Creek (Red Beach), 15 m (50 feet) north of the Harrier Pad at Red Beach, disturbed grassland habitat on an eroding coastal bluff, 33°17′09″N, 117°27′17″W, 30 m (100 feet) elevation, 13 Jun 1992, ***K. L. Marsden 13VI92A*** (holotype: SD 142722; isotypes: BCMEX, CAS, DAV, LA, MO, RSA, SDSU, UC, UCR, UCSB, US).

Differt a *Eryngio pinnatisecto* indumentis minus scabris, habitibus prostratis, axibus primaribus brevioribus (1–6 cm), et floribus capitulorum paucioribus.

Plants herbaceous perennials, 0.5–2 dm tall; growth apparently colonial, several individuals often clumped together giving the appearance of one plant, clumps up to 5 dm in diameter; roots fascicled, adventitious, arising from a short, erect rootstock; rootstock (a caudex) brown, as wide as long, 5–10 mm, giving rise to basal leaves at apex, slightly thickened relative to aerial stems; aerial stems a central primary axis (continuous with rootstock) plus (0–)1(–2) lateral primary axes arising from apex of rootstock (Fig. 1); central primary axis erect, 1–6 cm long at maturity (Fig. 5); branching of primary axes dichasial, at apex giving rise to two cauline leaves, a terminal pedunculate head, and (1–)2 secondary axes; this dichasial pattern repeated up to 6 times in secondary and subsequent axes (Fig. 1); all aerial axes ribbed, ribs scaberulous; leaves basal and cauline; basal leaves arising from apex of rootstock, sheathing, crowded; first 3–7 leaves typically linear to acicular, unlobed, with transverse septa; later leaves pinnately to bipinnately divided (Figs. 2B, 3A), 8–25 cm long, oblanceolate in outline, septate only in petiole region, ascending at first, drooping with maturity, withering or senescing prior to or at the onset of flowering; leaf lobes mostly narrowly elliptic to lanceolate, often apiculate at maturity; cauline leaves opposite, resembling basal leaves but not septate, size diminishing with distance from rootstock; inflorescence a penduncluate, congested head (Fig. 2C), inflorescence bracts absent, flowers 9–19 per head, head size (including number of flowers) diminishing with distance from rootstock; peduncles 2–3 cm long; flowers bisexual, actinomorphic, erect, sessile, 3–4 mm long (Fig. 2D); flower bracts (Figs. 2C, D, 4) 5–21 mm long (decreasing in size from

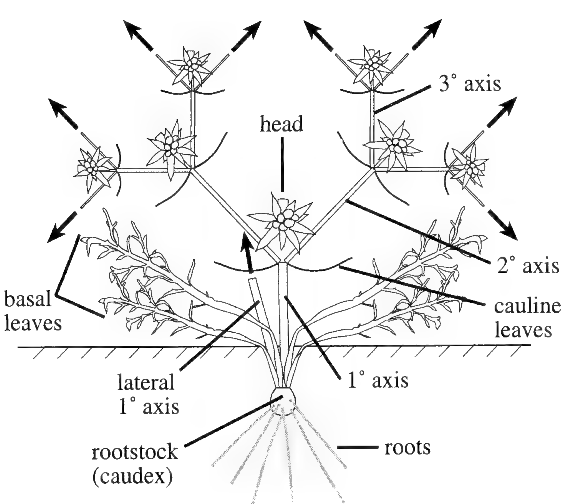

FIG. 1. Diagram of *Eryngium pendletonensis* growth habit. Note that axes actually have a sprawling, not erect, habit.

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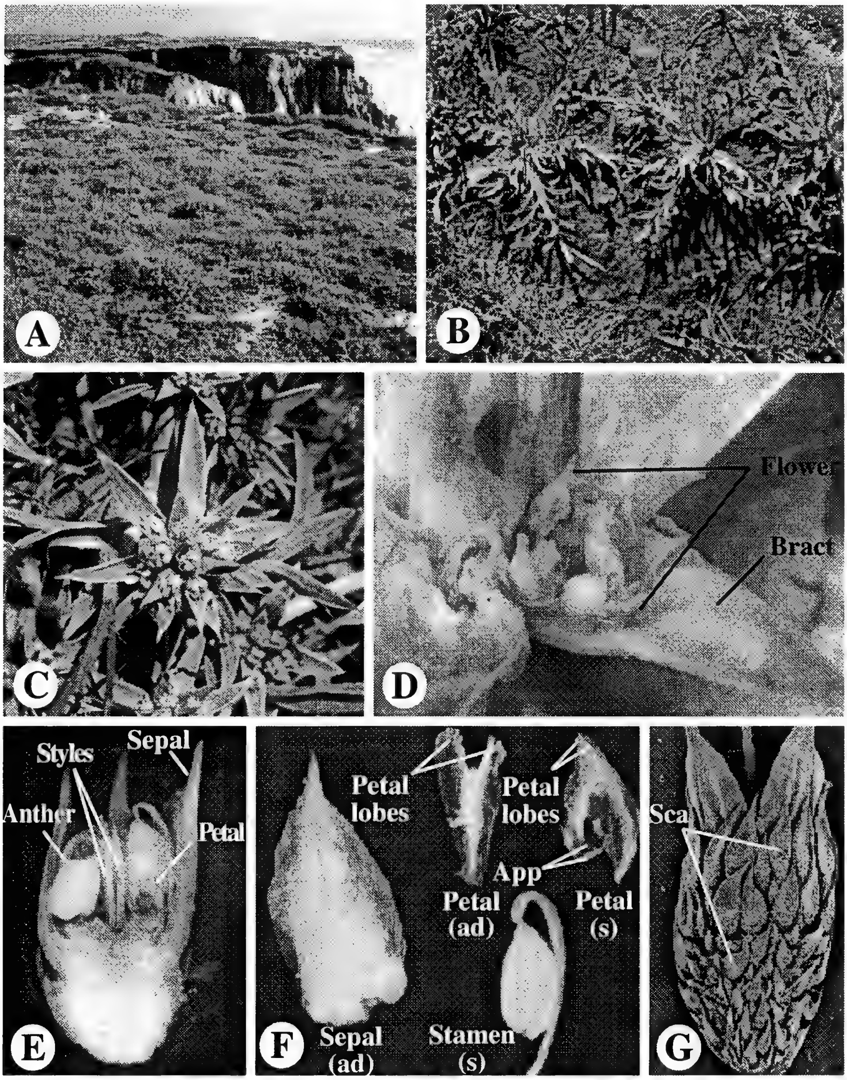

FIG. 2. *Eryngium pendletonensis.* A. Habitat, type locality. B. Whole plant, prior to flowering. C. Head with flowers subtended by bracts. D. Close-up of flower and bract. E. Flower close-up, with facing sepals, petals, and stamens removed. F. Dissected floral parts. G. Mature fruit, showing numerous scales (scanning electron micrograph). Abbreviations: App = appendages of petal; Sca = scales of fruit; (ad) = adaxial side facing; (s) = side view (adaxial at left).

base to apex of head), sessile, narrowly triangular to lanceolate, flat to conduplicate, apically acuminate-spinose, margins entire, thickened, abaxial surfaces mostly with very sparse to dense, minute scabrosity, especially along the veins, with white membranous basal sheaths at lower third, sheaths open, wrapping around the ovary, margins sometimes overlapping; perianth dichlamydeous, imbricate; calyx aposepalous, approximately 2 mm long, green; sepals oblong to ovate, 1-veined, with widely scarious margins, each apex with an apiculate process (Fig. 2E, F); corolla apopetalous; petals ca. 1 mm long, white, membranous, delicate, caducous, 1-veined, surface folded along central vein such that abaxial surfaces face one another (reduplicate); apex incurved to near petal base, ending in 2 elongate appendages; folded surfaces forming fimbriate lobes at mid-region (Fig. 2E, F); androecium uniseriate; stamens 5, apostemonous, whorled, antisepalous; filaments incurved early in development, extended and ca. 2.1 mm long at maturity; anthers yellow, narrowly oblong, thecae angled in cross-section, basifixed, longitudinally dehiscent; ovary inferior, 1–1.2 mm long, obovoid, slightly angled, covered with overlapping, hyaline scales persistent in fruit; carpels and locules 2; placentation apical-axile; ovules 1 per carpel; stylopodium low, 2-lobed; styles 2, ascending; stigmas terminal, obscure; fruits oblance-ovoid, prismatic, 5-angled and ribbed; scales lanceolate to lance-ovate, acuminate,

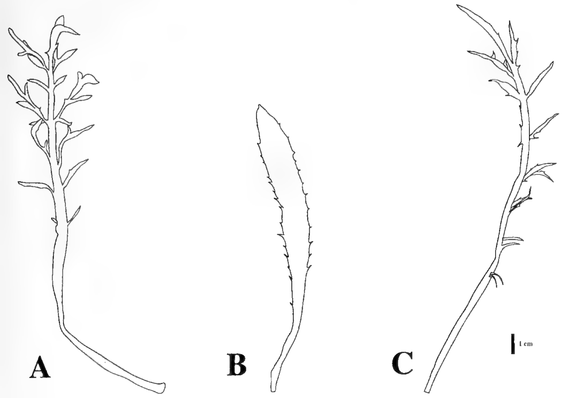

FIG. 3. Leaf outlines. A. *Eyngium pendletonensis*. B. *E. armatum*. C. *E. pinnatisectum*.

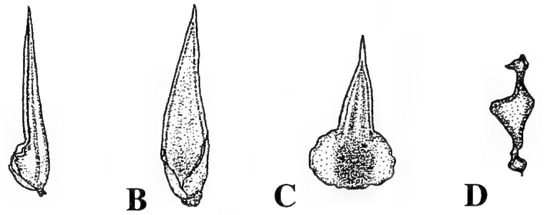

FIG. 4. *Eryngium pendletonensis* flower bracts. A. Outer flower bract, side view, adaxial at left. B. Outer flower bract, adaxial side facing. C. Inner flower bract, flattened to show scarious base, adaxial side facing. D. Outer bract cross-section at mid-region, showing thickened margins.

variable in size (Fig. 2G); cotyledons linear. Chromosome number: $2n=16$ II (counted at metaphase I of microsporogenesis; equivalent to $2n=32$; see Strother & Nesom 1997).

Paratype. Near Oceanside, southern California, 16 Apr 1902, G. B. Grant, *s.n.*, (DS 129228).

Distribution, habitat, phenology, and rarity. *Eryngium pendletonensis* is a narrow endemic to San Diego County, CA, in ca. 25 square kilometers (9 square miles) of Camp Pendleton Marine Corps Base (ranging within 33°21′04″–33°33′11″N; 117°23′27″–117°31′40″W), where it occurs along exposed coastal bluffs (Fig. 2A) and grasslands. Clay soils of the Huerhuero series (Bowman 1973) are the substrate type. The vegetation type of the surrounding area is disturbed native grassland or sparse Coastal Sage Scrub. Common associates include *Artemisia californica* Less., *Dudleya blochmaniae* (Eastw.) Moran, *Hemizonia fasciculata* (DC.) Torrey & A. Gray, *Lasthenia californica* Lindley, *Chlorogalum parviflorum* S. Watson, *Linanthus dianthiflorus* (Benth.) E. Greene, *Isocoma menziesii* (Hook. & Arn.) G. Nesom, *Grindelia camporum* E. Greene var. *bracteosum* (J. Howell) M. A. Lane, *Sisyrinchium bellum* S. Watson, *Brodiaea filifolia* S. Watson, *Juncus bufonius* L., *Nasella pulchra* (A. Hitchc.) Buckworth, *Vulpia myuros* (L.) C. Gmelin, *Avena barbata* Link, and *Bromus* spp.

Plants flower from April to June. Flowering is diurnal and is roughly synchronous within a population. Heads remain largely intact in fruit. Small beetles, flies, native bees, and wasps have been observed visiting the flowers.

Factors contributing to the rarity of *Eryngium pendletonensis* include its narrow habitat specificity and small geographic range. The species has a patchy distribution and can be locally abundant within subpopulations. Although no population trend data are available, ongoing military training activities pose a threat to this species. Populations that occur on the coastal bluffs are especially at risk.

Relationships. Within *Eryngium* sect. *Armata*, *E. pendletonensis* resembles *E. armatum* (S. Watson) J. Coulter & Rose and *E. pinnatisectum* Jepson in having flower bracts with thickened, entire margins (Fig. 4). All other species in this section have flower bracts with unthickened, spinose margins. *Eryngium pendletonensis* differs from *E. armatum* in that the latter has undivided, serrate leaves (Fig. 3B). *Eryngium pendletonensis* differs from *E. pinnatisectum* (Fig. 3C) in that the former has a shorter primary axis (Fig. 5), a sprawling (as opposed to more erect) habit, fewer flowers per head, and reduced scabrosity on flower bracts and ribs of stem axes, resulting in a mostly greenish coloration (as opposed to silvery in *E. pinnatisectum*).

REVISED KEY TO THE SPECIES OF ERYNGIUM IN CALIFORNIA

(Appropriate section modified from the Jepson Manual, Hickman 1993, 1996)

4. Bracts and bractlets very rigid, margins gen entire, prominently thickened
5. Lf unlobed, margin gen sharply serrate to irregularly cut . . . . *E. armatum*
5′ Lf pinnately to bipinnately lobed

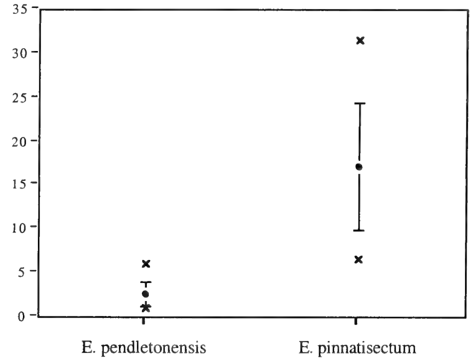

FIG. 5. Primary axis length (in centimeters) of *E. pendletonensis* (sample size = 42 individuals) and *E. pinnatisectum* (sample size = 23 individuals). Means = ●; ranges = x; bars = ±1 standard deviation of the mean.

6. Pl erect, silvery, primary stem axis 7–32 cm; n&c SNF . . . . *E. pinnatisectum*
6′ Pl sprawling, greenish, primary stem axis 1–6 cm; SCo. . . . . *E. pendletonensis*
4′ Bracts and bractlets ± flexible, margin gen sharply toothed, not thickened

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October 21, 1999
Evolution and Ecology of *Arctostaphylos*
Dr. Tom Parker, Professor
San Francisco State University

November 18, 1999
Seed Predation, Seed Dormancy, and Plant Population
Dynamics in the Yellow Bush Lupine
Dr. Ellen Simms, Director
University of California Botanic Garden

January 20, 2000
New Directions for the California Native Plant
Society's Rare Plant Program
Dr. Ann Dennis, Director
Cal Flora Project

February 19, 2000 ANNUAL MEETING (at UCB)
What do We Know about the Origin of Angiosperms?
Dr. Jim Doyle, Professor of Botany
University of California Davis

March 16, 2000
Floristic Tour of Iran
Dr. Fosiee Tahbaz, Research Associate
University of California Herbaria

April 20, 2000
Origin of the California Tarweeds
Dr. Bruce Baldwin, Curator,
the Jepson Herbarium
University of California Berkeley

May 18, 2000
Evolution and Distribution of the North American Thistles
Dr. Dean Kelch, Research Associate,
the Jepson Herbarium
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MADROÑO, Vol. 46, No. 2, pp. 69–79, 1999

CANOPY GAPS, ZONATION AND TOPOGRAPHY STRUCTURE: A NORTHERN COASTAL SCRUB COMMUNITY ON CALIFORNIA COASTAL BLUFFS

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San Francisco, CA 94132

ABSTRACT

We examined northern coastal scrub vegetation in relation to canopy gap formation, zonation and topographic relief on coastal escarpments (bluffs) in San Mateo County, CA. Vegetation was sampled in quadrats, along line transects and within gaps in the canopy of the dominant shrub *Baccharis pilularis* DC. (*Baccharis* gaps) on three topographically distinct coastal bluffs. *Baccharis* gaps were also sampled for area, light penetration, distance from the bluff edge, and residual branch height. Thirty-seven species were encountered in quadrats at the three sampling sites. *Baccharis pilularis* and *Eriophyllum staechadifolium* Lagasca were the dominant species, together comprising 67% cover at the three sites. Canopy gaps averaged 0.96 m^2 in area and occupied 58% of the area sampled. Species composition and relative abundance was strongly influenced by percent canopy gap. Cover of *Scrophularia californica* Cham. & Schldl. was found to increase with increasing percent canopy gap. Thirty-eight percent of species occurred exclusively in quadrats dominated by canopy gaps. Species richness showed a positive relationship to percent canopy gap and to *Baccharis* gaps with greater light penetration. Line transects indicated distinct species and gap zonation on the three bluff sites sampled. Differences in species composition, species relative abundance and vegetation height were also found among the three coastal bluff sites. At the spatial scale of an individual bluff, our results suggest that canopy gaps and zonation are important in maintaining the diversity of northern coastal scrub in San Mateo County. Variation in topographic relief among neighboring bluff sites also appears to play a role in maintaining species diversity at larger spatial scales.

Northern coastal scrub occurs in a narrow and discontinuous region along the Pacific coast of North America from southern Oregon to Point Sur, Monterey Co., CA (Munz and Keck 1968; Ornduff 1974; Heady et al. 1988). The vegetation is characterized by low (<2 m) shrubs and a conspicuous herbaceous component (Heady et al. 1988). Throughout much of its range, northern coastal scrub occurs with coastal prairie and together they form a mosaic that is interrupted by oak woodland, mixed evergreen forest, closed-cone pine forest and fresh and saltwater marshes (Ornduff 1974; Axelrod 1978; Bakker 1984; personal observation).

Few studies have examined the community structure and diversity of northern coastal scrub vegetation. These investigations have focused on scrub invasion of grassland (McBride and Heady 1968; Hobbs and Mooney 1986; Williams et al. 1987), the effects of fire and grazing suppression (Elliot and Wehausen 1974; McBride 1974) and vegetation patterns in relation to slope-aspect (Grams et al. 1977), salt spray (Barbour 1978; Holton Jr. and Johnson 1979), and north-south range transitions (Heady et al. 1988).

There is little information on northern coastal scrub community structure and diversity in distinctly maritime locations in central California (but see Barbour 1978; Holton Jr. and Johnson 1979). Here, northern coastal scrub occurs on a topographically diverse system of coastal escarpments, or bluffs. These bluffs are exposed to different intensities of wind, solar radiation and sea-salt deposition, each of which can influence plant community structure (Boyce 1954; Malloch 1972; Barbour 1978; Holton Jr. and Johnson 1979). Northern coastal scrub on coastal bluffs is distinct in species composition and physiognomy from that occurring inland (Heady et al. 1988). The vegetation in many locations is prostrate (≤ 0.2 m) and large openings (gaps) in the canopy of the dominant shrub, *Baccharis pilularis* DC., are a prominent feature of the scrub vegetation. These patterns, and the factors responsible for creating them, have not been well studied, nor has their influence on plant diversity been investigated.

We investigated the influence of canopy gaps, zonation, and topographic relief on northern coastal scrub community structure and diversity on coastal escarpments in San Mateo Co., CA. We hypothesized that canopy gaps play a role in maintaining species diversity at a local spatial scale (i.e., within individual bluffs). To test this hypothesis, we investigated the relationship between the extent of canopy gaps and species composition, relative abundance and richness. In addition, we examined the relationship between gap structure and species diversity. We also hypothesized that coastal scrub

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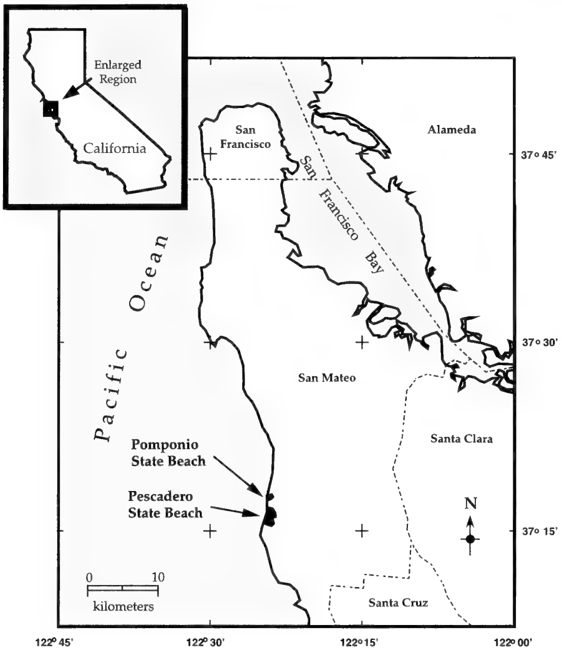

FIG. 1. Location of the three bluff sites studied. Site 2 was located at Pomponio State Beach and Sites 1 and 3 were located at Pescadero State Beach.

species would show zonation with respect to distance from the bluff edge. This hypothesis was tested by sampling vegetation along line transects extending away from the cliff edge. Finally, we hypothesized that variation in topographic relief among coastal bluffs is important in maintaining species diversity at larger spatial scales. This hypothesis is based on the assumption that differences in topographic relief among bluffs should expose individual escarpments to distinct environmental conditions (e.g., wind impact, solar radiation, and salt spray deposition), thereby altering scrub community composition. To examine this we compared bluff sites with respect to species composition and abundance.

STUDY AREA

Physical environment. This study was conducted within Pescadero and Pomponio State Beaches in San Mateo Co., CA. (37°17′N, 122°24′W) (Fig. 1). The study sites were located on coastal terrace escarpments derived from uplifted Pleistocene marine sediments of mixed origin (Wagner and Nelson 1961). Coastal terrace escarpments, or bluffs, are a common topographic feature along this coast and range widely in elevation, slope and aspect. Bluffs in this region may range in elevation from 20 to 50 m, with cliffs at their coastal margins.

The climate is Mediterranean, with mild, wet winters and warm, dry summers. Due to the maritime influence, temperatures are cool year round. At San Gregorio, approximately 5 km north of the study sites, mean annual temperature is 13°C (U.S. Weather Bureau 1979–1989). Temperatures range from a monthly mean low of 10°C in January, to a monthly mean high of 16°C in August. Mean annual precipitation at San Gregorio is 773 mm, with over 95% falling between September and April (U.S. Weather Bureau, 1979–1989). Although official records are not kept on its occurrence, summer fog is common along the central California coast and may provide additional moisture in the form of fog drip.

North-northwesterly winds are constant, with the highest velocities in winter and spring. Average wind speed is 21.7 km/h at Pescadero (California Surface Wind Climatology 1992). Sea-salt aerosols are carried by the wind and deposited on the soil and vegetation (Clayton 1972; Barbour 1978).

Vegetation. Northern coastal scrub is composed of a diverse community of shrubs, perennial herbs, and vines. Characteristic species include *Baccharis pilularis, Eriophyllum staechadifolium* Lagasca, *Gaultheria shallon* Pursh, *Eriogonum latifolium* Smith, *Erigeron glaucus* Ker-Gawler, *Heracleum lanatum* Michaux, *Anaphalis margaritacea* (L.) Benth. & Hook., and *Rubus* spp. On the San Mateo Co. coast, the physiognomy and species composition of northern coastal scrub differ as a function of exposure to ocean influence (Clayton 1972). The vegetation on the immediate coast is lower in stature (<1 m) than shrubland several hundred meters from the beach (Clayton 1972; Heady et al. 1988; personal observation). A prostrate form of *Baccharis pilularis,* which was noted by Hoover (1970) in San Luis Obispo Co., by Clayton (1972) in San Mateo Co., and by Holton Jr. and Johnson (1979) at Point Reyes Peninsula, also occurs on these bluffs and ranges from extremely prostrate (<0.1 m) to approximately 1 m in height.

Openings in the vegetation canopy are a prominent feature of northern coastal scrub on coastal bluffs in San Mateo Co. (Fig. 2). We refer to these openings as canopy gaps and define them as contiguous regions within one or more shrubs of the same species that are virtually devoid of leaves and ≥ 0.2 m in diameter. Although the individual shrub in which a canopy gap occurs may be alive or dead, branches are generally still present within gaps. Canopy gaps occur primarily within the crowns of live *B. pilularis.* Although less frequent, gaps also occur in *E. staechadifolium* and *Lupinus arboreus* Sims.

METHODS

Site selection. Three bluff sites were chosen that differed in slope, aspect and apparent exposure to wind and sea-salt deposition (Table 1, Fig. 1). The three sites were numbered in order of presumed maritime influence, Site 1 being the most exposed and Site 3 the least. Sites were intact stands of

FIG. 2. Site 2, showing the extent and distribution of *Baccharis* gaps. Arrow indicates a *Baccharis* gap.

northern coastal scrub that showed minimal signs of human disturbance.

Vegetation sampling. To examine the role of canopy gaps, zonation, and topography on plant species distribution and diversity, we sampled vegetation in quadrats, along line transects and within individual gaps in the canopy of *Baccharis pilularis.* We refer to these gaps as *Baccharis* gaps. Sampling was completed between April and July 1992.

Quadrats. We estimated species relative percent cover and percent frequency from fifty-eight 1 × 0.75 m quadrats. Vegetation height and distance from the cliff edge were also determined for each quadrat. In addition, the proportion of a quadrat constituting a canopy gap (i.e., percent gap), as previously defined, was estimated. Canopy gaps were classified as "*Baccharis* gaps," if they occurred within this shrub, or "Other gap." Sites were sampled in a stratified random fashion to ensure adequate representation of each site. Eight quadrats were sampled at Site 1, thirty-two quadrats at Site 2, and eighteen at Site 3. Species area curves for each site indicated that samples adequately captured the diversity present.

Throughout this study, the presence of unstable cliffs at Site 1 and the position of Site 3 on the bluff required that we sample these sites at 7 and 24 m from the cliff edge, respectively. A more stable bluff at Site 2 allowed sampling up to 0.5 m from the cliff edge.

Line transects. We examined zonation by sampling vegetation and canopy gaps along line transects at each site. Three transects per site were randomly placed, running parallel to the direction of

TABLE 1. AREA, ELEVATION, SLOPE AND ASPECT OF THE THREE COASTAL BLUFF SITES STUDIED. * NA = not applicable.

Site	Area (ha)	Elevation (m)	Slope	Aspect
1	0.1	37	20°	275°
2	0.5	45	0°	NA*
3	0.2	38	8°	90°

TABLE 2. DEFINITIONS OF THE 3 CLASSES USED TO INDEX RELATIVE LIGHT PENETRATION IN *BACCHARIS* GAP SAMPLES.

Gap class	Definition
1	None to very few branches within the gap; maximum light penetration at the soil level.
2	Moderate density of small diameter branches within the gap; moderate light penetration at the soil level.
3	High density of small branches within the gap; low light penetration at the soil level.

TABLE 3. SPECIES RELATIVE COVER (% COVER) AND FREQUENCY (% FREQ.) AT EACH SITE AND FOR ALL SITES COMBINED. Cover and frequency values were determined from quadrat samples. No entry indicates that the species was not encountered.

	Site							
	1		2		3		All sites	
Species	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.
Shrubs								
Baccharis pilularis	24.3	100	59.8	94	32.3	89	46.4	93
Eriophyllum staechadifolium	19.7	100	5.9	44	49.2	89	20.2	66
Lupinus arboreus	—	—	0.5	16	—	—	0.3	9
Artemisia californica	—	—	0.8	3	—	—	0.5	2
Perennial Herbs								
Erigeron glaucus	7.9	50	14.3	72	—	—	9.3	47
Achillea millefolium	1.7	38	3.4	53	4.8	50	3.5	50
Scrophularia californica subsp. *californica*	2.2	63	5.3	34	1.7	11	3.8	31
Iris douglasiana	9.2	75	0.2	3	—	—	1.6	12
Castilleja latifolia	—	—	1.1	16	—	—	0.6	9
Aster lentus	0.6	13	0.6	6	0.7	6	0.6	7
Angelica hendersonii	3.7	25	—	—	—	—	0.6	3
Solidago canadensis subsp. *elongata*	4.5	13	—	—	—	—	0.7	2
Horkelia californica subsp. *californica*	—	—	—	—	0.9	6	0.3	2
Stachys ajugoides subsp. *rigida*	0.5	13	—	—	—	—	<0.1	2
Gnaphalium purpureum	—	—	<0.1	3	—	—	<0.1	2
Gnaphalium stramineum	—	—	<0.1	3	—	—	<0.1	2
Perennial Vines								
Rubus ursinus	6.8	38	1.0	6	—	—	1.7	9
Satureja douglasii	4.0	13	1.2	9	—	—	1.3	7
Carpobrotus edulis	—	—	0.4	3	—	—	0.2	2
Perennial Grasses								
Agrostis densiflora	—	—	<0.1	3	0.2	6	0.1	3
Bromus carinatus var. *maritimus*	—	—	0.5	6	—	—	0.3	3
Deschampsia elongata	—	—	<0.1	3	—	—	<0.1	3
Perennial Rushes/Sedges								
Juncus patens	1.4	38	2.1	19	—	—	1.4	16
Juncus sp.	—	—	—	—	0.5	6	0.1	2
Carex obnupta	—	—	1.3	9	—	—	0.7	5
Carex sp.	—	—	<0.1	3	—	—	<0.1	2
Ferns								
Polypodium californicum	4.8	38	—	—	—	—	0.8	5
Dryopteris arguta	0.3	13	—	—	—	—	<0.1	2

TABLE 3. CONTINUED

Species	Site 1		Site 2		Site 3		All sites	
	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.
Annual Herbs								
Daucus pusillus	0.2	13	<0.1	3	—	—	<0.1	3
Centaurium davyi	—	—	<0.1	3	—	—	<0.1	2
Sonchus asper subsp. *asper*	—	—	<0.1	3	—	—	<0.1	2
Annual Vines								
Galium aparine	3.8	63	—	—	4.5	67	1.9	29
Pterostegia drymarioides	2.7	75	—	—	1.6	28	0.9	19
Anagallis arvensis	0.8	25	0.1	6	1.7	33	0.7	17
Annual Grasses								
Vulpia bromoides	0.8	25	0.9	28	1.9	17	1.1	24
Agrostis sp.	—	—	<0.1	6	<0.1	6	<0.1	3
Aira caryophyllea	—	—	<0.1	6	—	—	<0.1	2

the prevailing north-northwesterly winds (~135°). Transects were 20 m at Site 1 and 30 m at Sites 2 and 3. Percent vegetation cover, percent gap, and vegetation height were recorded in 0.5 m units along transects.

Baccharis *gaps.* We sampled canopy gaps occurring in *B. pilularis* to investigate relationships between gap structure and species diversity. Fifty-eight *Baccharis* gaps were sampled at the three bluff sites, eight at Site 1, thirty-two at Site 2, and eighteen at Site 3. *Baccharis* gaps were selected within sites in a stratified random fashion. Gap area (m^2), height of the branch material within gaps, and distance to the nearest cliff edge were recorded for each gap. In addition, *Baccharis* gaps were assigned to one of 3 classes, which indexed the relative degree of light penetration into the gap. *Baccharis* gap classes are defined in Table 2.

Data analyses. We used principal component analysis (PCA) and multivariate analysis of covariance (MANCOVA) to test differences in community composition and relative abundance among sites and with respect to percent canopy gap. In the PCA we used a variance-covariance matrix with cover values of species that occurred more than once in the data set (i.e., 24 species, accounting for 98% of total plant cover). The broken-stick method was used to determine the number of axes retained (Jackson 1993). We then used the principal component scores of the first two principal component axes in a MANCOVA to test community-level differences among the three sites and with respect to percent canopy gap (Morin et al. 1990). Percent gap was used as the covariate. Pearson's product moment correlation was used to examine species relationships with the principal component axes.

To evaluate the relationship between species cover and percent canopy gap in quadrat samples, we used regression analysis on arcsine-square root transformed cover values. Regression was also used to assess the relationship between species richness and canopy gap variables as well as between bluff position and vegetation height. We compared species cover and percent canopy gap along line transects using either the Mann-Whitney U test (Site 1) or the Kruskal-Wallis test (Sites 2 and 3). Differences in species richness among the three gap classes were compared using the Kruskal-Wallis test. Tukey's Studentized Range test was used to distinguish treatment means in all parametric analyses. Means in all Kruskal-Wallis tests were distinguished using Dunn's multiple comparison test.

We conducted the PCA using PC-ORD version 3.01 (McCune and Mefford 1997). Parametric analyses were performed using Statistical Analysis Software version 6.12 (SAS Institute 1990). Nonparametric analyses were conducted using GraphPad Prism version 3.00, GraphPad Software, San Diego, CA.

TABLE 4. MEAN (±1 SE) % AREA OCCUPIED AND SIZE OF *BACCHARIS* GAPS AND OTHER GAPS IN VEGETATION SAMPLES AT EACH BLUFF SITE AND FOR ALL SITES COMBINED.

		Sites			
Gap type	Variable	1	2	3	All sites
Baccharis	% Area	53 (10)	49 (5.4)	34 (8.1)	45 (3.7)
	Size (m^2)	0.95 (0.26)	0.97 (0.24)	0.94 (0.16)	0.96 (0.15)
Other	% Area	12 (6.3)	9.4 (5.0)	21 (9.0)	13 (3.5)

RESULTS

General vegetation patterns. Of the thirty-seven plant species encountered in quadrats from the three coastal bluff sites, twenty occurred at Site 1, twenty-seven at Site 2, and thirteen at Site 3 (Table 3). *Baccharis pilularis* and *Eriophyllum staechadifolium* were the dominant species, together comprising 67% cover at the three sites. Other common species encountered in quadrats were the perennial herbs *Erigeron glaucus, Achillea millefolium* L. and *Scrophularia californica* Cham. & Schldl.

Canopy gaps in *B. pilularis* (*Baccharis* gaps) were a common structural feature on the three bluff sites, with 45% of the area sampled occupied by these gaps; Other gaps occupied 13% of the area sampled (Table 4). Although percent area occupied by *Baccharis* gaps and Other gaps varied across sites, no significant differences were detected. *Baccharis* gaps averaged 0.96 ± 0.15 m^2 in area and ranged from 0.14 to 7.68 m^2, with 90% of gaps less than 2 m^2.

Quadrat samples. Overall differences in the scrub community among the three bluff sites are illustrated in a PCA diagram (Fig. 3). The two axes retained in the analysis accounted for 81% of the total variance, with Axis 1 accounting for 60.6% and Axis 2 20.6% of the variance (Table 5). Coastal scrub species composition and abundance differed significantly across the three bluff sites (MANCOVA: $P < 0.001$). Means comparisons showed that Axis 1 distinguished Site 2 from Sites 1 and 3, and Axis 2 distinguished Site 3 from Sites 1 and 2. Based on correlations of individual species in the ordination (Table 5), Axis 1 separated quadrats among sites based on the abundance of *B. pilularis* at Site 2 and *E. staechadifolium* and *Anagallis arvensis* L. at Sites 1 and 3. Likewise, Axis 2 distinguished samples based on the abundance of *E. staechadifolium* at Site 3 versus *E. glaucus* and *S. californica* at Sites 1 and 2.

A highly significant effect of percent canopy gap on plant species composition and abundance was also detected in the MANCOVA ($P < 0.001$). Thus, irrespective of site differences, a substantial amount of variation in species composition and abundance was explained by the extent of canopy gaps. This is illustrated in the PCA diagram (Fig. 3), which distinguishes samples with ≥ 50% canopy gap from those with < 50% canopy gap.

Cover of *S. californica* showed a significant positive relationship to percent canopy gap, as indicated by regression analysis ($R^2 = 0.067$; $P = 0.049$). No significant relationships were observed for other species. However, when quadrats were separated into those with ≥ 50% canopy gap versus those with < 50% canopy gap, fourteen species occurred exclusively in quadrats dominated by canopy gap and were not encountered in other samples. Several of these species are typical coastal prairie species (e.g., *Agrostis densiflora* Vasey, *Centaurium davyi* (Jepson) Abrams, *Agrostis* sp. and *Aira caryophyllea* L.). *Carpobrotus edulis* (L.) N.E. Br., which is an invasive perennial vine in coastal California, was also found only in gap-dominated samples. By contrast three species occurred exclusively in vegetation-dominated quadrats.

Although there was substantial variation in the data, a significant positive relationship was observed between species richness and percent canopy gap in quadrat samples (Fig. 4). Using the 50% cut-off between vegetation- and gap-dominated samples, quadrats with ≥ 50% *Baccharis* gap had a mean of 4.3 ± 0.5 species compared to 2.7 ± 0.3 in the remaining samples (mean ± SE).

TABLE 5. EIGENVECTORS (EIGEN.) AND PEARSON CORRELATION COEFFICIENTS (R) FOR THE FIRST TWO PRINCIPAL COMPONENT AXES DERIVED FROM THE PCA. Species shown were significantly correlated to at least one axis. Eigenvalues for Axis 1 and 2 are 4.28 and 1.44, respectively. Boldface correlation coefficients are significant at $P < 0.05$.

	Axis 1		Axis 2	
Species	Eigen.	r	Eigen.	r
Baccharis pilularis	0.9345	**0.98**	0.3460	0.21
Eriophyllum staechadifolium	−0.3420	**−0.55**	0.8798	**0.82**
Erigeron glaucus	0.0778	0.22	−0.2989	**−0.49**
Scrophularia californica	−0.0077	−0.04	−0.1024	**−0.30**
Anagallis arvensis	−0.0126	**−0.30**	0.0150	0.20

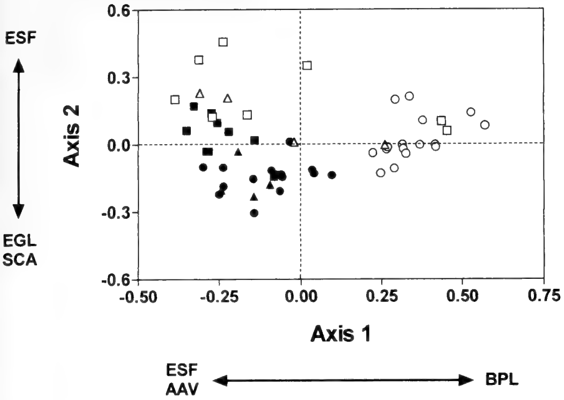

FIG. 3. Ordination of 58 quadrats from Sites 1–3 by principal component analysis along two axes. Black symbols are samples with ≥ 50% canopy gap; white symbols are samples with < 50% gap. Site 1, squares; Site 2, circles; Site 3, triangles. Arrows indicate significant correlations between individual species and axes. BPL = *B. pilularis*; EGL = *E. glaucus*; ESF = *E. staechadifolium*; AAV = *A. arvensis*.

Line transects. Cover of *E. glaucus* increased significantly in 10 m distance classes along transects at Sites 1 and 2 ($P < 0.001$ and $P = 0.012$, respectively; Fig. 5) but was not encountered at Site 3. In contrast, cover of *S. californica* decreased significantly along transects extending away from the cliff edge at Site 2 ($P = 0.01$). *Rubus ursinus* Cham. & Schldl. which was also not encountered at Site 3, decreased significantly away from the cliff edge at Sites 1 and 2 ($P < 0.001$ and $P = 0.027$, respectively). Significantly higher cover near the cliff edge was also detected for *E. staechadifolium* and *A. millefolium* at Site 2 but the spatial patterns were less clear. *Vulpia bromoides* (L.) S.F. Gray was the only species that showed zonation at Site 3, decreasing in abundance at 24 m and farther from the cliff edge.

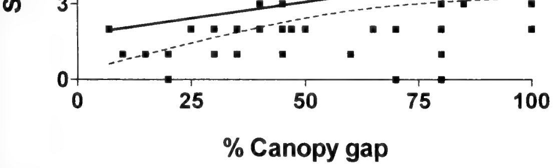

FIG. 4. Regression of species richness versus percent canopy gap for the 58 quadrats sampled. Dashed lines indicate 95% C.I. above and below the least squares fit line ($R^2 = 0.083$; $P = 0.028$).

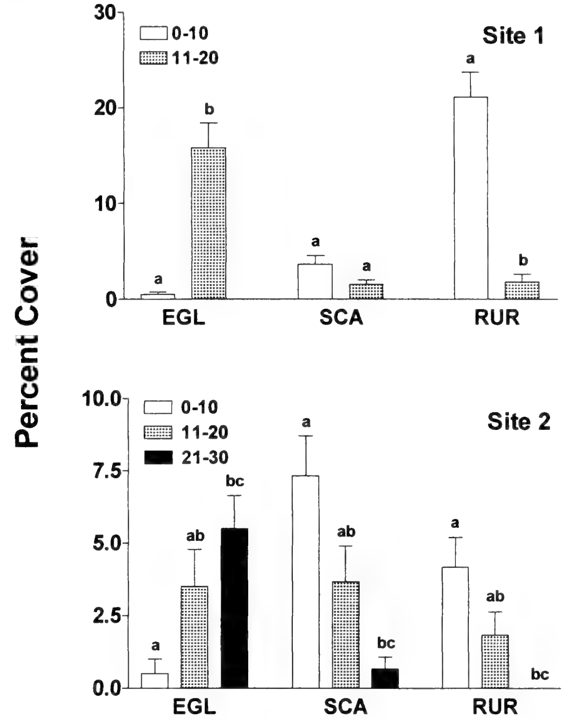

FIG. 5. Comparison of percent cover of *E. glaucus* (EGL), *S. californica* (SCA) and *R. ursinus* (RUR) in 10 m distance classes along transects at Sites 1 and 2. Values are means (±1 SE) of the three transects per site. Lower numbered distance classes are nearest to the cliff edge.

Zonation was also observed for *Baccharis* gaps and Other gaps (Table 6), although it was site-specific. No zonation of *Baccharis* gaps was observed at Sites 1 and 3. However, the extent of *Baccharis* gaps at Site 2 was lower within 20 m of the cliff edge than farther away. Other gaps showed significant zonation at Sites 1 and 3 but the spatial patterns were opposite. At Site 1, the extent of Other gaps in the nearest distance class to the cliff edge was higher than farther away. In contrast, at Site 3 the extent of Other gaps was highest in the farthest distance class from the cliff edge and lowest in the nearest distance class. No zonation was observed for Other gaps at Site 2.

TABLE 6. MEAN PERCENT *BACCHARIS* GAP (BG) AND OTHER GAP (OG) IN 10 M DISTANCE CLASSES ALONG TRANSECTS AT EACH SITE. Column means with different superscript letters are significantly different at $P < 0.05$.

	1		2		3	
	Sites					
Distance class (m)	BG	OG	BG	OG	BG	OG
0–10	42.3^{a}	25.0^{a}	27.0^{a}	3.0^{a}	39.5^{a}	17.8^{a}
11–20	44.5^{a}	12.0^{b}	35.8^{a}	7.7^{a}	40.0^{a}	23.5^{ab}
21–30	—	—	54.5^{b}	0.0^{a}	29.8^{a}	36.5^{b}

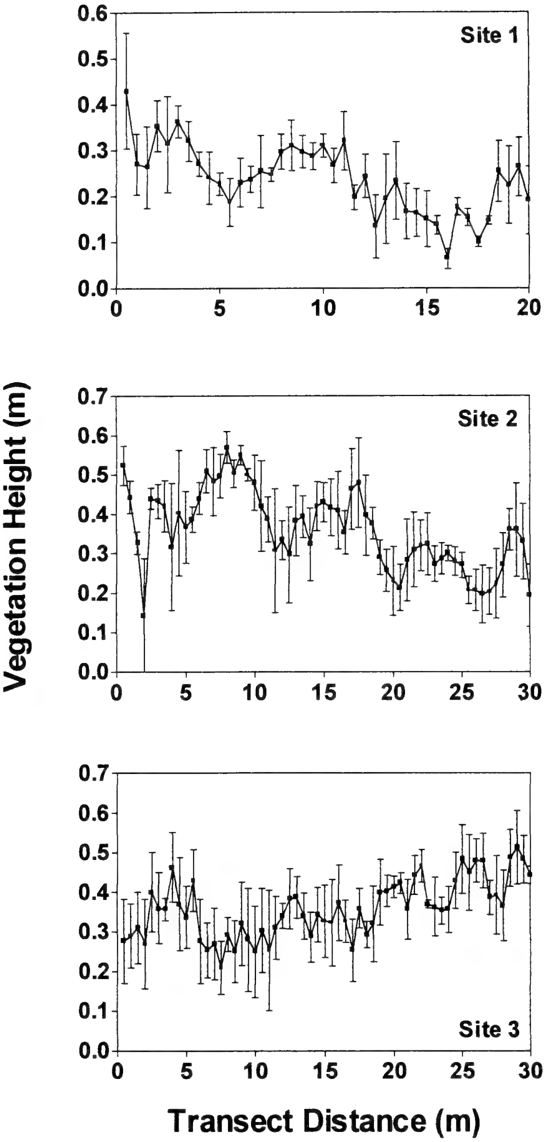

FIG. 6. Mean vegetation height along line transects at each site. Points are means of the three transects per site. Bars indicate ± 1 SE. Note the difference in scale on the x-axis for Site 1.

Mean vegetation height was lower at Site 1 than at Sites 2 or 3 ($P = 0.005$). The latter two sites did not differ from one another. Scrub height decreased with increasing distance from the bluff edge at Sites 1 and 2 ($R^2 = 0.539$, $P < 0.001$ and $R^2 = 0.438$, $P < 0.001$ respectively), but Site 3 showed the reverse pattern ($R^2 = 0.387$, $P < 0.001$) (Fig. 6). Sites 1 and 2 also exhibited a notable sinusoid pattern in vegetation height along transects.

Baccharis *gap samples.* Despite a fair amount of variability in the data, species richness showed a significant positive relationship to *Baccharis* gap area ($R^2 = 0.084$; $P = 0.028$) and a negative relationship to gap height ($R^2 = 0.199$; $P < 0.001$). However, no relationship was observed between species richness and gap distance from the nearest cliff edge. Species richness was highest in *Baccharis* gaps with the greatest light penetration ($P < 0.001$). The most open gaps (class 1) had 7 ± 1.5 species per gap versus 2.7 ± 0.7 in the most densely branched gaps (class 3) (mean ± SE). Gap class 2 had an intermediate number of species per gap (4.5 ± 0.4) and was significantly different than gap class 3 (mean ± SE). Although *Baccharis* gaps with the greatest light penetration were somewhat larger than gaps in class 2, they were not larger than those with the lowest light penetration (class 3).

DISCUSSION

Our results indicate that canopy gaps, zonation, and topography influence the distribution of scrub species on coastal bluffs in this study and that these factors may be important in the maintenance of northern coastal scrub species diversity. Canopy gaps, zonation, and topographic relief appear to be important at two distinct spatial scales. At the scale of an individual bluff (local scale), canopy gaps and zonation were important factors governing species distribution and diversity. At a larger landscape scale, coastal bluff topographic heterogeneity influenced the distribution of species among bluff sites. Differential exposure to wind, sea-salt aerosols, fog, and solar radiation may be important in generating these patterns at both spatial scales.

Local scale patterns. On individual coastal bluffs, canopy gaps and zonation were important in governing northern coastal scrub species distribution and diversity. In particular, canopy gaps had a strong influence on species composition and relative abundance and a large number of rare species occurred exclusively in gap-dominated (≥50% gap) quadrats. We also observed a positive relationship between species richness and percent canopy gap. Zonation was also observed, with the distribution of several species, canopy gaps and vegetation height influenced by bluff position.

Species zonation and vegetation height patterns observed on individual bluffs may be due to differences in soil moisture and the impact of wind and salt spray within bluffs. The importance of wind and salt spray as a constraint on the growth of coastal bluff species is well known (Oosting and Billings 1942; Boyce 1954; Malloch 1972). Barbour (1978) found that small-scale variation in salt spray deposition played an important role in influencing the distribution of northern coastal scrub vegetation at Point Reyes National Seashore. In this study moisture levels nearest the cliff edge may be higher due to stronger winds, decreased evapotranspiration, and greater insulation by taller and denser vegetation near the cliff edge. This could account for the distribution of several species typical of mesic habitats that occurred adjacent to the bluff edge (e.g., *R. ursinus*; Fig. 5). A greater impact of wind—and potentially salt spray—farther inland could also account for the decreased vegetation height observed away from the bluff edge at Sites 1 and 2. Decreased vegetation height away from the cliff edge at Sites 1 and 2 may have influenced zonation of several of the perennial herbs.

Differences in species composition between canopy gaps and scrub vegetation suggest that species responded differently to the contrasting conditions present in these two distinct habitat patches. In this study 38% of species were encountered only in quadrats dominated by canopy gaps compared to 8% in vegetation-dominated samples. Such a large proportion of "gap species" could explain the higher species richness we found in quadrats with higher percent gap. Although it occurred in both gap and scrub vegetation, the rhizomatous species *S. californica* occurred more often in gaps than the surrounding scrub. Indeed, a rhizomatous habit may be advantageous in this vegetation because clonal reproduction would allow for rapid establishment and colonization in newly formed gaps. Such establishment patterns by rhizomatous species have been observed in studies of old-field succession and disturbance (Beckwith 1954; Bazzaz 1979; Sebens and Thorne 1985).

Small spatial scale variation in salt spray deposition (Barbour 1978) and sensitivity to salt spray by the three gap-forming shrubs in this study suggest that sea-salt deposition could be an important factor generating canopy gaps in this vegetation. Holton Jr. and Johnson (1979) observed that the leaves of *B. pilularis* were significantly damaged by salt spray, more so than either *E. staechadifolium* or *L. arboreus.* This might explain why canopy gaps were most prevalent in *B. pilularis* (*Baccharis* gaps were encountered in 93% of samples versus 33% for Other gaps). Localized pockets of differential impact by wind and salt spray could also explain the patchy nature of gaps. Leaf senescence on the windward side of these shrubs and the wind-shaped growth form of the most exposed individuals also suggest that wind and salt spray deposition influence gap formation (Baxter, 1992). Although canopy gaps in *B. pilularis* could be caused by herbivory, it seems unlikely that the pattern of herbivory would mirror that of gaps, and we observed no evidence that this might be the case. Despite circumstantial evidence supporting the role of sea-salt deposition in gap formation, this mechanism needs to be tested in future studies.

Our observation that the smallest *Baccharis* gaps had the highest density of young branches and the largest gaps had few branches and were the most open and decayed suggests that *Baccharis* gaps may enlarge over time. The wide range of gap sizes and branch densities found in this vegetation also suggest that there is a mosaic of canopy gaps of different ages and, therefore, in different stages of succession.

Our results regarding the role of canopy gaps are consistent with a non-equilibrium patch dynamical system mediated by natural disturbance. Non-equilibrium disturbance-mediated dynamics have been proposed elsewhere as a mechanism driving species coexistence and the maintenance of species diversity (Pickett 1980). This mechanism suggests that over the entire community a mosaic of patches of different successional ages exist, all recovering from past disturbances and together providing a wider range of habitats or conditions to which species may become adapted (Grubb 1977; Denslow 1980, 1985). A patchy distribution of resources could also buffer competitive interactions (Chesson and Huntly 1989) or limit the ability of some species to colonize new patches (Tilman 1994). Differential species tolerances and resource requirements are also important in determining species coexistence in heterogeneous environments (Tilman 1982; Keddy 1984).

Consistent with disturbance-mediated gaps in other systems (Levin and Paine 1974), canopy gaps in the scrub vegetation introduce a high degree of structural and resource heterogeneity. For example, light levels in gaps are higher than under the surrounding scrub canopy and, together with low litter inputs, increased solar radiation likely reduces within-gap moisture levels. Soil nutrients may also be less available due to greater soil leaching, low leaf litter inputs and lower rates of nutrient mineralization. However, canopy gaps in northern coastal scrub differ from other disturbance-mediated gaps in that they form over a long period of time and occupy an unusually large cumulative area (45% aerial coverage), which appears to be recolonized slowly.

Landscape patterns. Differences in species composition and abundance among the three coastal bluff sites in this study suggest that topographic relief influences northern coastal scrub species composition and relative abundance. This is consistent with Grams et al. (1977), who suggested that soil moisture, as determined by site exposure, is an important determinant of northern coastal scrub species composition. Although environmental factors were not measured, it is likely that variation in wind, sea-salt deposition, fog, and solar radiation among our topographically distinct bluff sites influenced plant species composition by affecting the moisture regime among sites.

By influencing evapotranspiration rates, and soil water availability, wind and the deposition of sea-salts onto the soil and vegetation can have a strong influence on coastal species, including those in California coastal communities (Barbour 1978; Ogden 1979). Indeed, increased soil salinity levels caused by sea salt deposition were observed to increase plant water stress (Boyce 1954), suggesting lower soil water availability.

Because salt spray deposition increases with increasing wind speed (Malloch 1972), the level of salt spray deposition should vary depending on bluff exposure. Sites exposed to the direct impact of the prevailing winds should receive the highest inputs of sea-salts and show the greatest vegetation response to salt spray deposition. Low mean vegetation height at Site 1 suggests increased wind impact, perhaps in combination with elevated salt spray deposition. Notably, a preliminary assessment of salt spray deposition at the three bluff sites resulted in 8 of 9 filter paper collector strips at Site 1 being torn off of the microscope slides on which they were mounted (no evidence of animal removal was observed). Filter paper strips remained intact at the other two sites. Although this suggests higher wind velocity at Site 1, it could not be determined if higher levels of salt spray were actually deposited at this site.

Differences among bluffs in solar radiation or precipitation via fog drip may also alter soil moisture and influence the distribution of species. For example, *E. staechadifolium,* which was most abundant at Site 3, is often found in mesic habitats (Grams et al. 1977), suggesting that Site 3 may be wetter than Sites 1 or 2. Similarly, the presence at Site 2 of *Artemisia californica* Less. and *Satureja douglasii* (Benth.) Briq., which tend to occur in drier locations (Grams et al. 1977), suggests that this site may be relatively dry.

Although bluff topography may influence the composition and distribution of northern coastal scrub species by affecting the moisture regime of individual escarpments, this appears to occur in a complex way. For instance, the tendency of ocean-facing bluffs to be xeric from direct exposure to prevailing winds and salt deposition may be counteracted by additional input of precipitation via fog drip. In this way fog may act to mediate evapotranspirative moisture loss on exposed sites. Indeed, several species that typically occur in mesic habitats were found at Site 1, which is most exposed to the impacts of wind and salt spray.

In conclusion, canopy gaps, zonation, and topography played an important role in influencing the distribution of northern coastal scrub species on coastal bluffs in this study. As a consequence, these factors may be important in the maintenance of northern coastal scrub species diversity on maritime bluffs. Efforts to preserve this vegetation may be best achieved by maintaining local- and landscape-level heterogeneity through preservation of a range of bluff habitats each varying in extent and topographic relief.

ACKNOWLEDGMENTS

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REVISITING NATIVE *PINUS RADIATA* FORESTS AFTER TWENTY-NINE YEARS

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ABSTRACT

Repeat sampling of 19 native *Pinus radiata* D. Don stands, each about one ha, was conducted after a 28–29 year interval. Tree density decreased from 636 per ha in 1965–1966 to 460 in 1994, probably due to mortality of young *P. radiata.*

In these unburned stands, tree seedling densities were low for all species, and similar for both sample times although the density by stand was variable—from 11 to 790 per ha in 1965–1966 and 15 to 986 per ha in 1994. Two-thirds of the tree seedlings sampled were *Quercus agrifolia* Nee, easily growing under the *P. radiata* canopies.

Tree sapling densities were also low, averaging 177 per ha in 1965–1966 and 99 in 1994. In 1965–1966 only 58% of the saplings were *P. radiata,* and in 1994 only 50% were *P. radiata.* The rest, except for a single *Arbutus menziesii* Pursh, were *Q. agrifolia,* having tolerated heavy deer browsing as seedlings for years and finally producing a central stem emerging as a sapling.

The stands reflect a sequence of maturation, from dense *P. radiata* poles to sparse large *P. radiata* trees with small *Q. agrifolia* trees below. Stands that were logged in the past (decades prior to 1965–1966) had high numbers of *Q. agrifolia* (seedlings, saplings and trees) below those few large *P. radiata* trees left (for unknown reasons) after logging.

Of the 38 stands of *P. radiata* sampled in 1965–1966 on the Monterey Peninsula, 12 had been seriously modified by human activity by 1994.

There have been many studies examining the management of *Pinus radiata* D. Don forests, but mostly of plantations and especially in Australia and New Zealand (Scott 1960; Pert 1963). Few reports describe the natural *P. radiata* forests in California (Roy 1966; McDonald and Laacke 1990), and there are only brief comments in these reports that refer to changes in the forests over time. This study adds to the sparse information on temporal variation in the natural *P. radiata* forests by examining changes in a series of stands first studied in 1965–1966 (Vogl et al. 1977) and then restudied in 1994 (this report).

Stand Selection in 1965–1966. In the early summers of 1965 and 1966 I sampled the trees, tree saplings and tree seedlings, shrubs and forbs in 48 approximately one ha natural *P. radiata* stands in California (Vogl et al. 1977). The 48 stands were scattered over the natural range of this species and included four near Año Nuevo Point, six near Cambria, and 38 on the Monterey Peninsula. My goal in 1965–1966 was to provide a quantitative description of the vegetation in the natural *P. radiata* forests in California. At that time an attempt to establish an 800 ha State Monterey Pines Park on the Monterey Peninsula was failing. With such a large block of the natural *P. radiata* forest at risk of development, it seemed appropriate to obtain some measure of the relationship between ground flora and canopy in the natural forest before more widespread modification occurred. Since then, fortunately, Jacks Peak Regional Park was established on the Peninsula embracing 212 ha of mostly natural *P. radiata* forest. According to Deghi et al. (1995) 42% (1174 ha) of the *P. radiata* forest at Monterey is now permanently protected.

The native stands of *P. radiata* were heavily logged for their high quality timber since the time of settlement, and were also grazed and subjected to fires. Thus the use of "natural" in describing a particular stand has its critics. At the least, my sample stands in 1965–1966 excluded the urban forests (Deghi et al. 1995), the forest remnants on golf courses and in housing developments, and planted stands. Selection of a stand was based on apparent dominance by *P. radiata* trees. Those stands selected represented a range of previous and existing conditions, including logging, grazing and burning, variation in elevation and distance from the ocean, and variation in soils. The natural *P. radiata* forests occur over a variety of geological parent materials, and on soils from four orders embracing thirteen soil series (McDonald and Laacke 1990; Deghi et al. 1995). Some of the sample stands at Monterey occurred on the marine terraces mapped by Cylinder (1995), but most occurred further inland on Santa Lucia and Sheridan soils. Because of the range of conditions tolerated in stand selection, some stands sampled were not dominated by *P. radiata*; this occurred in stands that were logged in the past and had numerous *Quercus agrifolia* Nee trees.

I did not sample any stands in the Huckleberry Hill area at Monterey where *P. radiata* occurs with *Cupressus macrocarpa* Gordon, *C. goveniana* Gordon and *P. muricata* D. Don.

Stand Selection in 1994. In February of 1994, I attempted to re-sample the 38 stands of *P. radiata* on the Monterey Peninsula. Notes entered on U.S. Geological Survey quadrangle maps used in the original study provided locations of the stands. Some of the stands occurred on steep terrain in undeveloped areas without unique constructed landmarks and as a consequence four stands could not be re-located. None of these four stands were absent because of cutting or fire. One other stand could not be re-located because an identifying road had been eliminated. In addition, three stands were partially cut for housing developments, three burned completely in the 1987 Del Monte Properties (once Pacific Improvement Co., then Del Monte Properties Co., and now Pebble Beach Properties) wildfire, and one was clear-cut for a golf course.

Five stands appeared partially logged, since larger dbh trees present in 1965–1966 were missing in 1994; stumps and firewood blocks were present in one of these stands in 1994 but no dead trunks or remnants of dead trunks were present in any. A broad range of conditions was embraced by the sampled stands in 1965–1966, including previous logging, but my goal in 1994 was to assess any natural changes over the intervening 28–29 yr and so these five stands apparently logged since 1965–1966 were rejected.

In two other stands, tree dbh comparisons between 1965–1966 and 1994 indicated a mis-match of location since the larger dbh of trees in 1994 could not possibly have been attained in the 28–29 yr interval.

Thus, with 12 stands modified by cutting or fire since 1965–1966, and seven stands not accurately relocated, sample data from only 19 of the original 38 stands at Monterey were used in this study. Nine of the 19 were initially sampled in 1965, while the other ten were initially sampled in 1966.

METHODS

In each of the 19 stands I sampled tree seedlings, saplings and trees at ten points using the point-centered quarter method (as in 1965–1966), where the stem is sampled that occurs nearest to a point in each of the four quadrats around the point. This was the method of choice for an expeditious survey of the forest in 1965–1966, but it is not the best method for assessing diameter growth, sapling survival or seedling success over time (permanent plots with marked stems would have been much more appropriate). It needs to be emphasized that the trees sampled in 1994 were not the identical trees sampled in 1965–1966—rather a random set of 40 trees (and saplings and seedlings) in the same stand was sampled in each period. The stands sampled were relatively homogeneous patches on uniform topography in a larger matrix of *P. radiata* forest. Ten quarter points were sampled in each stand, with four quadrats at each point for a total of 760 quadrats in the 19 stands. My intent was to sample live individuals of 40 trees, 40 saplings and 40 seedlings in the 40 quadrats of each stand, but in addition to live saplings I also sampled dead saplings in those stands with an unusually large number. The criterion for tree seedlings was a dbh less than 2.5 cm, for tree saplings a dbh 2.5 to 10 cm, and for trees a dbh more than 10 cm, all at 1.4 m above ground level. Any tree stem emerging at ground level or forking below 1.4 m height was considered an individual, even in multiple-stemmed *Q. agrifolia.* Tree height was measured with a clinometer. Tree seedlings were sparse in all stands and saplings were sparse in many stands, so search for them was extended only 30 m away from the points; area expands rapidly with distance away from the points, and so does the possibility of overlooking seedlings or small saplings. Where seedlings or saplings were not found within 30 m from a point, distance was recorded as 30 m for determining stand density; at this average distance with the point-centered quarter method, the calculated number of individuals per ha is 11. For species composition, quadrats with no seedlings or saplings within 30 m were considered unoccupied.

Annual rings were counted in 1965 on 26 fresh *P. radiata* stumps along a cleared powerline on Pebble Beach Properties, and in 1966 at a Carmel Valley sawmill on a deck of 41 *P. radiata* logs cut along Highway 1 over Carmel Hill.

In 1965–1966 small numbers of beef cattle (ca. 20) were observed on the properties encompassing six of the 19 relocated stands, but in 1994 cattle (small numbers again) were present in only two of the 19 stands.

RESULTS

Pinus radiata and *Q. agrifolia* were the only tree species recorded at the sample points in the 19 stands at Monterey in both 1965–1966 and 1994. (However, in 1965 a few individuals of *Pinus attenuata* Lemmon and *Pseudotsuga menziesii* (Mirbel) Franco were recorded at the sample points in one stand near Año Nuevo Pt.) Similarly, tree seedlings and saplings at the sample points in the 19 stands were all *P. radiata* or *Q. agrifolia,* except for three seedlings of *Arbutus menziesii* Pursh in 1965–1966 and one in 1994 and one sapling of *A. menziesii* in 1994.

Table 1 summarizes the measurements of trees, saplings, and seedlings from the 760 quadrats in the 19 stands relocated in 1994 and from the 760 quadrats in these same stands in 1965–1966. The only values significantly different over the time interval were the average number of trees per ha and the average dbh (Fig. 1). The average number of trees per ha decreased over the 28–29 yr interval; however, the average number per ha was nearly the same in 1994 (462) as in 1965–1966 (455) if five stands with unusually high numbers of trees per ha

TABLE 1. CHANGES IN 19 *P. RADIATA* STANDS FROM 1965-1966 TO 1994. Data from 760 quadrats in each time period.

	1965–1966	1994
Trees		
No. *P. radiata*	640	626
No. *Q. agrifolia*	120	134
Ave. No. per ha	636	460
Ave. stand dbh (cm)	34	40.2
Ave. *P. radiata* dbh (cm)	37.2	44.3
Ave. *Q. agrifolia* dbh (cm)	21.1	18.7
No. *P. radiata* 10–21 cm dbh	194	140
No. *P. radiata* 22–31 cm dbh	169	102
No. *P. radiata* >31 cm dbh	277	384
No. *P. radiata* >100 cm dbh	1	4
No. *Q. agrifolia* 10–21 cm dbh	87	97
No. *Q. agrifolia* 22–31 cm dbh	19	24
No. *Q. agrifolia* >31 cm dbh	14	13
No. *Q. agrifolia* >50 cm dbh	7	3
Tree seedlings		
Ave. No. per ha	160	252
No. *P. radiata*	118	229
No. *Q. agrifolia*	330	371
No. *A. menziesii*	3	1
No. occupied quadrats	451	601
Tree saplings		
Ave. No. per ha	177	99
No. *P. radiata*	328	324
No. *Q. agrifolia*	238	329
No. *A. menziesii*	0	1
No. occupied quadrats	566	654

(882 to 1359 in 1965–1966) (Figs. 2 and 3) are excluded. In 1965–1966, 78% of the 200 trees measured in these five stands were only 10–31 cm dbh, compared to 35% in 1994. All but three of the 200 trees in 1965–1966 were *P. radiata.* There was a 60% decrease, from 1148 to 461 in the average number of trees per ha in these five stands over the time interval.

The number of trees per ha in these "mature" *P. radiata* stands (excluding the five young stands with high numbers of poles per ha in 1965–1966) should reflect the highest natural stand density of *P. radiata* forests. The five stands with highest densities in the other 14 stands (of the 19) had an average of 575 trees per ha (512 to 646) in 1965–1966 and an ave of 641 (585 to 693) in 1994.

Average tree dbh increased slightly over the time interval but the measured average embraces several processes. Some trees grew in diameter during this time, but some died and their absence in 1994 would affect the average dbh. In 1965–1966 eight large, dead *P. radiata* snags were noted near the sample points, and 13 in 1994. Decay is rapid on these sites, so these numbers of snags are probably minimal. Disease, fire or perhaps some other factor could have killed these trees. The most susceptible to fire would have been young trees with thin bark and low canopies, but decay hides this evidence.

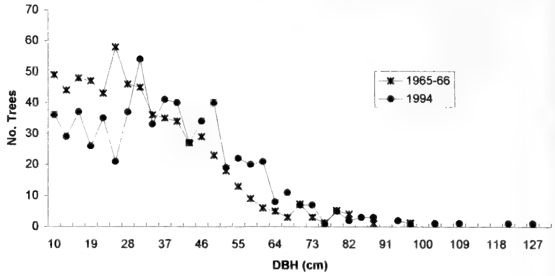

FIG. 1. Distribution of tree dbh, for *P. radiata* only, in all 19 stands. N-640 in 1965–1966, 626 in 1994.

Fire scars and/or charred bark on large *P. radiata* trees were noted in four of the 19 stands in 1965–1966, and in three different stands in 1994. *Fusarium subglutinans* (Wollenweb. and Reinking) Nelson, Toussoun, and Marasas (*F. moniliforme* J. Sheld. var *subglutinans* Wollenweb. and Reinking) (pine pitch canker) was just being noticed ca. 1994 on *P. radiata* in urban areas (=planted trees?) of the Peninsula, but was not apparent (i.e. canopies with dead needles) in my sample stands.

In addition, some saplings grew to tree size in the 28–29 yr period, lowering the average dbh. In 1994, 72% of *Q. agrifolia* trees were 10–21 cm dbh, a size that could easily have grown to trees from saplings in 1965–1966 and account for the slight measured decrease in *Q. agrifolia* average dbh over the time interval.

No annual rings were counted on trees or stumps of *P. radiata* in 1994. From rings counted in 1965–1966 on fresh stumps and logs, age is quite variable among trees with the same dbh. In the deck of 41 *P. radiata* logs, 24 to 44 rings were counted on 6 logs all 33 cm diameter, and 31 to 59 rings were counted on 6 logs all 61 cm diameter.

Tree sapling density was not significantly different between the two sampling periods, with density variable from 11 to 948 per ha in 1965–1966 and from 18 to 245 per ha in 1994. None of the 19 stands were grown to saplings in 1965–1966, rather I selected stands with tree-size individuals. Thus the sapling densities measured are low compared to densities occurring after hot fires. Many saplings die when pole size dbh is reached. To illustrate, the average dbh of *P. radiata* trees in the two stands with the smallest trees (all *P. radiata*) in 1965–

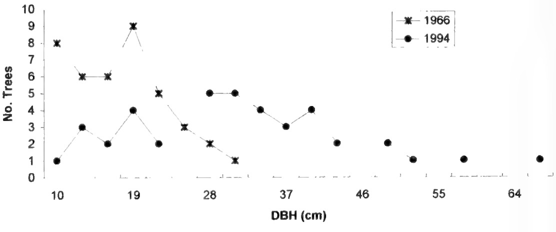

FIG. 2. Distribution of tree dbh in a young stand, all *P. radiata.*

FIG. 3. A 1994 view of the stand in Figure 2. Tree ht is ca. 18 m. This relatively young stand is located at ca. 215 m elevation on the east slope of the summit in the former Presidio of Monterey.

1966 was 19 and 20 cm. The number of saplings (all *P. radiata*) per ha in these two stands in 1965–1966 was 499 and 89. In the first stand 21 of the 40 quadrats were unoccupied by saplings and in the 19 quadrats with saplings 14 were deformed. The second stand had an unusually large number of dead saplings, 215 per ha. Thus it appeared that *P. radiata* sapling mortality occurred when average tree dbh reached somewhat less than 20 cm; from the available age-diameter data *P. radiata* trees at 20 cm dbh are approximately 20 to 25 yr old.

The proportion of saplings as *P. radiata* in all 19 stands did not change much over the time interval, at 58% in 1965–1966 and 50% in 1994, but the number of quadrats occupied by *Q. agrifolia* saplings increased by more than one-third.

Tree seedling density was not significantly different over the time interval, with density variable from 11 to 790 per ha in 1965–1966 and 15 to 986 in 1994. Seedling density appeared higher in 1994 than in 1965–1966 since the number of occupied quadrats increased by a third. Only one-fourth of the seedlings recorded in the 19 stands in 1965–1966 were *P. radiata,* and only one-third in 1994—the rest (except for four *A. menziesii*) were *Q. agrifolia.*

The *P. radiata* seedlings found in 1994 occurred in two sizes: 5–8 cm tall and 1–3 m tall (individuals taller than this have dbh in the sapling class i.e., 2.5 to 10 cm dbh, although a very few tall seedlings were measured at the sample points, four at 3 m height and two at 6 m). The shorter seedlings are probably several yr old, with root development as the major growth. Once a substantial root system has developed, shoot growth apparently proceeds rapidly which can account for the hiatus in height between the two sizes of seedlings. All *P. radiata* seedlings occurred with natural growth form, evidence that deer and cattle did not browse them.

Eight of the 19 stands in 1965–1966 had fewer than 17 tree seedlings per ha, and fewer than 13 quadrats were occupied by seedlings. Six of these eight stands had a dense, 1 to 1.5 m tall shrub cover of *Vaccinium ovatum* Pursh and/or *Arctostaphylos tomentosa* (Pursh) Lindley which could have limited sunlight for successful seedling establishment by *P. radiata.*

The 19 stands resampled in 1994 were far from being homogeneous. Some appeared to be pole stands originating after fire, while others were older stands with a wide range of tree dbh. Logged stands (previous to the 1965–1966 sampling) had an even wider range of tree dbh, skewed to larger trees and with numerous *Q. agrifolia* seedlings and saplings among and under the *P. radiata* trees. The average values in Table 1 mask obvious differences among the 19 stands, which can be arranged into groups based on the distribution of tree dbh. Three dissim-

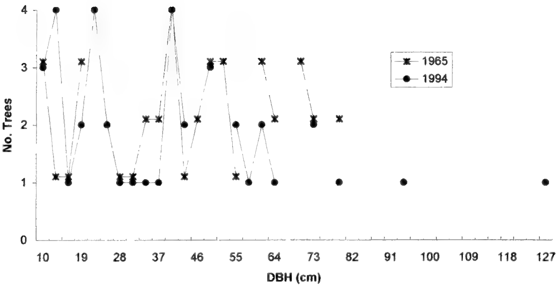

FIG. 4. Distribution of tree dbh in an old stand, nearly all *P. radiata* but with two *Q. agrifolia* in 1966 and three in 1996.

ilar stands will be used to emphasize the greatest differences.

In a young stand sampled in 1966 the average dbh for the trees (all *P. radiata*) was 20 cm and the distance measurements indicated a dense stand of 1200 trees per ha. Also present in 1966 were ca. 20 large, dead *P. radiata* trees per ha, all with charred bases; their presence suggests this was a stand of older trees that burned over in a hot fire. From my annual ring counts on logs and stumps the 20 cm dbh trees here were probably 20 to 25 yr old so this fire could have occurred in the early 1940's. By 1994 only 370 trees occurred per ha (Figs. 2 and 3), so major tree mortality occurred in the interval between sampling. There were 89 live *P. radiata* saplings per ha in 1966, but there also were 215 dead saplings per ha in 1966, indicating high mortality of *P. radiata* saplings at this early stage of stand development. One third of the 40 saplings in 1994 were *Q. agrifolia,* evidence that *Q. agrifolia* begins invasion of *P. radiata* stands in the early stages; they were sparse however, with only 30 per ha. There were practically no seedlings of either *P. radiata* or *Q. agrifolia,* with nearly all of the distances over 30 m in both 1966 and 1994 (i.e., no seedlings were found within 30 m from the quarter points). The dense shading cover of *Vaccinium ovatum* in this stand may have accounted for the low seedling density.

An older stand provides a second example of variation among the 19 stands. None of the trees sampled in 1966 in the young stand above were larger than 34 cm dbh, while in this older stand in 1965 dbh reached 84 cm (Figs. 4 and 5). The largest *P. radiata* sampled in all 19 stands in 1994 occurred here at 128 cm dbh. There were only 333 trees per ha in 1965, which contrasts with the 1200 per ha in the young stand above. Sapling density was low in 1965, at 25 per ha and consisted entirely of *P. radiata,* but increased to 73 per ha by 1994 with three of the 40 as *Q. agrifolia.* In 1965 there were 56 seedlings per ha in this stand, and most of them were *Q. agrifolia* (they were not seedlings of

FIG. 5. A 1994 view of the stand in Figure 4. This older stand is located at ca. 150 m elevation on an east-west ridge, 0.5 km southwest of Jacks Peak County Park.

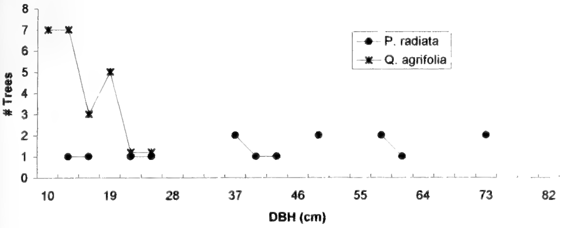

FIG. 6. Distribution of tree dbh in 1994 for 16 *P. radiata* and 24 *Q. agrifolia* from a stand logged prior to 1965.

a few yr, but rather browsed older bushes spreading laterally without any upright stem over 2.5 cm dbh). The canopy of this older stand on an east-west ridge top was apparently open enough for successful establishment of some *P. radiata* seedlings even without surface fire. By 1994 there were 359 seedlings per ha, all of them *P. radiata* (there were *Q. agrifolia* bushes still present, but at the higher density of the *P. radiata* seedlings *Q. agrifolia* individuals were not close enough to the sample points (=dense enough) to be recorded.

