MADROÑO

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For his unparalleled investigations of the origin and evolution of the vegetation of western North America, his distinguished contributions to our understanding of the role of fossil floras in unlocking the secrets of paleoclimate, his early appreciation of the importance of plate tectonics as a controlling factor in determining the distribution of plants and animals, and his contribution of a very substantial body of literature that has consistently inspired his fellow scientists, volume 28 of Madroño is dedicated to DANIEL I. AXELROD.

Dan, we know you consider the herbs that we love to be a "ground cover," unworthy of notice, but we forgive you because, largely through your own insightful analyses, together with lots of tough rock-splitting in the hot Nevada sun, you have made the communities in which they occur the best known in the world from the standpoint of their Tertiary history. Besides, you have never given us a dull moment, and we recall with enthusiasm your many fine speeches and seminars. May your years be filled with equability, punctuated with just enough climatic and edaphic stress to add variety and zest!

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ECOLOGICAL RELATIONSHIPS OF QUERCUS DOUGLASII (FAGACEAE) IN THE FOOTHILL ZONE OF SEQUOIA NATIONAL PARK, CALIFORNIA

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Abstract

Quercus douglasii (blue oak) forms the dominant element of foothill woodland communities in the lower foothill zone of Sequoia National Park below 500 m on north-facing slopes and 600–800 m on south-facing slopes. Small stands of this species occur up to 1500 m on dry slopes with relatively deep soils. Densities of *Q. douglasii* range from 111–321 trees per hectare. Soils beneath stands of *Q. douglasii* are significantly lower in total nitrogen, total phosphorus, and organic matter content than adjacent sites with mixed-evergreen woodland. Maximum water stress during the end of a two-year drought in 1977 reached −50 bars with little overnight recovery. Moderately low summer water potentials were also present in 1978, a wet year, but with overnight recovery to relatively low dawn stress. Mean levels of precipitation in 1979 produced intermediate values of water potential. Phenological patterns of *Q. douglasii* are variable among sites studied. Stem elongation begins in February or March and continues for 2–3 months. Leaf production began as stem elongation slowed in two sites but occurred contemporaneously with stem elongation at a third. Leaf fall occurs within a month after maximum water stress is reached. Catkins are developed from preformed buds from the previous growing season. No flowering was observed during the spring of 1978, despite abundant precipitation, because of the preceding two-year drought. Establishment of seedlings is an irregular event related to environmental stress, predation, and land-use history including fire frequency. The greatest proportion of trees at Sequoia National Park are estimated to be 60–100 years in age, with few young trees present.

The foothills of the Sierra Nevada contain a mosaic of plant communities, including the distinctive blue-oak woodland dominated by *Quercus douglasii*. While few studies to date have focused specifically on the ecological relationships of *Q. douglasii,* some data are available on this species in the Coast Ranges of California. Ecological studies of *Q. douglasii* have treated seedling survival and establishment (Griffin, 1971), community structure (Leonard, 1956; Johnson et al., 1959; White, 1966; Brooks, 1969; Vankat and Major, 1978; Pillsbury, 1978) rooting characteristics (Lewis and Burgy, 1964) and water potential relationships (Griffin, 1973). While a comprehensive description of blue-oak woodland vegetation in California can be found in Griffin

(1977), no study in the past has integrated data on community structure, water relations, and phenology into a clear treatment of the ecology of *Q. douglasii*. In this paper we discuss the interaction of seasonal drought stress and qualitative and quantitative aspects of phenology of *Q. douglasii* in the foothill zone of Sequoia National Park. Quantitative stand structure is also treated as reflected by soil and environmental patterns and the dynamics of seedling establishment.

Quercus douglasii, distributed throughout the foothills of the Coast Ranges and Sierra Nevada of California, often occurs with other oak species but is usually restricted to relatively dry sites (Griffin, 1973). Its ability to survive in such areas has been attributed to a deep root system and to its deciduous nature (Griffin, 1973). These facts suggest an interaction between environmental conditions and plant responses to water stress and seasonal patterns.

Physiologically, *Q. douglasii* must be able to withstand or avoid drought characteristic of the hot and dry summers of California's Mediterranean climate. The responses of plant characteristics to limited moisture availability and the consequent physiological stresses are an important aspect of successful ecological adaptation in Mediterranean-climate species. For example, timing and duration of phenological events (specifically leaf longevity, amount of new growth, and reproductive effort) are all related to climatic patterns (Leith, 1974). In addition to these physiological and phenological factors, the distribution and structure of *Q. douglasii* communities are affected by conditions of seedling establishment and the historical background of land use, including fire history and grazing practices. Our goal in this paper is to integrate all of these factors in discussing the ecological relationships of *Q. douglasii* in Sequoia National Park.

Methods

A vegetation inventory of the foothill zone of Sequoia National Park was carried out in spring 1977, including 20 stands of foothill woodland and nine additional stands of mixed evergreen woodland with *Q. douglasii*. These stands were sampled by means of two 25-m line-intercept transects. Data recorded for each stand included cover and height of woody species and the physical characteristics of the stands, including aspect, slope angle, elevation and soil type. Stands with *Quercus douglasii* were found between 338 and 1173 m elevation.

Soil samples were collected from each stand by pooling 30 subsamples from the top 10 cm of mineral soil. Analyses of N, P, K, Ca, Mg, $N-NH_4$, $N-NO_3$, soluble P, loss on ignition, and pH were carried out at the Soil Testing Laboratory of the University of Alaska, Palmer, following standard methods (Allen et al., 1974). Textural analysis and

determinations of soil water-holding capacity were made at U.C. Irvine using standard hydrometer and soil pressure-plate techniques.

Three permanent study sites representing blue-oak woodland communities were selected in 1977 for detailed studies of water relations, phenological patterns, and growth rates of *Q. douglasii*. The Ash Mountain site at 520 m has a southerly exposure with only a gradual slope. This site receives a greater amount of solar radiation than the other two. Surface soil moisture was lower and ambient temperatures were higher here than at the other two sites during our study. The community composition is that of a typical blue-oak woodland, with widely spaced trees forming a savanna with a grass and herb understory. The Flume site, at 634 m, has a northwestern exposure and a 30° slope. The community is a buckeye-woodland phase of a blue-oak woodland with a more closed canopy than the Ash Mountain site. Buckeye Campground, at 830 m, has a westerly exposure and a 30° slope. Temperatures are coolest at this site due to its location in a canyon that channels cold air drainage. This stand is also a buckeye-woodland phase of blue-oak woodland. The canopy is closed with an herbaceous understory.

Water-stress measurements were made using a Scholander-type pressure chamber (Scholander et al., 1965; Ritchie and Hinckley, 1975). Predawn and midday readings were carried out over a 12-month period. During the growing season, March to May, measurements were made at 2-week intervals, otherwise at 4-week intervals. The sampling regime included measurements for 3–5 branches from each of two different trees. Water-potential values were calculated as the average of mean readings from each plant and the standard errors of these means were usually less than 1 bar. Midday samples were collected from branches in full sun to represent maximum diurnal stress conditions. The bomb chamber was pressurized during measurement at 0.5 bars/sec with "balancing pressure" recorded with the first appearance of xylem sap on the cut surface of the sample twig. Weather data, including temperature, relative humidity, and rainfall were monitored at permanent weather stations established at each site.

Qualitative observations of phenological stage (i.e., presence of leaf buds, new leaves, flowers, fruit, mature and senescent leaves) were recorded at the same intervals as the water stress measurements. Measurements of branch elongation were made at each site on five permanently tagged branches of each of five individuals (N = 25).

Results and Discussion

Blue-oak woodlands in the southern Sierra Nevada, the dominant phase of the foothill woodland community (Griffin, 1977), extend upward from approximately 200 m (possibly lower before the influence
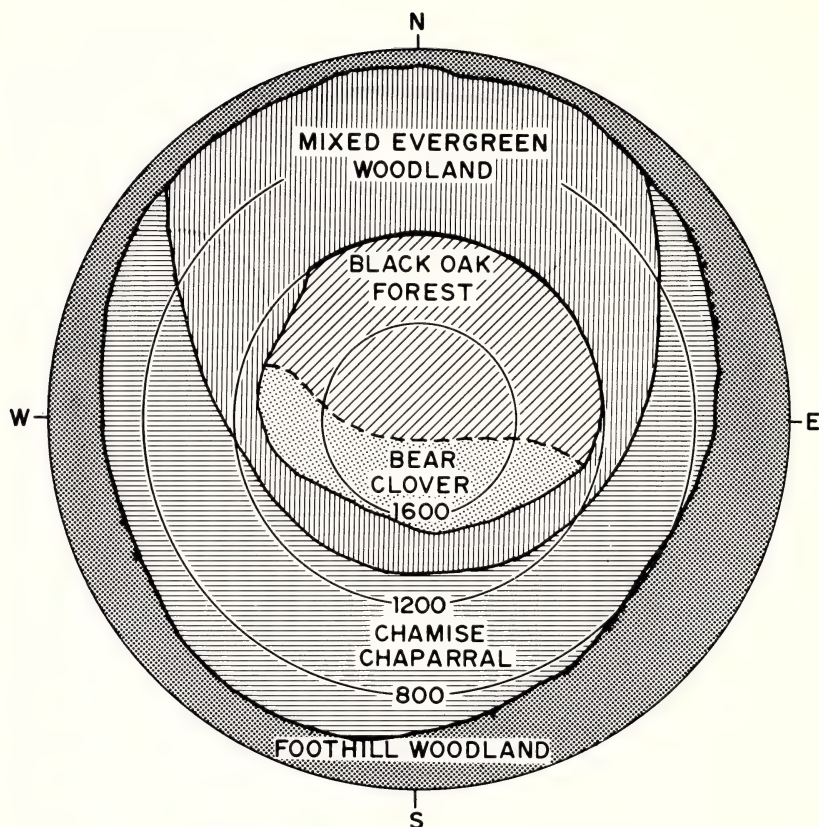
Fig. 1. Polar diagram of the distribution of foothill woodland and other major community types in the foothill zone of Sequoia National Park. Elevations are shown in meters.

of agricultural activities). They are replaced at 500–800 m by ever-green-dominated communities (Fig. 1). On north-facing slopes this community is replaced at about 500 m by mixed evergreen woodland dominated by *Aesculus californica, Quercus wislizenii,* and evergreen shrub species. On south-facing slopes it may extend up to 600–800 m where it is replaced by chamise chaparral. In many areas complex mosaics of communities occur, with blue-oak woodland on drier sites and mixed-evergreen woodland on more mesic sites, or blue-oak woodland on deeper soils and chaparral on shallower soils. Small stands of foothill woodland can be found at higher elevations up to 1500 m on relatively dry ridge lines, where soils are moderately deep or bedrock fractured. In these higher sites *Q. douglasii* is replaced by *Q. kelloggii* (black oak), but the open, savanna-like structure of stands

TABLE 1.   CANOPY COVER (PERCENT), TOTAL WOODY PLANT COVER (PERCENT) AND MEAN HEIGHT (M) OF *Quercus douglasii* IN WOODLAND COMMUNITIES OF SEQUOIA NATIONAL PARK. Cover ranges are given in parentheses.

Community type	No. of stands sampled	Mean cover of *Q. douglasii*	Woody plant cover	Mean height of *Q. douglasii*
Foothill woodland				
Blue-oak woodland	10	42 (23–74)	70	7.7
Buckeye woodland	7	22 (26–40)	75	5.1
Black-oak woodland	3	6 (0–19)	74	6.0
Mixed-evergreen woodland				
Oak-buckeye woodland	9	3 (0–20)	94	6.0

remains much the same. These stands are quite distinct from typical black-oak forest.

Cover of *Q. douglasii* ranged from 23–79 percent in the 10 stands of blue-oak woodland we sampled (Table 1). Densities of blue oaks in these stands range from 111 to 321 trees per hectare (Brooks, 1969). The mean height of *Q. douglasii* is greater in this community than in woodland communities and decreases as cover of *Q. douglasii* decreases (Table 1). Herbaceous understories in blue-oak woodlands are invariably dense and dominated by introduced annual grasses. Woody shrubs and trees including *Aesculus californica, Arctostaphylos viscida, Quercus wislizenii, Rhamnus ilicifolia, Toxicodendron diversilobum, Quercus chrysolepis, Quercus dumosa,* and *Ceanothus cuneatus* are frequently present but never dominant.

In the buckeye-woodland phase of the foothill woodland, *Aesculus californica* and evergreen shrubby species combined have greater coverage than *Q. douglasii* (Table 1). *Aesculus* generally has 20 percent or more coverage in these stands. Herbaceous species also provide a continuous ground cover in this phase of foothill woodland, but the denser canopy structure in comparison to the blue-oak phase (Table 1) leads to a dominance of broad-leaved, herbaceous species over grasses.

Quercus douglasii occurs infrequently as a minor element in mixed-evergreen woodland. Its cover may reach 20 percent in such stands, but evergreen oaks are more dominant. We have termed these communities, with or without blue oak, as the oak-buckeye phase of mixed-evergreen woodland.

Soil characteristics of foothill-woodland communities differ from those of the oak-buckeye phase of mixed-evergreen woodland in many respects despite the common parent materials. Values for mean total nitrogen, total phosphorus, and loss on ignition are all much lower in
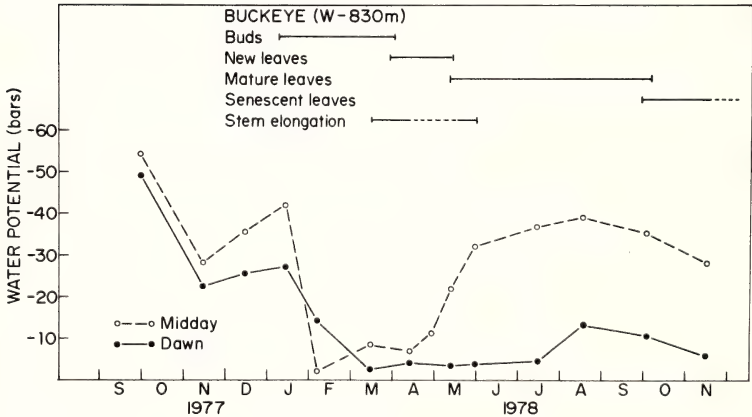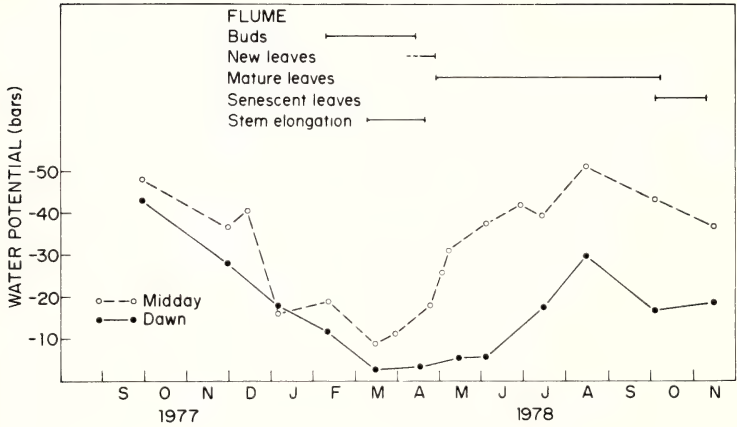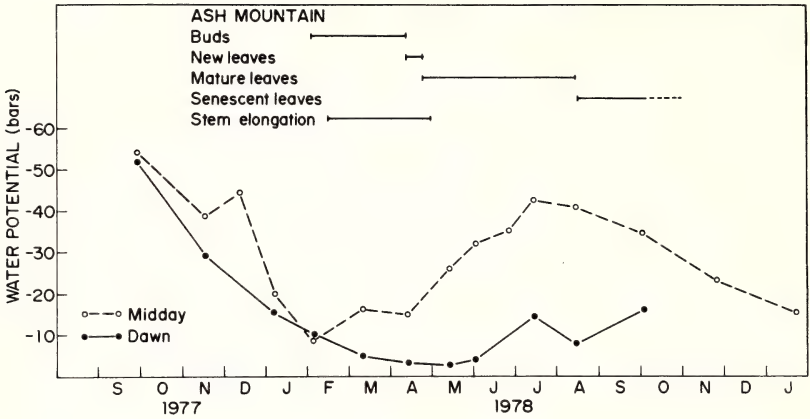
TABLE 2.   SOIL CHARACTERISTICS OF COMMUNITIES WITH *Quercus douglasii* IN SEQUOIA NATIONAL PARK. Nutrients are reported as ppm (±s.d.). Soil particle-size classes, loss on ignition and moisture content are reported as percents (±s.d.).

| | Foothill woodland | | | Mixed-evergreen woodland |
	Blue-oak woodland	Buckeye woodland	Black-oak woodland	Oak-buckeye woodland
Total N	1920 ± 830	1900 ± 310	2130 ± 570	2990 ± 1310
Total P	650 ± 300	620 ± 190	720 ± 520	1040 ± 650
K	455 ± 281	353 ± 395	353 ± 79	460 ± 195
Ca	1695 ± 734	1793 ± 504	1738 ± 422	2426 ± 998
Mg	134 ± 60	150 ± 59	150 ± 28	186 ± 89
N-NH$_4$	16.3 ± 8	20.1 ± 27	13.7 ± 1.9	12.8 ± 4.5
N-NO$_3$	11.4 ± 5.2	10.7 ± 7.6	6.8 ± 1.8	11.0 ± 3.9
Soluble P	52 ± 36	57 ± 15	64 ± 85	74 ± 60
pH	6.53 ± 0.39	675 ± 0.16	6.45 ± 0.10	6.59 ± 0.34
Loss on ignition	6.6 ± 3.2	6.8 ± 2	8.7 ± 2.2	11.0 ± 4.6
Sand	79.8 ± 6.5	82.2 ± 3.4	82.1 ± 1.6	80.2 ± 3.6
Clay	9.0 ± 5.4	6.8 ± 2.3	5.8 ± 1.3	7.1 ± 1.7
15-bar soil moisture content	7.5 ± 2.9	7.8 ± 2.3	9.9 ± 1.0	12.3 ± 6.1

the foothill woodland, indicating lower soil fertility (Table 2). Cation contents and available forms of nitrogen and phosphorous are not significantly different. Soils in all community types are sandy loams, with a mean sand content of about 80 percent. The higher organic matter content of the oak-buckeye communities, however, gives these soils a higher moisture content at −15 bars water potential.

Seasonal water-stress patterns in *Quercus douglasii* reflect patterns in precipitation. Although *Q. douglasii* is able to use water from relatively great depths (Lewis and Burghy, 1964), it must rely on a limited ground-water supply that apparently is depleted by autumn.

Quercus douglasii showed similar seasonal patterns in dawn and midday water potentials at all three study sites over 1977–1978 (Figs. 2–4). The highest stress at all sites occurred during the initial (September, 1977) measurement at the end of a severe two-year drought. With the onset of precipitation in November, water potentials began to increase, although that increase was much slower than in evergreen shrubs at the same sites. There was a secondary peak of stress at all

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FIGS. 2–4.   Seasonal water potentials at dawn and midday and qualitative phenology of *Quercus douglasii*. FIG. 2 (top). Ash Mountain site. FIG. 3 (middle). Flume site. FIG. 4 (bottom). Buckeye Campground site.
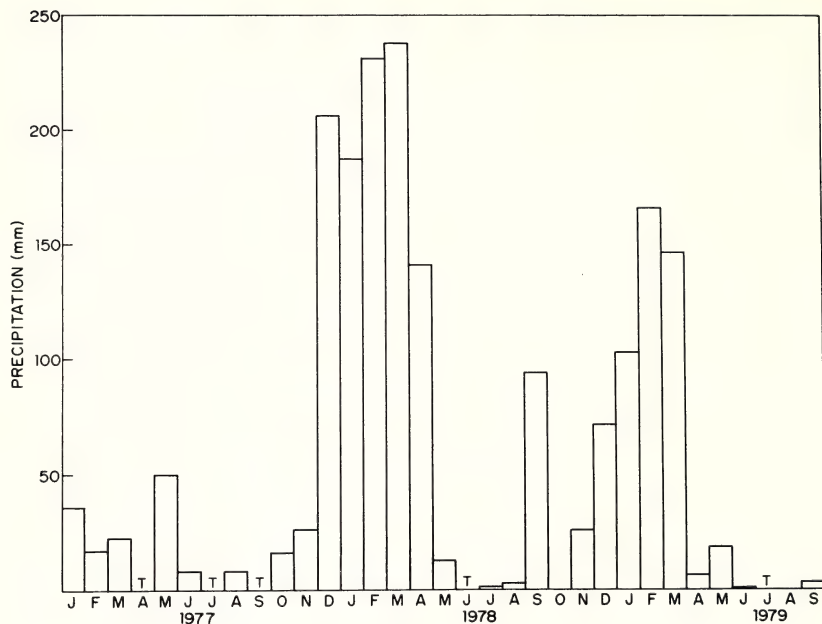
FIG. 5.   Monthly precipitation for Ash Mountain over the 1977–1979 period of study. Trace precipitation is indicated by a "T".

sites; in December at the Flume and Ash Mountain and during De-cember–January at Buckeye Campground, reflecting continued drought conditions following initial fall rains (Fig. 5). The highest water potentials occurred in February and March when the soil was recharged with water. Minimum water potentials occurred in July at Ash Mountain and in August at the other two sites.

Extreme summer water potentials are low for all three years from 1977–1979, but there is a large difference between the dawn water potentials of the drought (1977) and mesic (1978) years (Fig. 6). In 1977 the greatest difference between dawn and midday values was −6 bars. The following year the differences ranged from −21 to −30 bars, indicating considerable overnight recovery. Intermediate values of water potential and dawn-to-midday stress differentials were gen-erally present in 1979 when precipitation was close to mean levels. Maximum 1979 water stress at the Flume site, however, exceeded that reached during the drought of 1977.

Intensive studies of the water relations of *Quercus douglasii* trees in the coast ranges of Monterey County over a three-year period found minimum dawn water potentials of −40 bars (Griffin, 1973). This is higher than our minimum dawn water potential (below −50 bars in
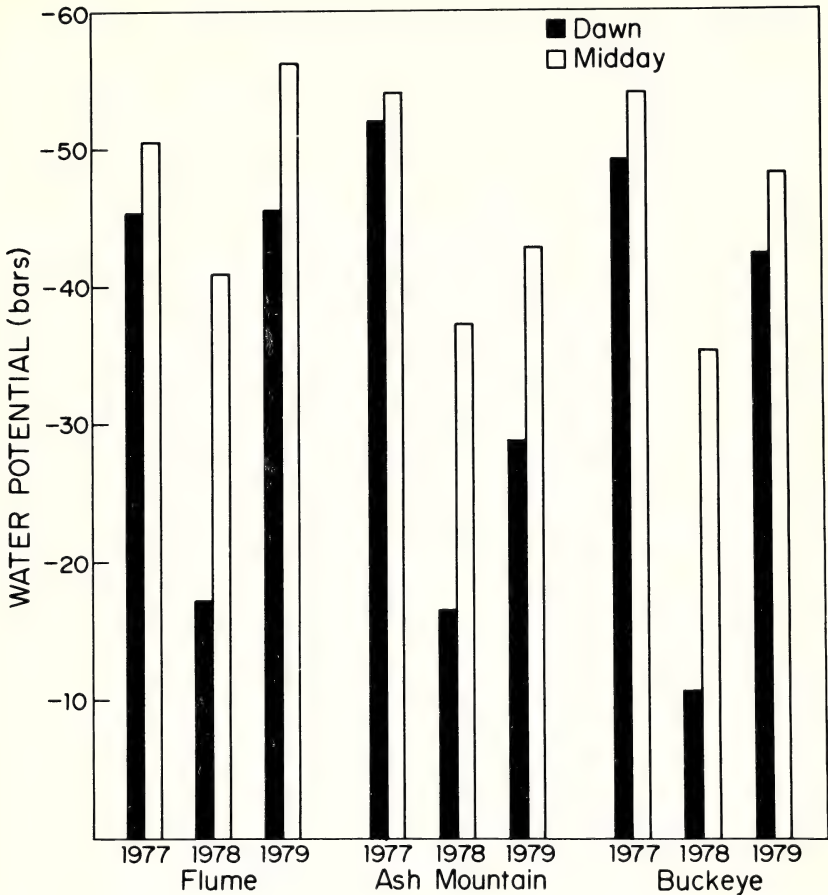
Fig. 6.   Minimum water potentials for 1977–1979 in three populations of *Quercus douglasii*.

both 1977 and 1979). The density of *Q. douglasii* on slopes with shallow soils has been shown to be directly related to water stress (Griffin, 1973).

Phenological patterns and periods of vegetative growth among sites showed variability. The greatest amount of growth and development occurred from March through May when surface soil moisture was highest, temperatures were increasing (Table 3) and water uptake by plants was highest (Figs. 2–4).

Stem elongation preceded the major phenological events (Figs. 2–4). Trees at Ash Mountain showed a pattern of gradual stem elonga-
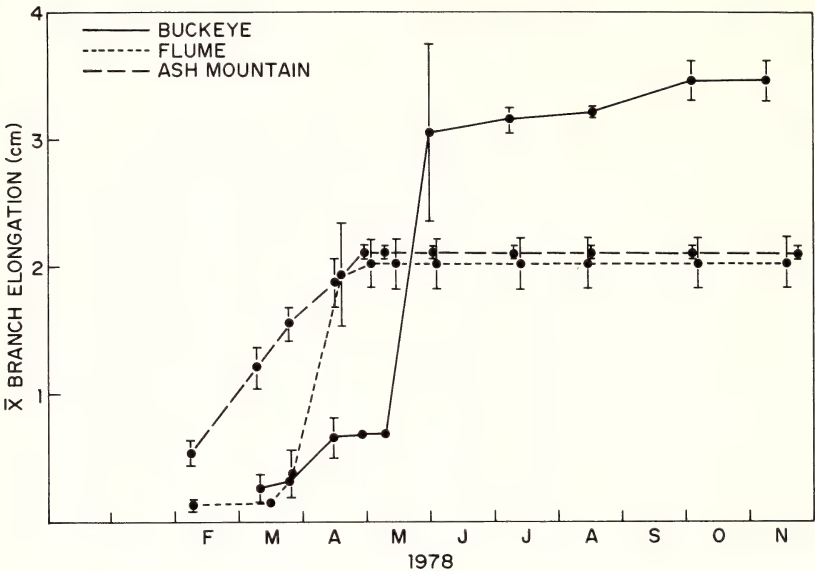
FIG. 7. Seasonal pattern of stem elongation in three populations of *Quercus doug-lasii*. Brackets enclose one standard error around the mean.

tion from February through April, while growth at the other two sites occurred rapidly over a shorter period of time (Fig. 7). This rapid growth occurred at the Flume site in March and at Buckeye Campground, the coolest of the sites, in May. Total mean stem elongation for the Flume, Ash Mountain, and Buckeye Campground sites was 2.0, 2.1, and 3.7 cm, respectively.

The first initiation of bud swelling occurred one to two months earlier at Buckeye Campground than at the other two sites despite the cooler temperatures (Figs. 2–4). New leaves formed after the main

TABLE 3. MEAN MONTHLY HIGH AND LOW TEMPERATURES (°C) DURING THE 1978 GROWING SEASON AT THE *Quercus douglasii* STUDY SITES. Data for March are means for a single week.

	Ash Mountain		Buckeye Campground		Flume	
	High	Low	High	Low	High	Low
February	15.2	4.2	11.6	3.6	10.5	4.2
March	19.3	7.7	13.5	5.7	12.2	7.2
April	17.9	7.0	—	—	13.5	6.3
May	23.6	11.0	21.6	9.1	21.5	10.7
June	27.5	14.0	26.8	13.9	27.9	15.9

branch elongation at Ash Mountain and Flume, but at Buckeye the appearance of new leaves and branch elongation continued simultaneously. New leaves appeared at all sites by the end of March and were mature by mid-April, with a blue-green caste and a thick cuticle. The leaves remained on the trees throughout the major portion of summer and began to fall at the end of August when trees were under maximum water stress. By October all trees had lost the majority of their leaves and remained leafless until the following March.

Flowering in *Q. douglasii* is determined by conditions of the previous growing season, because reproductive buds are formed at that time. No flowering was observed during the 1978 season at any site, reflecting conditions of drought in 1977. However, many catkins developed after the appearance of new leaves at the Ash Mountain site in 1979. There was also somewhat greater stem elongation during this season. Average elongation was 1.5 cm on 20 March 1978 and, for the same branches a year later (16 March 1979), elongation 2.2 cm.

Studies of oak community structure by Griffin (1971, 1976) and White (1966) have shown that a combination of favorable conditions must occur for successful reproduction and establishment. With their limited root systems, seedlings of *Q. douglasii* must endure much lower summer water potentials than mature trees (Griffin, 1973). Not only are temperature and rainfall important, but also such factors as acorn and seedling predation, grazing pressure, and fire history. Phenological variability from season to season has been shown by Griffin (1971) and in unpublished National Park Service data. Establishment every year is not necessary for populations of long-lived species, such as oaks, to maintain themselves. When the correct combination of favorable conditions occur, the result is the establishment of a cohort of oaks of similar ages (Griffin, 1977).

Quercus douglasii stands in Sequoia National Park have a high proportion of even-aged individuals of similar size (Brooks, 1969). The greatest proportion of trees are between 60 and 100 years old and 12 to 30 cm dbh. Stand density affects diameters to some degree, so that dense stands (163 trees/ha) have trees with an average dbh of 18 cm and open stands (25 trees/ha) show a greater average dbh of 36 cm in the Coast Range of Central California (White, 1966). The factors responsible for the increased density of *Q. douglasii* in Sequoia National Park and other areas in California are believed to be changes in land-use history and concurrent occurrence of favorable establishment conditions in the 1860's and 1870's (Vankat and Major, 1978). During this period grazing was increased and increased density of *Q. douglasii* was favored by removing herbaceous competition for oak seedlings and decreasing fuel levels so that fires were not as intense or frequent. In addition to direct effects on oak seedlings, fire has an indirect effect on young blue oaks by increasing vulnerability to insect damage (Lawrence, 1966).

The survival of *Q. douglasii* in drier habitats is the result of a coordination between physiological and phenological characteristics in response to environmental conditions. Initial distribution of blue oaks and subsequent stand structure are affected by patterns of climate and physical events.

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HYBRIDIZATION BETWEEN *COWANIA MEXICANA* VAR. *STANSBURIANA* AND *PURSHIA GLANDULOSA* (ROSACEAE)

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Abstract

The hybrid combination *Cowania mexicana* var. *stansburiana* × *Purshia glandulosa* has been observed at two locations in Inyo Co., California. Morphological intermediacy, reduced fertility, and the addition of species-specific flavonoids document hybridization in the narrow altitudinal zone of the species' overlap at these localities. A unique aspect of this study is that leaf flavonoid complements of the two species and hybrids are the same whereas petal flavonoid complements are different subsets of the leaf flavonoid constituents. The discovery of this hybrid documents the third possible hybrid combination among three taxa (including *P. tridentata*) that are currently classified within two genera and magnifies the question of the logic of this classification.

Cowania mexicana var. *stansburiana* (Torr.) Jeps. and *Purshia glandulosa* Curran are long-lived shrubs or small trees of the Rosaceae. Within the southern Great Basin, they form a significant component of the vegetation from 850–2700 m (Fig. 1). These two species, with *P. tridentata* (Pursh) DC., have been the subjects of numerous studies because of their conspicuous abundance and importance as range plants. Ecological (Nord, 1965; Mortenson, 1970) and range management studies (USDA, 1937; Plummer et al., 1968; USDA, 1975; Blauer et al., 1975) make up the bulk of the literature.

Cowania, with three or four species, and *Purshia,* consisting of two species, have been regarded as well-defined genera because of obvious differences in number of carpels, appearance of fruits, and other divergent morphological characters. In spite of this, several authors have noted interspecific and intergeneric hybridization (Brandegee, 1903; Stebbins, 1959; Stutz and Thomas, 1963; Nord, 1965; Blauer et al., 1975).

This paper presents morphological, chemical, and fertility data that document hybridization between *Cowania mexicana* var. *stansburiana* and *Purshia glandulosa*. Although this hybrid combination has been suggested as possible and probable (Brandegee, 1903; Thomas, 1957; Stutz and Thomas, 1963), no documentation of either artificial or natural hybrids exists. The results of this study are of special interest in that they document the third possible hybrid combination among three taxa that are currently classified within two genera.
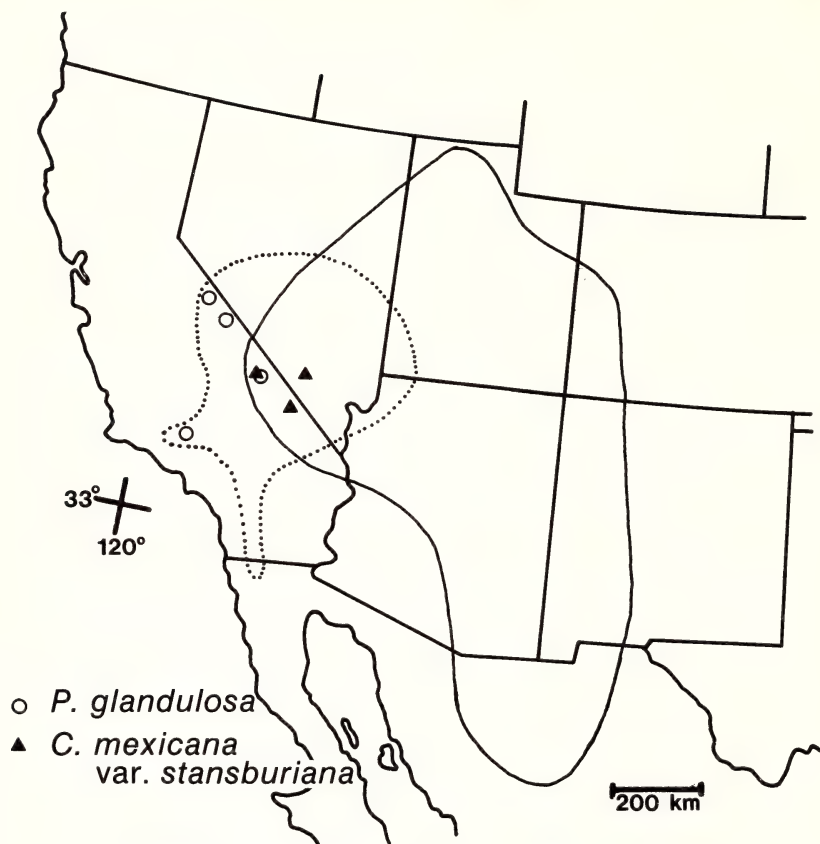
FIG. 1. Geographic distribution of *P. glandulosa* (dotted line) and *C. mexicana* var. *stansburiana* (solid line), and locations of populations used in this study.

Brandegee (1903), describing a plant he collected in the Providence Mountains of southeastern California and that he called *Cowania mexicana* var. *dubia,* stated that "this form was also collected by Dr. C. A. Purpus on Morey Peak, Nevada in 1898, and he considered it a hybrid between *Cowania* and *Purshia.*" No indication was given by Brandegee of which species of *Purshia* Purpus considered to be parental, although a Purpus specimen (*6356,* UC) is clearly labelled *Cowania Mexicana* × *Purshia glandulosa*. Subsequent collections and observations in the Providence Mountains indicate that *P. glandulosa* and *C. mexicana* var. *stansburiana* are abundant there, but *P. tridentata* does not occur that far south (Munz, 1959). Nord (1965) interpreted Brandegee's *C. mexicana* var. *dubia,* from the Providence Mountains, and Purpus' collection from Morey Peak, Nevada, as hy-

brids between *P. tridentata* and *C. mexicana* var. *stansburiana* and proposed the hybrid be called "Purpus cliffrose (*C. mexicana* var. *dubia* Bdg.)".

Stebbins (1959), using his observations and the preliminary data of H. Stutz, P. Plummer, A. Holmgren, W. S. Boyle, and L. K. Thomas, concluded that sympatric hybridization and introgression between *P. tridentata* and *C. mexicana* var. *stansburiana* is widespread. In the same paper, Stebbins (1959) stated that *P. tridentata* and *P. glandulosa* form such extensive hybrid swarms that the identity of the parental types is completely obliterated, although no quantitative data were presented. These putative hybrid swarms occur along the eastern side of the Sierra Nevada and elsewhere in central and eastern California (Koehler, unpubl. data).

Stutz and Thomas (1963) documented that *C. mexicana* var. *stansburiana* and *P. tridentata* frequently form fertile hybrids in nature, ranging from a relatively few putative F_1 hybrids to situations that suggest the presence of F_2 segregates as well as F_1 and backcross derivatives, depending on the slope exposure of parental populations. These authors also suggested that *P. glandulosa* appears to be a stabilized segregate from hybrids of *C. mexicana* var. *stansburiana* and *P. tridentata*.

Artificial hybridization by pollinating emasculated flowers of *C. mexicana* var. *stansburiana* with pollen from *P. tridentata* has produced viable seeds and seedlings (Blauer et al., 1975).

Knobloch (1972) listed 2993 reports of intergeneric hybridization in flowering plants and stated that hindrance of acceptance of hybridization as a potent evolutionary force results from lack of knowledge of the extent of the process in nature. The bulk of literature dealing with homogamic intergeneric hybridization describes crosses that were artificially derived, such as *Helianthus* × *Viguiera* (Heiser, 1963), *Lycopersicon* × *Solanum* (Rick, 1951, 1960), *Lychnis* × *Silene* and *Melandrium* × *Silene* (Kruckeberg, 1962), *Hordeum* × *Agropyron* (Kruse, 1974), *Tripsacum* × *Zea* (Mangelsdorf and Reeves, 1938), and others in the Gramineae (Stebbins, 1950). Observations of natural intergeneric hybridization such as *Cowania* × *Purshia* (Stutz and Thomas, 1963) and *Encelia* × *Geraea* (Kyhos, 1967) are limited, except in the Orchidaceae where natural hybrids between genera are common (Pijl and Dodson, 1966).

METHODS

Two mixed stands of *C. mexicana* var. *stansburiana* and *P. glandulosa* containing putative hybrids were observed in the field and specimens were collected for study. Specimens from monotypic stands of each species were also collected for comparison (Fig. 1). The putative hybrids occur on the east flank of Cerro Gordo and Waucoba

TABLE 1.   MORPHOLOGICAL COMPARISON OF *Cowania mexicana* VAR. *stansburiana*, *Purshia glandulosa*, AND PUTATIVE HYBRIDS. Numerical values represent the mean of 10 measurements on each of 5 individuals from 4 populations (20 plants) of *P. glandulosa* and of 5 individuals from 3 populations (15 plants) of *C. m.* var. *stansburiana* and of the 14 hybrids. Numbers in parenthesis are the ranges of means of 10 measurements/individual.