Another stand, apparently logged prior to sampling in 1965, provides a third example of variation among the stands. In contrast to the two previous stands, there were many *Q. agrifolia* trees present (Figs. 6 and 7). In 1965 11 of the 40 trees in the sample were small *Q. agrifolia* trees, with none larger than 14 cm dbh. In 1994, 24 of the 40 trees sampled were small *Q. agrifolia* trees, averaging 16 cm dbh with the largest at 23 cm. These *Q. agrifolia* trees were mostly multiple-stemmed, from the ground level. They accounted for the calculated high density of trees—1566 per ha in 1965 and 1340 in 1994. The *P. radiata* trees in this stand were large and sparse, so few were recorded at the sample points. In 1994 a second set of 40 trees were recorded, sampling only *P. radiata.* These measurements indicated a density of 171 *P. radiata* trees per ha with an ave dbh of 63 cm with the largest at 97 cm. These were tall, straight-trunked trees, without large, low spreading branches and there was no apparent reason for not having harvested them when the logging took place. Nearly all the saplings and seedlings at the sample points in this stand were *Q. agrifolia,* with 222 saplings and 49 seedlings per ha in 1994. *Pinus radiata* reproduction was poor under these small *Q. agrifolia* trees with their shading canopy and thick, persistent leaf litter. It seems likely that without a hot fire, *Q. agrifolia* will attain dominance in this stand.

DISCUSSION

Tree density and diameter. Mortality of young *P. radiata* is a probable cause for the decrease in tree

FIG. 7. A 1994 view of the logged (prior to 1965) stand in Figure 6, where *Q. agrifolia* is becoming dominant. The trunks of four remaining, sparse, large *P. radiata* trees ca. 23 m tall are visible. This stand is located on a north slope at ca. 135 m elevation, in Roach Canyon about halfway from Carmel Valley Road up to Jacks Peak.

density between 1965–1966 and 1994; subsequent fall-down and decay eliminates noticeable evidence. While some *P. radiata* poles may have died between 1965–1966 and 1994, the number of *P. radiata* trees over 31 cm dbh increased (Table 1). Observation did not reveal high mortality such as many dead snags among older *P. radiata* trees; widespread logging in the past undoubtedly removed many of the larger trees, leaving few to reach senescence by 1994.

Only five *P. radiata* trees over 100 cm dbh were found in the 19 stands. To emphasize the paucity of large trees in the contemporary *P. radiata* forests beyond the data in Table 1, the number of *P. radiata* over 100 cm dbh in the 29 other stands sampled in 1965–1966 was only 8 (out of 988 measured) and the number of *Q. agrifolia* trees over 50 cm dbh was only 6 (out of 166 measured). The two largest *P. radiata* trees measured by Jepson (1910) were 114 and 137 cm dbh. The oldest *P. radiata* tree cut in a 1946–1947 logging operation that felled nearly three million bd ft on the present Pebble Beach Properties was 70 yr, with an 81 cm dbh (Stoddard 1947). These measurements suggest that *P. radiata* attains a dbh of at least one m before senescence. The largest *P. radiata* trees in this study were open-grown with low spreading branches. The high incidence of knots from the retained lower branches may have been a reason for not harvesting these trees. The full-sun environment enabling them to attain their open-grown stature could have been due to intensive logging or to surface fires that thinned the adjacent trees.

Very few large *Q. agrifolia* trees occurred in the 19 stands (Table 1)—*P. radiata* forests are fire-prone and the thin bark of *Q. agrifolia* is a poor insulator. The largest *Q. agrifolia* tree found with a pronounced fire-scar occurred outside the sample stands with a dbh of 55 cm. The largest *Q. agrifolia* tree measured in the sampled stands was 88 cm dbh. Larger trees of *Q. agrifolia* commonly occur in canyon bottoms where the thick, moist, persistent leaf litter and shading canopy of *Q. agrifolia* are not conducive to spread of surface fire—the largest tree found (outside the sample stands) in a canyon bottom was 114 cm dbh.

Tree seedlings and saplings. Even though closed-cone *P. radiata* trees depend upon hot fires for a dense seed rain and a bare soil seed-bed, some cones open in ambient air temperatures giving a sparse seed rain in most years. Consequently, a few *P. radiata* seedlings are usually present even in the layer of persistent *P. radiata* needles and *Q. agrifolia* leaves. *Pinus radiata* seedlings often occur on ridge tops, where the litter layer is thinner and the topography apparently allows more sunlight at seedling level. Over time, low densities of *P. radiata* seedlings enter the sapling class, so that in effect an 'all-age' stand of *P. radiata* occurs even though the size-class distribution is markedly skewed to the trees that originated after the last hot fire.

With hot fires, closed-cone *P. radiata* trees shed a heavy seed rain onto bare soil and seedling germination and survival are excellent. After the 1959 and 1987 wildfires on the Huckleberry Hill area of the present Pebble Beach Properties, seedling densities appeared to me to be at least 100,000 per ha. Fenton (1951) recorded more than 2,400,000 seedlings per ha following fire in *P. radiata* forests in New Zealand. Jepson (1910) counted 612 four-yr old *P. radiata* seedlings on 100 sq ft of a burned stand in Pacific Grove; this converts to 658,500 per ha. The wildfires on Huckleberry Hill are the only hot fires that have occurred in the *P. radiata* forest in the past 40 yr. Larkey (1972) recorded hot fires on Del Monte Properties (now Pebble Beach Properties) in 1901 and 1905, but provided no location or size of area burned. More recently, wildfires in the *P. radiata* forests of the Monterey Peninsula have been prevented or rapidly controlled. I saw only one recent burn during 1965–1966, a fraction of one ha on private land, resulting in dense, 30–56 cm tall *P. radiata* seedlings after only one growing season (Vogl et al. 1977). In February of 1994 I saw only one recent burn, again on a tiny area, under a powerline on private land and with no vegetative recovery at the time. While fire scars and/or charred bark were noted in a few stands in both 1965–1966 and 1994, I could not ascertain the time of the fires producing these scars nor their effect on forest structure. The only contemporary prescribed burns under *P. radiata* on the Peninsula that I am aware are conducted in Point Lobos State Reserve; the management goal there, however, is to reduce *P. radiata* seedling and sapling density to produce more open forests (McGowan 1994).

Quercus agrifolia seedlings are common under *P. radiata* trees beyond pole size, easily tolerating the open shade. However, very few small, newly developed *Q. agrifolia* seedlings were present in the 19 stands. Instead, most common were short, spreading *Q. agrifolia* bushes due to repeated deer browsing and persisting for years. Without this browsing, growth would expectedly progress to the sapling and then tree stage, changing the stand composition to more *Q. agrifolia.* Even with the browsing, a central stem from the bush ultimately grows above the reach of deer and enters the sapling stage. The number of quadrats out of 760 occupied by *Q. agrifolia* saplings increased over the 28–29 yr—31% in 1965–1966 to 43% in 1994 (Table 1), increasing in 15 of the 19 stands.

The densities of *P. radiata* seedlings and saplings were very low in the 19 stands, compared to observed densities after the 1959 and 1987 crown fires. There may not be enough *P. radiata* reproduction to perpetuate these stands as *P. radiata* forests in the absence of hot fires, especially with the apparent increasing success of *Q. agrifolia* as the stands mature.

Stand age. Of the 626 *P. radiata* trees sampled in 1994, 12% were larger than 61 cm dbh. While the published *P. radiata* age-dbh data (Larsen 1932; Lindsay 1937; McDonald 1959) seems inadequate, some of it recorded 6–7 decades ago and based on small samples, the data indicate trees at 60 cm dbh are 65 to 100 yr old. Taking Roy's (1966) 80–90 yr ave life span for *P. radiata,* more frequent senescent trees might be expected soon in the *P. radiata* forests.

CONCLUSIONS

This study gave a measure of landscape development rate as forest acreage lost over time. Between 1965–1966 and 1994 four of the 38 stands sampled in 1965–1966 were removed by cutting for housing or a golf course. Five stands appeared to have been appreciably logged, but were still *P. radiata* forest. Three stands were destroyed by wildfire (although the dense reproduction of *P. radiata* seedlings following the fire in effect renewed these stands as *P. radiata* forests). Thus one-third of the 38 stands were seriously modified by human activity in the 28–29 yr interval (assuming the wildfire was human ignited). This degree of modification may not be representative since most of the 38 stands were some distance from the fringe of development.

Many of the 38 stands in 1965–1966 had low densities of *P. radiata* seedlings. In only 6 of these stands did this low density appear to be a consequence of dense, shading understory shrubs. The crowns of the *P. radiata* trees had abundant closed cones, and what seems needed is fire to open these cones for a seed rain and also to remove the litter exposing bare soil for successful seedling establishment.

The *P. radiata* forests are getting older. Only three of the 38 stands from 1965–1966 were "renewed" by fire by 1994, and the 1987 wildfire was an unintentional event. While low densities of *P. radiata* saplings did occur in the 19 stands sampled in 1994, I doubt that they occur in sufficient number to adequately perpetuate the stands in a condition similar to the *P. radiata* forests of today. With one-eighth of the *P. radiata* trees measured in 1994 over 61 cm dbh, which are ca. 65–100 yr old, senescence can be expected to increase soon in these stands.

The fate of the *P. radiata* forests on the Monterey Peninsula with complete fire control probably involves increasing dominance by *Q. agrifolia.* Logging of *P. radiata* appears to accelerate dominance by *Q. agrifolia.* It seems unlikely that hot fires can be used as a forest management tool on the Monterey Peninsula, a highly urbanized-recreational area. However even moderate, prescribed fires could probably injure or kill thin-barked *Q. agrifolia* saplings and young trees. With heavy deer browsing being the only apparent current yet ineffective limitation on *Q. agrifolia,* with continued logging of *P. radiata,* and without prescribed fires, the gradual increase in dominance by *Q. agrifolia* over time could change the character of the Peninsula from a *P. radiata* to a *Q. agrifolia* setting.

ACKNOWLEDGMENTS

Both the 1965–1966 and 1994 studies of *P. radiata* forests were funded by the University of California, Hastings Natural History Reservation, Carmel Valley. Housing for the 1994 study was graciously provided by Karen and Hugo Ferlito of Carmel. My thanks to Dr. David Jowett for statistical advice and to Dr. Robin White for her critical review of the manuscript. Two anonymous reviewers made important suggestions for improving the manuscript. My wife Betty recorded the measurements in the field in 1994 and also, unfortunately, suffered from the ubiquitous *Rhus.*

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LESQUERELLA NAVAJOENSIS (BRASSICACEAE), A NEW SPECIES OF THE *L. HITCHCOCKII* COMPLEX FROM NEW MEXICO

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ABSTRACT

Lesquerella navajoensis is a newly described perennial, cushion-forming species from northwestern New Mexico. It occurs on mesa rims of Todilto Limestone with other low-growing, wind-tolerant species and with or near a low form of *L. fendleri.* The species is apparently very rare and may be threatened by limestone mining activities. *Lesquerella navajoensis* belongs to a small group of species that include *L. hitchcockii, L. tumulosa, L. rubicundula,* and, as first reported here, *L. arizonica.* These species, except *L. arizonica,* are also rare or infrequent. This new species is most similar to the very narrow endemic *L. tumulosa* which is listed as Endangered by the U. S. Fish and Wildlife Service. In addition to molecular characteristics, *L. navajoensis* differs in having strongly mucilaginous seeds, petals that are slightly orange at the junction of the blade and claw, and petals that are presented as flat rather than arched. A key is provided to the species of the *L. hitchcockii* Complex.

This distinctive new species was first shown to me on 28 May 1997 by Ken Heil (San Juan College) growing on a mesa rim northeast of Thoreau, NM. At that locality, the species grows immediately adjacent to an active limestone quarry. A mine road is no more than 25 meters from the nearest individuals. In the summer of 1998, Daniela Roth (Navajo Natural Heritage Program) aided me in searching for additional populations of the species that are not so immediately threatened. We searched a number of similar habitats north of Thoreau, and although most similar habitats do not contain the species, we were able to find one large population that at present is not threatened by mining, road construction, or grazing.

Lesquerella navajoensis O'Kane, sp. nov. (Figs. 1 and 2)—TYPE: USA, New Mexico, McKinley Co., ca. 2 air mi NE of Thoreau on bench below and SE of Mt. Powell, 35°26′8″N 108°12′26″W, 7600′ (2316m) elev., 23 May 1998, *Steve L. O'Kane, Jr. 4232 & Daniela Roth* (holotype, MO; isotypes, BRY, COLO, GH, ISTC, NMC, RM, UNM).

Herba perennis, depresso-pulvinata, caudice autem confertissime ramosissimo, multicipiti; folii integris, lineari-oblanceolatis undique indumento argenteo-stellatis 3–8–(13) mm longis, 0.7–1.4 mm latis; sepala luteo-viridis 3.7–4.8 mm longa, elliptica; petala lutea, spatulata, 5.2–6.5 mm longa cum oculus aurantiaca; inflorescentiis congestis nonelongatis; pedicelli recti vel subsigmoidei; fructis glabis, ovatis, rubicundulis sessilibus, 3–4.9 mm longis; stylo 1.8–3 mm longo; loculis cum 1 seminibus; semina suborbiculata, immarginata humida mucilaginosa.

Herbs, perennial, pulvinate-caespitose and soboliferous from a densely ramified caudex arising from a thick taproot, forming low-hemispherical cushions up to 19 cm in diameter. Herbage silvery-gray, densely covered with a crust of overlapping, stellate trichomes; trichomes generally with 5 main rays, each twice bifurcate into 20 tuberculate tips, rays somewhat fused in center by a thin, narrow webbing and arising from a slightly raised, moderately tuberculate umbo (Fig. 2). Stems numerous, crowded, buried among the leaves and not exceeding them, clothed below the leaves with marcescent leaf bases, arising from divisions of a branched, woody caudex. Leaves entire, linear-oblanceolate, tapering to base with no distinction between blade and petiole, 3–8–(13) mm long, 0.7–1.4 mm wide. Flowers and fruits in dense, few-flowered, subcorymbose racemes at apex of flowering stems, not or barely exceeding the leaves. Pedicels straight to slightly sigmoid. Sepals yellow-green, elliptic, 3.7–4.8 mm long, inner pair not or only slightly saccate at base. Petals 5.2–6.5 mm long, spatulate, deep yellow, faintly orange at junction of blade and claw, blades diverging at 90° from claw and, therefore, flower flat-topped. Stamens tetradynamous, filaments linear. Fruit sessile to substipitate, becoming reddish to copper-colored at maturity, interior and exterior glabrous, 3–4.9 mm long, 2.2–3.1 mm wide, ovate, often compressed at margins apically, acute at apex, base rounded-truncate; replum ovate to broadly elliptic to obovate; septum perforate in center or not at all; ovules 2–4 in each locule from funicles attached in apical half; style 1.8–3 mm long at maturity, somewhat wider just below the slightly expanded stigma. Seeds usually 1 per locule, 1.5–2.4 mm × 1.3–1.9 mm, suborbicular-ovoid, plump but somewhat flattened, brown, cotyledons accumbent, strongly mucilaginous when wetted.

Paratypes. USA, New Mexico, McKinley Co.: NE of Thoreau on Hwy. 57, SW-facing rim of mesa adjacect to mine. 35°26′14″N 108°7′31″W, T14N

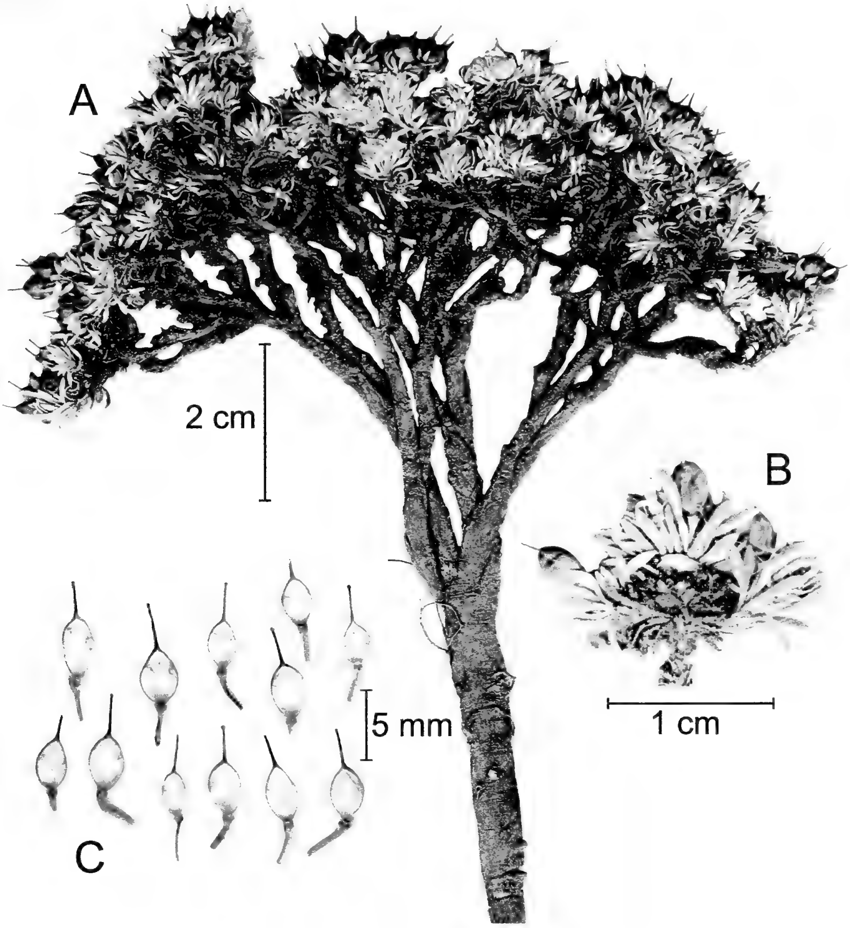

FIG. 1. *Lesquerella navajoensis* O'Kane. A. Habit. Branches are not visible in life as the plants form cushions with their leaves at ground level. B. Branch tip showing several short stems and mature siliques. C. Repla and septa from dehisced siliques. (Images scanned in greyscale at 1200 dpi from pressed material of the type collection).

R12W Sec. 17, 7270′ (2216 m) elev., 28 May 1997, *Steve L. O'Kane, Jr. 3850 & Ken Heil* (BRY, GH, ISTC, RM, SJNM, UNM, Navajo Natural Heritage Inventory); NW of Thoreau on edge of mesa near limestone quarry, 35°26′17″N 108°7′34″W, T14N R12W Sec. 17 SW¼ SE¼, 7400′ (2256 m) elev., 20 May 1998, *Steve L. O'Kane, Jr. 4220* (BRY, COLO, GH, MO, NMC, RM, RSA).

Habitat characteristics. Lesquerella navajoensis is limited to windward (west-facing), windswept mesa rims and nearby habitat with little vegetative cover and high insolation. Because of high winds and shifting substrate, the associated species are low-growing and usually mat-forming, e.g., *Eriogonum shockleyi* S. Watson. Back from the mesa rims, short-statured trees of *Pinus edulis* Engelm. are the dominant species. *Lesquerella navajoensis* is a calciphile apparently limited to the nearly white Todilto Limestone Member of the Morrison Formation which forms local mesa rims as a cap above the Entrada Formation (Green 1976; Robertson 1990). At the type locality some plants are located behind the mesa rim among *P. edulis* in reddish soil formed from the mixing of decomposed Todilto Limestone and colluvial sand from the Summerville Formation above. Plants are found in reddish soil only on the windward margins of the mesa, suggesting that these plants have spread as seed from the preferred mesa rim habitat by strong prevailing west and southwest winds. The seeds of *L. navajoensis* are strongly mucilaginous, forming a halo up to 2 mm thick when wetted. I have concluded from observations made of other species of *Lesquerella* growing in shifting or barren substrates (e.g., *L. pruiosa* Greene) that this mucilage is an adaptation allowing some seeds to become glued to the substrate. In this way, all seeds are not lost to water movement or to strong winds as long as some seed experience precipitation shortly after being released from the siliques.

Taxonomic relationships. Lesquerella navajoensis immediately suggests kinship with a small group

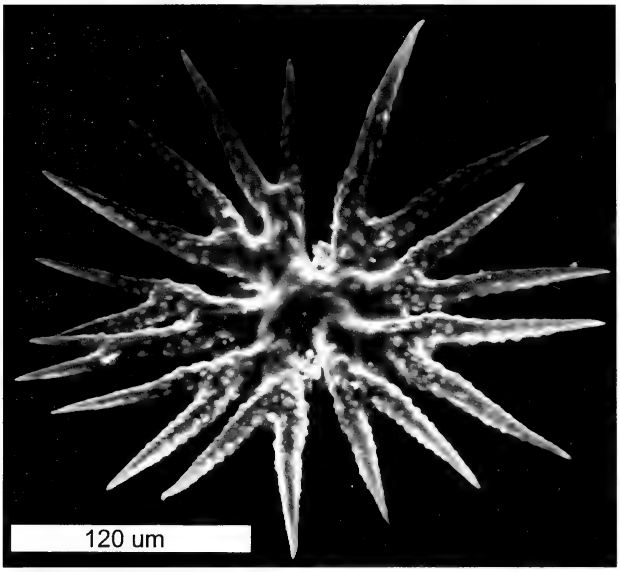

FIG. 2. SEM photomicrograph (holotype) of an adaxial leaf trichome of *Lesquerella navajoensis*. Scale bar is 120 μm, original magnification 250×, specimen coated with 25 nm of gold-palladium.

of species which includes *L. hitchcockii* Munz, *L. tumulosa* (Barneby) Reveal, and *L. rubicundula* Rollins. This group has engendered a small literature of its own due to strong morphological ties and the fact the constituent species are all rare or very rare (Maguire and Holmgren 1951; Barneby 1966; Reveal 1970; Munz 1930). The group historically has been composed of species with small, linear to spatulate leaves, a pulviate-caespitose or at least mat-forming habit, and siliques that are strikingly reddish at maturity, glabrous, and have relatively long styles (Rollins and Shaw 1973). I have been examining the relationships of these, and other species of *Lesquerella* using DNA sequences of the internal transcribed spacer of ribosomal DNA and inter-simple sequence repeat (ISSR) length variation (data not given here). Based on these data sets, species of the *L. hitchcockii* complex are shown to be closely related. Molecular data also indicate that *Lesquerella arizonica* Watson is a member of this complex, a relationship not previously recognized. *Lesquerella arizonica* has strongly pubescent rather than glabrous fruits and the fruits are not reddish. These morphological differences aside, however, the plants have similar small leaves and a pulvinate-caespitose habit like the rest of the complex. *Lesquerella navajoensis* is most morphologically similar to *L. tumulosa,* a species endemic to a few barren, white hills near Kodachrome State Park in south-central Utah, a great-circle distance of 407 km (253 miles) from the nearest locality for *L. navajoensis.* Given the rarity of the two species and the distance between them, it is certain that no gene flow exists between these morphologically similar entities. In life, the flowers of *L. navajoensis* have a light orange "eye" where the blade and claw meet, whereas the petals of *L. tumulosa* are uniformly yellow. The mature seeds of *L. navajoensis* are strongly mucilaginous, whereas those of of *L. tumulosa* are not. The ability to exude mucilage is retained for many years on well preserved herbarium material of other species of *Lesquerella* (personal observation). The petals of *L. navajoensis* bend at nearly a 90° angle where the blade and claw meet which makes the flower distinctly flat-topped. The petals of *L. tumulosa* arch from the claw and the petals are, therefore, curved and the flowers do not appear distinctly flat-topped.

A short-statured form of *Lesquerella fendleri* (A. Gray) Watson grows interspersed with or near *L. navajoensis* at both of the known localities for *L. navajoensis. Lesquerella fendleri,* however, is not found at the rim of the mesa where insolation and wind are maximum. The presence of *L. fendleri* may explain why the new species was for so long overlooked. *Lesquerella fendleri* and *L. navajoensis* are easily distinguished as follows. *L. fendleri* has a deep orange "eye", the veins of the petals near the eye are also orange, the petals are much larger, and the stellate trichomes are webbed for at least half the length of the rays. *L. navajoensis* has a faint orange eye and no orange veins, the flowers are much smaller, and the trichomes have only a narrow webbing (seen at >100× magnification). Additionally, *L. navajoensis* flowers and forms fruits earlier than does *L. fendleri.* Few if any flowers of both species are contemporaneous.

KEY TO THE SPECIES OF THE *LESQURELLA HITCHCOCKII* COMPLEX

1. Plants spreading or prostrate from elongated stems,

neither densely caespitose nor cushion-forming (but may form loose mats when growing on flat substrates); siliques glabrous.

2. Leaves linear to linear-oblanceolate, no distinction between petiole and blade; trichomes smooth or less commonly weakly tuberculate under high magnification; south-central Utah . . . . *L. rubicundula*
2. Leaves spathulate to broadly oblanceolate, the blade distinctly narrowing to a petiole; trichomes covered with well-developed tubercles under high magnification; Nevada and south-central Utah . . . . *L. hitchcockii*

1. Plants compact, essentially erect, densely caespitose or cushion-forming; siliques glabrous or pubescent.
   3. Siliques glabrous; plants cushion-forming from a large, many-branched caudex.
      4. Flowers with a faint orange "eye", the blade of the petals bent at right angles to the claw; seeds strongly mucilaginous when wet; northwestern New Mexico near Thoreau . . . . *L. navajoensis*
      4. Flowers uniformly yellow, the blade of the petals arching from the claw; seeds not mucilaginous when wet; south-central Utah near Cannonville . . . . *L. tumulosa*
   3. Siliques densely pubescent with stellate trichomes; plants merely caespitose, not cushion-forming; . . . . *L. arizonica*

Because the type locality is located on Tribal Lands and because to walk among these plants in full flower is to "walk in beauty", the specific epithet commemorates the people of the Navajo Nation, the Diné.

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THE NICKEL HYPERACCUMULATOR *STREPTANTHUS POLYGALOIDES* (BRASSICACEAE) IS ATTACKED BY THE PARASITIC PLANT *CUSCUTA CALIFORNICA* (CUSCUTACEAE)

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ABSTRACT

Metal hyperaccumulator plants can be defended from herbivore/pathogen attack by elevated tissue metal contents. We encountered the parasite *Cuscuta californica* Hook. & Arn. growing on a Ni hyperaccumulator (*Streptanthus polygaloides* A. Gray) and investigated this host/parasite relationship. Elemental levels in plant samples, and the Ni level in soil samples, were measured for two hosts: *S. polygaloides* and the nonhyperaccumulator *Lessingia nemaclada* E. Greene. Levels of 12 elements in parasitized and nonparasitized hosts, and corresponding *C. californica* samples, differed only for *S. polygaloides,* where significant differences were detected for six elements. Parasitized and nonparasitized *S. polygaloides* had similar amounts of Ni, K, P, Co and Pb, but parasitized plants had higher Ca than nonparasitized ones. *Cuscuta californica* had higher K and P, and lower Ni, Co and Pb than host *S. polygaloides. Cuscuta californica* parasitizing *S. polygaloides* contained 800 μg Ni/g, whereas that from *L. nemaclada* contained only 11 μg Ni/g. We concluded that hyperaccumulated Ni did not prevent attack of *S. polygaloides* by *C. californica.* We also tested the hypothesis that high-Ni *C. californica* was defended from generalist insect folivores. High- and low-Ni *C. californica* fed to neonate *Spodoptera exigua* larvae affected neither larval survival nor larval mass. We concluded that the elevated Ni content of *C. californica* parasitizing *S. polygaloides* did not benefit *C. californica* by defending it from a generalist herbivore.

Hyperaccumulators are plants that contain unusually elevated levels of metals in their tissues. Baker and Brooks (1989) reviewed hyperaccumulators of seven metals: Ni, Cu, Co, Zn, Pb, Cr and Mn. They define hyperaccumulators of Ni, Cu, Cr, Pb and Co as plants containing >1000 μg metal/g dry mass. Hyperaccumulators of Zn and Mn have >10,000 μg metal/g in their tissues. Nickel is the metal hyperaccumulated by the largest number of plant species, currently over 300 species (Brooks 1998), with each of the other metals hyperaccumulated by fewer than 30 species (Brooks 1998).

Although metal hyperaccumulation was defined over two decades ago by Brooks et al. (1977), the ecological function(s) of metal hyperaccumulation are only now being investigated. Boyd and Martens (1992) summarized five hypothetical (and not mutually exclusive) explanations for the hyperaccumulation of metals. These were: (1) metal tolerance/disposal; (2) drought resistance; (3) interference with neighboring plant species; (4) inadvertent uptake; and, (5) defense against herbivores/pathogens. Of these, the defense hypothesis has been supported by several recent experimental investigations. A harmful effect of hyperaccumulated Ni in plant tissues has been shown for lepidopteran folivores (Boyd and Martens 1994; Boyd and Moar 1999; Martens and Boyd 1994), a pathogenic bacterium (Boyd et al. 1994) and a pathogenic fungus (Boyd et al. 1994). In addition, Pollard and Baker (1997) demonstrated deterrence of herbivory by hyperaccumulated Zn for several types of invertebrate herbivores. For *Streptanthus polygaloides* A. Gray, hyperaccumulated Ni has been shown to cause acute toxicity in several invertebrate folivores (Boyd and Moar 1999; Martens and Boyd 1994) and negative effects on two plant pathogens (Boyd et al. 1994). Boyd (1998) reviewed the available experimental evidence and concluded that defense is a likely function of at least some hyperaccumulated metals.

Plant defense mediated by hyperaccumulated metals differs from other plant chemical defenses in at least two important ways. First, the toxic principle (metal ion) is translocated from the soil rather than constructed via biochemical pathways, and, second, metal-based defenses (due to their elemental nature) cannot be degraded by enzymatic attack. Hyperaccumulated metals thus constitute "elemental defenses" (Martens and Boyd 1994), and therefore differ from the more widespread secondary chemical defenses of plants.

As with other plant defenses, elemental defenses are not inviolate and are circumvented by some organisms. Investigations into how a defensive mechanism is circumvented help define the effectiveness and limitations of plant defense tactics (e.g., Becerra 1994). There is evidence that elemental defenses do not protect hyperaccumulators from some herbivores. For example, Boyd and Martens (1999) showed that the aphid *Acyrthosiphon pisum* was able to feed without apparent harm on Ni-hyperaccumulating plants of *Streptanthus polygaloides.*

As an additional case, we discovered a population of *S. polygaloides* that was parasitized by *Cuscuta californica* Hook. & Arn. var. *breviflora* Engelm. (Cuscutaceae). Parasitic plants attack many plant species (Kuijt 1969) and can have an important influence on host survival and reproductive success (Riches and Parker 1995; Pennings and Callaway 1996). They also may obtain defensive chemicals from their hosts that can defend the parasites from herbivory (e.g., Atsatt 1977; Schneider and Stermitz 1990). The research reported here examined the apparent failure of Ni hyperaccumulation to defend *S. polygaloides* against attack. We also hypothesized that, if *C. californica* plants attacking *S. polygaloides* contained elevated Ni contents, this Ni might defend *Cuscuta* against generalist folivores. Specific questions addressed are:

(1) Does *C. californica* parasitizing *S. polygaloides* receive metal from its host?
(2) Do parasitized *S. polygaloides* plants have elemental levels similar to nonparasitized plants?
(3) Do the elemental parasite/host relationships of *C. californica* and *S. polygaloides* differ from those for a nonhyperaccumulator serpentine soil plant parasitized by *C. californica*?
(4) What are the relationships between soil, host, and parasite Ni levels?
(5) Does the elevated Ni content of *C. californica* parasitizing *S. polygaloides* benefit *C. californica* by protecting it from a generalist folivore?

METHODS

Study site. The study site is located in the Red Hills Management Area administered by the U. S. Department of Interior, Bureau of Land Management. Located in Tuolumne County, CA, this area is a large serpentine exposure that is occupied by serpentine chaparral, with the surrounding soils covered by oak savanna and oak woodland (Favre 1987). The serpentine chaparral is dominated by *Ceanothus cuneatus* (Hook.) Nutt. with a scattered overstory of *Pinus sabiniana* Douglas (Favre 1987).

Study species. Three plant species (two hosts, one parasite) were included in this study. One host species, *S. polygaloides* (Brassicaceae), is an annual Ni hyperaccumulator endemic to serpentine soils in the western foothills of the Sierra Nevada (Reeves et al. 1981; Kruckeberg and Reeves 1995). This species is a 2.5–9 dm-tall annual (Munz and Keck 1968) that hyperaccumulates Ni in all plant parts, ranging from a minimum of 1100 μg/g (dry mass) in fruits to as much as 16,400 μg/g in flowers (Reeves et al. 1981). The second host species, found in the Red Hills but not endemic to serpentine soils (Munz and Keck 1968), was *Lessingia nemaclada* E. Greene (Asteraceae). This species was selected for comparison because it also was parasitized by *C. californica* on the study site. This species, a 1–8 dm-tall annual common on dry gravelly slopes on the western side of the Sierra Nevada, ranges in elevation from 245–1070 m (Munz and Keck 1968). The third species is a parasitic member of the Cuscutaceae, *Cuscuta californica* var. *breviflora* (= *C. occidentalis* Millsp.). This taxon is reported from various hosts (*Grindelia* spp., *Solanum* spp., etc.) in many plant communities, ranging from the coast of California to Washington and Colorado (Munz and Keck 1968).

Plant and soil samples. We collected aboveground biomass samples of parasitized and nonparasitized *L. nemaclada* and *S. polygaloides* during early July 1995. The area chosen for study covered several hectares and contained a high density of plants of both host species. *Streptanthus polygaloides* plants selected for sampling were growing in a relatively dense stand that contained few *L. nemaclada* or other herbaceous associates. Patches of *C. californica*-parasitized *S. polygaloides* were selected and the aboveground material harvested and separated into *C. californica* and *S. polygaloides* components. Host density was great enough to allow a single *C. californica* stem to extend between a number of individual host plants. Care was taken to ensure that the *C. californica* sample did not include any host *S. polygaloides* biomass, but the host plant samples did contain some adhering *C. californica* stems. For each *C. californica*-parasitized *S. polygaloides* patch sampled, the nearest comparable nonparasitized patch was located and aboveground biomass harvested. All of the nonparasitized *S. polygaloides* patches were <2 m from the corresponding parasitized patch. For both parasitized and nonparasitized patches, samples from three local areas were composited into a single sample for analysis. A total of four sets of *S. polygaloides* composite samples were collected. We also collected soil samples to determine if soil Ni levels influenced *C. californica* presence or Ni levels in either host or parasite biomass. A soil sample was collected from each biomass sampling site from directly beneath the harvested host plants. Any litter present was removed to expose mineral soil, and a sample of the upper 5 cm of soil was removed. Soil samples were composited in the same manner as plant samples, to result in a soil sample that corresponded with each plant sample collected.

Lessingia nemaclada was sampled in a similar manner. Dense patches of *L. nemaclada* were located in two separate areas each ca. 200 m from the area in which *S. polygaloides* was sampled. Some *S. polygaloides* plants were present in both of the *L. nemaclada* sampling areas. *Lessingia nemaclada* plants were more widely dispersed than were *S. polygaloides* plants, so that each *L. nemaclada* sample was a composite of plants from many different locations in the same general area. Plants were classified as parasitized or nonparasitized and aboveground biomass was collected into separate composite samples. Two composite samples of parasitized *L. nemaclada,* and two composite samples of nonparasitized *L. nemaclada,* were collected from each of the two areas, for a total of four parasitized and four nonparasitized samples of *L. nemaclada.* As with *S. polygaloides,* soil samples were also collected. A soil sample was collected (in the same manner described above) from each location and soil samples were composited in parallel with the compositing of the biomass samples. Therefore, each *L. nemaclada* soil and biomass sample was composed of several subsamples from a particular location. Aboveground *C. californica*-parasitized material was separated into *C. californica* and *L. nemaclada* components. As with *S. polygaloides* samples, care was taken to ensure that the *C. californica* sample did not contain any host biomass, but the host plant samples contained some of the adhering *C. californica* stems.

Defense of C. californica *by Ni.* We hypothesized that the Ni content of *C. californica* parasitizing *S. polygaloides* may defend *C. californica* against polyphagous insect herbivores. We tested this hypothesis during the 1998 field season, using larvae of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). Larvae of this insect were an appropriate selection as a representative polyphagous insect herbivore because of their broad host range (Metcalf and Metcalf 1993) and because *Spodoptera exigua* has been used as a "bioassay" herbivore in other research we have conducted on the Ni-based defense of *S. polygaloides* (Boyd and Moar 1999). We obtained larvae for this experiment from a laboratory colony established from insects collected from Alabama cotton fields and maintained on artificial diet (Chalfant 1975) at 28°C with a light-dark period of 12:12 h.

Neonate larvae were fed *C. californica* stems collected in 1998 from the Red Hills study site that parasitized either *S. polygaloides* or other herbaceous hosts. Four or five neonate larvae were placed on top of samples of freshly-collected *C. californica* stems within small plastic petri plates. A small piece of moistened sponge was included in each petri plate to help maintain the freshness of the plant material. Fifteen plates each of high-Ni *C. californica* (collected from *S. polygaloides*) and low-Ni *C. californica* (collected from herbaceous nonhyperaccumulator species) were started on June 15. Two days later, we began a second run using another hatching of neonates and a second set of 15 petri plates (each) for high- and low-Ni *C. californica.* Larvae were fed fresh field-collected *C. californica* stems every 3–5 days, at which time we removed from the petri plates any plant material that remained from the previous feeding. Larval survival was noted on days that larvae were fed. The experiment was conducted at room temperature and under ambient light conditions. Both runs were terminated on July 1, when fresh *C. californica* stems became difficult to find. Larvae still alive on July 1 were frozen, dried at 60°C for several days, weighed and the mean mass of the survivors in each petri dish was calculated. A sample of high- and low-Ni *C. californica* stems used to feed larvae was set aside for Ni analysis (procedure described below) midway through the feeding experiment.

Elemental analyses. Dried plant samples were ground and elemental analysis was performed for 12 elements for all plant samples except the *C. californica* samples from the *Spodoptera* feeding experiment, which were only analyzed for Ni content. Plant samples were dry-ashed at 485°C, further oxidized with boiling 1 M HNO_3, dissolved in boiling 1 M HCl, filtered, and analyzed for Ca, K, Mg, P, Cu, Fe, Mn, Cr, Pb, Co, and Zn using an inductively-coupled argon plasma spectrometer (ICAP 9000, Jarrell-Ash, Franklin, MA). Nickel was determined by analyzing the extract with an atomic absorption spectrophotometer (IL 251, Instrumentation Laboratory, Franklin, MA).

Soil samples were dried, ground and a subsample used to quantify extractable Ni. Soil samples were double-acid extracted using 20 mL of extractant (0.05 M HCl/0.025 M H_2SO_4) shaken with 5 g of dry soil for 5 min. The extract was analyzed for Ni using an atomic absorption spectrophotometer.

Data analyses. Concentrations of each element for each host species were analyzed by one-way Analysis of Variance (ANOVA) to determine whether elemental concentrations varied between nonparasitized host, parasitized host, and *C. californica* tissue samples. Fisher's Protected Least Significant Difference (PLSD) test was used for post-hoc means separation at $\propto = 0.05$ (Abacus Concepts 1992). Soil Ni data were analyzed by two-way ANOVA, with host species and the presence or absence of *C. californica* as main effects and including the interaction term. Regression analysis was used to further explore relationships between soil, host, and parasite Ni levels for each of the host species. For Ni data from host plants that were nonparasitized, host plant Ni content (dependent variable) was related to soil Ni (independent variable). Data sets from parasitized host plants were analyzed by examining the relationship between: (1) host plant Ni (dependent variable) and soil Ni content (independent variable), (2) *C. californica* Ni (dependent variable) and soil Ni (independent variable), and (3) *C. californica* Ni (dependent variable) and host plant Ni (independent variable).

The relationship between host and parasite was further explored by calculating quotients of elements in parasite versus host tissue (Pate 1995). The level of a given element in a *C. californica* sample was compared to that of the corresponding sample of its host plant by dividing the parasite's value by that of the host plant. Because concentrations of Co, Cr and Pb were very low (quantities were below our detection limit in several cases), quotients were not calculated for those elements. One-way ANOVAs tested the significance of host plant identity (*L. nemaclada* or *S. polygaloides*) on quotients for each element. Fisher's PLSD test was used for post-hoc means separation at ∝ = 0.05 (Abacus Concepts 1992). Quotients were transformed (arcsine square root transformation) prior to ANOVA to better meet assumptions underlying ANOVA (Zar 1996).

Data from the *Spodoptera* feeding experiment were analyzed to determine if larval survival or growth were influenced by the hyperaccumulation status of *C. californica*'s host plant. Survival data were analyzed via survival analysis, using the actuarial (life table) estimation method (Abacus Concepts 1994). Larval weight data, log-transformed to better fit ANOVA assumptions (Zar 1996), were analyzed by one-way ANOVA to determine if the Ni content of *C. californica* influenced larval growth.

RESULTS

Elemental contents of *Lessingia nemaclada* samples did not differ significantly between parasitized, nonparasitized, and *Cuscuta californica* samples (Table 1). This was not the case for samples from *Streptanthus polygaloides,* for which significant variation was detected for six of the 12 elements examined. This variation was due to differences in elemental contents between *S. polygaloides* and *C. californica,* rather than between parasitized and nonparasitized *S. polygaloides* plants. Parasitized and nonparasitized *S. polygaloides* had similar amounts of Ni, K, P, Co, and Pb (Table 1). Only Ca differed between these samples, being significantly higher in parasitized than in nonparasitized *S. polygaloides. Cuscuta californica* had higher K and P, and lower Ni, Co and Pb contents, than *S. polygaloides.* Calcium values for *C. californica* were similar to those for nonparasitized *S. polygaloides,* but significantly less than for parasitized *S. polygaloides* (Table 1).

Cuscuta californica parasitizing *S. polygaloides* contained a mean of 800 μg Ni/g, whereas *C. californica* parasitizing *L. nemaclada* had only 11.3μg Ni/g, a 70-fold difference (Table 1). Nickel contents of *C. californica* reflected the large difference in Ni between *S. polygaloides* and *L. nemaclada* (Table 1).

Two-way ANOVA of soil Ni values detected significant variation between host plant species (mean square = 4660, $F_{1,12}$ = 21.5, P = 0.0006), but *C. californica* infection (mean square = 452, $F_{1,12}$ = 2.08, P = 0.174) and the interaction term (mean square = 7.56, $F_{1,12}$ = 0.35, P = 0.855) were nonsignificant. Mean extractable Ni content of all eight *S. polygaloides* soil samples was 42 μg/g (SE = 3.9), whereas that for the eight *L. nemaclada* samples was almost two-fold greater (76 μg Ni/g, SE = 6.3).

There were no statistically significant linear regressions for *L. nemaclada* samples (Table 2). The same was found for *S. polygaloides* samples, with one exception: that between soil Ni and *C. californica* Ni for parasitized *S. polygaloides* plants (Table

TABLE 1. ELEMENTAL COMPOSITION OF PLANT SAMPLES, EXPRESSED AS μG/G DRY WEIGHT. Data are means (SE), n = 4. Plant material for *S. polygaloides* that varied significantly in composition for an element (as shown by ANOVA) is denoted by superscripts. Differing superscripts indicate significant post-hoc means separation (∝ = 0.05) by Fisher's PLSD test. No samples from *L. nemaclada* differed significantly in composition for any element measured.

	Plant material: *Streptanthus polygaloides*			Plant material: *Lessingia nemaclada*		
Element	Nonparasitized	Parasitized	*Cuscuta*	Nonparasitized	Parasitized	*Cuscuta*
Ni	2620^{a} (373)	3130^{a} (249)	800^{b} (153)	17.5 (4.2)	27.0 (8.4)	11.3 (1.8)
K	9140^{a} (2560)	6340^{a} (816)	16,000^{b} (1058)	8060 (346)	9090 (640)	11,300 (3180)
P	1440^{a} (122)	1260^{a} (176)	3470^{b} (252)	866 (186)	973 (280)	1280 (422)
Ca	2420^{a} (437)	3540^{b} (359)	2140^{a} (216)	3430 (206)	3670 (319)	2170 (857)
Co	2.3^{a,b} (0.88)	3.7^{b} (0.33)	0.69^{a} (0.34)	0.83 (0.53)	0.86 (0.42)	3.3 (3.2)
Pb	4.4^{a,b} (2.0)	7.0^{b} (0.68)	0.61^{a} (0.36)	0.45 (0.45)	1.7 (0.7)	8.4 (8.4)
Mg	2050 (326)	2440 (281)	2050 (171)	2010 (218)	2930 (223)	2150 (442)
Fe	118 (36)	76.8 (10)	111 (38)	269 (77)	494 (132)	158 (49)
Zn	35.2 (5.9)	47.2 (4.0)	39.8 (3.2)	26.5 (2.2)	29.7 (3.6)	27.1 (8.4)
Mn	11.6 (1.7)	10.4 (1.2)	13.6 (2.2)	20.3 (2.1)	25.4 (4.0)	17.9 (7.0)
Cu	3.0 (0.68)	2.9 (0.90)	2.8 (0.80)	5.5 (0.66)	6.3 (1.6)	5.2 (1.5)
Cr	2.0 (0.95)	1.0 (0.36)	1.6 (1.4)	4.0 (1.6)	7.8 (3.5)	5.8 (4.9)

TABLE 2. RELATIONSHIPS BETWEEN HOST, PARASITE, AND SOIL NI CONTENTS AS REVEALED BY LINEAR REGRESSIONS. Regressions are presented between pairs of variables selected from each of the four datasets generated in the experiment. For all regressions, df = 1.

Dependent/Independent variables	Mean square	F	P
	L. nemaclada: No *Cuscuta* present		
L. nemaclada Ni/soil Ni	0.260	0.002	0.97
	L. nemaclada: Parasitized		
L. nemaclada Ni/soil Ni	322	1.24	0.38
C. californica Ni/soil Ni	9.98	1.42	0.36
C. californica Ni/*L. nemaclada* Ni	0.119	0.010	0.93
	S. polygaloides: No *Cuscuta* present		
S. polygaloides Ni/soil Ni	70,500	0.088	0.79
	S. polygaloides: Parasitized		
S. polygaloides Ni/soil Ni	119,000	1.49	0.35
C. californica Ni/soil Ni	264,000	33.2	0.029
C. californica Ni/*S. polygaloides* Ni	491,000	3.87	0.19

2). The regression for this analysis accounted for 94.3% of the variation in the data ($r^2 = 0.943$, $Y = 2502 - 47.3\ X$) and described an inverse relationship between these two variables. This inverse relationship was unanticipated, and may be a chance result stemming from small sample size.

Elemental parasite/host quotients for *C. californica* ranged widely, and for some elements varied due to host identity. Mean quotients varied from a low of 0.25 for Ni to a high of 2.8 for P, both with *S. polygaloides* as host (Table 3). Quotients for most elements did not vary due to host (Table 3). Exceptions were Ni, with a significantly higher quotient on *L. nemaclada* than on *S. polygaloides* (ANOVA: mean square = 0.238, $F_{1,6} = 6.65$, P = 0.0418), and K and P, both of which had significantly higher quotients on *S. polygaloides* (respective ANOVA's: mean square = 0.622, $F_{1,6} = 10.3$, P = 0.0185; and mean square = 0.645, $F_{1,5} = 9.61$, P = 0.0268). Quotients for Ca and Mg were <1 for both host species, whereas quotients for Fe, Mn, Cu and Zn showed no consistent trend relative to unity for either host (Table 3).

TABLE 3. ELEMENTAL QUOTIENTS FOR *CUSCUTA CALIFORNICA* VAR. *BREVIFLORA* PARASITIZING *LESSINGIA NEMACLADA* OR *STREPTANTHUS POLYGALOIDES*. Data are means (SE), n = 4. Differing superscripts for mean quotients of an element denote significantly differing means (Fisher's PLSD test, ∝ = 0.05).

Element	*Lessingia nemaclada*	*Streptanthus polygaloides*
Ni	0.60^a (0.13)	0.25^b (0.036)
K	1.2^a (0.35)	2.6^b (0.18)
P	1.4^a (0.38)	2.8^b (0.16)
Ca	0.59 (0.23)	0.61 (0.040)
Mg	0.72 (0.12)	0.87 (0.090)
Fe	0.33 (0.042)	1.6 (0.65)
Mn	0.71 (0.27)	1.4 (0.37)
Cu	0.91 (0.33)	1.3 (0.45)
Zn	1.0 (0.42)	0.85 (0.064)

Stems of high-Ni *C. californica* (*S. polygaloides* as host) and low-Ni *C. californica* (nonhyperaccumulators as hosts) were equivalent diets for *Spodoptera* larvae. For both runs, larval survival was initially greater for those fed high-Ni leaves. By the time the experiment was terminated, survival had dropped to similarly low levels (ca. 50%) for larvae fed *C. californica* from either type of host (Fig. 1). Survival analysis revealed no significant effect of *C. californica* host on larval survival (Mantel-Cox logrank test, $\chi^2 = 0.019$, df = 1, P = 0.89).

Larval growth also was unaffected by *C. californica* Ni content. Mean larval mass at the end of the experiment was similar for larvae fed high-Ni *C. californica* stems (6.8 ± 3.9 mg, mean ± SE, n = 29) and those fed low-Ni stems (6.6 ± 4.4 mg, mean ± SE, n = 28). ANOVA indicated no significant effect of *C. californica* host on mean larval mass (mean square = 0.001, $F_{1,55} = 0.011$, P =

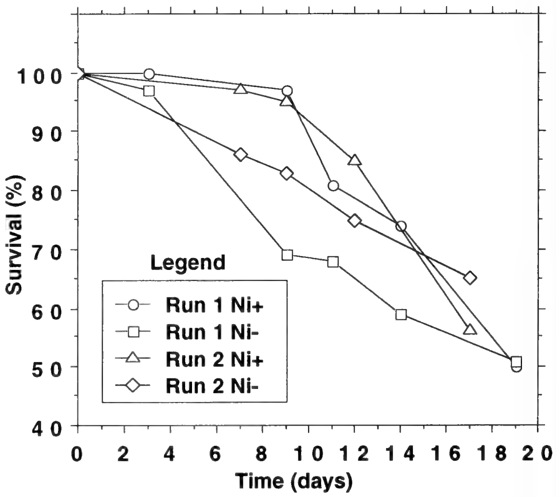

FIG. 1. Survival of *Spodoptera exigua* larvae fed *Cuscuta californica* collected from *S. polygaloides* (Ni+ *Cuscuta*) and *L. nemaclada* (Ni− *Cuscuta*).

0.92). *Cuscuta californica* stems used for this experiment had lower Ni contents than those collected in 1995. The 1998 sample of *C. californica* from *S. polygaloides* contained 470 μg Ni/g, whereas the mean for samples from 1995 was 800 μg/g (Table 1). The sample of *C. californica* collected from nonhyperaccumulator hosts in 1998 contained 28 μg Ni/g, versus 13 μg/g from *C. californica* parasitizing *L. nemaclada* in 1995 (Table 1).

DISCUSSION

Hyperaccumulated Ni did not prevent *Streptanthus polygaloides* from being attacked by *C. californica.* In the field, *C. californica* parasitizing *S. polygaloides* appeared as vigorous as nearby *C. californica* that used other herbaceous species as hosts. Because all plant defenses can be circumvented to some extent by some organisms (Levin 1976), this study helps to define the limitations of the Ni-based elemental defense of *S. polygaloides.* Whereas hyperaccumulated Ni negatively affects generalist folivores (Boyd and Martens 1994: Martens and Boyd 1994; Boyd and Moar 1999), organisms tapping vascular tissues are not similarly affected. Boyd and Martens (1999) showed that the pea aphid (*Acyrthosiphon pisum* [Harris]; Homoptera: Aphididae), a phloem-feeder as with many aphid species (Dixon 1985), was not harmed by feeding on Ni-hyperaccumulating *S. polygaloides* plants. Unlike aphids, *C. californica* may tap both phloem and xylem tissues (e.g., Lee and Lee 1989). The high Ni content of *C. californica* observed here, and the low Ni content of aphids feeding on high-Ni *S. polygaloides* reported by Boyd and Martens (1999), suggest that the Ni level in phloem fluid of *S. polygaloides* is relatively low and that the Ni present in *C. californica* arrives largely through the xylem connections. The latter idea is bolstered by the report of Kramer et al. (1996) that Ni in the Ni hyperaccumulator *Alyssum lesbiacum* is transported in xylem (as a histidine-Ni complex).

Our results show that this population of *C. californica* is remarkably Ni-tolerant, since these plants were able to withstand the elevated tissue Ni levels that we measured in *C. californica* parasitizing *S. polygaloides* (see Table 1). MacNicol and Beckett (1985) suggest that unadapted plants can withstand tissue Ni concentrations of approximately 10 μg/g without suffering a reduction in growth. Reeves (1992) pointed out that most plants growing on serpentine soils contain <100 μg Ni/g in their tissues. The mean value reported here for *C. californica* parasitizing *S. polygaloides,* 800 μg/g, therefore is exceptionally high relative to most serpentine species. Although the mean fell short of the 1000 μg/g level used to define hyperaccumulator status (Brooks 1987; Baker and Brooks 1989), one *C. californica* sample reached 1220 μg Ni/g. To our knowledge, these values are the highest Ni contents of any parasitic plant yet reported. It is unlikely that soil contamination contributed greatly to these Ni values. Reeves (1992) points out that high levels of Co (>50 μg/g) may indicate soil contamination. Levels of Co in our specimens were low, with means ranging from 0.69–3.7 μg/g (Table 1). Further evidence against soil contamination is shown by the low Cr values of our samples, which ranged from 1–8 μg/g (Table 1). Brooks et al. (1995) state that low Cr concentrations of plant samples imply lack of contamination by serpentine soils, as these soils often have elevated Cr concentrations.

Boyd and Martens (1998a) suggested that elemental defenses of plants may be circumvented in several ways by organisms that attack those plants: (1) by selective feeding on low-metal tissue; (2) by use of a generalist diet to dilute high-metal food; and, (3) by genuine tolerance of high metal levels. For *C. californica,* the relatively high Ni content when growing on *S. polygaloides* indicates that this population of *C. californica* possesses a high level of metal tolerance. Thus, *C. californica* is one of the first organisms documented to attack a metal-hyperaccumulator plant by way of physiological metal tolerance. However, we should note that the Ni content of *C. californica,* relative to its *S. polygaloides* host, was lower than for all other elements analyzed (see quotients in Table 3). The lessened concentrations of some heavy metals (Ni, Co, Pb) in *C. californica* parasitizing *S. polygaloides* (Table 1) implies discrimination against those elements during uptake by the parasite. We suggest that the high Ni content of *C. californica* from *S. polygaloides* results from its inability to be more effective in excluding metals from its tissues.

The high Ni levels found in *C. californica* tissue did not protect it from herbivory by *Spodoptera exigua* larvae. Neither acute toxicity nor sublethal (growth-reducing) effects were detected in our feeding experiment. This implies that *C. californica* does not receive a defensive benefit from the Ni it obtains from host *S. polygaloides.* This differs from some cases of chemical defense in insects, in which a chemical from a plant species is used by the insect in its own defense (see Duffey 1980), and from examples where parasitic plants obtain defensive chemicals from their hosts (e.g., Atsatt 1977; Schneider and Stermitz 1990; Marvier 1996). In this first test involving a Ni-based defense, we found no evidence of a protective benefit accruing to high-Ni *C. californica* plants.

To our knowledge, this report is the first definitive record of a parasitic plant obtaining high amounts of metal from a hyperaccumulator host. Reeves (1992) reported that the root parasite *Orobanche rechingeri* was believed to parasitize the Ni hyperaccumulator *Alyssum lesbiacum.* The parasite contained 600 μg Ni/g, but it was unclear if the Ni came from the host or directly from the serpentine soil. Because *C. californica* contacts soil only as a seedling and depends solely on its host for mineral nutrition during subsequent life history stages

(Kuijt 1969; Pate 1995), there is little doubt as to the source of the Ni found in *C. californica* tissues. Study of other parasite/hyperaccumulator interactions will determine if the case reported here is a representative outcome for parasite/hyperaccumulator interactions. Because parasitic plants are very widespread (Musselman and Press 1995) and occur on serpentine substrates (e.g., Kruckeberg 1984; Callizo 1992), it seems certain that more cases of parasitism of metal hyperaccumulators will be uncovered in the future.

Our results also have implications regarding the type of defense represented by metals. Plant defenses can be either constitutive or inducible (Karban and Baldwin 1997), and we know of little available evidence that bears on this point regarding metal-based elemental defenses (Boyd 1998; Boyd and Martens 1998b). To our knowledge, the only published information pertinent to this question is a study by de Varennes et al. (1996) using the Ni hyperaccumulator *Alyssum pintodasilvae* Dudley. They found that plants regrowing after an initial harvest of aboveground biomass contained 3.4–5 times more Zn than the first harvest of plant material. In our study of *S. polygaloides,* Ni levels did not vary significantly between parasitized and nonparasitized plants. Therefore, we conclude that the degree of Ni hyperaccumulation was not affected by *C. californica* attack and that Ni hyperaccumulation in *S. polygaloides* represents a constitutive, rather than inducible, defense.

Finally, this report has implications for applied uses of metal hyperaccumulators. Metal hyperaccumulators may be useful as "phytoextractors" of metals, either from metal-contaminated sites (McGrath et al. 1993) or as a way to "phytomine" metals from naturally metalliferous soils (Nicks and Chambers 1995). Parasitic plants, including some species of *Cuscuta* (Kuijt 1969), can become pests in agricultural situations (e.g., Riches and Parker 1995). Given the high levels of elemental defenses in a metal-hyperaccumulating "phytoextractor" plant, one might suspect that such plants would be well-defended against attack by insects, parasitic plants, etc. Our research shows that, at least in the case of *S. polygaloides,* plants hyperaccumulating Ni are not safe from attack by *C. californica.* Phytoextraction or phytomining industries must therefore be prepared to protect their metal-hyperaccumulating plants against parasitic plant pests using other techniques.

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MORPHOLOGICAL DIFFERENTIATION AMONG MADREAN SKY ISLAND POPULATIONS OF *CASTILLEJA AUSTROMONTANA* (SCROPHULARIACEAE)

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Abstract

Populations of *Castilleja austromontana* (Scrophulariaceae) occur at high elevations (>2050 m) on the Madrean sky islands of southern Arizona, adjacent New Mexico and northern México. These mountaintop habitat islands are cooler and wetter than the desert and semi-desert grasslands below. We examined 41 vegetative, floral and seed characters for plants from six sky islands in Arizona. Univariate and multivariate analyses indicate strong morphological differentiation among populations. Discriminant functions analysis placed 88% of plants correctly, indicating that plants from different populations are morphologically distinct. Selection may contribute to the observed differentiation, but we have no basis for inferring the direction or strength of selection on vegetative traits. Sky island populations apparently share the same pollinators, so divergent selection on floral traits seems unlikely. Past and present gene flow may also be involved as our results conform, at least in part, to an isolation by distance model. The magnitude of character differences combined with inferences of population sizes suggests that genetic drift may also contribute to the differentiation observed.

Evolutionary biologists have long recognized that islands, both real and habitat, provide special opportunities to study population differentiation and speciation due to geographic isolation (MacArthur and Wilson 1967; Carlquist 1974; Grant 1986, 1998 and papers therein; Wagner and Funk 1995 and papers therein; Francisco-Ortega et al. 1996; Givnish 1998). Gene flow will be reduced among populations on geographically isolated islands compared to contiguous populations. When gene flow is absent or rare, populations may differentiate over time as a result of selection or genetic drift (Wright 1943; Mayr 1954). Thus, island systems are ideal for studies of both the processes that hold populations together (i.e., gene flow) and those that result in differentiation (i.e., selection, genetic drift).

In the Basin and Range province of the southwestern United States and northwestern México, a series of mountain ranges provide island-like habitats for plants and animals that require more mesic and temperate conditions than those offered by the deserts, scrublands and grasslands that now occupy the intervening basins (Marshall 1957). These Madrean sky islands developed as a series of deformation mountains produced by continental rifting that occurred between 12 and 6 million years BP (Nations and Stump 1981; Morrison 1991). At present, 17 Madrean sky islands are high enough to support mixed conifer forest (ca. 2500 m elev., somewhat lower toward the north and higher toward the south). They form an archipelago that connects extensive and continuous highlands to the north (the Central Mountain Province and the Colorado Plateau above the Mogollon Rim in Arizona) and south (the Sierra Madre Occidental that extends to within ~75 km of the Arizona-México border) (Fig. 1). As first documented by Shreve (1915; see also Heald 1950; Niering and Lowe 1984; Brown 1994; Warshall 1995), the Madrean sky islands support almost the same range of vegetation zones as occurs in all of the western United States, from open juniper woodlands just above semi-desert grasslands to spruce-fir forest on the summits of the highest mountains.

Here we report morphological differentiation among populations of *Castilleja austromontana* Standl. & Blumer (Scrophulariaceae), an herbaceous perennial that occurs on most of the Madrean sky islands. *Castilleja austromontana* is found above 2050 m elev., and therefore occurs as isolated populations in the highest of sky island habitats. We used data from vegetative, floral and seed characters for individuals from six sky island populations to address three questions: (1) Are populations distinguishable by the examined morphological traits? (2) If so, which traits most strongly differentiate the populations? (3) Can morphological divergence among populations be related to geography?

Materials and Methods

Castilleja austromontana is found as far north as the White Mountains of Arizona (Apache County) and the Sangre de Cristo Mountains of northern

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TABLE 1. LOCATION OF POPULATIONS OF *CASTILLEJA AUSTROMONTANA* FROM WHICH SAMPLES WERE TAKEN. Abbreviations following the name of each mountain range are those used in Tables 2 and 4.

Catalina Mountains (Cat): Mount Lemmon, ca. 2 miles above Ski Valley, 2750 m elev., Pima County, Arizona. *S. Slentz 44* (ARIZ).
Santa Rita Mountains (SR): About 200 meters below Baldy Saddle, Old Baldy Trail, Mount Wrightson, 2500 m elev., Santa Cruz County, Arizona. *S. Slentz and L. McDade 40* (ARIZ).
Pinaleno Mountains (Pin): Hospital Flat, 2750 m elev., Graham Country, Arizona. *S. McLaughlin and J. Bowers 6431* (ARIZ).
Rincon Mountains (Rin): Italian Ranch Trail, Italian Spring, Saguaro National Park East, 2400 m elev., Pima Country, Arizona. *S. Slentz 48* (ARIZ).
Huachuca Mountains (Hua): Carr Canyon Trail, 0.75 miles above Reef Area Campground, 2400 m elev., Cochise Country, Arizona. *S. Slentz 43* (ARIZ).
White Mountains (Wht): Lee Valley Recreation Area, ca. 3 miles south of Sunrise Lake on State Rt. 273, 2800 m elev., Apache County, Arizona. *S. Slentz 45* (ARIZ).

New Mexico and at least as far south as the limit of the sky island region in the northern Mexican states of Sonora and Chihuahua. Nothing is known about the age of the species nor is there a phylogenetic hypothesis for *Castilleja.* Flowering of *Castilleja austromontana* coincides with the summer wet season (July–September), and plants die back to the ground with the onset of winter. Our observations (44 hours on the Huachuca, Catalina and White Mountains) indicate that flowers of *C. austromontana* are visited and likely pollinated by hummingbirds. Individuals of *Selasphorus rufus* (Rufous Hummingbird) and possibly *S. platycercus* (Broadtailed Hummingbird) were observed to contact anthers and stigmas, and patches of pollen were seen on the heads of some visiting birds. There have been no detailed studies of the breeding systems of plants of this species. The seeds of *C. austromontana* have no special dispersal mechanism and seem to fall passively from dehiscing fruits. All *Castilleja* studied to date are autotrophic root parasites (Heckard 1962, Marvier 1996); nothing is known about the nutritional status or hosts of *C. austromontana.*

Collection Sites and Protocol. Field sites were located from specimens at the University of Arizona herbarium (ARIZ). We collected plants from one area on each of six different mountain ranges (Table 1; Fig. 1). During 1995 and 1996, we made at least one collecting trip to each mountain range during the flowering season to gather specimens for scoring vegetative and floral characters. These were followed by a later trip to collect mature fruits. Individual flowering plants were sampled by first determining the extent of the population, then walking a transect along the longest dimension of the population and collecting from individuals at intervals chosen to achieve the desired sample size (15–20 individuals per population) across this longest dimension. Individual plants produce one to many stems from a root crown and are clearly distinct from other individuals. One flowering stem from each individual was snapped off just above the root stock at ground level. Only fresh flowers and their subtending bracts were scored (freshness was assessed by presence of pollen on recently dehisced anthers).

Plants sampled for seed collection were chosen in the same manner. Infructescences from six to 11 individuals were collected from each population except the White Mountains, where mature fruits could not be collected. Seeds were sampled only from mature, partially dehisced capsules; only filled, apparently viable seeds were used. Because individuals from which flowering stems were collected were not marked, it was not possible to collect infructescences from the same individuals.

Morphometrics. A total of 41 characters was recorded from each flowering stem (35 measurements + 6 meristics); of these, 11 were vegetative and 30 were floral characters (Fig. 2, Appendix 1). Data were recorded from four leaves, three bracts, and three flowers per individual (Fig. 2). The sampling scheme for leaves and bracts specifically sought to capture positional differences in these structures: leaf and bract size and shape may vary along the stem or rachis, respectively, in *Castilleja.* We therefore included the measurements for each individual leaf and bract in the analyses. We calculated means of corolla and calyx measurements for the three flowers sampled from each plant and used these means in all analyses. In addition, to examine leaf and bract shape, we combined length and width measurements of individual leaves and bracts. The ratio of corolla to galea length varies in *Castilleja*; we determined this ratio for individual flowers and then calculated a mean value for each individual. The data set for univariate analysis thus includes a total of 39 characters (Table 2); of these, eight are ratios and the six calyx and corolla characters each represent means of three measurements. All measurements were log-transformed. Because entire bracts have cleft depths of zero, we added 0.5 to each value for depth of bract clefts prior to log-transformation. Meristic variables were square-root transformed.

The intricate surface characteristics of the seeds, as viewed with the SEM, have proven useful in taxonomic work with *Castilleja* (Chuang and Heckard 1992; Lockwood 1992). Initial experiments

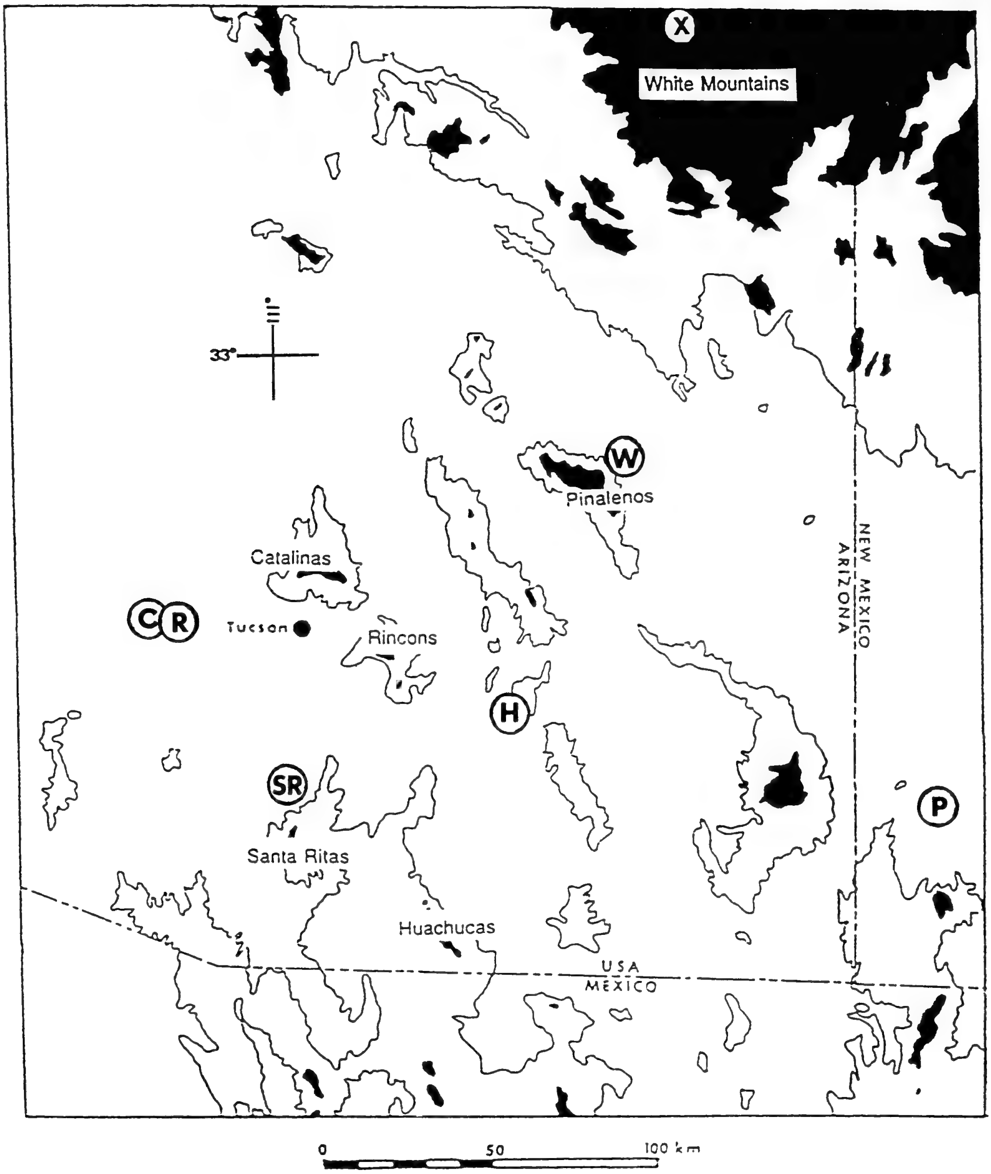

FIG. 1. The Madrean sky islands in southeastern Arizona and adjacent western New Mexico and northern Mexico. 1500 m contour lines outline mountain ranges. Shaded areas are >2500 m elevation, corresponding to approximate range of habitat of *Castilleja austromontana*. Circles indicate relative placement of plant populations by multidimensional scaling (the MDS result was scaled so that its dimensions matched those of the physical map; C = Catalina Mountains, H = Huachuca Mountains, P = Pinaleño Mountains; R = Rincon Mountains; SR = Santa Rita Mountains; W = White Mountains). An X indicates the collection location for the White Mountain population.

with techniques for preparing seeds (including dehydration and critical point drying) indicated that there were no differences between seeds prepared using these methods versus simply placed directly onto SEM specimen stubs. Several seeds from the same fruit were then placed onto a stub; stubs were coated with 30–60 nm of gold-palladium and viewed using an I.S.I. DS-130 scanning electron microscope. Several photographs were taken of at least one seed from each of 6–11 plants per population for examination of seed characters. To facilitate standardization of measurements, seeds chosen to be photographed were in the same orientation, i.e., with the longest dimension of the seed parallel to the long axis of the photo. The SEM was periodically recalibrated by photographing a micrometer and adjusting the scale that appears on each photograph accordingly. Four measurements plus one meristic character were scored for each seed (Fig. 3, Appendix 1). To examine seed shape, we

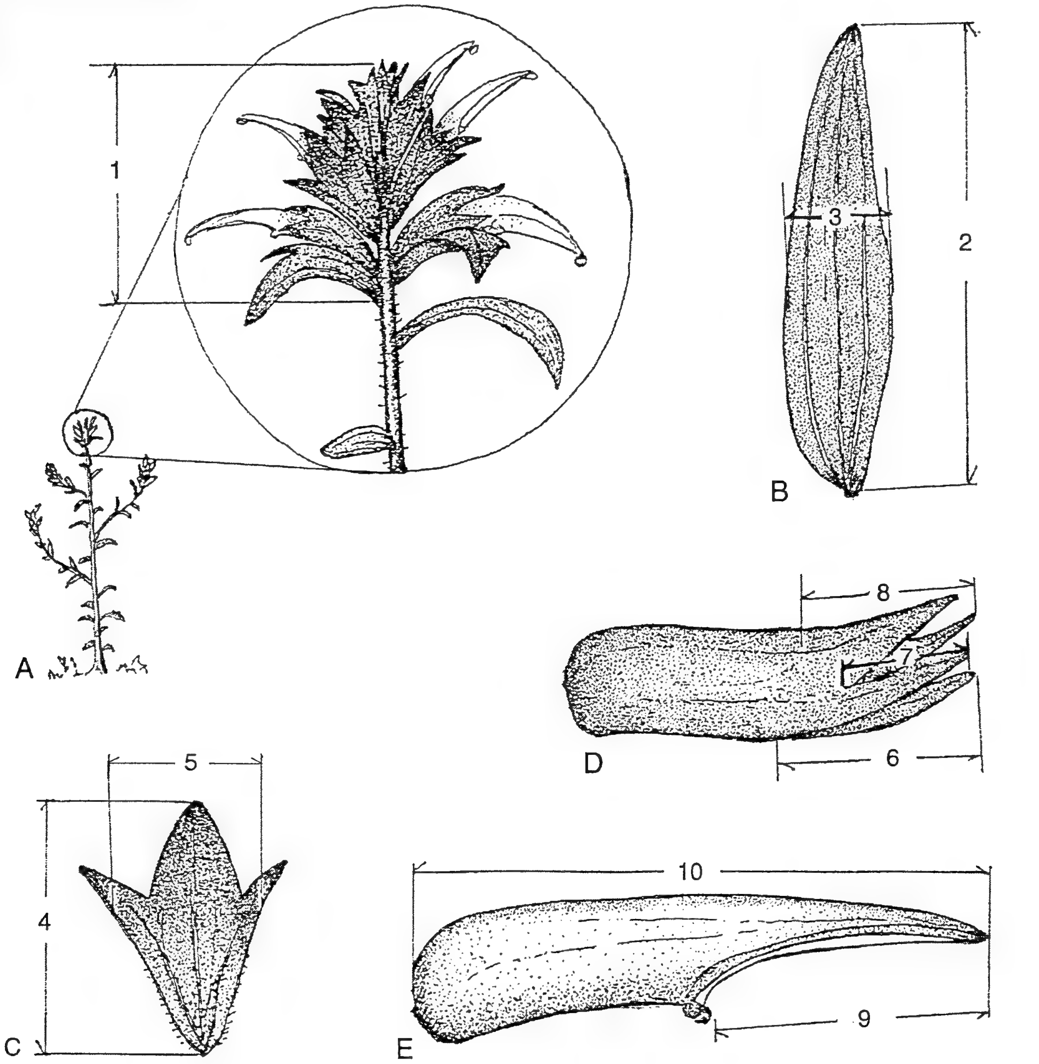

FIG. 2. *Castilleja austromontana.* A. Schematic illustration of plant with enlarged terminal raceme; B. leaf; C. floral bract; D. calyx; E. corolla. Numbered dimensions indicate measurements taken (Appendix 1, Table 1): 1 Raceme length; 2 Leaf length; 3 Leaf width; 4 Bract length; 5 Bract width; 6 Anterior calyx cleft depth; 7 Lateral calyx cleft depth; 8 Posterior calyx cleft depth; 9 Galea length; 10 Corolla length. Drawn by S. Slentz.

combined length and width measurements of individual seeds. When more than one seed was measured from an individual plant, within-plant means of each character were used in the analyses. As with the vegetative + floral data, measurements were log-transformed and meristic data were square-root transformed.