Character	*C.m.*	Hybrids	*P.g.*
Pistil number	5.0 (4.2–6.4)	2.4 (2.0–3.0)	1.2 (1.0–1.3)
Style length in fruit (cm)	3.8 (3.0–4.3)	1.9 (1.6–2.2)	0.7 (0.6–0.8)
Style pubescence in fruit	plumose	short villous	puberulent
Achene shape	oblong	intermediate	obovate
Achene ratio, L/W	3.6 (3.0–4.3)	2.3 (2.2–2.7)	2.0 (1.9–2.2)
Achene pubescence	villous	villous-hirsute	short pubescent
Hypanthium pubescence	glabrous	sparse	tomentulose
Stamen series	2	2 (see text)	1
Number of stamens	>80	52.0 (43–70)	<30
Petal shape	obovate	intermediate	spatulate

Mountain, located respectively near the south and north ends of Saline Valley, Inyo County, California. On Cerro Gordo, *C. mexicana* var. *stansburiana* ranges from 1600 to 2200 m and *P. glandulosa* ranges from 1350 to 1800 m. At Waucoba Mt. the two species range from 1850 to 2100 m and from 1700 to 2000 m, respectively. Hybrids were growing along roads and in washes paralleling roads in a narrow altitudinal zone of species overlap. Fourteen apparent hybrids were found at the two localities. No other mixed stands or hybrids were encountered in these mountains or in other ranges of the region.

A variety of morphological characters distinguish the parental taxa and hybrids. Table 1 shows the most striking and consistent differences. A hybrid-index value for each of the 49 plants studied was derived by assigning the character states given in Table 1 a value of 2 for *Cowania*-like characters and a value of 0 for *Purshia*-like characters; intermediate states were assigned a value of 1. Voucher specimens are deposited at UCSB.

Fertility was estimated from pollen stained for at least 24 hours in 1 percent aniline blue in lactophenol. Five hundred pollen grains were scored from each of 10 specimens of each population. Ten flowers were sampled from each of the 14 putative hybrids. Pollen grains that stained evenly were considered viable; unstained and unevenly stained grains were considered inviable.

Comparison of flavonoids of flowers and leaves was performed by standard techniques (Harborne, 1967, 1968, 1973; Mabry et al., 1970). Twelve flavonoids were identified and individual plants were compared by two-dimensional paper chromatography using identified compounds as markers.
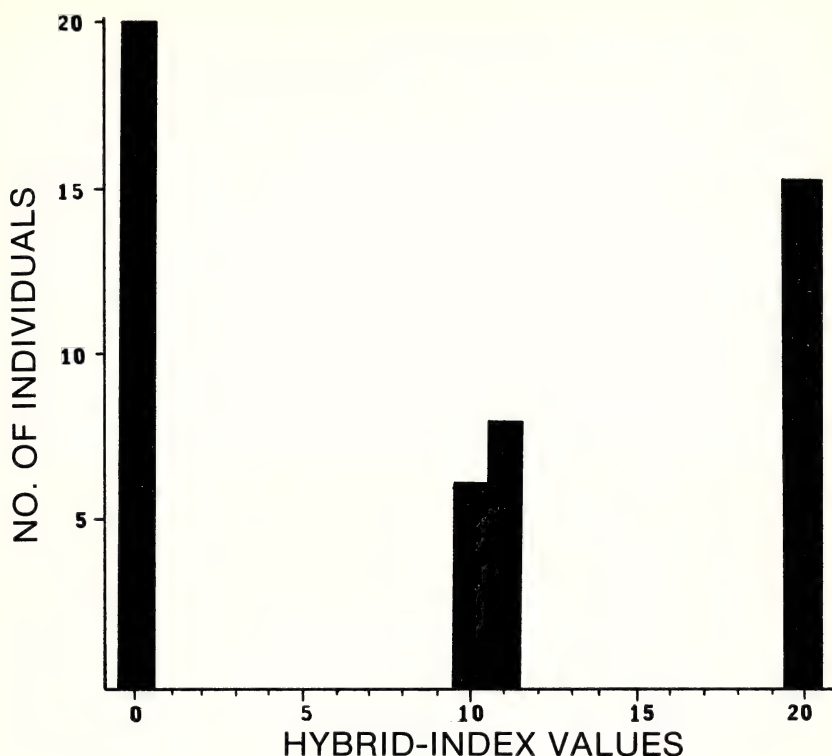
FIG. 2.   Histogram of the hybrid-index values for 49 plants. The character states given in Table 1 were assigned a value of 20 for *Cowania*-like characters and a value of 0 for *Purshia*-like characters; intermediate states were assigned a value of 10.

RESULTS

Morphological comparison.   Several floral and mature fruit characteristics distinguish *C. mexicana* var. *stansburiana, P. glandulosa,* and the putative hybrids (Table 1; Figs. 2–3). Some contrasting characters and a typical intermediate are shown in Figs. 4 and 5. Vegetative characters such as leaf shape, number of lobes per leaf, leaf margin revolution, and glandularity, as used in earlier studies of hybridization between *P. tridentata* and *C. mexicana* var. *stansburiana* (Thomas, 1957; Stutz and Thomas, 1963), were too variable within and overlapping between populations to be of value. Field identification of individuals in overlapping and contiguous areas was difficult when both flowers and fruits were lacking.

Pollen stainability.   Cowania mexicana var. *stansburiana* averaged 93.4 percent stainable pollen, ranging from 84.0 to 99.0 percent
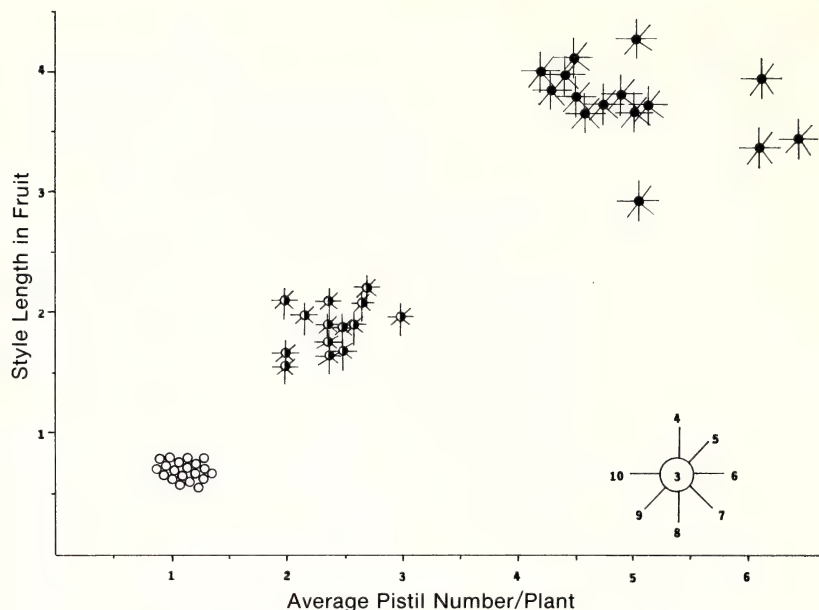
Fig. 3. Scatter diagram for 49 plants. The symbol in the lower right-hand corner indicates the character numbers listed in Table 1. Black circle and full-length glyph indicate *Cowania*-like characters. Open circle and no glyph indicate *Purshia*-like characters. Intermediate characters score as half values.

for all plants sampled from three populations. *Purshia glandulosa* averaged 81.2 percent stainable pollen, ranging from 22.8 to 99.4 percent for all plants sampled from four populations. Stainability of hybrid pollen was comparatively low, averaging 24.4 percent and ranging from 7.8 to 55.8 percent. Six hybrids were higher than the lowest value recorded for *P. glandulosa*, while three individuals of *P. glandulosa* were below the highest value recorded for hybrids. Forty-five percent of *P. glandulosa* individuals had percentages below the lowest value recorded for *C. mexicana* var. *stansburiana*.

Flavonoid constituents. Twelve compounds were identified from bulk leaf extracts of *C. mexicana* var. *stansburiana* and *P. glandulosa*. The two species and the hybrids possess the same leaf flavonoids (Fig. 6; Table 2). A corresponding analysis of petals showed that the two species differ significantly (Table 2). Petal extracts of the two species shared five quercetin glycosides. *Purshia glandulosa* petal extracts yielded a rhamnetin 3-O-glycoside not found in petals of *C. mexicana* var. *stansburiana*, while the latter species contained the aglycone quercetin and five glycosides based on the aglycones luteolin, gossypetin and corniculatusin not found in petal extracts of *P. glandu-*
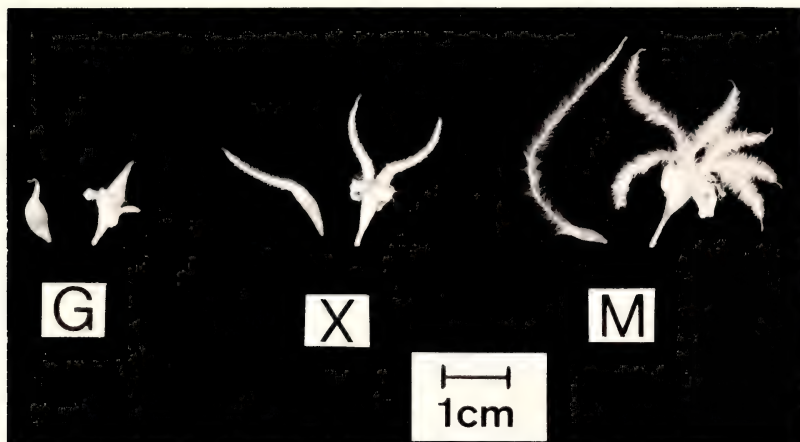
FIG. 4.   Fruits of *P. glandulosa* (G), *C. mexicana* var. *stansburiana* (M), and a hybrid (X).

losa. Flavonoids extracted from petals of hybrids matched the combined petal flavonoid complements of *P. glandulosa* and *C. mexicana* var. *stansburiana* (Fig. 7). No flavonoids unique to the hybrids were found. Six hybrids lacked sufficient petals to determine their flavonoid complements.

DISCUSSION

Hybridization occurred in the overlap zone of populations at two locations, separated by forty miles, in the Inyo Mountains of south-
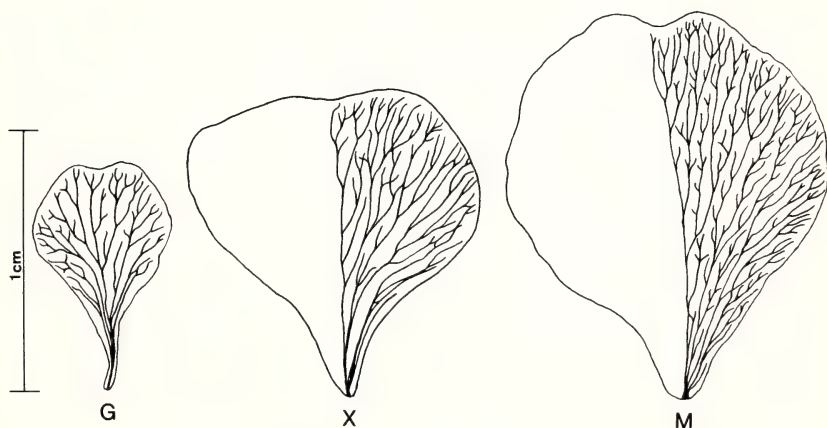
FIG. 5.   Drawing of petals of *P. glandulosa* (G), *C. mexicana* var. *stansburiana* (M), and a hybrid (X).
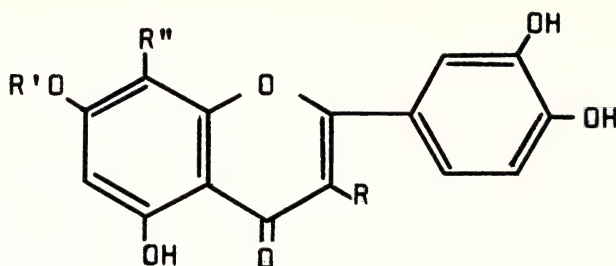
Fig. 6. The compounds isolated in this study were based on the aglycones represented above (LUTEOLIN; R = R' = R" = H. QUERCETIN; R = OH, R' = R" = H. RHAMNETIN; R = OH, R' = CH$_3$, R" = H. GOSSYPETIN; R = R" = OH, R' = H. CORNICULATUSIN; R = OH, R' = H, R" = OCH$_3$).

eastern California. Hybrids grew in obviously disturbed areas near roadsides. Although the surrounding terrain at both sites is very rugged, broken, and naturally disturbed, several trips to both sites yielded no other obvious hybrids. The onset of flowering in both species is gradual from low to high elevation and the flowers are short-lived. This tends to reduce pollen flow between the species at these sites because *C. mexicana* var. *stansburiana* occurs generally at the higher elevation and *P. glandulosa* at the lower. This is similar to the isolation between *C. mexicana* var. *stansburiana* and *P. tridentata* (Stutz and Thomas, 1963). Pollinator specificity is not known. No sterility because of differences in chromosome number is expected because both species have $n = 9$ (Baldwin, 1951; Blauer et al., 1975).

TABLE 2. FLAVONOID COMPOUNDS OF PETAL EXTRACTS OF *C. mexicana* VAR. *stansburiana*, *P. glandulosa*, AND PUTATIVE HYBRIDS. The 12 compounds are all found in and are the major flavonoid constituents of the leaves of the two species and the hybrids.

Compound	Cowania	Hybrids	Purshia
Luteolin 7-0-Glucoside	×	×	
Gossypetin 3-0-Glucogalactoside	×	×	
Corniculatusin 3-0-Glucoside	×	×	
Corniculatusin 3-0-Rutinoside	×	×	
Corniculatusin 3-0-Diglycoside	×	×	
Quercetin (as the free aglycone)	×	×	
Quercetin 3-0-Glucoside	×	×	×
Quercetin 3-0-Galactoside	×	×	×
Quercetin 3-0-Rutinoside	×	×	×
Quercetin 3-0-Glucoxyloside	×	×	×
Quercetin 7-0-Glucoside	×	×	×
Rhamnetin 3-0-Glycoside		×	×
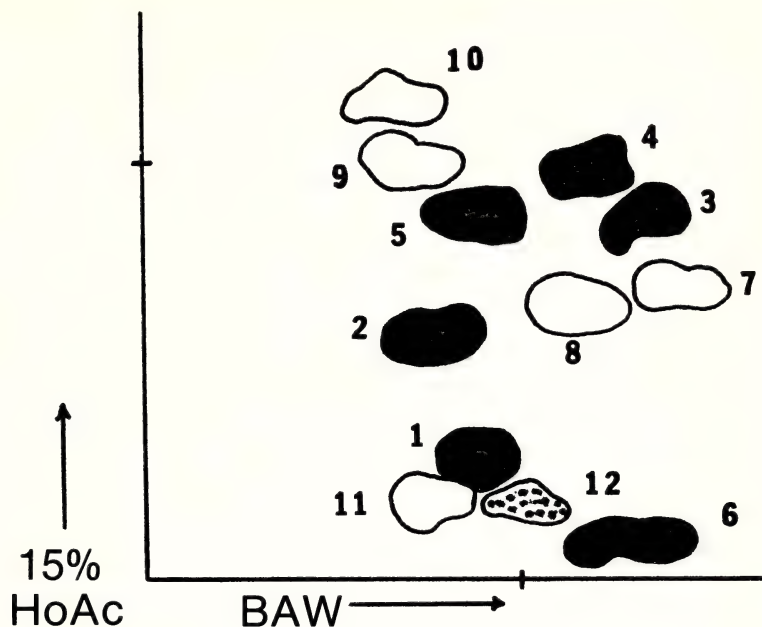
FIG. 7.   Diagrammatic representation of the spots revealed on paper chromatograms of the petal extracts of *C. mexicana* var. *stansburiana* × *P. glandulosa* hybrids. The unshaded spots are common to both putative parental species, the shaded spots are specific to *C. mexicana* var. *stansburiana,* and the speckled spot is specific to *P. glandulosa.* The numbers refer to the compounds listed in Table 2. R_f 0.50 indicated by cross lines on axes.

No other mixed populations or hybrids were encountered in the Inyo Mountains or other mountains of this region. Mountain ranges to the south and east, such as the Providence and New York Mountains of California, and the Spring and Palmetto Mountains of Nevada, contain numerous populations of each species but mixed stands are rare and no hybrids were observed. Contact between the species is relatively rare and in turn hybridization rare in the mountains near the California-Nevada border.

Pollen stainability. Average pollen fertilities of the two parental species is high. Overall fertility of the fourteen hybrids is significantly reduced. The range (7.8–55.8 percent) suggests that the hybrids are varied in their genetic make-up. Pollen fertility of *P. glandulosa* was low compared with *C. mexicana* var. *stansburiana* and *P. tridentata,* which had an average of 94.5 percent and a range of 90.0–97.6 percent (Koehler, unpubl. data). This is consistent with the hypothesis that *P. glandulosa* is a segregation product of *C. mexicana* var. *stansburiana* × *P. tridentata* that retains genetic variability. With *P. glandu-*

losa retaining heterozygosity one might expect a broad fertility range in F_1 hybrids of *C. mexicana* var. *stansburiana* × *P. glandulosa*.

Morphological comparison. Morphological data demonstrate the overall intermediacy of hybrids in relation to the parents. Only one character, stamen series, failed to score in a range dissimilar to either species in any of the hybrids. Stamen insertion in hybrids was highly irregular but best characterized as two series. Except for stamen series, the hybrids had a character state distinct from either species for each of the observed characters. Interplant variation in most characters indicated a high degree of morphological variability comparable with that expressed in the broad range of pollen fertility.

Flavonoid constituents. Although leaf flavonoid complements of *C. mexicana* var. *stansburiana* and *P. glandulosa* are the same, petal flavonoid complements are distinctive. Therefore, qualitative data showing addition of petal flavonoids in morphologically intermediate plants lends strong support to the theory of their hybrid origin. It has been shown that flavonoid compounds are often inherited as simple dominant characters, involving only one or a few genes (Alston, 1964; Brehm and Ownbey, 1965, 1968; Ownbey and Brehm, 1965), and addition of flavonoids has been observed in many studies of hybridization (e.g., Alston et al., 1962; Alston and Turner, 1963; Smith and Levin, 1963; Crawford, 1974).

A unique aspect of the results is that the sum of the twelve petal flavonoids is found in the leaves of both species. This indicates that both parental species have the same overall genetic complement for the production of flavonoids but that different modifier genes are operative in the production of petal flavonoids. Genes controlling flavonoid synthesis in these taxa apparently fall into three classes: those controlling general production, those modifying chemical structure, and those controlling distribution within the whole plant. The difference in specific petal flavonoid complements is not a relatively simple one such as the production of variants that differ only slightly in structure, but is based on the presence or absence of different compounds that are themselves uncommonly substituted.

These data indicate a close relationship between *C. mexicana* var. *stansburiana* and *P. glandulosa* in their identical leaf flavonoid complements, yet their petal flavonoid complements demonstrate a basic difference that supports morphological and ecological differences. The chemical data also emphasize the importance of studying floral as well as vegetative flavonoids.

Relationship to previous Cowania-Purshia studies. Examination of the type specimen of *Cowania mexicana* var. *dubia,* collected by T. S. Brandegee in the Providence Mountains of southeastern California in 1902, and of a specimen Brandegee considered to be of the same variety, collected by C. A. Purpus on Morey Peak, Nevada in 1898, indicates that they are both hybrid plants derived from *P. glan-*

dulosa × *C. mexicana* var. *stansburiana*. Both specimens have characteristics ascribed to the hybrids of this study. Several comparisons, such as pollen stainability and flavonoid analysis, could not be made but their morphological characters fall easily into the ranges of hybrids examined in this study. It was considered by one author (Nord, 1965) that these specimens were hybrids between *P. tridentata* and *C. mexicana* var. *stansburiana*. This suggestion can be negated on several points. The Providence Mountains are geographically removed from the southern limit of *P. tridentata* by approximately 268 km, but *P. glandulosa* and *C. mexicana* var. *stansburiana* populations can be found within a few kilometers of each other there. Morey Peak, Nevada, where Purpus collected his specimen, lies within the range of all three taxa. However, the specimen lacks distinctive *P. tridentata* characteristics, is similar to hybrids of this study, and was labelled *Cowania Mexicana* × *Purshia glandulosa* by Purpus, suggesting that it is also a hybrid derived from *C. mexicana* var. *stansburiana* and *P. glandulosa*. It is noteworthy that in 1898 Purpus recognized this plant as an intergeneric hybrid.

There seems little doubt that hybridization occurs between *C. mexicana* var. *stansburiana* and *P. glandulosa*. The data identify a well-established syndrome of hybridity: reduced fertility, morphological intermediacy, and the addition of species-specific flavonoids. The range of pollen fertility was suggestive of hybridization beyond the first filial generation, but petal flavonoid complements of eight hybrid individuals are the exact summation of parental complements. These eight individuals had pollen fertility averages below 21 percent and were the lowest of the 14 discovered hybrids in this regard. If these plants were the result of backcrossing, selfing, or intercrossing of F_1 hybrids, the effects of segregation on the flavonoid constituents would be expected in the petal flavonoid complements.

This documentation of hybridization between *C. mexicana* var. *stansburiana* and *P. glandulosa* closes the ring of possible hybrid combinations in this three-taxon complex and magnifies the question of the logic of the current classification. The occurrence of hybridization among the three taxa allows a strong case for merging the taxa into one genus. The data of this study and others (Thomas, 1957; Stebbins, 1959; Stutz and Thomas, 1963; Blauer et al., 1975) indicate a close genetic relationship that is clouded by seemingly major differences in carpel characters. However, without comprehensive study that includes the other taxa of *Cowania,* submerging taxa that long have been considered distinct and are important range plants would be premature.

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ANNOUNCEMENT

PAPERS IN WESTERN PLANT ECOLOGY HONORING JACK MAJOR

A symposium to honor Dr. Jack Major on the occasion of his retirement will be held at the University of California, Davis, on Friday, 29 May 1981, 9 a.m. to 5 p.m. Twelve to 13 papers will be presented, each 25 minutes long.

People wishing to contribute papers are invited to submit abstracts to Dr. Michael Barbour before 15 February.

The symposium will be co-sponsored by the California Botanical Society; the Botany Department, UC Davis; and UC Davis Institute of Ecology. The proceedings will be published in the Institute of Ecology series. Admission will be free.

An honorary dinner will be held from 7–9 p.m.

For further information and dinner reservations, call or write: DR. MICHAEL BARBOUR, Botany Department, UC Davis 95616: (916) 752-2956.

COVER OF PLANTS WITH EXTRAFLORAL NECTARIES AT FOUR NORTHERN CALIFORNIA SITES

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Abstract

Percent cover of plants with extrafloral nectaries was investigated in three California habitats with the same physiognomy as habitats previously studied in Nebraska (perennial native grassland, riparian forest, deciduous forest). In contrast to Nebraska where cover of plants with extrafloral nectaries reached 14 percent, no plants with extrafloral nectaries were found in any California transect. Chaparral was also studied; no plants with extrafloral nectaries were found.

A number of plant species with extrafloral nectaries (EFNs) have been shown to be involved in a mutualism with ants (Bentley, 1977; Deuth, 1977; Tilman, 1978; Inouye and Taylor, 1979; Koptur, 1979; O'Dowd, 1979; Pickett and Clark, 1979; Keeler, 1980b). Extrafloral nectaries are glands on a plant that secrete a nectar rich in sugars and amino acids, but are not involved in pollination. For ecological studies, function rather than morphology is considered the crucial aspect of the definition of an EFN.

Little is known about the distribution of plants with EFNs. Bentley (1976) and Keeler (1979) found that 0–80 percent of the plants in tropical habitats (Costa Rica and Jamaica) had EFNs, and that this correlated with ant abundance. In Nebraska, Keeler (1980a) found 0–14 percent of the cover to have EFNs. The percent cover of plants with EFNs in Nebraska was correlated strongly with abundance of foraging ants and secondarily with plant species diversity (H'), but not with rainfall or frost-free season.

This study was undertaken to test for a relationship between biome and the abundance of plants with EFNs. Three California communities with plant associations similar to the Nebraska ecosystems previously studied (prairie, riparian forest, and deciduous forest) were analyzed. The similar habitats are probably the result of similar rainfall (40–80 cm/yr). Adjacent chaparral was also investigated.

Methods

Vegetation analysis was carried out in natural habitats using a point-intercept method. Plants nearest to randomly chosen points along a transect were identified and scored for presence of EFNs. At each site, 500–1000 points were recorded on two transects. Simultaneously, abundance of ants was estimated using response of ants to karo syrup

and tuna fish baits (about 1 ml of each at 25 spots 2 m apart). Number and species of ants on baits at 15, 30, 60, 120, and 180 min. were recorded; the number of baits found reflects forager density, and number of species per bait probably indicates the diversity of the ant community.

The California sites were as follows: 1) Native grassland. Bunchgrass prairie 6.5 km north of Stonyford, Colusa County, on the Lodoga Rd., 370 m. This was a *Stipa* prairie with abundant annual forbs. 2) Riparian forest understory. Two sites along the Sacramento River, off Route 45 south of Princeton, Colusa Co., were studied; opposite Road 64, and along Reservation Road, 25 m. The canopy was dominated by cottonwoods, the understory by *Vitis americana, Ribes* spp., and *Rhus diversiloba*. 3) Deciduous forest understory. The study area was in Mendocino National Forest, Colusa Co., near Deafy Glade, 1370 m. The canopy was dominated by deciduous oaks (*Quercus garryana, Q. kelloggii*); the understory contained a variety of forbs, especially *Lupinus* sp. 4) Also studied was a chaparral site at 610 m in Mendocino National Forest along road 18N01 east of the Mill Creek campsite.

All studies were carried out 10–30 May 1979. This time was chosen for maximal plant and animal activity. The season had been cool and wet through the previous week. The days on which the study was carried out were warm, clear, and windy. Annual forbs were still flowering at the prairie site and *Stipa* was in bud. While it is possible that some extrafloral nectaries function at other times, the availability of water and the peak animal (both ant and herbivore) activity suggest April–May as the likely time for greatest EFN activity.

Air temperature was noted for all experiments. It ranged from 16°C to 33°C for 0900–1200 hr PDST, when ant baiting was carried out.

RESULTS

Not one plant with EFNs was found in any of the transects or observed at any of these sites (Table 1). Frequency of ants discovering baits was astonishingly low, in particular at the prairie site, where in one three-hour experiment, not one of 25 pairs of baits was found by ants. The California sites had significantly fewer ant species per bait as judged by the Wilcoxon two-sample test ($n = 10,6$; $C = 53$, $p < 0.01$; Sokal and Rohlf, 1969). Adding in the chaparral sites, there are still significantly fewer ants per bait at the northern California sites ($n = 10,8$; $C = 9$; $p < 0.001$) than at the Nebraska sites.

DISCUSSION

No species with extrafloral nectaries were found at any of the California sites. No native plants with extrafloral nectaries are known from the California habitats studied (pers. obs.; H. G. Baker, pers.

TABLE 1.   PERCENT COVER OF PLANTS WITH EXTRAFLORAL NECTARIES AND BAIT VISITATION BY ANTS FOR EIGHT TRANSECTS THROUGH FOUR VEGETATION TYPES IN NORTHERN CALIFORNIA.

Sites	Percent cover of EFN	# points sampled	% baits found in 180 min.	Mean ant spp/bait
Prairie	0	554	12	0.12
	0	865	0	0
Riparian forest understory	0	1064	33	0.43
	0	1045	55	0.55
Deciduous forest understory	0	659	87	1.61
	0	542	100	2.71
Chaparral	0	420	86	1.29
	0	544	86	1.52

comm., 1976). Some of northern California's introduced species do have EFNs, and have been shown to benefit by mutualism with ants (Koptur, 1979). Furthermore, *Helianthella californica* (Asteraceae), a forb of the Sierra Nevada, has EFNs and is found at the same latitudes as the sites studied. However, all Nebraska transects had plants with EFNs except tallgrass prairie. Even in tallgrass prairie, species with EFNs were noted outside the transect (Keeler, 1980a). This suggests that in reality, plants with EFNs are less abundant in northern California than they are in comparable habitats in Nebraska. Why this type of plant defense is not favored in these northern California habitats is not clear at this time.

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CHIOCOCCA HENRICKSONII (RUBIACEAE), A NEW SPECIES FROM THE CHIHUAHUAN DESERT REGION

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ABSTRACT

Two specimens from desertic mountains of Coahuila, Mexico, are described as **Chiococca henricksonii**, distinguished by its extreme xeromorphy, microphylly, and inflorescences that are reduced to solitary flowers. Tetramerous flowers are reported in the genus for the first time. *Chiococca henricksonii* appears to have relationships to *C. alba, C. pachyphylla,* and *C. petrina.*

Chiococca henricksonii M. C. Johnston, sp. nov.

Frutex humilis rupestris caulibus divaricatis hispidulis, folia coriacea elliptica hispidula laminis 4–6(–9) mm longis, flores solitarii 4–5-meri, calycibus hispidulis (Fig. 1).

Low shrub; branches numerous, divaricate, short, with internodes 1–4(–8) mm long, densely hispidulous with white, erect hairs 0.1 mm long; leaves coriaceous, hispidulous; blades elliptical, 4–6(–9) mm long; petioles 1–1.5(–2) mm long; flowers solitary, axillary; pedicels 1–1.5(–2) mm long, hispidulous; sepals 4–5, oblong, obtuse, ca. 1 mm long, hispidulous, pale green at first, persistent and darkly pigmented in fruit; corolla "dark yellow" (*Johnston 8738*), funnelform, ca. 7 mm long including tube ca. 4.5 mm long, gradually dilated upward, and 4–5 obtuse spreading lobes (apparently valvate in bud), caducous; stamens 4–5, ca. 6 mm long, inserted at very base of corolla-tube, paddle-shaped, with free filaments ca. 3 mm long and oblong acute anthers ca. 3 mm long, about half exserted beyond the corolla-tube and reaching about the midpoint of the corolla-lobes; ovary hispidulous; drupe (apparently slightly immature) laterally compressed, suborbicular, ca. 4 mm long and broad not including persistent sepals, white; seeds 2, brownish, narrowly ovoid.

TYPE: Mexico, Coahuila, 1–2 km n. of Puerto Colorado, near crest at sw. end of Sierra de la Fragua (near 26°45′N, 102°30′W), high limestone ridge with forest of *Pinus pinceana* Gordon, shrub flat against rock, rooted in solution-holes, fruit white with black stigma, above 1750 m, 2 Sep 1941, *I. M. Johnston 8738*. (Holotype: LL; isotypes: GH, MICH).

PARATYPE: Mexico, Coahuila, ca. 2.4 km sw. of Las Delicias on e. side of Sierra de las Delicias, at margin of scree-slope along canyon
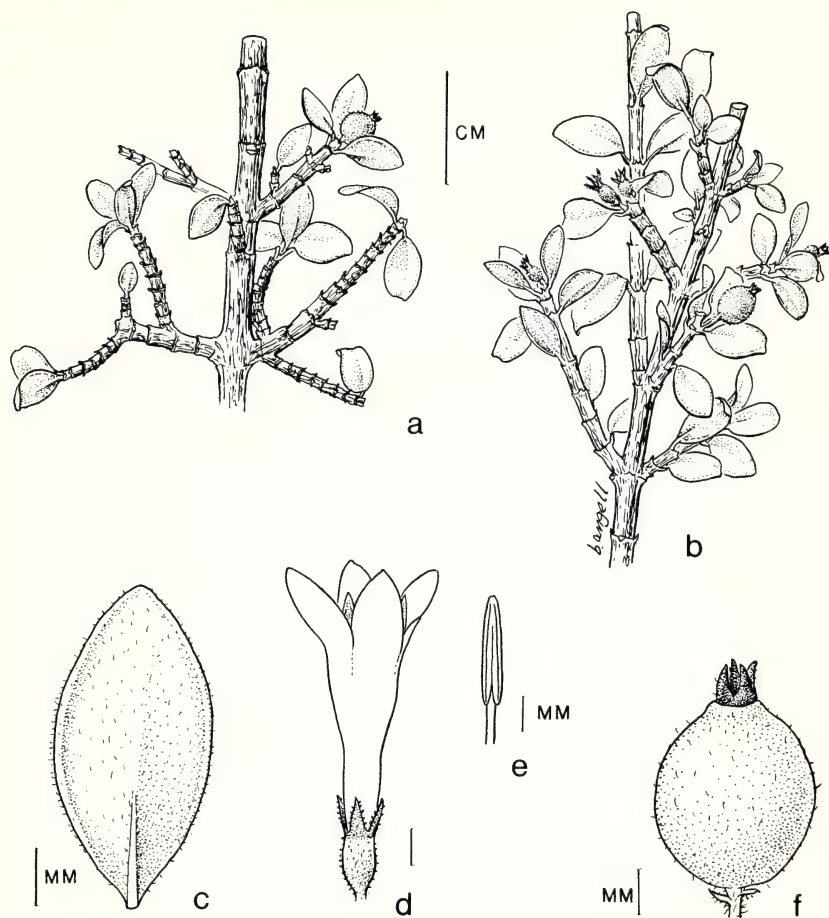
FIG. 1. *Chiococca henricksonii* M. C. Johnston, drawn from *I. M. Johnston 8738*. a. Mature stem showing characteristic shoots after leaves fall. b. Mature stem with leaves of current season and fruit. c. Leaf, abaxial view. d. Flower. e. Anther, adaxial view. f. Almost mature fruit, showing subtending bracts.

ca. 400 m above main spring (26°14′N, 102°49′W), with *Agave lecheguilla, Hechtia, Acacia, Dasylirion, Tecoma, Viguiera, Leucophyllum, Euphorbia,* small shrub with snow-white fruits and one fasciated branchlet, ca. 1600 m, 15 Aug 1973, *Henrickson 12471* (LL, MEXU).

In Standley (1926), *Johnston 8738,* with its constantly tetramerous flowers, keys to the apparently closely related, monotypic, Yucatanian *Asemnanthe* Hooker f. But *Henrickson 12471,* otherwise identical to *Johnston 8738,* has constantly pentamerous flowers as in the rest of the genus *Chiococca.* I conclude that in this case the number of sepals

and petals is not of taxonomic value, but that the diagnosis of *Chiococca* must be modified to take into account rare cases of tetramery. Without much more thorough study, I decline to pass judgment on the merit of retaining *Asemnanthe* as a distinct genus.

Chiococca henricksonii is apparently related to *C. alba* (L.) Hitchcock, which is widespread in warmer parts of America, and to *C. pachyphylla* Wernham of the Sierra Madre Oriental. It is quite distinct in habit, foliage, pubescence, and inflorescence from those two species. *Chiococca henricksonii* may find its closest relative in the almost equally xerophytic and microphyllous *C. petrina* Wiggins of Sonora and extreme western Chihuahua. The leaf-blades of *C. petrina* average slightly larger than those of *C. henricksonii* and its larger flowers are borne in racemes.

The two known localities for *Chiococca henricksonii* are only 70 km apart and lie in some of the driest, most rigorous parts of the Chihuahuan Desert Region in southwestern Coahuila, where a number of other local endemic species have been discovered. Although gypseous substrates are common in the general region, the substrates at the two localities are essentially pure limestone (Henrickson, pers. comm., 1980; T. L. Wendt and E. Lott, pers. comm., 1980).

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A NEW SUBSPECIES OF COMAROSTAPHYLIS POLIFOLIA (ERICACEAE) FROM COAHUILA, MEXICO

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ABSTRACT

Comarostaphylis polifolia subsp. **coahuilensis** is described from the mountains of the central Chihuahuan Desert in Coahuila, Mexico. A discussion of fruit structure supports the generic separation of *Comarostaphylis* from *Arctostaphylos* and *Arbutus*.

Recent field studies in connection with M. C. Johnston's Chihuahuan Desert Flora Project have brought forth collections of a distinct taxon of *Comarostaphylis* from six mountain ranges in south and central Coahuila. These collections appear to lie within the general variation that Standley (1924) advocated for *Arctostaphylos* (*Comarostaphylis*) *polifolia* H.B.K.

Comarostaphylis was first segregated from *Arctostaphylos* by Zuccarini (1837) on the basis of gynoecial and fruit characters. The gynoecium of *Comarostaphylis* consists of 5 (rarely 4) carpels, each with 1 ovule, and the fruit is a drupe with a reddish to blackish, granular or warty exocarp, a thin mesocarp, and a solid, bony, thick-walled, spheroidal endocarp stone that contains (4–)5 seeds each with a distinct conical grayish cap on the apical end. *Arctostaphylos,* in contrast, may have 5–9(–10) carpels each with 1 ovule, but the mature fruit is brownish, has a smooth exocarp, mealy mesocarp, and seeds are enclosed in separate portions of the endocarp, which may then consist of 5–9(–10) separate segments. In other species of *Arctostaphylos,* the endocarp segments may be variously combined into groups of 2 or 3, or in one species (*A. glauca* Lindl.), as in *Comarostaphylis* and *Xylococcus,* they are combined into a single, solid, but often vertically ridged endocarp stone.

Fruits of *Comarostaphylis* are superficially similar to those of *Arbutus* in that both have warty or granular exocarps. *Arbutus,* however, has several ovules per carpel and the seeds are enclosed in a cartilaginous to lignified endocarp wall that is open, i.e. not lignified, along the dorsal trace of each carpel.

I cannot agree with the placement of *Comarostaphylis* within *Arctostaphylos* as has been done in Standley (1924) and Standley and Williams (1966). I support the contention (Adams, 1940) that each of these genera, as well as *Xylococcus* and *Ornithostaphylos,* is worthy of generic recognition.

Small (1914) recognized *Comarostaphylis* as a distinct genus with 22 species, six of which he described as new. Standley (1924) placed *Comarostaphylis* within *Arctostaphylos,* recognizing only 14 species and combining five of Small's species into his *Arctostaphylos polifolia* H.B.K. with a comment that the key characters used by Small (1914) to distinguish these segregates were "utterly worthless". As recognized by Standley (1924), the delineation of taxon *polifolia,* one of the oldest names within *Comarostaphylis,* has been greatly broadened to include specimens with puberulent, canescent, or glandular stems and inflorescences and entire, linear to oblong-lanceolate, revolute to flattened, glabrous to glaucous, puberulent, villous to somewhat glandular leaves. This entire complex of taxa is also quite variable in floral features. Ovaries can be glabrous to weakly pilose or villous and corolla size also varies through the range of the species. At present the actual circumscription of the species is not known as a comprehensive study has not been made of the variation encountered in the field. Our specimens from the mountains of the Chihuahuan Desert appear to fit within the morphological range of *C. polifolia* in the broadest sense. To name this new taxon at a rank equal to *C. polifolia* is not defensible, in my opinion. I here present the taxon as a new subspecies of *C. polifolia* in anticipation that further studies will recognize additional, geographically distinct, minor variants of the species at the rank of subspecies (e.g., *A. novoleonsis* Rehder).