Statistical Analyses. The vegetative + floral data set was treated separately from the seed data because the plants from which seeds were taken were not matched with those from which flowering stems were taken. All analyses were conducted in SAS (SAS Institute 1988) except that NTSYS (Rohlf 1993) was used for multidimensional scaling (see below). One-way analyses of variance were used to determine which variables showed significant variation among populations. Student-Newman-Keuls a posteriori tests were used to assess which populations were significantly different from one another for each character. The vegetative + floral data set was subjected to principal components analysis (PCA) to examine relationships among characters. Ratios were omitted from the PCA because covariation between characters will be detected by multivariate methods automatically. Because only five seed variables were measured, the seed data were not analyzed using PCA. Correlation matrices were used for PCA because both metric and meristic characters were included.

Discriminant functions analysis (DFA) was used to determine how effectively the character data distinguish plants from different mountain ranges.

Table 2. Results of ANOVA for Morphological Characters Ordered by Plant Structure. Results of the Student-Newman-Keuls a posteriori test are reported for each variable, with populations ordered from high values to low. See Table 1 for key to abbreviations of mountains. Lines below mountain abbreviations connect populations that are not significantly different. Asterisks indicate p-values that are judged significant by the sequential Bonferroni test.

Character	Results of ANOVA	a posteriori test
Vegetative:		
Leaf length 1	$F = 1.83$; 5, 83 df; $p = 0.1166$	
Leaf length 2	$F = 2.71$; 5, 83 df; $p = 0.0255$	Wht Pin Hua Cat SR Rin
Leaf length 3	$F = 3.64$; 5, 83 df; $p = 0.0050$	Wht Rin Pin Hua SR Cat
Leaf length 4	$F = 1.95$; 5, 82 df; $p = 0.0950$	
Leaf width 1	$F = 8.51$; 5, 83 df; $p < 0.0001$*	Pin Hua Rin SR Cat Wht
Leaf width 2	$F = 6.04$; 5, 83 df; $p < 0.0001$*	Pin Hua Cat SR Rin Wht
Leaf width 3	$F = 2.01$; 5, 83 df; $p = 0.0858$	
Leaf width 4	$F = 1.92$; 5, 82 df; $p = 0.0999$	
Leaf length/width 1	$F = 0.48$; 5, 83 df; $p = 0.7901$	
Leaf length/width 2	$F = 5.45$; 5, 83 df; $p = 0.0002$*	Wht Cat Hua SR Rin Pin
Leaf length/width 3	$F = 6.12$; 5, 83 df; $p < 0.0001$*	Wht Rin Hua Cat SR Pin
Leaf length/width 4	$F = 3.78$; 5, 82 df; $p = 0.0039$	Wht Rin Hua Cat Pin SR
No. lateral branches	$F = 4.84$; 5, 49 df; $p = 0.0011$*	Cat Rin Hua SR Pin Wht
Apical stem width	$F = 4.51$; 5, 77 df; $p = 0.0012$*	Rin SR Hua Pin Wht Cat
Basal stem width	$F = 3.12$; 5, 78 df; $p = 0.0129$	Hua Cat Rin Pin Wht SR
Reproductive:		
No. of racemes	$F = 3.64$; 5, 63 df; $p = 0.0059$	Rin Cat Hua Pin SR Wht
No. of flowers	$F = 1.95$; 5, 82 df; $p = 0.0943$	
Raceme length	$F = 1.65$; 5, 82 df; $p = 0.1572$	
Bracts:		
Bract length 1	$F = 2.34$; 5, 83 df; $p = 0.0489$	Wht SR Rin Hua Pin Cat
Bract length 2	$F = 2.74$; 5, 83 df; $p = 0.0244$	SR Wht Pin Rin Hua Cat
Bract length 3	$F = 2.95$; 5, 83 df; $p = 0.0168$	Wht SR Pin Rin Hua Cat
Bract width 1	$F = 1.20$; 5, 83 df; $p = 0.3185$	
Bract width 2	$F = 1.62$; 5, 83 df; $p = 0.1646$	
Bract width 3	$F = 2.56$; 5, 83 df; $p = 0.0332$	SR Wht Hua Rin Cat Pin
Length/Width 1	$F = 2.57$; 5, 83 df; $p = 0.0325$	Wht Rin Hua Pin SR Cat
Length/Width 2	$F = 2.09$; 5, 83 df; $p = 0.0753$	
Length/Width 3	$F = 3.88$; 5, 83 df; $p = 0.0033$	Pin Wht Rin Cat Hua SR
Mean cleft depth 1	$F = 4.49$; 5, 83 df; $p = 0.0011$*	Pin Cat Wht Hua SR Rin
Mean cleft depth 2	$F = 4.31$; 5, 83 df; $p = 0.0016$	Wht Pin Hua Cat SR Rin
Mean cleft depth 3	$F = 4.49$; 5, 83 df; $p = 0.0011$*	Wht Pin Hua Cat SR Rin
No. of clefts 1	$F = 3.41$; 5, 83 df; $p = 0.0075$	Pin Cat Wht SR Hua Rin
No. of clefts 2	$F = 2.26$; 5, 83 df; $p = 0.0560$	
No. of clefts 3	$F = 3.36$; 5, 83 df; $p = 0.0082$	Wht Pin SR Cat Hua Rin
Calyx:		
Mean anterior cleft	$F = 7.11$; 5, 83 df; $p = 0.0001$*	Wht Pin Hua SR Rin Cat
Mean lateral cleft	$F = 6.29$; 5, 83 df; $p = 0.0001$*	Pin Wht SR Hua Cat Rin
Mean posterior cleft	$F = 9.80$; 5, 83 df; $p = 0.0001$*	Wht Pin SR Hua Rin Cat
Corolla:		
Mean corolla length	$F = 8.62$; 5, 83 df; $p = 0.0001$*	Pin Hua Wht SR Rin Cat
Mean galea length	$F = 3.21$; 5, 83 df; $p = 0.0106$	Pin Wht Hua Rin SR Cat
Mean corolla/galea	$F = 3.56$; 5, 83 df; $p = 0.0057$	SR Pin Hua Wht Cat Rin
Seeds:		
Seed length	$F = 18.75$; 4, 37 df; $p < 0.0001$*	Pin Hua Cat Rin SR
Seed width	$F = 4.52$; 4, 37 df; $p = 0.0022$	Pin Cat Hua Rin SR
Seed length/width	$F = 1.10$; 4, 37 df; $p = 0.3724$	
No. midline cells	$F = 29.09$; 4, 37 df; $p < 0.0001$*	Pin Cat SR Hua Rin
No. layers of testa	$F = 15.28$; 4, 37 df; $p < 0.0001$*	Cat Hua Pin SR Rin
Wall width	$F = 12.13$; 4, 37 df; $p < 0.0001$*	Pin Hua Rin Cat SR

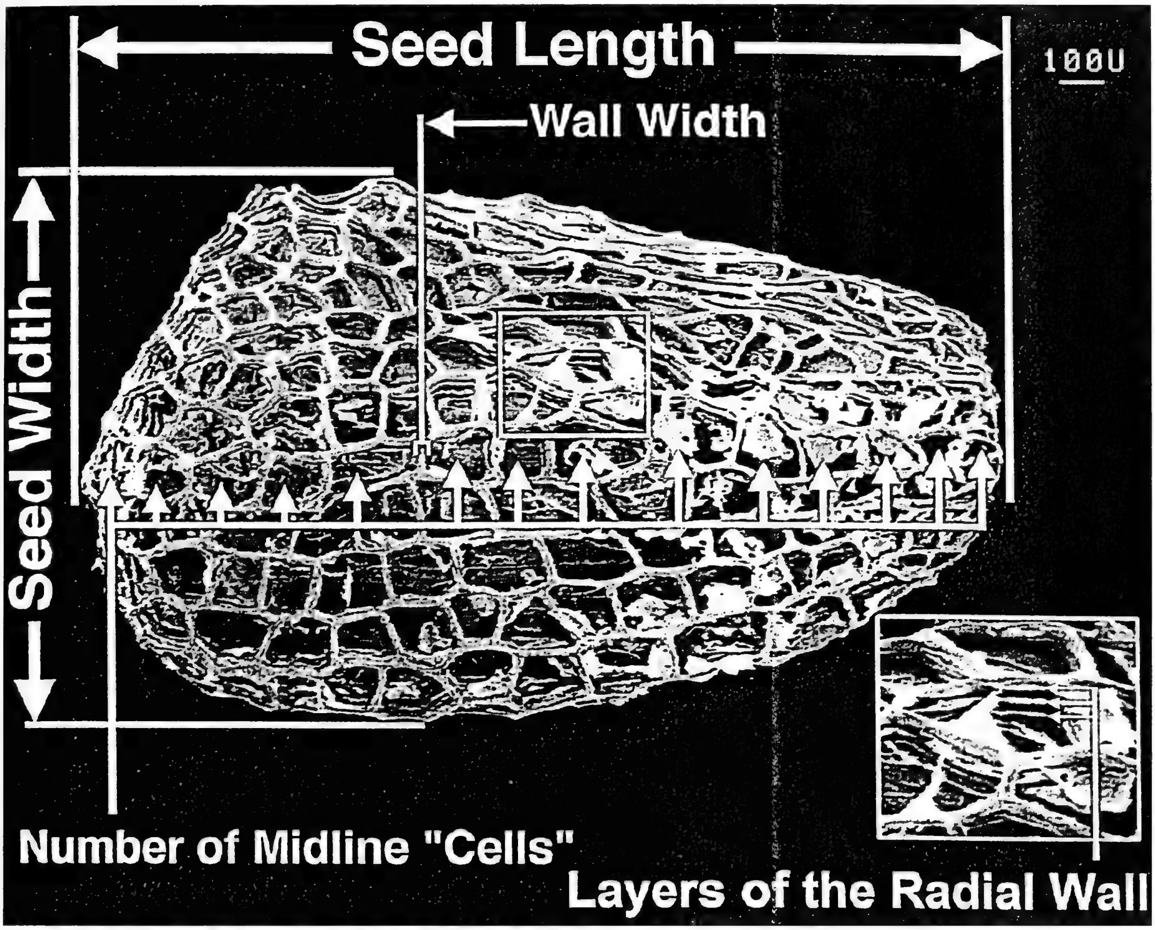

FIG. 3. Scanning electron micrograph of seed of *Castilleja austromontana*; seed length, width, and wall width were measured as indicated. Wall width was measured on a cell perpendicular to the line of vision. Number of midline cells = 14 on this seed as indicated by arrows. Enlarged cell in box illustrates layers of the radial walls (three in this case).

Character data were log transformed only if their distributions were non-normal as DFA is not affected by scaling of individual variables (Manly 1994). For seven plants from the Pinaleños, basal and apical stem widths were not measured; as a result, these plants were excluded by DFA. To maximize the number of plants included, we conducted an additional DFA excluding the two characters that were missing for these plants.

Non-metric multidimensional scaling (MDS) creates map-like diagrams that optimize the placement of each population relative to all others; the algorithm minimizes "stress," measured as the difference between pairwise distances in the diagram produced by MDS and the original distances. MDS is widely used in the social and biological sciences; a number of authors have used this technique to study the relationship between genetic or phenotypic distance and geographic distance (e.g., Wright and Ladiges 1997; Krauss 1996; Ruiz-Garcia 1997). Guiller, Bellido, and Madec (1998) found MDS to be superior to other ordination methods; these authors provide a useful overview of the method and an explanation of its performance. Here we use MDS as a heuristic technique to visualize patterns of phenotypic distance in the context of geographic distances. Pairwise Mahalanobis distances between populations were calculated in SAS and entered into NTSYS for the MDS analysis for each of the two *Castilleja* data sets. We scaled the diagram produced by this analysis so that its dimensions matched those of the physical map depicted in Fig. 1. The MDS results were then overlaid on the geographic map of the sky island region to compare relative phenotypic and geographic distances (Fig. 1).

RESULTS

Twenty-eight of 39 vegetative + floral characters and all seed characters except ratio of seed length/width varied significantly among populations (Table 2). Twelve vegetative + floral characters and four seed characters vary significantly among pop-

TABLE 3. EIGENVECTORS ON FIRST THREE PRINCIPAL COMPONENTS FOR CHARACTERS INCLUDED IN PRINCIPAL COMPONENT ANALYSIS OF THE VEGETATIVE AND REPRODUCTIVE DATA EXCLUDING SEEDS AND RATIOS. Analysis included all characters. The first three principal components account for 52.9% of the total variation. See Appendix 1 for explanation of characters.

Characters	PC1	PC2	PC3
Bract length 2	0.2736	0.1076	−0.1530
Leaf length 4	0.2703	0.0622	−0.0533
Mean anterior calyx cleft depth	0.2653	−0.0975	−0.0242
Leaf length 3	0.2630	0.0495	−0.0786
Bract length 1	0.2619	0.1452	−0.1370
Mean posterior calyx cleft depth	0.2528	−0.1973	0.0011
Mean corolla length	0.2461	0.0168	−0.0076
Bract length 3	0.2402	−0.0080	−0.2036
Bract width 2	0.2344	−0.0382	0.1694
Leaf width 3	0.2262	0.0857	0.1295
Leaf width 4	0.2188	0.1475	0.1563
Mean galea length	0.1916	0.0443	−0.0159
Raceme length	0.1907	0.0358	0.1193
Number of racemes	−0.1825	0.1042	0.2325
Number of lateral branches	−0.1807	0.1228	0.2234
Bract width 1	0.1739	0.2196	0.1607
Bract width 3	0.1731	0.1393	0.0733
Mean lateral calyx cleft depth	0.1609	−0.1291	−0.0052
Leaf length 2	0.1422	0.0328	0.0363
Number of flowers per raceme	0.1244	−0.0002	0.2762
Bract 3, mean cleft depth	0.1225	−0.2549	0.1069
Bract 2, mean cleft depth	0.1204	−0.3384	0.1773
Leaf width 2	0.1194	0.2331	0.1976
Bract 2, number of clefts	0.1027	−0.2743	0.2194
Bract 3, number of clefts	0.0592	−0.3596	0.2684
Leaf length 1	−0.0502	0.2115	0.2808
Basal stem width	−0.0415	0.1710	0.3017
Leaf width 1	−0.0305	0.3290	0.2622
Bract 1, number of clefts	−0.0295	−0.2443	0.2698
Bract 1, mean cleft depth	0.0266	−0.2354	0.2871
Apical stem width	−0.0262	0.1100	0.1219
Eigenvalue	8.95	4.14	3.32
% variance explained	28.88%	13.36%	10.69%

ulations even after adjusting threshold probability values via the sequential Bonferroni test (Rice 1989) (Table 2). Characters that vary significantly among populations are from diverse plant structures (Table 2). Leaf shape (i.e., length/width) and size differ among populations, with plants from the White Mountains having leaves that are relatively longer and narrower than those of plants from the other sky islands. Plants from the White Mountains also have relatively few branches. Bracts differ in cleftedness (i.e., both number and depth of clefts), as well as in shape (length/width) and length among sky islands. Plants from the White Mountains and the Pinaleños have calyces that are more deeply cleft than those of other sky island populations. Corollas differ in total length and in galea length; flowers of plants from the Pinaleños are largest whereas those from the Catalinas are smallest. Plants from the Pinaleños have long, wide seeds with many cells along the midline and wide walls compared to seeds from plants from the Santa Ritas or Rincons. Seeds from plants from the Catalinas have the most layers of the radial wall and those from the Rincons the fewest; seeds from plants in the Pinaleños are intermediate for this character.

For the analysis including vegetative + floral data, the first three principal components each account for >10% of the variation among individuals, but together explain only 52.9% of total variation. PC1 accounts for 28.9% of the standardized variance in the data. The characters that contribute most to PC1 are length of bract 2, depths of the calyx clefts, and corolla length (Table 3). Raceme length, bract length and width, and leaf length and width also contribute substantially. The characters contributing most to PC2 involve cleftedness of bracts (i.e., both number and depth of clefts), and bract length (Table 3). This component explains an additional 13.4% of the standardized variance. Characters contributing most to PC3 are basal and apical stem width, number of flowers per raceme, and leaf width. The third principal component accounts for 10.7% of the standardized variance.

The next two principal components each account for more than 5% of the total variation for a cumulative total of 68% of total variation accounted

TABLE 4. NUMBER (ABOVE) AND PROPORTION (BELOW) OF PLANTS FROM SOURCE LOCATIONS (LEFT) THAT WERE IDENTIFIED BY DISCRIMINANT FUNCTIONS ANALYSIS OF VEGETATIVE + FLORAL DATA AS FROM THE LOCATIONS LISTED ABOVE. Characters were excluded for which data were missing for some plants. See Table 1 for key to abbreviations of mountains.

	Cat	Hua	Pin	Rin	SR	Wht
Cat	10	1	0	2	0	0
	76.9	7.7	0.0	15.4	0.0	0.0
Hua	1	12	0	0	0	0
	7.7	**92.3**	0.0	0.0	0.0	0.0
Pin	0	0	15	0	0	0
	0.0	0.0	**100.0**	0.0	0.0	0.0
Rin	1	0	0	8	2	0
	9.1	0.0	0.0	**72.7**	18.2	0.0
SR	1	0	0	1	16	0
	5.6	0.0	0.0	5.6	**88.9**	0.0
Wht	0	0	1	0	0	15
	0.0	0.0	6.3	0.0	0.0	**93.8**

for by the first five principal components. Sixteen principal components must be considered in order to explain more than 95% of the variation. Following Legendre and Legendre (1998) and considering only PCs with eigenvalues >1 restricts us to the first eight PCs which account for only 81% of the variation. Although there are no established guidelines for judging the power of a PCA to explain variation, Sneath and Sokal (1973) suggest that three PCs satisfactorily illustrate patterns of variation in most systematic studies. This is not the case here, indicating that many characters vary independently of others such that morphological variation among sky island populations of *Castilleja* defies reduction to a few orthogonal principal components.

Discriminant functions analysis including all plants (i.e., omitting basal and apical stem width which were missing for seven plants from the Pinaleños) indicated that plants can be linked to their source population with considerable accuracy: 88% (76 of 86 plants) are correctly assigned (Table 4). Nine of ten errors involved plants from the southern four populations (i.e., the Catalinas, Rincons, Santa Ritas and Huachucas) and no plants from the Pinaleños were misplaced.

Seeds of *C. austromontana* are of Lockwood's (1992) Type 1; the outer membrane is essentially completely ruptured and lost at maturity, the outer tangential wall is smooth, and the radial walls of the "cells" are unornamented. Seed characters vary among populations (Table 2) and discriminant functions placed more than ¾ of plants correctly based on seed characters (Table 5). Errors were most frequent regarding seeds from the Huachucas; nearly half were incorrectly placed. However, no seeds from the Pinaleños were misclassified as being from other sky islands nor were seeds from other populations placed on the Pinaleños. Seed morphology among plants on the Pinaleños is distinctive; these seeds are large with wider walls than those of plants from other sky islands.

TABLE 5. NUMBER (ABOVE) AND PROPORTION (BELOW) OF PLANTS FROM SOURCE LOCATIONS (LEFT) THAT WERE IDENTIFIED BY DISCRIMINANT FUNCTIONS ANALYSIS OF SEED DATA AS FROM THE LOCATIONS LISTED ABOVE. See Table 1 for key to abbreviations of mountains.

	CAT	HUA	PIN	RIN	SR
CAT	5	1	0	1	1
	62.5	12.5	0.0	12.5	12.5
HUA	1	6	0	2	2
	9.1	**54.6**	0.0	18.2	18.2
PIN	0	0	9	0	0
	0.0	0.0	**100.0**	0.0	0.0
RIN	0	0	0	6	0
	0.0	0.0	0.0	**100.0**	0.0
SR	2	0	0	0	6
	25.0	0.0	0.0	0.0	**75.0**

Superimposing the diagram from the MDS analysis of vegetative + floral characters on the map of the sky island region indicates that, among the Catalinas, Rincons, Santa Ritas, and Huachucas, physical and relative phenotypic distances are roughly congruent (Fig. 1). Relative to these four, the White Mountains are placed nearer and Pinaleños farther by MDS based on phenotypic distances than their geographic distances suggest.

The MDS analysis of seed data (not shown) placed the Pinaleño population distantly from the other four populations which were proximate and approximately equidistant from each other.

DISCUSSION

Our results demonstrate morphological differentiation among populations of *Castilleja austromontana* on Madrean sky islands. DFA associated 88% of plants with the population from which they were collected, and PCA indicates that many vegetative and reproductive characters contribute to this differentiation. At one extreme, plants on the White and Pinaleño Mountains tend to be relatively small in stature, with long leaves and bracts, long corollas, and deep bract and calyx clefts. At the other extreme, on the Catalina and Rincon Mountains, plants tend to be relatively tall with smaller leaves and flowers, and shallow clefts in bracts and calyces. Plants on the Huachuca and Santa Rita Mountains have structures that are intermediate in size and shape between these extremes.

It is important to note that we do not know the cause of this morphological variation. It is possible that the characters are phenotypically plastic and that our results reflect environmental differences among mountains. These plants are likely root parasites, so that common garden or reciprocal sowing or transplant approaches to examine this possibility will be difficult at best. Because the sizes and shapes of reproductive structures are generally understood to be under selection associated with achieving successful pollination and thus reproduction, these are often less phenotypically plastic than vegetative characters (e.g., Bradshaw 1965; Davis 1983; Apelgren and Lernstal 1991). Our results indicate that both vegetative and floral characters vary among sky island populations, suggesting that we are not dealing solely with phenotypic variants. However, data from other sources will be necessary to confirm that the differentiation that we see is genetically based. To the extent that the characters studied here have a genetic basis, they may also be genetically correlated and thus not reflect a suite of independent genetic differences. However, PCA suggests that many characters are independent of each other, at least in their phenotypic expression.

Selection, gene flow, and genetic drift may all contribute to the patterns of differentiation that we have documented. Contrasting selective regimes may be responsible for the morphological differences among plants from different sky island populations. We have no basis at present for specific hypotheses regarding the direction or magnitude of selection except that disruptive selection on corolla morphology is unlikely because pollinator relationships appear to be uniform.

Some inferences regarding gene flow are possible based upon geographic distances, pollinator relationships, and vegetation history. If gene flow (whether by pollen or migrants) is negatively related to geographic distance, then proximate populations should be more similar than populations that are distant and thus rarely exchange genes. The physical distances among the Catalina, Rincon, Santa Rita, and Huachuca populations are fairly congruent with phenotypic distances among plant populations from these ranges (Fig. 1) in accord with a gene flow or isolation by distance explanation. In contrast, the placement by MDS based on phenotypic distance of the White Mountain and Pinaleño populations relative to the other four is not congruent with geographic distances (Fig. 1). In this light, the behavior of pollinators may be informative.

As described above, observations suggest that the same hummingbird species visit flowers of *C. austromontana* across the species' range. Individuals of *Selasphorus platycercus* breed on the sky islands at the elevation of the *Castilleja* populations and thus should move pollen within ranges. In contrast, Rufous-tailed Hummingbirds (*S. rufus*) pass through these mountains during the late summer and early fall migration south to their winter range (the birds fly at lower elevation during their spring migration north because they precede the spring thaw at high elevation) (Grant and Grant 1967; Johnsgard 1983). If relative phenotypic distance reflects gene flow, then our data suggest a more direct route between the southern populations and the White Mountains than would be expected based on geographic distance. Unfortunately, migration routes are understood only in broad geographic terms, not at the level of routes followed by individual birds.

Vegetation history of these mountain ranges yields some ideas about past patterns of gene flow. During the late Pleistocene and Holocene, cycles of climate change were associated with glaciations farther north and at higher elevations. Fossil packrat middens provide direct evidence of vegetation changes associated with climatic changes during the last 40,000+ years (Van Devender, Thompson and Betancourt 1989; Betancourt et al. 1990 and references therein). During periods of glacial maxima, vegetation zones on the sky islands were substantially lower than they are today. The most complete evidence, from the most recent glacial maximum (i.e., 20,000 to 8,000 years BP), indicates that the habitat in which *C. austromontana* occurs ranged 500–600 m lower than at present. This would presumably have increased the area of suitable habitats on the sky islands and also increased connectivity among them. Higher connectivity would have likely increased gene flow between populations that are proximate (e.g., Catalinas and Rincons) and between those that are separated by valleys of relatively high elevation (e.g., Huachucas and Santa Ritas). Both the geographic distance and topographic complexity between these four sky islands and the Pinaleños and White Mountains preclude simple predictions of the impact of climate change on gene flow.

Finally, genetic drift occurs in populations that are isolated, especially if they are small (Lande 1976; Hartl and Clark 1989). We do not have census data for these populations, but some inferences are possible based upon areal extent of suitable habitat. The area inhabited by *C. austromontana* in the White Mountains is vast such that this population should be least susceptible to chance effects. In contrast, the area of suitable habitat for *C. austromontana* on all of the sky islands is far more limited and all of these populations may be subject to drift. This is especially true if warm interglacial periods produced an upward elevational shift in climatic zones comparable to the well-documented downward shift associated with glacial maxima.

Lande (1976:32) derived an equation to estimate the population size (N*) below which drift may influence morphological evolution:

$$N^* = \frac{(1.96)^2 h^2 t}{(z/\delta)^2}$$

where h^2 is heritability, t is number of elapsed generations, z is the difference in character means between two samples (i.e., the magnitude of morphological change observed), and δ is the standard deviation of the character. We estimated values for this population size threshold in *C. austromontana* using our data for corolla length from the Huachucas and Santa Ritas. Heritability has not been estimated for corolla length in *C. austromontana,* but

Campbell (1996) obtained h^2 values between 0.24 and 0.74 for another Asteridae, *Ipomopsis aggregata* (Polemoniaceae). It seems likely that h^2 for corolla length in *C. austromontana* falls within this rather large range. Further, we can estimate time since these populations were in contact: because of the relatively high basin between these two ranges, we hypothesize that there would have been nearly continuous habitat for *C. austromontana* during the last glacial maximum, ca. 10,000 years BP. Generation time is not known for these plants and we used 5 and 10 yr values as reasonable for herbaceous perennials. The range of parameters explored gives estimates from 21,000 ($h^2 = 0.24$, generation time = 10 yr) to 130,000 individuals ($h^2 = 0.74$, generation time = 5 yr); that is, drift cannot be ruled out if population sizes are lower than these values. Based on field experience and on areas of suitable habitat among sky islands, it seems likely that only the White Mountains could have as many as 20,000 individuals. These results are consistent with the hypothesis that drift is at least partly responsible for the differences that we see among sky island populations.

There are no other quantitative studies of plant population differentiation among Madrean sky island plants. Maddison and McMahon (in press) have documented substantial morphological and behavioral differences among male spiders (*Habronattus*: Salticidae) on different sky islands. Snails of the genus *Sonorella* (Helminthoglyptidae; Miller 1967) and beetles (*Scaphinotus,* Carabidae; Ball 1966) are reported to be highly differentiated among the Madrean sky islands although quantitative or phylogeographic studies are lacking. Such studies are underway for spiders (S. Masta personal communication) and lizards and snakes (K. Zamudio and H. Greene, Cornell University, personal communication). Other sky island systems (e.g., the tepuis of Venezuela) have been the focus of floristic and evolutionary studies above the species level (Givnish et al. 1997), but we are not aware of any research to document intraspecific patterns of differentiation there. Plant populations on true island systems have been studied by a number of researchers, but patterns of intraspecific differentiation have received relatively little attention (but see Francisco-Ortega et al. 1993; Hotta et al. 1985), in part because there appears to be little genetic divergence within many island lineages (Givnish 1998).

In sum, our results confirm that the Madrean sky islands are likely to be evolutionary hot spots and that further research is warranted. In the case of *C. austromontana,* additional populations should be studied, particularly from the southern portion of the Madrean sky island province (i.e., the Mexican sky islands between the international border and the "mainland" of the Sierra Madre Occidental). Genetic data that can be ordered (e.g., DNA sequences) would permit us to test more explicitly our ideas regarding gene flow and genetic drift, as well as to add a phylogeographic component (sensu Avise 1989, 1994; Templeton 1998). Further, parallel studies on other groups of plants with both similar and contrasting life histories, pollination systems and dispersal mechanisms will deepen our understanding of both the correlates and determinants of population differentiation.

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APPENDIX 1. EXPLANATION OF CHARACTERS MEASURED OR COUNTED FOR *CASTILLEJA AUSTROMONTANA*. See Figures 2 and 3 for illustrations of structures measured. Terminology follows Chuang and Heckard (1992).

Vegetative:

Basal Stem Width was measured just above the root stock.

Apical Stem Width was measured directly below the inflorescence.

Leaf Length (Fig. 2B-2) and *Leaf Width* (Fig. 2B-3) were measured for four leaves per sampled stem including the most proximal (leaf 1), most distal (i.e., last vegetative leaf below the most proximal floral bract; leaf 4), and two intermediates at ca. ⅓ and ⅔ of total stem height.

Number of Lateral Branches includes both vegetative and reproductive branches.

Floral:

Number of Racemes is number of branches bearing an inflorescence.

Number of Flowers on the raceme selected for measurement of floral characters.

Raceme Length was measured from directly below the most proximal floral bract to the tip of apical bud (Fig. 2A-1).

Bract, Calyx and Corolla: three nodes were sampled and scored for bract, calyx and corolla characters; these were the most proximal (1), most distal (3), and approximately median (2) flowering nodes.

Bract Length (Fig. 2C-4) and *Bract Width* (Fig. 2C-5)

Number of Clefts per Bract was counted on each of the three sampled bracts; bracts have from zero (entire) to four deep clefts on each lateral margin.

Mean Cleft Depth per Bract of all clefts on a given bract. Because number and position of clefts varied among bracts, it was not possible to compare individual clefts. This variable attempts to capture 'cleftedness,' which clearly varied among plants, without comparing individual clefts.

Calyx: Depths of the anterior (Fig. 2D-6), lateral (Fig. 2D-7), and posterior (Fig. 2D-8) calyx clefts were measured as the straight line distances from the base of each cleft to the apex of an adjacent calyx lobe. For analysis, measurements for the three sampled calyces were combined as mean depths of anterior, lateral and posterior clefts.

Corolla Length is from the apex of the posterior lobes of the corolla to the posterior base of the corolla (Fig. 2E-10). For analysis, measurements for the three sampled corollas were combined as mean corolla length.

Galea Length is from the apex of the posterior lobes of the corolla across the mouth of the corolla to the apex of the anterior lip (Fig. 2E-9). For analysis, measurements were combined as mean galea length.

Seeds: All variables were scored from SEM photomicrographs (Fig. 3). When more than one seed per individual was photographed, measurements or counts were averaged for analysis.

Seed Length was measured from the hilium to the opposite end of the long axis of the seed.

Seed Width was measured at the widest point of the seed as photographed in the standard orientation.

Number of Layers of the Radial Wall is the number of layers of "scalariform thickenings on the radial walls" (Lockwood, 1992:225).

Number of Midline Cells: We counted number of cells in the longest row along the midline of the seed.

Radial Wall Width: Width of the radial wall of testa cells measured at the widest point on a cell directly perpendicular to the line of sight.

Derived Variables: These ratios were calculated for each leaf, bract, and corolla measured; ratio of seed length/seed width was calculated based on within-plant mean length and width values (see Table 2).

Leaf Length/Leaf Width: This variable describes leaf shape; leaves with low ratios are more ovate than those with higher ratios.

Bract Length/Bract Width: This variable describes bract shape; bracts with low ratios are more ovate than those with higher ratios.

Corolla length/Galea length: This variable describes the corolla shape. Flowers with low ratios have long galeas relative to corolla length, and those with higher ratios have short galeas relative to corolla length.

Seed Length/Seed Width: This variable describes seed shape; seeds with low ratios are more ovate than those with higher ratios.

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NOTEWORTHY COLLECTIONS

ARIZONA

CRYPTANTHA DUMETORUM (Greene ex A. Gray) Greene (BORAGINACEAE).—Mohave Co., Sacramento Wash, ahout 1 mi. northwest of Yucca. In gravelly sand of broad desert wash with *Larrea tridentata, Acacia greggii, Tessaria sericea,* etc. T17N, R19W, 34°54′N, 114°10′W, elev. 1700 ft, 2 April 1998, Brasher 2986, ASU.

Previous knowledge. This species is known from southeastern California, southern Nevada, and southwestern Utah flanking Mohave Co. on two sides and approaching very closely at Needles, CA.

Significance. Cryptantha dumetorum has long been assumed to be in Mohave, Co., AZ (Kearney & Peebles, *Arizona Flora,* 1951; Higgins, *Great Basin Naturalist* 39(4):293–350, 1979) but never documented until now; thus this collection is an anticipated state record and the first collection east of the Colorado River.

—JEFFREY W. BRASHER, Herbarium, Department of Plant Biology, Box 871601, Arizona State University, Tempe, AZ 85287.

CALIFORNIA

DICENTRA CHRYSANTHA (Hook. & Arn.) Walp. (PAPAVERACEAE).—Inyo Co., Coso Range, canyon ca. 1.2 km W of Silver Pk., 36°09′N, 117°43′W, alt. 2000–2135 m, brushy pinyon woodland with *Pinus monophylla* Torrey & Frémont, *Chrysothamnus nauseosus* (Pallas) Britton, *Artemisia tridentata* Nutt., *Ceanothus greggii* A. Gray, etc., one colony on dry wash bank near springs with *Forestiera pubescens* Nutt., 12 Oct 1997, *A. C. Sanders et al. 21579* (RSA, UCR); Moist soil at Wild Horse Spg., 2006 m, USGS Coso Pk. Quad., T21S R39E NE 1/4 sec. 1, 21 Jul 1974, *R. L. Zembel, CHSA* 349 (RSA).

Previous knowledge. In chaparral on coastal slope of California from Baja California north to the northwest coast (P. A. Munz, A Flora of Southern California, 1974; C. Clark, in Hickman (ed.), The Jepson Manual, Higher Plants of California, 1993), but not reported from the Mojave Desert in these or any other available flora (e.g., M. DeDecker, Flora of the Northern Mojave Desert, California, 1984; E. Jaeger, Desert Wildflowers, 1941; R. F. Thorne, et al., Aliso 10:71–186, 1981; R. Stone and V. Sumida (eds.), The Kingston Range of California: A Resource Survey, Publ. 10, UC Santa Cruz Env. Field Prog., 1983).

Significance. First records of the species from the Mojave Desert, Coso Range and Inyo County. A range extension of ca. 70 km ENE from the upper Kern River drainage on the W slope of the Sierra Nevada. The species also occurs on the desert slope of the southern Sierra, but farther south, near Butterbredt Peak in Kern County. Other chaparral associated species occur in the higher ranges of the Mojave Desert, some even crossing the desert and appearing in Arizona. This record suggests that *Dicentra* should be added to the list of taxa that occurred on what is now the Mojave Desert during the Pleistocene when woodland communities were widespread (P. Raven and D. Axelrod, Origin and Relationships of the California Flora, Univ. of California Publ. Botany 72, 1978.) *Dicentra chrysantha* should be sought at additional localities in eastern Kern and western Inyo counties.

EUPHORBIA ABRAMSIANA Wheeler [*CHAMAESYCE ABRAMSIANA* (Wheeler) Koutnick] (EUPHORBIACEAE).—San Bernardino Co., Providence Mtns., Eastern Mojave Desert, road over Foshay Pass, E side of range, 9.2 km E of Essex Road, rocky, andesitic? slopes with *Larrea, Ferocactus, Yucca schidigera* K. E. Ortgies, *Opuntia acanthocarpa* Engelm. & J. Bigelow, *Bouteloua barbata* Lagasea, 3 Oct 1990, *Steve Boyd 5176* (RSA); Pass between Vontrigger Hills and Hackberry Mtns., E side of Lanfair Rd., 18 km N of jtn with Goffs Rd., scrub vegetation with *Larrea, Opuntia acanthocarpa, Acacia greggii* A. Gray, *Bouteloua barbata, Bouteloua aristidoides* (Kunth) Griseb. 4 Oct 1990, *Steve Boyd 5191A* (RSA).

Previous knowledge. Known from the southeastern corner of the Colorado Desert in California (Imperial Co.), eastward into Arizona and southward in western Mexico to Sinaloa (L. C. Wheeler, Rhodora 43:97–154, 168–286, 1941; J. C. Hickman, *loc. cit.*; P. A. Munz, *loc. cit.*).

Significance. First reports for the Mojave Desert and San Bernardino County. This species is among a suite of California desert taxa which have been documented infrequently and are closely associated with exceptional summer and early fall precipitation. These include *Euphorbia exstipulata* Engelm., *Munroa squarrosa* (Nutt.) Torrey, *Nama dichotomum* (Ruiz Lopez & Pawn) Choisy, *Portulaca halimoides* L., *Sanvitalia abertii* A. Gray, and *Schkuhria multiflora* Hook. & Arn. Late season precipitation in the eastern Mojave Desert was particularly heavy in 1990.

HOLOCARPHA HEERMANNII (E. Greene) Keck (ASTERACEAE).—Los Angeles Co., Liebre Mountains region, north base of Portal Ridge along the Broad Canyon Motorway, east of the mouth of Broad Canyon, edge of the Antelope Valley, near 34°43′11.3″N, 118°27′12.2″W, T7N R15W NE1/4 SW1/4 SE1/4 sec. 3, elev. 940–951 m, gently rolling hills with deep sandy loam at interface between grassland and scrub, vegetation a relatively open scrub of *Pinus sabiniana* Douglas, *Adenostoma fasciculatum* Hook & Arn., *Quercus john-tuckeri* K. Nixon & C. H. Muller, *Eriogonum fasciculatum* (Benth.) Torrey & A. Gray, and *Chrysothamnus nauseosus* (Pallas) Britton, grading into xeric grassland with *Stipa speciosa* Trin. & Rupr., *Poa secunda* J. S. Presl, *Melica imperfecta* Trin., *Bromus* spp., *Avena* spp., and *Corethrogyne filaginifolia* (Hook & Arn.) Nutt., 18 Jun 1997, *Steve Boyd & Lauren Raz 9984* (RSA).

Previous knowledge. Known from the foothills surrounding the southern half of the Central Valley, generally in grassy habitats below 1300 m (P. A. Munz & D. D. Keck, A California Flora, 1959; L. Abrams & R. S. Ferris, Illustrated Flora of the Pacific States Vol. IV, 1960; J. C. Hickman, *loc. cit.*).

Significance. First report from within the Mojave Desert region (Antelope Valley) and first record for Los Angeles County.

—STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden 1500 N. College Avenue, Claremont, CA 91711 and ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124.

CHLORIS TRUNCATA R. Br. (POACEAE).—Riverside Co., Perris, Nuevo Rd. at edge of irrigated alfalfa field, just east of San Jacinto River crossing, T4S R3W S28, 33°48′N, 117°12′W, 435 m alt., common in plowed field, most plants not yet mature, 22 Sep 1996, *S. D. White 4535A* (UCR); Temecula area, Borel Rd., 0.2 km W of turnoff to Lake Skinner, T7S R2W S13, 33°34′N, 117°02′W, vinyard weed, alt. 488 m, 26 Mar 1997, *A. C. Sanders 20095* (UCR); Lake Skinner area, large clay patch adjacent to entrance park road, 1 km NE of Borel Rd., T7S R1W S7, 33°34.5′N, 117°02′W, gentle N-facing slope with grassland and coastal sage scrub, assoc. with *Lotus humistratus* E. Greene, *L. hamatus* E. Greene, *Harpagonella palmeri* A. Gray, *Plantago erecta* E. Morris, *Convolvulus simulans* Perry, *Trifolium albopurpureum* Torrey & A. Gray, etc., common on roadside, all plants within 3 dm of pavement, alt. 500 m, 26 Mar 1997, *A. C. Sanders 20138* (UCR).

Previous knowledge. An introduced weed from Australia, first reported in North America and California from a collection made in 1995 in a vinyard in Temecula, Riverside Co. (Sanders, Madroño 43:524–532, 1996).

Significance. These records extend the range of this recently reported weed about 28 km to the NNW, add additional localities in the Temecula vinyard district, and (document the occurrence of this species in a natural area), thus further demonstrating that it is a well-established member of the California flora. The two locations near Lake Skinner are 3–5 km NE of the original California locality.

GALIUM PARISIENSE L. (RUBIACEAE).—Los Angeles Co., Rancho Santa Ana Botanic Garden [Claremont], 2 May 1972, *C. W. Tilforth 524* (RSA); San Gabriel Mtns., Elsmere Canyon, T3N R15W sec. 7, alt. 442–466 m, 26 Jun 1967, *L. C. Wheeler 9879* (RSA), det. V. Soza; Liebre Mountains, Castaic Creek drainage from Fish Canyon downstream to power plant, just north of upper end of Castaic Lake, near 34°36′00″N, 118°39′45″W, T6N R17W E1/2 E1/2 sec. 22, SW1/4 sec. 23, alt. 470–500 m, 23 May 1996, *S. Boyd & O. Mistretta 8816,* (RSA, UCR); Orange Co., Rancho Mission Viejo, tributary to Trampas Canyon, along Christianitos Rd., 2.4 km ESE Viejo survey mark, UTM 446500mE, 3707350mN, alt. 128 meters, 26 May 1988, *F. M. Roberts & K. Keane 4013,* (RSA), det. T. S. Ross; San Bernardino Co., San Bernardino Mtns., east side of Water Canyon, a tributary of Wildwood Canyon from the north, SW foot of Pisgah Peak, Porter Ranch, chaparral, T2S R1W SE/4 sec. 4, NE/4 sec. 9, 14 May 1993, *A. C. Sanders & E. J. Lott 14031,* (RSA, UCR); San Bernardino Mtns., Pisgah Peak Rd., 1.5 km above Oak Glen Rd., NW foot of Pisgah Peak, slopes of a wide N-draining canyon, chaparral, T1S R1W NW/4 SW/4 sec. 33, alt. 1100 m, 14 May 1993, *A. C. Sanders & E. J. Lott 14039,* (RSA, UCR); eastern San Gabriel Mtns., west fork Stoddard Canyon, ca. 1 km SE of Stoddard Flats, 100 m E of Cucamonga Truck Tr. (FS Road 1N35), Mt. Baldy quad, T1N R7W SE/16 SW/4 sec. 6, alt. 1341 m, 30 Apr. 1994, *D. Swinney 2808,* (RSA), det. R. F. Thorne; San Diego Co., 1.5 km north of Julian, oak woodland, 6 June 1979, *G. K. Helmkamp s.n.* (UCR).

Previous knowledge. A Eurasian weed, reported in California by P. A. Munz (1974, A Flora of Southern California) from Santa Barbara Co. north. E. Lathrop and R. F. Thorne (1978, Aliso 9:197–288) first reported the taxon from southern California, citing a specimen collected at the western base of the Santa Ana Mountains in Orange Co. Additional documentation from the southern Santa Ana Mtns. was provided by S. Boyd et al. (1995, Aliso 14:109–139). Oddly, the range for this plant cited by L. Dempster (1993, in J. C. Hickman, ed., The Jepson Manual: Higher Plants of California) completely excludes it from southern California.

Significance. The above collections provide additional documentation that this plant has become widespread and well established in cismontane southern California. The only coastal slope counties in southern California lacking records of this species are Riverside and Ventura.

RANUNCULUS TESTICULATUS Crantz (RANUNCULACEAE).—San Bernardino Co., San Bernardino Mtns., south shore of Big Bear Lake, vernally moist clay flats with *Sidalcea pedata, A. Gray* T2N R1E, NW/4 S20, alt. 2075 m, May 1982, *T. Krantz s.n.* (UCR), det. by A. C. Sanders.

Previous knowledge. A Eurasian weed first reported for California by P. A. Munz (Supplement to A California Flora, 1968), but not reported for southern California either there or in subsequent floras (e.g., J. C. Hickman, *loc. cit.*; P. A. Munz, 1974). Recently reported from the Cuyamaca Mtns. of San Diego Co. (J. Hirshberg & D. Clemmons, Phytologia 81:69–102, 1996).

Significance. First record for San Bernardino Co. and the San Bernardino Mtns. and a second record for southern California. This distinctive species should be watched for in other southern California mountains.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124 and STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden 1500 N. College Avenue, Claremont, CA 91711.

CAMPYLOPUS INTROFLEXUS (Hedw.) Brid. (Musci) (DICRANACEAE).—Marin Co., Point Reyes National Seashore, Limantour Beach, 38°02′N, 122°53′W, elev. 5 m, ca. 40 m south of the parking lot and 20 m north of the saltmarsh in the easternmost arm of Drake's Estero; a population of about 5 colonies, each less than 10 cm × 10 cm in area, associated with cryptogamic crusts at the base of a mostly barren and sandy, gentle slope. 24 April, 1999, *Terry J. O'Brien 3353* (UC).

Previous knowledge. First confirmed to occur in North America and in California from collections made in Humboldt and Mendocino counties (J.-P. Frahm, The Bryologist 83:570–588, 1980). The only specimen from Lassen Co. (Showers *1909*; in UC; transferred from HSC) also reported in the same literature, is annotated by Frahm as *Campylopus pilifer* Brid., suggesting that *C. introflexus* does not occur in this county nor far inland in California. Frahm (Dicranaceae: Campylopodioideae, Paraleucobryoideae, Flora Neotropica, No. 54, 1991) later reported that *C. introflexus* is known from California and Oregon, and first discovered in this region in 1972. One specimen in UC (Steve Selva *l*) was collected in 1971, but there are no collections prior to this year, so it appears that the species was not collected in California or elsewhere in North America before 1971. Other more recent collections of *C. introflexus* in UC are from additional localities in Mendocino Co. and Humboldt Co., and from Curry Co. in Oregon.

Significance. First record of *C. introflexus* in California from south of Mendocino Co., suggesting that the range is expanding. The species appears to be a neophyte introduced to California (J.-P. Frahm, 1980), as the natural distribution is the temperate southern hemisphere (S. R. Gradstein & H. J. M. Sipman, The Bryologist 81:114–121, 1978).

The apparent range expansion in California is a concern for species and habitat conservation along the temperate Pacific Coast. In Europe, *Campylopus introflexus* also is an introduction from the southern hemisphere, first discovered in Britain in 1941 (P. W. Richards, Trans. Brit. Bryol. Soc., 4:404–417, 1963), and has since expanded rapidly throughout much of the continent (L. Söderström, *in* Bryophytes and Lichens in a Changing Environment, J. W. Bates and A. M. Farmer, eds., 1992). In temperate regions of Europe, *C. introflexus* has a wide ecological range and is a highly effective colonist that once established is a better competitor than native species. There the substrate is primarily nonalkaline soils or roofing, and colonies are found in sites subject to human disturbance, on dunes, in heathlands, grasslands or open woodlands (R. Biermann & F. J. A. Daniels, Phytocoenologia 27:257–273, 1997; M. Equihar & M. B. Usher, J. of Ecology, 81: 359–365, 1993; Meulen, F. van der, H. van der Hagen & B. Kruijsen, Proc. K. Nederlandse Akad. van Wetenschappen, Ser. C, Biol. and Med. Sciences, 90:73–80, 1987; Richards 1963; H. Stierperaere & E. Jacques, Belg. J. Bot., 128:117–123, 1995). UC herbarium specimens indicate a similar ecological range in California and Oregon. In some natural habitats in California, such as the the pygmy forests in Mendocino Co., colonies of *C. introflexus* have formed loose carpets over patches of soil, suggesting a potential for competition with other native bryophytes or vascular plants. These observations highlight the need to closely monitor the distribution and ecology of *C. introflexus* along thc Pacific Coast, to better understand whether it is a threat to the native flora.

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REVIEW

Adaptation. Edited by MICHAEL R. ROSE and GEORGE V. LAUDER. 1996. xiii + 511 pages. ill., map. Paperback $41.00. Academic Press, San Diego. ISBN 0-12-5964218.

Two decades ago the paper by Gould and Lewontin (Proceedings of the Royal Society, London B 205:581–598, 1979) was required reading for students of evolutionary biology. Their critique of the "adaptationist program" attacked the assumption that the task at hand was to show how natural selection had molded the features of an organism into an optimal fit with the current environment. Instead, they emphasized the role of developmental constraints, stochastic processes and evolutionary history. All of which would produce an imperfect collection of traits. Harper (E.I. Newman, ed. The plant community as a working mechanism, pp. 11–25, 1982) added his voice by warning plant biologists against a glib adaptationism.

The present book shows that a newer but wiser adaptationism is possible. The authors are well-recognized scientists, albeit almost all based in the U.S. They espouse divergent, at times conflicting, views but share a critical attitude about the study of adaptation. The four chapters of Part I cover conceptual matters: ideas of adaptation and design before and after Darwin, the relevance of engineering and optimization models, the evolutionary genetics of adaptation. The six middle chapters of Part II range from DNA sequences to the exotic fossils of the Burgess Shale. What holds this part together is an engagement with data. For example, Sinervo and Basolo review elegant experimental manipulations of vertebrate traits like egg size and tail length that test adaptive hypotheses. Larson and Losos demonstrate how phylogenetic analysis can clarify the contribution of adaptation to character evolution. After a short general history, Reznick and Travis describe their work in the field on natural selection in fish populations. Drawing on the more recent tools of molecular biology, Hudson looks at adaptation at the protein and DNA level. For changes in sequences that are not strongly conserved, he finds it difficult to separate adaptive from non-adaptive causes. The authors of the four chapters in Part III think about adaptation from outside the box. Here one can learn about the adaptations of clades, kin selection and metapopulations, genomic parasites, and artificial adaptive systems, including robots.

In general, the chapters are clearly written, and readers of *Madrono* will want to refer to their contents. However, not one of the chapters gives more than a glance to adaptation in plants. The geographic location of the editors makes this omission hard to understand, and obviously their book is of less value to biologists interested in plant adaptation.

—ROBERT R. NAKAMURA. Department of Biology and Microbiology, California State University, Los Angeles, CA 90032-8201.

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CHARACTER VARIATION AND GEOGRAPHIC DISTRIBUTION OF *CLARKIA XANTIANA* A. GRAY (ONAGRACEAE): FLOWERS AND PHENOLOGY DISTINGUISH TWO SUBSPECIES

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ABSTRACT

This paper presents an analysis of variation in morphology and phenology in the California winter annual, *Clarkia xantiana* A. Gray (Onagraceae), along with an analysis of its geographic distribution. A set of characters associated with breeding system and flowering time clearly separate *C. xantiana* populations into two distinct sets: one large-flowered, late-flowering, highly protandrous, and having stigmas exserted several mm beyond anthers; and the other small-flowered, early-flowering, and exhibiting little or no protandry or anther-stigma separation. The latter set corresponds to the previously recognized *C. xantiana* subsp. *parviflora* (Eastw.). Harlan Lewis, although published key characters alone would not reliably distinguish these populations from *C. xantiana* subsp. *xantiana.* Surveys did not substantially extend the known limits of *C. xantiana*'s range (from the southern Sierra Nevada and Greenhorn Mountains south to the San Gabriel Mountains, with the greatest concentration in the lower Kern River drainage). The surveys did, however, reveal that subsp. *parviflora* is much more abundant and widespread than reported previously. In certain arid sections of the range, all populations resemble subsp. *parviflora.* Thus, there is an association of autogamy with dry environments. In a central zone the subspecies coexist, often occurring at the same sites, but with flowering times displaced several weeks. Pink- and white-flowered forms of subsp. *parviflora* are both common and widespread. Except for flower pigmentation, they are not clearly distinguishable by the characters measured here. This study will facilitate further investigation of the evolution of breeding systems and life history in *C. xantiana.*

Clarkia xantiana A. Gray (Onagraceae) is a winter annual of oak woodland, chaparral, and pinyon-juniper woodland, occurring from the southern Sierra Nevada and Greenhorn Mountains to the San Gabriel Mountains, in inland central and southern California (Lewis and Lewis 1955; Hickman 1993). A recent taxonomic treatment (Lewis and Raven 1992) describes *C. xantiana* subsp. *parviflora* (Eastw.) Harlan Lewis comb. nov., which is distinguished from *C. xantiana* subsp. *xantiana* by smaller petals (6–12 mm vs. 12–20 mm) and stigmas that are not exserted beyond the anthers, flower features commonly associated with self-pollination (Ornduff 1969; Jain 1976; Wyatt 1983). In subsp. *parviflora,* receptive stigmas often contact open anthers at anthesis, whereas stigmas of subsp. *xantiana* mature substantially later than anthers, as well as extending several millimeters beyond them (Moore and Lewis 1965). That is, subsp. *parviflora* has little dichogamy (temporal separation of anthers and stigmas) or herkogamy (spatial separation of anthers and stigmas), facilitating autogamous self-pollination. In addition, subsp. *parviflora* has distinctively earlier flowering, and it exhibits a white petal-color form, in addition to the pink form that subsp. *xantiana* exhibits (Moore and Lewis 1965). White-flowered individuals are extremely rare in subsp. *xantiana* (personal observation).

Until now, subsp. *parviflora* has been reported from only a few locations in the Kern River drainage, most notably in Tulare County, along the North Fork of the Kern River, near its confluence with South Creek, where it co-occurs with subsp. *xantiana* (Moore and Lewis 1965; Gottlieb 1984; Lewis and Raven 1992). Thus, subsp. *parviflora* is considered to be extremely rare (Skinner and Pavlik 1994). Studies of chromosome organization in populations at the Kern River-South Creek confluence (Moore and Lewis 1965) and studies of isozyme frequencies in those and other populations (Gottlieb 1984) have been taken to indicate that *C. xantiana* subsp. *xantiana* is the progenitor of *C. xantiana* subsp. *parviflora,* with white-flowered *parviflora* being derived from pink-flowered *parviflora.*

This paper presents an analysis of variation in selected morphological and phenological characters in *C. xantiana,* along with an extensive analysis of the species' geographic range. The purposes of the study were: (1) to carry out a phenetic analysis of morphological and phenological characters, including the floral characters that distinguish the subspecies, to evaluate the correspondence between the published subspecific designations and patterns of character variation among populations; (2) to characterize carefully the geographic range of *C. xantiana,* and especially to search for additional populations of the reportedly rare subsp. *parviflora* and delimit the ranges of the two subspecies; and (3) to examine patterns of geographic variation in characters. This analysis should facilitate additional study of the evolutionary origin of self-pollination and other features in *C. xantiana.*

METHODS

Locating populations. Guided by previous distribution reports (Lewis and Lewis 1955), herbarium records, and colleagues (T.P. Holtsford personal communication), we located 96 sites with *C. xantiana* populations between 1995 and 1998. An area of the reported range (Lewis and Lewis 1955) in which we did not locate populations was the vicinity of Tejon Pass, where Kern, Los Angeles, and Ventura Counties meet.

In our analysis, a "population" refers to a distinct aggregation of individuals, separated from other such aggregations by 100 meters to tens of kilometers. It is probable that some nearby populations are more properly considered to be patches within larger metapopulations. At some sites, there were two or more distinct aggregations of individuals closer than 100 meters. At some of these sites, aggregations of autogamous pink- and/or white-flowered individuals with small petals and very little or no anther-stigma separation would begin to flower several weeks earlier than aggregations of individuals with larger, pink petals, substantial protandry, and strongly exserted stigmas. At other sites, aggregations of pink-flowered autogamous individuals co-occurred with aggregations of white-flowered autogamous individuals. Whenever more than one of the three morphs co-occurred, we considered aggregations of each morph to comprise an independent population (Moore and Lewis 1965; Gottlieb 1984). In all, we identified 125 actively flowering populations at the 96 sites. We deposited voucher specimens from 62 populations at the University of California Herbarium (UC).

Scoring characters. From May through July 1998, we collected data on flowering phenology and floral and vegetative morphology for 93 populations at 67 sites, scoring 10 haphazardly-selected individuals per population for 14 characters. We measured all dimensions to the nearest 0.5 mm. We attempted to visit populations early in their flowering periods, so that we could also estimate the Julian date on which the population began to flower. Thus, flowering time is a single estimate of each population's date of flowering onset, rather than a mean among plants.

Five of the characters are flower dimensions. All these we measured on the youngest (i.e., uppermost) female-mature flower on the central stem. Petal length was scored on a haphazardly selected petal (from among the four present in the flower), from the petal's base to its edge, perpendicular to the base. Petal width we measured as the maximum width of that petal. Style length we measured from the base to the underside of the stigma. Anther-stigma distance we measured as the minimum distance, measured from the base of the style, from any open anther to the stigmatic surface (Holtsford and Ellstrand 1992). Finally, we measured ovary length, and we scored a sixth, qualitative character: the presence (1) or absence (0) of dark spots on one or more petals, which is a polymorphic character in *C. xantiana* (Lewis and Lewis 1955; E. Twieg et al. unpublished).

Two of the characters are indexes of anther dehiscence within flowers, measured on the youngest flower on the central stem, whether or not it was in female phase. *Clarkia xantiana* flowers have two whorls of four stamens each, with the outer whorl possessing longer anthers. "Short-anther phenology" and "long-anther phenology" refer to the degree of dehiscence (in fourths) of anthers of the inner whorl and those of the outer whorl, respectively.

Because we visited populations only once for the purpose of taking measurements, we could not measure directly the duration of protandry within individual flowers, which correlates with outcrossing rate in the closely related *Clarkia tembloriensis* Vasek (Holtsford and Ellstrand 1992). Instead, we used two indexes of protandry that have been applied previously in *Clarkia* (Vasek 1968). "Stigma receptivity" is the degree (in fourths) to which opposing stigma lobes approach 180° apart, their position at receptivity. Thus it is an index of female maturity for the youngest open flower. Low values of stigma receptivity represent high levels of protandry. "Flowers of protandry" is the number of open flowers on the central stem above the first receptive flower. High values of this character represent high levels of actual protandry, though the precision of this relationship depends on the extent to which the rates of flower opening and organ maturation are uniform within and among plants.

The remaining four characters are vegetative. "Node of first flower" is the number, counted from the base, of the lowest node on the central stem at which a flower appears. "Leaf length" and "leaf width" are the maximum length and width of the leaf at that node, respectively. "Node of last branch" is the highest node on the central stem at which a branch appears, whether expanded or not.

Phenetic analysis. After calculating character means by population, we examined patterns of character variation and covariation among *C. xantiana* populations in three ways. First, we examined frequency-distributions of population means for all characters. Second, we calculated pairwise correlation coefficients between all characters. Third, we performed multivariate analyses (principal component analysis, discriminate function analysis, and unweighted-pair-group-mean cluster analysis) of character means. We present only the principal component analysis here, as other analyses yielded similar results. Flowering time increased signifi-

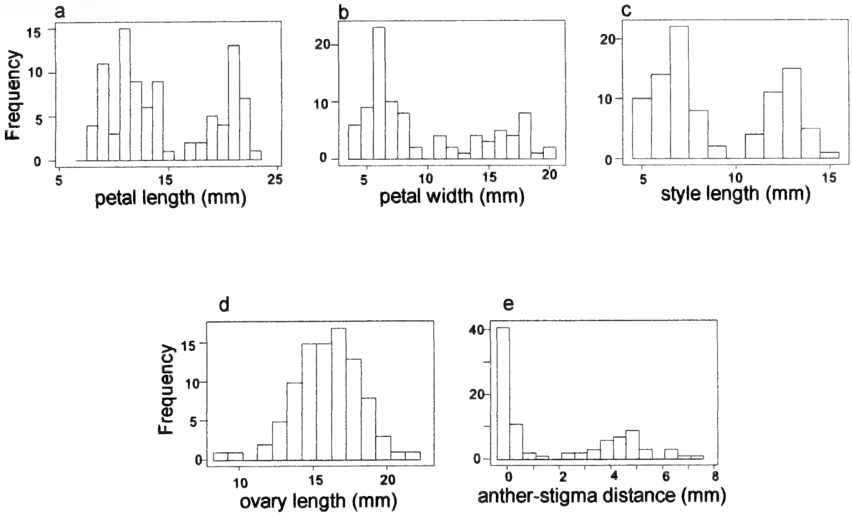

FIG. 1. Among-population distributions of flower dimensions in *Clarkia xantiana.* All scales in mm. Histograms for (a) petal length, (b) petal width, (c) style length, (d) ovary length, and (e) anther-stigma distance.

cantly with elevation (Julian flowering date = 135 + 0.0105 [elevation in m] days, $P < 0.01$). We therefore used residuals from this linear regression in place of raw Julian dates in the correlation and multivariate analyses. Actual Julian flowering dates ranged from about 120 (late April) to about 180 (early July). A table of each population's character values and geographic location appears at *http://www.grinnell.edu/individuals/eckhart/clarkiatable.html.* We used Minitab 12.1 to perform statistical analysis.

RESULTS

Character variation. Four of five flower dimensions exhibited bimodal distributions among populations, ovary length being the exception (Fig. 1). Though many populations lay below the 12 mm petal-length and 0 mm anther-stigma distance thresholds that define the published key characters of subsp. *parviflora,* the obvious gaps in these characters' distributions did not correspond precisely to those cutoffs (Fig. 1a, e).

Bimodality was also common among the distributions of phenological characters (Fig. 2). Flowering time (adjusted for elevation) was strongly bimodal, with approximately 3 weeks between modes (Fig. 2a). Stigma receptivity (Fig. 2b) and flowers of protandry (Fig. 2e) were also clearly bimodal. Populations tended to have youngest flowers with stigmas fully receptive (and therefore zero flowers of protandry) or fully closed (and therefore >1 day of protandry). In most populations, short anthers were fully dehisced at anthesis (Fig. 2c), while long anthers lagged behind, with a broad range of degrees of dehiscence on youngest flowers (Fig. 2d).

In contrast to flower dimensions and phenology, vegetative character distributions appeared to be unimodal (Fig. 3a-d). The ranges, however, were substantial, from approximately two-fold in node of last branch (Fig. 3a) and node of first flower (Fig. 3b), to a seven-fold range in leaf length (Fig. 3c).

Petal spotting was found to be highly polymorphic. Although there were several populations in which the (rather small [$n = 10$]) samples were completely spotted or completely spotless, the majority of populations had intermediate frequencies of spotted individuals (Fig. 3e).

Character correlations. Correlation analysis revealed strong associations between sets of characters (Table 1). There were strong positive correlations between petal and style dimensions, vegetative size, flowers of protandry, flowering time, and anther-stigma separation, and strong negative correlations between this set of characters and flower organ phenology. In other words, large-flowered populations tended to flower late, and they tended to have strongly exserted stigmas, high levels of protandry, slowly dehiscing anthers, and large vegetative size (i.e., large leaves and high nodes of last branching and first flowering).

Plotting the two key characters, petal length and anther-stigma distance, against each other revealed that the covariation in these characters was clustered in this set of populations, but it did not correspond precisely to the published thresholds for inclusion in the two named subspecies. There was a set of small-flowered populations with little anther-stigma separation, but some populations that lacked any anther-stigma separation possessed petal lengths up to 14 mm (not 12 mm), and there were a few populations with substantial anther-stigma separations that had petals no longer than those of some apparently autogamous populations (Fig. 4). A clearer break occurred between populations with

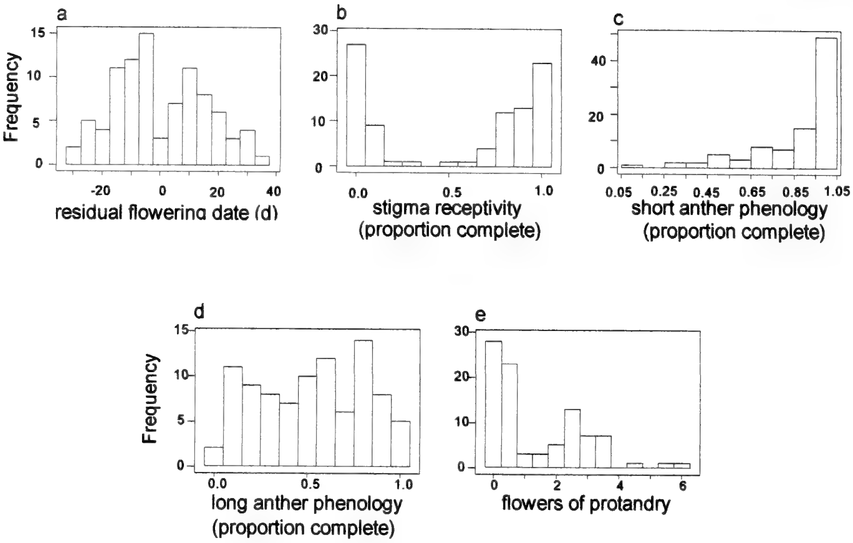

FIG. 2. Among-population distributions of phenological traits in *Clarkia xantiana*. Histogram for (a) residual flowering date (i.e., Julian day adjusted for the effect of elevation), (b) stigma receptivity, (c) short anther phenology, (d) long anther phenology, and (e) flowers of protandry.

mean anther-stigma distances less than 2 mm and those with greater distances.

Principal component analysis. As expected, given the strong patterns of correlation among characters, principal component analysis assisted in summarizing them. The first principal component accounted for almost 60% of the variance, and the next two accounted for an additional 20% (Table 2). Other components accounted for ≤7% each. The first component captured the major pattern of correlations detailed above, with substantial negative loadings for flower and vegetative dimensions, anther-stigma separation, protandry (i.e., a negative loading for flowers of protandry and a positive loading for stigma receptivity), and flowering time, along with substantial positive loadings for anther phenology. Thus, the first component is an index of small size and rapid maturation of organs and whole plants. The second principal component had large positive loadings for leaf dimensions, nodes of first flowering and last branching, ovary length, and petal-spotting, while it had a large negative

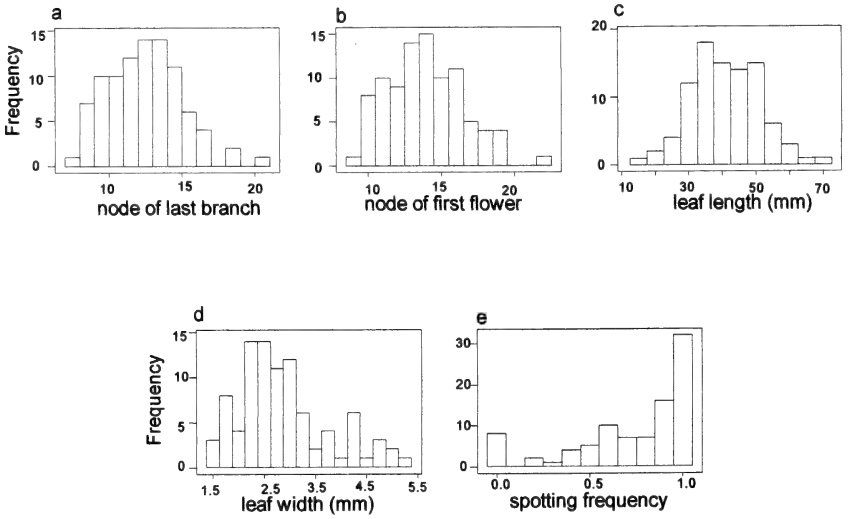

FIG. 3. Among-population distributions of vegetative traits and petal spotting in *Clarkia xantiana*. Histograms for (a) node of last branch, (b) node of first flower, (c) leaf length, (d) leaf width, and (e) frequency of petal spotting among individuals.

TABLE 1. CHARACTER CORRELATIONS AMONG POPULATIONS. n = 93. Abbreviations: PL = petal length; SL = style length; OL = ovary length; AS = anther-stigma distance; SA = short anther phenology; LA = long anther phenology; SR = stigma receptivity; PR = flowers of protandry; NL = node of last branch; NF = node of first flower; LL = leaf length; LW = leaf width; FT = residual flowering time, correcting for the effect of elevation on flowering time. All correlations with absolute values ≥ 0.36 (in boldface) are significant at $P < 0.05$, after Bonferroni correction for multiple comparisons.

	PL	PW	SL	OL	AS	SA	LA	SR	PR	PS	NL	NF	LL	LW
PL	**0.95**													
SL	**0.95**	**0.91**												
OL	−0.19	−0.22	−0.22											
AS	**0.90**	**0.87**	**0.95**	−0.27										
SA	**−0.40**	−0.35	**−0.43**	0.21	**−0.41**									
LA	**−0.75**	**−0.73**	**−0.80**	**0.36**	**−0.81**	**0.65**								
SR	**−0.91**	**−0.89**	**−0.95**	**0.40**	**−0.93**	**0.49**	**0.86**							
PR	**0.85**	**0.79**	**0.90**	−0.28	**0.90**	**−0.57**	**−0.84**	**−0.91**						
PS	0.02	0.02	0.07	−0.08	0.07	−0.24	−0.19	−0.10	0.13					
NL	**0.53**	**0.54**	**0.59**	−0.19	**0.62**	−0.23	**−0.60**	**−0.62**	**0.63**	0.23				
NF	**0.51**	**0.50**	**0.56**	−0.14	**0.59**	−0.24	**−0.57**	**−0.59**	**0.60**	0.27	**0.97**			
LL	**0.62**	**0.54**	**0.63**	0.11	**0.62**	**−0.36**	**−0.63**	**−0.63**	**0.67**	0.14	**0.56**	**0.56**		
LW	**0.54**	**0.43**	**0.60**	0.06	**0.65**	**−0.40**	**−0.58**	**−0.58**	**0.65**	0.06	**0.40**	**0.42**	**0.77**	
FT	**0.71**	**0.66**	**0.73**	**−0.43**	**0.67**	**−0.39**	**−0.61**	**−0.74**	**0.64**	−0.04	0.30	0.28	0.34	**0.40**

loading for flowering time. This component represents an index of large vegetative size and long ovaries, along with early flowering. As character loadings on the third principal component were dominated by ovary length (positive) and spotting (negative), this component represents an index of the combination of long ovaries and having high frequencies of individuals with spotted petals.

A scatterplot of the first two principal components identified two distinct clusters of populations, differentiated by the first component but not the second (Fig. 5a) (The third component showed no evidence of separation [data not shown]). Those populations with positive values of the first principal component (i.e., the cluster on the right) had morphology and phenology that resemble subsp. *parviflora,* while those in the left cluster had morphology and phenology that resemble subsp. *xantiana.* Not all of the populations in these clusters, however, strictly fitted the published key characters of the subspecies. A few populations in the right cluster had petal lengths greater than 12 mm (Fig. 5b) and/or anther-stigma distances slightly greater than 1 mm (Fig. 5c). One population in the left cluster had a mean petal length less than 12 mm but an anther-stigma distance greater than 2 mm (Fig. 5b, c). Three populations appear to be outliers between the clusters (Fig. 5a, see arrows). These were not similar to each other, nor did they come from any particular region. (Clockwise from the top, these populations were: 5aw, on Sierra Way in Tulare County; 34p, near the "5,000 ft" sign on the Sherman Pass Road, in Tulare County; and 86x, in Sand Canyon, north of Tehachapi Pass, in Kern County). Within each main cluster, the first two principal components correlated negatively (with a slope within each group of −0.50, $P < 0.001$). This suggests that, within each set of populations, the tendency to have small, rapidly maturing flower organs correlated negatively with large vegetative size and late flowering.

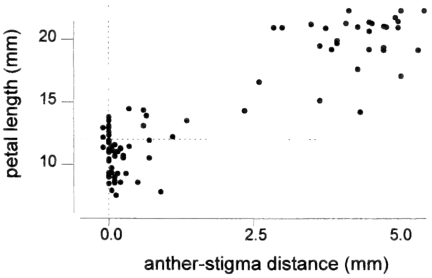

FIG. 4. Scatterplot of mean petal length against mean anther-stigma distance for sampled populations. Dashed lines indicate the thresholds of published key characters distinguishing subsp. *xantiana* from subsp. *parviflora.*

White- and pink-flowered populations in the right cluster showed no separation from each other along these axes (Fig. 5d). Cluster analysis and discriminant function analysis confirmed that this set of characters (other than flower color) do not distinguish white- from pink-flowered populations (analysis not shown).

Geographic distribution. The surveys did not substantially extend the absolute limits of *C. xantiana*'s known range (from the southern Sierra Nevada and Greenhorn Mountains [Inyo and Tulare Counties] south to the San Gabriel Mountains [Los Angeles County], with the greatest concentration in the lower Kern River drainage [Kern County], Fig. 6). The surveys did, however, provide considerable detail within the range.

The distribution maps distinguish areas according to whether they contained only populations with positive values of the first principal compo-

TABLE 2. CHARACTER LOADINGS ON FIRST THREE PRINCIPAL COMPONENTS OF THE ANALYSIS OF POPULATION CHARACTER VALUES.

Character	Loading on PC 1 (60% of variance)	Loading on PC2 (10% of variance)	Loading on PC3 (9% of variance)
Petal length	−0.307	−0.134	0.160
Petal width	−0.294	−0.156	0.103
Style length	−0.319	−0.097	0.106
Ovary length	0.099	0.425	0.570
Anther-stigma distance	−0.316	−0.064	0.079
Short anther phenology	0.182	0.046	0.199
Long anther phenology	0.300	0.024	0.124
Stigma receptivity	0.323	0.125	0.029
Flowers of protandry	−0.316	−0.019	0.007
Spot frequency	−0.049	0.348	−0.550
Node of last branch	−0.237	0.370	−0.224
Node of first flower	−0.230	0.412	−0.225
Leaf length	−0.244	0.346	0.256
Leaf width	−0.227	0.224	0.311
Flowering time (residual)	−0.240	−0.385	−0.009

nent, only populations with negative values of the first principal component, or a mixture of both kinds of populations (Fig. 6). This is equivalent (with the exception of one population) to distinguishing populations on the basis of anther-stigma distance alone, with anther-stigma distances greater than 2 mm corresponding to the left cluster (Fig. 5c). Taking populations with positive values of the first principal component to represent subsp. *parviflora,* such populations are much more abundant and widespread than reported previously, and they occupy a distinctive geographic distribution (Fig. 6). In the northeastern section of the range, all populations are of subsp. *parviflora.* Nearer the southwestern range limits, all populations are of subsp. *xantiana,* while there is one subsp. *parviflora* population in the southeast (population 27p, Fig. 6a). In a central zone, the subspecies coexist, often co-

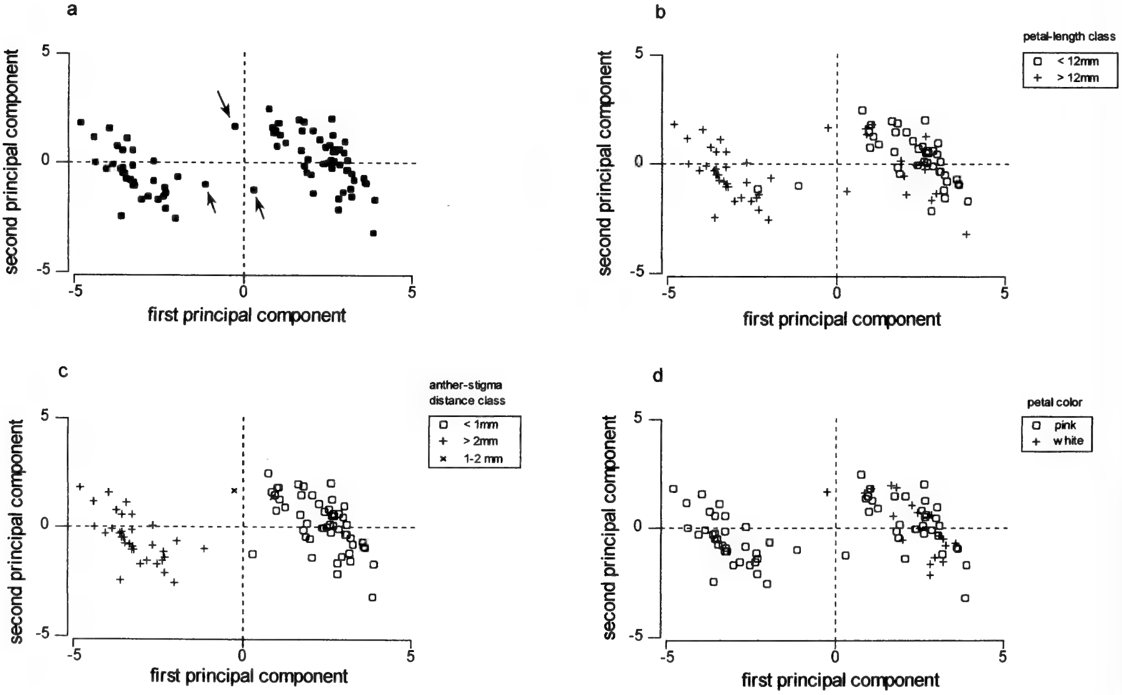

FIG. 5. Scatterplots of second principal component against the first. Each point represents a population. (a) Not coded. Arrows indicate apparent outliers. (b) Coded by petal-length class, according to symbols shown. (c) Coded by anther-stigma distance class, as shown. (d) Coded by flower color, as shown.

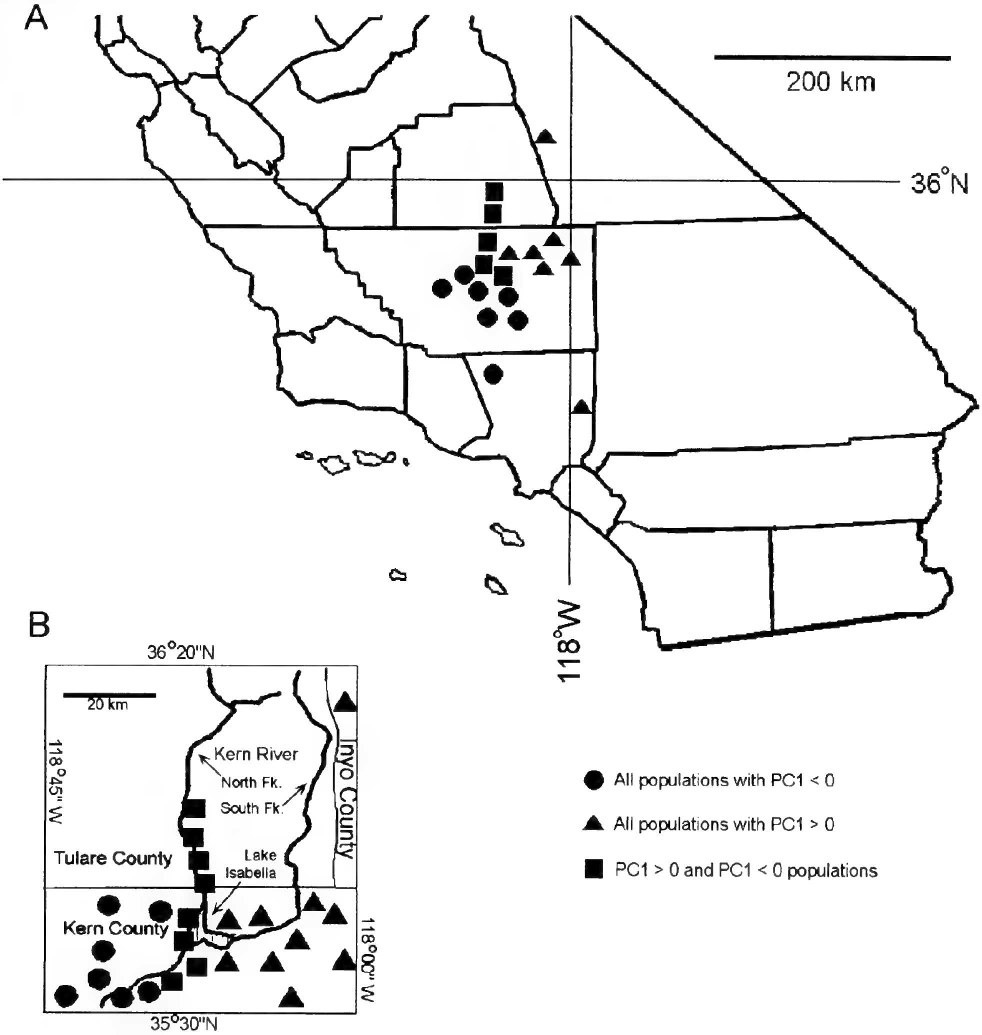

FIG. 6. Geographic distribution of *C. xantiana* in California. (a) Large-scale distribution. Sites are distinguished according to whether they contain populations only in the left cluster of Figure 5 (first principal component <0; i.e., large-flowered, late-flowering populations with substantial herkogamy and protandry), only in the right cluster of Figure 5 (first principal component >0; i.e., small-flowered, early-flowering populations with little herkogamy or protandry), or contain populations in both clusters. (b) Enlargement of the northern section of the range.

occurring at the same sites (Fig. 6). Pink- and white-flowered forms of subsp. *parviflora* were both found to be common and widespread, pink-flowered populations being slightly more abundant (44 pink-flowered populations versus 33 white-flowered ones). We did not encounter white-flowered populations outside the Kern River drainage.

DISCUSSION

Phenetics. Character variation in *C. xantiana* falls into two clusters of populations, corresponding to the two named subspecies. The clusters, however, are not separated with complete precision or reliability by the characters proposed previously to distinguish subsp. *xantiana* from subsp. *parviflora* (Lewis and Raven 1992; Hickman 1993). In particular, petal length is not a reliable indicator of whether a population belongs to one or the other cluster, and stigmas are sometimes exserted slightly beyond anthers in populations that clearly belong to subsp. *parviflora*. In defining the pattern of variation, petal length and anther-stigma separation are only two in a suite of correlated characters, including other flower dimensions, flower organ phenology, flowering time, and, to a lesser extent, patterns of meristem commitment (e.g., node of first flowering) and leaf dimensions. Nevertheless, anther-stigma separation is the most reliable single character for discriminating between the subspecies, as this character: (1) has a discontinuous phenotypic distribution; and (2) correlates most clearly (though not perfectly) with concordant patterns of variation in other traits, making it a reasonable surrogate for the complex morphological and phenological index that separates the clusters in this analysis (Fig. 5c). Thus, for identification purposes, it is reasonably straightforward to consider subsp. *parviflora* to include specimens with anther-stigma separations less than 2 mm, petals 8–15 mm long, little or no protandry, and occurring mostly near and east of the North Fork of the Kern River (Kern, Tulare, and Inyo Counties) or in the north-central San Gabriel Mountains (Los Angeles County). Where the subspecies co-occur, the displacement of flowering time is also diagnostic, with subsp. *parviflora* flowering 2–4 weeks earlier than subsp. *xantiana.* Further refinement of this evaluation awaits an assessment of the developmental, genetic, phylogenetic, and selective causes and consequences of character variation in *C. xantiana.*

Very few populations are phenotypically intermediate between the clusters, consistent with the hypothesis that subspecies differences in flowering time and breeding system reduce gene flow between them, even where they co-occur (Moore and Lewis 1965; Gottlieb 1984). Alternatively, disruptive selection may maintain the distinctness of sympatric populations.

Geographic distribution. Subspecies *parviflora* is widespread, and both pink and white-flowered populations are common. The area of this subspecies' geographic range may actually exceed that of subsp. *xantiana.* Thus, the autogamous subspecies of *C. xantiana* does not appear to be in immediate jeopardy of extinction.

The subspecies' distributions overlap but do not coincide. Each subspecies occupies a zone by itself, while the two also occupy a contact zone along the lower Kern River and its north fork. Population genetic analysis will be necessary to resolve whether this represents a secondary contact zone between populations that have diverged in allopatry or a primary contact zone in place where the initial divergence occurred.

Storm tracks and topography in this region create high-to-low precipitation gradients from west to east in the southern Sierra Nevada and associated ranges, and from southwest to northeast in the Transverse Ranges (National Climatic Data Center). Thus, the areas in which each subspecies occurs alone are distinctively different in precipitation. Subspecies *parviflora* occupies relatively arid sections of the species range. This association between early flowering, self-pollination, and arid environments is not unusual in annual plants (see Guerrant 1989, and references therein). Noting this association, Guerrant (1989) suggested that by favoring early maturation in drought-prone environments, selection may cause the evolution of self-pollination as a correlated character. This might be expected, as one developmental mechanism that hastens flowering is reduced floral development time, which would facilitate self pollination by reducing herkogamy and protandry. As this hypothesis would predict, the present data set reveals an association between early flowering, small flowers, and reduced protandry and herkogamy among populations. Moore and Lewis (1965) reported similar correlations among F_2 individuals after crossing subsp. *xantiana* and subsp. *parviflora* populations from the Kern River-South Creek confluence.

This is not the final word on *C. xantiana*'s distribution or variation, as there are inadequately explored areas where the species might occur (e.g., the Kern Plateau, the southern Tehachapi Mountains, the Tejon Pass area, and the northwestern San Gabriel Mountains). Nevertheless, this paper's findings compel, and should facilitate, further study of the evolution of autogamy in *C. xantiana.*

The present findings already shed some light on breeding-system evolution in this species, though significant questions remain. Moore and Lewis (1965) studied three sympatric populations, one of each flower color and size morph, from the Kern River-South Creek confluence. They found that the pink-flowered subsp. *parviflora* population was karyotypically similar to the subsp. *xantiana* population, while the white-flowered subsp. *parviflora* population differed from the others by an inversion and possibly also a translocation. Assuming that self-pollination is derived (as in the genus in general), they inferred that self-pollination arose first, followed by white petal color. Gottlieb (1984) examined allele frequencies at 40 isozyme loci in these three populations, and at 17 loci in three additional *C. xantiana* populations from elsewhere in the Kern River drainage. The white and pink-flowered subsp. *parviflora* populations at South Creek were found to be identical at 32 loci and monomorphic for different alleles at the other 8, indicating inbreeding within populations and lack of hybridization between them. As these subsp. *parviflora* populations contained some alleles found in allopatric *C. xantiana* populations but not in the sympatric one, Gottlieb (1984) inferred that pink-flowered subsp. *parviflora,* at least, may not actually have originated at that location. The present study's revelation that subsp. *parviflora* is quite common casts additional doubt on the hypothesis that the three populations at the Moore and Lewis site are related as direct progenitors and derivatives. In addition, the present paper's findings suggest that one of the subsp. *xantiana* populations used in Gottlieb (1984) may have been subsp. *parviflora,* as it occurs in the region where we found only that subspecies. That particular population, unlike the subsp. *parviflora* populations at South Creek, exhibited some heterozygosity and polymorphism (Gottlieb 1984), which suggests that not all populations of subsp. *parviflora* are as strictly self-pollinating as those at South Creek. Furthermore, the presence of populations fitting the multivariate description of subsp. *parviflora* that occur at very distant sites (e.g., Inyo and Los Angeles Counties) suggests that there may even have been more than one origin of self-pollination (and its associated characters) in *C. xantiana.* How are populations of *C. xantiana* related to each other? How many origins of the morphology, phenology, and breeding system of subsp. *parviflora* have occurred? What is the relationship between floral character variation and actual rates of outcrossing (e.g. Holtsford and Ellstrand 1992). Analysis of population genetics (and phylogenetics) on a large geographic scale will be necessary to resolve these questions.

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SEED VIABILITY AND GERMINATION BEHAVIOR OF THE DESERT SHRUB *ENCELIA FARINOSA* TORREY AND A. GRAY (COMPOSITAE)

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ABSTRACT

Restoration and revegetation of arid and semi-arid landscapes requires an understanding of the targeted environmental conditions, physiological requirements of the plant species, and horticultural tools available to complete the project. *Encelia farinosa* Torrey & A. Gray is a shrub widely adapted to desert and coastal sage shrublands. It is often included in seed mixes intended for revegetation of disturbed arid lands. However, the successful establishment of shrubs in wild lands and the ability to grow *Encelia farinosa* under horticultural conditions has been hampered by poor germination percentages, typically 2–5%. In this study, we endeavored to establish the source of germination failure and to test methods for increasing germination. We found that nearly half the seeds collected from field sites or donated from a commercial source were not viable. The seed coats were either completely empty or contained embryos and endosperm unresponsive to the metabolic indicator Triphenyl-tetrazolium chloride, indicative of dead tissues. Of the remaining seeds, soaking seeds in gibberellic acid, a well-known germination stimulant, enhanced germination. The ecological significance of such a large number of non-viable seeds is not understood, but for restoration purposes, the data suggests pretreatment with gibberellic acid may increase establishment of genetically mixed stands.

Encelia farinosa Torrey & A. Gray (Compositae) is an arid-zone shrub with floral structures that are typical of the family. The seeds are flattened achenes similar in appearance to small sunflower seeds. The edges of the achenes are ciliate and the faces are slightly pubescent which may aid in animal dispersion (Keator 1994). This species is native to the deserts of California, Utah, Arizona, and New Mexico as well as parts of northwestern Mexico (Clark 1993). It is also a common component in the drier sites of the Mediterranean coastal sage scrublands of southern California and tends to occupy alluvial fans and rocky aprons, especially on south facing slopes (Clark 1993; Keator 1994). *Encelia farinosa* is facultatively drought deciduous, normally loosing its leaves during dry summers. It will, however, remain evergreen or flush new leaves when even small amounts of rainfall or irrigation are introduced (Smith and Nobel 1986; Ehleringer and Cook 1990). The ecophysiology of this plant is among the best studied of the desert-adapted species. This is, in part, because of its abundance in nature and its large and accessible leaves (Nobel et al. 1998). However, where disturbance has eliminated this species, little is known about the reestablishment of natural stands.

The understanding of restoration and revegetation processes in disturbed arid and semi-arid habitats is becoming more important as human utilization and the intrinsic value of arid ecosystems continue to increase. Adjustments in desert management such as abandonment of military installations, curtailing of mining operation, restrictions in livestock utilization and heightened interest in the recreational value of deserts have increased the interest in reestablishment of native desert vegetation (Bainbridge et al. 1995). In related semi-arid ecosystems such as coastal sage scrub, the listing of many plant and animal species as rare, threatened, and endangered has driven legal requirements to restore appropriate habitats (Bowler 1990; Minnich and Dezzani 1998). However, re-establishment and management of native arid and semi-arid vegetation has proved challenging due to severe environmental stresses such as water limitations and high temperatures. (Mooney 1982; Call and Roudy 1991; Bainbridge et al. 1995). Many unique adaptations allowing plants to germinate and survive under these conditions have evolved. Among those adaptations are germination strategies designed to inhibit or trigger emergence depending on environmental conditions (Went 1948; Bowers 1994).

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The reported germination percentages for *Encelia farinosa* are typically 2–5% under ordinary horticultural conditions (Emery 1988; Szarek et al. 1996). Although some work has been published regarding germination under natural field conditions (Went 1948; Bowers 1994), less is known for horticultural approaches. The ability to raise seedlings under horticultural conditions for scientific study, ornamental use, or for restoration purposes is important for progress in these endeavors. It may be even more important in restoration projects where natural germination and seedling survival is poor, or where rapid revegetations is preferred. *Encelia farinosa* is easily propagated from stem cuttings (Joshua Tree Nursery personal communication), but concerns about overly uniform genetic backgrounds in clonal populations makes this a less desirable option in fragmented habitats where loss of genetic diversity could lead to local extinctions.

The objectives of this work are twofold: 1) to determine the causes of low germination in seeds from natural populations and from commercial sources and 2) to identify readily available seed treatments for enhancing germination.

MATERIALS AND METHODS

Seed collection and storage. Three seed sources were used: two collected from local populations and one donated from a commercial source. The locally collected populations were from two coastal sage sites, Box Springs Mountain and Lake Skinner, approximately 70 km apart in Riverside County, CA. The collected seeds from each site were pooled from many individuals in the population. The commercially available seed was acquired from S&S Seed in Carpinteria, CA and consisted of a mixed population of individuals collected from southern California. Harvesting and storage of the S&S seed is presumed to be optimal for commercial purposes. Seeds from the three different sources were divided into two groups; one was stored in a standard refrigerator at about 5°–10°C and the other group was stored in the dark at room temperature. The seeds were stored in paper bags and were neither cleaned nor sorted prior to storage.

Prior to planting, each seed was selected individually after visual inspection under a dissecting microscope. Seeds containing obvious defects, signs of predation or those smaller or larger than the population means were rejected. Acceptable seeds were pooled and redistributed as required for each experiment.

Viability determination. Seed viability was tested in the bulk population prior to germination testing, and in the ungerminated seeds following the germination tests using a Triphenyl-tetrazolium (TZ) staining technique. For the evaluation of embryo viability in the bulk seed populations (Box Springs, Lake Skinner and S&S Seed), 200 uniform seeds from each source were selected for intact, uniform appearance and then divided into 10 replicates of 20 seeds. The seeds were soaked in a 1 mM $CaCl_2$ solution at 37°C for 1 hr to initiate imbibition and then dissected for TZ staining.

For evaluation of viability after the petri dish germination trial, the ungerminated seeds were scored for the presence or absence of fungal contamination and the uncontaminated seeds dissected for TZ staining. In the post-germination viability tests, the seeds were scored by the following criteria: fungal contamination, presence or absence of embryo and endosperm, and viability stain. A similar approach of scoring ungerminated seeds from the vermiculite pots studies was attempted in order to compare the differences in germination between these studies. However retrieval of the ungerminated seeds from the vermiculite pot studies was unsuccessful.

Triphenyl-tetrazolium chloride (TZ) staining is an indicator of metabolic activity. The method used was adapted from Das and Sen-madi (1992). For staining, the seed coats were removed from each seed and the exposed embryo and endosperm were placed into a solution of 0.5% TZ dissolved in 0.1 mM $CaCl_2$. Stain-treated seeds were incubated in a water bath at 50°C for 30 minutes and then inspected under a dissection microscope. Viable seeds indicated metabolic activity by the presence of a strong pink/red coloring of the embryo. Occasionally staining of the endosperm, but not the embryo, was observed. When this occurred the seeds were not scored as viable. The intensity and degree of staining varied markedly from seed to seed, but there did not seem to be any correlation between magnitude of staining and the seed source, age, or germination potential.

Germination percentages on different substrates. Germination percentages were determined by two methods, petri dishes lined with germination blotter paper and in pots containing sterile vermiculite. The petri dish method is typical of standard germination tests and vermiculite is typically used for seedling establishment prior to transplanting into potting soil. Seeds to be tested in petri dishes were transferred after visual inspection to disposable petri dishes lined with 2 layers of blotter paper. The blotter paper was premoistened to saturation with 1 mM $CaCl_2$ and any standing solution was removed. Twenty seeds were placed in each dish and the dishes were sealed with parafilm to reduce evaporation. The petri dishes were placed in an incubator under low light (approximately 50 μmol m^{-2} s^{-1}) at a constant temperature of 25°C. Each dish was opened every two days to enumerate germinated seeds and to replace the $CaCl_2$ when necessary. Emergence of the radical was scored as germination and once counted, the germinated seed was removed. The evaluations typically ran 10 days after which further germination was infrequent. At

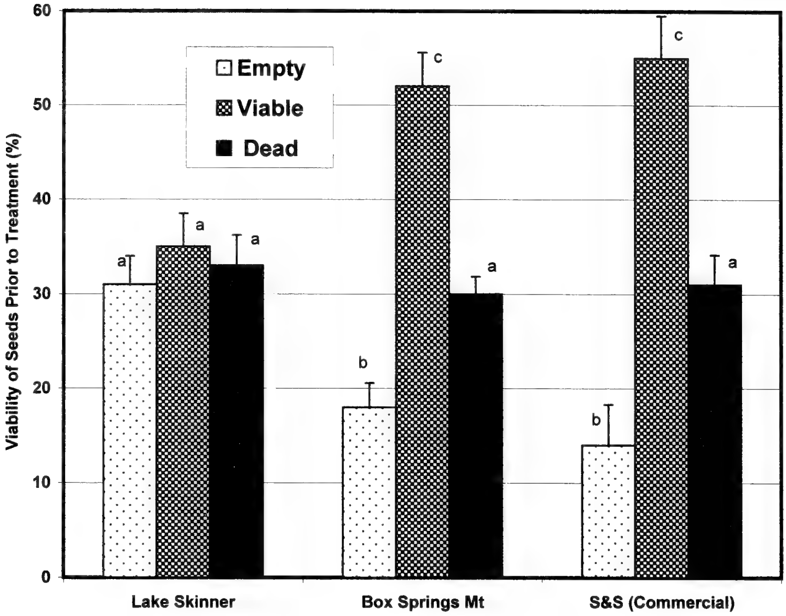

FIG. 1. Percent viability as determined by tetrazolium staining. Three bulk populations were evaluated: two collected locally and one donated by a commercial source. The seeds were stored at 5–10°C for 6 months prior to testing. Letter designations denote significant differences at the $P < 0.01$ level and error bars indicate SEM.

the conclusion of the evaluations, the remaining seeds were inspected as described above.

To estimate the germination percentages in vermiculite, following visual inspection seeds were transferred to 4 inch pots partially filled with moist, sterile, expanded vermiculite (McConkey Co., Sumner, WA). The pots were kept in a glasshouse with an average light level of two-thirds full sunlight and a temperature regime of 80°F days, 65°F nights. Complete germination generally required 2 weeks. Seedlings were not removed until the end of the experiment whereupon they were transplanted into potting soil. The success of transplanting was 100%.

Germination responses to chemical treatments. Seeds were treated with the following chemical solutions that have been reported to enhance germination in some plant species: 0.5 mM $Ca(NO_3)_2$, 1 mM $CaCO_3$, and 100 ppm gibberelic acid. One mM $CaCl_2$ was used as a control (Bewley and Black 1994). Some experiments included a combined 0.5-mM $Ca(NO_3)_2$ and gibberelic acid treatment. Each experimental unit contained 20 seeds and was replicated 5 times per treatment using both petri dishes and vermiculate as substrates.

Preliminary experiments investigated chemical treatment, incubation temperature, and duration and appropriate germination substrate. For determination of exposure time, seeds were soaked in solutions at room temperature or at 37°C for 0.5, 1, 3 or 6 hours. The elevated temperature proved more reliable than room temperature (data not shown) and soaking the seeds for more than 3 hours was fatal in most cases (data not shown). Germination trials using native soils or potting media produced poor results regardless of the treatments applied, therefore experiments were conducted using standard petri dish and vermiculite techniques only. Once the parameters were established, the experiments described were conducted once for the locally collected seed source and twice for the commercially available seeds. Data shown are from commercial source experiments, because the results would be easiest to replicate by others.

Statistical analysis. Germination percentages were analyzed by one-way ANOVA using SigmaStat, version 2.0 by Jandel Scientific Software (San Rafael, CA, USA). Statistical significance of the differences were generally set at $P < 0.01$, but the specific rejection criteria of each experiment is indicated in the text.

RESULTS

Seed viability—untreated seeds. Dissection and TZ staining indicated that a large proportion of the *Encelia farinosa* seeds were either empty (absence of endosperm) or contained a dead embryo (Fig. 1). A comparison of the three seed sources indicated no significant difference in the percent of seeds with a dead embryo, approximately one-third of the total. However, seeds collected from Lake Skinner had a significantly greater ($P < 0.01$) percentage of empty seeds than the other two sources even though the outer appearance of the seed was normal. No significant difference in the percentage

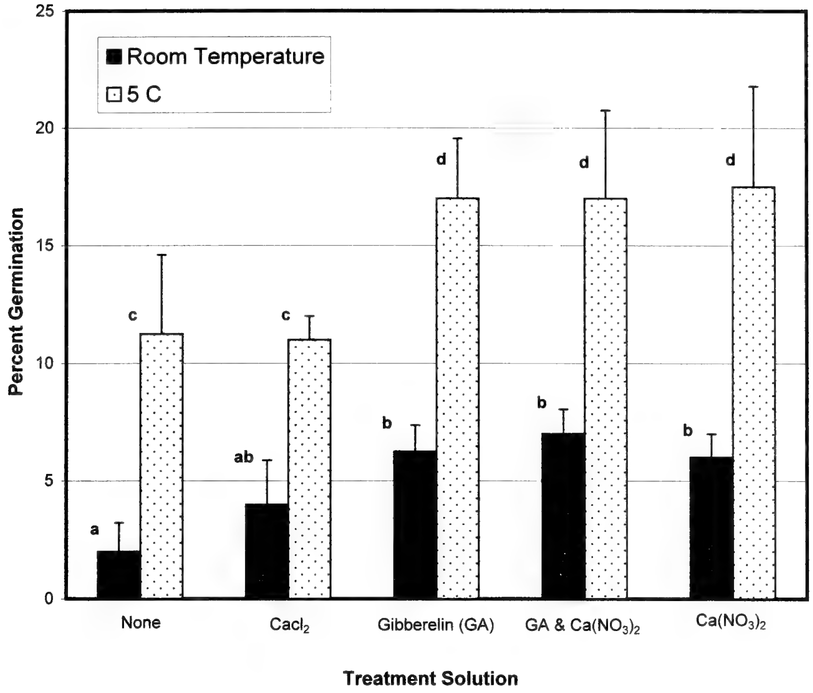

FIG. 2. Comparison of the effects of storage temperature on germination response to four common seed treatments. Data shown is from seeds donated by S&S Seeds, but all seed sources indicated similar responses. Seeds were soaked 30 minutes at room temperature in each of the solutions indicated. Please refer to the materials and methods for solution details. Letter designations denote significant differences at the $P < 0.01$ level and error bars indicate SEM.

of empty seeds was found between the Box Springs Mt and the commercial seed sources (18% and 14% respectively). Seeds collected from Lake Skinner showed the lowest percentage of viable seeds compared to the Box Springs and commercial sources. On average, only 35% of the seeds collected from Lake Skinner would be expected to germinate as compared to slightly more than 50% from the other two sources.

Effect of storage temperature and chemical treatment on germination. Germination was significantly affected by storage conditions. Seeds stored for six months in a standard refrigerator held to approximately 5° to 10°C exhibited two to three times greater germination percentages than seeds stored at room temperature (Fig. 2). Under both storage regimes, seeds were placed in paper bags, kept as dry as possible and were not deliberately stratified (Emery 1988; Bewly and Black 1994).

The response to commonly used germination stimulants indicated trends of greater germination with chemical treatment under both room temperature and cold storage regimes. Seeds stored at room temperature (black bars, Fig. 2) germinated at significantly higher percentages ($P < 0.01$) when soaked in gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$. The $CaCl_2$ treatment resulted in an intermediate response that was not significantly different from untreated seeds, or from seeds receiving gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$. Seeds stored under cold conditions (shaded bars) exhibited germination percentages that fell into two classes. Mean germination percentages were identical for untreated seeds and seeds treated with $CaCl_2$. Seeds soaked in $Ca(NO_3)_2$, gibberelic acid or a combination of both solutions showed an average of 50% greater germination than those untreated or soaked in $CaCl_2$. Analysis of variance identified significant differences between the germination percentages of untreated seeds and seeds soaked in gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$ at the 95% confidence interval. No difference in germination between the untreated seeds and the $CaCl_2$ treated seeds was noted, and there was no difference among the gibberellic acid and NO_3^- treatments.

Chemical treatments—petri dish tests. Soaking seeds in commonly used germination stimulants resulted in a mix of germination responses (Fig. 3). Seeds were selected from the refrigerator-stored batches, and soaked for 30 minutes, 1 or 3 hours at 37°C. In the treatments using $CaCl_2$ and $Ca(NO_3)_2$, differences in the soaking times did not result in any significant differences ($P < 0.01$) in germination percentages. In the treatments using $CaCO_3$ and gibberellic acid, however, an increase in the soaking time suggested a trend in increased

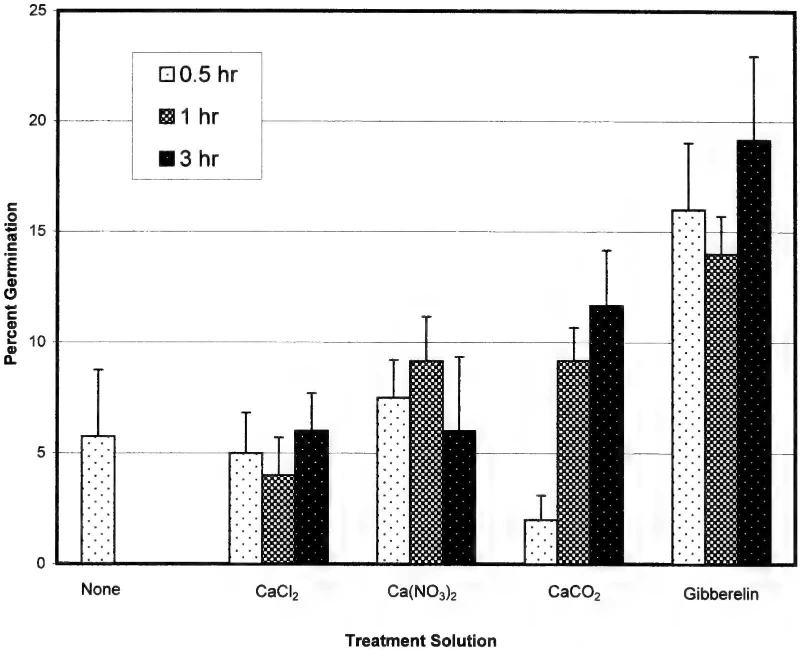

FIG. 3. Evaluation of chemical treatments and exposure times for enhanced germination of *Encelia farinosa* seeds incubated in petri dishes. Data shown are from commercially available seeds stored under cold conditions. Similar responses were observed for seeds collected from local sites.

germination. On average, gibberellic acid doubled germination as compared to $CaCl_2$, $CaCO_3$, and $Ca(NO_3)_2$. Germination percentages among these three calcium salts were not significantly different. Contrary to the results shown in the storage temperature experiment (at 5°C; Fig. 2), $Ca(NO_3)_2$ did not result in any clear, significant increases in germination as compared to the $CaCl_2$ treatment. A comparison of germination percentages in seeds treated with $CaCl_2$ or $Ca(NO_3)_2$ for 1 hour resulted in a significant difference at the $P < 0.1$ level suggesting a slight, but inconsistent response to nitrate.

Maximum germination even in the gibberellic acid treatment was still less than 20% and between 5% and 10% for most of the other treatments. This is considerably less than the 50% maximum germination indicated by evaluating the bulk seed populations (Fig. 1).

Seed viability—ungerminated seeds. Viability tests performed on seed that did not germinate after the 10 days in petri dishes indicated that between 50% and 60% of those seeds contained a dead embryo and between 5% and 10% of the seeds coats were empty (Fig. 4). Fungal infection, presumably from seed borne spores, claimed 20% to 30% of the seeds, leaving approximately 5% of those ungerminated seeds with viable embryos.

Chemical treatment—vermiculite pots. The overall pattern of enhanced germination with chemical treatment observed in the petri dish trials was replicated in the pot studies (Fig. 5). As with the petri dish trials, there was no a clear pattern of increased germination rate with increased soaking times in the different chemical treatments. Germination in general, however, was better in vermiculite than in the petri dishes. On average, vermiculite produced a 50% increase in germination in the $CaCl_2$ treatment, a 3-fold increase in $CaCO_3$, a 3-fold increase in $Ca(NO_3)_2$ treatment, and a little more than 2-fold increase in the gibberellic acid treated seeds over the petri dish germinations. Germination remained significantly higher in the gibberellic acid treated seeds, but the trend was for seeds soaked for 3 hours to yield less than seeds soaked for 1 hour. Seeds soaked in $CaCl_2$ for 3 hours had significantly lower germination percentages than most of the other treatments.

DISCUSSION

Encelia farinosa is not known to have any germination barriers such as those reported for many arid and semi-arid species (Emery 1988; De Hart 1994; Kigel 1995), even though germination rates of 2 to 5% are typically encountered. The low germination rate of *Encelia farinosa* has made sexual propagation of this species problematic for nurseries and restoration projects. The source of this poor germination response has not been identified. However the data presented here clearly shows that a significant portion of the seed population—as much as 65%—will never germinate because they lack embryonic or endosperm tissues, or the embryos

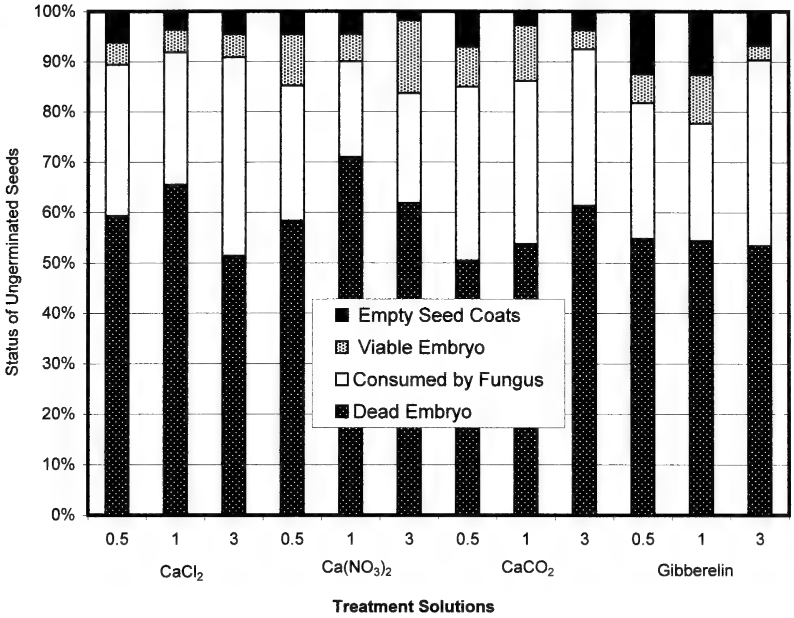

FIG. 4. Status of ungerminated seeds after chemical treatment and 10 day incubations. Ungerminated seeds were scored for fungal contamination. Seeds with little or no contamination were dissected and treated with 0.5% tetrazolium of determination of embryo viability.

are not metabolically active. Under horticultural conditions, a significant portion of the population also succumbed to fungal infection. It is possible that infection was enhanced by the absence of viable embryo. The data further suggest that some portion of the seeds identified as viable prior to planting, lost viability during the germination test. The reason for this remains unclear.

Cool storage temperatures significantly increased germination of seeds that had been held for 6

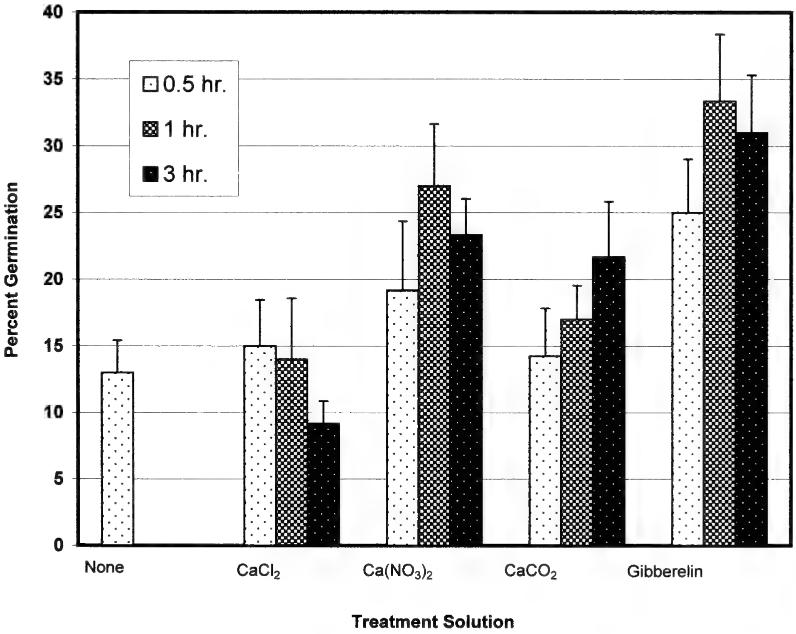

FIG. 5. Evaluation of chemical treatments and exposure times for enhanced germination of *Encelia farinosa* seeds planted in vermiculite and grown in the glasshouse. Data shown are from commercially available seeds stored under cold conditions. Similar responses were observed for seeds collected from local sites.

months or more. Cool storage serves two functions: the reduced temperatures slow metabolic activity of both seeds and infectious microbes and secondly, cool temperatures contain less water. The dryer the atmosphere, the longer a seed retains its dormant condition (Bewley and Black 1994). When seeds are exposed to cool, *moist* conditions such as refrigeration storage in damp peat moss, stratification can occur. This common seed treatment is most effective for temperate species and is thought to preclude early germination until the correct environmental signal is received to indicate spring (Bewley and Black 1994). *Encelia farinosa* is not known to respond to stratification, and because seeds were not stored in this manner, we do not believe that the enhanced germination of the cold-stored seed was due to stratification. However, the possibility of a dry chilling requirement in this species has not been evaluated and cannot be ruled out at this point.

Of the seeds stored under cool conditions a consistent 30% from each of three pooled populations contained seeds with non-viable embryos. Significant portions of the remaining seeds were only empty seed coats leaving the viable population between 30% and 50%. It should be noted, however, that this determination was made from a visually inspected and uniform population of seeds. These populations were specifically selected as undamaged, and representative of the healthy population mean in terms of size and weight. The seeds that were rejected during inspection were not accurately counted, but we estimate a percentage of about 25% were unsuitable because of insect predation, broken seed coats, or size and mass outside of the population mean. When this is taken into account (and assuming that the rejected seeds would not have germinated), maximum germination percentages from the bulk population are expected to be between 20% and 40%, if every viable seed sprouted.

Untreated germination percentages were about 5% for seeds tested in petri dishes and 12% for seeds evaluated in vermiculite (control bars in Figs. 3 and 5). Gibberellic acid significantly increased the germination percentages in all of the experiments under all conditions. The application of the plant growth regulators gibberellin, cytokinin, and ethylene to break dormancy is widely recognized (Powell 1988). Of the three, gibberellin is the most commonly used and frequently substitutes for other germination signals such as light and chilling requirements. However, not all plants respond to gibberellin (Powell 1988, Bewley and Black 1994). In cereal grains, applications of gibberellic acid stimulate the activity of several enzyme systems including the initiation of hydrolysis of starch to glucose. Other plant families seem to respond to applications of gibberellic acids with changes in enzyme activity, but the numbers of species investigated is quite limited (Jacobsen and Chandler 1988, Bewley and Black 1994). During cell development exogenous applications of gibberellic acid stimulates cell elongation (Métraux 1988). Given the observation that *Encelia farinosa* does not respond to stratification, nor seems to have any specific light requirements, it seems reasonable to surmise that the germination responses to gibberellic acid is due to induced enzyme activity.

The germination rate was clearly better in vermiculite as compared to petri dishes (Figs. 3 and 5), but both methods were superior to the germination percentages of seeds planted in artificial potting media or native soils (data not shown). There were many environmental differences between these two methods, and as a rule the goals of these two methods were different. Vermiculite provides no substantial nutrient source (Troeh and Thompson 1993), but the greenhouse environment provided more light, better aeration, and most likely more compatible moisture regime suitable for transplanting germinated seedlings for establishment. While petri dish methods are rarely used for establishment of potted plants, they are often used to estimate viable seed content. We did not attempt to optimize the incubator conditions used for the experiments and it is likely that other parameters may have increased seedling yield. In any event the relative responses to the seed treatments remain consistent between the two methods even if the total germination varied.

We found that it was nearly impossible, based on microscopic observation of undissected seeds or mass of dried seeds, to predict which individuals would contain a viable embryo. The dried seeds, when harvested or as released from the flower head, are very flat but swelled rapidly with imbibition. Unfortunately, even seeds without an embryo or an endosperm often swelled with imbibition. Also, there was no consistent relationship between seed viability and position on the flower head (data not shown). Many of the outer-most and innermost seeds were underdeveloped, but these were usually eliminated during visual inspection. We could devise no method for identifying and selecting viable seeds prior to planting.

The adaptive advantage of this poor seed set under natural conditions is unclear. A typical *Encelia farinosa* shrub produces tens of thousands of seeds. Perhaps by hiding the "good" seeds among the "bad" seed, the viable seeds are more likely to escape predation. It seems unlikely that this is the result of environmental conditions because of the two field sites. Box Springs Mt. is the more highly disturbed and influenced by urban pollution (Allen et al. 1997). Yet, Box Springs Mt. had the more viable population of viable seeds. Although the history of the commercial seeds is unknown, we assume that they were collected from relatively pristine desert populations. Other than the greater percentage of empty seed coats observed from the Lake Skinner seeds, all three sources behaved remarkably similarly.

In conclusion: the most significant cause of the poor germination in *Encelia farinosa* is lack of viable embryos in nearly 50% of the seeds tested. Storage at 5° to 10°C resulted in better germination percentages than seeds stored at room temperature. Soaking the seeds in 0.1% gibberellic acid for 30 minutes to 1 hour at 37°C improved germination by about 2 fold as compared to no treatment. And finally germination in horticultural vermiculite followed by transplantation into sterile potting media resulting in about 30% germination and a successfully reared population of seedlings.

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FINGERPRINTING *JUNIPERUS COMMUNIS* L. CULTIVARS USING RAPD MARKERS

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ABSTRACT

Eight of eleven cultivars of *Juniperus communis* L. growing at Rancho Santa Ana Botanic Garden exhibit a morphology atypical of the wild populations from which they were reportedly derived. The "exotic" morphology consists of branchlets arranged at almost 90° to the branch axis and more spreading leaves that are of a bluer color than those of the wild plants. One of the "exotic" cultivars additionally shows a chimaeric distribution of acicular and scale-like leaves along its branches. Scale-like leaves are characteristics of *Juniperus* section *Sabina* and not section *Juniperus,* to which *J. communis* belongs. A RAPD marker study was initiated to compare RAPD fingerprints of the cultivars with those of their putative wild ancestors and representatives of other *Juniperus* species in both sections. Results suggested that the eight cultivars having an "exotic" morphology were either hybrids between *J. communis* and *J. chinensis,* or pedomorphic forms of *J. chinensis.* The three remaining cultivars that have a "native" morphology clustered with *J. communis* progenitors.

Rancho Santa Ana Botanic Garden (RSABG) is home to eleven plants of *Juniperus communis* L. (common juniper). All were established from cuttings reportedly taken from wild populations native to the California Floristic Province (Raven and Axelrod 1978). However, not all the plants in question exhibit the morphology generally seen in the wild. Instead of having a prostrate habit and somewhat incurved leaves, plants produce branches with fairly upright branchlets and spreading leaves. Given that RSABG specializes in the cultivation of plants native to California, a RAPD (Random Amplified Polymorphic DNA) marker study was initiated with the aim of tracing the origins of the putatively "exotic" specimens and to match up the remaining junipers with their wild progenitors.

Cultivars at Rancho Santa Ana Botanic Garden. Table 1 summarizes the salient characteristics and collection information of the junipers included in this study. Five of the eleven plants are of known geographic origin, but documentation for the remainder is either questionable or missing. Four distinctive morphologies are represented. The "exotic" form consists of long branches from which short branchlets emerge at an upward angle of almost 90°. Leaves are short and spreading and the entire plant is blue-green in color. This suite of traits is seen in CV1, CV3, CV4, CV6, and CV8–CV10. CV7 also differs by its greener foliage, a more spreading habit, and a chimaeric distribution of leaf shapes along its branches and branchlets. Zones of acicular, spreading leaves alternate with appressed, scale-like leaves reminiscent of species in section *Sabina.* The three remaining cultivars resemble *J. communis* found in the wild. CV2 has longer, incurved, leaves and a less prostrate habit with a moderately erect stem. A mat-like habit and incurved leaves characterize cultivars CV5 and CV11 (Table 1). The former is of greener and the latter of bluer coloring.

Juniperus communis *Varieties in the Western United States. Juniperus communis* is a circumboreal species of juniper (Franco 1962) characterized by acicular leaves. Two varieties of *J. communis* (Cronquist et al. 1972; Flora of North America Committee 1993) are encountered in the western United States. *Juniperus communis* var. *depressa* Pursh is native to the Great Basin Floristic Province. It ranges farther north into Alaska and eastward across much of Canada and the Great Lakes region, arching south along the east coast to North Carolina. *Juniperus communis* var. *montana* Aiton occurs from British Columbia southward into California in the Cascade Ranges, North Coast Ranges, and Sierra Nevada. The two varieties differ in habit, leaf size and shape and width of the glaucous stomatal band on the adaxial leaf surface. Although both are low-growing, variety *depressa* develops a somewhat erect main stem whereas variety *montana* is entirely prostrate. Leaf dimensions are ca. 1.0–1.6 mm broad × (6) 10–18 mm long (*depressa*), and (1.2) 1.5–1.8 mm broad × 5–10 (12) mm long (*montana*) (Cronquist et al. 1972). The glaucous stomatal band is as broad as, or narrower, than each green margin (*depressa*) or 2–3 times as broad as each green margin (*montana*). Two other varieties are occasionally distinguished in California. *Juniperus communis* var. *jackii* Rehder (Rehder 1940) differs from var. *montana* by having longer, more sparsely branched lateral branches. It is a form common to serpentinite substrates in inland coastal

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TABLE 1. DESIGNATION, ACCESSION NUMBER (WHERE KNOWN), LABEL OR PUTATIVE GEOGRAPHIC ORIGIN (WHERE KNOWN) AND SALIENT DISTINGUISHING CHARACTERISTICS OF CULTIVARS GROWING ON THE GROUNDS OF RANCHO SANTA ANA BOTANIC GARDEN.

Sample designation	Accession number	Label/putative geographic origin	Habitat and morphology
CV1	7106	CA, Mono County, 'Tioga'	fairly prostrate, long branches, branchlets upturned, leaves short & spreading, blue-green
CV2	9619	OR, Hood River County, Mt. Hood	erect main stem, long incurved leaves
CV3	13,360	OR, Curry County, 'Gold Beach'?	as CV1
CV4	?	?	as CV1
CV5	17,328	OR, Curry County, 'Gold Beach'	mat-like, long branches, leaves short & incurved, green; wild population no longer readily accessible
CV6	15,826	?	as CV1
CV7	15,826	?	branches spreading, some leaves scale-like, chimaeric distribution of acicular and scale-like leaves
CV8	?	?	as CV1, but foliage greener and branchlets inserted more evenly all around branch axis
CV9	7106	CA, Mono County, 'Tioga'	as CV1
CV10	7106	CA, Mono County, 'Tioga'	as CV1
CV11	17,329	CA, Del Norte County, 'Point St. George'?	mat-like, long branches, leaves short & incurved, blue-green; wild population extirpated

areas of northern California and Oregon. *Juniperus communis* var. *sibirica* Rydb. describes a very prostrate, almost mat-like, form found on coastal bluffs in the extreme northwest of California and southwestern Oregon, and at Ebbett's Pass in the Sierra Nevada. According to Roof (1973), this variety is characterized by leaves that are more incurved, making it less prickly to the touch than *J. communis* vars. *jackii* or *montana.*

RAPD analysis was chosen as a quick and relatively inexpensive means of getting a fingerprint of the genome of each plant which could then be compared against similar fingerprints generated from the native populations. This technique has been applied successfully to *Juniperus* in other studies (Adams and Demeke 1993) addressing affinities between species of *Juniperus.*

METHODS

Plant Material. Plant material was gathered from all *J. communis* cultivars growing at RSABG and from seven wild populations growing at localities from which the original cultivar cuttings had reportedly been collected. In some cases, plants had been acquired from a nursery that had reportedly established its plants from wild-collected stock. Where the source populations were no longer alive or accessible (CV11 and CV5, respectively) adjacent populations were collected instead. Details of collecting locality and morphology of the native populations are summarized in Table 2. The seven wild-collected populations represent *J. communis* vars. *montana* (*mo*A–*mo*C, *mo*G) and *depressa* (*de*D–*de*F). Under the alternative taxonomic scheme (Table 2), populations *mo*A and *mo*G correspond to *J. communis* var. *sibirica,* and populations *mo*B and *mo*C to *J. communis* var. *jackii.* The fourteen cultivars added to the analysis after completion of the preliminary screens are identified in Table 3. They represent different cultivars of species of creeping juniper commonly sold in the nursery trade and are henceforth called "commercial" cultivars.

DNA Analysis. Leaf samples weighing 0.2–0.5 g were ground in liquid nitrogen, followed by extraction of genomic DNA using a modification of Doyle and Doyle (1987). Reaction mixtures (25 μl) for amplification of RAPD bands contained 0.1–1.0 μl genomic DNA (10 ng/μl), 18.8 μl dH_2O, 2.5 μl sequencing buffer (Tris-HCl (pH 9.0), KCl, $MgCl_2$, glycerin), 1.5 μl dNTP's (2.5 mM), 1.0 μl primer (10 pmol/μl), and 0.05 μl *Taq* polymerase. Details of primer nucleotide sequences are given in Table 4. Amplifications were performed on a PTC-100 thermocycler (MJ Research, Inc.) programmed for 1 cycle at 94°C for 1 min, 44 cycles at 94°C for 1 min, 42°C for 1 min and 72°C for 2 min, followed by a final extension time of 7 min at 72°C. Reaction product was run out on a 1.5% agarose gel, stained with ethidium bromide to visualize the bands, and electrophoregrams were photographed on a UV transilluminator (Fotodyne). Product size was determined using a DNA standard (1 kb ladder; Gibco BRL, Inc.). Bands were scored as present or absent by the first and last author. The scores were analyzed using the clustering algorithm UPGMA (Unweighted pair group method with arithmetic averages; average link) and Neighbor-Joining (NJ) available on PAUP* version 4.0 β1 (Swofford 1998).

RESULTS

Of a total of 65 primers screened for RAPD analysis, six showed scorable and reproducible banding patterns and were entered into the final analysis. Scorable bands per primer ranged from one (Operon A1) to nine (UBC-244). A total of 34 bands were scored.

The preliminary analysis, which included all RSABG cultivars (CV), *J. communis* var. *depressa* (*de*) and all but the Ebbett's Pass population of *J. communis* var. *montana* (*mo*), revealed a strikingly different banding pattern of cultivars CV1, CV3, CV4, and CV6 through CV10. All had numerous bands that were missing from the three remaining cultivars and all wild populations. Clearly, the ancestry of these cultivars included an as yet unsampled genotype. The three cultivars having a set of bands more consistent with that of the wild populations were CV2, CV5 and CV11.

To identify the unknown parent or parental component, fourteen creeping cultivars of *J. chinensis* (3), *J. conferta* (1), *J. horizontalis* (6) and *J. sabina* (4) were added to the study (Table 3). Figures 1 and 2 show the resulting UPGMA and NJ phenograms. In both figures, the "exotic" and "commercial" cultivars were more similar to each other, forming a "non-native cluster", than to any of the wild populations ("native cluster"). Among the "commercial" cultivars, all *J. horizontalis* cultivars except *hor* 6 ('Wiltonii') formed a well-defined cluster, and another cluster contained all *J. sabina* cultivars, as well as *hor* 6. Perhaps *hor* 6 was mislabeled at the nursery of origin or has been mistakenly attributed to *J. horizontalis. Juniperus conferta* clustered with *J. sabina* (UPGMA; Fig. 1) or at the base of a cluster including the "exotics" and "commercial" cultivars (NJ; Fig. 2). *Juniperus chinensis* var. *sargentii* 'Viridis' (*chi* 3), did not cluster with the other two *J. chinensis* cultivars, regardless of the distance algorithm used. Instead, it clustered at the base of a cluster including the exotic RSABG cultivars, *chi* 1 and *chi* 2, and *J. horizontalis* (excluding *hor* 6).

Both clustering algorithms placed the "exotic" RSABG cultivars in a cluster with *J. chinensis* var. *procumbens* 'Nana' (*chi* 1) and *J. chinensis* 'San Jose' (*chi* 2). CV7 associated more closely with *chi* 1 and *chi* 2 than the other "exotics" in the NJ phenogram (Fig. 2). Even when *chi* 1 or *chi* 2 were excluded from the analysis the "exotics" still clustered with the "commercial" cultivars (not shown).

Only three RSABG cultivars clustered with the

Table 2. Designation, Scientific Name, Collection Locality, Habitat and Salient Distinguishing Features of Wild Populations of *Juniperus communis* Varieties. Nomenclature follows Flora of North America Committee 1993; names in parentheses are those used in Roof (1973). Sample designations consist of the first two letters of the varietal epithet (italic font), followed by the population (capital letter) and sample number, where more than one sample per population was obtained.

Sample designation	*J. communis* variety	Collection locality	Habitat notes	Habit and morphology
*mo*A1–*mo*A7	*montana* (sibirica)	OR, Curry County: Cape Sebastian	Coastal	mat-like, long branches, leaves short & incurved
*mo*B1–*mo*B6	*montana* (*jackii*)	CA, Del Norte County: Gasquet Toll Road; two sites ca. 1 mile apart	Near coast, serpentinite substrate	prostrate, very long branches
*mo*C1–*mo*C2	*montana* (*jackii*)	CA, Humboldt County: Onion Mountain/Onion Lake intersection	Near coast, serpentinite substrate	prostrate, fairly long branches (young plants)
*de*D	*depressa* (*saxatilis*)	UT, Iron County: between Cedar Breaks National Monument and Panguitch	Great Basin	erect main stem, leaves long & incurved
*de*E	*depressa* (*saxatilis*)	UT, Iron County: Cedar Breaks National Monument	Great Basin	erect main stem, leaves long & incurved
*de*F	*depressa* (*saxatilis*)	NV, White Pine County: Wheeler Mtn., Great Basin National Park	Great Basin	erect main stem, leaves long & incurved
*mo*G1–*mo*G3	*montana* (*sibirica*)	CA, Alpine County: Ebbett's Pass, Sierra Nevada	Sierra Nevada	mat-like, long branches, leaves short & incurved

TABLE 3. DESIGNATION, SPECIES AND CULTIVAR NAME, AND SECTIONAL PLACEMENT OF FOURTEEN "COMMERCIAL" CULTIVARS OF JUNIPER SPECIES ADDED TO THE STUDY TO TRACE THE PARENTAGE OF THE "EXOTIC" RSABG CULTIVARS.

Sample designation	Juniper species and cultivar name	Sectional placement
chi 1	*J. chinensis* var. *procumbens* 'Nana'	section *Sabina*
chi 2	*J. chinensis* 'San Jose'	section *Sabina*
chi 3	*J. chinensis* var. *sargentii* 'Viridis'	section *Sabina*
con 1	*J. conferta* 'Emerald Sea'	section *Juniperus*
hor 1	*J. horizontalis* 'Blue Chip'	section *Sabina*
hor 2	*J. horizontalis* 'Emerald Isle' ('Emerald Spreader'?)	section *Sabina*
hor 3	*J. horizontalis* 'Hughes'	section *Sabina*
hor 4	*J. horizontalis* 'Yukon Belle'	section *Sabina*
hor 5	*J. horizontalis* 'Prince of Wales'	section *Sabina*
hor 6	*J. horizontalis* 'Wiltonii'	section *Sabina*
sab 1	*J. sabina* 'Calgary Carpet'	section *Sabina*
sab 2	*J. sabina* 'Arcadia'	section *Sabina*
sab 3	*J. sabina* 'Moor-Dense'	section *Sabina*
sab 4	*J. sabina* 'Tamariscifolia'	section *Sabina*

native populations (Figs. 1 and 2). CV5 clustered with *mo*A1–*mo*A4 (Fig. 1) or *mo*B4 (Fig. 2). CV11 was placed in a cluster with *mo*A5 (Fig. 1) or with *mo*G1–*mo*G3 (Fig. 2). The long-leaved CV2 was less likely to group with any cluster. In the NJ phenogram (Fig. 2), it clustered with a four taxon cluster containing *mo*B3 and *de*D, *de*E and *de*F. However, UPGMA positioned CV2 at the base of the "native cluster" (Fig. 1). Results pertaining to the wild populations are discussed elsewhere (Ashworth et al., in prep.).

DISCUSSION

Phenetic analysis suggests that nine of eleven cultivars growing at RSABG are either similar to *J. chinensis* or are the result of hybridization between *J. communis* and *J. chinensis.* Given that all "exotics" showed banding patterns far more reminiscent of *J. chinensis* (*chi* 1 or *chi* 2) than their purported *J. communis* progenitor, rather than showing additivity, could reflect multiple backcrossing to the former (Hawkins and Harris 1998; Rieseberg and Ellstrand 1993). Variability within the wild populations makes it difficult to select among the *J. communis* varieties as the putative native ancestor. When all bands shared between the "exotics" and *chi* 1 or *chi* 2 are excluded from the cluster analysis, most "exotics" associate closest with *J. communis* var. *montana* population *mo*C1 (not shown). However, the large proportion of bands shared with *chi* 1 and especially *chi* 2 (73–85%) does not exclude the possibility of a pure *J. chinensis* origin. Under this scenario, the plants may represent pedomorphic *J. chinensis* mutants that retain acicular (juvenile) foliage instead of developing scale leaves typical of (mature) *J. chinensis.* Mutants are of common occurrence in *Juniperus* (p. 413, Flora of North America Committee 1993; Hall 1952).

If hybridity is invoked, the "exotics" may represent *J. communis* × *J. chinensis* hybrids that have undergone multiple backcrossing to *J. chinensis.* The NJ tree (Fig. 2) places CV7 closer to *chi* 1 and *chi* 2 than it does the other "exotics," possibly suggesting additional backcrossing events to *J. chinensis,* but this is not true of the UPGMA phenogram (Fig. 1). In the case of F_1 hybrids and morphological data, UPGMA has been shown to give more predictable placement of a hybrid with one or both parents than NJ (McDade 1997), but relative performances are unknown for more complex breeding histories, let alone for RAPD data and cases involving mutants. The placement of CV7 closest to *chi* 1 and *chi* 2 is, however, consistent with the observation that CV7 exhibits several *J. chinensis* characteristics, notably scale-like leaves and spreading branches, that are not found in the other "exotics". Overall, the RAPD data are in good agreement with morphology. All cultivars at RSABG suggested to be "exotic" by virtue of their less prostrate growth and more prickly leaves, display banding patterns atypical of the wild-collected plants while the cultivars of native appearance cluster with the wild populations. CV5 and CV11 exhibit the prostrate growth habit associated with native populations of *J. communis* var. *montana.* The blue-green foliage of CV11 and the green foliage of CV5 match

TABLE 4. NUCLEOTIDE SEQUENCES OF THE RAPD PRIMERS USED TO FINGERPRINT *JUNIPERUS* GENOTYPES IN THIS STUDY. All nucleotide sequences are cited in a 3′ to 5′ orientation.

Primer name	Nucleotide sequence
OPERON A1	CAG GCC CTT C
OPERON B18	CCA CAG CAG T
UBC-108	GTA TTG CCC T
UBC-111	AGT AGA CGG G
UBC-184	CAA ACG GCA C
UBC-244	CAG CCA ACC G
UBC-329	GCG AAC CTC C

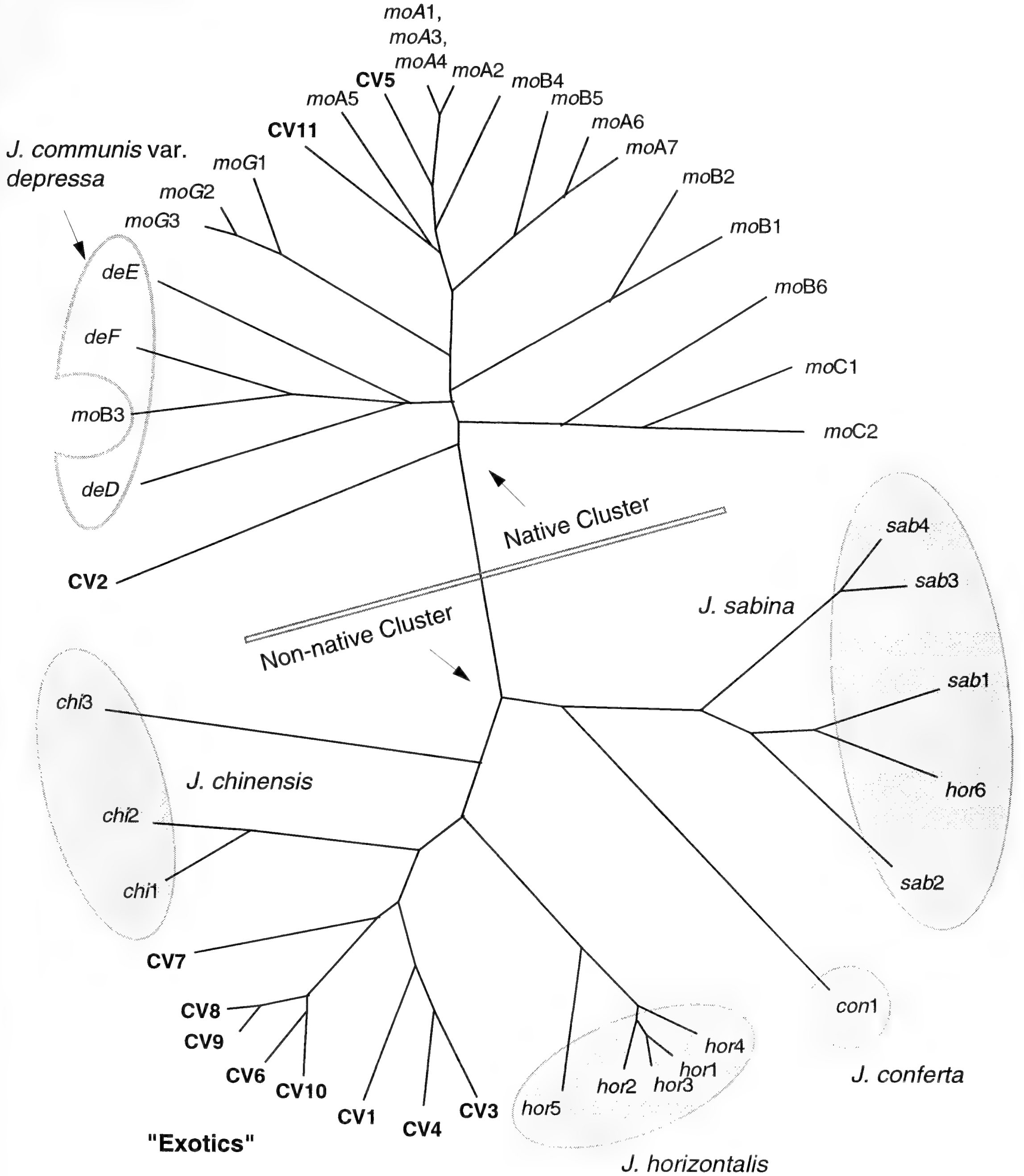

FIG. 1. Unrooted UPGMA phenogram, showing two distinct clusters that group plants with typical *Juniperus communis* morphology (native cluster) and "exotic" morphology (non-native cluster). All RSABG cultivars (CV1–CV11) are bolded. Shaded ovals highlight the four species of juniper other than *J. communis*. Members of *J. communis* var. *depressa* are also indicated. All other individuals represent *J. communis* var. *montana*. Sample designations are identical to those used in Tables 1–3.

Roof's (1973) description of the Point St. George and Gold Beach populations, respectively. CV2 resembles *J. communis* var. *depressa* in habit and leaf size, an affinity receiving partial support from the RAPD data (NJ; Fig. 2).

CONCLUSIONS

This study of dwarf junipers illustrates that a relatively simple molecular technique can be used to test a hypothesis based on observations of aberrant

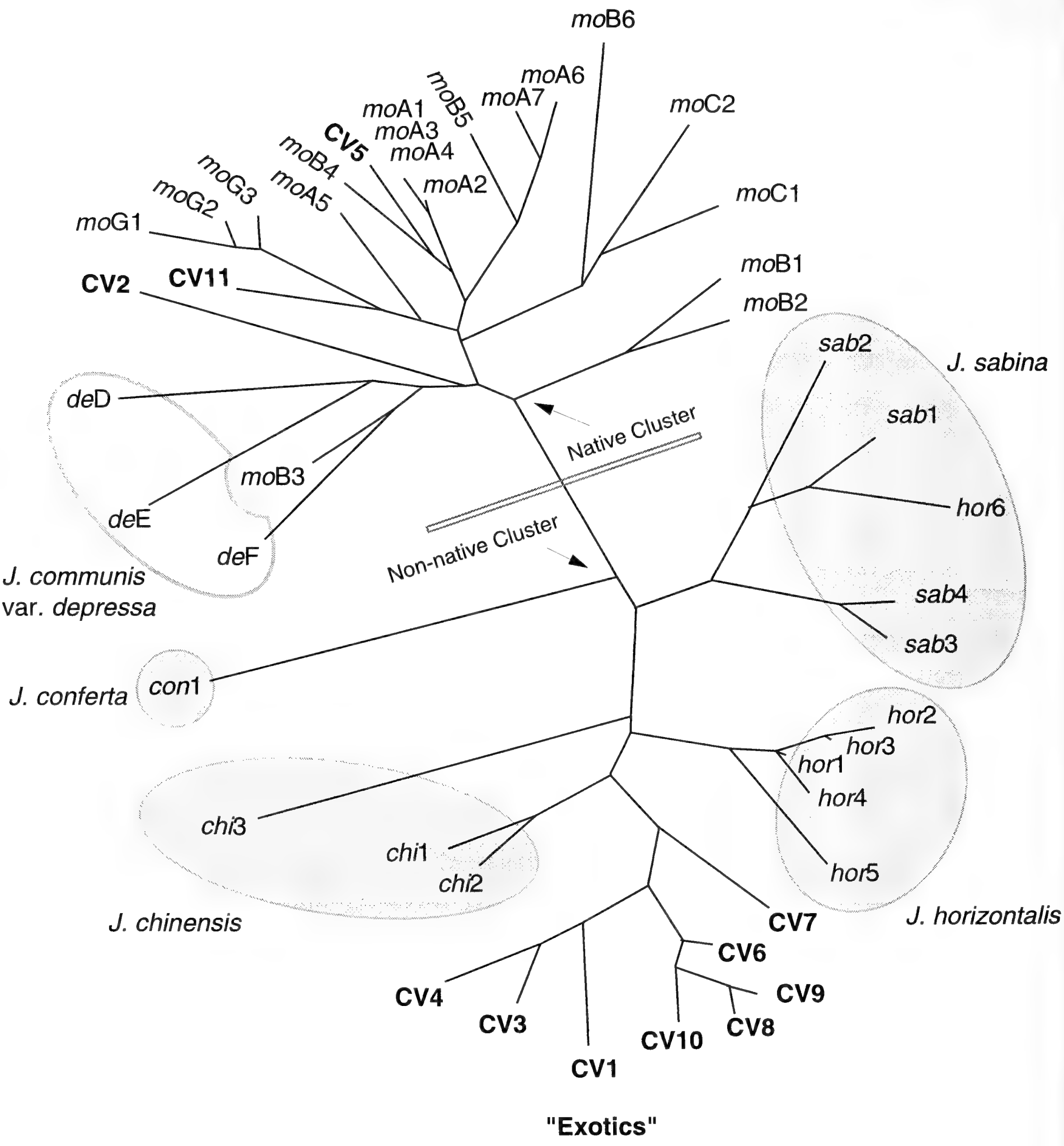

FIG. 2. Unrooted NJ phenogram. Abbreviations and explanations as in Figure 1.

plant morphology. Although the precise parentage of the "exotic" cultivars is unknown, the RAPD fingerprints nonetheless point to a major contribution from *J. chinensis.* Careful research into garden records suggests that all "exotics" trace back to three plants acquired from Louis L. Edmunds, Danville, CA, in 1950. These had been purportedly collected as cuttings from "just east of Tioga Pass summit" in 1938. The most likely explanation is a nursery mix-up, mislabeling, or inadvertent hybridization with *J. chinensis* (suggesting propagation from seed) in the intervening twelve years. It seems unlikely that the original plants from Tioga Pass were themselves hybrids or *J. chinensis* mutants, even though many species of this wind-pollinated genus are able to interbreed (e.g., Flora of North America Committee 1993) and *J. chinensis* has been in cultivation since the last century (Rehder 1940).

ACKNOWLEDGMENTS

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MORPHOLOGICAL VARIATION IN *MALACOTHAMNUS FASCICULATUS* (TORREY & A. GRAY) E. GREENE (MALVACEAE) AND RELATED SPECIES

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ABSTRACT

Character polymorphism is widespread and species delimitation is unresolved among 11 species of *Malacothamnus* currently recognized in California and Baja California. To evaluate variation among characters used in previous taxonomic treatments and to identify characters most useful for discriminating among four species closely associated with *M. fasciculatus,* we analyzed 26 morphological characters from 46 exemplar specimens using cluster, ordination, and statistical analyses. Although many vegetative and reproductive characters exhibited high levels of variation among and within OTU's, bractlet and calyx characters demonstrated maximum utility for discriminating among species in principal components and discriminant functions analyses. OTU's representing previously segregated "varieties" of *M. fasciculatus* (Torrey & A. Gray) E. Greene did not group together nor did conspecific OTU's, except for three OTU's representing the San Clemente Island endemic, *M. clementinus* (Munz & I. M. Johnston) Kearney. The absence of well-defined gaps in many characters and intergradation resulting from gene flow and/or recent divergence from ancestral species impede delimitation at the species and infraspecific levels whether a phenetic or phylogenetic approach is employed. *Malacothamnus fasciculatus* and *M. fremontii* A. Gray are particularly variable and difficult to define unambiguously using morphological data.

INTRODUCTION

Malacothamnus Greene is a genus of woody or suffrutescent perennials with 11 species currently recognized in California and Baja California (Bates 1963, 1993). Distributed from Mendocino and Tehama Counties in northern California to Rosario, Baja California Norte, species of *Malacothamnus* are primarily associated with chaparral and coastal sage scrub communities. The common names of *Malacothamnus,* chaparral mallow and bush mallow, reflect its habit and habitat preferences.

Established by E. L. Greene (1906), *Malacothamnus* is characterized by uniovulate, unappendaged, completely dehiscent carpels; ascending ovules; and a shrubby habit. Later treatments place *Malacothamnus* in Tribe Malveae, Subtribe Abutilinae (Kearney 1951a, b). Bates (1968) did not recognize subtribes, but regrouped the Malveae into "alliances" and suggested a *Malacothamnus* alliance consisting of *Malacothamnus* (**n** = 17), *Iliamna* Greene (**n** = 33), and *Phymosia* Desvaux (**n** = 17). Based on cytological evidence coupled with inference of Tertiary floristic evolution, Bates (1967, 1968) suggested that the three genera are derived from a *Phymosia*-like ancestor. Eastwood (1939) proposed that the California *Malvastrum* (*Malacothamnus*) was an old genus of previously greater abundance, but now in decline. Kearney (1951b) noted that the lack of pronounced morphological differences among species of *Malacothamnus* suggested a recent origin for the genus.

Although the genus *Malacothamnus* is morphologically distinct within Malvaceae, species and varietal delimitations are problematic because of character intergradation and morphological variation both within and among populations (Kearney 1951b; Bates 1963, 1993). The degree of taxonomic uncertainty and instability is evident when considering the widely fluctuating number of species recognized in different treatments. Whereas Greene (1906) recognized nine species, subsequent treatments recognized from one (Bates 1963) to twenty-seven (Eastwood 1936) species and a variable number of infraspecific taxa. In the most recent treatments of the California species, Kearney (1951b) recognized 19 species and six varieties and Munz and Keck (1968) delimited 18 species, one subspecies, and six varieties. In the Jepson Manual (Hickman 1993), Bates recognized ten species without infraspecific taxa; taxa previously ranked as subspecies (Bates 1963) were elevated to species level without changes in circumscriptions (Bates, personal communication). Skinner et al. (1995) noted that several *Malacothamnus* taxa are of "uncertain distinctiveness" and calculated that 75% of the taxa in the genus are taxonomically uncertain.

Few characters unique to any species have been identified in previous taxonomic treatments. Generally, combinations of overlapping characters have been used to delimit species (Kearney 1951b; Bates 1963, 1993). These recent treatments have employed type and density of calyx pubescence, length and shape of the calyx lobes, length and shape of the bractlets, relative length of the involucel bractlets and calyx lobes, type of inflorescence, and shape and texture of the leaves (Kearney 1951b; Bates 1963, 1993). For example, *M. fremontii* A. Gray and *M. davidsonii* (Robinson) E. Greene can be identified by thick, often densely pubescent leaf blades, but other species are not easily distinguished based on leaf characters. Bates (1963) provided an example where polymorphism in leaf shape in a single population of about 50 individuals of *M. fasciculatus* (Torrey & A. Gray) E. Greene encompassed almost all the variation found throughout the genus. Differences in habit among species sometimes may be observed, which may result from environmental factors such as water stress, fire, and competition, affecting growth form (Bates 1963).

The basic floral arrangement within *Malacothamnus* is a cyme arranged into terminal heads, spikes, or open panicles (Bates 1963); variation can be found in the length, number of nodes, branching, internode length, and leafiness of the inflorescence (Bates 1963). Examples include *M. densiflorus* (S. Watson) E. Greene, which is distinguished by a densely flowered, spike-like inflorescence with elongate internodes; and *M. palmeri* (S. Watson) E. Greene, which has a densely flowered, head-like or short, spike-like inflorescence subtended by conspicuous bracts (Bates 1993). Involucel bractlet and calyx characters also have been used to delimit species, but exhibit polymorphism within and among species (Kearney 1951b; Bates 1963, 1993). Within *Malacothamnus,* bractlet length ranges from 2.5 to 21 mm and calyx length varies from 5 to 19 mm (Bates 1993). A single species, *M. densiflorus,* encompasses most of the range for these characters; its bractlets vary from 5 to 15 mm in length and its calyces from 6 to 14 mm. Unlike leaf, inflorescence, bractlet, and calyx characters, morphology of the corolla, pistil, stamen, carpels, and seeds provide few characters used to segregate species (Kearney 1951b; Bates 1963).

Similar to problems in species delimitation and identification, infraspecific taxa in *M. fasciculatus* are notoriously difficult to identify. Although extreme morphological forms are evident, intergradation among habit, leaf shape and pubescence, inflorescence structure, and carpel characters is widespread. Five varieties of *M. fasciculatus* were described previously by Kearney (1951b) and eight subspecies by Bates (1963) in an unpublished dissertation. Later, Bates (1993) recognized no infraspecific taxa in *M. fasciculatus.* In a study of molecular variation in *M. fasciculatus,* Swensen et al. (1995) provided data that indicated var. *nesioticus* is genetically distinct from other varieties of *M. fasciculatus.*

We conducted this study to initiate analyses of character variation within and among species of *Malacothamnus.* Although previous taxonomic and floristic treatments (Kearney 1951b; Bates 1963) emphasized the lack of constant, unique characters and the high level of variability found within species, there have been no explicit numerical studies of the amount and pattern of variation nor statistical analyses of characters that differentiate species. *Malacothamnus fasciculatus* is morphologically and geographically diverse, has been examined at the molecular level (Swensen et al. 1995), and intergrades commonly with other sympatric species, particularly in the southern portion of its range. The present study focused on variation in morphological characters among five intergrading species: *M. clementinus* (Munz & I. M. Johnston) Kearney, *M. davidsonii, M. densiflorus, M. fasciculatus,* and *M. fremontii.* The primary objectives of the study were to assess variation among characters used in previous taxonomic treatments, to identify characters that discriminate among species, and to test hypotheses of taxonomic delimitation of species and varieties.