Comarostaphylis polifolia (H.B.K.) Zucc. subsp. **coahuilensis** Henrickson, subsp. nov.

Frutices saepe humiles nodosi vel arbores parvae ad 1.5 m altae; rami hornotini purpureo-brunnei, dense albo-puberulentes vel canescentes. Laminae foliorum oblongo-ellipticae vel anguste oblongo-ovatae, planae vel conduplicatae ad costum, apice saepissime mucronatae, sparse puberulentes, supra glabratae nitidae, subtus glaucae superpersistente pubescentes. Racemi terminales puberulentes pilis crispis glandulosis; lobi calycis deltoidei, glandulosi puberulentesque ciliati roseoli; corolla ovoidae vel elliptoco-urceolatae, pallide roseolae vel roseolae, lobis orbicularibus vel ovatis reflexis (Fig. 1).

Low, rounded, somewhat gnarled shrubs to miniature trees 0.2–1.5 m high; young stems maroon-brown, densely white puberulent, hirtellous to subcanescent with trichomes 0.05–2 mm long; bark reddish brown, flaking, weathering gray in old stems. Leaves congested at stem tips; petioles 3–7 mm long, flattened to grooved adaxially, puberulent as young stems; blades oblong-elliptical to narrowly oblong-ovate, oblong-obovate, 2–4(–4.5) cm long, 7–11(–20) mm wide, subcoriaceous to coriaceous, flat or conduplicately folded along midrib, obtuse to rounded or acute but mostly mucronate at apex, rounded to cuneate at base, entire, rarely slightly toothed, revolute to undulate, callose-thickened at margins, sparsely puberulent to glabrate, shining
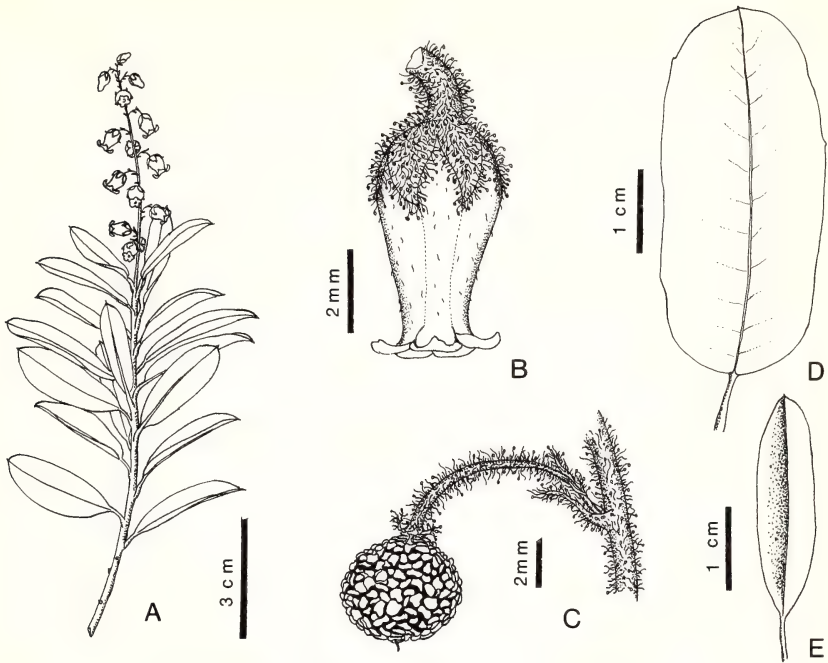
FIG. 1. *Comarostaphylis polifolia* subsp. *coahuilensis* Henrickson. A. Stem showing orientation of leaves and inflorescence (*Johnston et al. 10842*, LL). B. Flower with glandular sepals (*Johnston et al. 10842*, LL). C. Immature fruit on glandular-puberulent pedicel with bracts and rachis shown (*Henrickson 13600*, TEX). D–E. Extremes in leaf size from original collections. D. Subcoriaceous large leaf with slight tooth formation (*Chiang et al. 9075*, LL). E. Coriaceous leaf, folded along midrib (*Johnston et al. 11682*, LL).

green above, sparsely but more persistently puberulent with trichomes 0.1–0.5 mm long, glaucous, gray-green to yellow-green beneath. Racemes terminal, 2.5–4.5 cm long, rachis and pedicels curly-puberulent and with stalked glands 0.2–0.5 mm long, glands red or not; pedicels 3.7–7(–10) mm long, with 3 bracts, the basal to 6 mm long, the upper bracts narrowly acuminate, to 1 mm long. Flower calyx 4–5 mm broad, lobes to 1.5 mm long, triangular, acute to acuminate, glandular and puberulent, ciliate, reddish; corollas ovoid to elliptically urceolate, pale pink to rose, 5–8(–9) mm long, 3–5 mm wide, glabrous without, pilose within, lobes erect to reflexed, orbicular to ovate, 0.8–1.0 mm long, 0.8–1.5 mm wide, ciliate, papillate within; stamens 10, filaments 1.3–2.2 mm long, dilated, pilose at base; anthers ovoid 0.9–1.2 mm long, pink, appendages 0.4–0.6 mm long; ovary sparsely pilose, basal disk weakly 10-ribbed, sparsely pilose-ciliate; style 4–5 mm long. Drupe 4–6 mm in diameter; endocarp 3.0–3.5 mm broad, spheroidal;

seeds ovoid, 1.7–2.2 mm long, the gray conical cap one-third its length.

Type: Mexico, Coahuila, Cañon de Calabazas in Sierra Mojada, s. of Esmeralda (near 27°16'N, 103°41'W), flowers pink, 6 May 1973, *Johnston, Wendt,* and *Chiang 10881.* (Holotype: LL; isotype: MEXU).

Paratypes: Mexico, Coahuila, Sierra Mojada, s. of La Esmeralda (near 27°16'N, 103°41'W), 1 Sep 1972, *Chiang et al. 9075* (LL): Sierra de Parras, ca. 16 km (10 mi) w. of Parras de la Fuente (near 25°26'N, 102°16'W), 4 Nov 1972, *Chiang et al. 10061* (LL); e. face of Sierra de Almagre (near 27°36'N, 103°53'W), 5 May 1973, *Johnston et al. 10842* (LL); n. side Sierra de Paila, Mina El Aguirreno (near 26°06'N, 101°36'W), 5 Jul 1973, *Johnston et al. 11682* (LL): Sierra de Paila, upper Cañon Corazón del Toro (near 25°54'N, 101°38'W), 5 Nov 1972, *Wendt et al. 10101* (LL); n. side Sierra de Organos (near 26°41'N, 103°03'W), 8 Aug 1973, *Henrickson 12148* (TEX); s. part Sierra de los Organos (near 26°44'N, 103°01'W), 8 Aug 1973, *Johnston et al. 12143* (LL); crest of Sierra de la Madera, above Cañon de la Hacienda (near 27°03'N, 102°24'W), 27 Sep 1973, *Henrickson 13600* (TEX).

The new taxon is known only from limestone areas at 1500–2800 m where it occurs in open chaparral with *Quercus* spp., *Acacia, Dasylirion, Leucophyllum, Fraxinus greggii, Sophora, Lindleya, Ptelea, Agave* and on the southern crests of mountains in forests of *Pinus strobiformis, P. arizonica, Abies coahuilensis, Pseudotsuga menziesii, Quercus greggii,* and *Cupressus arizonica,* often in association with *Arctostaphylos pungens* and *Philadelphus.*

The new taxon fits well into the *C. polifolia* complex as interpreted by Standley (1924) but is distinguished by the tendency to have a small shrub habit, often conduplicately folded, oblong-lanceolate to flat, oblong-ovate leaves, closely pubescent to hirtellous stems, glandular-pubescent rachis and pedicels, and by its northern distribution. When comparing this new taxon with the species recognized by Small (1914) in his North American Flora treatment it would tend to key to *C. hartwegiana* Klotzsch from which the new taxon differs in broader leaves, non-glandular twigs, and more northern distribution. The new taxon also fits within the general description of *C. caeciliana* (Loes.) Small from Oaxaca but is not so tomentose.

The nine collections on the new taxon are uniform except for small differences in leaf shape, those from more exposed sites tending to have smaller, more oblong-elliptical, entire, coriaceous leaves (Fig. 1E) than those of plants of presumed more protected sites (Fig. 1D). One specimen from the Sierra de la Paila (*Wendt et al. 10101*), lacks glandular hairs on the inflorescence while others in that collection are glandular (Fig. 1C). The new taxon is also variable in growth habit.

On exposed cliffs plants only 1.5 dm tall but 1 m broad have been observed. In protected sites plants may develop into small trees.

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NOTEWORTHY COLLECTIONS

WOLFFIA PUNCTATA Griseb. (LEMNACEAE).—USA, CA, San Diego Co., Lake Hodges, 5 km s. of Escondido, e. side of hwy I-15 (33°3'16"N, 117°3'45"W), 152 m, 14 Jun 1980, *Armstrong s.n.* (SD 105410). Scattered individuals, with ave. density of 10–12 per 250 ml of water, floating at surface near shoreline among dense homogeneous population of *Lemna gibba.* Verified by R. F. Thorne, Jun 1980.
Previous knowledge. Known from WA, OR, c. and ne. US, s. to the West Indies. A minute, free-floating rootless angiosperm, barely visible without magnification. Often associated with *Lemna, Spirodela,* and *Azolla.* The genus has likely been overlooked many times because of its small size. (Herbaria consulted: RSA, SD; published sources: Daubs, Ill. Biol. Monogr. 34. 1965; Mason, A fl. marshes Calif. 1957.)
Significance. First record of *Wolffia* in s. CA, a se. extension for *W. punctata* of 975 km from Fall River Mills, Shasta Co. According to Daubs (op. cit.), two spp. of *Wolffia* are native to CA: *W. punctata* and *W. columbiana. W. arrhiza* (and its synonym, *W. cylindracea*) are listed, apparently incorrectly, for CA by Mason (op. cit.).—WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069. (Received and accepted 16 Jul 1980; final version received 24 Jul 1980.)

OROBANCHE UNIFLORA L. subsp. OCCIDENTALIS (Greene) Abrams ex Ferris (OROBANCHACEAE).—USA, AZ: Gila Co., 3-bar Wildlife Area (e. of Four Peaks), 30 Apr

1958, *Dick Saunders s.n.* (ASU); Mohave Co., Hualapai Mts., upper Frees Wash on n. side of Dean Peak: T20N R15W S16 nw.¼, steep canyon, one plant seen, 1900 m, 16 Jun 1979, *Butterwick 5149 & Parfitt* (ASU, JEPS); T20N R15W S16 sw.¼, one clump in moist humus of stream bed near *Erigeron* and *Solidago*, some flowers underground (cleistogamous?) and producing fruits, 2070 m, 11 Aug 1979, *Butterwick 5435 & Parfitt* (ASU, JEPS). Verified by L. R. Heckard, 1979.

Previous knowledge.　　The species is known from Newfoundland to Quebec and Yukon, s. to n. FL. TX, and s. CA. AZ is specifically mentioned (Thieret, J. Arnold Arboretum 52:425. 1971) as lacking a report of *O. uniflora*. Identification of the subsp. follows the treatment of Abrams and Ferris, which recognizes two subspecific taxa of w. N. Amer. in addition to the typical subsp. of e. N. Amer. According to Heckard (pers. comm., 1980) the infraspecific taxa are not sharply defined and a critical reexamination of the species is needed. (Herbaria consulted: ARIZ, ASC, ASU, MNA; published sources: Abrams and Ferris, Illus. fl. Pac. States. 1960; Munz, A fl. S. Calif. 1974; Hitchcock et al., Vasc. pls. Pac. Northw. 5. 1959; Watson, Syst. f *Orobanche* sect. *Gymnocaulis,* M.A. thesis, Calif. State Univ. Chico. 1975; Barkley, Man. fl. pls. Kans. 1968; Correll and Johnston, Man. vasc. pls. Tex. 1970; Harrington, Man. pls. Colo., ed. 2. 1964.)

Significance.　　First records for AZ, a se. range extension of the subsp. The AZ specimens will be an important link in a comparative study of the e. and w. populations of the species (Heckard, pers. comm., 1980). Underground (cleistogamous?) flowers and fruits have not been reported previously.—BRUCE D. PARFITT, Department of Botany and Microbiology, Arizona State University, Tempe 85281 and MARY BUTTERWICK, Bureau of Land Management, 2929 W. Clarendon Ave., Phoenix, AZ 85017. (Received 28 Mar 1980; accepted 10 Jul 1980; final version received 28 Jul 1980.)

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HAZARDIA ORCUTTII (Gray) Greene (COMPOSITAE).—USA, CA, San Diego Co., Heritage Park housing development e. of El Camino Real, s. of Encinitas (near 33°03′N, 117°15′W), 75 m, 25 Aug 1979, *Oberbauer 188* (SD). A vigorous population of several hundred individuals on crumbly clay soil at the interface of coastal sage scrub and chaparral. Verified by Reid Moran, Sep 1979.

Previous knowledge.　　Known only from nw. Baja Calif. along coastal plains and hills from Colonet to about 5 km s. of the international border at La Joya (Clark, Madroño 26:105–127. 1979; R. Moran, pers. comm., 1979).

Significance.　　First record for USA and CA, a disjunction of 60 km. Found in an area approved for a housing development. The environmental impact report for the development failed to mention this species as well as several other "rare and endangered" plants.—THOMAS A. OBERBAUER, Department of Planning and Land Use, County of San Diego, 1600 Pacific Coast Highway, San Diego, CA 92101. (Received 18 Aug 1980; final version received and accepted 19 Sep 1980.)

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Herbaria consulted for all taxa: CAS, DS, FSC, JEPS, UC; published sources for all taxa: Abrams, Illus. fl. Pac. States 1949–1960; Hitchcock, Man. grasses U.S. 1935; Hitchcock and Chase, Man. grasses U.S. 1950; Munz, A Calif. fl. 1959; Powell, Inv. rare endang. vasc. pls. Calif. 1974; Smith et al., Inv. rare endang. vasc. pls. Calif., ed. 2. 1980. All *Evans, Haines,* and *Haines and Evans* vouchers are deposited in both FSC and JEPS.

MADIA SUBSPICATA Keck (ASTERACEAE).—USA, CA, Fresno Co.: Haslett Basin, USFS engineer's camp (T11S R25E S23), 568 m, 29 May 1975, *Haines and Evans C-75373*; along hwy 168, 1.6 km above Tollhouse Village (T10S R24E S31), 768 m, 8 May 1953, *Quibell 1868* (FSC); 6 km w. by air from Prather, ne. corner Table Mt. (T10S R22E S20), 560 m, 15 Apr 1978, *Haines 78006*; Deep Creek Basin (T11S R25E S19–20), 792 m, 24 May 1977, *Haines and Evans 77036*. Growing under the driplines of trees and shrubs in foothill-woodland. Common in these scattered populations; associated with *Quercus douglasii, Q. wislizenii, Arctostaphylos mariposa, Bromus diandrus,* and *Erodium cicutarium*.

Previous knowledge.   Scattered sites from Mariposa to Butte cos. (Munz).

Significance.   First records s. of Mariposa Co.; a range extension of ca. 100 km. Considered, but not included by Smith et al. (op. cit.).

RAFINESQUIA CALIFORNICA Nutt. (ASTERACEAE).—USA, CA: Fresno Co.: Haslett Basin, USFS engineer's camp (T11S R25E S23), 568 m, 6 Jun 1975, *Haines and Evans C-75411*; hwy 180, 15 km e. of Centerville (T14S R24E S14), 175 m, 2 Jun 1974, *Haines 74214*; Inyo Co.: Great Falls Canyon, 11.3 km n. of Trona, 806 m, 15 Apr 1940, *Alexander and Kellogg 1077* (UC); Johnson Canyon, Panamint Range, 1075 m, 27 Apr 1940, *Jepson 1972* (JEPS); Stanislaus Co.: Hill n. of Del Puerto Canyon, 13 Apr 1940, *Hoover 4338* (JEPS); Arroyo del Puerto, Mount Hamilton Range, 461 m, 9 May 1935, *Mason 8311* (UC); Calaveras Co.: Stanislaus River at crossing of Copperopolis-Sonora Road, 154 m, 22 May 1921, *Tracy 5709* (JEPS).

Previous knowledge.   Cismontane California n. to Humboldt and Kern cos.; to UT, AZ, L. Cal. Most frequent in disturbed places.

Significance.   Extends dist. in Sierra Nevada n. to Calaveras Co. and e. to Inyo Co. A range extension of ca. 400 km.

CRYPTANTHA MURICATA (H. & A.) Nels. & Macbr. var. MURICATA (BORAGINACEAE).—USA, CA: Fresno Co.: Haslett Basin, USFS Rd. 10S69, 4.5 km e. of Rd. 10S02 (T11S R25E S24), 870 m, open areas with *Mimulus gracilipes, M. bolanderi, M. viscidus,* and *Ceanothus cuneatus,* 19 May 1975, *Haines and Evans C-75310*; Jose Basin (T10S R23E S4), 768 m, in an open area with *M. gracilipes, Eriodictyon californicum,* and *Plagiobothrys tenellus,* 30 Apr 1974, *Haines 74203*; above Sampson Flats, below Delilah Lookout (T13S R26E S13), 1382 m, 24 May 1941, *Simonian 849* (FSC); Madera Co.: 2.4 km se. of South Fork, e. of Mammoth Rd. (T8S R23E S17), 920 m, 5 Jun 1957, *Brock 159* (FSC).

Previous knowledge.   Gravelly or rocky soils, many plant communities; Coast Ranges from Contra Costa Co. s., Sierra Nevada of Kern Co. to Orange Co.

Significance.   First Sierran records n. of Kern Co., an extension of ca. 160 km.

CAREX TUMULICOLA Mkze. (CYPERACEAE).—USA, CA, Fresno Co.: Haslett Basin, USFS engineer's camp (T11S R25E S23), 568 m, 25 Mar 1975, *Haines and Evans C-75089,* common in moist areas with *Plectritis californica, Bromus mollis, Plagiobothrys nothofulvus,* and *Erodium obtusiplicatum.*
  Previous knowledge. Meadows and grassy slopes; Santa Cruz Id., Coast Ranges from Monterey to Del Norte and Siskiyou cos., Madera to Tuolumne cos. in the Sierra Nevada, into w. OR and WA.
  Significance. First record for Fresno Co., a range extension of ca. 35 km.

EPILOBIUM MINUTUM Lindl. ex Hook. (ONAGRACEAE).—USA, CA, Fresno Co.: Haslett Basin, USFS Rd. 10S69, 4.5 km e. of Rd. 10S02 (T11S R25E S24), 768 m, 10 May 1975, *Haines and Evans C-75237,* openings in chaparral, around the bases of shrubs with *Ceanothus cuneatus, Quercus wislizenii, Mimulus viscidus,* and *Cryptantha muricata.*
  Previous knowledge. Dry open places, Coast Ranges from Santa Barbara Co. to Del Norte and Siskiyou cos.; Sierra Nevada from Madera Co. n.; to B. C., NE.
  Significance. First record for Fresno Co., an extension of ca. 35 km s.