The five species examined in this study are widespread in southern California and Baja California Norte, and one species is distributed in northern as well as southern California. *Malacothamnus fasciculatus* as delimited by Kearney (1951b) ranges from Santa Barbara County to Baja California Norte. Kearney (1951b) recognized five varieties: vars. *fasciculatus* Greene, *laxiflorus* (Gray) Kearney, and *nuttallii* (Abrams) Kearney are restricted to mainland California, whereas var. *catalinensis* (Eastw.) Kearney (found on Santa Catalina Island and coastal Ventura to San Diego Counties) and var. *nesioticus* (B. L. Rob.) Kearney (restricted to Santa Cruz Island) have populations on the California Islands. Also widely distributed are *M. fremontii,* ranging from Tehama to Riverside Counties and *M. densiflorus,* which is distributed from Riverside County to northern Baja California Norte. The federally and state listed endangered species *M. clementinus* (Smith & Berg 1988) is endemic to San Clemente Island. Populations of *M. davidsonii* are separated by the Transverse Ranges between Los Angeles County and San Luis Obispo and Monterey Counties.

MATERIALS AND METHODS

We examined variation among 26 morphological characters among five species of *Malacothamnus* using clustering, ordination, and statistical analyses. Taxonomic identity was determined using keys and descriptions from the Jepson Manual (Hickman 1993) and, for "varieties" of *M. fasciculatus,* Kearney's treatment (1951b) and Munz and Keck (1968) were used. One representative individual from each of 46 collections representing natural populations (Table 1, Fig. 1) was selected as an exemplar operational taxonomic unit (OTU). The OTU's were chosen from herbarium specimens or from collections of the first author; they were selected to span the geographic and morphological range of each species analyzed (Fig. 1). The widespread species

TABLE 1. SPECIMENS REPRESENTING NUMBERED OTU'S OF FIVE SPECIES OF *MALACOTHAMNUS* USED IN INVESTIGATIONS OF MORPHOLOGICAL VARIATION. All locations are in the state of California unless otherwise noted.

M. clementinus (Munz & Johnston) Kearney

13. San Bernardino Co., Victorville, North Verde Ranch, *Raven 16625,* CAS. 14. Los Angeles Co., San Clemente Island, Lemon Tank, *Beauchamp & Douglas 3236,* SD. 15. Los Angeles Co., San Clemente Island, China Canyon, *Moran, Beauchamp, & Oberbauer 22697,* UC.

M. davidsonii (B. L. Rob.) Greene

11. San Luis Obispo Co., Bee Rock, *Hardham s.n.,* CAS. 12. Los Angeles Co., San Fernando Wash, *Davidson s.n.,* CAS. 16. Los Angeles Co., Big Tujunga, *Lyon s.n.,* CAS. 17. Monterey Co., Lake San Antonio, *Jensen 45,* UC.

M. densiflorus (S. Watson) Greene

9. Mexico, Baja, Valle Redondo, *Fosberg 8368,* UC. 10. Riverside Co., Santa Ana Mtns., above Glen Ivy, *Howell 1056,* UC. 18. San Diego Co., Barrett Lake, *Benesh & Anderson 35,* OKL. 39. San Diego Co., Ramona, *Brandegee s.n.,* UC. 46. Mexico, Baja, San Pedro Martir Mtn., *Robertson 55,* UC.

M. fasciculatus (Nutt. ex Torr. & Gray) Greene

"*var. catalinensis* (Eastwood) Kearney"

5. Los Angeles Co., Santa Catalina Island, Middle Ranch Dam, *Fosberg 54770,* UC. 6. Orange Co., Laguna, *Peirson 4662,* SD. 19. Los Angeles Co., Santa Catalina Island; Black Jack Mtn., *Thorne 36518,* SBBG. 21. Ventura Co., Santa Monica Mtns. beyond Hidden Valley on Sherwood Rd., *Holbrook s.n.,* SBBG.

"var. *fasciculatus* (Nutt. *ex* Torr. & Gray) Greene"

20. San Diego Co., 2 mi E of San Ysidro on Otay Mesa, *Gander 219.13,* SD. 31. Riverside Co., El Toro Peak, San Jacinto Mtns., Santa Rosa Range, *Hall 765,* UC. 32. San Diego Co., Fallbrook; ca. 6 mi NE, *Benesh & Anderson 39,* OKL. 33. Mexico, Baja, Punta Banda near Arbolitos, *Thorne & Charlton 58685,* RSA. 34. Mexico, Baja, Rancho Estela, *Moran 24380,* SD. 35. Mexico, Baja, El Condor, Sierra Juarez, *Moran 13578,* SD. 37. San Mateo Co., Spring Valley, *Cougdon s.n.,* JEPS. 40. Mexico, Baja, Upper Arroyo Copal, Sierra San Pedro Martir, *Moran 15499,* SD. 41. Mexico, Baja, Santa Rosa, *Moran & Thorne 14427,* RSA. 44. San Bernardino Co., San Bernardino Mtns., State Hwy 18 ca 0.5 mi above Waterman Canyon Road, *Raven & Beeks 16759,* UC. 45. Mexico, Baja, Socorro Wash (Arroyo Hondo), *Thorne, Wisura, Peterson, & Annable 58011,* RSA.

"var. *laxiflorus* (Gray) Kearney"

22. Los Angeles Co., Altadena, *Ramsey & Ramsey 3084,* RSA. 23. Orange Co., Crystal Cove State Park, El Moro Canyon, *Benesh 57,* OKL. 24. San Bernardino Co., Cajon Pass, *Benesh 53,* OKL. 27. Ventura Co., Point Mugu, *Vanderwier & Murphey 78,* SBBG. 30. Riverside Co., Garner Valley, *Tilforth & Wisura 1916,* RSA. 36. San Diego Co., Camp Pendleton, Horno Canyon, *Beauchamp & Swickard 1518,* SD.

"var. *nesioticus* (B. L. Rob.) Greene"

7. Santa Barbara Co., Santa Cruz Island, *Brandegee 1888,* UC.

TABLE 1. (CONTINUED).

"var. *nuttallii* (Abrams) Kearney"

3. Santa Barbara Co., upper Cachuma Dam area, *Smith 4940,* SBBG. 4. Los Angeles Co., Santa Monica Mountains, *Howe 2164,* SD. 25. Santa Barbara Co., Santa Barbara, *Benesh 63,* OKL. 26. Ventura Co., Lake Casitas, near East Casitas Pass, *Benesh 64,* OKL. 43. Santa Barbara Co., Gaviota Pass, *Abrams 5030,* UC.

M. fremontii (Torr. ex Gray) Torr. ex Greene

1. Santa Barbara Co., Vandenburg AFB, *Nichols 664,* JEP. 2. Sutter Co., North Butte, *Ewan & Ewan 9597,* JEP. 8. Madera Co., Oakhurst, *Wolf 2433,* SBBG. 28. Los Angeles Co., Pine Canyon, *Hoffman s.n.,* SBBG. 29. Ventura Co., Lockwood Valley, *unknown s.n.,* SBBG. 38. San Bernardino Co., Baldwin Lake, *Tilforth & Wisura 2107,* RSA. 42. Riverside Co., San Jacinto Mtn., *Purer 6472,* CAS.

M. fasciculatus and *M. fremontii* were disproportionately represented in their southern range where they and other species are sympatric.

Eleven quantitative and 15 qualitative characters were chosen to represent vegetative and reproductive structures (Table 2). Characters were selected based on their inclusion as diagnostic features in previous taxonomic treatments (Kearney 1951b; Munz and Keck 1968; Bates 1963, 1993). For each OTU, we obtained a minimum of 10 measurements for each character whenever possible. Several measurements of bractlet, calyx, and leaf length and/or width were converted to a ratio (characters 2, 7, 17, 18; Table 2) to describe shape and relative dimensions rather than absolute size. Lack of sufficient suitable material on herbarium specimens precluded the use of leaf size, carpel characters, and seed characters in our analysis. Preliminary analyses also revealed that several characters not included in our analysis were either variable on a single individual, too subjective to be coded accurately, or difficult to detect (e.g., leaf lobing, leaf margin, leaf apex, leaf thickness, pubescence color, inflorescence type, and bractlet shape).

Analyses were performed using NTSYS-pc (Rohlf 1993) and SYSTAT (SPSS Inc. 1997). A standardized data matrix was used to compute a dissimilarity matrix using the average taxonomic distance coefficient and a cophenetic correlation coefficient. A clustering phenogram was generated using the UPGMA (unweighted pair-group method using arithmetic averages) method. A Principal Components Analysis (PCA) was performed by computing a correlation matrix, calculating eigenvectors for the first three axes, and projecting the OTU's onto the components.

Using the SYSTAT software package (SPSS Inc. 1997), discriminant functions analysis was used to determine which combination of characters provided maximum discrimination among recognized species and "varieties" of *M. fasciculatus.* Because this method does not allow missing data, seven of

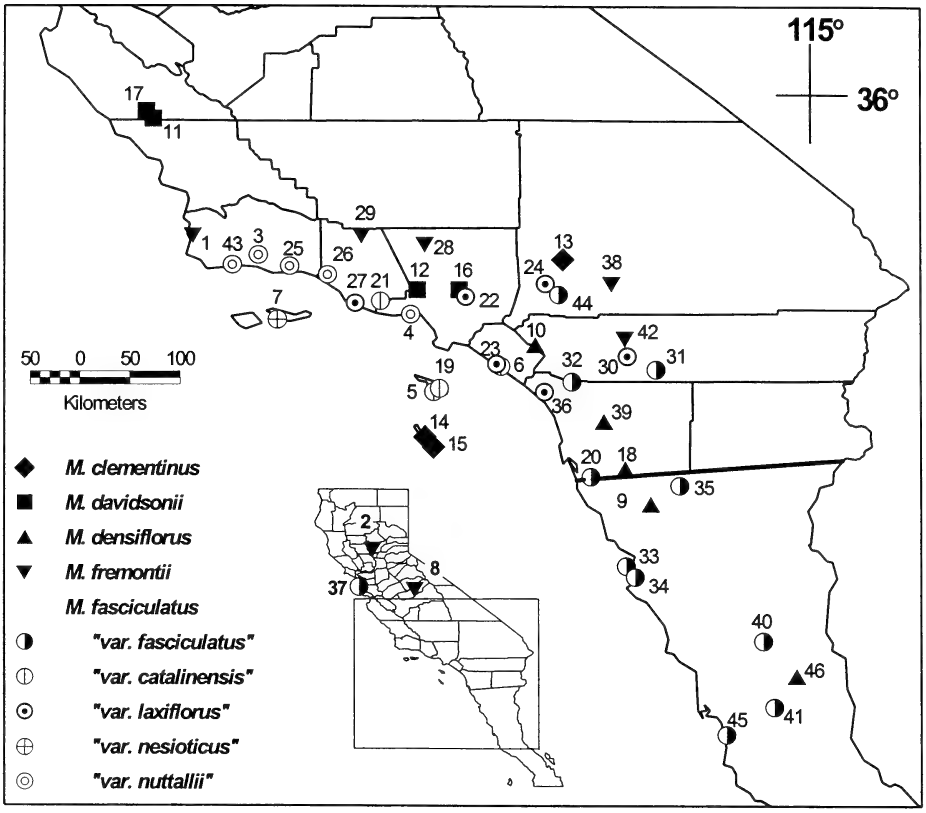

FIG. 1. Collection localities for 46 specimens of five species of *Malacothamnus* analyzed for morphological variation. Solid symbols represent species described in The Jepson Manual (Hickman 1993; Bates 1993). Shaded symbols represent "varieties" of *M. fasciculatus* as delimited by Kearney (1951b; Munz & Keck 1968).

1288 entries (0.54%) from the data matrix were estimated by using the average of other OTU's of the same species. Standard and jackknifed classifications were produced to test group relationships. In the standard procedure, the centroid of each group of like taxa was computed, and then each OTU was examined to determine to which group it was most similar. When the OTU was most similar to the group representing that taxon, it was scored as a correct identification. When it was most similar to a group representing another taxon, it was scored as an incorrect classification. For the jackknifed classification, an OTU was removed, the centroid recalculated, and the OTU identified as to which group it was most similar. This was repeated for each OTU, producing a less biased number of correct classifications. Three discriminant functions analyses were performed: species level only, species and all "varieties" of *M. fasciculatus,* and species and "varieties" of *M. fasciculatus* except "var. *nesioticus*". The latter analysis was performed because "var. *nesioticus*" was represented by only a single OTU, which confounded the jackknifed classification.

RESULTS

The UPGMA phenogram (Fig. 2) had four major clusters and a cophenetic correlation value of 0.840. Cluster I was composed of two OTU's of *M. fremontii* and an OTU representing *M. fasciculatus* "var. *fasciculatus*" of unusual appearance from the southern limits of its range in Baja California Norte. Cluster II was the most complex grouping in the phenogram, and could be further subdivided into three groups, excluding the outlying "var. *fasciculatus*" (OTU 37) from San Mateo County. With the two aforementioned exceptions, all other OTU's representing *M. fasciculatus* were found within cluster II along with OTU's of three other species. Cluster IIa consisted of 10 OTU's representing *M. fremontii, M. davidsonii,* and three "varieties" of *M. fasciculatus.* The closest phenetic similarity among all OTU's was in this cluster between *M. davidsonii* and *M. fasciculatus* "var. *laxiflorus*" (OTU's 17 and 24). Cluster IIb comprised OTU's representing all five "varieties" of *M. fasciculatus* as well as one OTU of *M. davidsonii* from Los Angeles County. The OTU representing the Santa Cruz Island endemic *M. fasciculatus* "var. *nesioti-*

TABLE 2. MORPHOLOGICAL CHARACTERS EXAMINED AMONG FIVE SPECIES OF *MALACOTHAMNUS* AND PURPORTED VARIETIES OF *M. FASCICULATUS*. Characters useful for differentiating among species in principal components analysis (PCA) are indicated by an asterisk (*). Characters useful for differentiating species in discriminant functions analysis are indicated by a plus sign (+).

	1.	stem pubescence type: loose (0), appressed (1)
	2.	leaf blade length/width
	3.	leaf base: cordate (0), truncate (1)
* +	4.	bractlet length
*	5.	bractlets concolorous throughout: absent (0), present (1)
*	6.	bractlet concolorous with calyx: absent (0), present (1)
* +	7.	bractlet length/calyx length
	8.	calyx length from base to tip of lobe
*	9.	calyx outer pubescence type: rigid (0), soft or pliant (1)
* +	10.	sepal lobes in bud recurved at margins: absent (0), present (1)
*	11.	sepal lobes in bud: divergent (0), connivent (1)
	12.	sepal lobe shape: triangular (0), ovate (1)
	13.	sepal lobe apex: acute (0), acuminate (1)
*	14.	sepal lobe constricted at base: absent (0), present (1)
*	15.	sepal lobe length
	16.	sepal lobe width at base
	17.	sepal length/width
	18.	sepal lobe length/calyx tube length
	19.	sepal lobes obscured by pubescence: absent (0), present (1)
+	20.	sepal pubescence: short-stalked (0), long-stalked (1)
	21.	sepal pubescence: number of arms
*	22.	sepal pubescence: length of arms
	23.	sepal lobe pubescence type within: glabrous (0), tomentose (1), pilose (2), hispid (3)
	24.	inflorescence: unbranched (0), branched (1)
	25.	flower clusters: dense (0), open (1)
	26.	length of staminal column

cus" clustered most closely with "var. *nuttallii*" from Los Angeles County, whereas OTU's of "var. *catalinensis*", including two from Santa Catalina Island, did not group together.

Only *M. densiflorus* and *M. fasciculatus* OTU's were contained in Cluster IIc, which included specimens from south-central Riverside County to the southern limits of the North American range in Baja California. Cluster III was composed of two subclusters of OTU's representing *M. fremontii* and *M. clementinus*. The *M. clementinus* OTU's included a (cultivated?) specimen from San Bernardino County. Cluster IV comprised two *M. densiflorus* OTU's that are less similar to each other than are most of the other clusters.

The three-dimensional PCA model (Fig. 3) revealed groupings similar to those in the UPGMA phenogram. The first three components constituted 49 percent of the total variation: 28%, 11%, and 10%, respectively. Characters with high loadings (Table 3) included characters 4, 7, 11, 15, and 22 in the first component; 9, 10, and 14 in the second component; and 5 and 6 in the third component. The PCA model also did not reveal discrete groupings corresponding to species boundaries, but instead depicted loose groups with considerable overlap among taxa. OTU's representing *M. clementinus, M. densiflorus,* and *M. fremontii* were generally separated from *M. fasciculatus* and *M. davidsonii* along the first axis. There were no discrete groupings among OTU's corresponding to varieties of *M. fasciculatus*. As in the UPGMA phenogram, the PCA model placed *M. davidsonii* within the *M. fasciculatus* complex.

Discriminant functions analysis identified four characters as most useful for classifying species: 4, 7, 10, and 20 (Table 2). The OTU's were correctly classified to species an average of 67% (Table 4) in the standard classification. Whereas *M. densiflorus* was classified correctly 100% of the time, the lowest value, 56%, resulted when 12 *M. fasciculatus* OTU's were misclassified as *M. davidsonii* (10) or *M. densiflorus* (2). In the jackknifed classification, a 52% average correct classification was obtained. The lowest value, 44%, resulted when 15 OTU's of *M. fasciculatus* were incorrectly classified.

When "varieties" of *M. fasciculatus* were included as taxa, characters 7 and 10 (Table 2) were the most useful for discriminating among species and "varieties" using discriminant functions analysis. The correct classification percentages were relatively unchanged by the exclusion of the one OTU of "var. *nesioticus*". The standard classification was correct 43% of the time when "var. *nesioticus*" was included (Table 4) and 47% when it was removed compared to jackknifed percentages of 35% when "var. *nesioticus*" was included and 36% when it was excluded. *Malacothamnus davidsonii* and *M. fasciculatus* "var. *laxiflorus*" were consistently classified incorrectly in analyses including varieties. For example, OTU's of *M. dav-*

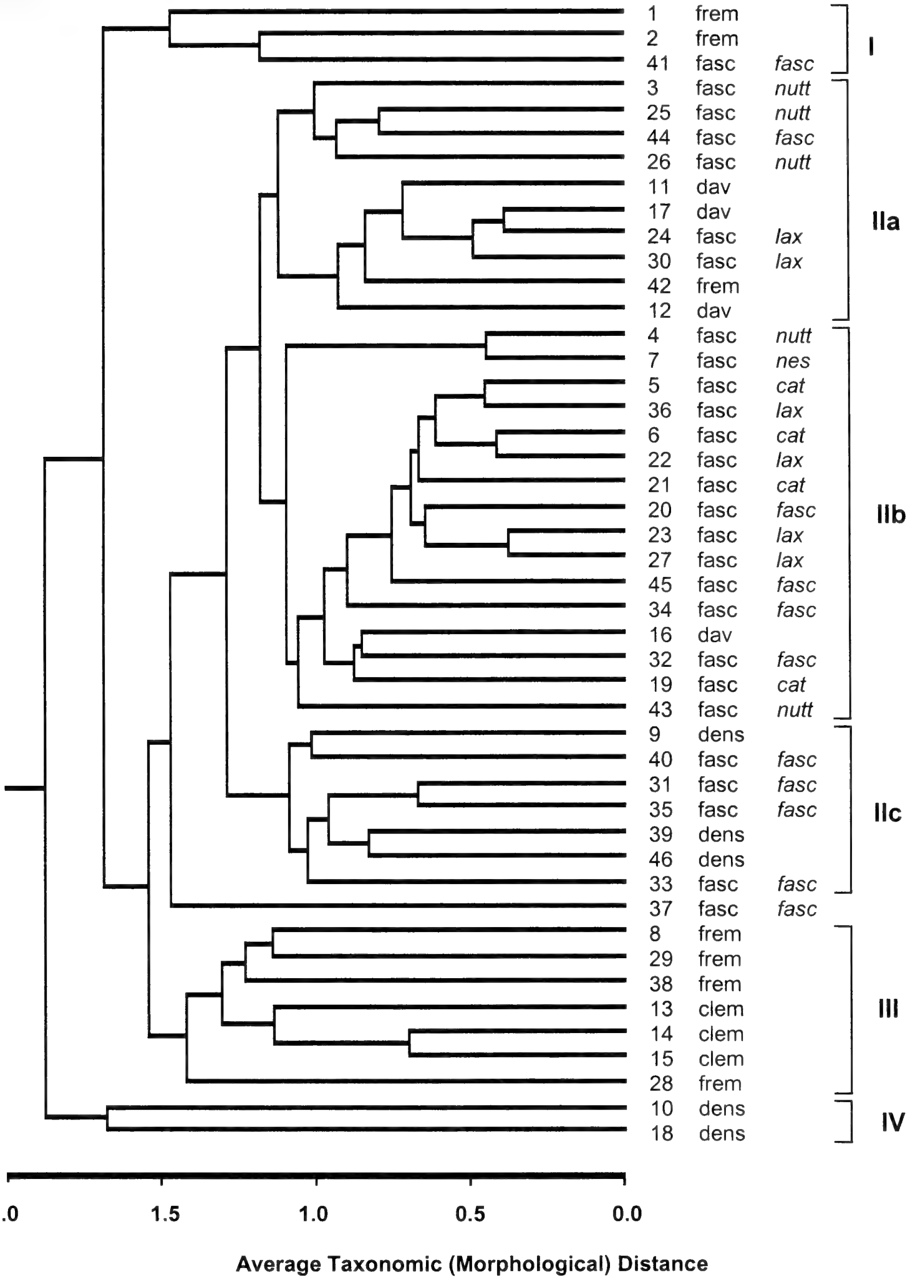

FIG. 2. UPGMA phenogram derived from average taxonomic distance coefficients using 26 morphological characters from 46 OTU's of five species of *Malacothamnus*. OTU numbers and locations are listed in Table 1. The cophenetic correlation is 0.840.

idsonii were classified as "var. *nesioticus*", "var. *nuttallii*" or "var. *laxiflorus*".

DISCUSSION

Character variation and life history traits. The diverse taxonomic interpretations within *Malacothamnus* reflect complex patterns of morphological variation. Our observations and analyses confirm that many characters used previously exhibited high levels of variability within species, populations, and, even, single individuals. This point often was commented upon to varying degrees by previous workers (Kearney 1951b; Bates 1963, 1993), but there has been no quantification or documentation of character variation until the present study. We found that most vegetative characters used previously to delimit and characterize species, particularly those describing the vestiture, lobing, apex,

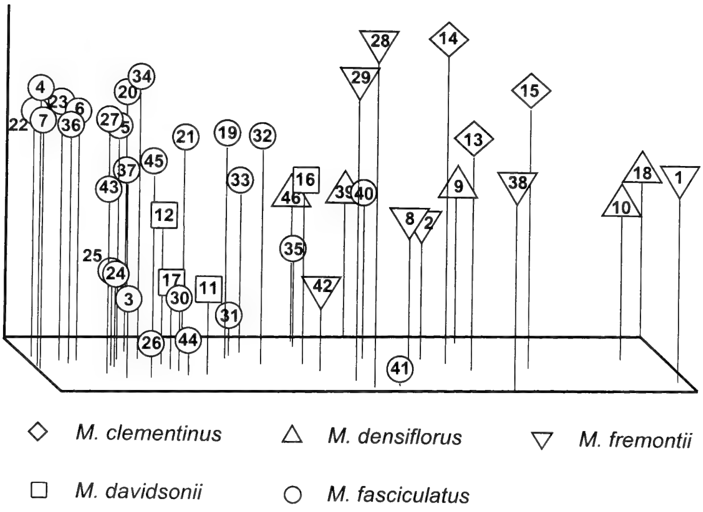

FIG. 3. Three-dimensional model produced in principal components analysis using 26 morphological characters in five species of *Malacothamnus*. OTU numbers and locations are listed in Table 1.

and margins of leaves, were too variable on specimens to code or to describe accurately the phenotype of a collection or OTU. Our study is at least partially supportive of Bates' (1963) comment that some characters are vague or difficult to quantify, but are apparent to those familiar with the genus. This was particularly noteworthy for *M. davidsonii*, whose "coarse" habit, "stout" branches, and "densely" pubescent leaves are readily observable in field populations, but difficult to observe and quantify on herbarium specimens. Consequently, only one stem and two leaf characters were included in the analyses out of 26 total characters. Of the three vegetative characters identified, none were indicated as "useful" for discriminating among species in our analyses.

Reproductive characters, especially those de-

TABLE 3. EIGENVALUES PRODUCED IN PCA FOR 26 MORPHOLOGICAL CHARACTERS AMONG FIVE SPECIES OF *MALACOTHAMNUS*. Character numbers refer to Table 2.

Character	Component 1	Component 2	Component 3
1	−0.185	−0.233	0.361
2	−0.070	0.235	0.059
3	0.019	0.248	−0.458
4	0.899	0.168	0.117
5	0.490	−0.068	−0.632
6	0.256	0.129	−0.750
7	0.802	0.343	0.244
8	0.678	−0.320	−0.223
9	0.426	−0.496	−0.020
10	−0.630	0.483	−0.422
11	−0.780	0.231	−0.370
12	−0.040	0.303	0.177
13	0.012	0.416	0.088
14	0.433	0.563	−0.239
15	0.788	−0.308	−0.327
16	0.152	−0.215	−0.210
17	0.713	−0.287	−0.324
18	0.681	−0.228	−0.332
19	−0.563	−0.395	−0.146
20	0.480	−0.418	0.388
21	−0.524	−0.365	−0.365
22	0.760	0.308	0.217
23	0.092	0.305	−0.273
24	−0.489	−0.436	−0.191
25	−0.500	−0.385	−0.060
26	0.125	−0.211	0.086

TABLE 4. PERCENTAGE OF TAXA CORRECTLY CLASSIFIED IN DISCRIMINANT FUNCTIONS ANALYSIS OF 26 MORPHOLOGICAL CHARACTERS AMONG FIVE SPECIES OF *MALACOTHAMNUS*. Results are presented for comparisons among species only and among species and all "varieties" of *M. fasciculatus*. See text for discussion of results when "var. *nesioticus*" was removed from the analysis.

	Percent correctly classified			
	Species only		Including "varieties" of *M. fasciculatus*	
Taxa	Standard	Jackknifed	Standard	Jackknifed
M. clementinus	67	67	100	67
M. davidsonii	75	50	0	0
M. densiflorus	100	60	80	80
M. fremontii	86	71	29	29
M. fasciculatus	56	44	—	—
"var. *catalinensis*"	—	—	75	75
"var. *fasciculatus*"	—	—	45	36
"var. *laxiflorus*"	—	—	0	0
"var. *nesioticus*"	—	—	100	0
"var. *nuttallii*"	—	—	40	20
Total	67	52	43	35

scribing the bractlets and calyx, were more consistent within OTU's, were easier to code, made up the majority of characters subjected to numerical analyses, and comprised all 11 characters that discriminated most effectively among species in the PCA and/or discriminant functions analyses (Table 2). Other reproductive characters describing the inflorescence and staminal column exhibited little utility for discriminating among species. Three characters exhibited high levels of discrimination among species in both PCA and discriminant functions analyses, and represent characters of maximum taxonomic utility: bractlet length, bractlet length/calyx length, and the presence or absence of recurving sepal lobe margins in bud. Another five qualitative and three quantitative characters were significant in either PCA or discriminant functions analyses: bractlets concolorous with calyx, bractlets concolorous throughout, outer calyx pubescence texture, divergence of sepal lobes in bud, sepal lobe constriction at base, sepal lobe length, and length of the arms and stalks of the sepal pubescence.

Variation patterns observed among species reflect historical factors such as biogeography and phylogeny, and genetic factors such as population structure, mating system, reproductive isolation, and seed dispersal (Avise 1994). Populations of *M. fasciculatus* and related species vary in size from few to numerous individuals, consist often of clones because of reproduction via rhizomes (Bates 1963; Swensen et al. 1995), and are characterized by lack of fertility barriers (Bates 1963). Artificial hybridization experiments revealed widespread cross-compatibilities and interfertilities among species (Bates 1963). Natural hybridization between species also has been postulated; Bates (1963) identified four regions of sympatry with interspecific hybrid swarms. Bates (1963) suggested that "random but recurrent hybridization and isolation of populations has probably been a major factor in the evolution of morphological diversity in *Malacothamnus.*"

Variable compatibility systems may be present among species of *Malacothamnus*; *M. fasciculatus* and *M. palmeri* are self-incompatible, whereas self-compatibility has been observed in *M. fremontii* and *M. jonesii* (Bates 1963). Additionally, Bates (1963) observed that although the flowers of *Malacothamnus* are bisexual and pollen is released while stigmas are receptive, insects commonly visit the flowers. He concluded that species of *Malacothamnus* have a mixed mating system but are predominantly outcrossing. However, in an examination of genetic variation within *M. fasciculatus,* Swensen et al. (1995) reported a value of isozyme differentiation among ten populations ($G_{st} = 0.584$) which is most concordant with that of a selfing species (Loveless and Hamrick 1984; Hamrick and Godt 1990). Because of the lack of interspecific reproductive barriers, gene flow among populations and species may be partly responsible for character intergradation in *Malacothamnus* (Loveless and Hamrick 1984; Briggs and Walters 1985). Additionally, replenishment of alleles from the soil seed bank may contribute to heterogeneity within and among populations (Huenneke 1991). Germination experiments indicate that *Malacothamnus* seeds remain viable for more than 50 years (Bates 1963; Benesh unpublished data) and germinate rapidly following a fire (Bates 1963).

Taxonomic implications and species delimitation. Among 46 OTU's included in clustering and ordination analyses, only those representing *M. clementinus* formed a distinct cluster and grouped with OTU's of *M. fremontii.* Sampled specimens of other species were intermixed in the UPGMA phenogram and PCA model. *Malacothamnus fasciculatus* was the most widely sampled species and encompassed the most morphological variation. Similar to the interspecific pattern, OTU's representing segregated "varieties" of *M. fasciculatus* were completely intermixed and clustered with those of three other species: *M. fremontii, M. davidsonii,* and *M. densiflorus.* The 16 specimens in cluster IIb of the phenogram (Fig. 2) formed the most internally consistent taxonomic grouping, with one *M. davidsonii* in a group of *M. fasciculatus* OTU's.

The general lack of resolution delimiting species of *Malacothamnus* using numerous characters and a phenetic approach indicate polymorphism among species was extensive. In our study, multivariate techniques did not identify any well-defined morphological and geographic cluster within *Malacothamnus.* The pattern of morphological and geographical variation was widespread among the five species sampled, and character intergradation was not restricted to particular species pairs or to a few areas of sympatry. Conspecific OTU's were generally spatially separated on the phenogram (e.g., OTU's 16+32+19 and OTU's 17+24+30), except for cluster IIc where three *M. densiflorus* specimens grouped with four OTU's of *M. fasciculatus* in an area of sympatry and purported hybridization (Bates 1963). Although found at elevations less than 650 meters throughout much of its range (Bates 1963), inland populations of *M. fasciculatus* in Riverside and San Diego Counties and northern Baja California Norte can be found at higher elevations, resulting in sympatry with *M. densiflorus* (Fig. 4). Bates (1963) recognized this area as a zone of introgression and suggested that delimitation of *M. densiflorus* and *M. fasciculatus* is arbitrary in this region.

Because comparatively few characters exhibited significant taxonomic utility (Table 2), it is useful to consider whether a phylogenetic approach to species delimitation (e.g., Nixon and Wheeler 1990, Davis and Nixon 1992), based on uniform and unique characters or combinations of characters, is more useful than the phenetic methods used in this study. Population (OTU)-based data have been used

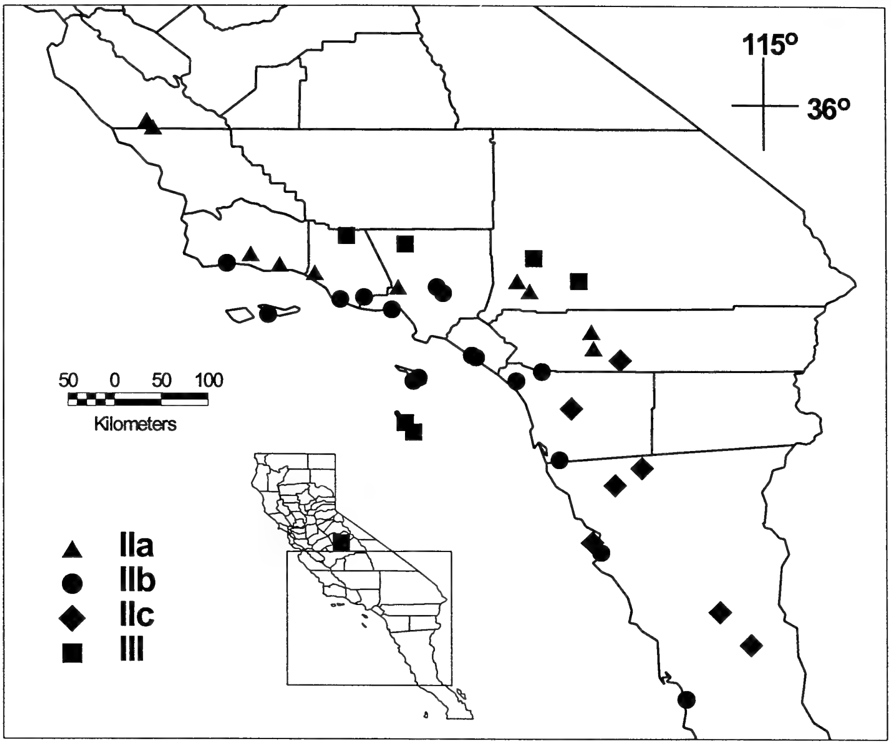

FIG. 4. Collection locations for specimens of five species of *Malacothamnus* analyzed for morphological variation. Cluster designations correspond to the clusters produced in the UPGMA phenogram (Fig. 2). Only clusters II and III are shown.

successfully to identify lineage-defining characters in several groups (e.g., Davis and Manos 1991), and several species of *Malacothamnus* can be delimited using morphological data with this procedure. For example, *M. densiflorus* can be defined by a unique character combination of an unbranched, elongated inflorescence, dense flower clusters, and large bractlet and calyx lengths. *Malacothamnus clementinus* is identified by the association of isodiametric leaves (similar to *M. fasciculatus*) and recurved sepal lobes in bud (similar to *M. fremontii).* The combination of "stout" branches and "dense" leaf pubescence of *M. davidsonii* also are unique in the genus and are used to define this species by several workers (Kearney 1951b; Bates 1963, 1993). However, in *M. davidsonii* as in *M. fasciculatus, M. fremontii,* and other species in *Malacothamnus,* lineage-defining characters are often difficult to detect in herbarium specimens, vary greatly among and within populations, and are difficult to divide into discrete character states. The absence of well-defined gaps in many characters and intergradation resulting from gene flow and/or recent divergence from ancestral species pose serious problems to species delimitation within *Malacothamnus* whether a phenetic or phylogenetic approach is employed.

Malacothamnus fasciculatus and *M. fremontii* encompass the largest geographical range and morphological variation among the species investigated and in the genus (Bates 1963). Illustrating the discordant views of species boundaries and the extent of phenotypic variation among these species, Bates (1993) submerged five and three specific epithets to synonymy within *M. fasciculatus* and *M. fremontii,* respectively. Other than geographic locality (e.g., "var. *catalinensis", "*var. *nesioticus")*, varieties of *M. fasciculatus* were equally difficult to characterize and were not recognized in the Jepson Manual (Hickman 1993). Because of complex patterns of intergradation among morphological characters, we were not able to identify any unique character combinations for *M. fasciculatus* or *M. fremontii.*

Using molecular data, Swensen et al. (1995) examined variation among varieties of *M. fasciculatus* to assess the genetic distinctness of the two known populations of the Santa Cruz Island endemic, *M. fasciculatus* "var. *nesioticus*". Sampling within *M. fasciculatus* was from six counties and was based on ten populations in the isozyme studies and seven populations in the RAPD and rDNA analyses. Swensen et al. (1995) concluded that the pattern of molecular variation supported Kearney's (1951b) varietal delimitations within *M. fasciculatus,* and that "var. *nesioticus*" was the most divergent genetically among sampled populations with unique isozyme and RAPD alleles and rDNA restriction sites. Our morphological analyses indicate a conclusion similar to Bates (1963, 1993) is warranted. There is extensive morphological intergradation among "varieties" of *M. fasciculatus* and we are unable to characterize any variety unambiguously, including "var. *nesioticus.*"

Biogeographic implications. Populations of two species examined in this study, *M. fasciculatus* and *M. clementinus,* are considered California Island endemics or island-mainland disjuncts. Whereas *M. clementinus* is restricted to San Clemente Island, previously segregated "varieties" of *M. fasciculatus* included a Santa Cruz Island endemic ("var. *nesioticus*") and a Santa Catalina Island and mainland disjunct ("var. *catalinensis*"). Our results supported the status of the endangered species *M. clementinus* as a distinct morphotype in *Malacothamnus* that may be found occurring naturally only on San Clemente Island. *Malacothamnus clementinus* forms the most morphologically coherent group for any species examined, and its three OTU's are most similar morphologically to four OTU's of *M. fremontii* collected at elevations ranging from 1160 to 1500 meters in Los Angeles, Madera, San Bernardino, and Ventura Counties. Our analyses included an OTU (P. H. Raven #16625, annotated by Bates) from San Bernardino County, but it was unclear if it was a human-facilitated introduction. Bates (1963, 1993) previously noted the similarities between *M. clementinus* and *M. fremontii* in calyx characters, and suggested that *M. clementinus* represented a "generalized" form of *Malacothamnus* that persisted in refugial habitats in San Clemente Island (Raven and Axelrod 1978).

Mainland and island OTU's representing *M. fasciculatus* "var. *catalinensis*" did not group together in our morphological analyses, indicating polymorphism among Santa Catalina Island and mainland populations formerly placed in "var. *catalinensis*". We present no morphological evidence to characterize "var. *catalinensis*" or to support its status as a California Island endemic or island-mainland disjunct. For *M. fasciculatus* "var. *nesioticus*", its coherence as a distinctive morphotype within *M. fasciculatus* and as a Santa Cruz Island endemic could not be tested because only one OTU was examined. Swensen et al. (1993) found that the two known populations of "var. *nesioticus*" were more dissimilar genetically to each other than either population was to other "varieties". Our PCA indicated that the Santa Cruz Island OTU was most similar to a collection of *M. fasciculatus* "var. *nuttallii*" from the Santa Monica Mountains in Los Angeles county. This morphological grouping is geographically proximate and also is consistent with the hypothesized physiographic and geological correspondence of the northern California Islands with the western Transverse Ranges (Valentine and Lipps 1967, Sorlien 1994).

The rare species *M. davidsonii* is disjunct between the South Coast Ranges and Los Angeles County. The four OTU's representing these disjunct regions did not group together, but exhibited the closest morphological similarity to *M. fasciculatus* and, to a lesser extent, *M. fremontii.* Our data support Bates' (1963, 1993) observation of the intergradation between *M. davidsonii* with *M. fasciculatus.* As in this and other examples of character intergradation between species, this study cannot differentiate between hypotheses of interspecific hybridization or primary (and incomplete) divergence from ancestral species. Future studies employing molecular markers may represent the best approach to investigate specific instances of gene flow, species delimitations, and interspecific relationships.

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NOTES

TYPIFICATIONS OF NORTH AMERICAN *SALIX* (SALICACEAE), MOSTLY MEXICAN. Robert D. Dorn, Box 1471, Cheyenne, WY 82003.

Types encountered in the course of other studies or received too late to incorporate into other papers are dealt with in this note.

Salix cana M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(4):344. 1843. TYPE: MEXICO, Veracruz, Fl. Aout. bord des Ruisseaux In Volcan D'Orizaba à 12,000 pd, Nov–Apr 1840, *Galeotti 69* (holotype, BR, lost; lectotype, designated here, P!; isolectotype, G!).

The application of this name has been uncertain ever since it was described. This is partly because the original description does not totally match the type specimens and partly because only three additional collections are known. The following description is based on the lectotype and isolectotype, which are vegetative, and the other collections cited below.

Trees about 4 m high (ca. 7–9 m for the type); year-old branchlets reddish-brown, glabrous (pubescent); branchlets of year greenish or yellowish, becoming reddish-brown, pubescent (glabrous); expanded leaf blades narrowly elliptic, 3–5 cm long, 0.6–0.9 cm wide, acute at tip, less sharply acute at base, glaucescent on underside, entire, pubescent with some reddish hairs, becoming glabrous on upperside or sometimes on both sides, petioles 1–3 (4) mm long, stipules lacking; staminate aments subprecocious, 0.6–1 cm long, sessile or nearly so but with small leaves at base, stamens 2, anthers 0.4–0.5 mm long, filaments pubescent toward base, floral bracts light to dark brown, oblanceolate to obovate, 1–1.5 mm long, pubescent with relatively short, straight hairs; pistillate aments subprecocious, 0.8–1.2 cm long, subsessile with small leaves at base, pistils 2–3 mm long, pubescent, styles 0.2–0.3 mm long, stipes mostly 1–2 mm long, floral bracts 1.5–2.5 mm long, dark brown to black, short-pubescent. *Abies* and *Pinus* forests, stream sides, and humid ravines, 2750–3700 m.

Other specimens examined. MEXICO, Hidalgo, Mpio. de Real del Monte, Peñas Largas, cerca de Tezoantla, 2750 m, staminate, 12 Mar 1970, *Rzedowski 27135* (LL, US). This collection most closely matches the type. Mexico, Mpio. Ixtapaluca, Estación Experimental de Investigación y Enseñanza de Zoquiapan, 8 km al S de Río Frio, Cañada Temascatitla, ca. 200 m del Camino 4, hacia abajo, pistillate, 18 Mar 1979, *Vega Aviña 585* (F). This collection is only tentatively placed here because the leaves are too young for comparison with the type and the floral bracts are darker than *Rzedowski 27135*. Veracruz, Mpio. Calcahualco, glacier fed beginnings of Río Jamapa just upstream from where (impassable) road from Coscomatepec-Escola-Jacal crosses Río Jamapa on way to Miguel Hidalgo & Tlachichuca in Edo. Puebla, 5 km SW of Jacal, 3450 m, vegetative, 8 Jul 1982, *Nee & Diggs 24848* (F).

This species resembles *Salix geyeriana* Andersson so I would tentatively place it in Section *Cinerella* (*Vetrix*).

Salix endlichii Seemen, Repert. Spec. Nov. Regni Veg. 5:19. 1908. TYPE: MEXICO, Chihuahua, In den Tälern der westlichen Sierra Madre, 2250–2400 m, 16–17 Apr 1906, *Endlich 1225a, 1226* (syntypes, B, destroyed; duplicates not located).

Schneider (J. Arnold Arbor. 3:78. 1921) was unable to find the type collections at B before the willow collection there was destroyed. No duplicates have been located. The original description does not match any known American willow, although it resembles *S. cana*. It must remain uncertain until material matching the description is collected or duplicates of the syntypes surface. A brief description from the original follows.

Shrub to 1 m; leaves narrowly lanceolate, to 1.6 cm long, 0.3 cm wide, entire, glabrous, gray-green (glaucous?) on underside, petioles to 0.1 cm, stipules none; aments coetaneous, sessile, subglobose, to 0.7 cm long; stamens 2, filaments pubescent, nectary 1; capsules pubescent, stipe half as long as capsule, style short, nectary 1, floral bracts oblong, light brown with darker tip, sparsely crisp-puberulent and bearded.

Salix latifolia M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(4):344. 1843, non Forbes, Salict. Woburn. 235, t. 118. 1829. *Salix oxylepis* C. K. Schneid., Bot. Gaz. 65:34. 1918. TYPE: MEXICO, Veracruz, Fl. en Aout. bord des Ruisseaux à 12,500 pd Volcan D'Orizaba, Jun-Oct 1840, *Galeotti 70* (holotype: BR, lost; lectotype designated here, P!)

This somewhat deformed specimen is the same as *Salix paradoxa* Humb., Bonpl. & Kunth.

Salix pameachiana Barratt, Salices Amer. No. 16. 1840. TYPE: USA, Connecticut, "Middletown," staminate shoot, Apr 26, *Barratt s. n.* (lectotype designated here, NY!).

This material is the same as *Salix alba* L. representing an early naturalization.

Salix paradoxa Humb., Bonpl. & Kunth var. *ajuscana* C. K. Schneid., Bot. Gaz. 65:37. 1918. TYPE: MEXICO, [Federal District], La Cima de Ajusco, 3200 m, 21 May 1898, pistillate, *Pringle 6795* (lectotype designated here, GH!, photo A!; isolectotypes, A!, F!, MEXU!, NY!, RM!, US!).

This is merely a pubescent extreme of *Salix paradoxa*. The isolectotype at F is also the holotype of *Salix pringlei* Rowlee.

Salix rowleei C. K. Schneid. var. *cana* C. K. Schneid., Bot. Gaz. 65:34. 1918. TYPE: MEXICO, Federal District, La Cima de Ajusco, 3100 m, 16 Apr 1898, *Pringle 6794* (lectotype designated here, GH!, photo A!; isolectotypes, A!, MEXU!, RM!, US!).

Salix rowleei is merely a glabrous-capsuled form of *Salix paradoxa*.

Salix stipulacea M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10(4):343. 1843. TYPE: MEXICO, "Croît an bord du Rio Grande de Mextitlan," Ravins près Real del Monte, 5000, "Fl. en octobre," Nov–Apr 1840, *Galeotti 75* (holotype, BR, lost; lectotype designated here, P!).

This is similar to *Salix humboldtiana* Willd. and *Salix nigra* Marshall. The proper disposition must await detailed study.

Salix waghornei Rydb., Bull. New York Bot. Gard. 1:271. 1899. TYPE: Probably eastern CANADA, "Salix cordifolia Fl. Bor. Am." Torrey Herbarium, pistillate (lectotype designated here, NY!).
This is the same as *Salix arctica* Pall.

I thank Ronald Hartman for use of the facilities at RM, the curators of the cited herbaria from which specimens were borrowed, the curators of BR, CU, and L for searching for type material, and the staff at RM for assistance with loans.

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NOTES

OBSERVATIONS ON THE POLLINATION BIOLOGY AND FLOWERING PHENOLOGY OF TEXAN *MATELEA RETICULATA* (ENGELM. EX A. GRAY) WOODS. (ASCLEPIADACEAE).

Alexander Krings, Zilker Botanical Garden, 2220 Barton Springs Rd., Austin, TX 78746.

Although the pollination mechanisms of Asclepiadaceae have received considerable attention, the majority of research has focused on the genus *Asclepias* (e.g., Kephart, American Journal of Botany 68(2): 226–232, 1981; Willson et al., American Midland Naturalist 102:23–32, 1979; Willson and Price, Evolution 31:495–511, 1977; Willson and Rathke, American Midland Naturalist 92:47–57, 1974). As Liede (Madroño 41(4):266–276, 1994) points out, relatively few pollination observations have been made on other taxa and the majority of these have focused on Old World species (see also ASCLEPOL: http://www.uni-bayreuth.de/departments/planta2/research/Pollina /as_pol_d.htm). Only three studies of New World taxa besides *Asclepias* are known (e.g., *Fischeria*: Skutch, Brenesia 30:13–20, 1988; *Funastrum*: Kunze and Liede, Systematics and Evolution 178:95–105, 1991; *Matelea*: Liede, Madroño 41(4): 266–276, 1994) and none of Texan populations. In order to increase our depauperate understanding of Texan vining asclepiads, this study sought to: (1) identify the floral visitors of Texan *Matelea reticulata*, (2) track the vines' flowering phenology, and (3) analyze visitor activity based on pollinarium removal rates and pollinium insertion rates. The species was chosen due to its natural occurrence on our Garden grounds and to allow comparison with previously studied Mexican populations by Liede (Madroño 41(4):266–276, 1994).

A naturally occurring population of *Matelea reticulata* was studied in a *Quercus virginiana-Juniperus ashei* dominated forest patch on the grounds of Zilker Botanical Garden, Austin, Texas from 20 July–5 Aug 1999. The vines grew to 6 m into the canopy of a *Juniperus ashei* tree. On 20 July, inflorescences of the intertwining vines were labeled with small, cardboard labels. On 22 July 1999, insect visitors were observed from 09:30–12:00 and 14:00–16:30. Visitors were caught in a small, cylindric plastic container and killed by exposure to ethyl alcohol. The container could comfortably be held in one hand (5 cm diam. × 2.5 cm deep) and proved a more effective capturing device in the crowded canopy than standard insect nets. At least one representative of all visiting species was captured. Following the five hours of visitor observation, all open and senesced flowers of the tagged inflorescences were collected in a baseline harvest and preserved in 70% ethyl alcohol. These flowers were then analyzed under the microscope for pollinarium removal and pollinium insertion. From 23 July–5 Aug, newly opened flowers on the tagged inflorescences were marked on the abaxial petal surface with colored, water-resistant ink on a daily basis (between 15:00 and 17:30). A different color ink was used each day to allow tracking of flower longevity. Previously marked, senesced flowers were collected as newly opened flowers were marked. All collected senesced flowers were analyzed under a microscope for pollinarium removal and pollinium insertion. Captured insects were identified by the author and deposited at Zilker Botanical Garden.

Insect activity was sparse. Within a five hour observation period, only thirty-four floral visitation events occurred. However, the number of insect taxa and visitation events is potentially underestimated as the observation period did not extend to dawn or dusk and the capturing of insects may have interfered with visitation frequency. Nonetheless, separate anecdotal observations at least support a relative low frequency of visitation in the absence of capturing activity.

Visitors were flies, except for one wasp in the Chalcidoidea. The wasp was a frequent, active visitor, landing on the broad petals and moving toward the base of the staminal column to partake of the nectar. Minute in size, 1 mm or less, the wasp is not much bigger than a pollinium and thus unlikely powerful enough to dislodge an entire pollinarium. It was never observed near the upper portions of the staminal column where the corpuscula are displayed.

The fly visitors belonged to three families: Drosophilidae, Lonchaeideae, and Sarcophagidae. Pollinaria were found exclusively on the labella of the haustellum of the Sarcophagids. No pollinaria were found on flies in the other families—due to their small size (<3 mm), it is unlikely that they are active pollinators of *M. reticulata*. Only flies (Calliphoridae, Muscidae, and Tachinidae) were found visiting a Mexican population of *M. reticulata* (Liede, Madroño 41(4):266–276, 1994).

In contrast to the Mexican population of *M. reticulata* studied by Liede (Madroño 41(4):266–276, 1994), which bore inflorescences displaying no more than six open flowers simultaneously, vines of the present study bore inflorescences displaying no more than three open flowers simultaneously. In addition, a strong musky fragrance was detected throughout the study period at various times of day. No fragrance was detected in the population studied by Liede (Madroño 41(4):266–276, 1994).

The total number of open flowers reached a peak on 25 July with 48 open flowers and declined steadily thereafter (Fig. 1). Clearly the study period

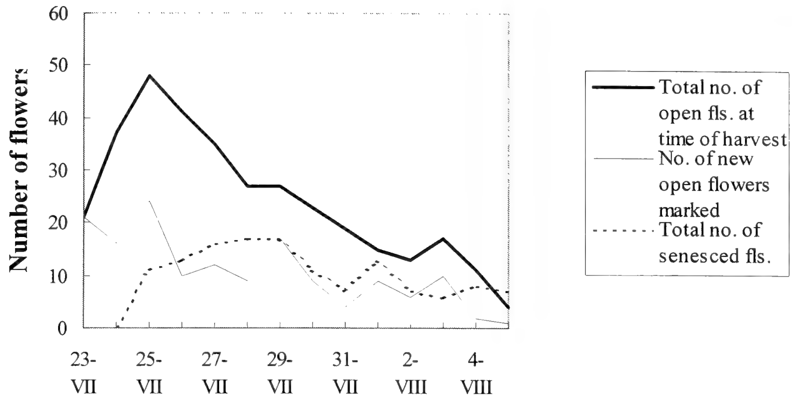

FIG. 1. Number of newly opened flowers, senesced flowers, and total open flowers per day of a Texan population of *Matelea reticulata* from 23 Jul–5 Aug 1999.

coincided partly with the end of the flowering of the population. By 9 Aug, no open flowers were displayed as all inflorescences (including the non-tagged) had senesced.

Floral longevity was short, as 43.84% of all flowers marked over the period from 23 July–4 Aug senesced after two days. Flowers senescing within two and three days account for 72.61% of all flowers. Almost nine percent of flowers were unaccounted for and probably eaten by Tussock moth caterpillars (Arctiidae) which were removed from the vines whenever detected.

The sparse insect activity was reflected in pollinarium removal rates. The average number of pollinaria removed per flower on the baseline flower harvest date of 22 July was 0.54 (Fig. 2A). The average number of pollinaria removed per flower in *M. reticulata* decreased over the study period from this baseline harvest high (Fig. 2A).

As found by Liede for Mexican *Matelea reticulata* (Madroño 41(4):266–276, 1994), and in contrast to studies on N. American *Asclepias* (e.g., Chaplin and Walker, Ecology 63:1857–1870, 1982; Willson and Rathke, American Midland Naturalist 92:47–57, 1974) pollinarium removal did not increase with umbel size ($r = -0.16$, $t = -2.59$, $P > 0.08$). Twice as many flowers had only one pollinarium removed (27.85%) as those that had two removed (12.66%). No flowers in any inflorescence size class had three or more pollinaria removed (Table 1). There was no significant difference between Liede (Madroño 41(4):266–276, 1994) and the present study in the number of flowers in all inflorescence size classes with one or two pollinaria removed ($P = 0.429$).

Figure 2B depicts the daily percentage of senesced flowers with removed pollinaria. The mean daily percentage of flowers in this class over the period from 25 July–1 Aug is 26.89% (SD = 13.50). In only one of the eight flowers not senescing until four days, had pollinaria been removed. Although over 1.5 times as many flowers senesced after two days than after three days, there is no significant difference in pollinarium removal rates between flowers in these senescence classes over the period of the study ($F_{0.95_{1,22}} = 0.02 < 4.30$, $P = 0.88$).

Not surprisingly based on the sparse insect visitation, pollinium insertion rates were also quite low (Fig. 2C). The peak daily pollinium insertion rate of 0.24 was achieved on 28 July. No inserted pollinia were detected in senesced flowers in eight of the fifteen days of study.

The average pollinarium removal rate from the baseline flower harvest of 0.54 pollinaria removed/flower (Figure 2A) is remarkably low compared to the previously reported 0.94 pollinaria removed/flower for Mexican *Matelea reticulata* (Liede, Madroño 41(4):266–276, 1994). Removal rates for other New World Asclepiads are considerably higher (e.g., Mexican *Funastrum* had 2.5 pollinaria removed/flower (Kunze and Liede, Systematics and Evolution 178:95–105, 1991) and N. American *Asclepias* had 3.6 pollinaria removed/flower (Lynch, Madroño 24:159–177, 1977). Weather could be a factor in the low pollinarium removal rates, but there is relatively little variability in Austin's climate in the summer months to drastically affect insect behavior. Although insect observation occurred a day after brief, scattered showers, temperatures quickly warmed to above 35°C and the day continued, as previous and subsequent days, to be characterized by sunny skies with occasional, scattered clouds. Perhaps, the annual drought conditions experienced from the end of June through the start of August could be a factor.

Another potential factor in the pollinarium removal rate could be proximity to edge. The population studied by Liede (Madroño 41(4):266–276, 1994) occurred entirely in open habitat, whereas the vines of the present study grew in a forest patch at least 5–7 m from any edge.

Proximity to edge could influence the visibility of flowers and thus potentially affect pollinator activity. Some flies, however, have been found to re-

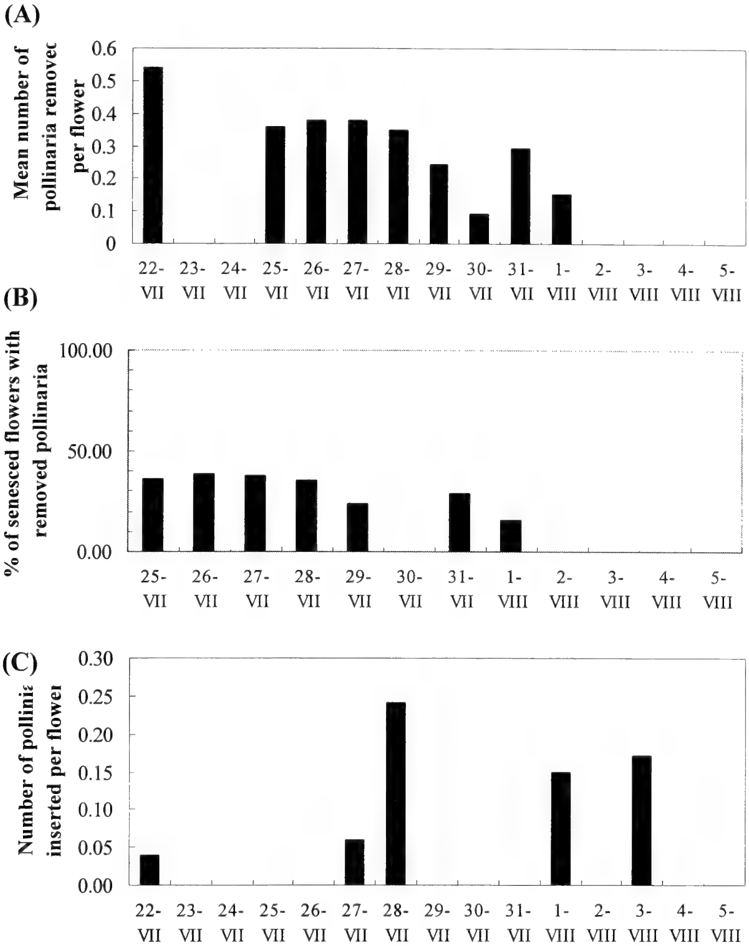

FIG. 2. (A) Pollinarium removal from flowers of *Matelea reticulata* over the period 22 July–5 Aug 1999. Both senesced and open flowers were analyzed from the baseline harvest of July 22. Subsequently only senesced flowers were analyzed. On July 23–24, no flowers had yet senesced, so none were analyzed. (B) Percent of senesced flowers with removed pollinaria (poll.) out of total number of senesced flowers over the period of 25 July–5 Aug 1999. (C) Pollinium insertion rates in *Matelea reticulata* from 22 July–5 Aug 1999. Both open and senesced flowers are included in the analysis for the baseline harvest 22 July. Only senesced flowers are analyzed from 23 July–5 Aug. No flowers senesced on 23 or 24 July.

spond more to olfactory than visual cues (Roy and Raguso, Oecologia 109:414–426, 1997). Interestingly, the scentless, highly visible Mexican population seems to have had higher pollinator visitation rates then the scented, "obscured" Texan population (or, perhaps, simply more effective pollinators?).

In addition, populations growing in full sunlight may produce more flowers (and thus potentially increase pollinator attraction) than shade-grown populations. Liede (Madroño 41(4):266–276, 1994) found an average of 2.24 flowers per inflorescence in Mexican *M. reticulata*, whereas the present study only found an average of 1.41 flowers per inflorescence in Texan *M. reticulata*.

To what extent the brief lifespan of individual flowers (72.61% senesced within 2–3 days) plays a role in pollinarium removal rates, also remains unclear. Unfortunately, no comparable flower longevity data could be found. Floral maintenance costs associated with water loss through floral transpiration and/or nectar production can be substantial (Ashman and Schoen, Nature 371:788–791, 1994; Nobel, Botanical Gazette 138:1–6, 1977) and could account for the brief flower lifespans. Certainly a longer lifespan would seem to increase the probability of insect visitation and thus pollinarium removal and pollinium insertion. A long flowering period would likewise increase the probability of insect visitation by lessening the effects of brief unfavorable conditions for pollinators (Willson and Rathke, American Midland Naturalist 92:47–57, 1974) and could thus potentially compensate for reduced individual flower longevity. Populations of this species generally flower from April through October (Correll and Johnston, Manual of the Vas-

TABLE 1. NUMBER OF FLOWERS OF *MATELEA RETICULATA* REMOVED ON 22 JULY 1999, IN FOUR INFLORESCENCE SIZE AND SIX POLLINARIUM (POLL.) REMOVAL CLASSES. Numbers in parentheses reported by Liede (1994). Numbers given for total pollinaria, pollinaria removed/inflorescence, and pollinaria removed/flower in the smallest inflorescence size class, have been corrected for the minor miscalculations in Liede (1994).

	Flowers/inflorescence				
	1	2	3	>3	No. of Flowers
No. of infl.	26 (11)	25 (39)	1 (17)	0 (5)	
Total flowers	26 (11)	50 (78)	3 (51)	0 (21)	79 (161)
Rem. poll./fl.					
0	15 (4)	31 (34)	1 (21)	0 (8)	47
1	9 (3)	13 (25)	0 (17)	0 (9)	22
2	2 (1)	6 (13)	2 (10)	0 (3)	10
3	0 (2)	0 (4)	0 (2)	0 (1)	0
4	0 (2)	0 (2)	0 (1)	0 (0)	0
5	0 (0)	0 (0)	0 (0)	0 (0)	0
Total poll.	13 (19)	25 (71)	4 (47)	0 (18)	
poll./infl.	0.50 (1.7)	1.00 (1.8)	4.00 (2.8)	0.00 (3.6)	
poll./fl.	0.50 (1.7)	0.50 (0.91)	1.33 (0.92)	0.00 (0.85)	

cular Plants of Texas, University of Texas Press, Dallas, 1979), but it remains unknown whether individual vines flower continuously for such a long period.

Although contrary evidence has been reported for *Asclepias* (Willson and Rathke, American Midland Naturalist 92:47–57, 1974), no support was found in either the present study or by Liede (Madroño 41(4):266–276, 1994) that pollinarium removal increases significantly with increasing inflorescence size in *Matelea reticulata* (Table 1). However, beyond concerns of potentially generally low visitation rates and very small inflorescence sizes (compared to *Asclepias*), a greater problem exists in that the investigative method may not be optimal for addressing such an issue. Data maybe skewed because the size of the inflorescence during the flower harvest may not accurately reflect its previous size—an obvious potential influence of pollinator activity. What if, for instance, a freshly opened and a senesced flower are collected from a two-flowered inflorescence. For the duration of its life, the senesced flower was the only open flower on the inflorescence. The freshly opened flower could have just opened that morning (before the harvest). For the duration of its brief life, it was the only open flower on the inflorescence. However, when harvested by the researcher, both will be considered belonging to the two-flower size inflorescence, eventhough at no point were two open flowers presented to visitors simultaneously. Although flower expansion was not observed on an hourly basis, the daily tracking of individual flowers in the present study supports the existence of such scenarios. The results of Liede (Madroño 41(4):266–276, 1994) and the present study, with regard to increased pollinarium removal with increased inflorescence size, are thus poor evidence for resolving the issue. It is recommended that future studies on the influence of inflorescence size be conducted through a more controlled experimental approach.

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CONSTANCEA, A NEW GENUS FOR *ERIOPHYLLUM NEVINII* (COMPOSITAE–HELIANTHEAE S. LAT.)

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ABSTRACT

A new genus, *Constancea*, for *Eriophyllum nevinii*, is erected in light of evidence that *Eriophyllum* is polyphyletic. *Constancea*, endemic to the southern Channel Islands of California, appears to be the sole representative of a lineage that diverged early in the history of either subtribe Baeriinae or the putatively-sister clade comprising most other $x = 19$ genera of helenioid Heliantheae (i.e., *Arnica*, *Eatonella* s. str., *Hulsea*, and *Venegasia*) plus Madiinae. Morphological characteristics of *Constancea* shared with other, closely related $x = 19$ helenioid lineages but rare or absent in the clade comprising *Eriophyllum*, *Pseudobahia*, and *Syntrichopappus* include well-developed petioles, phyllaries in more than one series and exceeding the number of ray florets, and pappus scales unequal or a longer pair opposite and ± equal.

Results of phylogenetic studies of helenioid Heliantheae lead me to conclude that *Eriophyllum* Lag. is not monophyletic. Based on rDNA trees, *E. nevinii* A. Gray, a subshrub endemic to the southern Channel Islands of southern California, appears to be more distantly related to other members of *Eriophyllum* sensu Constance (1937) than are *Pseudobahia* (A. Gray) Rydb., *Syntrichopappus* A. Gray, and, probably, all other members of Baeriinae Benth. (Baldwin and Wessa in press and in prep.). Mooring (1997) raised questions about the phylogenetic position of *E. nevinii* upon reporting chromosome counts for the species of $2n = 19$ II, a number not previously known for *Eriophyllum* or Baeriinae in general.

In a hypothetical phylogeny of *Eriophyllum* proposed by Mooring (1997), *E. nevinii* occupies a basal position in the group, from which taxa of lower chromosome number and, ultimately, of annual habit descended. Phylogenetic data from external and internal transcribed spacer sequences of 18–26S rDNA (Baldwin and Wessa in press and in prep.) together with chromosomal and morphological considerations lead me to conclude that *E. nevinii* is indeed distantly related to other members of *Eriophyllum*, including the morphologically and ecologically similar *E. staechadifolium* Lag. (the type species of *Eriophyllum*), and that the base chromosome number of all of Baeriinae may be $x = 19$. *Eriophyllum nevinii* appears to represent a basally divergent lineage either in Baeriinae or in the putatively-sister clade including almost all other $x = 19$ taxa in helenioid Heliantheae [i.e., *Arnica* L. (including *Mallotopus* Franch. & Sav. and *Whitneya* A. Gray), *Eatonella* A. Gray s. str., *Hulsea* Torr. & A. Gray, and *Venegasia* DC.] plus Madiinae Benth. sensu Carlquist (1959).

Morphologically, *Eriophyllum nevinii* possesses characteristics that are shared with one or more closely related $x = 19$ taxa or with pappose members of the Baeriinae genus *Monolopia* DC. [i.e., *M.* (*Lembertia*) *congdonii* (A. Gray) B. G. Baldwin], but are rare or absent in the clade comprising *Pseudobahia*, *Syntrichopappus*, and all other members of *Eriophyllum* sensu Constance (1937). For example, *E. nevinii* possesses well-developed petioles (as in at least some members of *Arnica*, *Hulsea*, and *Venegasia*), phyllaries in more than one series and exceeding the number of ray florets (as in *Hulsea*, *Venegasia*, and most species of *Arnica*), and pappus scales unequal or a longer pair opposite and ± equal (similar to pappi of *Eatonella*, *Hulsea*, and *Monolopia congdonii*).

On the basis of molecular, chromosomal, and morphological evidence, I propose a new genus for *Eriophyllum nevinii*. Other nomenclatural changes are necessary for members of the clade comprising *Pseudobahia, Syntrichopappus,* and *Eriophyllum* sensu Constance (1937) minus *E. nevinii* to provide a taxonomy of only monophyletic genera. Those changes must await completion of ongoing phylogenetic investigations (Baldwin and Wessa in prep.).

Constancea B. G. Baldwin, gen. nov.—TYPE: *Eriophyllum nevinii* A. Gray. ≡ *Constancea nevinii* (A. Gray) B. G. Baldwin.

A Heliantheae ceteris characteribus combinatis differt: habitu suffruticoso; foliis alternis petiolatis ≤ ca. 25 cm longis, laminis albo-tomentosis late ovatis plerumque bipinnatifidis; capitulescentiis corymbiformis capitulis confertis; involucris campanulatis ca. 3–5 mm diametris; phyllariis ca. 8–16 albo-tomentosis ca. 2 seriatis (numeris phyllariorum semper > numeris flosculis radiorum); flosculis radiorum 4–9, corollis flavis et laminis 2–3 mm longis; lobis corollarum flosculorum discorum 5; receptaculis epaleatis; cypselis atris; squamis papporum 2–6+, ± connatis basim, omnibus magnopere inaequalibus et irregularibus vel longiore pari opposito et ± aequali, omnibus enervis, <2.5 mm longis; $2n=19$ II.

Subshrubs, to ca. 1 (–2) m high. *Stems* decumbent, branched mostly near base, ≤ ca. 1 cm diam., densely white-tomentose, to glabrate. *Leaves* alternate, petiolate, crowded along proximal stem, ≤25 cm long; blades broadly ovate, pinnatifid to mostly bipinnatifid into linear lobes, slightly revolute, densely white-tomentose on both surfaces to glabrate adaxially, lobe apices obtuse. *Capitulescences* corymbiform, sparsely leafy near base, minutely and sparsely bracteate distally, lightly tomentose to glabrate, the heads crowded. *Peduncles* mostly ≤5 mm long. *Involucres* campanulate, ca. 3–5 mm diam. *Phyllaries* ca. 8–16, more than number of ray florets, in ca. 2 series, narrowly linear to oblong, oblanceolate, or somewhat irregular in shape, the inner narrower than the outer, ca. 4–6 mm long, white-tomentose, apices obtuse. *Ray florets* 4–9, pistillate, fertile, corollas yellow, tubes ca. 2–3 mm long and glandular-hairy to nearly glabrous, laminae 2–3 mm long, ca. 1–2 mm wide, shallowly 2–3-lobed. *Disc florets* ca. 10–27, bisexual, corollas yellow, 2–4 mm long, the tubes shorter than the narrowly funnelform throats, sparsely glandular-hairy, 5-lobed. *Anthers* yellow. *Style branches* papillose adaxially. *Receptacles* flat or convex, epaleate, glabrous. *Cypselae* dull, black, prismatic or flattened, narrowly clavate, ca. 2–3 mm long, with scattered, minute, appressed hairs (mostly on angles) or ± glabrate. *Pappus scales* 2–6+, basally connate, whitish to tawny, highly irregular and unequal or a longer pair opposite and ± equal, unnerved, apically acute or erose, <2.5 mm long. *Chromosome number* $2n=19$ II (fide Mooring 1997).

Distribution and ecology. Constancea is endemic to three of the southern Channel Islands of southern California (Santa Barbara Island, Santa Catalina Island, and San Clemente Island), where populations occur in coastal sage scrub and on exposed cliffs. *Constancea* has been negatively impacted by grazing of feral ungulates and appears on List 1B (plants rare, threatened, or endangered in California and elsewhere) of the California Native Plant Society (Skinner and Pavlik 1994).

Constancea nevinii (A. Gray) B. G. Baldwin, comb. nov.—*Eriophyllum nevinii* A. Gray, Synoptical Flora of North America, Ed. 2. Vol. 1. Part 2 (New York: Ivison, Blakeman, Taylor, and Co.): 452. 1886.—TYPE: USA, California, San Clemente Island, "on rocks overhanging the sea" (in protologue), Apr 1885, *Nevin* (Rev. J. C. Nevin) *and Lyon* (W. S. Lyon) *s.n.* (holotype, GH!).

Constancea is named for Professor Emeritus Lincoln Constance, world-renowned plant systematist and Umbelliferae expert, who conducted his dissertation research under Willis Linn Jepson on the systematics of *Eriophyllum* and judged *E. nevinii* to be "a beautifully distinct . . . species."

ACKNOWLEDGMENTS

I am especially grateful to the *Eriophyllum* experts John S. Mooring and Dale E. Johnson for generously encouraging me to work on molecular phylogenetics of *Eriophyllum* and relatives. I also thank Steve Junak, John S. Mooring, and the U. C. Berkeley Botanical Garden for providing plant material of *E. nevinii*; John L. Strother for assisting with the Latin diagnosis and offering advice; JLS and David J. Keil for reviewing the manuscript; Kristina A. Schierenbeck for expeditious editing of the manuscript; Bridget L. Wessa for molecular lab assistance; and Margriet Wetherwax for greenhouse assistance. This paper is based on research supported by the National Science Foundation (DEB–9458237), the Lawrence R. Heckard Endowment Fund, and Roderick Park and other generous Friends of the Jepson Herbarium.

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NOTEWORTHY COLLECTIONS

ARIZONA

CASTILLEJA NERVATA Eastwood (SCROPHULARIACEAE).—Santa Cruz Co., Sonoita Valley, 6300 ft, August 1874, *J. T. Rothrock 626* (F).

Previous knowledge. This is a widespread and characteristic species in the Sierra Madre Occidental of Mexico from Oaxaca to Sonora. *C. nervata* is known in the United States from only two collections in the Chiricahua Mountains and one each in the Rincon and Santa Rita Mountains of southeastern Arizona, where it was originally recognized by the synonymous name, *C. cruenta* Standley.

Significance. Recently located in the undetermined collections at F, this is the fifth and earliest verified collection of this species north of Mexico. This specimen, in flower and fruit, was probably collected either in the southern Santa Rita Mountains or in the northern Patagonia Mountains, where the elevations reach as high as 6300 ft.

OREGON

CASTILLEJA MENDOCINENSIS Pennell (SCROPHULARIACEAE).—Curry Co., Otter Point State Park, westernmost portion, in coastal scrub vegetation on flat upper portion and outer margins of coastal bluffs and sandstone headlands, ca. 42°25′N, 124°26′W, ca. 30–40 m elev., 27 July 1998, *M. Egger 1017* (OSC, WTU); Agate Beach, near Wedderburn, 14 June 1928, *L. Leach 1910* (ORE) (this sheet also contains one stem of *C. affinis* Hook. & Arn. ssp. *litoralis* (Pennell) Chuang & Heckard); Agate Beach, sloping secondary beach, 10–11 June 1929, *L. Leach 2540* (ORE).

Previous knowledge. Known only from the immediate coast in Mendocino and Humboldt Counties, California. An unpublished annotation by L. F. Henderson on *Leach 2540* names it as a new variety of *Castilleja latifolia* Hook & Arn., a closely related species of the central California coast. Field observations in 1998 indicate that the coastal bluff habitat of this species at Otter Point State Park is being subjected to severe erosional forces, at least partly due to frequent off-trail trampling by recreational users of the headlands portion of the park. Some specimens collected in thickly vegetated areas back from the immediate headlands show evidence of introgression with the sympatric *C. affinis* ssp. *litoralis,* which is widespread in similar habitat throughout the region.

Significance. First verified collections of this species for Oregon.

CASTILLEJA THOMPSONII Pennell (SCROPHULARIACEAE).—Wasco Co., Mt. Hood National Forest, above spur rd to Flag Point from U.S. Forest Service Rd 2730, on steep, open hillside in mixed coniferous forest, T3S, R11E, Sec. 7, ca. 1615 m elev., 15 July 1996, *M. Egger 779* (OSC, WTU); Near Frailey Point, above USFS Rd 2730, N of Jordan Creek on a bench over a basalt outcrop, south aspect, T2S, R11E, Sec. 33, 25 May 1982, *C. Wright s.n.* (OSC?).