ARGEMONE MUNITA Dur. & Hilg. subsp. ROTUNDATA (Rydb.) G. Ownbey (PAPAVERACEAE).—USA, CA, Fresno Co.: w. slope of Bald Mt., 4.5 km n. of Dinkey Cr. Rd. (T9S R25E S26), 2058 m, 20 Jul 1974, *Haines and Evans C-74023;* Tamarack Ridge, 5 km e. of hwy 168 (T9S R26E S18), 2235 m, 16 Sep 1975, *Haines and Evans C-75648;* Sugar Pine Hill near Rancheria Cr. (T11S R27E S25), 2012 m, 3 Oct 1975, *Haines and Evans C-75714;* USFS Rd. 10S70, 1.3 km n. of McKinley Grove Rd. near Tule Meadow (T11S R27E S4), 2181 m, 3 Oct 1975, *Haines and Evans C-75716;* along road to Mushroom Rock, 6.4 km w. of Huntington Lake Rd. (T8S R25E S17), 2335 m, 3 Oct 1975, *Haines and Evans C-75708.* All locations are on disturbed sites in mixed conifer forest, associated with *Abies concolor, A. magnifica,* and *Ceanothus cordulatus.*
  Previous knowledge. Mts. of Mojave Desert, San Bernardino and San Gabriel mts., e. slope Sierra Nevada to Shasta Co.; local populations in Lake and Colusa cos. (Munz).
  Significance. First records for w. Sierra Nevada.

APERA SPICA-VENTI (L.) Beauv. (POACEAE).—USA, CA: Fresno Co., along USFS Rd. 10S02, 1.6 km ne. of the jct. of Rd. 10S69 in Haslett Basin (T11S R25E S14), 838 m, 6 Jun 1975, *Haines and Evans C-75419,* commonly distributed on open slopes with *Quercus wislizenii, Bromus diandrus, B. mollis;* San Luis Obispo Co.: hwy 166, 41 km w. of New Cuyama (T12N R30W S27), 427 m, 2 Nov 1975, *Evans 75053,* with *B. diandrus* and *B. mollis* in grassy openings.
  Previous knowledge. European weed, scattered locations from OR to ME (Hitchcock and Chase). *Diagnostic characters.* Keys to *Agrostis tenuis* var. *aristata* in Munz (p. 1520) but is long awned from near the tip of the lemma (vs. awned from near the base of the lemma) and lemma firm at maturity (vs. membranaceous at maturity). Verified with European collections in UC.
  Significance. First records for CA, a range extension of ca. 1200 km from Portland, OR.

RHAMNUS RUBRA Greene subsp. YOSEMITANA C. B. Wolf (RHAMNACEAE).—USA, CA: Fresno Co.: w. slope Bald Mt., 4.5 km n. of Dinkey Cr. Rd., 2058 m, 4 Aug 1975, *Haines and Evans C-75611,* growing in rocky areas with *Quercus kelloggii, Arctostaphylos patula,* and *Sitanion hystrix;* between Zumwalt Meadow and Bubbs Cr., Kings Canyon, 28 Jul 1940, *Howell 15601* (CAS); Huntington Lake, 2150 m, 16 Jul 1917, *Grant 1097* (JEPS); Florence Lake, 2243 m, 5 Jul 1952, *Raven 4242* (CAS); Tulare Co.: Hockett Meadow, 2611 m, Jun 1870, *Purpus 1785* (UC); Mineral King, 24 Jul 1942, *Howell 17096* (CAS); Inyo Co.: Summes Creek, 2304 m, 18 Jul 1955, *Raven 8313* (CAS); Calaveras Co., Big Tree Meadow, 1536 m, May 1865, *Davy 1543* (UC);

Sierra Co., w. side of Yuba Pass, 1536 m, 21 Aug 1951, *Howell 28279* (CAS); Butte Co., 3.2 km s. of Big Bar Mt., 8 Jun 1941, *Quick 41-09* (CAS).

Previous knowledge. Known only from Tuolumne, Mariposa, and Mono cos. (Munz).

Significance. Extends range ca. 105 km n. to Sierra Co., ca. 130 km s. to Tulare Co., and ca. 35 km e. to Inyo Co.

MIMULUS GRACILIPES Rob. (SCROPHULARIACEAE).—USA, CA, Fresno Co.: Haslett Basin, USFS engineer's camp (T11S R25E S23), 568 m, 11 May 1975, *Haines and Evans C-75245,* growing with *M. bolanderi, M. viscida, Ceanothus cuneatus*; Haslett Basin, along USFS Rd. 10S69 (T11S R25E S24), 4.5 km e. of road 10S02, 870 m, 13 Apr 1975, *Haines and Evans C-75142,* common in small openings in chaparral, with *Plagiobothrys tenellus, Quercus wislizenii, Cryptantha muricata, M. viscidus, M. bolanderi*; jct. of Mill Cr. Rd. and Sand Cr. Rd., 0.8 km w. of Miramonte, 950 m, 1 May 1960, *Linderman s.n.* (FSC); Carpenteria Botanical Area, 6.4 km w. of Lodge Rd. on hwy 168 (T10S R23E S23), 973 m, 2 May 1974, *Stebbins 74123* (FSC); N. Burrough Rd. 0.8 km e. of Burrough Valley Rd., 522 m, 17 May 1964, *Hardwick 144b* (FSC); 7.6 km e. of Auberry Rd., 925 m: 30 May 1963, *Weiler 63120* (FSC); 7 May 1964, *Webb 0108* (FSC); Auberry Rd., 1137 m, 25 Apr 1941, *Petersen 316* (FSC); upper Jose Basin, 1137 m, 22 May 1957, *Quibell and Brock 6* (FSC); 32 km from Auberry on USFS Rd. 9S07, 1230 m, 24 Apr 1962, *Kirkhart 9* (FSC).

Previous knowledge. Mormon Bar, Mariposa Co. (Munz).

Significance. Extends the known range ca. 120 km s. These collections are the basis for the designation "rare but not endangered" in Smith et al. (op. cit.).—ROBERT D. HAINES, Tulare County Department of Agriculture, Visalia, CA 93277 and CHARLES J. EVANS, Pacific Southwest Forest and Range Experiment Station, 2081 E. Sierra Avenue, Fresno, CA 93710. (Received 3 Jun 1980; revision received and accepted 19 Sep 1980.)

Herbaria consulted for all taxa: ARIZ, ASU, COLO, CS, MO, NMC, RM, UNM, UT, UTC; published sources for all taxa: Barneby, Contr. N.Y. Bot. Gard. 13. 1964; Blake, Leafl. W. Bot. 6:71. 1950; Cronquist, Brittonia 6:121–300. 1947; Cronquist et al., Intermt. fl. 1. 1972; Epling, Repert. Spec. Nov. Beih. 110:1–380. 1939; Federal Register 41(117):24523–24572. 16 Jun 1976; Fernald, Gray's Man. Bot., ed. 8. 1950; Gould, The grasses Tex. 1975; Harrington, Man. pls. Colo. 1964; Kearney and Peebles, Ariz. fl., ed. 2. 1960; Martin, Brittonia 7:91–111. 1950; Martin and Hutchins, A N. Mex. fl. 1980; McDougall, Seed pls. N. Ariz. 1973; Munz, A Calif. fl. 1959; Parfitt et al., Madroño 26:141–144. 1979; Strother, Brittonia 26:177–202. 1974; Wagner and Sabo, Rep. N. Mex. threat. endang. pl. spp. U.S.D.I. Fish Wildl. Serv., unpubl. reports. 1977.

ERIGERON COMPACTUS Blake var. CONSIMILIS (Cronq.) (ASTERACEAE).—USA, NM, McKinley Co., Zuni Mts., Six Mile Canyon (T14N R15W S18), clay hills, 220 m, 18 Jun 1977, *Wagner and Sabo 3180* (UNM).

Previous knowledge. Uintah Basin, UT to ne. AZ, Navajo and Apache cos. (Cronquist).

Significance. First record for NM; a se. extension of 120 km for the species.

TETRADYMIA SPINOSA Hook. & Arn. (ASTERACEAE).—USA, NM: Sandoval Co., 2 km ne. of La Ventana, 2015 m, 10 Oct 1975, *Wagner 1989* (UNM); San Juan Co.: 2.1 km n. of Aztec on hwy 550, *Keil 10868* (ASU); *Harper NM7* (UT); 10 km s. of Bisti Trading Post, w. of hwy 371 (T23N R13W S25), edge of badlands on sandstone/siltstone interface, 1820 m: 6 Jun 1977, *Marley 424* (MO); 24 May 1978, *Marley 1234* (UNM); 21 km se. of Bisti, 1.4 km ne. of Black L. (T23N R12W S26/35), heavily eroded area of gray clay over soft coal, arroyo bottom, slopes with *Xanthocephalum sarothrae, Atriplex confertifolia, Sarcobatus vermiculatus, Lycium pallidum,* 8 Jun 1976, *Spellenberg et al. 4116* (NMC).

Previous knowledge. OR to WY, s. to NM and w. to CA (Strother).

Significance. First record for Sandoval Co.; 110 km se. range extension (*Wagner 1989*). Widely-spaced localities may suggest a marginal distribution, but may also reflect lack of floristic study in nw. NM.

CHORISPORA TENELLA (Pall.) DC. (BRASSICACEAE).—USA, NM, Bernalillo Co., Albuquerque, Univ. NM campus, e. side of Biology Bldg., disturbed ground, 25 Apr 1975, *Wagner 22* (UNM). Other observations have been made from 1974–1976 along the Rio Grande flood plain in Sandoval Co., near the town of Bernalillo, and in Bernalillo Co. along hwy I-40 near the Rio Grande overpass.

Previous knowledge. Introduced from Asia, naturalized in N.A. in scattered areas from MA, IA, and NE w. to WA and CA (McDougall). Rapidly spreading in CO (Harrington).

Significance. First record for NM. Now well established in c. NM along the Rio Grande and along hwy I-40 near Albuquerque.

DIPLOTAXIS MURALIS (L.) DC. (BRASSICACEAE).—USA, NM: Lincoln Co., foothills of Capitan Mts. along F.S. Rd. 56 (T8S R15E S29), grazed pinyon-juniper woodland, 2000 m, 1 Aug 1976, *Wagner and Sabo 2120* (GH); Grant Co., hwy 90 at Santa Rita, road shoulders, 1880 m, 10 Aug 1977, *Wagner and Sabo 3434* (UNM). Determined by R. Rollins, GH, 1980.

Previous knowledge. Naturalized from Europe. Widely scattered as a weed in e. Canada, most of the U.S., including TX and AZ. Known from Tucson as early as 1913 (Kearney and Peebles, p. 337) but not collected in NM prior to *Wagner and Sabo 2120* (R. Rollins, pers. comm., 1980).

Significance. First records for NM. Wide separation, small population size, and lack of previous collections suggest recent establishment of *D. muralis* in NM.

MALCOLMIA AFRICANA (L.) R.Br. (BRASSICACEAE).—USA, NM, San Juan Co.: se. of Fruitland, T29N R16W S13 nw. ¼ se. ¼, 14 May 1979, *Kramp 96* (ASU); 1.2 km n. of jct. of hwy 550 and county Rd. 52 and 524, T30N R15W, rolling hills and benches, Mancos Shale, with *Atriplex corrugata, Mentzelia albicaulis*, and *Oenothera caespitosa*, 1600 m, 17 May 1979, *Marley 1810* (UNM); 18.5 km n. of Shiprock on hwy 666, w. of Blue Hill, Mancos Shale with *Atriplex corrugata, A. cuneata,* and *Sclerocactus mesae-verdae,* 1600 m, 13 May 1977, *Wagner and Sabo: 2890* (UNM); *2893* (NMC).

Previous knowledge. Naturalized from Mediterranean region (Harrington). In N.A., w.-c. CO to NV and Mojave Co., AZ (McDougall).

Significance. First records for NM, the se.-most collections in N.A.

SCLEROCACTUS MESAE-VERDAE (Boissevain ex Hill & Salisbury) Benson (CACTACEAE).—USA, NM, San Juan Co., e. of Chuska Mts., along hwy 666, 1.6 km s. of Sheep Springs, Menefee Fm., barren, overgrazed sandstone and siltstone hills, 1800 m, 10 Jul 1979, *Marley and Heil 1990* (MO).

Previous knowledge. Endemic to Mancos Shale, below 1650 m in nw. San Juan Co., NM, and se. Montezuma Co., CO; s.-most collection 8 km. s. of Shiprock along the South Hogback (Wagner and Sabo, op.cit.; Ken Heil, pers. comm., 1979).

Significance. Extends the geographical range (65 km), elevational range (150 m), and documents a new substrate type. Proposed for Federal Endangered status (Fed. Reg. op. cit.), but probably should be considered only for Threatened status.

ASTRAGALUS MONUMENTALIS Barneby (FABACEAE).—USA, NM, McKinley Co.: sandy slopes, vic. Peach Spring Canyon, T17N R16W S10, Point Lookout Fm., 2050 m, 25 May 1976, *Manthey 853* (NY); sandy soils, w. fork Coyote Canyon, T17N R16W S2, pinyon-juniper woodland, 17 May 1977, *Manthey 1692* (UNM). Determined by R. Barneby, NY, 1977.

Previous knowledge. Canyons of the Colorado and lower San Juan rivers in San Juan Co., UT, and n. Navajo Co., AZ. A member of Sect. *Desperati* Barneby Subsect. *Naturitenses* Barneby along with two other highly disjunct, specialized, and recently evolved astragali: *A. naturitensis* Payson, known only from the Dolores R. and McElmo Cr. in Montrose and Montezuma cos., CO; and *A. deterior* (Barneby) Barneby, known only from Mesa Verde and Montezuma cos., CO. These three rare, local species are a closely related assemblage that has evolved in the Colorado Plateau region and is entirely endemic to it (Barneby).

Significance. First record for NM; 140 km se. of closest sites in AZ and 220 km se. of those in UT. These collections emphasize the floristic affinities of nw. NM with the Colorado Plateau, especially with the Canyon Lands Section (Cronquist et al.), to which *Astragalus monumentalis* is endemic.

SALVIA MICROPHYLLA Kunth var. WISLIZENII A. Gray (LAMIACEAE).—USA, NM, Hidalgo Co., Big Hatchet Mts., Thompson Canyon, T3S R15W, limestone soil, 1800 m, 7 Sep 1952, *Castetter 5266* (UNM). Specimen had been misidentified.

Previous knowledge. Pima and Cochise cos., AZ, s. to San Luis Potosí and Durango, Mex. (Epling). Common in Chiricahua Mts., AZ. Synonym: *S. lemmonii* A. Gray.

Significance. First record for NM; 80-km e. extension from Chiricahua Mts.

BROMUS DIANDRUS Roth (POACEAE).—USA, NM, Bernalillo Co., Albuquerque, 1710 Gold St. SE, residential lot, disturbed ground, 1650 m, 10 Jun 1975, *Wagner 1315* (UNM).

Previous knowledge. Common from B.C. to ID, s. to AZ and CA (McDougall, Gould). Local in MD and D.C. and occasional n. to MA (Fernald). Has gone under the name *B. rigidus* Roth., a closely related Mediterranean species (Gould).

Significance. First record for NM.

RANUNCULUS TESTICULATUS Crantz (RANUNCULACEAE).—USA, NM, San Juan Co., 1 km e. of hwy 666, 1 km s. of NM-CO line, flat plains of Mancos Shale with *Atriplex cuneata, Sporobolus airoides,* and *Cymopterus purpureus,* 1625 m, 20 Mar 1979, *Marley 1991* (UNM).

Previous knowledge. Introduced recently from Mediterranean region (Harrington). In N.A. spreading WA to WY, s. to w. CO, UT, n. AZ, and OR (Parfitt et al.).

Significance. First record for NM; 50-km s. extension from w. CO and 100-km ne. extension from recently reported populations in AZ (Parfitt et al.).

CERCOCARPUS INTRICATUS S. Wats. (ROSACEAE).—USA, NM, San Juan Co., North Hogback, above Mine Cr., Mesa Verde Sandstone, shallow sandy soils, with *Artemisia* sp., *Xanthocephalum sarothrae, Rhus trilobata,* and *Juniperus monosperma,* 1750 m, 13 May 1977, *Wagner and Sabo: 2928* (MO); *2929* (UNM).

Previous knowledge. s. CA, s. and c. NV, UT, and CO, and n. AZ (Martin).

Significance. First record for NM, 110 km s. of the s.-most CO site and 90 km ne. of the w.-most AZ site.—GREGORY A. MARLEY, 4934 Constance, Apt. C, New Orleans, LA 70115 and WARREN L. WAGNER, Missouri Botanical Garden, P. O. Box 299, St. Louis 63166. (Received 18 Jun 1980; accepted 7 Jul 1980; final version received 25 Aug 1980.)

NOTES AND NEWS

NECTAR-SUGARS AND POLLINATOR TYPES IN CALIFORNIA *Trichostema* (LABIA-TAE).—The relative proportions of glucose, fructose, and sucrose in nectar vary, with either the monosaccharides or disaccharide predominating (Percival, New Phytol. 60:235–281. 1961). The three sugars contain about an equal number of calories per gram (Stiles, Ecology 56:285–301. 1975). Energy costs in the formation of saccharide bonds may select against the use of oligosaccharides but this may be counterbalanced by pollinator preferences. For example, hummingbirds prefer sucrose-rich nectar (Stiles, Condor 78:10–26. 1976) and in a survey of hummingbird-pollinated species, Baker and Baker (Phytochem. Bull. 12:43–45. 1979) found sucrose-rich nectar to prevail.

In this note, data on nectar sugars and pollinator types are presented for five California species of *Trichostema*. Populations were sampled in the following areas: *T. lanatum* (Santa Monica Mountains); *T. lanceolatum* and *T. ovatum* (Central Valley); *T. laxum* (North Coast Range) and *T. parishii* (San Gabriel Mountains). More specific locations and a description of pollination mechanisms and nectar production are found elsewhere (Spira, M.A. thesis, Calif. State Univ., Chico. 1978; Spira, Amer. J. Bot. 67:278–284. 1980). Nectar samples were collected and analyzed using techniques described in Baker and Baker (op. cit.).

The hummingbird-pollinated *Trichostema lanatum* has sucrose-dominant nectar (1.08 sucrose:1 glucose + fructose) while bee-pollinated *T. lanceolatum* (0.43:1), *T. ovatum* (0.43:1) and *T. laxum* (0.25:1) have glucose-fructose dominant nectars. Both hummingbird pollination (Moldenke, *In*: Thrower and Bradbury, eds., Chile-Calif. Medit. scrub atlas. 1977) and insect pollination (Spira, 1980, op. cit.) occur in *T. parishii*, which has a sucrose-dominant nectar (1.24:1). These data provide additional evidence that a tendency toward sucrose-dominant nectars is associated with hummingbird pollination, in spite of the increased cost in producing it.

WALNUT POLLEN IN LATE-HOLOCENE SEDIMENTS OF THE SACRAMENTO-SAN JOAQUIN DELTA, CALIFORNIA.—Thompson (Madroño 17:1–10. 1963) has reviewed the origin and distribution of *Juglans hindsii* Jepson in central California, has noted the paucity of fossil material of Pleistocene-Holocene age, and has suggested (p. 8) that "verification of Pleistocene remains, perhaps through fossil walnut pollens from the San Joaquin Delta peats, would greatly reinforce our understanding of pre-Holocene distribution." While it is now known, based on radiocarbon-dated peats and peaty mucks, that the modern Delta is post-Pleistocene (Shlemon and Begg, *In*: Suggate and Cresswell, eds., Quaternary studies. 1975), the presence of walnut pollen within Delta sediments still is significant, because it adds to the known areal distribution of walnut in central California a temporal dimension extending back 5000–6000 years.

As part of a paleo-environmental study of the Delta supported by the California Department of Water Resources (West, report on file, Calif. Dept. Parks Rec. 1977), cores were collected from Clifton Court and Roberts Island in the southeast corner of the Delta. Both cores provided discontinuous pollen records from more than 4300 radiocarbon years ago. In the Clifton Court core, walnut pollen is present in small amounts (<1 percent) in four samples, one from immediately below a peaty muck dated to 2950 ± 150 B.P. (GX 4221) and the others from 2, 8, and 10 cm below the lowest dated peaty muck (4340 ± 150 B.P.; GX 4223). In the Roberts Island core, *Juglans* pollen is present only in the uppermost of the prehistoric peat layers and in each of the overlying historic age samples. The Roberts Island core samples have not been dated by radiocarbon methods but the sediments, stratigraphy, and pollen spectra are similar to those of the Clifton Court core and are assumed to be of an equivalent age. Some of the

larger-sized (45–49 μm) walnut pollen grains in the historic-age sediments of the Roberts Island core may be derived from *Juglans regia* L. growing in orchards adjacent to the Delta (unpubl. data; Stone and Broome, *In*: Nilsson, ed., World pollen spore fl. 4. 1975).

In all instances *Juglans* pollen is well preserved and does not appear to be redeposited from earlier sediments in the Sacramento-San Joaquin drainage systems. Accordingly, I believe that the *Juglans* is in primary deposits derived from trees growing within the drainage system over the last 5000 years.

Thompson's suggestion regarding the presence of walnut pollen in the Delta deposits is correct. Although the available pollen record does not preclude the dispersal of walnut in central California by prehistoric human activity, it does indicate that the trees were present in the Delta thousands of years prior to the earliest known Euro-American entry into the area.—G. JAMES WEST, Department of Anthropology, University of California, Davis 95616. (Received 2 Nov 1979; revision received and accepted 26 Sep 1980.)

AGES OF INVASIVE TREES IN DANA MEADOWS, YOSEMITE NATIONAL PARK, CALIFORNIA.—Throughout the high elevations of the Sierra Nevada, meadows are commonly invaded by lodgepole pine (*Pinus contorta*). In 1978, I investigated the age structure of trees in Dana Meadows, about 2 km south of the Tioga Pass entrance station to Yosemite National Park. These meadows are bordered by monotypic stands of lodgepole pine. On both the north and south sides of the meadow, five belt transects 2 m wide were located 30 m apart. Each of the ten transects was extended perpendicularly from the forest-meadow ecotone into the meadow to the most distant tree encountered; transect lengths varied from 10.4 m to 100 m. The largest number of trees in a transect was 32, and the smallest was 5. An eleventh sample, a quadrat 10 m by 2 m and containing 23 trees, was established within the meadow in an area of dense young trees. All trees rooted within the sample areas were cored at their bases with an increment borer; ages were estimated to be the number of rings on the cores plus 2. Trees too small to core were cut at their bases and the rings counted on the stumps. In addition to the trees within the samples, the four largest trees well within the meadow, which occurred in a stand of 12 individuals, were cored. In total, the ages of 149 trees were determined; these were aggregated into five-year age-classes for analysis.

Invasion by large numbers of trees apparently began about 1925, although all five-year periods between 1910 and 1975 were represented by trees; a few trees germinated and survived within the meadow in still earlier years (Table 1). The oldest tree within the transects germinated about 1866 (other germination dates for trees in this stand: 1887, 1902, 1910). In general, the older trees appeared healthy, but 40 percent of the trees established after 1950 had dead leaders. In addition, 16 dead trees were encountered in the 11 sample areas; judging by size-age correlations, none of these was older than 30 years when it died.

The distribution of trees of certain conditions and ages along the transects produced only weak patterns. The dead trees were not restricted to particular locations along the transects, but most of the trees with dead tops were not immediately adjacent to the forest edge. The correlation between position on the transects and age was not significant ($r^2 = 0.08$), although trees encountered in the outermost segment of the transects were often younger than those closer to the forest, and the oldest trees within each transect usually tended to be closer to the forest edge than to the end of the transect in the meadow. These patterns suggest that invasion into open meadow by a few individuals is followed by subsequent germination and survival of other trees.

The invasion date of 1925 is more recent than the dates of initial tree establishment reported by either Boche (Factors affecting meadow-forest borders in Yosemite National Park, California. M.S. thesis, U.C.L.A. 1974) for meadows in the lodgepole forests of Yosemite (1898–1909), or Vankat and Major (J. Biogeogr. 5:377–402. 1978) for meadows in the lodgepole forests of the southern Sierra (1910). In his review of three other

TABLE 1. SPRING TEMPERATURE DEVIATIONS, ANNUAL PRECIPITATION, AND NUMBERS OF TREES GERMINATING IN FIVE-YEAR PERIODS FROM 1865. Spring temperatures are deviations of five-year means from the mean monthly temperatures for March, April, and May. Precipitation values are percents of the mean for the period covered. Climatic data are from NOAA for Yosemite Valley.

Period	Spring temp. (°C)	Annual precip.	No. of trees germinating
1865–			1
1870–			0
1875–			0
1880–			0
1885–			1
1890–			0
1895–			1
1900–			2
1905–		122	0
1910–		93	3
1915–	+0.5	84	2
1920–	−2.2	87	3
1925–	+0.7	89	12
1930–	+0.8	76	13
1935–	−0.1	119	14
1940–	+0.3	116	12
1945–	+0.1	95	5
1950–	+0.2	104	12
1955–	+0.1	105	23
1960–	−0.6	99	14
1965–	+0.2	120	18
1970–	+0.4	105	13
1975–	−0.5	83	0

studies of such tree invasions in the southern Sierra Nevada, Wood (Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. Ph.D. dissertation, Calif. Inst. Tech. 1975) found that the initial establishment dates of meadow trees were reported as 1903, 1906, and 1924. Part of the disparity in dates probably reflects site-specific differences in environmental or historical factors, but it may also result from different criteria for identifying the "beginning" of tree invasions. If 1910 is recognized as the date of initial invasion in Dana Meadows, for example, the data presented here become more consistent with other studies.

The identification of the date when the tree invasion "began" becomes especially significant when trying to correlate it with events that may have caused the unstable ecotone. Regardless of which dates are used, climatic fluctuation seems an unlikely trigger for the recent establishment of meadow trees in Dana Meadows or elsewhere in the Sierra Nevada. Warm dry weather has been suggested as a cause of tree invasion in Sierran meadows because such weather desiccates competing herbaceous vegetation and reduces suffocating soil moisture (Boche, op. cit; Wood, op. cit.). Franklin and Dyrness (U.S. For. Serv. Gen. Tech. Rept. PNW-8. 1973) found convincing the association between warm dry weather and a period of tree establishment in subalpine meadows in the Pacific Northwest. These warm dry periods early in this century, however, were apparently not unprecedented in the recent past in the Sierra Nevada; particularly noteworthy is the warm dry episode in the mid 1800's (Fritts, Monthly Weather Rev. 93:421–443. 1965; Bradley, Monthly Weather Rev. 104:501–512. 1976), a relatively recent period with weather presumably favorable for tree invasion when

trees did not become established in Dana Meadows or other subalpine meadows in the Sierra Nevada. The relatively cold dry conditions since 1975 may have contributed to both the lack of recent tree establishment and the high proportion of die-back among small trees. As a period, however, the years of massive tree invasion were not characterized by consistent and distinctive climatic conditions (Table 1).

Other possible causes are environmental changes involving people. Suppression of frequent fires is sometimes considered responsible for these invasions, although the only empirical study of this agency in a Sierran lodgepole forest focuses on a wet meadow and not a dry-mesic meadow such as Dana Meadows (DeBenedetti and Parsons, J. Forest (Washington) 77:477–479. 1979). The model of Vankat and Major, which suggests a lag of a decade between the cessation of sheep grazing and the establishment of meadow trees, seems not to fit the data in this study; sheep were not eliminated from Dana Meadows until 1905, decades following the germination of the oldest tree (1866) and far predating the beginning of massive invasion (1925). Yet, their model fits the data better if the date of 1910 is used as the beginning of the invasion; such an interpretation would then also conform more closely with that of Dunwiddie (Arctic and Alpine Res. 9:393–399. 1977) who found that trees invaded a subalpine meadow in Wyoming soon after the cessation of grazing by sheep.

It is difficult to isolate possible single causes of these tree invasions, however, by looking simply at the chronology of events. Particularly troublesome is the fact that sheepherders probably burned meadowlands in the Sierra regularly, and thus the elimination of sheep grazing involved a great reduction not only in grazing intensity but also in fire frequency. The interactions among environmental variables also detract from the attempt to find a single cause of invasion. Heavy grazing, for example, may create conditions conducive to tree invasion, but trees may not become established unless the climatic conditions are also suitable. Compounding these difficulties is the likelihood that the occasional establishment of single trees (pre-1910 or pre-1925 in Dana Meadows) is a different phenomenon (reflecting distinctive causes) from the massive establishment of trees so common in the meadows of the Sierra Nevada (after 1925 in Dana Meadows).

It is popular to suggest that forest-meadow ecotones are in "dynamic equilibrium", in that they may fluctuate with short-term changes in environmental conditions but remain stable over longer periods of time. The high frequency of young trees that are either dead or dying supports such a view for Dana Meadows. The apparent health of older trees, however, even those well within the meadow, implies that the invasion is better interpreted as a "directional" change in the vegetation.—THOMAS R. VALE, Department of Geography, University of Wisconsin, Madison 53706. (Received 7 Mar 1980; revision received 12 Sep 1980; accepted 22 Sep 1980.)

BOOKS RECEIVED AND LITERATURE OF INTEREST

Flora of the Central Wasatch Front, Utah. By LOIS A. ARNOW, BEVERLY J. ALBEE, and ANN M. WYCKOFF. xiv + 663 p. Univ. Utah Printing Service, Salt Lake City. ed 2, 1980. No price listed. Will be reviewed in a subsequent issue.

Inventory of Rare and Endangered Vascular Plants of California. By JAMES PAYNE SMITH, JR., R. JANE COLE, and JOHN O. SAWYER, JR. in collaboration with W. Robert Powell. viii + 115 p. California Native Plant Society Special Publication 1, Berkeley. ed. 2, 1980. $7.50. Available from CNPS, 2380 Ellsworth, Suite D, Berkeley, CA 94704. Will be reviewed in a subsequent issue.

Rare, Threatened and Endangered Vascular Plants in Oregon—an Interim Report. By JEAN L. SIDDALL, KENTON L. CHAMBERS, and DAVID H. WAGNER. Oregon Natural Area Preserves Advisory Committee, Salem. 1979. iv + 109 p. Available (apparently free) from Division of State Lands, 1445 State St., Salem, OR 97310.

Threatened and Endangered Plants of Alaska. By DAVID F. MURRAY. vii + 59 p., illus. Published cooperatively by USDA (Forest Service) and USDI (BLM). 1980. No price listed.

Desert Plants. Edited by FRANK S. CROSSWHITE. Published by the Boyce Thompson Southwestern Arboretum, Box AB, Superior, AZ 85273. This new journal is oriented to the general public rather than to professional botanists and, judging from promotional literature, will cover botanical history, ethnobotany, agriculture, horticulture, flora, vegetation, and conservation of the desert regions of the southwest.

Scientific Research in Sequoia and Kings Canyon National Parks: an Annotated Bibliography. By DAVID J. PARSONS and VIRGINIA A. KING. ii + 70 p. Sequoia Natural History Association, Three Rivers, CA. 1980. Available from NTIS (document PB 80-187-313), 5285 Port Royal Road, Springfield, VA 22161. $8.00 (paper) or $3.50 (microfiche). Nearly 350 references to work both published and unpublished, organized by general topic (Fire Ecology, Geology and Soils, Vegetation, Wilderness Use and Impact, etc).

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An international symposium on brushland management will be held in San Diego, 22–26 June 1981. The focus will be on regions having Mediterranean-type climates, including the Mediterranean Basin, southwestern United States, Africa, Chile, and Australia. Symposium topics will include the effects of brushland management on vegetation, wildlife, soils, and hydrology; the use of prescribed burning; and new ways to make better use of brushlands. More information is available from: Chairman, Dynamics and Management of Mediterranean-type Ecosystems, Pacific SW For. and Range Expt. Station, 4955 Canyon Crest Drive, Riverside, CA 92507.

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All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 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 @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

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STRAND AND DUNE VEGETATION AT SALINAS RIVER STATE BEACH, CALIFORNIA

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ABSTRACT

At Salinas River State Beach, Monterey Bay, California, beach and dune vegetation is relatively undisturbed. Nine zones of vegetation are distinguished along a line inland from the shore: beach, foredune, foredune hollow, mid-dune, mid-dune hollow, and reardune, the last divided into foreslope, crown, leeslope, and inland margin zones. These zones were arrived at through analysis of physiography, plant cover, density, species richness, and changing size of selected species. In general, low plants (such as *Carpobrotus aequilaterus, Convolvulus soldanella,* and *Abronia latifolia* with trailing stems, and *Artemisia pycnocephala* with thick pubescence) are characteristic of the foredunes to mid-dunes. Woody shrubs (such as *Haplopappus ericoides, Lupinus chamissonis,* and *Eriophyllum staechadifolium*) along with smaller herbs and subshrubs (such as *Dudleya farinosa* and *Eriogonum latifolium*) dominate the mid-dunes through reardunes.

Although several studies of the zonation of beach and dune vegetation along the California shoreline have been undertaken (for summaries see Breckon and Barbour, 1974; McBride and Stone, 1976; Barbour and Johnson, 1977), such analysis within Monterey Bay has begun only recently (Bluestone, 1970; Gordon, 1979). The closest area investigated has been the Monterey Peninsula, which marks the southern extent of the bay (Cooper, 1967; McBride and Stone, 1976).

Quantitative documentation of the beach and dune vegetation within Monterey Bay is particularly important at this time because increasing human activities are significantly altering the character of many of the beach and dune areas (Gordon, 1979). Because some of the best examples of natural beach and dune vegetation within Monterey Bay are found at Salinas River State Beach, the zones described in this study might serve as a paradigm for other sites in the area.

METHODS

Study area. Salinas River State Beach is located in the southern half of Monterey Bay, 5 km south of Moss Landing and Elkhorn Slough. Wave action and longshore currents transport sand derived from eroded marine terraces and various rivers in the northern part of the bay, and deposit it in the southern half of the bay where the dunes tracts formed are among the largest along the California Coast (Shepard and Wanless, 1971). The crests of the dune ridges tend to lie at right angles to the direction of the dominant winds, which blow onshore from a northwesterly direction.

A maritime climate of little seasonal temperature fluctuation prevails. Although rainfall is concentrated in the winter months, summer fogs moderate the hotter dry season from late spring to early fall by reducing the temperature and providing moisture along the shoreline (Moss Landing Marine Laboratory, 1971). Annual precipitation is 460 mm. On the average there is only one day of frost per year. The mean air temperature is 10°C during January and 16°C during July. Because surface water supply is limited and salt-laden winds are constant throughout the year, some have considered the beach and dune habitat essentially xeric (Purer, 1936; Martin and Clements, 1939). It is likely that soluble mineral and organic content in the soil is limited, as it is for the California coastal sand areas in general (Cooper, 1967). Accumulation of organic litter and compaction of sand are greater where plant density and cover values are highest.

Beginning at least 7500 years ago, the Costanoan Indians, or culturally similar predecessors, may have altered the beach and dune vegetation to some extent with their hunting and gathering, and limited use of fire (Gordon, 1979). A Costanoan site is located near the inland margin of the transect described here. Browsing by livestock of later settlers beginning with the Spanish probably altered this vegetation further. However, the frequency and amount of alteration was probably little enough to allow native plant growth to reestablish readily. Recent human activity on the beach and dunes has accelerated alarmingly within the last 20 years leaving visible scars, such as the three sand trails that parallel the coastline and run through the study site as shown in Fig. 1A. Furthermore, the deflation area shown adjacent to the transect may have been caused by human activities, and a recent fire may have occurred on the leeside of the reardune (Gordon, 1979). Other cultural imprints considered are the introduced species. These include *Carpobrotus edulis* from southern Africa, *Ammophila arenaria* from Europe, and *Tetragonia tetragonioides* from Australasia.

Quantitative sampling. A total of 372 contiguous 1-m^2 quadrats was taken along a line inland from the shoreline at Salinas River State Beach. Along the same line during June and July of 1977, 1978, and 1980, I recorded density (number of individuals per m^2) and percent cover for each species in each quadrat.

Zones were defined by changes in topography or vegetation. Important vegetation changes included density, cover, and species composition. Also considered was the changing size of *Haplopappus ericoides* and *Eriophyllum staechadifolium,* which are wide-ranging shrubs that illustrate how diameter and height change along the transect. Species considered to be zone dominants were those with more than 10 percent cover; subdominants had 5-10 percent cover.

Nomenclature follows Munz (1959), except for the names *Carpo-*
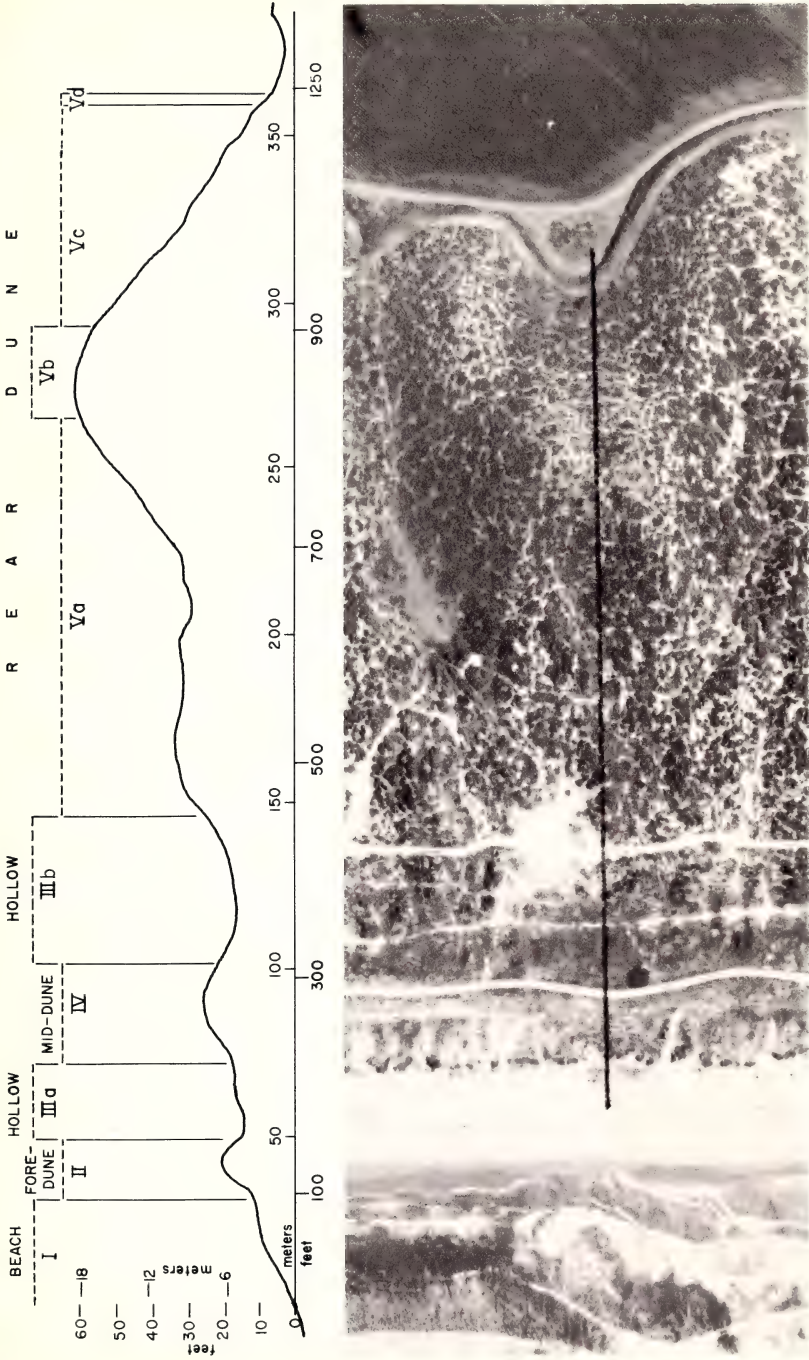
Fig. 1. The study area at Salinas River State Beach. A (above). Cross section along the transect. B (below). Aerial photograph taken by Bestor Engineering, Monterey, CA. The transect is superimposed.

brotus aequilaterus and *C. edulis,* which follow Brown (1928). All taxa were compared with specimens in CAS and DS.