Previous knowledge. Previously known from the Columbia River Basin and adjacent mountainous areas in Washington and from the Okanogan Valley of South-central British Columbia. The identity of the 1982 collection by Carolyn Wright was confirmed by Robert Meinke (personal communication 1996), but subsequent searches of *Castilleja* specimens found at OSC (author, R. Meinke personal communication 1996; S. Sundberg personal communication 1996) failed to locate this collection. Thus, the identity of the Wilson collection could not be independently confirmed for the present study.

Significance. First collections of this species for Oregon.

JALISCO, MEXICO

CASTILLEJA SPIRANTHOIDES Standley (SCROPHULARIACEAE).—Sierra du Nayarit (Territoire Huichol), no date given, *L. Diguet s.n.* (NY).

Previous knowledge. Known from several collections from the Sierra Madre Occidental in Sinaloa and from a single collection from southwestern Durango (M. González et al. 1693, TEX!, MICH!). The Gonzalez collection is the type of what field work and examination of types by the author indicates is the synonymous taxon, *Castelleja gonzalezii* G. L. Nesom (Phytologia 76(6): 465, 1994). While no date is indicated on it, the Diguet collection is most likely the earliest known of *C. spiranthoides.* The aging sheet bears an older style accession stamp with no accession number from NY, as well as a notation that the sheet was "presented by the Duke de Loubat through the American Museum of Natural History". Leon Diguet's field work in the Huichol region of Nayarit and Jalisco was primarily in the last decade of the nineteenth and the first decade of the twentieth centuries. The holotype and earliest previously known collection of *C. spiranthoides* (Jesus González Ortega 6896, F!) is from 1931.

Significance. Recently located in the undetermined collections at NY, this is the first collection of this species for the state of Jalisco, representing a southward extension of the known range of this species of approximately 120 km.

SINALOA, MEXICO

CASTILLEJA CHLOROSCEPTRON G. L. Nesom (SCROPHULARIACEAE). Mpio. De Concordia, upper Rio Presidio drainage, upper Arroyo San Diego watershed, ca. 2 km WNW of El Palmito and ca. 1.5 km in from trailhead along Hwy. 40 near km post 205.5, growing in forest duff on moderately steep slopes in relatively open pine-oak madrone cloud forest overlooking Rancho El Liebre Barranca, ca. 0.1–0.2 km upslope to the NE from "Alden's Rock" overlook, 23°34.5′N, 105°51′W, 2140–2170 m elev., 1 September 1997, *M. Egger 908* (UC, UCR, WTU).

Previous knowledge. Known from a handful of collections from the upper regions of the Sierra Madre Occidental from southwestern Durango northward into extreme southwestern Chihuahua (Cerro Mohinora).

Significance. First but not unexpected collection of this distinctive but inconspicuous species for the state of Sinaloa.

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REVIEW

Land of chamise and pines. Historical accounts and current status of Northern Baja California's Vegetation. By R. J. MINNICH and E. FRANCO VIZCAÍNO. University of California Publications in Botany. Vol. 80. University of California Press, Berkeley, CA. 166 p. Softcover $00.00 ISBN 0-520-09825-0.

Northern Baja California is a remarkable area rich in biotic diversity, and home to unique ecosystems and dramatic landscapes. It is of special interest to those who wish to understand the relation of humans to landscapes because of the contrast this relatively sparsely settled region provides with the more developed and intensively managed regions that lie across the international boundary. Minnich and Franco Vizcaíno's book is addressed to both these big issues. It provides a good overall discussion of the present vegetation but also explores the changes that have occurred by reviewing the early reports of the region and comparing these to what is found at the same sites today. In the penultimate chapter, a discussion of the stability of the vegetation is provided that brings together the historical evidence with what is known from current studies, and comparisons are drawn with the situation in the U. S.

The description of the vegetation is authoritative, and the included map will be a useful reference for anyone interested in the region. The vegetation classification adopted is similar to the Holland system used north of the border, and seems appropriate given the benefits and limitations of mapping from air photos.

I found the sections dealing with the historical accounts of most interest. They provide a detailed analysis of expedition reports and diaries from the 18th to 20th centuries. The authors are to be commended for a thoughtful approach to these. Unlike some others who have used historical sources, they are cautious in interpretation. For example, they note that *pasto*, generally translated into English as grassland, actually has a broader meaning that can include any area dominated by herbaceous vegetation suitable as forage for domestic animals. Similarly, they caution that all of the accounts were biased in that certain rare vegetation types were almost invariably noted (e.g., palm groves) whereas the abundant background vegetation types seem to have often been ignored. Despite the caution, there are interpretations with which one might quibble. Equating "couch grass, *Triticum repens*" with *Agrostis exarata* seems dubious. Likewise it seems a stretch to say that "*caña*" must be *Adenostoma fasciculatum*, and odd to decide that something described as "domestic bean" must have been *Lotus* rather than *Lathyrus*.

Here and elsewhere specialists may raise objections in detail, but most will probably buy the main conclusion which follows from the historical analysis: the explorers for the most part made reliable observations and these show that there has been no major change in the distribution of vegetation types in the 235 years since the first detailed accounts were written. Where oaks were reported in 1800, oaks are almost always present today; and hills that were covered with mescal and coastal scrub in 1769 still are—unless of course a city or highway has been built on top of them. The exception, discussed at some length in different parts of the book, is the change wrought by introduced species, especially the annual grasses. The authors find in Baja California the same depressing evidence of a loss of beauty and diversity that has been commented on for the Mediterranean-climate regions of alta California. Multi-colored floral vistas that elicited rapturous comment from travel-hardened colonial explorers are now dreary annual grasslands.

The conclusion that the landscape has been surprisingly stable is reinforced in the penultimate chapter. There can be little doubt that a large part of this consistency is attributable to the limited human population in the region, even up to the present. Large areas of the interior have never had permanent settlements, and data in the book show that in 1940 there were fewer than 80,000 people in all of Baja California. In the last 50 years the population has grown much faster, but even so, the 1990 population of 1.6 M is concentrated mostly along the coasts and in the cultivatable interior alluvial valley bottoms.

But one way a small population can have a large effect is through the use of fire, and fire is very much a part of the past and present of northern Baja California. Many now believe that North America at the time of first European contact was not a wilderness with pinpricks of human presence, but rather a garden cultivated by skilled landscape managers, with fire as their primary tool. Might this have been the case in northern Baja California? Though Minnich and Franco Vizcaíno do not directly address this question, their arguments about the stability of vegetation over time are incompatible with the skilled landscape manager hypothesis. They state that the vegetation is "self-regulating" and that "the rate at which vegetation burns is controlled more by successional processes and fuel buildup than by exogenous factors including ignition rates". They also argue that even where exotic species have invaded, they have replaced native species with broadly similar lifeforms, leaving the structural mosaic little changed outside of cities and areas subject to intensive agriculture.

This view should be unwelcome to the "cultivated garden" proponents, but would, if true, offer great comfort to the rest of us. According to Minnich and Franco Vizcaíno vegetation will be stable if we merely stand back and let nature and any arsonists who want to help it along take their course. Fires, whether caused by humans or lightning cannot destabilize the landscape. But, they argue, human intervention in the form of fire suppression puts everything at risk by intervening in the natural cycle of growth and destruction. This, they assert, is exactly what has happened north of the border. They do not suggest that wildland arson be decriminalized and fire suppressionists sent to jail, but this would seem a logical deduction from their theory.

I believe, however, that complacency about the self-regulating properties of vegetation is ill-advised, especially in a region formerly remote, but now experiencing population pressures. Studies elsewhere have underscored the importance of weather, something of which managers are acutely aware. In chaparral, a fire may fizzle on Friday but explode unmanageably on Monday if the weather changes. This demonstrates that the fire regime will likely change if there are changes in the patterns of coincidence of ignition events and weather-controlled propensity to burn. Unless a stand of vegetation is tested multiple times each year with an opportunity to burn, it cannot be assumed to be immune to fire. In a sparsely populated region, such testing is primarily by lightning. As populations grow, the number of human-caused ignition tests will also tend to increase, even if the laws discourage it. The result is that areas adjacent to dense human populations are likely to be burned more than they would have been prior to the increase in population. The resilience of chaparral can be counted on to prevent immediate and catastrophic change as a result of one or a few fires in most (but not all!) instances, but granting this does not rule out a pronounced cumulative effect.

Most troubling is the failure of the authors to allow one very important fact—the positive feedback between exotic invasion and fire—to influence their belief that fire is benign in Northern Baja California. This is odd, because they discuss the fire/exotic grass connection at several points, noting that aggressive burning will increase invasive grasses at the expense of native woody vegetation. But if this is true, it is hard to see how the authors can ignore the possibility that a *laissez-faire* attitude to fire may lead to widespread degradation of the regional vegetation as development and human populations increase. It is fervently hoped that the responsible agencies in Mexico will take the author's assurance of stability as a hypothesis to be evaluated and not a demonstrated scientific fact.

This book can be recommended for its description of the vegetation and detailed presentation of the historical record. The interpretations of vegetation dynamics, and especially the predictions of the future, however, are problematical and if adopted uncritically by land managers, could prove dangerous.

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Madroño, Vol. 46, No. 3, p. 165, 1999

ERRATA

Impact of a Non-Native Plant on Seed Dispersal of a Native by Cheryl H. Vanier and Lawrence R. Walker. Madroño Volume 46, No. 1, pp. 46–48.

When this article was printed, we inadvertently left out the following Acknowledgments and Literature Cited sections. We apologize to the authors for this error.

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A New Variety of Azorella diversifolia *(Apiaceae) from Southern Chile* by James C. Zech. Madroño Volume 44, No. 2, pp. 193–196.

Azorella diversifolia var. **antillanca** isotypes are deposited in CONC, GH, UC, and LP (Museo de La Plata not LB).

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ADULT SEX RATIO OF *PHORADENDRON JUNIPERINUM* IN TEN SEVERELY INFECTED *JUNIPERUS MONOSPERMA* IN NORTHERN ARIZONA

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ABSTRACT

The adult sex ratio of *Phoradendron juniperinum* A. Gray (juniper mistletoe) was determined on ten severely infected *Juniperus monosperma* (Engelm.) Sarg. (one-seeded junipers) near Flagstaff, AZ. The adult sex ratio of *P. juniperinum* has previously been reported to be male-biased. Although two trees did have a male-biased sex ratio, two trees had a female-biased sex ratio, and the overall sex ratio of this population of *P. juniperinum* was essentially 1:1. The sex ratio of adult *P. juniperinum* was also examined on the south, east, west, and north sides (quadrants) of each tree. There was a large amount of variation in the sex ratio by quadrant among individual trees. However, the overall sex ratio was not significantly different from a 1:1 ratio in the south, east, and north quadrant, while the west quadrant had a female-biased sex ratio. The sex ratio of adult *P. juniperinum* also varied by height when the data were pooled for all trees. Our results also indicate that the total number of *P. juniperinum* (adults and non-reproductive plants combined) was usually greater on the south sides of trees with fewer on the north sides. The reasons for the distribution of *P. juniperinum* within the crowns of host trees are discussed in relation to how this parasitic plant is disseminated.

Phoradendron juniperinum A. Gray (juniper mistletoe) is a dioecious parasitic flowering plant that commonly occurs on several different *Juniperus* spp. in the western United States (Wiens 1964; Hawksworth and Scharpf 1981). The sex ratio of several dioecious mistletoes has been reported to be female-biased (Showler 1974; Barlow and Wiens 1976; Wiens and Barlow 1979; Nixon and Todzia 1985; Wiens et al. 1996). However, *P. juniperinum* has been reported to have a male-biased sex ratio (Dawson et al. 1990a), as have many other dioecious plants (Willson 1981). In addition, Dawson et al. (1990a) reported that the male-biased sex ratio for *P. juniperinum* was statistically significant on the east and south sides of the 30 *Juniperus osteosperma* (Torrey) Little (Utah juniper) they sampled in southern Utah. Although they reported that there were more male plants on the north sides of the trees sampled, the male-bias was not statistically significant and, on the west sides of the trees, the sex ratio was essentially 1:1.

Wiens et al. (1996) reported a female-biased sex ratio for *Arceuthobium tsugense* (C. Rosend.) G. Jones (hemlock dwarf mistletoe) when it occurred on its principal host *Tsuga heterophylla* (Raf.) Sarg. (western hemlock). However, when this mistletoe occurred on other hosts, its sex ratio was essentially 1:1. Because Dawson et al. (1990a) only examined the sex ratio of *P. juniperinum* on one host (*J. osteosperma*), we undertook this study to determine if *P. juniperinum* also has a male-biased sex ratio when parasitizing a different host, *Juniperus monosperma* (Engelm.) (one-seeded juniper) Sarg. In addition, we investigated the distribution of male, female, and non-reproductive *P. juniperinum* within host trees, as did Dawson et al. (1990a).

MATERIALS AND METHODS

Our study site was located in the Coconino National Forest east of Flagstaff, AZ, in Sections 16 and 21 of Township 22 North, Range 9 East at elevations between 1920 and 2010 m. The study area was in the pinyon-juniper vegetation type (Barrett 1980). Soil in the area consisted of lava, ash, and volcanic cinders with low moisture and nutrient availability.

Ten *J. monosperma* were selected for sampling based on the following criteria: 1) greater than 4 m in height with rounded, uniform live crowns; 2) severe mistletoe infection in the live crown; 3) easily accessible from all sides; and 4) not shaded by other trees on any side of the tree's crown. An example of tree form and mistletoe infection severity is illustrated in Figure 1.

The study was conducted from 20 August to 2 October, 1999, when male *P. juniperinum* were at, or just past, anthesis so their gender could be easily determined. In late September and early October, when many males were past their peak anthesis, male plants could be distinguished from most adult female plants because female plants usually had maturing fruits. Those adult females that did not have maturing fruits still had mature female flowers which occurred on single segments and in pairs on

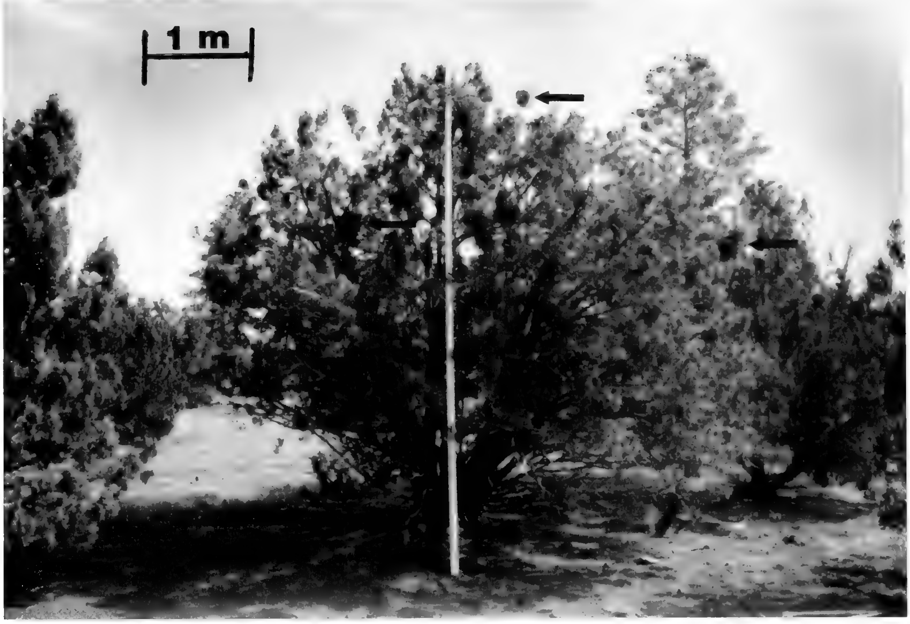

FIG. 1. Tree 5 illustrating the uniform crown and severe juniper mistletoe infection typical of the *Juniperus monosperma* sampled near Flagstaff, AZ. The three arrows indicate the location of obvious juniper mistletoe plants. Not all of the mistletoe plants can be seen in this figure as this tree had over 450 plants on it.

the distal ends of shoots (Wiens 1964). After peak anthesis adult male plants usually had old flowers still attached.

Whenever a plant could not be positively identified as male or female, it was classified as non-reproductive. Non-reproductive plants usually represented young plants that had not yet produced flowers (Dawson et al. 1990a), or adult plants that had no flowers or fruits on them. Adult plants without flowers or fruits could not be accurately sexed by their color, size, or habit. Although we searched each tree carefully for *P. juniperinum,* we undoubtedly did not sample every small, non-reproductive plant on each tree. Many non-reproductive plants were less than ten cm in height, occurred on small branches, and since they frequently were nearly the same color as *J. monosperma* foliage, were difficult to detect. In addition, dead *P. juniperinum* were not included in the sample because their sex could not be accurately determined. Non-reproductive plants were not recorded on Tree 1. After sampling the first tree and discovering that many plants were non-reproductive, we sampled non-reproductive plants on all subsequent trees.

For each tree, we recorded its sex (*J. monosperma* is dioecious), diameter to the nearest 0.25 cm around all the stems at the ground line of each tree (*J. monosperma* usually has multiple stems, Fig. 1), total height to the nearest 0.1 m, height to the bottom of the live crown to the nearest 0.1 m, and *P. juniperinum* rating. The mistletoe rating used was a modification of the 6-class dwarf mistletoe rating system (Hawksworth 1977). The system we used divided the live crown of each tree into three equal thirds and each third was rated as: 0—no *P. juniperinum* occurred in the third; 1—less than half of the branches traversing the third had one or more *P. juniperinum* within that third; or 2—more than half of the branches traversing a crown third had one or more *P. juniperinum.* Ratings for each third were then summed to give a total rating from 0 to 6 for each tree. This modification of the 6-class system was necessary because the habit of *J. monosperma* consists of multiple trunks emanating from the same general location on the ground and therefore, the same branch or trunk could occur in each third of the live crown. Thus, a branch could have a *P. juniperinum* infection in each of the thirds and contribute to the overall rating three times. In the 6-class dwarf mistletoe system each branch is only considered for a single third depending on its origin on the main trunk of the tree being rated. This works well for coniferous trees with a single trunk with radiating branches, but is not adequate for rating *J. monosperma* which has multiple main trunks.

Each tree's live crown was partitioned into north, east, south, and west quadrants by placing a series of surveying flags in the ground below the crown running at the following azimuths: 45, 135, 225, and 315 degrees (compass declination of 12.5 degrees East). Quadrants between the azimuths 315–45, 45–135, 135–225, and 225–315 degrees will be referred to as the north, east, south and west quadrants, respectively.

Individual *P. juniperinum* were cut from trees us-

TABLE 1. SEX, BASE DIAMETER, HEIGHT, HEIGHT TO LIVE CROWN, AND MISTLETOE RATINGS FOR TEN *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. [1] M—Male; F—Female. [2] See text for explanation of the mistletoe rating used.

					Mistletoe rating[2]			
Tree	Sex[1]	Base diameter (cm)	Height (m)	Height live crown (m)	Bottom third	Middle third	Top third	Total
1	M	51.8	7.1	0.4	1	1	2	4
2	F	68.1	5.5	0.3	1	2	2	5
3	F	53.3	4.5	0.3	2	2	2	6
4	F	62.5	4.6	0.3	1	2	2	5
5	M	93.7	5.7	0.1	1	2	2	5
6	M	61.5	4.8	0.3	1	2	2	5
7	M	80.0	4.9	0.4	1	2	2	5
8	M	66.5	4.6	0.3	1	2	2	5
9	F	69.6	4.7	0.1	1	1	2	4
10	F	64.8	4.1	0.1	1	1	2	4
Mean		67.2	5.1	0.3	1.1	1.7	2	4.8

ing hand pruners, pruning poles, or pruning saws. Before each plant was removed from a branch, its height in the tree to the nearest 0.1 m was determined using a 7.8 m long leveling rod graduated in 0.1 m intervals. In some instances, large central trunk branches with multiple *P. juniperinum* infections were cut at a measured height and placed on the ground. Before these branches were cut, marks were placed on each branch at 0.5-m intervals. The leveling rod was then placed along the branch on the ground, aligned with the correct heights, and used to determine heights of *P. juniperinum* as they were removed from the branch. After each *P. juniperinum* was removed from a tree branch it was carefully examined for male flowers, female flowers, or maturing fruits. A 10×-hand lens was used whenever necessary to determine male flowers from females (Wiens 1964). All observed *P. juniperinum* in a quadrant were removed and sexed before moving into the next quadrant of a tree. The sex (male, female, or non-reproductive), quadrant (N, E, S, W), and height of each *P. juniperinum* were recorded and transferred to an electronic spreadsheet (Microsoft Excel).

TABLE 2. NUMBER OF ADULT JUNIPER MISTLETOE PLANTS AND SEX RATIOS ON TEN *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. * Sex ratios that exhibit a significant sex bias. Chi-square statistics ($P \leq 0.05$).

Tree	Adult plants	Sex ratio (% females)	P
1	233	39*	0.001
2	1011	52	0.157
3	670	51	0.699
4	657	56*	0.003
5	452	49	0.510
6	541	48	0.414
7	937	57*	0.001
8	484	48	0.413
9	274	41*	0.004
10	165	44	0.312
Total	5414	51	0.211

A chi-square analysis was used to determine if the ratio of male to female *P. juniperinum* exhibited a sex bias. We determined this relationship by one-meter height classes and compass aspect (quadrants). As previously noted, Dawson et al. (1990a) reported a male-biased sex ratio for *P. juniperinum* on *J. osteosperma* and so we hypothesized that *P. juniperinum* would also have a male-biased sex ratio on *J. monosperma.* Dawson et al. (1990a) analyzed their data using a log likelihood ratio chi-square statistic (g values) while we used the chi-square statistic (p values). Since g is approximately distributed as chi-square, both methods commonly result in the same conclusions (Zar 1984), particularly when large samples are used. We used a p value of ≤ 0.05 to determine the existence of statistically significant differences.

RESULTS

Sex, base diameters, heights, and *P. juniperinum* ratings of the ten *Juniperus monosperma* sampled are presented in Table 1. Five of these trees were males and five were females. Diameters at the base of these trees ranged from 51.8 to 93.7 cm (mean 67.2 cm) and heights varied from 4.1 to 7.1 m (mean 5.1 m). *Phoradendron juniperinum* ratings ranged from 4 to 6 (mean 4.8). Most trees (7) had severe levels of infection in the upper two thirds of their live crowns. All of the trees, except Tree 3, had lower levels of infection (*P. juniperinum* ratings of 1) in the lower third of their live crowns.

We sampled 5414 adult plants (an average of 541 plants/tree) that could be accurately sexed on the ten trees and another 3154 non-reproductive plants (an average of 350 plants/tree) on nine of the ten trees. Of the 5414 plants we sexed, 2661 (49%) were males and 2753 (51%) were females. The difference in the number of male and female plants in our sample was not significantly different from the number expected for a 1:1 sex ratio; therefore, the sex ratio of *P. juniperinum* on the ten trees was essentially 1:1 (Table 2).

TABLE 3. NUMBER OF MALE AND FEMALE MISTLETOE PLANTS BY QUADRANTS FOR TEN *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. * Sex ratios that exhibit a significant sex bias. Chi-square statistics ($P \leq 0.05$). [1] M—Male; F—Female.

	Quadrant							
	South		East		West		North	
Tree	M[1]	F	M	F	M	F	M	F
1	51	29*	53	30*	3	3	30	24
2	166	202	105	123	127	123	85	80
3	63	78	106	106	87	96	74	60
4	86	107	107	133	37	60*	61	66
5	17	19	53	59	72	72	91	69
6	110	94	66	59	45	44	59	64
7	117	165*	99	63*	122	204*	68	99*
8	71	55	71	71	41	50	68	57
9	30	15*	50	28*	46	40	35	30
10	36	24	24	27	15	11	14	14
Total	747	788	734	699	595	703*	585	563

Six trees did not have a statistically significant difference in sex ratio from 1:1 (Table 2). Two trees had a male-biased sex ratio (Trees 1 and 9) and two trees had a female-biased sex ratio (Trees 4 and 7). Although two of the trees with female-biased sex ratios represented trees with large sample sizes (937 and 657 plants, respectively), more trees (6 versus 4 trees) had more male plants than female plants. Therefore, the overall sex ratio of *P. juniperinum* population on the ten trees did not have a statistically significant sex bias towards either sex. We did not observe any pattern in male or female bias based on the sex, base diameter, or height of the host trees (Tables 1, 2).

The distribution of male and female plants by quadrant is presented in Table 3. Although there were statistically significant differences in the sex ratios for some quadrants for several of the trees, the overall sex ratio of adult plants in the south, east, and north quadrants was essentially 1:1. The west quadrant had a statistically significant female-biased sex ratio (Table 3).

The total number of male and female plants, by one-meter height classes, is presented in Table 4. There was a highly statistically significant ($P \leq 0.01$) male-biased sex ratio in the lower crowns (1.1–2.0 m) and the very tops of two trees (6.1–7.0 m). However, only 229 and 63 plants, respectively, were sampled in these height classes. The upper crown of several trees had more female plants than male plants, and this resulted in a statistically significant female-biased sex ratio (52% female) in the 3.1–4.0 m height class which had a large sample of plants (2365).

TABLE 4. NUMBER OF MALE AND FEMALE MISTLETOE PLANTS BY ONE-METER HEIGHT CLASSES FOR TEN *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. * Sex ratios that exhibit a significant sex bias. Chi-square statistics ($P \leq 0.05$).

Height class (m)	Adult plants	Sex ratio (% females)	P
0.1–1.0	16	44	0.617
1.1–2.0	229	39*	0.001
2.1–3.0	1554	51	0.722
3.1–4.0	2365	52*	0.018
4.1–5.0	1055	52	0.186
5.1–6.0	132	47	0.486
6.1–7.0	63	33*	0.008
Total	5414	51	0.211

The distribution of adult plants by one-meter height classes for individual trees is presented in Table 5. The general pattern of infection was the same in all trees sampled. Generally, there were few adult plants in the top meter of each tree. Most of the adult plants were usually within the middle of the trees (Table 5). The lower two meters of each tree had the fewest numbers of adult plants. In contrast, the majority of non-reproductive plants were usually found below two meters in height in a tree (Table 6). The shift in distribution of non-reproductive plants, as compared to adult plants, to lower parts of the live crowns is evident when Tables 5 and 6 are compared. Most of the non-reproductive plants we observed in the lower crown (<one meter in height) were small plants <10 cm tall.

Table 6 also presents the distribution of *P. juniperinum* (male, female, and non-reproductive plants combined) by one-meter height classes. Most of the plants (59%) were in the middle to upper parts of the live crown of the host trees (2.1–4.0 m). Twenty-three percent of the plants were in the lower crown (<two meters in height), but most of these plants (89%) were non-reproductive.

The distribution of *P. juniperinum* (male, female, and non-reproductive plants combined) by quadrants is presented in Table 7. If we assume there should be the same number of *P. juniperinum* in each quadrant, there were a significantly greater number of plants in the south quadrant and a significantly lower number of plants in the north quad-

TABLE 5. NUMBER OF ADULT MISTLETOE PLANTS (MALE AND FEMALE COMBINED) BY ONE-METER HEIGHT CLASSES FOR TEN *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. — [1] No plants sampled because tree height was less than the height class (Table 1).

Height class (m)	Number of adult plants Tree number 1	2	3	4	5	6	7	8	9	10	Total
0.1–1.0	0	0	2	0	7	0	5	1	1	0	16
1.1–2.0	0	27	28	15	18	58	41	18	13	11	229
2.1–3.0	21	301	184	165	155	154	218	190	86	80	1554
3.1–4.0	40	340	397	341	144	246	462	186	135	74	2365
4.1–5.0	43	291	59	136	104	83	211	89	39	—	1055
5.1–6.0	56	52	—[1]	—	24	—	—	—	—	—	132
6.1–7.0	63	—	—	—	—	—	—	—	—	—	63
Total	223	1011	670	657	452	541	937	484	274	165	5414

rant than expected when the data for trees 2–10 were pooled. The number of plants in the east and west quadrants was not statistically significant from the expected value. When these data were examined for individual trees, some trees had significantly fewer plants than expected in the south quadrant and significantly more plants in the north quadrant, while others had significantly more plants than expected in the east or west quadrants. However, the distribution of *P. juniperinum* in individual trees followed an overall pattern of more plants in the south quadrant and fewer plants in the north quadrant. But a large amount of variation in this general pattern occurred among trees (Table 7).

DISCUSSION

Although Dawson et al. (1990a) reported a statistically significant male-biased adult sex ratio for *P. juniperinum* in southern Utah, we found that the adult sex ratio for the *P. juniperinum* population we sampled on *J. monosperma* in northern Arizona was essentially 1:1. Our results demonstrate the variation in sex ratio that can occur among individual trees. This tree-to-tree variation has been demonstrated in other studies of mistletoe sex ratio (Nixon and Todzia 1985; Mathiasen and Shaw 1998). Because of this tree-to-tree variation, a large sample of mistletoe plants should be sampled for dioecious mistletoe sex ratio studies and data should be analyzed using the results for the entire sample population and not on an individual tree basis. If a large number of adult mistletoe plants (e.g., >2000) is sampled and a statistically significant deviation from the expected 1:1 sex ratio is found, then specific genetic, physiological, and/or environmental mechanisms for the sex ratio bias may be in operation. However, Dawson et al. (1990a) only sampled a total of 466 adult plants on thirty *J. osteosperma* in their study of *P. juniperinum* sex ratio. This represents an average of approximately 15 plants/tree. We sampled over 5400 adult plants, an average of over 500 adult plants per tree, and found that although the sex ratio of *P. juniperinum* varies among individual trees, the overall sex ratio of this *P. juniperinum* population did not differ significantly from a 1:1 ratio.

Dawson et al. (1990a) also reported a significantly male-biased adult plant sex ratio for plants occurring at a height of 3–4 m in the *J. osteosperma* they sampled. We also found significant differences in sex ratio for adult *P. juniperinum* at different heights within host trees, but the sex bias varied by height class. At 3–4 m in height, the adult sex ratio in the trees we sampled was significantly

TABLE 6. NUMBER OF NON-REPRODUCTIVE MISTLETOE PLANTS BY ONE-METER HEIGHT CLASSES FOR NINE *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. —[1] No plants sampled because tree height was less than the height class (Table 1). [2] Male, female, and non-reproductive plants combined. Includes Tree 1 data from Table 5.

Height class (m)	Number of non-reproductive plants Tree number 2	3	4	5	6	7	8	9	10	Total	All plants total[2]	% of all plants
0.1–1.0	9	142	11	8	72	174	5	11		436	452	5
1.1–2.0	143	358	104	41	184	386	29	38	4	1303	1532	18
2.1–3.0	60	87	81	22	82	174	41	42	20	610	2164	25
3.1–4.0	32	114	57	16	82	118	41	82	21	559	2924	34
4.1–5.0	33	23	18	18	23	65	9	38	17	227	1282	15
5.1–6.0	9	—[1]	—	10	—	—	—	—	—	19	151	2
6.1–7.0	—	—	—	—	—	—	—	—	—	—	63	1
Total	286	724	271	115	443	917	125	211	62	3154	8568	100

TABLE 7. NUMBER OF MISTLETOE PLANTS (ALL CLASSES) IN EACH QUADRANT FOR NINE *JUNIPERUS MONOSPERMA* SAMPLED NEAR FLAGSTAFF, AZ. * Significant deviation from an expected equal distribution of plants in each quadrant. Chi-square statistics ($P \leq 0.05$). [1] Expected value assumes an equal distribution of plants in each quadrant.

	Quadrant					
Tree	South	East	West	North	Total	Expected[1]
2	436*	274*	332	255*	1297	324
3	378*	352	380*	284*	1394	349
4	285*	367*	110*	166*	928	232
5	45*	127	193*	202*	567	141
6	372*	234	162*	216*	984	246
7	679*	324*	598*	253*	1854	464
8	178*	173*	103*	155	609	152
9	88*	149*	145*	103*	485	121
10	67	74*	32*	54	227	57
Total	2528*	2074	2055	1688*	8345	2086

female-biased instead of male-biased. However, in other height classes within our trees (2.1–3.0 and 6.1–7.0 m) we found a significant male-biased sex ratio (Table 4). Because Dawson et al. (1990a) only sampled 466 adult plants, their sample sizes for the height classes they examined were correspondingly small. For example, in the height class with the male-biased sex ratio they had a sample size of 129 adult plants. We also had relatively small sample sizes for the two height classes demonstrating a male-biased sex ratio (229 and 63 plants, Table 4). We conclude that these sample sizes are not large enough to validate a sex bias in these height classes. However, we had a large sample size (2365 plants) for the height class with a female-biased sex ratio (3.1–4.0 m). Therefore, significantly more female plants than male plants occurred in some parts of the crowns of the *J. monosperma* we sampled. A similar situation has also been reported for *Arceuthobium tsugense* in the lower crowns of *Tsuga heterophylla* (Wiens et al. 1996; Mathiasen and Shaw 1998). However, the 3.1–4.0 m height class actually represents the upper crowns of most of the *J. monosperma* we sampled (Tables 1 and 4). The female-biased sex ratio in the upper crown of many of the trees we sampled may be the result of greater longevity of female *P. juniperinum* (Wiens et al. 1996; Nixon and Todzia 1985; Mathiasen and Shaw 1998). However, we have no data to support this argument because we did not age the *P. juniperinum* we sampled.

Dawson et al. (1990a) initially hypothesized that the east side of host junipers should be the most favorable locations for *P. juniperinum* if carbon and water relations are important parameters influencing the micro-distributions of male and female *P. juniperinum*. They reported that *P. juniperinum* sex ratios were most male-biased on the east sides of the *J. osteosperma* they sampled, but females were more common on the west and north sides of their trees. They considered these latter exposures to be less favorable sites for female *P. juniperinum* because they assumed female plants have a higher reproductive cost than males and that these exposures are not as favorable to energy or water balance. Our results indicate that there are not significantly more male or female *P. juniperinum* on the east sides of host trees. We also found a significantly higher number of female *P. juniperinum* than males on the west sides of the trees we sampled. However, assuming that we can expect the same number of plants (males, females, and non-reproductive) on each side of severely infected trees, the overall number of *P. juniperinum* was not significantly greater on the west or east sides of the trees. However, the number of plants was significantly greater on the south sides and the north sides had significantly fewer *P. juniperinum*. Because *P. juniperinum* may derive a significant amount of its carbon, water, and minerals via xylem sap (Marshall and Ehleringer 1990), there is no reason to expect that *P. juniperinum* should occur in locations most favorable to their energy or water balance. Our results, and those of Dawson et al. (1990a, b) and Marshall et al. (1993), support this conclusion.

Although we did find variation in the number of *P. juniperinum* by quadrant, we do not feel these differences are the result of physiological adaptations of *P. juniperinum* to environmental conditions. An examination of our data for individual trees indicates quadrants often had significantly greater or fewer numbers of plants than an equal distribution (Table 7).

Because of this variation, we contend that adult *P. juniperinum* gender data should not be grouped by quadrants for statistical analysis of sex ratios. Therefore, we contend that it is more appropriate to use male and female plant counts for the entire sample population, as we did for the ten trees we sampled, when determining the sex ratio for a *P. juniperinum* population. Because we did not detect a statistically significant sex-bias for the *P. juniperinum* population we sampled on *J. monosperma* using a large sample of over 5400 plants, we cannot conclude that specific genetic, physiological, and/or environmental mechanisms are operating to cause a sex ratio bias in this population. We propose that the distribution of *P. juniperinum* within host trees is a result of how *P. juniperinum* is disseminated.

Seeds of *Phoradendron* are primarily disseminated among trees by birds (Sutton 1951; Kuijt 1969; Scharpf and Hawksworth 1974; Hawksworth and Scharpf 1981; Calder 1983). Avian vectors of *Phoradendron* spp. have been observed to perch or feed frequently at the same location on trees (Cowles 1936; Crouch 1943). Because these vectors could then defecate seeds they have consumed at these locations, this would suggest that more infections should occur directly below frequented perches. For instance, if birds consistently land on the south side of juniper trees during the winter months when the *P. juniperinum* fruits are mature, because of exposure to greater solar insolation, then this could explain why we found more *P. juniperinum* on the south sides of the trees we sampled.

Although birds (e.g., Western bluebirds, Townsend's solitaires, and American robins) have been observed eating *P. juniperinum* seeds and are undoubtedly involved in seed dissemination among host trees (Gehring and Whitham 1992), no investigations of within-tree dissemination have been completed for *P. juniperinum.* It has usually been assumed that within-tree intensification occurs because birds are attracted to mistletoe-infected trees, spend long periods of time feeding on mistletoe fruits, and hence, defecate mistletoe seeds on the same tree (Hawksworth and Scharpf 1981). This pattern has been reported for the *Phoradendron californicum* Nutt. (desert mistletoe) (Cowles 1936). Cowles (1936) also reported that large accumulations of *P. californicum* seeds occur directly beneath perches on host trees frequently used by the birds responsible for seed dissemination of *P. californicum.*

Although we did not observe accumulations of *P. juniperinum* seeds in the host trees we sampled, we did observe many individual *P. juniperinum* seeds scattered on *J. monosperma* branches we had pruned from trees. Some of these seeds had bird feces on them, but many had no indication of bird dissemination. Many of these seeds occurred on small host branches less than five mm in diameter. Because many of these seeds were on small branches at the edge of the crown, not directly below a probable perch for a vector, it is unlikely they were bird-disseminated. If these seeds were bird-disseminated, then it would have to be a case of "fly-over:" birds leaving trees defecated seeds and these seeds landed on the tree and adhered to the small branches. Therefore, the actual role played by avian vectors in the within-tree dispersal of *P. juniperinum* needs further research.

Another possibility is that many of the seeds we observed on small branches represent self-dispersal by gravity and/or rain and wind. Female *P. juniperinum* produce hundreds of fruits. Some of the mature fruits not eaten by birds could fall through the crown of the host tree or seeds may fall from over-mature fruits. Since the fruits and seeds of the *P. juniperinum* are sticky (particularly the seeds), self-dispersed fruits and seeds are certainly capable of adhering to branches and foliage as they fall through the crown. Self-dispersal by gravity is not thought to be a principal means of seed dispersal for true mistletoes (Calder 1983; Liddy 1983). But a few investigators have postulated this means of dissemination for some mistletoes (Blakely 1922; McLuckie 1922) and the species of *Korthalsella* in New Zealand are primarily self-dispersed by gravity and rain (Stevenson 1934). We hypothesize that the initial location of infection in junipers greatly influences where subsequent infections will occur within individual trees because we propose that self-dispersal of *P. juniperinum* is more common than previously believed. Therefore, which side and at what height avian vectors of *P. juniperinum* tend to perch for feeding, observation, or hiding on host trees will directly influence the distribution of subsequent within-tree infection. Although we believe self-dispersal is a principal means of within-tree dissemination for *P. juniperinum,* further research is needed to test this hypothesis.

Birds initiate many new infections in the upper crown of host trees, because they tend to perch near the tops of trees (Cowles 1936; Hawksworth and Scharpf 1981; Gehring and Whitham 1992). Infections then spread to the middle and lower crown by self-dispersal mechanisms and some subsequent bird dissemination from the same tree and other infected trees may occur. The large number of small, young, non-reproductive plants in the lower crown of the host trees we sampled supports our hypothesis of a "top-down" spread of *P. juniperinum* infections by self-dispersal. Dawson et al. (1990b) also hypothesized that there is a great amount of self-dispersal within host trees by *P. juniperinum,* but they called this process "intra-tree-dispersal."

Most of the *P. juniperinum* were found in the middle to upper crowns of the host trees and these were primarily adult plants. In contrast, most of the non-reproductive plants were found in the lower crown. This pattern is probably the result of the host tree's crown structure and within-tree self-dispersal of *P. juniperinum.* The crown structure of *J. monosperma* usually has its greatest branch and foliage biomass at 2–4 m above the ground (Born and Chojnacky 1985). This greater biomass provides more surface area on which *P. juniperinum* seeds can adhere and germinate. Therefore, more infections, and hence more plants, should occur in this region of greater crown biomass as our results and those of Dawson et al. (1990a, b) demonstrate.

We plan to sample additional severely infected *J. monosperma* at other locations to determine if other *P. juniperinum* populations have a 1:1 adult sex ratio on this host. We also plan to expand this research to include a determination of the sex ratio for *P. juniperinum* populations on *J. osteosperma* in northern Arizona. However, we now hypothesize that if a large number of *P. juniperinum* is sampled from severely infected *J. osteosperma,* the overall sex ratio will be essentially 1:1 as it was for the population of *P. juniperinum* we sampled on *J. monosperma* in this study.

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PREDICTABILITY OF PRIMARY SUCCESSIONAL WETLANDS ON PUMICE, MOUNT ST. HELENS

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ABSTRACT

This study describes wetland vegetation developing on young volcanic surfaces at Mount St. Helens. Canonical correspondence analysis (CCA) revealed that habitat types reflecting moisture regimes were the best predictors of species composition and that elevation and geographical position were also significant predictors. Explained variation was significant and had increased from 19% to 31% in the five years since these wetlands were first sampled. Ten community types derived by TWINSPAN were cohesive when mapped in the CCA space. They represent more developed versions of community types previously identified in the study area. Understories of plots with over 70% *Salix* cover were internally more similar than those with less than 10% *Salix* cover, suggesting that biotic effects may be reducing variation. Similarity among plots connected by rapidly moving water was higher than that among plots supported by seeps and among drier plots. This suggests that dispersal limitations continue to influence understory species composition in isolated vegetation. The results of this study suggest that wetland vegetation is beginning to demonstrate deterministic effects due to competition and stronger coupling to moisture regimes.

Wetlands forming on newly emplaced substrates are unusual. Those forming on Mount St. Helens offer an opportunity to test basic hypotheses about community assembly. Davey and Rothery (1993) proposed that assembly in Antarctic sinkholes was stochastic, but vegetation had not developed sufficiently there to determine the long-term effects of chance establishment. Motzkin et al. (1999) demonstrated that forest development in New England was controlled largely by unique historical factors. Fort & Richards (1998) suggested that the lack of seeds in a barren playa inhibited succession, and Fastie (1995) demonstrated that dispersal strongly affected the course of primary succession in glacier valleys. There are no long-term studies of wetland formation on primary substrates, so the situation on Mount St. Helens provides a unique opportunity to explore the potential transition from a stochastic assembly to vegetation controlled by more deterministic factors (cf. Walker 1993, 1999).

Colonization of newly formed substrates requires physical facilitation (Bjärnason 1991; del Moral 1993a) and eventual colonization (Kalliola et al. 1991; del Moral and Bliss 1993). If a site is sufficiently isolated, limited dispersal produces initially variable vegetation (Wood and del Moral 1988; Clarkson 1990; del Moral 1993b; del Moral and Grishin 1999). Titus et al. (1999) studied wetlands established after the 1980 eruption of Mount St. Helens on the Pumice Plain. They concluded that similar sites might develop different plant communities due to stochastic effects. They also found only weak interactions between environmental factors and species composition. Developing dominance was predicted to reduce variation between sites by altering the competitive environment and by reducing habitat variation (del Moral 1999; Dlugosch and del Moral 1999).

This study centers on a subset of the primary wetlands examined by Titus et al. (1999). The purposes are to determine if increasing *Salix* dominance has reduced floristic variation and whether links between vegetation and the environment have developed. Wetland vegetation has developed rapidly, so it is here that biotic factors should first become apparent on pumice. Earlier studies on Mount St. Helens suggested that homogeneity increases as species expand from the site of their initial establishment (del Moral 1998). However, there is as yet scant evidence that dominance reduces heterogeneity in early primary succession on Mount St. Helens. The relationship between the woody species and within-community variation was used to explore the putative shift from stochastic to deterministic control of vegetation. I will describe the relationships between species and their environment and explore the evidence that vegetation is responding deterministically to environmental or biotic factors.

METHODS

Study area. All wetlands were on the Pumice Plains of Mount St. Helens between the south shore of Spirit Lake and the lower slope of the cone. A wetland was defined by the presence of saturated soils during July. Elevations ranged from 1035 m to 1340 m. Plots were established as close to sites sampled by Titus et al. (1999) in 1993 and 1994 as could be determined from his map. Of the 79 plots sampled in this study, at least 68 were floristically similar to and within a few meters of sites studied by Titus et al. (1999). However, direct comparisons were not possible because I could not relocate the plots exactly. The factors of slope and aspect used in that study were not used, but were replaced by elevation, erosion and geographic position variables that incorporated the potential variation.

Environmental data. Each plot was located using a global positioning system device and the positions placed on a topographic map. Positions were divided into five categories in two dimensions each (rotated 30° from true north). Elevations were divided into nine segments with approximately equal numbers of plots. Erosion was determined in three categories: sediments being removed, little erosion, or sediments being deposited. Tsuyuzaki et al. (1997) showed that erosion strongly influenced seedling survival.

Composites of five subsurface soil samples were obtained from each plot between 2 and 8 cm. Soils were dried at 105°C. Texture was estimated by sieving 100 g of each sample through 2 mm, 250 μm and 63 μm screens to form four fractions (gravel, coarse sand, sand, and fines). Soil pH was determined from a 1:1 soil paste of a 50 g subset of each sample. Organic matter was determined from a 20 g subset by loss on ignition at 400°C after 24 h.

Habitats were assigned to one of five categories: rapidly moving spring-fed streams (Spring), slow, low volume seep-fed courses (Seep), snow-fed stagnant trickles (Stagnant), habitats isolated from moving water (Isolated), and drier sites (Drier). Both springs and seeps remain active throughout the growing season. Stagnant habitats are low-gradient sites that often dry out during late summer. Isolated wetlands form in depressions that may be supported by ground water. Drier sites were either alluvial, with little to no stream flow, or rocky and narrow.

Vegetation sampling. Sites were sampled during July and August 1998 using 5 by 20 m plots established within the wetland. Sites were selected using a map of previously sampled sites and composition compared to field data collected by Titus et al. (1999). Woody species cover was determined directly over the whole plot by visual estimate. Mean herb layer cover was determined from five 1-m^2 quadrats placed regularly along the long axis of the plot adjacent to any surface water. R. N. Fuller and I sampled the first 20 plots together to ensure comparability in cover determinations and species identification. Thereafter, we each sampled plots independently, but calibrated our determinations frequently. Species not sampled but within the 5 by 20 m plot were given a value of 0.1%.

Vascular plant nomenclature follows the Integrated Taxonomic Information System (found at: www.itis.usda.gov). Two wetland mosses were sampled and could be distinguished in the field. Based on Vitt et al. (1988), photographs and consultation with Paul Yurky (personal communication), the two dominant mosses were identified as *Philonotis fontana* and *Brachythecium* sp. (either *B. rivulare* or *R. frigidum*), widely distributed highland mosses. *Cratoneuron* spp. are found along streams in this area, but were not sampled. Upland mosses encountered on dry margins of some samples included *Racomitrium* spp., *Polytrichum* spp. and *Oligotrichum.* Species were assigned to one of five wetland indicator categories based on Reed (1988) to assess the degree to which communities reflected wetland conditions. Hydrophytic species are defined as those that always (obligate), usually (facultative wetland) or often (facultative) occur in wetlands. Species that seldom (facultative upland) or rarely (upland) occur in wetlands suggest dry conditions. Nonvascular plants reported here are assumed to be hydrophytic based on their occurrence in saturated soil.

Classification. The plots were classified with two-way indicator species analysis (TWINSPAN; Hill and Gauch 1979), comparable to the previous study (Titus et al. 1999). I used cut-levels of 0, 2, 5, 10 and 20%, five divisions and deleted species with fewer than four occurrences (see McCune and Mefford 1997 for details.)

Indirect ordination. Patterns within the data were sought by detrended correspondence analysis (DCA; Hill and Gauch 1980). I used untransformed percent cover, deleted species with fewer than four occurrences and down-weighted species whose frequency was less than 20%. Axes were rescaled and divided into 26 segments for detrending. Nonmetric multidimensional scaling (NMS; Minchin 1987) gave similar results and is not reported. NMS showed that the matrix was three-dimensional. I used a multiple regression of the environmental values to predict DCA axis scores and to provide an estimate of their relationship to species patterns.

Direct ordination. I used canonical correspondence analysis (CCA; McCune and Mefford 1997) to evaluate relationships between environmental factors and species cover. CCA determines the least squares linear regression of environmental variables on plot scores determined by correspondence analysis. New plot scores are calculated by a multiple regression of the environmental scores. I used eigenvalues, Pearson correlations between species and environmental axes and correlations of variables to each axis to describe the results. I used t-values associated with the regression coefficient of environmental factors using CANOCO 4.0 (ter Braak and Šmilauer 1998) only to help assess the importance of each variable rather than to test hypotheses. Monte Carlo simulations (n = 1000) were used to assess significance of eigenvalues and of species-environment correlations.

These continuous variables were used: elevation, erosion, soil pH, percent organic matter, gravel,

TABLE 1. SPECIES COMPOSITION OF PRIMARY WETLANDS. Species listed as determined by TWINSPAN two-way table. Species values in bold indicate 100% frequency. t ≤ 0.1% cover. Less common species are omitted. "Wet" indicates the wetland indicator value of the species: OBL (obligate, always in wetlands); FACW (facultative wetland, usually in wetlands); FAC (facultative, indifferent to wetland conditions); FACU (facultative upland, usually not in wetlands); and UPL (upland, rarely in wetlands). Numbers in parentheses after Community Type designation are the number of samples in the CT.

		Percent cover in community type									
Species	Wet	A (3)	B (9)	C (7)	D (15)	E (12)	F (6)	G (7)	H (8)	I (7)	J (5)
Aruncus dioicus	FACU		**4.1**							t	
Luzula parviflora	FAC		1.8		t	t				t	
Epilobium luteum	FACW	**8.1**	t			0.3					
Lupinus latifolius	UPL		1.9		1.2	t					
Hieracium albiflorum	UPL		t		0.1	0.1					
Mimulus lewisii	FACW		1.0	0.4	0.2	**6.4**	0.7				
Epilobium minutum	FACU	t	t	0.3	0.1	t	t	t			
Agrostis scabra	FAC			t	0.4				t		
Achillea millefolium	FACU				0.1	0.5	t	t			
Agrostis pallens	UPL				03	0.4		t			t
Marchantia polymorpha	FACW	1.3	t	0.3	0.2	8.7	5.9	0.6	0.7		
Philonotis fontana	FACW	**42.4**	2.1	**5.0**	**6.9**	**26.5**	6.4	2.1	4.0	t	t
Alnus viridus	FACW	3.3	3.3	0.5	1.3	0.8	0.2	t	0.4	t	
Epilobium angustifolium	FACU	**4.6**	5.8	0.9	0.1	5.2	t		0.2	t	11.8
Petasitis frigidus	FACW	2.8	0.5	0.3	t	1.0			0.4		
Brachythecium sp.	FACW			1.6	2.1	8.8	**34.6**	**10.5**	3.3		
Lupinus lepidus	UPL			t	**0.7**	0.5	t	0.1	t	t	t
Anaphalis margaritacea	UPL		2.3	0.7	**0.7**	1.4	0.1	0.1	0.1	0.1	0.3
Carex mertensii	FACW		**3.2**	1.1	0.5	**1.0**	0.5	**0.8**	0.4	0.3	
Carex microptera	FAC		0.4	t	t	t	t	0.1			
Agrostis exarata	FACW	t	0.8	0.5	**0.2**	0.9	0.1	0.1	1.1	0.5	0.9
Hypochaeris radicata	UPL		1.2	0.3	**0.2**	0.4	t	**0.5**	0.5	0.1	1.2
Salix stichensis	FACW	**92.7**	**48.4**	**36.1**	**11.7**	**50.3**	**25.3**	**21.2**	**20.4**	**46.8**	**4.3**
Juncus mertensianus	OBL		0.1		0.1	0.5	2.2	0.1	1.2		
Calamagrostis canadensis	FACW		0.1	**1.1**	0.1	0.8				0.4	0.6
Epilobium cilatium	FACW		0.4	**11.7**	**0.6**	**1.9**	**0.7**	**5.8**	**2.0**	0.1	**0.8**
Equisetum arvense	FAC	**2.5**	2.9	0.6	0.3	0.2	0.6	2.4	**19.8**	**18.9**	4.9
Juncus ensifolius	FACW				t	0.1	4.8	**4.3**	**2.4**	0.5	0.7
Juncus bufonius	FACW					0.2	0.5	**2.6**	**7.2**	0.7	**12.5**
Typha latifolia	OBL		t					0.1	1.7	0.1	**15.3**
Eleocharis macrostachya	OBL								4.9		0.1
Juncus articulatus	OBL						0.7	**4.5**	**2.0**	0.1	0.4

coarse sand, sand, and fines (silt and clay). In addition, the X and Y coordinates, in five geographic categories along northwest to southeast and northeast to southwest transects, were used. As described above, five categorical variables were used to characterize the habitats: spring, seep, stagnant, isolated and drier. Categorical values were treated as a set of binaries (ter Braak 1986). In order to avoid high variance inflation values (which occur when a set of variables are internally constrained), I eliminated "fines" and "isolated habitat" from the CCA.

Statistics. Plot structure (richness, percent cover, Shannon diversity, and evenness were calculated with PC-ORD (McCune and Mefford 1997). Richness is the number of species, percent cover is the total cover of species in the plot, Shannon diversity, is H′, the information theory statistic and evenness is H′/ln Richness. Evenness approaches 1.0 as dominance decreases. Descriptive statistics were calculated with Statistix 4.1 (Analytical Software 1994). Comparisons among multiple means were conducted by Bonferroni comparisons after any significant analyses of variance. I used percent similarity to assess relationships within groups of plots. It was calculated using MVSP 3.0 (Kovach 1998).

RESULTS

Classification. Ten community types (CT's) were identified with TWINSPAN. Table 1 summarizes the species composition of the more common species. Species are ordered so that their weighted mean cover shifts diagonally down the table. Values are the mean percent cover. The number of samples in each CT is given within parentheses. Characteristic species, those found in all samples of a CT, are in bold. These species may be common or rare, but they occur in all samples of a CT. Mean species richness, mean percent cover, Shannon diversity (H') and evenness are summarized in Table 2 by habitat and in Table 3 for each CT. Wetland

TABLE 2. STRUCTURE OF HABITAT TYPES. Richness is the mean number of species per plot in the habitat type; cover % is the mean total plant cover; H′ is the mean Shannon diversity index; and E is the mean Simpson equitability. Values within a column with different superscripts (if any) are significantly different ($P < 0.05$, Bonferroni comparison).

Habitat type	Richness	Cover %	H′	E
Springs	20.7^{a}	65.7	1.65^{a}	0.55
Seeps	14.6^{b}	68.8	1.49^{a}	0.57
Stagnant	12.3^{b}	106.5	1.28^{a}	0.52
Isolated	13.1^{b}	55.5	1.68^{a}	0.64
Drier	11.9^{b}	82.7	1.10^{b}	0.46

indicator status is shown and total percentage of hydrophytic species is summarized in Table 3. In these tables, all values within a column that share the same superscript are not significantly different ($P < 0.05$) from each other as determined by the conservative Bonferroni multi-comparison test.

Hydrophytic species dominated all CT's and accounted for between 80.9% and 99.9% of total cover. No upland or facultative upland species was prevalent, but some were common along the margins of CT's with less developed canopies.

A. *Salix sitchensis* Bong./*Epilobium luteum* Porsh/mixed mosses CT—This CT occurs in stagnant sites with moderate pH and organic matter. Soil has a low gravel fraction and moderate fine material. *Salix* dominance is strong, *Philonotis fontana* and *Brachythecium* are abundant and *Epilobium luteum* and *Equisetum arvense* L. are common. Species richness is very low and cover is very high.

B. *Salix sitchensis/Aruncus dioicus* (Walter) Fern./*Carex mertensii* Prescott CT—This CT is moderately eroded with coarse soils and moderate organic matter. It occurs along seeps, some of which may dry out. This CT occurs at lower elevations near Spirit Lake. *Salix* remains small and open, while *Alnus* and non-hydrophytic herbs such as *E. angustifolium* L., *Anaphalis* and *L. latifolius* occur on the margins of this type. Cover is moderate and richness relatively low.

C. *Salix sitchensis/Epilobium ciliatum-Calamagrostis canadensis* (Michaux) Beauv./mixed mosses CT—All plots are sustained by seeps with moderate to low erosion. Soils are coarse and lack fines. *Salix* is scattered, while *Epilobium* occurs consistently. Though there is constant low water flow, which helps support *Philonotis* and *Brachythecium,* the soil has poor water retention and late summer drought is likely. Richness is intermediate and cover is relatively low.

D. *Salix sitchensis*/mixed herbs/mixed mosses CT—This CT occurs at higher elevations with rapid stream flow. Soils are acid, with low organic matter. *Salix* is ubiquitous, but poorly developed. Characteristic species include the non-hydrophytic species *Lupinus lepidus* Douglas, *Anaphalis* and *Hypochaeris,* though these are not common and are confined to the wetland margins. *Philonotis* and *Brachythecium* are common in local stable patches. High species richness and diversity result from low cover by *Salix.* It appears that soil and snow movements frequently disturb this type and have retarded vegetation development.

E. *Salix sitchensis/Mimulus lewisii* Pursh-*E. ciliatum/Philonotis fontana* CT—These plots are eroded, with low organic matter, low pH and coarse substrates. They occur at higher elevations along streams or near seep sources with well-developed *Salix. Philonotis* and *Mimulus* characterize this type. The liverwort *Marchantia* is abundant where stream flow is high, but is otherwise lacking. The understory demonstrates high richness, cover and diversity.

F. *Salix sitchensis/Juncus* spp./*Brachythecium* sp. CT—This CT occurs at lower elevations in stagnant habitats near Spirit Lake. The organic fraction and fines are low, while pH is moderate. Though structurally similar to CT E, CT F has a more open *Salix* layer, several *Juncus* species and dominance by

TABLE 3. STRUCTURE OF COMMUNITY TYPES. Values within a column with different superscripts (if any) are significantly different ($P < 0.05$, Bonferroni comparison). Richness is the mean number of species per plot; cover % is the mean cover in the community type, H′ is the mean Shannon diversity index of the CT, E is the mean evenness of the CT, and % Hydrophytic is the cover of species considered to be hydrophytes, e.g., obligate, facultative wetland, or facultative species (cf. Reed 1988).

C.T.	Name	Richness	Cover %	H′	E	% Hydrophytic
A.	*Salix/Epilobium luteum*/mosses	10.0^{cd}	157.6^{a}	1.09^{ab}	0.484	97.9
B.	*Salix/Aruncus-Carex mertensii*	13.7^{bcd}	83.7^{bc}	1.34^{ab}	0.508	80.9
C.	*Salix/E. ciliatum-Calamagrostis*/mosses	13.0^{bcd}	67.5^{cd}	1.42^{ab}	0.596	96.4
D.	*Salix*/mixed herbs/mosses	20.5^{a}	28.9^{d}	1.68^{a}	0.562	91.5
E.	*Salix/Mimulus-E. ciliatum/Philonotis*	19.6^{ab}	117.6^{a}	1.61^{a}	0.540	92.6
F.	*Salix/Juncus* spp.*Brachythecium*	12.0^{cd}	85.5^{bc}	1.18^{ab}	0.481	99.9
G.	*Salix/Juncus* spp./-*E. ciliatum/Brachythecium*	16.0^{abc}	57.2^{cd}	1.70^{a}	0.613	99.1
H.	*Salix/Equisetum arvense-Juncus* spp.	14.2^{bcd}	72.9^{bc}	1.67^{a}	0.633	99.2
I.	*Salix/Equisetum arvense*	8.3^{d}	73.0^{c}	0.79^{b}	0.387	99.7
J.	*Typha latifolia-Juncus bufonius*	12.8^{bcd}	52.6^{cd}	1.52^{ab}	0.603	97.2

Brachythecium. It lacks *Petasites,* has little *Mimulus* or *Philonotis,* species normally associated with moving water. Richness and diversity are low and cover moderate.

G. *Salix sitchensis/Juncus* spp.-*E. ciliatum/Cratoneuron commutatus* CT—This CT occurs at lower elevations in dry and isolated habitats with little erosion. Soil pH is high and texture is coarse. *Salix* cover is low, but developing, and rushes are abundant in the wetter parts of this type. Cover is low, but richness and diversity are high.

H. *Salix sitchensis/Equisetum arvense-Juncus* spp. CT—This CT occurs primarily in dry and isolated sites at low elevations where erosion is nil. Organic matter is low, pH is high and fines are moderate. This CT is similar to CT G, but *Equisetum* is more abundant and *Brachythecium* is rare. Richness and diversity are intermediate.

I. *Salix sitchensis/Equisetum arvense* CT—This CT occurs in depositional sites at low elevations. Sites have high organic matter, moderate pH and a high level of fine material. *Salix* and *Equisetum* dominate, but sites are open. Richness and diversity are very low and various *Juncus* species occur sporadically.

J. *Typha latifolia* L.-*Juncus bufonius* L. CT—This CT occurs in narrow seeps with little erosion. *Typha latifolia* dominates and *J. bufonius* is abundant, but plots remain open. The margins contain a variety of upland species such as *Epilobium angustifolium* L., but richness is moderate. One plot had an abundance of *Epilobium ciliatum,* but was otherwise similar to the other plots in CT J.

Vegetation structure. The richness and cover of plots in each of the five habitat types are variable. Springs are significantly richer than all other habitats. Diversity within habitats varies considerably, but Drier sites are significantly lower (Table 2). The habitats do not differ significantly in cover or evenness.

CT's do differ in vegetative structure (Table 3). For each measure of vegetation structure, an initial one-way ANOVA was conducted. Despite large differences in evenness between CT's, the ANOVA was not significant due to high variance. Significant differences occurred among the other parameters. Subsequent Bonferroni comparisons indicated that there were four overlapping richness groups. Richness was greatest in the high elevation, eroded habitats found along faster moving streams (CT's D and E) and least in stagnant or dry sites (CT's A and I). Vegetation cover was high in protected, stagnant sites (CT A) and along seeps and streams (CT E) where *Salix* was well developed. Low cover is associated with high elevation, eroded sites (CT D) that, though similar to CT E, occur in narrower streambeds and lack *Salix* dominance. Low cover also occurs in depositional habitats where *Juncus* or *Typha* are common, but incompletely developed. The lowest diversity and least equitability occur in CT I, formed in a depositional habitat that is dominated by *Salix* and *Equisetum.* CT F, dominated by *Salix* and *E. ciliatum,* also has low richness, diversity and equitability. The more diverse CTs are those that have yet to develop a dense canopy and which have an open herb layer (e.g., CT's D, G, and H). The less diverse CT's occur in more stable habitats where dominance has developed (CT's A, F and I).

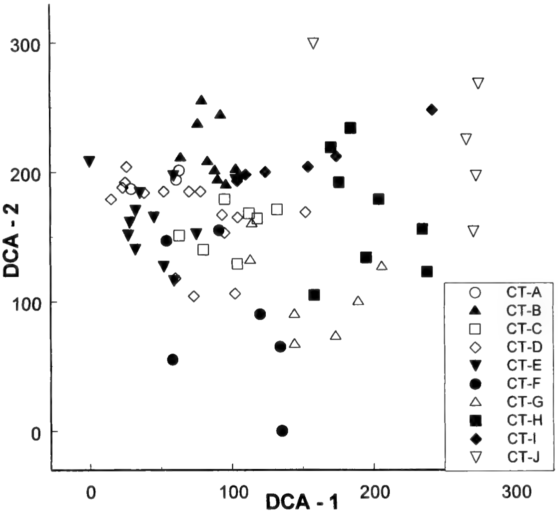

FIG. 1. Detrended correspondence analysis ordination of 79 wetland plots. Symbols are keyed to the 10 community types (CT) identified by TWINSPAN classifiction. Axes are scaled in turnover units such that plots separated by 400 units have no species in common.

Indirect ordination. Species composition was analyzed by DCA using percent cover. The eigenvalues for the first three axes were 0.348 (8.4%), 0.216 (5.2%) and 0.170 (4.1%), respectively. Each habitat type (not plotted) tends to occur in a distinct portion of the graph, but plots overlap considerably, particularly in only two dimensions. This implies that there is only a modest relationship between species composition and habitat type. The trend along DCA-1 is from plots along rapidly moving streams, through seeps to drier or depositional habitats (Fig. 1). Along DCA-2 a less pronounced trend is from stagnant to drier habitats. Isolated habitats overlap drier ones and seeps, suggesting that habitat classifications do not completely capture moisture effects. Along DCA-1, CT's D and E form one extreme and CT J the other. (One sample of CT J was unique in that it contained a high concentration of *Epilobium ciliatum,* a short-lived herb.) This reflects a gradient from *Salix* dominated sites with rapid stream flow and strong erosion to sites dominated by *Typha* and *J. bufonius* in isolated or depositional habitats. Along DCA-2, the trend is from CT F, dominated by *Salix, Brachythecium* and *Marchantia* to CT B, seep sites with margins dominated by upland species such as *Aruncus, C. mertensii*

Table 4. Standardized Canonical Coefficients and Intraset Correlations Between Environmental Factors and Constrained Ordinations. Statistical evaluations are exploratory and based on t-tests. $a = P < 0.05$; $b = P < 0.01$; $c = P < 0.001$.

	Canonical coefficients		Intraset correlation	
Variable	CCA-1	CCA-2	CCA-1	CCA-2
Erosion	0.10	0.05	−0.59	−0.13
pH	0.19^{a}	0.02	0.71	0.04
Gravel	−0.07	0.17	−0.25	−0.04
Coarse sand	0.02	0.09	−0.08	0.33
Fine sand	0.06	0.11	0.02	0.03
Organic	−0.10	−0.06	−0.10	−0.40
Elevation	0.07	-0.26^{a}	−0.72	−0.12
Spring	-0.52^{b}	0.04	−0.55	0.13
Seep	-0.40^{b}	-0.43^{c}	−0.14	−0.69
Stagnant	-0.42^{c}	0.01	−0.24	0.53
Drier	−0.09	-0.30^{b}	0.73	−0.17
X (NE to SW)	0.24^{a}	−0.02	0.77	0.14
Y (NW to SE)	−0.12	−0.05	−0.45	−0.20

and *E. angustifolium* and CT H, dominated by *Salix, Equisetum,* and *Juncus* spp.

DCA species patterns offer little additional insight. Inspection of the species graph from DCA shows that *Equisetum* and *Typha* dominate depositional wetlands. *Juncus ensifolius* Wikström, *J. articulatus* L., and *J. bufonius* are typical of some low-energy wetlands. In contrast, the upland species *J. parryi* Engelm. is common along stream margins, as are such typically upland species as *Agrostis pallens* Trin., *Carex mertensii, Hieracium albiflorum* Hook., and *Luzula parviflora* (Ehrh.) Desv.

Simple correlations of environmental factors to DCA scores (cf. Gauch 1982) suggested spatial correlations. The X-position value increased with DCA-1 ($r = 0.70$; $P < 0.01$) and decreased with elevation ($r = -0.65$; $P < 0.01$). Low DCA-1 scores were associated with Springs ($r = -0.57$; $P < 0.01$), while higher DCA-1 scores were associated with Drier sites ($r = 0.52$), Isolated sites ($r = 0.42$) and higher soil pH ($r = 0.59$). DCA-2 was weakly correlated with a gradient of Stagnant ($r = -0.37$) to Drier sites ($r = 0.28$, $P < 0.05$) and with fine soil ($r = 0.45$). A multiple regression of the environmental factors with DCA scores implied the relative strength of correlations of environmental factors to species patterns. Two analyses were conducted. First, without spatial variables, DCA-1 was predicted by these factors (multiple $r = 0.82$): stagnant ($P < 0.001$), fresh ($P < 0.001$), drier ($P < 0.004$) and seep ($P < 0.02$) habitats, soil pH ($P < 0.003$) and gravel ($P < 0.03$). The second analysis, with spatial factors included, was slightly better (multiple $r = 0.86$). The location in the X-position ($P < 0.001$) was the strongest predictor of the DCA-1 score of a plot, followed by stagnant ($P < 0.002$), pH ($P < 0.005$) and drier ($P < 0.01$). DCA-2 was unaffected by spatial factors. The regression (multiple $r = 0.68$) was associated with elevation ($P < 0.02$) and seeps ($P < 0.04$).

Direct ordination. CCA was applied to the species and environmental data (excluding fine texture and isolated habitats to eliminate co-linearity). Table 4 summarizes the standardized canonical coefficients and intraset correlations. The constrained plot ordination (community types) is overlain by the vectors to indicate relative importance of environmental variables (Fig. 2). The vectors are exaggerated two-fold. The Pearson correlation between plot positions determined by correspondence analysis and those predicted by a multiple regression of environmental values were 0.861, 0.746, and 0.732, respectively. The variances (eigenvalues) associated with each axis were 0.348, 0.216, and 0.170, respectively. These measured variables explained 30.4% of the species-environment correlation. These eigenvalues and species matrix to environment matrix correlations were significant (1000 Monte Carlo simulations, $P < 0.001$).

Significant canonical coefficients for CCA-1 (estimated from *t*-tests) were for the variables Stagnant ($P < 0.001$), Seep ($P < 0.01$), Spring ($P < 0.01$), X-position ($P < 0.05$) and pH ($P < 0.05$). Significant CCA-2 canonical coefficients were for Seep ($P < 0.001$), Drier ($P < 0.01$) and Elevation ($P < 0.05$). Intraset correlations indicate the degree to which a variable is correlated with the species axes. Bi-plot positions of environmental variables illustrate the strong effects of habitats, elevation, erosion, and position. Soil pH is the only significant soil factor. The overall relationships between these two axes and the environmental factors were relatively strong. The CT's segregate well in this space (Fig. 2), indicating that the environmental factors capture a significant portion of the species variation.

In order to test the hypothesis that *Salix sitchensis* was a deterministic factor that structured vegetation, a second CCA was completed, with *Salix* transferred to the environmental matrix. Inclusion of *Salix* altered the canonical regression because it

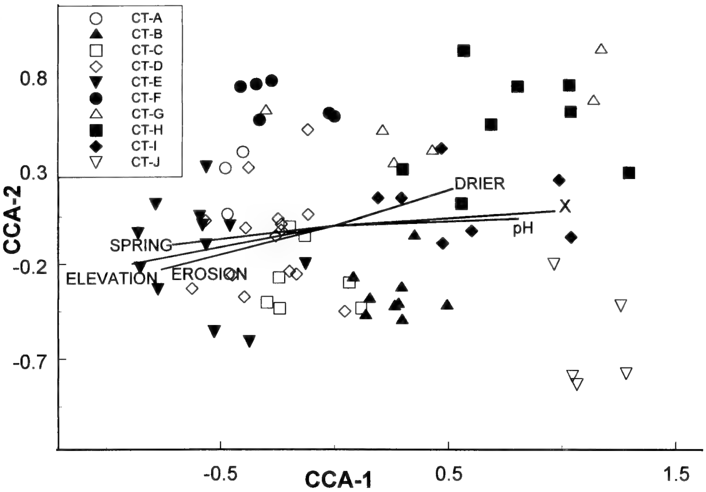

FIG. 2. Canonical correspondence analysis 79 wetland plots using 13 environmental variables. Only the variables with strong predictive power are shown as vectors. The length of the vector is proportional to the effect of the variable in predicting the position of a sample (length of vectors has been exaggerated two-fold for clarity). Spring = spring-fed stream habitats; Drier = depositional habitats likely to dry during late summer; X = position on grid of samples, from northwest to southeast); Elevation = elevation class from high to low; Erosion = degree of erosion from high to low; and pH = soil pH, from low to high.

is correlated with elevation. Pearson correlations improved to 0.926, 0.852 and 0.773 for the first three axes, respectively. The variances associated with these axes increased to 0.573, 0.314, and 0.256, respectively (34.1% of the species-environment variation). The significant regression coefficients along CCA-1 were Stagnant ($P < 0.001$), X-position ($P < 0.001$) and Seep ($P < 0.05$). For CCA-2, Seep ($P < 0.001$), *Salix* ($P < 0.01$), X-position ($P < 0.01$) and Drier ($P < 0.05$) were significant.

Plot similarity. Another analysis was used to determine if *Salix* reduced between-plot heterogeneity by constraining understory species composition. Plots were categorized by *Salix* cover as follows: <10% cover (n = 23 plots); 10 to 20% cover (n = 18); 21 to 50% (n = 13); 51 to 70% (n = 12); and >70% (n = 13). Cover of *Salix* and *Alnus* was removed since their inclusion guarantees that similarity will be relatively high and obscure understory relationships.

Mean similarity among *Salix* cover groups, from low to high, was: 14.7%, 19.3%, 17.8%, 14.4% and 21.0%. The only significant difference in mean similarity was between low *Salix* plots and high *Salix* plots ($P < 0.05$, Bonferroni comparison of all means).

Studies of uplands on the Pumice Plain (del Moral and Wood 1993) indicated that species established by nucleation, then expanded from initial foci. If wetlands form similarly, then there may be a negative relationship between the degree of isolation and similarity. Plots in the five habitats were studied for internal similarity. Analyses were conducted with all species and also with all tall woody species excluded (Table 5). If dispersal limited homogeneity development, then high similarities found in plots along active streams and low similarities in dry and isolated plots. Including shrub species, only Seeps were significantly less similar than Springs. Without shrubs, each of the habitat types displays low mean internal similarity. Springs had the highest values while Seeps and Dry habitats had the least internal similarity.

DISCUSSION

The present study suggested that significant changes have occurred during the five-year interval since the Titus et al. (1999) study. The rate of community development where erosion is strong is lower than where water flows are limited. Stable environments have developed dense shrub or dense ground layers, often both. The community types described in this study were floristically similar to

TABLE 5. PERCENT SIMILARITY WITHIN HABITAT TYPES. Parenthetical values are standard deviations. Values sharing a superscript in each row are not significantly different ($P < 0.05$, Bonferroni comparisons across each row).

Analysis	Spring	Seep	Stagnant	Isolated	Dry
All species	39.4 (18.9)^{a}	28.8 (19.6)^{b}	31.86 (19.7)^{ab}	36.1 (17.1)^{ab}	33.5 (23.0)^{ab}
No shrubs	32.5 (19.0)^{a}	15.9 (13.6)^{c}	24.7 (20.5)^{ab}	28.4 (20.9)^{ab}	18.6 (23.4)^{bc}

those previously identified by Titus et al. (1999, see also Tu et al. 1998), but were more developed.

Each CT is variable (Fig. 1) and all plots now contain some *Salix.* While Titus et al. (1999) noted four CT's dominated by different species of *Juncus* with little or no *Salix*; here all *Juncus* plots had substantial *Salix*. *Juncus* species were also common subordinates in several CTs. Many species generally not found in wetlands were common in the earlier study, particularly in open and seasonally wet habitats. Titus et al. (1999) predicted that species such as *Agrostis* spp., *Anaphalis margaritacea* (L.) Benth. & Hook., *Epilobium angustifolium, Lupinus lepidus,* and *Hypochaeris radicata* L. would decline in wetlands, and in fact they have.

The matches between the extant CT's and those previously defined are moderate. Differences due to *Salix* maturation and my inclusion of mosses and liverworts make it impractical to match community types closely. There were 81 species in this study, compared to 104 in the more extensive study of Titus et al. (1999). Richness changed little between studies, from 14.8 to 15.2 species per plot. The continued species accumulation in open plots was balanced by the reduction in richness in plots that developed closed canopies. Cover in the 86 comparable plots in the earlier study was 46% compared to 66% in the 79 plots of this study. Cover increased dramatically in CT's A, B, C, E, F, H and I, due mostly to tall shrubs. CT's D and J had lower cover. The latter resulted because we did not sample any dense *Typha* communities. Mean species richness declined in CT's A, B, C and E, which had large cover increases due to *Salix* and *Alnus.* This sugge,sts that dominance suppressed species richness.

The relationship between CT's and their environment remains weak, but detectable. The CTs' segregated efficiently in DCA. The species-based ordination is correlated with measures of the environment. DCA-1 reflects species changes from sites with rapid stream flow and less acid soils to sites that are isolated or drier, and which may accumulate organic matter. As these habitats develop, I predict that the relationships will strengthen.

In contrast to the previous study of Pumice Plain wetlands, community types also segregated well in CCA space. CT's D and E occur along fast-moving streams (Spring), while CT's B and C occur in Seeps and CT F tends to form in Stagnant habitats. CT A is a variant found in Stagnant habitats characterized by *Epilobium luteum.* Isolated habitats contain CT's G and H, and are dominated either by *Juncus* spp. or by *Equisetum arvense.* Finally, Drier habitats are a mix of CT's I and J, with some examples of G and H. CT J, with the highest scores of CCA-1, is plots dominated by *Typha latifolia,* with *J. bufonius* and little *Salix.* The other CT's found in drier habitats are dominated by wind-dispersed species (i.e., *Salix, Epilobium angustifolium, E. ciliatum, Juncus* spp. and *Equisetum arvense*). Weak tendencies towards the association of certain species with particular habitats noted by Titus et al. (1999) have strengthened. *Salix* has developed and expanded, while *Equisetum* and *Juncus* have become more restricted. These changes are consistent with expected patterns of early primary succession.

Titus et al. (1999) noted a large stochastic element within Pumice Plain wetlands. Their analysis accounted for only 19% of the species-environment variation. In this study, 30% of the variation was associated with environmental factors. Including *Salix,* 34% of the variation was associated with the regression. This increase occurred despite the exclusion of unique warm-water or high elevation sites and of complex spatial parameters. *Salix* cover developed from 10% in the previous study to 28% in this one.

Investigations of plot similarities provided evidence for developing deterministic control of vegetation structure. Plots with strong *Salix* dominance were significantly more homogeneous than those with low *Salix* cover. Understory species do not dominate sufficiently to reduce between plot similarity because there is substantial open space in the understory of most plots.

The interaction between degree of isolation and degree of similarity is complex. Spring habitats were consistently the most similar. This reflects their connectivity and the ability of species to be dispersed along stream corridors. Seep habitats do not readily disperse seeds along the watercourses and dispersal of species with poor wind dispersal is constrained. Dry habitats are variable in composition due to a substantial stochastic effect. Stagnant and Isolated habitats are intermediate. The species common in isolated habitats (e.g., *Juncus* spp., *Eleocharis macrostachya* Britton, *Equisetum* spp. and *Epilobium ciliatum*) are wind dispersed so that these habitats, though hydrologically isolated, may not be dispersal limited.

Several of the CT's described in this study have rough analogs throughout the region (Titus et al. 1996, 1998; Christy and Titus 1997), though these differ in structure from described associations owing to their immaturity. Associations dominated by *Salix sitchensis* are widespread (Kunze 1994), with a variety of understories, but none of the understories is recognized. A *S. sitchensis/Equisetum arvense-Petasites frigidus* (L.) Fries association was described by Christy (2000), and CT A could be assigned to this type. CT H and I are similar, but without *Petasites.* A *Marchantia polymorpha-Philonotis fontana* association was described for sites in Oregon and British Columbia (Christy 2000). CT E may be similar to this type, but with willows and *Mimulus lewisii. Typha latifolia* associations are widespread. Here it is joined by *Juncus bufonius* an early pioneer species. None of the CT's described in this study have exact analogs elsewhere in the region. However, unlike the case in the adjacent uplands (del Moral et al. 1995), none is so different from described associations that it would be surprising for them to develop into recognized associations. The wetland CT's remain poorly correlated with their environment and are internally variable, yet each is recognizable. This paradox may result because most wetland CT's developed from only a few predominantly wind-dispersed species that quickly occupied these habitats. Because the initial colonization was stochastic, similar habitats may have received dissimilar colonists, for example one of several possible *Juncus* species. Subsequent invasions may be limited by infertile soils, poor dispersal or by competition from existing plants, thus perpetuating low similarity among vegetation in similar habitats. Due to the gradual development of an overstory, slow spread of better-adapted species (Fuller 1999) and competitive interactions, vegetation in these wetlands is becoming more predictable.

An initially stochastic pattern has begun to develop such that mechanisms that structure vegetation are becoming more prevalent. The principal structuring mechanisms in this study are the moisture regime, which permits rapid development of plant biomass, and the competitive effects of *Salix.* Vegetation should become more predictable as species come into closer equilibrium with these factors and competitive effects among the herbs develop more fully.

ACKNOWLEDGMENTS

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FIELD ASSESSMENT OF THE CALIFORNIA GAP ANALYSIS PROGRAM DATABASE FOR SAN DIEGO COUNTY

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ABSTRACT

Given the key role played by biogenic hydrocarbons (BHC's) in photochemical smog formation and atmospheric chemistry, it is critical to generate accurate BHC emission inventories. Assembling such inventories requires reliable characterization of the areal coverage of important plant species in order to quantify the biomass of BHC-emitting vegetation. A recent GIS-based description of vegetation coverage in the natural areas of San Diego County is provided by the Gap Analysis Program (GAP) database. We conducted an assessment of this database through ground-based vegetation surveys prior to using the database to develop a BHC emission inventory for southern California. Quantitative vegetation surveys were conducted along belt transects in four polygons dominated by trees and along line transects in four polygons dominated by shrubs, in order to determine percent cover of major plant species. The species listed by GAP accounted for two-thirds to three-quarters of the relative cover in these selected polygons. About 60% of the species listed by GAP were found in high enough proportions in the field surveys to justify their listing. Summed over all eight polygons, BHC emission indices based on GAP data correlated with BHC emission indices generated with data from our field surveys. On balance, we judge the GAP GIS database to be a useful source of species composition and dominance information for the purpose of assembling BHC emission inventories, provided supplementary data on crown volumes are available from the literature or can be obtained in the field.

The emission of reactive hydrocarbons such as isoprene and monoterpenes by vegetation (i.e., biogenic hydrocarbons or BHC's) has been known for several decades (Went 1960; Rasmussen 1972). However, only in the last fifteen years has interest in the role of BHC's in photochemical smog formation and atmospheric chemistry expanded dramatically, both in the scientific and regulatory communities (Winer et. al. 1983; Lamb et al. 1987; Chamedies et al. 1988; NRC 1991; Corchnoy et al 1992; Winer et al. 1992; Arey et al. 1995; Geron et al 1995; Sharkey and Singsaas 1995; Benjamin et al. 1996, 1997; Guenther 1997; Benjamin and Winer 1998).

In the atmosphere, many BHC's are as reactive as, or more reactive than, volatile organic compounds (VOC) emitted from mobile or stationary anthropogenic sources (Carter 1994; Benjamin and Winer 1998), and there is a growing body of research suggesting BHC's can constitute a significant and even dominant contribution to the overall VOC inventory in both regional airsheds and the global atmosphere (Workshop on Biogenic Hydrocarbons [WBH] 1997). Given the enormous costs associated with further reducing VOC and NO_X emissions to meet state and federal air quality standards, it is critical to obtain data needed to assemble reliable BHC emission inventories, including composition and dominance of the plant species in an airshed, green leaf biomass for the dominant plant species, and quantitative rates of emission of individual organic compounds from these species.

Plant species distributions, BHC emission rates, and leaf mass constants have been developed for a substantial number of species relevant to certain areas of California (Winer et al. 1983, 1992; Miller and Winer 1984; Horie et al. 1991; Karlik and Winer 1998). With the proposal of a taxonomic methodology for assigning isoprene and monoterpene emission rates to unmeasured plant species (Benjamin et al. 1996), emission rates can in principle be estimated for many of the 6000 plant species in California without direct experimental measurements. Of the southern California airsheds, the vegetation spatial distribution and composition has been established for urban and natural areas within Orange County and the non-desert portions of Los Angeles, Riverside, and San Bernardino Counties (Winer et al. 1983; Miller and Winer 1984; Horie et al. 1991; Benjamin et al. 1997), and a limited BHC emission study for Santa Barbara and Ventura Counties has also been reported (Chinkin et al. 1996). However, a validated inventory of vegetation species composition and spatial distribution, specifically to develop a BHC emissions inventory, has not been established for the San Diego County airshed.

A potential source of information concerning vegetation in the natural areas of San Diego County is the Gap Analysis Program database (GAP), which is coordinated by the United States Geolog-

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ical Service–Biological Resources Division (formerly the National Biological Service) to identify the distribution and management status of plant communities. GAP compiled a geographic information system (GIS) database (based primarily on remote-sensing data) describing vegetation type and dominance in terms of areal coverage (Davis et al. 1994, 1995). Unlike other vegetation maps, which describe geographic areas using only plant communities, the California GAP describes vegetation in given geographic areas using dominant plant species. Because BHC emissions inventories rely on species-specific measurements of both leaf mass and BHC emission rates (Benjamin et al. 1997), GAP offers the advantage of providing species-specific vegetation distribution data. Moreover, the GAP GIS database is recent for southern California (Davis et al. 1995) and therefore more up to date than older vegetation databases employed in California, such as the vegetation type map (VTM) surveys conducted in the 1930's and CALVEG generated in the 1970's (Sawyer and Keeler-Wolf 1995). Although large-area, small-scale GIS databases based on remote-sensing data, such as GAP, offer a potentially inexpensive and simple approach to characterizing the distribution and species identity of natural vegetation within an airshed, use of such GIS databases in BHC emissions inventory development requires evaluation of their accuracy and reliability through ground-based observations.

We report here the results of a ground-based assessment of the GAP GIS database for San Diego County using vegetation surveys of representative GIS polygons. The surveys employed a modified stratified random sampling approach and a survey protocol based in part on the recommendations of the developers of the GAP database (Stoms et al. 1994). Data gathered from field surveys conducted from September 1997 to April 1998 in San Diego County were used to assess the utility of the GAP GIS database for predicting the distribution and species identity of vegetation, and for providing a quantitative description of plant species assemblages.

METHODS

Gap analysis program database. As noted earlier, GAP's purpose was to identify the distribution and management status of selected components of biodiversity. The central tool of this program was an ARC/INFO GIS database with plant species and vegetation class attributes associated with polygons within a defined geographic region. This database was generated from summer 1990 Landsat Thematic Mapper satellite imagery, 1990 high altitude color infrared photography, VTM surveys based on field surveys conducted between 1928 and 1940, and miscellaneous vegetation maps and ground surveys (Davis et al. 1995). Polygons were delimited based on climate, physiography, substrate, and disturbance regime. Landscape boundaries were subjectively determined through photointerpretation by expert personnel so that between-polygon variation was greater than within-polygon variation. The final result was a vegetation map with a 100 hectare minimum mapping unit and a 1:100,000 mapping scale (Davis et al. 1995).

For each polygon in the database, one primary and one secondary vegetation assemblage was listed. Each assemblage consisted of three co-dominant overstory species, each covering a minimum of 20% of the relative cover of the assemblage. The primary assemblage was defined as the assemblage covering the majority of the polygon, and the secondary assemblage as covering the remainder of the polygon. Relative cover is the proportion of total vegetation cover occupied by a given plant species, excluding certain vegetation such as plants below a pre-established height and bare ground. Overstory plants are those plants viewable directly from above. In addition, GAP listed the percent crown cover of each assemblage in the polygon in four classes.

Acquisition and preparation of the GAP database. The GAP database for the southwest ecoregion was obtained in August 1997 from the Department of Geography at the University of California at Santa Barbara. The southwest ecoregion covers all or portions of Santa Barbara, Ventura, Kern, Los Angeles, San Bernardino, Orange, and Riverside Counties and the western two-thirds of San Diego County. The remaining eastern third of San Diego County is located in the Sonoran ecoregion, which was not obtained for use in the present study because it is located far from the major urbanized centers of San Diego County, and because the ecoregion is composed mostly of deserts with little biomass. From the 2014 original polygons for the southwest ecoregion, the San Diego County subset of 437 polygons was extracted using ArcView 3.0a GIS software.

Vegetation survey protocol and methods. The vegetation survey protocol employed was initially based on recommendations for a GAP database validation study suggesting 1 square km sample units (Stoms et al. 1994). Because the GAP database is a large-area land cover map, use of a large sample element (e.g., 1 km^2) avoids quantifying heterogeneity below the intended resolution of the map. Stoms et al. (1994) noted other issues affecting vegetation surveying such as the need to obtain legal access from private land-owners, safety, and proximity of sample sites to roads. The specific shape of the vegetation survey unit was left unresolved in the guidelines.

In the present study, the specific survey protocol chosen depended on the type of vegetation being assessed. Within the polygons dominated by trees, surveys were performed in three sample elements consisting of two 6 m wide, 500 m long belt transects bisecting each other at right angles. Other researchers have demonstrated 6 m wide belt transects make the mechanics of sampling easier while not significantly compromising accuracy (Lindsey 1955). For these belt transects, the surveyors walked 250 m north, south, east, or west away from the centerpoint, using a magnetic compass to maintain course.

In the present study, one person measured the crown radii and diameter at breast height of trees and the crown height of shrubs (plants with more than one stem), while another measured the crown height of trees (plants with one stem) and recorded the field data. Crown radii in trees were measured with a 10 m tape in four directions (north, south, east, and west). Crown radii in shrubs were measured using two diameters perpendicular to each other. Readings were taken to the nearest tenth of a meter. Crown height of trees was obtained from a clinometer. From a distance of approximately 10–20 meters, the observer measured to the nearest meter the distance from the tree to the observer using an optical rangefinder. With a clinometer, the observer determined the crown height as a percentage of the observer's distance away from the tree.

Within polygons dominated by scrub or chaparral, one individual performed surveys in four sample elements, each consisting of two 300 m long line transects bisecting each other at right angles. Line transects have been used to estimate relative cover for chaparral (Bauer 1943) and for sage scrub (Kent and Coker 1992; Zippin and Vanderwier 1994). The individual surveyed along line transects using a 50 m tape and collected data on the identity of the topmost plant species directly over the meter tape, was determined the number of 0.1 m segments occupied by that plant species, and recorded the height of the crown for each individual plant to the nearest 0.1 m. The crowns were envisioned as rectangular prisms and measured as such. The 150 m transects running north, south, east, and west from the centerpoint were completed using three 50 m segments.

The survey team located the centerpoint of a particular sample element using a global positioning receiver (GPS) locked onto universal transmercator (UTM) coordinates gathered from the GAP database. A Garmin 12XL handheld GPS unit, with an accuracy of ± 100 m 99% of the time, was employed. The survey team then recorded the species identity and related data as described above. For forested polygons (areas where crowns of trees interlocked), only data from plants taller than waist height were recorded. For woodland polygons (areas where crowns of trees did not interlock), only plants taller than knee height were recorded. For scrub and chaparral, all plant species except for understory species and grasses were recorded. All plants were identified in the field, and samples of unidentifiable plants were taken to the herbarium at UCLA for identification.

Selection of polygons from the GAP database. Polygons were chosen for potential inclusion in the present study based on an index estimating their isoprene or monoterpene emissions. Use of these indices identified eighty polygons (Fig. 1) estimated to have the largest biogenic hydrocarbons emissions based on the presence of high-emitting plant species (Benjamin et al. 1996) and their areal coverage within a polygon.

Further selection from among the eighty polygons with the highest BHC emissions involved an iterative process accounting for representativeness and feasibility. In considering representativeness, roughly equal numbers of polygons were selected with woodland/forest vegetation and scrub/chaparral vegetation, the two main classes of natural vegetation in San Diego County. Polygons were selected to insure that all geographic regions of the county, except the desert regions, were represented. In considering feasibility, physical access and permission to survey vegetation on private or military property were important. Polygons with a large public land component (e.g., California State Parks, San Diego County Parks, United States National Forest System, Bureau of Land Management, and local parks) were favored due to the relative ease of gaining permission to conduct surveys on such properties compared with privately-owned properties.

The minimum square-shaped area needed to encompass a sample element within a polygon was determined to be 62.5 acres for forests and woodlands and 22.5 acres for scrub and chaparral, and owners of parcels of land of these sizes within selected polygons were identified using information from the San Diego County assessor's records. A letter was prepared requesting permission to conduct a vegetation survey, stating the goals of the research, and enclosing a form to be returned offering or denying access. Out of 69 mailers, 10 owners agreed to participate in the study, 15 declined and the rest were non-responders, for a success rate of about 14%. Those polygons with a large public land component and/or with many private land owners responding positively to the mailers were included for further consideration.

Based on these criteria and the time and resources available for this research, eight polygons were selected for the present study. Four polygons consisted primarily of woodland/forest vegetation, and four polygons consisted primarily of shrub/chaparral vegetation (Table 1). Of these eight polygons, five were estimated to be dominated by isoprene emissions, two were estimated to be dominated by monoterpene emissions, and one exhibited both high isoprene and high monoterpene emissions. Table 1 lists data for each of these eight polygons according to the GAP database, including the expected species assemblages and their relative proportion of the polygon and crown closure. In addition, Table 1 lists the polygon rank by the iso-

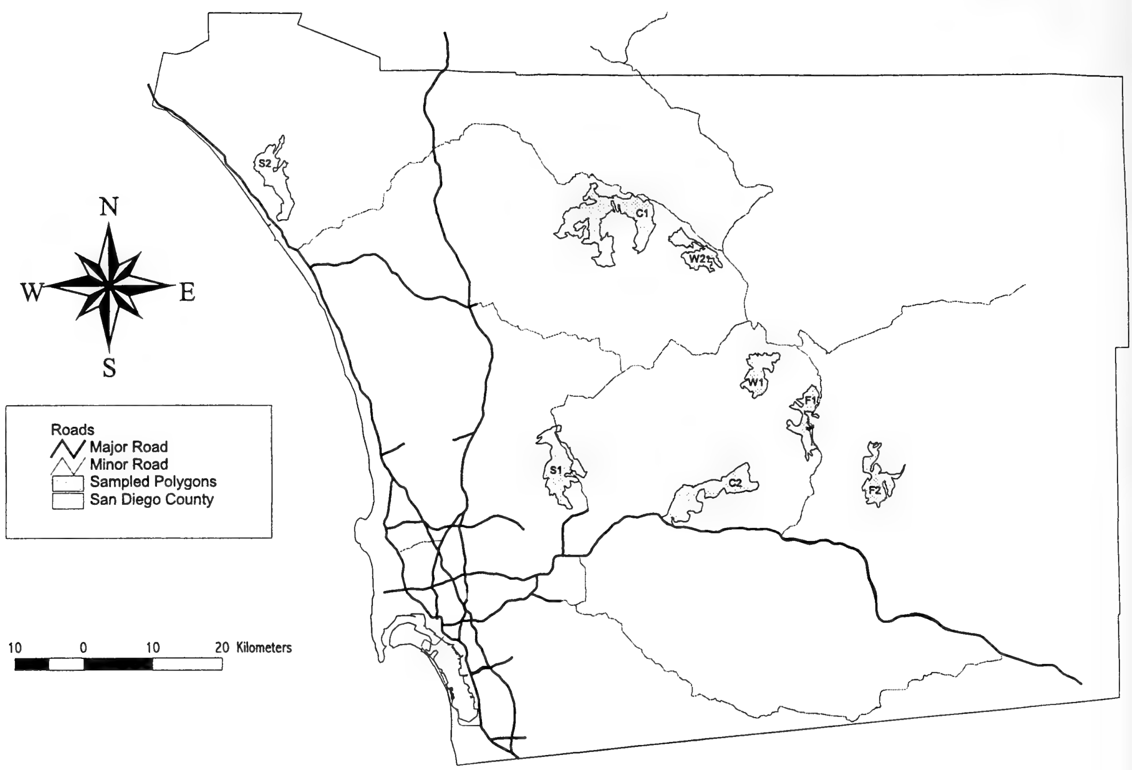

FIG. 1. GAP polygons surveyed in San Diego County for plant species composition and dominance.

prene or monoterpene emission index. Figure 1 shows the location of the polygons investigated in the present study.

Selection of sample elements within a polygon. After a polygon was chosen by the process described above, sample elements were selected. The centerpoints of the elements were located so all transects were at least 100 meters away from the polygon boundary. If permission was obtained to access most of the polygon, sample elements were selected by overlaying a 500 meter UTM grid on the polygon, assigning sequential numbers to every grid element within 1 km of a road, and randomly selecting the needed number of 500 meter grid elements. This method was similar to the one employed in the Utah GAP validation project (Edwards et al. 1995). Only four polygons had enough area accessible by roads or sufficient permission to be sampled. For the other four polygons, large portions were physically or legally inaccessible, and sample elements were chosen from within the accessible areas. To minimize bias in site selection for these four polygons, the final selection of sample elements was decided before entry into the polygon. In several cases, suitable survey sites were not available within the vicinity of a road, so hikes of up to two hours along a trail were needed to reach the desired area within the polygon.

Data analysis. As noted earlier, the GAP GIS database provides semi-quantitative information on the abundance and distribution of plant species. For each polygon, the GAP database lists species assemblages and the estimated areal proportion (p) of that assemblage within a polygon. Each species in a listed assemblage is a co-dominant, providing ≥20% relative cover. The expected relative cover of a species listed in the GAP database for a polygon is then ≥0.2p. For example, in polygon F1, *Quercus agrifolia* Nee is a co-dominant in an assemblage that occupies 60–70% of the polygon. Using a mean value of 65%, GAP predicts *Q. agrifolia* would cover ≥ 13% of the polygon.

The relative cover of plant species inferred from the GAP database by this procedure was compared with the cover data gathered from the field surveys in the eight selected polygons. First, the relative cover of each species within each sample element of a polygon was calculated. Then from the species relative cover for each sample element, the mean relative cover and upper limit of the two standard error (SE) confidence interval for the polygons were calculated, corresponding to an 85% confidence interval (McClave and Dietrich 1985).

If the upper limit of the confidence interval for the relative cover of a measured species was less than its GAP-predicted relative cover, then the species was considered an "incorrect" listing as a co-

TABLE 1. POLYGONS FROM THE GAP DATABASE SELECTED FOR FIELD SURVEY OF SPECIES COMPOSITION AND ABUNDANCE. [a] From GAP database (University of California at Santa Barbara Department of Geography 1997). [b] F = Forest, W = Woodland, C = Chaparral, S = Sage Scrub. [c] Ii = Isoprene emission index. [d] Im = Monoterpene emission index.

ID[b]	Area (ha)[a]	Primary or secondary[a]	Species assemblage[a]	Percentage of polygon[a]	Crown closure[a]	Rank by I_I[c]	Rank by I_M[d]
F1	1990	P	*Quercus kelloggii, Quercus chrysolepis,* and *Quercus agrifolia*	60–70%	60–100%	10	159
		S	*Pinus lambertiana, Pinus coulteri,* and *Libocedrus decurrens*	30–40%	60–100%		
F2	2317	P	*Quercus kelloggii* and *Pinus jeffreyi*	50–60%	40–59%	29	136
		S	*Quercus cornelius-mullerii, Cercocarpus betuloides,* and *Adenostoma fasciculatum*	40–50%	60–100%		
W1	1904	P	*Quercus agrifolia, Quercus engelmannii,* and *Quercus kelloggii*	60–70%	25–39%	9	170
		S	*Ceanothus leucodermis, Adenostoma fasciculatum,* and *Quercus berberidifolia*	30–40%	60–100%		
W2	1778	P	*Quercus kelloggii, Quercus agrifolia,* and *Quercus engelmannii*	60–70%	60–100%	16	249
		S	*Adenostoma fasciculatum, Arctostaphylos tomentosa,* and *Cercocarpus betuloides*	30–40%	60–100%		
C1	6578	P	*Quercus berberidifolia* and *Ceanothus leucodermis*	50–60%	60–100%	7	37
		S	*Adenostoma fasciculatum, Cercocarpus betuloides,* and *Ceanothus* sp.	40–50%	60–100%		
C2	3986	P	*Adenostoma fasciculatum, Quercus berberidifolia* and *Ceanothus leucodermis*	80–90%	60–10%	20	56
		S	*Ceanothus greggii* and *Arctostaphylos pungens*	10–20%	60–100%		
S1	3650	P	*Artemisia californica, Eriogonum fasciculatum,* and *Salvia apiana*	60–70%	40–59%	102	8
		S	*Adenostoma fasciculatum, Ceanothus oliganthus,* and *Quercus berberidifolia*	30–40%	40–59%		
S2	2718	P	*Artemisia californica, Salvia mellifera,* and *Malosma laurina*	80–90%	60–100%	251	2
		S	*Avena* spp., *Bromus* spp., etc. and *Baccharis pilularis*	10–20%	25–39%		

dominant in the GAP database. Otherwise, it was considered a "correct" listing. An observed species not listed by GAP as a co-dominant was considered a "potential" co-dominant if the upper limit of the uncertainty interval was greater than the predicted relative cover value of any co-dominant in the secondary assemblage in that polygon. For example, in polygon F1, the smallest predicted relative cover is that of a co-dominant in the secondary assemblage which provides 30–40% cover for that polygon. Using a mean value of 35% for the secondary assemblage in polygon F1 and a relative cover value of ≥20% for a co-dominant, then ≥7% of the polygon is expected to be covered by a co-dominant of a secondary assemblage in polygon F1. Any plant species not listed by GAP but observed in polygon F1 with a relative cover ≥ 7% was considered a potential co-dominant in that polygon.

Crown closure from the GAP database was also compared to the field data. Crown closure is equivalent to the percent coverage by all overstory plants within a polygon divided by the area of the polygon. A confidence interval within two SE was calculated from these data and compared with the data predicted from the GAP database.

RESULTS

Species composition and abundance within GAP polygons. Table 2 summarizes the overall results from the field surveys, listing the six most abundant overstory species observed for each polygon, the percent composition predicted from the GAP database, the percent composition determined by the field surveys, and the upper limits of a two SE interval of the percent composition. In the forest and wooded polygons, overstory plants accounted for 87–92% of the relative crown cover according to

TABLE 2. MEASURED SPECIES COVER COMPOSITION OF THE SIX MOST ABUNDANT PLANT SPECIES OBSERVED IN SELECTED GAP POLYGONS. * Species listed in the GAP database as a co-dominant, but not ranked in the top 6 species observed for the polygon.

Polygon	Species	Predicted cover (%)	Sampled cover (%) (s)	(s + 2 SE)
F1	*Quercus chrsyolepis*	≥13	23	70
	Pinus jeffreyi	—	19	47
	Quercus kelloggii	≥13	19	26
	Quercus agrifolia	≥13	11	24
	Arctostaphylos pungens	—	7	17
	Pinus coulteri	≥7	6	18
	**Calocedrus decurrens*	≥7	4	7
	**Pinus lambertinana*	≥7	0.0	—
	Total of six highest		85	
	GAP Co-dominants		64	
F2	*Quercus kelloggii*	≥11	34	37
	Pinus jeffreyi	≥11	18	39
	Quercus berberidifolia	—	13	23
	Ceanothus palmeri	—	11	26
	Cercocarpus betuloides	≥9	7	14
	Adenostoma fasciculatum	≥9	5	12
	**Quercus cornelius-mulleri*	≥9	0.0	—
	Total of six highest		88	
	GAP Co-dominants		65	
W1	*Quercus engelmannii*	≥13	39	56
	Quercus agrifolia	≥13	26	41
	Arctostaphylos gladulosa	—	10	27
	Adenostoma fasciculatum	≥7	8	25
	Salvia apiana	—	4	12
	Eriogonum fasciculatum	—	4	11
	**Quercus kelloggii*	≥13	2	3
	**Ceanothus leucodermis*	≥7	0.2	2
	Quercus berberidifolia	≥7	0.0	—
	Total of six highest		91	
	GAP Co-dominants		76	
W2	*Quercus engelmannii*	≥13	62	121
	Quercus kelloggii	≥13	17	46
	Quercus berberidifolia	—	10	27
	Quercus agrifolia	≥13	3	6
	Pinus coulteri	—	2	6
	Arctostaphylos glandulosa	—	2	4
	**Adenostoma fasciculatum*	≥7	1	3
	**Cercocarpus betuloides*	≥7	.05	1
	Arctostaphylos glandulosa	≥7	0	—
	Total of six highest		96	
	GAP Co-dominants		85	
C1	*Quercus berberidifolia*	≥11	39	67
	Adenostoma fasciculatum	≥9	36	54
	Eriogonum fasciculatum	—	5	15
	Quercus engelmannii	—	4	12
	Ceanothus crassifolius	—	2	4
	Heteromeles arbutifolia	—	2	4
	**Cercocarpus betuloides*	≥9	2	4
	**Ceanothus leucodermis*	≥11	0.4	1
	*Buckbrush	≥9	0.0	—
	Total of six highest		88	
	GAP Co-dominants		78	
C2	*Adenostoma fasciculatum*	≥17	51	73
	Xylococcus bicolor		13	25
	Eriogonum fasciculatum		8	15
	Quercus berberidifolia	≥17	5	6
	Malosma laurina		4	9
	Rhus ovata		4	7
	**Ceanothus greggii*	≥3	3	7
	**Ceanothus leucodermis*	≥17	1	1
	Total of six highest		85	
	GAP Co-dominants		59	
S1	*Eriogonum fasciculatum*	≥13	26	49
	Adenostoma fasciculatum	≥7	21	48
	Artemisia californica	≥13	20	33
	Malosma laurina	—	14	26
	Xylococcus bicolor	—	6	14
	Ceanothus oliganthus	≥7	3	10
	**Quercus berberidifolia*	≥7	1	3
	Salvia apiana	≥13	1	1
	Total of six highest		90	
	GAP Co-dominants		72	
S2	*Artemisia californica*	≥17	41	68
	Salvia mellifera	≥17	16	31
	Malosoma laurina	≥17	14	24
	Rhus integrifolia	—	6	15
	Baccharis pilularis	≥3	4	12
	Malacothamnus fasciculatus	—	4	10
	Total of six highest		85	
	GAP Co-dominants		75	

our data. In the polygons dominated by scrub and chaparral, there was little or no understory.

Most of the relative cover was attributable to a few species. For all polygons, the six most abundant species (many of them listed as GAP co-dominants) were responsible for over 80% of the relative cover (Table 2). In general, the GAP co-dominants provided roughly two-thirds to three-quarters of the relative cover observed in the field surveys. For polygons F1, F2, W1, W2, C1, C2, S1, and S2, GAP co-dominants provided 64%, 65%, 76%, 85%, 78%, 59%, 72%, and 75% of the observed relative cover, respectively.

For both forest/woodland and chaparral/scrub polygons, the observed relative cover of certain co-dominants in GAP polygons often substantially exceeded the minimum predicted values (Table 2). For example, in polygon F2, *Quercus kelloggi* Newb. provided 34% of the relative cover when ≥11% was predicted, and in polygon W1, *Q. engelmannii* E. Greene provided 39% of the relative cover when ≥13% was predicted. In polygon C1, *Q. berberidifolia* Liebm. and *Adenostoma fasciculatum* Hook. & Arn. provided 39% and 36% of the relative cover, respectively, when ≥11% and ≥9% were predicted by the GAP database. Thus, although a lower limit for species relative cover can be inferred from the data provided by the GAP database, an upper limit for species relative cover is not available from GAP.

TABLE 3. SPECIES LISTED CORRECTLY AND INCORRECTLY AS CO-DOMINANTS WITHIN SURVEYED GAP POLYGON ORDERED BY DECREASING MEAN RELATIVE COVER. (p) GAP primary assemblage species. (s) GAP secondary assemblage species. * Potential co-dominant listed as a co-dominant in an adjacent GAP polygon. † See test.

Polygon	GAP species observed in significantly large quantities†	GAP species not observed in significantly large quantities†	Potential co-dominants
F1	*Quercus chrysolepis* (p) *Quercus kelloggii* (p) *Quercus agrifolia* (p) *Pinus coulteri* (s) *Calocedrus decurrens* (s)	*Pinus lambertiana* (s)	*Pinus jeffreyi** *Arctostaphylos pungens* *Quercus berberidifolia**
F2	*Quercus kelloggii* (p) *Pinus jeffreyi* (p) *Cercocarpus betuloides* (s) *Adenostoma fasciculatum* (s)	*Quercus cornelius-mulleri* (s)	*Quercus berberidifolia* *Ceanothus palmeri** *Pinus coulteri*
W1	*Quercus engelmannii* (p) *Quercus agrifolia* (p) *Adenostoma fasciculatum* (s)	*Quercus kelloggii* (p) *Ceanothus leucodermis* (s) *Quercus berberidifolia* (s)	*Arctostaphylos glandulosa** *Eriogonum fasciculatum** *Salvia apiana**
W2	*Quercus engelmannii* (p) *Quercus kelloggii* (p)	*Quercus agrifolia* (p) *Adenostoma fasciculatum* (s) *Arctostaphylos tomentosa* (s) *Cercocarpus betuloides* (s)	*Quercus berberidifolia**
C1	*Quercus berberidifolia* (p) *Adenostoma fasciculatum* (s)	*Cercocarpus betuloides* (s) *Ceanothus leucodermis* (p) *Ceanothus cuneatus* (s)	*Eriogonum fasciculatum** *Quercus engelmannii**
C2	*Adenostoma fasciculatum* (p) *Ceanothus greggii* (s)	*Quercus berberidifolia* (p) *Ceanothus leucodermis* (p) *Arctostaphylos pungens* (s)	*Xyloccocus bicolor** *Eriogonum fasciculatum** *Malosma laurina** *Rhus ovata* *Cneoridium dumosum* *Ceanothus oliganthus* *Arctostaphylos glandulosa**
S1	*Eriogonum fasciculatum* (p) *Adenostoma fasciculatum* (p) *Artemisia californica* (s) *Ceanothus oliganthus* (s)	*Quercus berberidifolia* (s) *Salvia apiana* (p)	*Malosma laurina* *Xylococcus bicolor** *Salvia mellifera*
S2	*Artemisia californica* (p) *Salvia mellifera* (p) *Malosma laurina* (p) *Baccharis pilularis* (s) *Avena* spp., *Bromus* spp., etc. (s)		*Rhus integrifolia* *Malacothamnus fasciculatus* *Eriogonum fasciculatum** *Lotus scoparius*

For each polygon, Table 3 shows the number of species listed as GAP co-dominants which agreed with our field observations, the species listed by GAP but not observed in significant amounts in the field, and species that could have been listed as co-dominants based on their observed abundance.

For all the polygons taken together, 59% of the GAP co-dominants were observed in the field survey in large enough proportions to justify their co-dominant designation. Of the species listed as co-dominants in the primary assemblages, this percentage was 73%, whereas for species listed within the secondary assemblages, only 45% had sufficient abundance to match the predictions. The "correct" listing of GAP co-dominants was more common (61%) in forested or wooded polygons, with primary and secondary assemblage co-dominants confirmed in the field 82% and 42% of the time, respectively. Overall, agreement with GAP was less common in the chaparral and scrub polygons, with 57% of the GAP co-dominants observed in large enough proportions to justify their co-dominant designation, or 64% and 50%, respectively among primary and secondary assemblages.

There were several instances where species listed in either the primary or secondary assemblages were not observed at all in the polygon in our field surveys. In some cases, a taxonomically similar species was found instead. For example, we did not observe *Quercus cornelius-mulleri* K. Nixon & K. Steele (a scrub oak with tomentose hairs on the underside of the leaves) in polygon F2, but did observe *Q. berberidifolia.* In another case, the species listed in GAP did not even exist within San Diego County according to botanical experts, although a closely-related species was found instead in our study. For example, *Arctostaphylos tomentosa* (Pursh) Lindley was not recognized by Beauchamp (1986) as a species found in the county, but *A. glandulosa* Eastw., a similar hairy manzanita with a basal burl, was found in our surveys for polygon W2. In two other cases, a species listed by GAP was not observed in any of the sample elements we surveyed. *Pinus lambertiana* Douglas was not found in the sample elements in polygon F1, although California State Park personnel indicated they thrived at higher elevations within the polygon, away from roads and in areas close to the polygon boundary. In the other case, *Ceanothus cuneatus* was not found in any of the sample elements within polygon C1.

Similar to the experience with *Pinus lambertiana,* observations of polygon areas away from the chosen sample elements suggested that in some cases the elements chosen did not encompass representative vegetation found elsewhere in the polygon. For example, in polygon S1, large portions of roadside areas in the northern part of the polygon were covered with *Salvia apiana* Jepson. However, permission to access those areas was not granted and no sampling could be performed. In polygon C2, large portions of north-facing slopes in the southern part of the polygon were covered by continuous stands of *Quercus berberidifolia,* but permission was not granted to access those areas. Although unavoidable, these experiences indicate limits to the representativeness of our sampling protocol.

Conversely as noted above, numerous species within the polygons were observed in high enough abundance to warrant possible designation as a co-dominant although they were not listed in the GAP database (Table 3). The abundance of most of these species was modest, but given the SE interval about the mean sampled composition (Table 2), these species could be designated as co-dominants. Most of these species omitted from GAP were shrubs (e.g., *Arctostaphylos glandulosa, Quercus berberidifolia, Ceanothus palmeri* Trel., *Eriogonum fasciculatum* (Benth.) Torrey & A. Gray), except for *Pinus jeffreyi* Grev. & Balf. in polygon F1 and *P. coulteri* D. Don in polygon F2. Many (15 of 27) of these potential co-dominants were listed as co-dominants in *neighboring* GAP polygons (see Table 3), suggesting the influence of adjacent polygons on species composition of the surveyed polygons.

Crown closure. Table 4 summarizes the predicted and measured crown closure for the GAP polygons studied. When the GAP-predicted crown closure of both primary and secondary assemblages were the same, the measured crown closure was within both ranges (polygons F1, C1, and S1). When the GAP-predicted crown closure of both primary and secondary assemblages were different, the measured crown closure was within the crown closure range of one of the assemblages (polygon F2) or between the ranges of both assemblages (polygon W1).

DISCUSSION

Species composition within the GAP database. In our study, the apparent accuracy of the GAP database was high for forest/woodland species and lower for scrub/chaparral species. As noted earlier, the accuracy of the GAP database is linked to the accuracy of VTM and soil vegetation maps, and to more recent remote sensing data used to create this database. The original VTM and soil-vegetation maps may have been quite accurate for forests and woodlands because of the ease of conducting studies in those relatively open areas, combined with the economic incentive of producing accurate data for these potential timber sources. Scrub and chaparral have little or no commercial value and the effort required to maneuver through dense thickets discourages data collection.

For certain chaparral species, successional changes may explain some of the discrepancies in species composition between the GAP database and the present field study. Although previous studies estimating natural cover of vegetation for BHC inventory generation assumed little change in chaparral vegetation over time (Winer et al. 1983), this assumption may not be appropriate. Chaparral follows certain successional trends after fires (Hanes 1971; Keeley 1975; Hanes 1977; Barbour and Major 1977; Gordon and White 1994). *Ceanothus* chaparral and coastal sage scrub may emerge immediately after a fire depending on the elevation, aspect, and antecedent vegetative conditions, but may be displaced by chamise or scrub oak chaparral. *Ceanothus cuneatus* (Hook.) Nott. is one species which within 50 years can die out completely, and *C. leucodermis* E. Greene is eliminated after 40 years. Other species of *Ceanothus* tend to thin with time because recruitment of new individuals does not occur in the absence of fire. Some of the more underrepresented species in our field observations which were predicted by the GAP database were members of the genus *Ceanothus* (*C. leucodermis, C. oliganthus* Nott., *C. greggii,* A. Gray and

TABLE 4. PREDICTED AND MEASURED CROWN CLOSURE FOR SELECTED GAP POLYGONS.

Polygon	Primary or secondary	Predicted crown closure (%)	Measured crown closure (%) (c)	(c − 2SE, c + 2SE)
F1	P	60–100	72	(54, 90)
	S	60–100		
F2	P	40–59	54	(44, 63)
	S	60–100		
W1	P	25–39	42	(20, 63)
	S	60–100		
W2	P	60–100	56	(35, 76)
	S	60–100		
C1	P	60–100	81	(63, 99)
	S	60–100		
C2	P	60–100	74	(66, 83)
	S	60–100		
S1	P	40–59	54	(36, 72)
	S	40–59		
S2	P	60–100	63	(45, 80)
	S	25–39		

C. cuneatus). A successional process could explain the absence of *Ceanothus* species from some of the field data even though they were predicted in the GAP database.

However, explaining discrepancies in the chaparral and coastal sage scrub polygons is still at present speculative. Direct evidence for successional trends in chaparral and coastal sage scrub species is not readily available in the literature for San Diego County, nor can it be easily determined. Establishing successional trends requires knowing the species composition at historical times (as well as at present) and such historic information is not readily available for specific locations within San Diego County. It would be useful to re-examine the VTM plots for chaparral and coastal sage scrub and compare them to the VTM plots for blue oak woodlands evaluated by Allen-Diaz (1993) and to the fire maps compiled by the California Department of Forestry and Fire Protection. However, such evaluation was beyond the scope of this project.

Within forests and woodlands, studies have evaluated the accuracy of VTM plots over time. For example, Allen-Diaz (1993) found little natural change in species composition in VTM plots within blue oak woodlands in the Central Valley but some increase in the size and number of oak species individuals over a period of 50–60 years. Minnich et al. (1995) reported gradual species change in VTM plots within the San Bernardino Mountains from *Pinus ponderosa* Laws. and *P. lambertiana* to *Abies concolor* (Gordon & Glend.) Lindley and *Calocedrus decurrens* (Torrey) Florin attributable to fire suppression. Some of these changes were attributable to effects of air pollution on beetle-induced mortality and seedling recruitment of pine species (Miller et al. 1997). However, these studies did not report wholesale replacement of species within forested and wooded VTM plots.

Other discrepancies observed between GAP predictions and data from the surveyed sample elements could be attributed to the GAP database. For example, the GAP database predicted species which are not recognized by local botanists as present in the county. Some of these discrepancies appear to be due to taxonomic distinctions (*Arctostaphylos tomentosas* listed by GAP in place of *A. glandulosa* or *Quercus cornelius-mulleri* listed by GAP in place of *Q. berberidifolia*). Fortunately, these discrepancies may have little impact on the utility of the GAP database for use in assembling BHC emission inventories because taxonomically-related species were found instead. We have shown that taxonomy can be a strong predictor of BHC emission rates, especially at the genus level (Benjamin et al. 1996).

Despite the discrepancies between predicted and observed plant species cover, on average the utility of the GAP database for developing BHC emission inventories appears to be adequate. Even though some plant species predicted by the GAP database were not present or were present at lower levels than expected for a co-dominant species, these discrepancies will not necessarily translate into significant errors in BHC emission inventories. For the purpose of the development of such BHC emissions inventories, species composition errors have adverse effects only when a plant species listed in GAP as a co-dominant for a polygon should actually be a species with a significantly different measured BHC emission rate. For example, if a codominant listed by GAP is a high isoprene-emitting species, but the actual plant species which occurs in the polygon is a low- or non-emitting species, the resulting BHC emission flux calculated for that polygon will over-estimate isoprene emissions. In contrast, for cases where a low-emitting species occurs in place of another low-emitting species (for example, *Adenostoma fasciculatum* in place of *Cercocarpus betuloides* Torrey & A. Gray), the error may be significant with respect to correct species assignment in GAP, but have minimal effect on the resulting BHC emissions inventory.

In order to evaluate the significance of species discrepancies between the GAP listings and the field surveys, the indices identifying the polygons with the largest biogenic hydrocarbon emissions based on GAP (see above) were recalculated for the eight polygons investigated in this study using the observed percent covers of plant species within each polygon. Values of the indices were calculated by summing the isoprene or monoterpene emission rates of the plant species in a given polygon, weighted by their percent relative cover, and multiplying this sum by the area of the polygon. For all eight polygons, total isoprene emission and total monoterpene emissions were calculated based on the survey data, and these were compared with the totals generated during the polygon selection phase of the study based on the GAP data. Although for some individual polygons the discrepancy between the indices obtained for GAP species vs observed species was quite large, when summed over all eight polygons the differences in the total emission indices were negligible. Thus, the total isoprene emission for the eight polygons based on the survey data was only 7% greater than the total calculated using the GAP data, while the total monoterpene emission for the eight polygons based on the field survey data was just 2% lower than the GAP derived total. Clearly, the GAP GIS database can be a useful source of species composition and dominance information for the purpose of assembling BHC emission inventories when a sufficiently large number of polygons are averaged.

Finally, the observation of numerous species in high-enough abundance to be designated as codominants but not listed in the GAP database is to be expected given that GAP designates only six codominants per polygon, three in the primary assemblage and three in the secondary assemblage. A species assemblage with only three co-dominants may not necessarily capture the species composition within a polygon.

Limitations in the present GAP field assessment. Our survey data indicated a difference in the accuracy of primary versus secondary assemblages in GAP. Primary assemblage co-dominants were correctly listed by the GAP database more often than secondary assemblage species. In a GAP polygon, primary assemblages by definition are more prevalent. In the present study, a sample element was more likely to be placed in the more prevalent assemblage, resulting in the gathering of more data on primary assemblage species and higher representation by those species. With use of only three or four elements, there was a smaller chance of sampling a species from a secondary assemblage with a frequency proportional to the area occupied by that assemblage. In a study with more resources, and hence a larger number of randomly-placed sample elements, representation by species from either assemblage should be proportional to that assemblage's cover within the polygon.

Limitations in siting the sample elements may have accounted for other discrepancies as well. By sampling only near roads, away from polygon boundaries, and only with the permission of land owners, large areas were removed from inclusion in the study. These limitations were recognized and accepted as a condition to performing this type of survey. Observations from a distance and input from individuals knowledgeable about local botany were helpful in identifying additional plant species outside the selected sample elements but did not add to the quantitative characterization of vegetation cover reported here.

As noted earlier, the GAP assessment in San Diego County posed special problems in terms of sampling representative areas within privately-owned parts of a polygon. In the Utah GAP validation project, 42% of the state was under the control of the US Bureau of Land Management, with private interests owning only 21% (Edwards et al. 1995). In San Diego County, the San Diego County Association of Government (SANDAG) 1990 ownership database indicated private interests owned 41% of county land (SANDAG 1997). Private land owners typically purchase land in accessible areas within the vicinity of roads, and therefore, suitable public lands within the vicinity of roads for the purposes of conducting a GAP assessment were limited. Although a 14% success rate for our mailers seeking property access was high by the standards of some surveys, obtaining permission to access private property was a limiting factor in being able to site sample elements.

These access limitations present possible biases related to not being able to survey private lands. Observations from roadsides and hilltops suggested that land use on private lands in the areas investigated did not differ appreciably from land use on public lands in these areas. Nevertheless not being able to survey more private lands resulted in potential sampling bias from this constraint on selecting random sample elements. For example in polygons C2 and S1, certain areas were removed from the random selection process due to private ownership. If such areas had been available for sampling and could have been included in the random selection process, better correlation between survey data and the GAP database might have been observed.

Additional potential biases exist due to sampling only eight of the original 437 GAP polygons within western San Diego County. However, the sample size for our purposes was relatively large, since the eight polygons studied were selected from a subset of 40 polygons believed to be the highest isoprene or monoterpene emitting polygons, respectively. Thus, high-emitting polygons were well represented. Although a bias existed for undersampling the low-emitting polygons, the likelihood of low-emitting polygons actually being high-emitting polygons was not significant since a relatively small number of plant species are high-emitting (Benjamin et al. 1996).

Given the effort needed to gather the field data, it was necessary to reduce the area sampled. Moreover, the sample area required to estimate the true relative cover of individual species in a polygon was not known. The literature suggested surveying 7% of a forested area using parallel belt transects provided a 65% chance the sample mean of the basal area of the trees would be within 10% of the true mean for more common species (Bormann 1953). The effort needed to obtain an accurate measure of relative cover may be similar. In the present study, the belt transects directly sampled 1.8 hectares within polygons of about 1800 to 2300 hectares, or about 0.1% of the polygon area. The line transects approximating 3 m belt transects directly sampled 0.72 hectares in polygons ranging in size from 3600 to 6600 hectares, or about 0.01%. On the other hand, the effective size of our samples may be larger. The vegetation cover composition within the transects may approximate the cover composition of a square which immediately bounds the ends of the perpendicular transects. If this was the case, the three sample elements in each forest/woodland polygon may have effectively sampled 75 hectares or about 4% of the polygon area, while the four sample elements in the chaparral/scrub polygons may have effectively sampled 36 hectares or about 1% of the polygon area.

A more intensive sample design could have allowed the surveying of plants that were missed in the current surveys. The anecdotal comments about the existence of *P. lambertiana* at higher elevations in polygon F1 suggest a more intensive sampling effort could address these omissions. Although large sample elements avoids quantifying heterogeneity below the intended resolution of the map, using large sample elements given finite time and resources results in oversampling certain areas at the expense of undersampling other areas. An alternative using shorter transects or recording data along regular intervals (e.g., recording data along 50 m for every 100 m) could result in less time being invested per survey element, allowing for the inclusion of more survey elements. However, constraints resulting from the lack of permission to access certain properties make this option difficult to freely implement.

CONCLUSIONS

A ground-based assessment of the GAP database for San Diego County for the purpose of evaluating its utility in the development of BHC inventories revealed the database was a useful source for data on species composition and abundance. The species listed by GAP accounted for two-thirds to three-quarters of the relative cover in selected polygons. About 60% of the species listed by GAP were found in high enough proportions in the field surveys to justify their listing. For certain species listed in GAP but not found in high abundance in the field surveys, taxonomically similar species were found. Discrepancies between the field observations and the GAP database could be explained by inaccuracies of the initial data sources incorporated into GAP, successional changes, limitations in sampling design, the arbitrary limiting of GAP to six species per polygon, and bias in sample site selection towards areas accessible by roads and public ownership. Nevertheless, overall comparisons between the BHC emission indices calculated using GAP data and the corresponding BHC emission indices calculated based on our field survey plant cover data indicate the utility of the GAP database in the development of BHC emission inventories.

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DISJUNCT POPULATIONS OF *TRIFOLIUM BECKWITHII* (FABACEAE) IN EASTERN SOUTH DAKOTA: VICARIANCE OR RECENT LONG-DISTANCE DISPERSAL? A PRELIMINARY ANALYSIS

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ABSTRACT

Trifolium beckwithii Brewer ex. S. Wats. is widespread in the Sierra Nevada and northern Rocky Mountains but five disjunct populations have existed for at least a century in a considerably different habitat in eastern South Dakota. Genetic divergence of these populations was expected. RAPD profiles were compared between South Dakota and two montane populations. Unexpectedly, measures of genetic similarity between South Dakota and northern California populations were twice as great as those between South Dakota and southern Idaho populations. These data can be interpreted as an indication that *T. beckwithii* has been introduced relatively recently into South Dakota from a population genetically similar to the one sampled from northern California.

Trifolium beckwithii Brewer ex. S. Wats. is a low growing, rhizomatous, perennial clover endemic to the western U.S. and commonly known as buffalo or Beckwith's clover. Beckwith's clover is distinguished from congeneric species by spherical heads of subsessile purple or rose-purple flowers and with narrowly elliptic, glabrous leaflets. The species is found primarily in montane meadows of the Sierra Nevada Mountains in northern California and Oregon ranging eastward to the Rocky Mountains of southwestern Montana (Fig. 1). It typically occurs in moist, streamside meadows at elevations of 1,200 to 2,125 meters above mean sea level (msl) (Gillett 1972). Unexpectedly, disjunct populations of this species also occur historically at five sites in extreme eastern South Dakota in moist tallgrass prairies located in the upper Big Sioux River watershed. These sites are at only 500 to 600 meters above msl and about 1200 km east of the nearest population which is in southwestern Montana (Fig. 1). These sites are closely clustered and do not extend into nearby Minnesota (Cholewa personal communication). The earliest report of these disjunct populations extends back a century (Saunders 1899).

To our knowledge no other species of plant has this distribution. The most similar phytogeographical patterns are those of species that occur in the northern Rocky Mountains with disjunctions in the Black Hills of western South Dakota and/or along the Great Lakes, e.g., *Adenocaulon bicolor* Hook, *Habenaria unalascensis,* (Sprengel) S. Watson and *Vaccinium membranaceum* Hook. (Marquis and Voss 1981). Disjunct distributions can be explained in two ways: 1) vicariance; and 2) long distance dispersal. Under the first of these two hypotheses, *T. beckwithii* in eastern South Dakota is a relict of a widespread and relatively old distribution. The habitat of the South Dakota populations of *T. beckwithii* has been significantly different from that of the cordilleran populations for at least several thousand years; a habitat that was frequently burned, periodically grazed by large bison herds, and subjected to irregular periods of drought. Note that the rhizomatous habit of *T. beckwithii* is preadapted to the prairie regime. Under this hypothesis the South Dakota populations, long isolated from the montane populations and environment, would be expected to exhibit substantial divergence when compared with montane populations of the species, and would not be expected to show significantly greater similarity to any one of the montane populations.

Alternatively, the species may have been introduced from the more typical western populations relatively recently. Humans are the most likely agents of dispersal since neither seeds, fruits, nor vegetative cuttings of *T. beckwithii* appear to be harvested by birds or other wide-ranging species. According to this hypothesis, little divergence of *T. beckwithii* in South Dakota would be expected when compared to montane populations, and greater similarity would be observed with the parent population from which the South Dakota populations were derived.

Divergence patterns related to geography might be expected to be reflected in morphological characters. Consequently, 112 herbarium specimens representing both cordilleran and South Dakota populations were measured with respect to the following characters: lengths and widths of stems, petioles, peduncles, leaflets, stipules, and inflorescences; lengths of calyces and calyx teeth, total corolla, wing petals, keel petals, stamens, anthers, styles, pods, and seeds, and finally the number of seeds per fruit. Variation in vegetative features in

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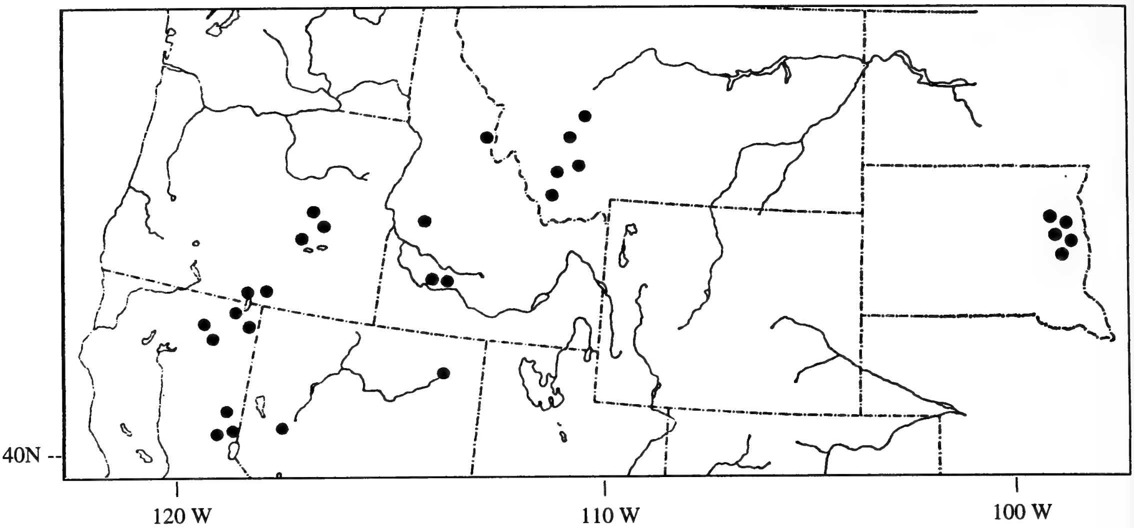

FIG. 1. Distribution of *Trifolium beckwithii,* adapted from Gillett (1972).

particular was considerable but with no correlation between variation in any features and geographic origin (Larson unpublished). Consequently, we chose to investigate genetic differences by assessing divergence in molecular characters.

Our specific objective was to assess the extent of divergence of a disjunct population of *T. beckwithii* in eastern South Dakota from two selected cordilleran populations by analysis of Random Amplified Polymorphic DNA's (RAPD's). The RAPD technique was first described by Williams et al. (1990). RAPD analysis allows the determination of the distribution of dominant DNA markers within populations. These markers are variable within populations of organisms and the technique has been successfully used to assess genetic variation in diverse plant species (reviewed in Newbury and Ford-Lloyd 1993). The RAPD technique does not require prior knowledge of target DNA sequences, an advantage when initiating research on a little-studied species.

MATERIALS AND METHODS

Material of *Trifolium beckwithii* was obtained from five individuals in each of three populations (Table 1). Seeds were obtained from the Western Regional Plant Introduction Station (WRPIS) at Pullman, Washington which had been collected from a site in Sierra County, northern California, near the Nevada border. These seeds were grown into 60-day old plants before harvest. Shoots were collected from a second site in Camas County in southern Idaho and immediately packed with silica gel for delivery to South Dakota State University prior to processing. Fresh shoots were also collected from a sparse population consisting of five individuals, in Rauville prairie in Codington County, South Dakota. Attempts at this same time (June 1997) to locate *Trifolium beckwithii* at two other previously documented sites for the species in South Dakota (Aurora Prairie, Brookings County and Quail Prairie, Deuel County) failed to locate any specimens either suggesting localized extinction or prolonged dormancy due to unseasonably wet and cool conditions.

Nucleic acids were extracted from leaves of each accession by the CTAB method (Doyle and Doyle 1987) and RNase-digested by standard procedures. Final concentrations of extracts were diluted to approximately 50 ng/μl. Sixty-three random decanucleotide primers were obtained for initial screening (Operon Technologies Inc., Alameda, CA). To min-

TABLE 1. COLLECTIONS OF *TRIFOLIUM BECKWITHII* USED FOR RAPD ANALYSIS.

Location	Date	Collectors	Voucher or WRPIS collection number
Sierra County, CA	Aug. 1995	N. Taylor, K. Quesenberry and J. Descries, Western Regional Plant Introduction Station, Pullman	C-107
Camas County, ID	May 1997	J. Smith, Boise State University	J. Smith, 3707
Codington County, SD	June 1997	M. Duvall and G. Larson, South Dakota State University, Brookings	G. Larson, s.n.

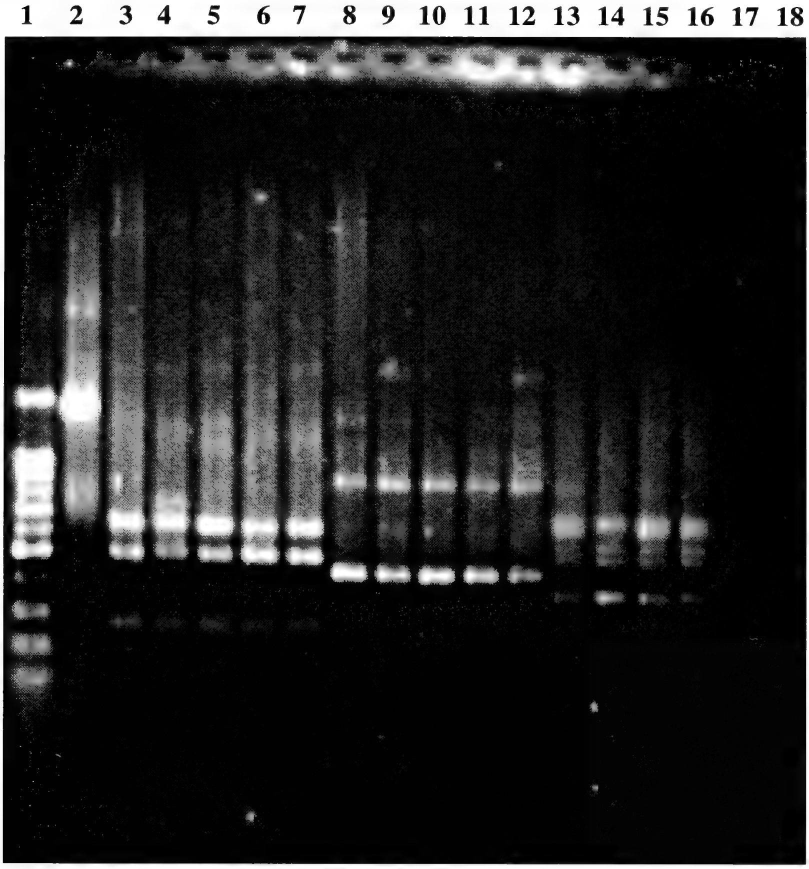

FIG. 2. Representative RAPD profiles (primer, OPB-11) of 15 individual accessions of *Trifolium beckwithii* from three sites after electrophoresis in a 0.8% agarose gel. Lane 1: 100 base pair ladder; Lane 2: amplification control; Lanes 3–7: northern California templates; Lanes 8–12: southern Idaho templates; Lanes 13–17: eastern South Dakota templates (note that the one template in lane 17 failed to amplify, as was typical); Lane 18: negative control (no template).

imize contamination, reactions were prepared in a laminar flow hood with a set of dedicated micropipettors using aerosol resistant tips. RAPD reactions were set up in Promega reaction buffer (final concentration of $MgCl_2$, 1.5 mM) with 0.02 mM dNTPs, 5 pmoles random primer, approximately 20 ng template DNA, and 1.25 units of Taq DNA Polymerase (Promega Corp., Madison, WI). At least one negative control was included with each set of reactions in which sterile water was substituted for the template DNA. Amplifications were performed in a PTC100 thermal cycler (MJ Research, Inc., Watertown, MA). After a hot start (94°C for 2.0 min), 45 amplification cycles of denaturation (94°C for 0.5 min), annealing (30°C for 1 min), and polymerization (72°C for 2 min) were performed with a final extension at 72°C for 10 minutes. Amplified fragments (20 μl of each reaction) were separated electrophoretically on 0.8% agarose gels in TBE, stained with ethidium bromide, visualized under short wavelength UV, and photographed. A 100 base pair ladder (Promega Corp., Madison, WI) provided molecular size markers. A representative photograph of a gel is given (Fig. 2). After the initial screening, primers which produced polymorphic RAPD profiles were run at least one additional time. Bands were observed directly on the photographs of the gels and scored as binary presence/absence data for each template. Jaccard coefficients (Table 2) were calculated for each pairwise comparison of individual accessions as a measure of genetic similarity (Jaccard 1908). These coefficients were selected since negative matches are appropriately excluded from the similarity measure. Mean Jaccard coefficients were calculated for each pairwise population comparison (Table 3). Unweighted pair group method of analysis (UPGMA) cluster analysis (Sokal and Sneath 1973) was performed on the binary data as implemented in PAUP* 4:0 (Swofford 1998, Fig. 3).

RESULTS

Of the 63 original random primers, 30 gave reproducible polymorphic profiles and no amplified

TABLE 2. PAIRWISE JACCARD COEFFICIENTS BY ACCESSION.

	CA2	CA3	CA4	CA5	ID1	ID2	ID3	ID4	ID5	SD1	SD2	SD3	SD4
CA1	0.643	0.695	0.717	0.690	0.160	0.141	0.116	0.123	0.105	0.225	0.230	0.338	0.237
CA2		0.633	0.683	0.600	0.197	0.188	0.175	0.203	0.192	0.258	0.197	0.308	0.203
CA3			0.817	0.793	0.162	0.212	0.200	0.183	0.202	0.246	0.209	0.368	0.197
CA4				0.754	0.157	0.204	0.193	0.176	0.195	0.254	0.200	0.352	0.188
CA5					0.197	0.217	0.190	0.188	0.207	0.235	0.179	0.319	0.167
ID1						0.579	0.589	0.555	0.571	0.159	0.133	0.111	0.119
ID2							0.904	0.678	0.690	0.107	0.083	0.139	0.086
ID3								0.661	0.617	0.093	0.084	0.141	0.087
ID4									0.736	0.132	0.091	0.151	0.094
ID5										0.141	0.101	0.158	0.104
SD1											0.605	0.622	0.639
SD2												0.511	0.636
SD3													0.500

products in the negative controls. One of the five individual DNA extracts from the South Dakota population consistently failed to amplify and eventually this accession was omitted from the analysis. A total of 105 bands were scored from the 30 primers over the remaining 14 accessions. Each accession of *Trifolium beckwithii* had a unique RAPD profile. The number of bands for each primer were: OPA2-6, OPA5-1, OPA7-2, OPA14-3, OPA15-3, OPA16-4, OPA18-4, OPB2-3, OPB6-1, OPB8-5, OPB10-4, OPB11-8, OPB12-3, OPB13-3, OPB14-3, OPB16-5, OPB20-3, OPC3-1, OPC6-3, OPC7-3, OPC8-6, OPC10-6, OPC13-5, OPC19-1, OPD1-2, OPD9-3, OPD12-5, OPD14-2, OPD15-4, and OPD16-3. The raw data matrix may be obtained from the first author on request.

Mean intrapopulational similarity measures were relatively high, as expected, ranging from 0.586 to 0.702 and were not significantly different from each other (Anova; $P < 0.005$). All individuals clustered into their respective populations in the UPGMA analysis (Fig. 3).

Mean similarity measures between populations were highest in the comparison between South Dakota and California (0.246), intermediate between the two montane populations (0.179), and lowest between South Dakota and Idaho (0.116 Table 3). Mean pairwise interpopulational similarity measures were, in every case, significantly different from each other (Anova; $P < 0.001$). The South Dakota accessions clustered with the northern California accessions in the UPGMA analysis (Fig. 3).

DISCUSSION

The distribution of *Trifolium beckwithii* is uniquely different from that of thousands of other plant species found in the western U.S. Such a distribution may suggest a similarly unique underlying origin. Perhaps the first attempt to explain this disjunct pattern was by a doctoral student working on a revision of native U.S. *Trifolium* spp. who suggested that the eastern populations had been introduced from the west (Martin 1943). Gillett (1972) disagreed because the most distantly separated South Dakota populations are nearly 100 km apart and the five individual sites are relatively isolated from each other necessitating either five separate introductions from farther west or a series of regional movements after the original introduction. Furthermore, *T. beckwithii* in eastern South Dakota is restricted to pristine native prairie habitats, a characteristic not expected of a recently introduced species. In either case no likely agent of dispersal is known.

Although Gillett did not propose an alternative explanation, a logical possibility is vicariance. Perhaps *T. beckwithii* in South Dakota was once part of a continuous range which originally extended across the state and into Montana, most likely during the retreat of Wisconsin glaciation (ca. 15,000 to 10,000 years ago), and has contracted into its current distribution because of unfavorable climatic changes or other factors. Note that *T. beckwithii* is preferred as forage by livestock (Larson and Duvall personal observation)

TABLE 3. MEAN PAIRWISE JACCARD COEFFICIENTS OF GENETIC SIMILARITY BY POPULATION.

	Montane, northern California	Montane, southern Idaho	Prairie, eastern South Dakota
Montane, northern California	0.702	0.179	0.246
Montane, southern Idaho		0.658	0.116
Prairie, eastern South Dakota			0.586

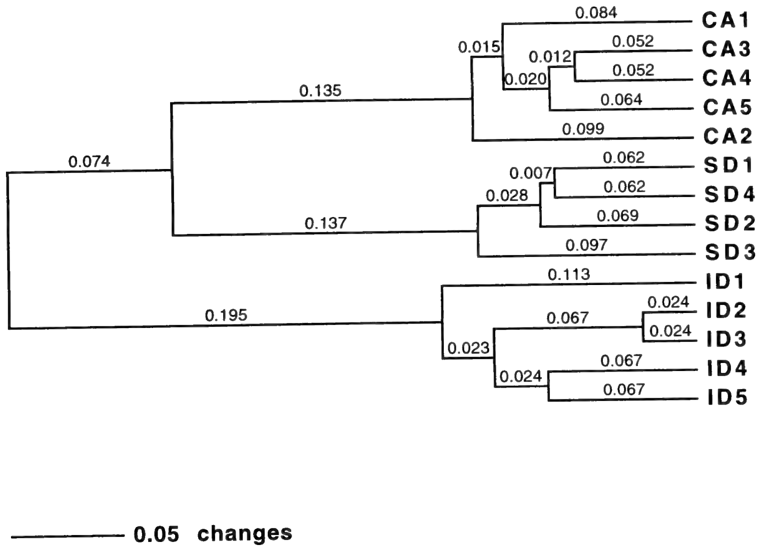

FIG. 3. UPGMA cluster analysis of 105 RAPD loci from 14 accessions of *Trifolium beckwithii* collected from three sites. Labels indicate the site of origin of each individual; CA1–5: northern California site; ID1–5: southern Idaho site; SD1–4: eastern South Dakota site. Branch lengths are given as calculated from simple matching coefficients. The scale bar represents a branch length of 0.05.

and perhaps by other grazing animals. Under this scenario, the implication is that *T. beckwithii,* the only clover native to South Dakota, should be considered endangered in the state, especially given evidence of its recent decline, and state conservation efforts and resources should be expended on behalf of this regionally rare species.

Paradoxically, the RAPDs data presented here do not support the vicariance scenario. Mean genetic measures among the three widely separated populations show a remarkable pattern. The eastern South Dakota and northern California populations have over twice the genetic similarity of the South Dakota and southern Idaho populations which are geographically nearer. Recall that this result has strong statistical support (interpopulational means are significantly different at $P < 0.001$). These data thus appear to support an original dispersal event, sometime prior to 1899, from a parent population genetically similar to the one sampled here from northern California. Given the isolation of South Dakota populations from cordilleran populations and the propensity for vegetative reproduction in *T. beckwithii,* preservation of the original genetic profile over the last century is likely. Note that genetic variation within each of the three populations sampled here is not significantly different suggesting that the propagation mechanisms which affect genetic diversity in the species are not geographically dependent.

These data thus suggest that *T. beckwithii* is a relatively recent immigrant to eastern South Dakota, and neither morphological nor molecular evidence indicate taxonomic distinction of the South Dakota isolate. However, given our limited sample size (five individuals in each of only three populations), recommendations for conservation measures at the federal level based on only these data would be premature and require additional populational analysis.

ACKNOWLEDGMENTS

We thank James F. Smith (Boise State University, Idaho) for collecting material from one population and Arvid Boe (South Dakota State University) for contacting the Western Regional Plant Introduction Station to obtain seeds and for helpful discussions. We also thank Barb Ingram for technical assistance. This research was supported by a grant from the South Dakota Department of Game, Fish, and Parks, Wildlife Division.

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NOTES

OBSERVATIONS ON THE MORPHOLOGY AND GEOGRAPHIC RANGE OF *ANTENNARIA DIOICA* (L.) GAERTN. (ASTERACEAE: GNAPHALIEAE).—Randall J. Bayer, CSIRO, Plant Industry, Australian National Herbarium, GPO Box 1600, Canberra, ACT, 2601, Australia.

ANTENNARIA DIOICA (L.) Gaertn. (Asteraceae: Gnaphalieae) is widely distributed across Eurasia from the British Isles to Japan and its range extends east into North America only in the western most Aleutian Islands (Bayer, 1993; Bayer and Stebbins, 1993). It is characterized by having glabrous adaxial leaf surfaces and phyllaries with pink or white laminae. The circumscription of *A. dioica* in North America has long been a topic of debate, as *A. marginata* (syn. = *A. dioica* var. *marginata* (Greene) Jeps.) of the southwestern United States bears a remarkable similarity to *A. dioica.* The two species differ in that *A. dioica* has the upper flowering stems lacking glandular hairs and the stolon surface is pubescent, but not densely woolly, whereas in *A. marginata* the upper flowering stem is usually beset with purple glandular hairs and the stolon surface is densely woolly obscuring the surface of the stolon. The species are also strongly allopatric, therefore it seems best to recognize the two as distinct species (Bayer and Stebbins, 1993). No other species in North America is so similar to *A. dioica* as to pose a difficulty in determination.

Recently, Chmielewski (1998) reported a large range extension for *A. dioica* from the Aleutian Islands to the Sierra Nevada, a distance of ca. 5,000 km. *Antennaria dioica* (*sensu* Bayer and Stebbins, 1993) has not previously been reported for California (Stebbins and Bayer, 1993). After examining the herbarium specimen upon which the range extension is based (California, Sierra Nevada, "Among granite fell-fields & scattered *Pinus albicaulis* near Margaret Lakes, east of Bishop Pass, no. Inyo Co. Elev. 10,800 ft., 7-19-62, *Betty H. Johnson #692,*" CAS 898202!), I came to the conclusion that this collection represents atypical individuals of *A. media* Greene (= *A. alpina* var. *media* (Greene) Jeps.).

Chmielewski (1998) states that "The single collection of *Antennaria dioica* that is the basis of this report consists of three staminate shoots . . .", however, also on the sheet are seven other staminate flowering stalks and their associated basal leaves and stolons.

These seven specimens are part of the same collection and in my view represent typical staminate plants of *Antennaria dioica*. They have strongly pubescent basal leaves, narrowly spathulate basal leaves, flagless[1] upper cauline leaves, and the papery laminae of the phyllaries are olivaceous to brown or black in color. The fact that the leaves of all ten flowering stalks mounted on the herbarium sheet lack flags distinguishes them from *A. alpina* (L.) Gaertn., which possesses prominent flags. The length of the staminate florets is greater than 3.5 mm, which separates these specimens from the closely related diploid species, *A. pulchella.* E. Greene, which has florets shorter than 3.0 mm (Bayer 1990). The observation that the adaxial surfaces of the leaves are pubescent and the capituli are relatively small and the laminae of the phyllaries are dark colored, distinguishes them from *A. marginata,* E. Greene which has leaves that are glabrous adaxially and has relatively large heads with white tipped phyllaries.

The three specimens (Fig. 1, arrows), referred to as *A. dioica* by Chmielewski (1998), appear to be those with pink flecking in the lamina of some of the phyllaries, although the entire sheet, i.e., all ten specimens, is annotated as *A. dioica* by chmielewski (Fig. 1). A fourth specimen with pink flecking in the lamina is in a fragment folder on the sheet. It appears that all of these specimens came from the same clone, as their leaves, stem height, phyllary color, and stage of maturity seem to be identical (Fig. 1, arrows). I would determine these three (four counting the specimen in the fragment folder) specimens as either *A. media* or later generation hybrids between *A. media* and *A. rosea* Greene, not *A. dioica.*

The basal leaves of the specimens are heavily pubescent on both the abaxial and adaxial surfaces and resemble the other eight specimens of *A. media* on the sheet. *Antennaria dioica* usually has glabrous adaxial leaf surface, less often are these surfaces subglabrous (Tutin et al. 1976; Hultén 1968; Bayer and Stebbins 1993). As for the phyllary color, my examination of the material leads me to conclude that these three staminate plants do not bear "pink bracted involucres" (c.f. Chmielewski 1998). The base of the papery lamina is olivaceous-black, the tips of some are white, whereas others are reddish-pink or white with reddish-pink flecks. The entire involucre of these three plants gives the impression of being white spotted with reddish-pink. Typical *A. dioica* has heads in which laminae are entirely white, pink or rose. Phyllary color in *A. dioica* is a sex-linked trait; the laminae of the *staminate* plants usually being white, whereas those of

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[1] Flags are flat, linear, scarious, tips that are similar to the tips of the phyllaries not to be confused with ordinary subulate or blunt leaf tips that are essentially green and herbaceous.

FIG. 1. Partial view of herbarium sheet (CAS #898202) showing staminate plants of *Antennaria media*; reputed specimens of *A. dioica* indicated with arrows. Scale as indicated on figure.

the *pistillate* plants are normally pink or rose (von Ubisch 1930), therefore the situation we see in these specimens is the opposite of the usual phyllary color in staminate *A. dioica.* Typical *A. dioica* do not usually have a large dark olivaceous or black spot at the juncture of the base of the phyllary and the papery lamina, as do the three (four) specimens in question. I believe that the pink flecking in these specimens is simply the expression of a rare character, not normally seen in *A. media.* The same rose flecking is also seen in the phyllaries of some specimens of *A. umbrinella* Rydb. (see discussion under *A. umbrinella* in Bayer and Stebbins 1993), whose laminae are normally light to dark brown. I also have made the same observation in *A. anaphaloides* Rydb and *A. pulcherrima* (Hook.) Greene (Bayer personal observation). It is also possible that the specimens in question represent later generation backcross hybrids between *A. media* and *A. rosea, E. Greene,* the pink or red phyllary character being a typical trait of *A. rosea* subsp *rosea.*

The protoplasts of pollen grains from a typical Scandanavian *A. dioica* (taken from CANB 11884 and stained with Alexander's stain (Alexander 1980)) are an average of 21.3 μ in diameter and 87.5% of the grains stained viable. The dark-phyllaried typical *A. media* specimens on the sheet, i.e., those without the pinkish flecking in the phyllaries, are an average of 27.2 μ in diameter with 90% viability. The size difference in the protoplasts is typical of diploid (*A. dioica*) vs. tetraploid (*A. media*) pollen (Bayer unpublished). If the three specimens in question were *A. dioica* one would expect the pollen to be around 21 μ in diameter and to be reasonably viable, thus distinguishing them from the other plants on the sheet. Unfortunately, they are sterile, the anthers are empty, not producing any identifiable pollen even though the flowering stalks are of mature height and the phyllaries are mature. This is highly supportive of the idea that these plants may represent hybrids between *A. media* and *A. rosea,* which grow in sympatry throughout the Sierra Nevada.

In summary, I believe the three specimens (four including the one in the fragment folder) in question on CAS 898202 (*Johnson #692*) to be somewhat atypical staminate plants of *A. media* with some pinkish or rose flecking in the laminae of the phyllaries. The reddish-pink phyllary color may be due to introgressive hybridization between *A. media* and *A. rosea.* I maintain that the distribution of *A. dioica* is mainly Eurasian, with a few populations in the Aleutian Islands of Alaska. Therefore, *Antennaria dioica* is not a part of the flora of California, and the only North American populations are in the Aleutian Islands.

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A NEW *BOERHAVIA* (NYCTAGINACEAE) FROM SONORA, MEXICO

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ABSTRACT

Boerhavia traubae (Nyctaginaceae: Nyctagineae; Nyctagininae) is described as a new species from Municipio de Yécora, Sonora, Mexico, in the immediate vicinity of the village of Yécora. It is restricted to mudflow deposits probably of late Miocene age. This delicate annual is distingushed from other species of *Boerhavia* by its small size, its persistent small bracts that are glabrous except for minute marginal trichomes, its few-flowered subumbellate inflorescences, and by its smooth clavate fruit with sharply acute ridges. It is estimated to be most closely related to *B. purpurascens* A. Gray and *B. wrightii* A. Gray.

RESUMEN

Boerhavia traubae (Nyctaginaceae: Nyctagineae; Nyctagininae) es descrita como una especie nueva de Sonora, México. Esta especie se encuentra en el municipio de Yécora, en los alrededores del pueblo de Yécora. Se encuentra restringida a los depósitos de lodolita del Mioceno o mas tarde. Esta anual delicada se distingue de otras especies de *Boerhavia* por su tamaño pequeño, sus brácteas pequeñas, persistentes y glabras excepto por tricomas diminutos en los márgenes, sus inflorescencias subumbeladas con pocas flores y por sus frutos clavados y lisos, con costillas prominentes agudas. Se estima que los relativos más cercanos de esta especie son *B. purpurascens* A. Gray y *B. wrightii* A. Gray.

Recent general collecting activities by Dr. Tom Van Devender, his wife, Ms. Ana Lilia Reina G., and their associates, toward the production of a flora of the Municipio de Yécora, in east central Sonora, Mexico, very near the Chihuahua border, have resulted in the discovery of several new plants. Specimens from the Yécora area, a botanically poorly known region, have provided holotypes or paratypes for 27 taxa since 1987, 16 since Dr. Van Devender and Ms. Reina began their study of the Yécora flora in 1995. Two such new taxa were the annual Asteraceae, *Pectis vandevenderi* B. L. Turner and *Tridax yecorana* B. L. Turner, associates of the distinct *Boerhavia,* here described. Herbaria abbreviations used in this paper follow Holmgren et al. (1990).

Boerhavia traubae Spellenb., sp. nov. (Fig. 1) —Type: SONORA, Mcpio. de Yécora, 1.6 km E of Yécora on Mex. Hwy. 16 at KM marker 281.5, 28°22.30′N, 108°54.71′W, elev. 1645 m, 15 Aug 1998, *Spellenberg, Brouillet & Todsen 12597* (holotype: NMC; isotypes: ARIZ, CIIDIR, ENCB, IEB, MEXU, MT, NY, USON). Paratypes: SONORA, all Mcpio. de Yécora: vicinity of cabañas on old road to Maycoba, 0.5 mi E of Arroyo Yécora, 28°23.5′N, 108°54.5′W, elev. 1550 m, 7 Sep 1995, *M. Fishbein et al. 2479* (ARIZ, MEXU, NMC); along westward extension of Avenida Juarez ca. 0.5 km W of cemetery, 28°22.50′N, 108°56.38′W, elev. 1645 m, 15 Aug 1998, *R. Spellenberg et al. 12596* (ASU, F, IEB, NMC, TEX); NW of cemetery in Yécora, 28°22′40″N, 108°56W′, elev. 1540 m, 2 Sep 1997, *W. Trauba s.n.* (NMC); 1.9 km SSW of Las Viboras on Mex. 16 on road to Trigo Moreno, 28°21′50″N, 108°49′34″W, elev. 1620 m, 17 Aug 1998, *T. Van Devender et al. 98-991* (ARIZ, ASU, CIIDIR, ENCB, MEXU, NMC, UC, USON); ca. 2 km NW of Yécora on old road to Santa Rosa, 28°22′45″N, 108°50′45″W, elev. 1560 m, 5 Sep 1996, *J. F. Wiens et al. 96-109* (NMC).

Herba annua tenella; caules 1–3, 10–30 cm alti patenter villosi; folia petiolata sursum parvescentia in caulibus, pro parte maxima in plantae tertia parte inferiore locata, folia inferiora petiolis 3–7 mm longis, laminis ovalibus vel oblongis, 5–16 mm longis, 4–9 mm latis; inflorescentia glabra ramis in fasciculos sumbellatos 1–5-florales terminantibus; bracteae florales 1–1.5 mm longae, late lanceolatae glabrae marginibus ciliatis; perianthum 2 mm longum super ovarium, 3.5 mm latum, pallide roseum; fructus clavatus, 2.5–2.8 mm longus, glaber laevis, aristis 5 acutis, ad basem sulcis quasi aequilatis.

Plants delicate annuals 10–30 cm tall, with 1–3 stems; *stems* with minute, bent white flat hairs near base, these becoming mixed with dense spreading

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FIG. 1. A) Habit of *B. traubae* (from isotype at IEB); B) Fruit; C) Bract from beneath flower. Illustration by Rogelia Cardenas.

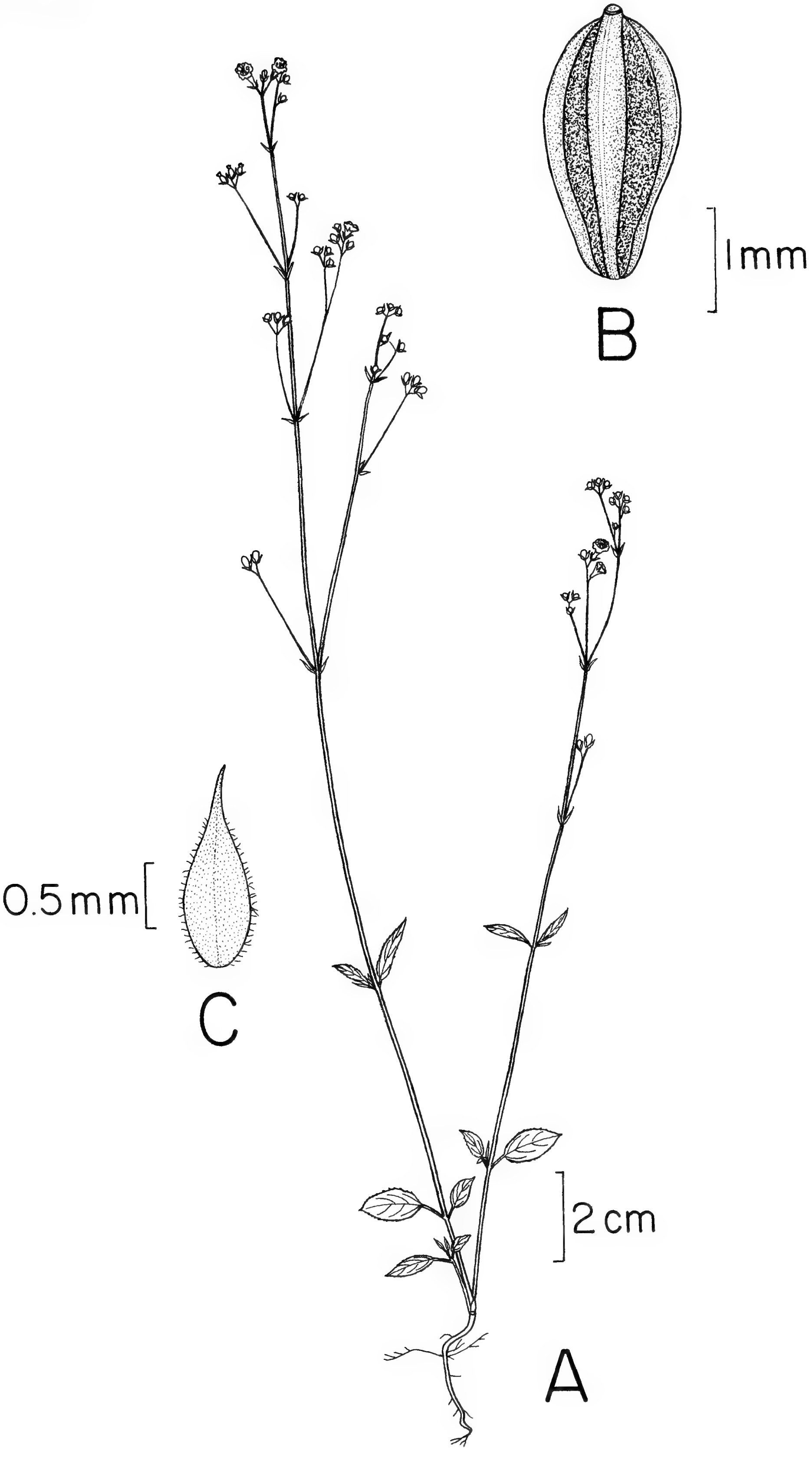
1mm
B
0.5mm
C
2cm
A

TABLE 1. COMPARISON OF FEATURES OF *BOERHAVIA PURPURASCENS*, *B. TRAUBAE*, AND *B. WRIGHTII*.

Character	*B. purpurascens*	*B. traubae*	*B. wrightii*
Stem pubescence near base of plant	Moderately pubescent with tack-shaped glandular hairs and with bent eglandular hairs	Few scattered tack-shaped glandular hairs; scattered minute bent eglandular hairs	Dense tack-shaped glandular hairs, often with spreading eglandular hairs, and with bent eglandular hairs
Pubescence on branches of inflorescence	Glabrous, or puberulent with bent hairs, or pubescent with tack-shaped glandular hairs and with bent hairs	Glabrous	Dense with tack-shaped glandular hairs and with bent hairs
Terminal clusters in inflorescence	Capitate, branches joining very near to same point	If >2 flowers, branches not all joining at same place	Racemose
Number of flowers per cluster	2–7	1–5	6–22
Bract length, mm	2.5–3.5	1.1–1.5	1.8–3.0
Ratio: bract length to fruit length	0.9–1.2	0.3–0.5	0.5–1.5
Bract pubescence	Glabrous or shaggy hairs on back; shaggy hairs on margin	Glabrous, or with few, small marginal hairs	Glabrous or few shaggy hairs on back; shaggy hairs on margin
Fruit length, mm	2.7–2.8	2.5–2.8	2.2–2.5
Number angles on fruit	5	5	4 (5)
Sulcus shape and sculpturing	Deeply concave; surface appearing pebbled; lightly rugose	Deeply concave, surface smooth; few low wrinkles	Shallowly "V" shaped or almost flat; prominently cross-rugose

brownish gland-tipped hairs beneath inflorescence, all pubescence decreasing within the inflorescence; *leaves* opposite, petiolate, few and mostly in the basal 1/3 of the plant, blades glabrous, petioles with a scattering of minute white hairs as on the stem, margins minutely crisped; leaves near base of plant with very slender petioles 3–7 mm long, the blades oval or oblong, reddish beneath, 5–16 mm long, 4–9 mm wide, more distal leaves rapidly decreasing in size, the petioles 1–3 mm long, the blades lanceolate, oblanceolate, or oblong, 8–20 mm long, 2–6 mm wide, the tip round or blunt, the leaves at the base of the inflorescence on petioles about 0.5–1 mm long, the blades linear, up to 12 mm long; *inflorescence* ½ or more the height of the plant, with a well-defined main axis, at most nodes with either 1 or 2 finer, short, strongly ascending branches terminating in compact subumbellate clusters of 1–5 flowers; *bracts* 1–3 beneath each flower, persistent into fruit, 1–1.5 mm long, broadly lanceolate, attenuate, glabrous except for minute cilia on margin; perianth above ovary broadly funnelform, pale pink, with reddish bands between the lobes, ca. 2 mm long, 3.5 mm broad, 5-lobed, the lobes emarginate; *stamens* exserted, 3–3.5 mm long, filaments pink, anthers pale yellow, ca. 0.5 mm long; *style* exserted to about the same length as the anthers; *fruit* 2.5–2.8 mm long, clavate, 5-angled, glabrous, angles forming narrow ribs about as high as broad, narrowly acute along the edge, the sulci concave, the sulcus surface smooth except for slight wrinkling.

Boerhavia traubae is named for one of the collectors of the species, Reverend William Trauba of the Capuchin order of Franciscan monks. At the time of our collection he was at the Iglesia de Nuestra Señora de Guadalupe in Yécora. Reverend Trauba is an avid collector of native plants within his area of responsibility, and has been of invaluable assistance to the efforts of Van Devender, Reina, and associates toward the production of a flora of the Municipio de Yécora. Personally, I am grateful for the wonderful hospitality of Rev. Trauba and his associates during my stay with the Van Devender—Reina entourage at the monastery in Yécora.

Boerhavia traubae is known to occur only on thin, gravelly soil pockets of exposed igneous outcrops of gently rolling conglomerate mudflow, among oaks, pines, and junipers at 1500–1700 m elevation, restricted to a few kilometers from the village of Yécora (the most distant known site is 9.2 air km E of Yecora, *Van Devender et al. 98-991*). These mudflows are estimated to be mid- to late Miocene in age, or younger (Reina G. et. al., 1999). From this unusual a habitat a number of other annuals and succulent perennials new to science have also been recently discovered, such as the *Pectis* and *Tridax* mentioned in the introductory paragraph.

Boerhavia traubae is a diminutive member of the section *Spicatae* as delimited by Heimerl (1934), a group of four to six species of arid-land annuals restricted to southwestern North America and western South America, the most common of which is

B. spicata Choisy (*sensu lato*). With its persistent bracts and its sharp ridges on the fruit, the *B. traubae* seems most closely related to *Boerhavia purpurascens* A. Gray, a species known to occur within 30 km to the WSW of Yécora in Sonora near La Concepcíon and 35 km to the WNW at Tepoca. Within the region *B. purpurascens* occurs at lower elevations (200–650 m) than *B. traubae* (1550–1650 m). From Sonora, *B. purpurascens* extends northward into southeastern Arizona and southwestern New Mexico at higher elevations, also occurring in open areas, but usually on deeper sandy or gravelly soils. The fruit of *B. purpurascens* is generally similar, slightly larger, and with a prominent granular appearance to the surface of the sulci. The similarity is sufficient that plants of *B. traubae* were first identified by me as diminutive *B. purpurascens* using Kearney and Peebles (1960), Standley (1918), and Wiggins (1964). Because of my earlier misidentification the collection *Fishbein et al. 2479* was published as *B. purpurascens* in Martin et al. (1998). *Boerhavia wrightii* A. Gray also has persistent bracts, but has different fruit and inflorescence structure. The three species are distinguished in Table 1.

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I thank Dr. Jerzy Rzedowski for assistance with the Latin description, Dr. John Strother and Dr. Alan Smith with the structure of the specific epithet, Mr. Rogelio Cardenas for the fine illustration, and Dr. Tom Van Devender and his wife, Ms. Ana Lilia Reina G., for assisting our efforts while collecting this novel species and for providing follow-up information. Ms. Reina also provided valued assistance with the Spanish abstract. Luis Alberto Pérez Alvarado, a student of *Boerhavia* in México, provided valuable comments in discussion of the new species, and kindly allowed access to types of Mexican *Boerhavia* species borrowed from major herbaria in the United States on loan to ENCB.

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HEDEOMA MATOMIANUM (LABIATAE), A NEW SPECIES FROM BAJA CALIFORNIA, MEXICO

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ABSTRACT

Hedeoma matomianum grows at 1400 m on Cerro Matomí, just south of the Sierra San Pedro Mártir. Two other species also grow in Baja California, both endemic: *H. tenuiflorum* Brandegee in the Sierra San Borja and *H. martirense* Moran in the high Sierra San Pedro Mártir. *Hedeoma matomianum* differs from both in its bushier habit and more compact inflorescence and in its shorter corolla (9–12 mm vs. 17–18 and 19–25 mm). Wiggins' Flora of Baja California (1980) lists only the *Hedeoma* of the Sierra San Borja; but it is misnamed as *H. nanum* Briq. subsp. *californicum* W. S. Stewart, which is not known in Baja California. That plant resembles *H. matomianum* in habit but differs in its less compact inflorescence and its smaller calyx and its shorter corolla (8–9 vs. 9–12 mm).

RESUMEN

Hedeoma matomianum crece a 1400 m en el Cerro Matomí, inmediatamente al sur de la Sierra de San Pedro Mártir. Otras dos especies, ambas endémicas, crecen también en Baja California: *H. tenuiflorum* Brandegee en la Sierra de San Borja y *H. martirense* Moran en la Sierra de San Pedro Mártir. *Hedeoma matomianum* difíere de ambas en su hábito más arbustivo, su inflorescencia más compacta, y su corola más corta (9–12 mm vs. 17–18 y 19–25 mm). La Flora de Baja California de Wiggins (1980) lista sólo la especie de *Hedeoma* de la Sierra de San Borja, pero la nombra incorrectamente como *H. nanum* Briq. subsp. *californicum* W. S. Stewart, la cual no es conocida en Baja California. Esta última planta (*H. nanum* subsp. *californicum*) se parece a *H. matomianum* en hábito, pero difíere en su inflorescencia menos compacta, cáliz más pequeño, y corola más corta (8–9 mm vs. 9–12 mm).

Cerro Matomí is a sharp 1643 m peak on the peninsular divide a quarter of the way down the peninsula of Baja California. It is some 30 km south of the Sierra San Pedro Mártir, far the highest range on the peninsula, a massif 70 km long and over 1800 m high, with one peak of 3095 m. Upper parts of the Sierra are a climatic island largely covered with coniferous forest, with no counterpart elsewhere in Baja California and none in any direction closer than the Santa Rosa Mountains of Southern California, some 250 km to the north.

Cerro Matomí is a lesser outpost of the Sierra, with *Pinus monophylla* Torrey & Frémont, *Juniperus californica* Carrière, and other northern plants, and with a dense growth of *Adenostoma fasciculatum* Hook. & Arn. (chamise) on the mesa just to the northeast. Some 15 flowering plants seem to reach their southern known limits at the peak (Moran 1983). Tinajas de Moraga, a series of tanks or pools in the bedrock of the arroyo bed at the SE base of the peak, is the northernmost known station for *Haplopappus odontolepis* Moran and the only known peninsular locality for *Purshia mexicana* (D. Don) Welsh var. *stansburyana* (Torrey) Welsh.

The peak is prominent on the skyline about 40 km NE from the main peninsular highway but is isolated from roads. I went there 2–5 May 1973, camping at Tinajas de Moraga (1150 m), about 6 hours on a slow mule from my starting point at Rancho el Metate. Apparently no other botanist has been there. In 1902 while collecting mammals (Elliott 1903) and some plants, Edmund Heller camped 12–30 June in Arroyo Matomí, just east of and below the peak; but his journal (Heller 1902) does not mention the peak.

On the rather bare gentler east slope below the steep rocky peak, I found a large stand (perhaps several hundred plants) of the unknown *Hedeoma* named here:

Hedeoma matomianum Moran, sp. nov. (Fig. 1) — TYPE: MEXICO, BAJA CALIFORNIA, Cerro Matomí, common at 1375 m on rather bare rocky east slope, near 30°22½′N, 115°07′W, 4 May 1973, **Reid Moran 20810** (holotype SD 88934; isotypes CAS and to go: BCMEX, BM, ENCB, F, GH, ICF, K, MEXU, MICH, MO, NY, RSA, US).

Planta perennis dense ramosa 1–2 dm alta, ramis dense hispidulis. Foliorum laminae ellipticae subacutae 5–8 × 2–5 mm, marginibus subintegris. Cymulae 1–3-floratae. Calyx 5–8 mm longus, tubo 4–5 mm longo, labio superiore ±2 mm longo valide sursum curvato intus pubescenti, segmentis triangulo-attenuatis ciliatis basi 0.8 mm latis, segmentis inferioribus 1.5–2.5 mm longis basi 0.5 mm latis. Corolla purpurea lavandulave tubulo-funnelforma 9–12 × 4–5 mm, tubo ±5–6 mm longo basi 0.5 mm crasso, fauce ±1–2 mm longa, labio superiore arcuato subgaleato ±2–2.5 mm longo, labio inferiore 3–4 mm longo. Stamina subexserta, filamentis 2.5–3 mm longis, fauce 6 mm supra corollae basin insertis. Ab *H. tenuifloro* Brandegee et *H. martirense* m. habitu fruticosiore inflorescentiaque compactiore et corolla breviore (9–12 mm vs. 17–18 et 19–25 mm) differt.

Densely branched perennial 1–2 dm high and to 3 dm wide, from a basal stem to 1 cm thick, the herbage with little odor. Stems of the season whitish, 5–15 cm tall, ±1 mm thick, little branched above base of new growth, densely hispidulous with downcurved trichomes to 0.1 mm long on lower stem and to 0.3 mm long on uppermost stem, the internodes mostly 5–15 mm long. Leaf blades thick, elliptic, subacute, 5–8 mm long, 2–5 mm wide, entire to faintly few-crenate or less often 1- or 2-toothed, hispidulous on both sides, glandular dorsally, with 2–3 pairs of strongly ascending veins slightly raised on dorsal surface and with margins slightly revolute-thickened, narrowed to petiole 1–4 mm long. Flowers at ±5–15 nodes in upper 5–10 cm of stem, in cymules mostly of 3 flowers, or upper flowers solitary; peduncles to 2 mm long and pedicels 1–4 mm long, the bracteoles acerose, 2–3 mm long. Calyx purplish, 5–8 mm long, ±1 mm thick, hispidulous below and with gradually shorter trichomes upward, the tube 4–5 mm long, somewhat sigmoid, with dense white annulus 0.8 mm high included at throat, the upper lip broad, ±2 mm long, strongly upcurved, pubescent within, divided nearly to middle into triangular-attenuate ciliate segments 0.8 mm wide at base, the lower two segments slightly upcurved, slender, attenuate, ciliate, 1.5–2.5 mm long, 0.5 mm wide at base. Corolla purple or lavender, tubular-funnelform, exserted 4–5 mm from calyx, 9–12 mm long, 4–5 mm wide, puberulent outside, the tube ± 5–6 mm long, ±0.5 mm thick at base and 0.8 mm above, the throat ±1–2 mm long, the upper lip arched, subgaleate, ±2–2.5 mm long, the lower lip 3–4 mm long, the lateral lobes slightly spreading, rounded, ±1 mm long and wide, the midlobe downcurved, retuse, ±1.5 mm long and 2 mm wide, puberulent along mid-line, with four ± parallel regular or irregular longitudinal stripes in throat and white between. Stamens slightly exserted, the filaments 2.5–3 mm long, inserted in throat ±6 mm from corolla base, the anther cells divaricate, ±0.6 mm long. Styles ±9 mm long. Nutlets unseen. Chromosomes: none noted. Flowering April and May.

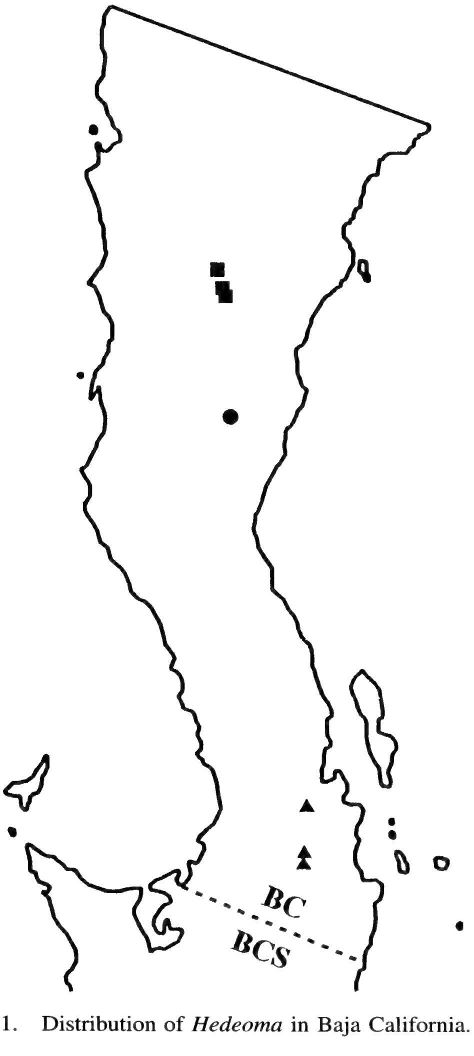

FIG. 1. Distribution of *Hedeoma* in Baja California.

Distribution. Known only from the type locality and vicinity; paratype from east slope of Cerro Matomí at 1425 m, **Moran 20794** (HCIB, SD, UC).

In Irving's (1980) revision of *Hedeoma,* the new species falls in *Hedeoma* subgenus *Saturejoides* Irving and section *Saturejoides* but does not agree with any of the species as described. Two other species grow in Baja California (Fig. 1), each known only in one mountain range: *H. tenuiflorum* Brandegee high in the Sierra San Borja, some 250 km to the SSE, and *H. martirense* Moran in the high Sierra San Pedro Mártir, some 80 km to the NNW. Irving placed these two together in his Wagner tree (1980, Fig. 1) and in his key; he called *H. martirense* "somewhat enigmatic, . . . [i]n many of its morphic features . . . show[ing] strong phenetic affinities" to *H. diffusum* E. Greene of northern Arizona, but in the rest of its characters "most closely related to *H. tenuiflorum*".

Hedeoma tenuiflorum is rare and little-known: Epling and Stewart (1939) and Irving (1980) cited only Brandegee's type collection of 1889 (holotype UC 122496!; isotypes PH, UC, US). This is from Rancho Viejo, which to judge from Brandegee's (1889) account and map, is near 28°28′N, 113°35′W, in the Sierra San Borja. Leaves of *Quercus turbinella* E. Greene (det. by Dennis Breedlove) with the holotype suggest that it probably grew at an elevation of 1200 m or more. Two later collections from the same sierra are essentially sterile, having only a few weathered old calyces; but they compare well with the holotype. These are: (1) **Moran 11504** (DS, SD) from north slope of red peak, Cerro el Sauco, 1450 m, 17 January 1964 [clump 2 dm high and wide; little odor]; and (2) **Moran 12806** (DS, SD, UC) from north slope near summit of Cerro la Chona, 1400 m, 19 March 1966.

Hedeoma martirense is locally common at 2300–2800 m near the crest of the north-central San Pedro Mártir, best developed in pine-fir forest on the upper east slope. Irving called it "unique" in the genus for the high insertion of the stamens—"just below the juncture of the upper and lower corolla lips". For the genus otherwise, he said the stamens arose from the middle of the corolla; but a quick check shows that this is not always true. In fact, the stamens are inserted in the throat also at least in *H. nanum* and in *H. tenuiflorum*; so other species need to be checked.

In *H. matomianum* the stamens again are inserted in the throat, as in the two other Baja Californian species. Despite the differences shown below and despite the lack of information about stamen insertion in other species, this fact at least suggests that these three may be closely related. Differences among the three Baja Californian species are shown in the following key.

1. Stems decumbent, rooting at nodes; cymules 1-flowered, at 1–4 nodes; corolla 19–25 mm long; upper calyx lobes united ca. ⅓; leaf-blades glabrous or sparsely scabrous ventrally . . . . . . *H. martirense*

1′ Stems erect, not rooting; cymules mostly 1–3-flowered, at 5–15 nodes; corolla 9–18 mm long; upper calyx lobes united ca. ½; leaf blades hispidulous ventrally.

2. Corolla slender, 17–18 mm long; stems 15–60 cm tall, the internodes 2–6 cm long; cymules at 5–10 nodes in upper 15–40 cm; calyx 8–9 mm long . . . . *H. tenuiflorum*

2′ Corolla funnelform, 9–12 mm long; stems 10–20 cm tall, the internodes 5–15 mm long; cymules at 5–15 nodes in upper 5–10 cm; calyx 5–8 mm long . . . . *H. matomianum*

R. S. Irving in 1968 annotated my SD specimens of both Sierra San Borja collections (**11504, 12806**) as *H. tenuiflorum* Brandegee, as they had been tentatively identified. However, in the same year he annotated the sterile DS specimen of my **11504** as *H. nanum* Briq. "var." *californicum* W. S. Stewart. That is a very different species, for which there seems to be no authentic Baja Californian record: at least Epling and Stewart (1939) and Irving (1980) cited none! Then under *Hedeoma* Wiggins (1980) showed only *H. nanum* Briq. subsp. *californicum* W. S. Stewart, "on N-facing slopes in Sierra San Borja . . . ." He evidently based this report on the DS specimen of *11504, H. tenuiflorum,* misidentified by Irving–though Wiggins' figure 386, drawn by Jeanne R. Janish for an earlier work (Abrams 1951, fig. 4421) doubtless is correct for subsp. *californicum.*

Although the only *Hedeoma* in Wiggins' Flora is wrongly named, *H. matomianum,* strangely enough, looks fairly similar to the one subspecies Wiggins did list. *Hedeoma nanum* Briq. is a variable annual or perennial of SE California to Nevada and Texas and southward in Mexico to San Luis Potosí. Stewart (in Epling and Stewart 1939) divided it into 4 subspecies and Irving (1980) into 3 varieties. *Hedeoma nanum* subsp. *californicum* Stewart grows in southernmost Nevada and in adjacent California and Arizona. The new species is similar in habit but differs in its more pubescent stems, its more compact inflorescence, with 1–3-flowered cymules, its longer calyx (tube 4–5 vs. 3–4 mm), with slightly longer and wider teeth, and notably its longer corolla (9–12 vs. 8–9 mm).

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Curators at CAS, DS, SD, and UC, lent the necessary specimens. Erik Jonsson told me of Edmond Heller's journal and kindly copied relevant parts. Jon Rebman and Judy Gibson dug out needed information, and they even made the map–not everyone would volunteer to do that. These two and Frank Almeda and Peter Fritsch all read versions of this account and made thoughtful suggestions. Exequiel Ezcurra came to the rescue with the Resumen. To all these friends I am grateful for their amiable and indispensable help. Funding for this study so far is zero, but contributions are earnestly solicited and would be gratefully received. Finally, I thank Kenton L. Chambers and Jan Barber, who kindly reviewed this paper for Madroño and made further suggestions.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

ASTRAGALUS AGNICIDUS Barneby (FABACEAE).—L. Davis 14 Sep 1999, USA, California, Mendocino Co., 14 air km E of Fort Bragg in Jackson Demonstration State Forest, along Parlin Drainage Road, T18N, R16W, NE 1/4S, 28, referred to as 'Road 330' population; elev ± 180 m (NMC). Majority of plants occur along disturbed logging haul road in active timber harvest area: road through mixed conifer and hardwood forest with previous logging history; with *Sequoia sempervirens, Pseudotsuga menziesii, Ceanothus* sp., *Polystichum* sp., *Cortaderia* sp., ± 5000 plants in population, 5% flowering, 95% fruiting. Two collections were made at the Road 330 Population in western Mendocino Co., Parlin Drainage area of Jackson State Demonstration Forest. Liam H. Davis (California Department of Fish and Game) and Fay A.Yee and John Griffen (California Department of Forestry and Fire Protection) surveyed two populations designated the Bear Gulch Population and the Road 330 Population. The Road 330 Population is approximately 800 m east of the Bear Gulch Population. The Bear Gulch Population is <100 plants. Seeds collected from three plants *in situ* at Road 330 Population were entered into Rancho Santa Ana Botanical Garden germ plasm bank.

Previous knowledge. Listed state endangered April 1982. Rediscovered in 1987 by R. Sutherland, R. Bittman, and K. Berg near Miranda in Humboldt County. This occurrence is located in an opening caused by a single tree removal. The occurrence is now voluntarily protected by the landowner, although the landowner attempted eradication in the early 1900's because of the plant's toxicity to sheep. This site is now partially fenced and the landowner no longer grazes sheep. (Berg and Bittman 1988, Skinner and Pavlik 1994). The duplicate was determined by L. Davis and R. Spellenberg (Spellenberg 1993).

Significance. First record for Mendocino County. Species now known from three occurrences.

1. BERG AND BITTMAN. 1988. Fremontia 16:1:13–14.
2. SKINNER AND PAVLIK. February 1994. California Native Plant Society's Inventory, 5th ed. Sacramento, CA.
3. SPELLENBERG, R. *in* J. Hickman. 1993. The Jepson Manual. UC Press.

—LIAM H. DAVIS, California Department of Fish and Game, P.O. Box 47, Yountville, CA 94599 and Roxanne Bittman, California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814.

CALIFORNIA

JAFFUELIOBRYUM RAUI (Aust.) Ther. (GRIMMIACEAE)—Riverside Co., San Bernardino National Forest, T6S R4E Sec. 27, Bull Canyon Road, 1700–1900 m, along a ridge on limestone rock outcrops in chamise chaparral, 27 April 1980, Judith A. Harpel 1177 (UBC, UC).

Previous knowledge. Known from mesic to more xeric areas in southeastern Alberta, eastern Montana to western North Dakota south to Texas, Utah, Arizona and New Mexico, disjunct to the Driftless Area of southwest Wisconsin, southeastern Minnesota and northeastern Iowa (Churchill Memoirs New York Botanical Garden. 45: 691–708, 1987).

Significance. First report of this species in California. The closest known populations occur in Mohave and Yavapai Counties in Arizona. The occurrence of this species in California may represent a relict population that developed during the Madro-Tertiary events of the Eocene. Additional populations may occur in southern California but due to its very small size and xeric substrate requirements this species has probably been overlooked.

—JUDITH A. S. HARPEL, Regional Interagency Bryologist/Lichen Coordinator, Gifford Pinchot National Forest, 10600 NE 51st Circle, Vancouver, WA 98682, jharpel@fs.fed.us or harpel@csci.clark.edu.

CALIFORNIA

ERIASTRUM HOOVERI (Jepson) H. Mason (POLEMONIACEAE).—Los Angeles Co., Antelope Valley: W of Lancaster, N. side of Avenue G, near 34°43′59.2″N 118°11′41.9″W, 27 Apr 1998, *Porter* 11834 (RSA); Mojave Desert: Antelope Valley, along Highway 138 (West Avenue D), west of the junction with Highway 14, at intersection with 40th Street, ca. 6.4 km southwest of Rosamond Dry Lake, near 34°46′35.5″N 118°12′09.4″W, 5 May 1998, *Boyd & Hughes* 10189 (RSA).

Previous knowledge. Eriastrum hooveri has been considered endemic to the southern San Joaquin Valley and southern inner Coast Ranges of Fresno, Kings, Kern, Santa Barbara, San Benito, San Luis Obispo, and Tulare counties (Hinshaw et al., 1998, Madroño 45:290–294; Skinner & Pavlik, C.N.P.S. Inventory of Rare and Endangered Vascular Plants of California, 5th ed., 1994; Patterson, *Eriastrum.* Pp. 826–828 in Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, 1993). This species is characteristically found in annual grassland and chenopod scrub habitats, often in sandy loam soils derived from alluvial and colluvial parent materials (Hinshaw et al. loc. cit.). Often, *E. hooveri* is found in association with cryptogamic soil crusts in relatively open habitats, but recent studies indicate the species is capable of withstanding some forms of physical disturbance and invading recently disturbed habitat (Holmstead & Anderson, 1998, Madroño 45:295–300). *Eriastrum hooveri* is currently listed as a Threatened Species under the federal endangered species act.

Significance. Our collections represent the first records for *Eriastrum hooveri* in Los Angeles County, and first records of the species in the Mojave Desert. The Antelope Valley populations represent a disjunction of ca. 140 km southeast from the nearest populations in Kern County.

The Los Angeles County collections are from the southwestern portion of the Rosamond Dry Lake basin, especially within the floodplain of Amargosa Creek and other drainages originating on the northerly flank of the Liebre Mountains. The habitat is characterized by an extensive network of small, interconnected, barren alkali pool beds separated by very low hummocks of semialkaline, sandy loam soil. The predominant vegetation on the hummocks is a low, open scrub of *Atriplex polycarpa, Kochia californica, Artemisia spinescens,* and *Tetradymia glabrata.* Numerous annuals are prevalent on the cryptogamic crust covered hummocks, including *Lepidium dictyotum, Goodmania luteola, Chorizanthe spinoas, Lasthenia californica, Malacothrix coulteri, Cryptantha nevadensis,* and *Plagiobothrys leptocladus.* At least during the relatively wet 1998 season, *Eriastrum hooveri* was locally common in this part of the Antelope Valley.

The distribution (population structure) of *Eriastrum hooveri* has been characterized as comprising four metapopulations: 1) the Kettleman Hills in Fresno and Kings counties; 2) the Carrizo Plain-Elkhorn Plain-Temblor Range-Caliente Mountains-Cuyama Valley-Sierra Madre Mountains in San Luis Obispo, Santa Barbara, and extreme western Kern counties; 3) the Lokern-Elk Hills-Buena Vista Hills-Coles Levee-Taft-Maricopa areas of Kern County; and 4) the Antelope Plain-Lost Hills-Semitropic Ridge region of Kern County (Sandoval & Cypher 1997, Hoover's wooly-star Profile, http://arnica.csustan.edu/esrpp/hoovers.htm). The Antelope Valley records apparently represent another distinct population system, effectively isolated from those of the San Joaquin Valley and inner Coast Ranges by the Tehachapi Mountains. Native habitat in the eastern Antelope Valley is becoming highly fragmented and degraded through rural development, road building, and marginal agriculture. Further surveys for *E. hooveri* near Rosamond Dry Lake and the eastern Antelope Valley are warranted.

—STEVE BOYD AND J. MARK PORTER. Rancho Santa Ana Botanic Garden 1500 N. College Avenue, Claremont, CA 91711.

OREGON

ALLIUM TRIQUETRUM L. (LILIACEAE).—Curry Co.: Langlois, sandy soil, apparently escaped, 21 Apr 1966, *W. L. Anderson* (OSC); Port Orford, in a vegetable/flower bed where persisting as a weed, 12 May 1996, *P. Cracas* (OSC); Lincoln Co.: Newport, along the south jetty road in a ditch with *Rumex, Stellaria, Elymus, Trifolium, Achillea, Lathyrus,* perennial from a bulb, flowers white, leaves keeled, scape strongly three angled, T11S, R11W, S17, elev. 1.5 m, 28 Apr 1998, *R. R. Halse 5315* (OSC—duplicates to be distributed).

Previous knowledge. This European native has escaped from cultivation along the central and northern California coast (J. C. Hickman [ed.], The Jepson Manual: Higher Plants of California, 1993).

Significance. First report for OR.

LONICERA PERICLYMENUM L. (CAPRIFOLIACEAE).—Lane Co.: In the Coast Range along State Hwy. 36, 2.7 km e of Blachly, woody vine in a thicket of brambles and willows, flowers fragrant, varying from yellow to white, assoc. genera: *Rubus discolor* Weihe & Nees, *R. laciniatus* Willd., *Salix, Phalaris,* T16S, R7W, S11, elev. 228 m, 9 Jun 1997, *R. R. Halse 5223* (OSC, BH, CAS, NY, RSA, WTU).

Previous knowledge. This Eurasian native sometimes escapes from cultivation in the eastern United States (H. A. Gleason and A. Cronquist, Manual of the Vascular Plants of Northeastern United States and Adjacent Canada, 2nd ed., 1991).

Significance. First report for OR.

PLANTAGO CORONOPUS L. (PLANTAGINACEAE).—Lincoln Co.: Newport, along the south jetty road, in sand with *Plantago lanceolata L., P. major L., Lupinus, Agrostis, Fragaria, Achillea, Polygonum,* T11S, R11W, S17, elev. 1.5 m, 29 Sep 1999, *R. R. Halse 5677* (OSC—duplicates to be distributed).

Previous knowledge. This native of Europe is found along the coast of California (J. C. Hickman, *loc. cit.*) and the southwest Oregon coast (M. E. Peck, A Manual of the Higher Plants of Oregon, 2nd ed., 1961).

Significance. Extends the distribution from Bandon in Coos Co., OR, ca. 170 km northward.

RAPISTRUM RUGOSUM (L.) All. (BRASSICACEAE).—Multnomah Co.: Portland, Lower Albina, on ballast, 21 Jul 1902, *E. P. Sheldon 9941* (OSC), det. by R. Halse, 1996.

Previous knowledge. A native of southern Europe this species is found in widely separated sites from California to the eastern United States (R. C. Rollins, Cruciferae of Continental North America, 1993).

Significance. First report for OR.

—RICHARD R. HALSE. Department of Botany & Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, OR 97331-2902.

MADROÑO, Vol. 46, No. 4, p. 217, 1999

REVIEW

Plant Life in the World's Mediterranean Climates. Peter Dallman. 1998. xiv + 258 pages. $29.95. California Native Plant Society Press and University of California Press, Berkeley. ISBN 0-520-20809-9.

To professional and lay botanists, horticulturists, and gardeners the world's mediterranean regions present an astonishing array of plant diversity, considering that the mediterranean climate occurs in only about 2% of the earth's land area. The mild weather conditions and long growing seasons contribute to a rich assemblage of plants and plant forms. The relatively small areas, widely disjunct from one another, offer an opportunity to witness and study parallel evolution among similar biotic regions. Peter Dallman, Chairman of the Strybing Arboretum Docent Council, has written a concise yet precise, and altogether entertaining treatment of the vegetation of the mediterranean regions of the world.

Chapter 1 sets the stage by discussing the Mediterranean Climate and its influence on plant growth. Chapter 2 on Plant and Climate Origins places climate into the context of why certain kinds of plants grow where they do, and what historical factors have influenced present and past climatic conditions in mediterranean regions. Chapter 3 summarizes various methods by which plants of mediterranean climates cope with the periods of drought, frequent fires, and nutrient-poor soils that characterize these areas. Chapter 4 treats the general types of Plant Communities that one encounters in mediterranean areas. It sets the stage for a comparative study of the five regions. The meat of the book lies in chapters 5 through 9, each covering one of the five mediterranean regions (California, central Chile, the western Cape, Australia, and the Mediterranean Basin, respectively). Each chapter is written parallel to the others, facilitating comparisons among regions. A brief discussion of landscape and climate is followed by a discussion of the important plant communities, organized as follows: sclerophyllous scrub communities; coastal scrub communities; woodlands and forests. Within the plant community segments discussions of the more important species are presented, often with clear and colorful illustrations. Each chapter ends with a short list of plants found in the region.

Upon reading about such interesting wild places, the natural reaction is, of course, "when do we go?" When is up to you, but in Chapter 10—Planning a Trip—Dallman provides us with the benefit of his extensive experience traveling these areas. He suggests specific localities in which to see the vegetation described in his book. This is bound to be extremely useful for the botanical traveller—almost a travel guide. And do you have trouble with the metric values that you will likely encounter as you travel abroad? Dallman provides at the end of the book an easy to use set of conversions.

In little more that 250 pages it is impossible to cover the detail that will certainly interest many a reader. If you want to dig deeper into the subject, Dallman has provided 11 pages of references on the plants and plant communities of the mediterranean climates.

The chapters are eminently readable for non-scientists. Dallman shows a talent for explanation without excessive verbiage. The illustrations are generally of high quality and add a definite attraction to the book. The color photographs, most of them by the author, are especially handsome, with high resolution and bright color reproduction. A few black and white photographs are a bit washed out and not up to the standard of the rest of the photos in the book. In some cases the photos have been reduced to a size too small to allow resolution of the subject. Likewise, several drawings seem primitive by today's standards. I wish that the publishers might have gone the extra (short) distance to ensure that all illustrations were of equal quality.

So for whom is this book written? Given its depth, I doubt that it would serve as a focus of a graduate seminar in mediterranean floristics and ecosystems—but I doubt that was Dallman's goal in writing this book. It certainly does provide an enjoyable introduction to some of the world's more interesting ecosystems. Further, a major strength of the book is its comparative approach. Many of us consider ourselves fortunate to have visited and studied at most any two of these regions. Dallman's offering provides an introductory view of all five regions at the same time. Even if you're not a traveller but want to grow mediterranean plants in your garden, there is ample information in Dallman's book to help you understand why plants from these regions do better in specific soils and climatic conditions.

When I teach California botany to my students each year, I remind them that what they are about to see is unlike any other region in the world, floristically and ecologically, and that this is due in large part to the mediterranean climate's affect on plants. *Plant Life in the World's Mediterranean Climates* gives us a well-organized view of these regions, and inspires a desire to explore further the differences and similarities of plant life in these regions.

—ROBERT PATTERSON, Department of Biology, San Francisco State University, San Francisco, CA 94132.

MADROÑO, Vol. 46, No. 4, pp. 218–219, 1999

REVIEW

Spatial Processes in Ecology.—D. Tilman and P. Kareiva (eds.) Spatial Ecology: The role of space in population dynamics and interspecific interactions. ca. 1997, Princeton University Press, Princeton, NJ, USA, 368 pages.

Ecologists are becoming increasingly aware of the potential impact of spatial processes on ecological phenomena. The incorporation of spatial considerations into models of population dynamics and interspecific interactions can drastically change predicted outcomes. This timely book provides a broad and stimulating sampling of current directions in the field of spatial ecology. The contributing authors analyze the role of space in processes such as: ecological invasions, metapopulation dynamics, host-parasitoid systems, disease dynamics, interspecific competition, and species extinctions. Many of these analyses clearly demonstrate a significant impact of space on the outcomes of ecological processes.

The book is an edited volume and the chapters vary greatly in both their style and content. Most notably, some chapters do an excellent job of melding theory and data to tell a complete story of the impact of space on the topic under consideration. For example, the chapter by Antonovics et al. utilizes extensive, long-term survey data as well as relevant theory to investigate the interaction between genetic variation and population dynamics in metapopulations of a pathogenic fungus and its host plant. The chapter by Hanski on metapopulation models and the chapter by Ferguson et al. on the dynamics of measles also clearly describe the relevant spatial theory and explore the applicability of this theory to relevant data.

Other chapters rely solely on a description of the theoretical aspects of a problem without ever discussing a real world application or an appropriate data set. Although the book is clearly based on theory, such analyses devoid of data may leave some readers feeling unsatisfied. While we don't consider the use of data to be an absolute requirement for a well-written book chapter, the chapters in this book that incorporate data are clearly stronger and more readable for a general audience. Too much of a gap already exists in the world of ecology between scientists generating theory, doing field work, and managing ecological systems. Including relevant data sets when discussing theoretical approaches is a good first step in integrating these three areas of ecology, and will allow appropriate theory to be more easily used by scientists to generate questions, interpret empirical results, or manage populations.

The strong variability among chapters results both from the variety of topics covered and from variation in clarity of writing. Although each chapter focuses on some aspect of spatial theory that may seem quite complex to the non-theoretician, most chapters do a good job of discussing the assumptions and implications of the theory in plain English. There are a few exceptions to this, however, and a general reader may find him/herself occasionally frustrated by the excessive technical jargon and math-speak of a few chapters.

The first chapter provides a good broad overview of the ways in which space has been incorporated into models of population dynamics and interspecific interactions in the past. This chapter is very readable and provides a great introduction to the book. Subsequent chapters vary in how interesting they will be to a general audience. While some of the chapters (such as the Ferguson et al. measles chapter) seem intended for a very specific audience of academics doing research in that field, and other chapters are targeted for the more generally interested academic ecologist, this book was clearly written for an academic audience. Although the chapters in the book at times seem to be striving to make a link between spatial theory and possible applications such as conservation, in the end this really isn't a book that will be of much interest or use to those outside of the academic community. For example, Roughgarden makes some progress towards applying spatial theory to real problems by deriving the "production functions" for a variety of spatial models. These production functions, in some systems, can be used to guide sustainable harvest of food species. However, the analysis has not yet been developed to the point where the information is useful or accessible to those making decisions about harvests. The spatial models discussed in the book tend towards complexity and the discussions in each chapter are model-driven without clear applications to current applied ecological problems.

The final chapter of the book deserves special mention. In this chapter, Steinberg and Kareiva discuss future possibilities for investigating the role of space via manipulative field experiments. Their analysis of how space can and cannot be investigated is both revealing and fascinating. From their discussion it seems clear that some aspects of the study of spatial ecology are not amenable to standard experimentation due to the weak expected effect of space on the experimental outcome (e.g. experiments would require unrealistically large numbers of replicates to demonstrate an effect).

If you are interested in the role of space in ecology and in understanding current thinking on how space may affect ecological phenomena, then this is the book for you. The list of authors is impressive and their expertise is clear. The book is also quite comprehensive, as we mentioned above, and will serve as a good summary of the role of space in ecology. If you are a resource manager or an endangered species expert, looking for some guidelines on how to deal with the spatial aspects of your system, you probably need to look elsewhere.

—CHRISTY A. BRIGHAM AND JASON D. HOEKSEMA. Department of Environmental Science and Policy, University of California–Davis.

MADROÑO, Vol. 46, No. 4, pp. 220, 1999

REVIEW

A Photographic Guide to Plants of the Tahoe Basin: Flowering Plants, Trees and Ferns.—Michael Graf. 1999. 308 pages. California Native Plant Society and University of California Press.

Graf has successfully compiled a regional botanical guide that is as close to the Platonic ideal of "guidebook" as I have encountered. I recommend a hike through the Tahoe Basin with this book in hand just to experience its lucidity, completeness and logic. To assemble a guide of this caliber requires an intense attention to detail, a knack for photography, tenacity and a love of botany.

Graf's guide is accessible to a beginning or casual botanist although they may find the phylogenetic arrangement (source not cited) of families hampering. It is a particularly good guide for the visual learner that finds the *Jepson Manual* daunting. All photos are taken in good light and are well printed. Furthermore, the photos are composed in a manner to reveal the most distinguishing characteristics of the species and its growth habit. Graf took the 367 photos included in the guide. Catching the angiosperms at peak bloom, despite an attenuated blooming period at this elevation, and compiling the photos was a monumental task.

The general characteristics of each family are explained, as are those for each photographed species. The descriptive entries of species include their height, temporal occurrence, habitat and general gross morphology. Taxonomic references are in agreement with those of the 1993 *Jepson Manual.* The less common congeners are described within the entry of the more common. Graf was careful to include very concise, yet clear, explanations of how congeners differ from one another. At the back of the book, morphological drawings from *Jepson Manual* and a brief glossary are provided to compliment the species descriptions.

Professional botanists will find this guide helpful as well. In the identification of plant species, descriptions and drawings are useful and backing this up with an herbarium specimen even more so, however, most gratifying for me is finding a name attached to a photo of the species. I conduct research in the southern portion of the El Dorado National Forest, an area that shares taxonomic overlap with the Tahoe Basin, and Graf's book was useful to confirm some of my species identifications. Graf includes taxa often overlooked due to their diminutive growth habits that can be upstaged by larger, fancier species. For example, my field site harbors Harkness linanthus (*Linanthus harknessii*), a species included in this guide. This phlox is a minor component of annual meadows and finding it requires belly botanizing of the most intense kind.

The species descriptions are preceded by a brief introduction on the Tahoe Basin that includes taxonomic organization, origins of the flora, vegetation ecology, vegetation communities and history. The overview is quite informative considering the limited amount of space dedicated to the whole of biogeography, evolutionary history and ecology of the region and Graf successfully recapitulates the plant ecology party line. Also included are details on edaphic, climatic and topographic effects on plant success in addition to intra- and interspecific interactions. This is apparently done to help explain the biogeography of the region and the patterns in the "climax" communities we see today.

Despite the decisive success of Graf's overview, introductory treatments of complicated and exciting topics in ecology are apt to exclude issues that specialists find fascinating. For example, Graf describes the traditional view of mycorrhizal-plant associations as wholly beneficial and mutualistic although a particularly hot area of research concerns the winnowing of this view. It remains to be determined the circumstances under which some of these fungi continue to be mutualistic; there may be a fine line between friend and foe. Furthermore, problems with concepts such as fungal-host specificity, fungal-mediated plant root connections and shared minerals and carbon between plants of different species and seedlings have the potential to turn plant-plant interaction studies on their heads.

The value and importance of this book cannot be overstated. Due to its thoroughness and beauty it will surely stand the test of time. It is a must have for plant enthusiasts hiking the Tahoe Basin.

—KELLY LYONS, Plant Ecologist/Ph.D. Candidate Dept. of Environmental Science and Policy, University of California, Davis, CA 95616, kelyons@ucdavis.edu

MADROÑO, Vol. 46, No. 4, p. 221, 1999

REVIEW

Ecology and Restoration of Northern California Coastal Dunes.—A. J. Pickart and J. O. Sawyer. 1998. California Native Plant Society, Sacramento, 172 pp.

For the first third of the way through, this paperback reads and looks like a natural history book. There are maps, discussions, and photographs of major plant communities (called series so as to parallel vegetation descriptions in the recent MANUAL OF CALIFORNIA VEGETATION by John Sawyer and Todd Keeler-Wolf). Information is also included about the biology and autecology of native dune plants and of invasive species that have significantly altered the topography and dynamics of California dunes.

But after this the book steps off into new territory. There is a chapter on restoration planning, including how to select the most discriminating variables to monitor and how to decide on the length of time for monitoring to continue. There is a sumary of successes and failures in the removal of invasive plants from California dunes, complete with costs per acre. Restoration can be an expensive undertaking, exceeding the cost of land purchase. For example, it takes about $35,000 to remove European beach grass (*Ammophila arenaria*) from one acre of dunes. The authors go on to compare the relative merits of removal and control by mechanical, chemical, fire, and other means.

This portion is a rich, detailed guidebook for others to follow elsewhere. Information on restoration includes optimal species to plant, where and when to collect their seeds, how to prepare the dune surface, rates of seed application, how to use vegetative transplants instead of seeds, whether to use soil amendments (including mycorrhizal inoculation), and how to stabilize the substrate with hydromulch, soil-binding emulsions, straw, netting, sand fences, or short-lived nursery crops.

Pickart and Sawyer's work is a new kind of book, which moves us from passive and descriptive natural history descriptions to activist and prescriptive restoration work. Many conservationists conclude that it is time for us to shift focus from preservation to restoration; that we should turn our attention to the matrix of degraded habitats that make up 90% of our landscapes, and to promote their enhancement.

A short final chapter addresses the role of restoration in conservation. "Skeptics fear," they write, "that restoration will be used . . . to justify the destruction of remaining areas." To counter such an argument, they point out the current poor status of restoration knowledge, the modest record of restoration success, and our dismal ability to monitor restoration projects in a way that we could learn from the failures. Clearly, restoration ecology is in an early stage of development and cannot be relied upon to take the place of more traditional conservation and preservation activities. Restoration, however, can and should accompany conservation and preservation.

Although the book limits itself to the California coast north of Sonoma County, its philosophical content and importance spill over to the entire Pacific Coast, from Baja California to Alaska.

—MICHAEL BARBOUR, Plant Ecologist, Environmental Horticulture Dept., University of California, Davis 95616.

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CORNELIUS H. MULLER

1909–1997

Professor of Botany, Emeritus
Santa Barbara

Cornelius H. Muller, botanist, Eminent Ecologist, and internationally recognized authority on the oaks, died January 26, 1997.

Neil, a Texan by temperament and schooling, was born July 22, 1909 in Collinsville, Illinois. All of his early schooling was in public schools in Cuero, Texas. He often credited his later success to 'the observational habits of my cowboy youth.' He received his B.A. and M.A. from the Department of Botany, University of Texas, Austin in 1932 and 1933. Neil received in Ph.D. from the University of Illinois, Urbana in 1938, in the Department of Botany. His dissertation was in the field of Plant Ecology with Dr. A. G. Vestal. His early botanical explorations led to 10 publications and descriptions of several new species, while still in graduate school. His first position was as Ecologist for the Illinois State Natural History Survey in 1938. He also held a position as Assistant Botanist (1938–1942) in the Division of Plant Exploration and Introduction, Bureau of Plant Industry, U.S. Department of Agriculture. In 1939, Neil married Katherine Kinsel. In 1942, he joined the Special Guayule Research Project in the southwest desert. This work was seminal in his latter research into plant interactions.

In 1945, Katherine resigned her position at the Santa Barbara College for a position at the Santa Barbara Botanic Garden. Neil was offered the position vacated by Katherine, and was appointed Assistant Professor of Science at the Santa Barbara College. Shortly after his employment, he founded a collection of botanical specimens, which later became The UCSB Herbarium, to aid in his classes in plant taxonomy. In 1947, he was appointed Research Associate at the Santa Barbara Botanic Garden. Neil became Assistant Professor of Botany in 1948, Associate Professor of Botany in 1950, and Full Professor in 1956. He was Faculty Research Lecturer in 1957. Neil was one of the original faculty at the Santa Barbara Campus when it became the 8th campus of the University of California in 1958. He served as acting Dean of the Graduate Division (1961–1962), and was one of the early participants in the Institute for Tropical Biology in San Jose, Costa Rica (1961–1962). Neil had twelve Ph.D students and two Masters students from 1966–1977. In 1974, Neal became Adjunct Professor in the Department of Botany, University of Texas, Austin. This allowed him to spend the hot months of the year in Austin. In 1975, he was selected as Eminent Ecologist, the highest honor bestowed by the Ecological Society of America. Neil became Emeritus Professor at UCSB in 1976. In 1982, his paper on "The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition" (1966), was selected by Current Contents as a Citation Classic, designating it as an extremely influential publication in the field of Ecology. By 1982, this paper had been cited over 125 times. Neil continued his interest on the history of early botanical explorations with work on the letters and collections of Jean Louis Berlandier culminating in a two-volume publication co-authored with Katherine Muller.

Cornelius Muller contributed importantly to two major scientific research areas. His active research life, which was most of his 87 years, spanned much of the history of plant ecology in the United States. In his work, he met or corresponded with many of the early workers in the burgeoning discipline of plant ecology. His ecological work tracks the development of the field of plant ecology from vegetation description to analysis to experimentation. His later investigations of plant interactions opened a new discipline of experimental investigations in chemical ecology. All of his ecological work was based on careful field observations and detailed experimentation to test hypotheses about the factors controlling plant distributions.

Neil's early work also addressed the taxonomic problems associated with plants in the American Southwest, and in Mexico and Central America. His extensive collections are to be found in herbaria around the world. His national and international reputation in plant taxonomy was first established by his study of oaks. The taxonomy of the oaks is a particularly challenging problem. Muller's work on the oaks drew from a number of areas in Botany. He published papers on the anatomy of species, the distribution of species, and their correlations with edaphic factors. He was one of a few early workers to recognize the role of hybridization in the relationships of the oak species. Neil's collections, species descriptions, and several volumes describing his work on the oaks made him a leading authority on the genus *Quercus.* This work spanned his entire career. He also named a number of new species, largely oaks. In honor of his work, two new species of oaks were named for him: *Quercus cornelius-*

mulleri Nixon and Steele (California) and *Quercus mulleri* Martinez (Mexico). He was honored by the California Botanical Society through dedication of Volume 35 of its journal *Madroño.* The UCSB Herbarium, now contained within the Museum of Systematics and Ecology at UCSB, is the repository for the Cornelius H. Muller Archives and many of his plant collections.

Neil published over 100 research papers from the 1930s to the 1990s. His early and his most recent investigations were joint efforts with his wife Katherine, who died in 1995. Neil's classes, seminars, and field trips at UCSB were legendary, and the quarterly Ecology Seminar founded by him is perhaps the longest, consistently offered one in the United States. The breadth and power of C. H. Muller's influence will continue to be felt for generations. It was Neil's wish that upon his demise his ashes be scattered over a field of bull-thistles somewhere in Texas.

—Nancy Vivrette
Wayne Ferren
Bruce Mahall

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President's Report for Volume 46

Welcome to the California Botanical Society's 1999–2000 program year. New and returning Council Members for the program year include myself; Wayne Ferren, Past President; Susan D'Alcamo, First Vice-President; Fosiee Tohbaz, Second Vice-President; Dean Kelch, Recording Secretary; Mary Butterwick, Treasurer; Sue Bainbridge, Corresponding Secretary; Council Members Jim Shevock, Diane Elam, and Bian Tan; Dennis Wall, Graduate Student Representative; and *Madroño* Editor, Kristina Schierenbeck. The Society thanks each of you! New Officers for this program year include Fosiee Tohbaz and Dean Kelch.

Susan D'Alcamo tried to retire early in her third year as First Vice-President. Although in "retirement," she organized an excellent slate of six speakers for the 1999–2000 program year Lecture Series. The Society greatly appreciates her help. Lectures are held on the third Thursday of each month from October through May, in the Valley Life Sciences Building at the University of California, Berkeley Campus. The lectures were well attended this year by members as well as many non-members. All members are invited and encouraged to attend the lectures and receptions. An informal reception followed each presentation which allowed an opportunity to mingle with the speaker, other botanists, and guests. The Jepson and University Herbaria furnished refreshments. The Council appreciates Dennis Wall's help with room reservations, projection equipment, and the reception. We again thank Brent Mishler and the Jepson and University Herbaria for providing space for the Council meetings, Lecture Series, and receptions.

Fosiee Tohbaz organized an outstanding Annual Banquet, which was held on 19 February 2000, at the U.C. Berkeley Faculty Men's Club. The guest speaker was Dr. Jim Doyle, Department of Evolution and Ecology. His lecture was entitled, "What do we know about the origin of angiosperms?" President Little presented "Outstanding Service Awards" to Board Members in recognition of their contributions to the organization. Recipients included Fosiee Tohbaz and Dennis Wall. The next Banquet will be held at Chico State.

The Society again acknowledges the contributions of Mary Butterwick as Treasurer for the Society. Although her third and final year ended mid-1999, her replacement was not confirmed until the end of 1999.

Mary therefore volunteered to continue her term through the 1999–2000 program year. Roy Buck will become the new Treasurer. Dean Kelch commenced his position this program year as the new Recording Secretary. Susan Bainbridge has done an outstanding job as Corresponding Secretary and has volunteered to remain as Corresponding Secretary for one more year. The Society also appreciates the contributions of Council Members Jim Shevock, Diane Elam, and Bian Tan. Kristina Schierenbeck continues to do an excellent job as Editor of *Madroño*. She has worked through a large backlog of manuscripts and is close to getting *Madroño* back on schedule. Nominations for her replacement are currently being solicited.

Council Members retiring after the 1999–2000 program year include myself (3 years as President), Susan D'Alcamo (3 years as First Vice-President), Mary Butterwick (4 years as Treasurer), Fosiee Tohbaz (1 year as 2nd Vice President), and Dennis Wall (2 years as Graduate Student Representative). New officers for the 2000–2001 program year include Bruce Baldwin, President; Rob Myatt, 1st Vice-President; Roy Buck, Treasurer; and Kirsten Johanus, Graduate Student Representative.

John LaDuke (University of North Dakota) and Curtis Clark (Cal Poly Pomona) have volunteered to establish a web site for the Society. The Council believes the web site is an excellent way for the Society to increase its membership. The lower than anticipated individual and institutional membership renewals for year 2000, are a concern to the Council as membership revenues are the only means by which *Madroño* can continue to be published. We believe renewals will increase after Madrono gets back on schedule, which will be soon. If you have not yet renewed please do so and encourage others to take out a student, individual, family, or institutional membership. It has been my pleasure to serve as the Society's President for the past three years and to work with the many outstanding volunteers who have served on the Council.

—R. John Little, Ph.D.
10 June 2000

MADROÑO, Vol. 46, No. 4, p. 225, 1999

EDITOR'S REPORT FOR VOLUME 46

This report serves to inform members of the California Botanical Society the status of *Madroño* from manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 45[4]) the journal received manuscripts for review, including Articles, Notes, and Noteworthy Collections; 60 of these have since been accepted for publication. The average time from article submission to publication has been remained stable at approximately six months. Very few manuscripts were rejected after review. Authors of *Madroño* articles are generally quite responsive to reviewer and editorial suggestions.

The larger page format implemented with volume 45 has reduced the number of pages per article thus more articles are required to fill each issue. Unfortunately, the need for more articles per issue has slowed the publication schedule. We hope to receive an increase in the number of manuscript submissions with the increased rate of publication.

Noteworthy collections continue to be a valuable contribution to the journal but have suffered from reduced attention due to editorial efforts with other manuscripts. The outlook for Noteworthy Collections is more optimistic for the next issue.

There are many individuals who contribute to the editorial process; Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who continues to assemble the Index and Table of Contents; Dieter Wilken and Margriet Wetherwax, who edit the Noteworthy Collections; David Parks, my editorial assistant; Michael Abruzzo, Chair of the Department of Biological Sciences at California State University Chico, who provides the funds to support David; Karen Ridgway at Allen Press; and members of the CBS executive council who enthusiastically support *Madroño* in every aspect. I continue to rely on the council of Robert Patterson, Wayne Ferren, Jon Keeley, John Strother, and Beth Painter for guidance about the editorial process. On behalf of the society, I thank the volunteer reviewers and the Board of Editors on whom we all depend to make the peer review process work for this valuable regional journal.

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Stanley Welch
Andrea Wolfe
David Wood

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DEDICATION

Kenton L. Chambers. In Baja California, summer 1955, shortly after completing his Ph.D. (left). At Oregon State University, 1989 (right).

This volume of *Madroño* is dedicated to Kenton L. Chambers, in honor of his 70th birthday. Ken has made important contributions to our knowledge of the flora of the western United States through his monographic and biosystematic studies of *Microseris* (Asteraceae) and related genera. A dedicated and inspiring instructor, he taught plant systematics, plant evolution, and agrostology to hundreds of students at Oregon State University, and served as major professor for 16 Ph.D. students and 16 M.Sc. students in plant systematics. Many of these students have gone on to careers in plant systematics. Ken is a preeminent authority on the flora of Oregon. Since his retirement from OSU in 1990, he has continued his herbarium and field studies and has been a major contributor to the Oregon Flora Project. Ken was a co-author with Jean Siddall and Dave Wagner of the first enumeration of rare, threatened and endangered vascular plants in Oregon, and his efforts towards plant conservation in Oregon continue to this day.

Ken was born in Los Angeles, California on September 27, 1929, and completed all of his education in the Golden State. He received his A.B. in Biology from Whittier College in 1950. Ken continued his studies at Stanford University, following in the footsteps of two of his instructors at Whittier College, Dr. Lois James and Dr. Henry J. (Harry) Thompson. In 1955, Ken completed his Ph.D. thesis, "A biosystematic study of the annual species of *Microseris*" under the supervision of Dr. Ira Wiggins.

Harry Thompson relayed anecdotes about Ken from his Whittier and Stanford days. Ken's career-long interest in Asteraceae apparently began at Whittier, when Ken took a field botany course from Harry. "Ken specialized in [the family] because everyone else in the course, including the instructor, knew very little about them. Ken made excellent plant collections in the class . . . and arranged them, using the Engler and Prantl system, in an orange crate. He brought the collection to Stanford where he took lots of kidding about his Orange Crate Herbarium."

After a year of post-doctoral research with Dr. Harlan Lewis at UCLA, Ken accepted a position in the Department of Botany at Yale University. Ken continued his *Microseris* research at Yale, and received the George R. Coolley Award in 1957 and in 1959, for the best papers presented at the American Society of Plant Taxonomists annual meetings. It was at Yale that Ken met Henrietta Chambers, and they married in 1958. Henny was also Ken's first Ph.D. student, conducting her thesis research on the genus *Pycnanthemum* (Lamiaceae). Ken and Henny have two children and four grandchildren.

In 1960, Ken was offered a position of Associate Professor in the Department of Botany and Plant Pathology at Oregon State College (renamed Oregon State University in 1961). There was to be a merger of the Botany and Zoology departments at Yale within the next year, and although he was encouraged to stay at Yale, Oregon State looked like a good opportunity for a plant systematist. His intuition was correct, and Ken had remained at OSU ever since.

Under Ken's direction, the OSU herbarium grew from 130,000 to nearly 200,000 specimens, and moved from antique wooden cases to steel cases. Ken's courses in plant systematics, plant evolution, and agrostology were famous for their depth and thoroughness. His plant systematics course included memorable field trips to the Columbia River Gorge, Central Oregon, the Cascades, and overnight trips to southern Oregon. Ken collected all of the plants for these classes (often with Henny's assistance on weekends). Upon retirement, he chose not to divulge the locations of his favorite collecting sites—he felt that after 30 years of annual culling, these populations deserved a respite!

Ken has over 75 scientific publications to his credit and has written dozens of articles for the Bulletin of the Native Plant Society of Oregon and the Oregon Flora Newsletter. Ken has been a member of the American Society of Plant Taxonomists (ASPT), American Association for the Advancement of Science, Botanical Society of America, American Institute of Biological Sciences (AIBS), California Botanical Society, and International Association of Plant Taxonomy. He served in a leadership capacity in many of these organizations, including ASPT president in 1979. He also served as local representative for the AIBS meetings in Corvallis in 1962 and 1975. Ken was a visiting National Science Foundation program director in 1967–68. Ken's botanical explorations focused on California and Oregon, however he also conducted fieldwork in Alaska, Baja California, Panama, and the Caribbean.

In 1978, Ken began a collaboration with a molecular geneticist, Dr. Konrad Bachmann, that continues to this day. Konrad's experimental organism had been frogs, but he became discouraged by the difficulty of keeping his genetic stocks alive and healthy in the lab. He came across Ken's 1955 thesis publication, and thought that *Microseris* would be a good plant to study the genetics of the composite head. This research has provided important insights into the quantitative genetics of floral and inflorescence traits in Asterceae.

In retirement, Ken has rediscovered his musical interests. He has participated in campus productions of Gilbert and Sullivan operettas, plays baritone horn in the Corvallis Community Band and sings in a madrigal group. He has also enjoyed several opportunities to botanize in California in spring, something that was impossible during his teaching days.

Ken was awarded the OSU Alumni Distinguished Professor Award in 1989. He has been honored as a Fellow of the American Association for the Advancement of Science and a Fellow of the Native Plant Society of Oregon. In 1990, he received a Certificate of Merit from the Botanical Society of America. It is fitting to conclude this tribute to Ken with the citation from this award: "Eminent biosystematist, internationally recognized for his studies of various genera of Asteraceae; a pioneer in the development of plant conservation in Oregon; stimulating teacher who has inspired many students to become botanists."

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INDEX TO VOLUME 46

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

DATES OF PUBLICATION OF MADROÑO, VOLUME 46

Number 1, pages 1–68, published 3 December 1999
Number 2, pages 69–116, published 30 December 1999
Number 3, pages 117–168, published 11 May 2000
Number 4, pages 169–232, published 26 September 2000

California Botanical Society—Meeting Program
2000–2001 Academic Year

All Meetings are held at 7:30 pm in room 2063
in the Valley Life Sciences Building on
the UC Berkeley campus.

September 21, 2000

Predicting the future of Sierran conifer forests: no lessons from the past.
John Battles, Professor, University of California, Berkeley

October 19, 2000

Diversity in California's serpentine plants: the roles of patchiness, grazing, and burning.
Susan Harrison, Professor, University of California, Davis

November 16, 2000

Restoration of oak woodlands and grasslands in California: an evolutionary perspective.
Kevin Rice, Professor, University of California, Davis

January 18, 2001

Explosive beauty: rare plant research and management at Lawrence Livermore National Lab's high explosive test facility, site 300.
Tina Carlsen, Project Leader and Ecologist, Lawrence Livermore National Lab

February 21, 2001

ANNUAL BANQUET and
SEMI-ANNUAL GRADUATE STUDENT MEETINGS
**NOTE CHANGE OF LOCATION: California State University, Chico

The role of geology in molding the California flora
Arthur Kruckeberg, Professor Emeritus, University of Washington

March 15, 2001

Molecular phylogenetic studies in Rosaceae.
Dan Potter, Professor, University of California, Davis

April 19, 2001

Defenders or pretenders? Interactions between an African acacia tree and four symbiotic ants.
Maureen Stanton, Professor, University of California, Davis

May 17, 2001

Using DNA fingerprinting to study *Sequoia sempervirens* populations in Big Basin Redwoods State Park.
Chris Brinegar, Professor, San Jose State University

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Membership in the California Botanical Society is open to individuals ($27 per year; family $30 per year; emeritus $17 per year; students $17 per year for a maximum of 7 years). Late fees may be assessed. Members of the Society receive MADROÑO free. Institutional subscriptions to MADROÑO are available ($60). Membership is based on a calendar year only. Life memberships are $540. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

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Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE-SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, 5 key words or phrases, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or 'erasable' paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units, except specimen citations, which may include English or metric measurements.

Authors of accepted papers will be asked to submit an electronic version of the manuscript. Microsoft Word 6.0 or WordPerfect 6.0 for Windows is the preferred software.

Line copy illustrations should be clean and legible, proportioned to the MADROÑO page. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include a scale and latitude and longitude or UTM references. In no case should original illustrations be sent prior to the acceptance of a manuscript. Illustrations should be sent flat. No illustrations larger than 27 5 43 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used by Sivinski, Robert C., in MADROÑO 41(4), 1994. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 8th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, Authors of Plant Names (1992) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted 5 free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $40 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $4.50 per line will be charged to authors.

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