RESULTS

The quantitative data, averaged over all three years, are arrayed by zone in Table 1. Transitions between zones were often gradational, but clusters of indicator species can be identified from the table. Each zone is described briefly below.

Zone I: Beach. Occasionally beach plants such as *Cakile maritima* are within the area of beach inundated by the sea at high tide. The dunes along the inland portions of the beach are exposed to constant onshore winds. They are small (less than 1 m high), scattered, and seasonally transient.

Cover, density, and species richness are the lowest encountered. No plant has more than 4 percent cover. Except for the grasses *Elymus mollis* and *Ammophila arenaria* that are found intermingling with other plants, each dune tends to be occupied by a single species. This is probably because the root system of a single establishing plant serves as a nucleus around which the dune is formed.

Zone II: Foredunes. The foredunes sharply demarcate the inland extent of the beach with an undulating ridge of sand that rises 2–4 m above the beach at an angle of 15–20° (Fig. 2). Strong onshore winds, abundant salt spray, and rapid displacement of sand further characterize this zone.

Cover, density, and species richness are still relatively low, but cover and density contrast strikingly with the beach zone. Many plants found in the more inland zones make their first appearance here. *Carpobrotus aequilaterus* is a strong dominant and *Elymus mollis* is subdominant. Many other plants grow intermingled, but no consistent patterns of association were observed.

Zone IIIa: Foredune hollows. This zone forms a shallow depression immediately inland from the foredunes that grades onto the middunes (Figs. 2, 3). Protection from wind by foredunes, accumulation of litter, and a possible freshwater table closer to the surface may help

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FIGS. 2–4. Beach to mid-dunes. FIG. 2 (top). Foredunes contrast sharply with beach on the left and grade into foredune hollows inland. *Carpobrotus aequilaterus* and other low plants dominate foredune crowns. FIG. 3 (middle). Greyish *Artemisia pycnocephala* of foredune hollows and mid-dunes (middle distance) contrast with the darker reardune foreslope dominated by *Haplopappus ericoides* (background). FIG. 4 (bottom). Vegetation characteristic of both seaward and inland zones mixes among undulating mid-dune ridges and depressions. Sand trail at left corresponds with thin middle trail in Fig. 1B.

TABLE 1. STAND DATA BY ZONE ALONG A SALINAS RIVER STATE BEACH TRANSECT. Data are from 372 contiguous 1-m² quadrats taken inland from the shoreline. The first number is mean density (plants per m²); the second is mean percent cover (per m²). Data represent the average of three samplings from 1977, 1979, and 1980. "+" = plant density <0.1. "*" = plants found in only one transect with a cover <1.0 percent. Zones are: I = Beach; II = Foredune; IIIa = Foredune hollow; IV = Mid-dune; IIIb = Mid-dune hollow; Va = Reardune foreslope; Vb = Reardune crown; Vc = Reardune leeslope; and Vd = Reardune margin.

Species	I	II	IIIa	IV	IIIb	Va	Vb	Vc	Vd
Ammophila arenaria	0.4, 1.8								
Atriplex leucophylla	+, 1.6								
Cakile edentula	*								
Elymus mollis	0.7, 3.3	2.8, 9.8	1.8, 4.4						
Cakile maritima	0.1, 2.8		+, 0.7						
Carpobrotus aequilaterus	+, 1.8	1.2, 15.8	1.3, 16.9	0.2, 3.1	0.1, 1.1				
Agoseris apargioides		+, 0.5							
Carpobrotus edulis		*							
Tetragonia tetragonioides		+, 0.7							
Lathyrus littoralis		0.1, 2.2	0.9, 7.1	0.6, 4.3		+, 0.6			
Armeria maritima		0.2, 0.8	0.2, 0.4						
Convolvulus soldanella		0.1, 1.7	1.1, 11.6	0.3, 4.4					
Franseria chamissonis		0.1, 3.7	0.2, 2.3	+, 0.8					
Oenothera chieranthifolia			0.2, 0.9						
Astragalus nuttallii			*						
Artemisia pycnocephala			2.7, 16.2	1.1, 14.1	0.7, 9.4				
Abronia latifolia			0.8, 8.9	0.7, 10.6	0.9, 1.8				
Castilleja latifolia			0.8, 3.7	0.2, 1.9	0.7, 0.7				
Haplopappus ericoides			0.1, 4.2	0.2, 5.0	0.6, 19.1	0.5, 21.7	0.4, 14.7	0.5, 20.1	
Poa douglasii			1.5, 1.0	1.3, 5.3	1.3, 5.5	0.2, 0.6			
Cryptantha leiocarpa			0.4, 0.9	0.1, 0.4	0.3, 0.2				
Dudleya farinosa			+, 0.2	0.2, 0.9	1.2, 14.3	0.9, 15.5	0.4, 2.8	0.6, 10.8	
Eriophyllum staechadifolium				0.1, 1.6	0.3, 7.6	0.1, 7.2	0.1, 1.2		
Lupinus chamissonis					0.4, 8.6	0.2, 8.3		0.1, 2.6	

TABLE 1. CONTINUED.

Species					Zones				
	I	II	IIIa	IV	IIIb	Va	Vb	Vc	Vd
Eschscholzia californica					0.2, 4.0	0.1, 0.3	0.2, 0.9		
Eriogonum latifolium					0.2, 0.9	0.3, 6.2	0.5, 5.2	0.7, 10.2	
Chorizanthe cuspidata						0.1, 0.2			
Abronia umbellata						0.1, 1.2	0.1, 1.1		
Corethrogyne filaginifolia						+, 0.3	0.9, 12.8	0.3, 5.8	
Eriogonum parvifolium							+, 0.2	+, 0.8	
Phacelia ramosissima							0.1, 1.2	0.2, 6.4	
Amsinckia spectabilis								0.3, 2.7	
Rosa californica								0.1, 1.9	
Marah fabaceus								0.1, 0.8	
Lotus scoparius								*	
Glycyrrhiza lepidota								0.2, 2.8	0.4, 2.1
Rhus diversiloba								0.1, 2.3	0.8, 4.9
Carex barbarae									19.2, 79.8
Baccharis pilularis									0.6, 9.3
Gilia capitata									0.6, 1.8
Rubus californica									0.2, 2.1
Breadth of zone (m)	30	20	25	35	50	115	30	62	5
Species richness	6	9	16	12	12	11	9	13	6
Total density (plants/m²)	1.2	4.5	12.0	5.0	6.6	2.5	2.7	3.2	21.8
Total cover	11.3	35.2	79.4	52.4	73.2	62.1	40.1	67.2	100.0

TABLE 2.　AVERAGE HEIGHT (H) AND DIAMETER (D) IN CM OF *Haplopappus ericoides* AND *Eriophyllum staechadifolium* ALONG A TRANSECT AT SALINAS RIVER STATE BEACH.

	Zones										
	IIIa		IV		IIIb		Va		Vb		Vc	
Species	H	D	H	D	H	D	H	D	H	D	H	D
Haplopappus ericoides	22	90	26	104	35	153	69	280	31	160	63	248
Eriophyllum staechadifolium			30	41	48	84	82	135				

explain why the density and species richness are the highest encountered (Oosting and Billings, 1942). Cover is also very high (78.5 percent), creating the impression in late spring and early summer of a dense mat of meadow wildflowers (Cowen, 1975).

Several plants appear first in this zone (Table 1). Dominants are *Artemisia pycnocephala, Carpobrotus aequilaterus,* and *Convolvulus soldanella.* Subdominants include *Abronia latifolia* and *Lathyrus littoralis.* The layered or storied vegetation that exists in this densely covered zone is due mainly to the trailing stems of *Carpobrotus aequilaterus, Abronia latifolia,* and *Convolvulus soldanella* threading beneath the more upright species (such as *Artemisia pycnocephala* and *Castelleja latifolia,* which may reach 35 cm in height). *Haplopappus ericoides,* which makes it first appearance here, is small (Table 2).

Because use of the area by off-road vehicles has abated somewhat since the area became a state park in 1971, some pioneer dune plants such as *Abronia latifolia, Oenothera cheiranthifolia, Lathyrus littoralis,* and *Convolvulus soldanella* are recolonizing strips of bare sand that make up about 12 percent of this zone.

Zone IV: Mid-dunes.　Because the mid-dunes consist of ridges and depressions that undulate in a series parallel to the beach, two different plant communities exist within this zone (Fig. 4). Some plants found on the wind-exposed ridges of unstable sand are characteristic of more seaward, low-lying, pioneer species such as *Carpobrotus aequilaterus,*

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FIGS. 5–7.　Mid-dune hollows to Reardune margin. FIG. 5 (top). Shrubby *Haplopappus ericoides* and herbaceous *Dudleya farinosa* dominate mid-dune hollows. Sand trail at center corresponds with most inland trail in Fig. 1B. FIG. 6 (middle). Dark *H. ericoides* that dominates the reardune foreslope contrasts with greyish reardune crest (background) dominated in part by *Corethrogyne filaginifolia.* FIG. 7 (bottom). Looking north from the leeward base of the reardune. Complete cover at the base contrasts with areas of exposed sand on the leeside. *Carex barbarae* is the dominant at the dune base. Shrubs are mainly *Baccharis pilularis.*

Artemisia pycnocephala, Convolvulus soldanella, Lathyrus littoralis, Abronia latifolia, Franseria chamissonis, and *Cryptantha leiocarpa.* Shrubs found on the leeward slopes and depressions between the crowns are characteristic of the more inland zones. These include *Haplopappus ericoides, Lupinus chamissonis,* and *Eriophyllum staechadifolium.*

This zone marks the transition between the two main life forms found along the transect—prostrate herbs and erect shrubs. Accordingly, species richness is high. The heterogeneous aspect makes comparison of density and cover with other zones difficult.

Zone IIIb: Mid-dune hollows.   The relief of this zone consists of a shallow hollow behind the mid-dunes that grades onto the foreslope rise of the reardunes (Fig. 5). The dominant plants **are** bushy and upright rather than procumbent. *Haplopappus ericoides* and *Eriophyllum staechadifolium* gradually increase in size from the more seaward mid-dunes but are noticeably smaller than those found on the reardune foreslope (Table 2). Possibly because of increased protection from salt spray and wind, plant cover, density, and species richness have high values.

The two dominant plants, *Haplopappus ericoides* and *Dudleya farinosa,* are almost always found together. Subdominants are *Artemisia pycnocephala, Poa douglasii, Lupinus chamissonis,* and *Eriophyllum staechadifolium.*

Zone V: Reardunes.   This is the largest, highest area, and it has greater relief than any other zone within the dune complex (Fig. 1). Four subzones can be recognized.

Zone Va: Reardune foreslope.   This subzone covers the largest area within the transect (Fig. 1). It rises gradually from the mid-dune hollow at about 12° and culminates in a rounded crest 19 m above sea level (Fig. 6).

The relatively low density and species richness and high cover may be due to the predominance of large shrubs of *Haplopappus ericoides, Lupinus chamissonis,* and *Eriophyllum staechadifolium. Haplopappus ericoides* and *Eriophyllum staechadifolium* show a decided increase in size from the mid-dune hollows almost doubling in size (Table 2). Shrubs are separated by strips of exposed sand (Fig. 1B). The resulting conspicuous mottled appearance and the larger size of dominant shrubs further distinguish this zone from more seaward ones.

Although *Haplopappus ericoides* and *Dudleya farinosa* are the dominant plants in terms of density and cover, *Haplopappus* is the dominant visually because of its relatively larger size. As in the mid-dune hollows, *Dudleya farinosa* usually grows in clusters intermingled with *Haplopappus ericoides.* Subdominant plants include *Lupinus chamissonis, Eriogonum latifolium,* and *Eriophyllum staechadifolium.*

Zone Vb: Reardune crest.   This broad dome-like crest is exposed directly to maritime winds. Ripple marks indicate active sand movement.

Several plant features distinguish this zone from those adjacent to it. Cover and species richness are lower (Table 1, Fig. 6). *Corethrogyne filaginifolia* is dominant here only. This pubescent plant gives a procumbent aspect to the zone that is also seen on the windswept foredunes and foredune hollows. *Haplopappus ericoides* is dominant but is only about half as large as the same plant found in the adjacent zones (Table 2). *Dudleya farinosa* has more than 10 percent cover in the adjacent zones but only 2.8 percent cover here. *Eriogonum latifolium* is subdominant.

Zone Vc: Reardune leeslope.   The angle of this slope (20°) is greater than that of the foreslope (12°). Cover, density, and species richness are considerably greater than on the crest. Riparian and dune plants intermingle on the innermost 15 m to form the densest vegetation within this zone (Fig. 7). Several species occur here for the first time. Dominants are *Haplopappus ericoides, Dudleya farinosa,* and *Eriogonum latifolium.* Subdominants are *Corethrogyne filaginifolia* and *Phacelia ramosissima.*

Zone Vd: Reardune base.   This most inland zone occupies the bank of an old stream channel. Complete cover (100 percent) makes the zone difficult to walk through (Fig. 7). Species richness per m^2 and density were the highest encountered. *Carex barbarae* is by far the dominant plant and *Baccharis pilularis* is subdominant.

Discussion

Physical factors controlling the distribution of coastal strand vegetation are difficult to establish. The most likely influences are salt, onshore winds, and associated substrate movement (Oosting, 1945). These conditions can affect plant distribution and life form by increasing the rate of plant water loss through increasing transpiration, by burying aerial plant parts, by exposing roots, and by mechanical injury from abrasion by wind-born sand (Reynoldson, 1932; Purer, 1936; Billings, 1966).

Possibly in response to wind, the more seaward plants are often procumbent, succulent, or pubescent, with flexible, trailing, and rooting stems. Most plants growing from the mid-dune depressions inland are generally less pubescent or succulent and more upright, woody, and shrub-like in appearance.

Although beach and dune plants are hardy, small alterations in their harsh environment can radically affect their survival. Future studies should investigate how disturbances within zones affect the plants within them and how successful these plants are in recolonizing disturbed areas.

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POSTFIRE RECOVERY OF CREOSOTE BUSH SCRUB VEGETATION IN THE WESTERN COLORADO DESERT

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Abstract

Postfire recovery of three desert shrubs, *Larrea tridentata*, *Hymenoclea salsola*, and *Opuntia echinocarpa* was examined five years after a fire in the Snow Creek area of southern California. *Larrea tridentata* resprouted and had nearly regained its estimated former cover. *O. echinocarpa* excepted, the community has shown substantial recovery. The upper distribution of these desert shrubs may be controlled in part by their susceptibility to periodic fire.

Desert vegetation of southern California is characterized by low biomass with substantial bare space between individual shrubs. Thus it is not surprising that wildfires are infrequent. As a result, remarkably little is known about the postfire recovery of such vegetation.

In early July, 1973, a brushfire spread along the steep north face of Mt. San Jacinto, burning about 3725 ha of timber and chaparral (U.S. Forest Service, undated). Along its northern perimeter the fire moved downslope onto the western edge of the Colorado Desert across an alluvial fan west of Snow Creek village (Fig. 1) where it was sustained by an unusually dense herb layer arising from the previous winter rains. Approximately 65 ha of desert scrub vegetation dominated by *Larrea tridentata*, *Hymenoclea salsola*, and *Opuntia echinocarpa* were incinerated before the fire's advance was halted by firemen near the 375 m contour line. The exact border is thus an artificial line rather than a function of fuel. In this paper, we assess postfire recovery of the dominant shrubs in this burned area by comparison with adjacent unburned stands. Also we attempt to compare shrub coverage before and after fire in the burned area.

Methods

Snags of *L. tridentata* and charred *O. echinocarpa* individuals allowed us to reconstruct the previous canopy extent. Many *H. salsola* plants were incinerated to ground level. Line intercepts and belt transects were used to sample both burned and unburned portions of the alluvial fan in April, 1978. Line intercepts were used for rapid and

accurate estimation of percent cover (Bauer, 1943) and belt transects were used to estimate plant frequencies.

Four 100-m line intercepts were extended at random intervals perpendicular to a 100-m baseline oriented parallel to contour in both study sites (Fig. 1). Both living and dead shrubs were recorded. Dead material in the unburned portion was not appreciable. Additionally in the sample sites the present ground cover of living herbs in the burned section was compared to the unburned section. Foliar cover of herbaceous species was visually estimated by three observers for both burned and unburned sites with average values recorded for the most common species. The relative similarity of the ephemeral vegetation on both sites was evaluated by calculating the percentage similarity (Czekanowski, 1909) and coefficient of community (Sørenson, 1948).

Two belt transects, 325 and 200 m in length, were extended up the alluvial fan from the unburned into the burned portions. Presence of perennial species was recorded above each square meter. Community and species nomenclature follow Munz (1974).

RESULTS

Table 1 indicates the percent frequency of occurrence of perennial plants in the belt transects. It also shows the percent cover of the three dominant shrubs in the burned and unburned sites. These data reveal that the estimated preburn cover of all three differed from that of the unburned site. Prior to the fire, *O. echinocarpa* and *H. salsola* occupied more area in the burned section than in the unburned section, whereas the reverse was true of *L. tridentata*. The lower *L. tridentata* cover in the burned site is probably best attributed to the ecoclinal nature of the alluvial fan vegetation. Prior to the fire, it extended no more than a few hundred meters above the study site where *Encelia farinosa* became dominant. Cover decreases in *L. tridentata* shrubs have also been observed along upper elevations of Colorado Desert (Burk, 1977) and Arizona bajadas (Barbour and Diaz, 1973). In the latter study, substantial patchy changes in floristic composition occurred with lateral displacement along a bajada, a condition we also noticed. Because *H. salsola* was commonly incinerated to ground level, its preburn cover was probably underestimated.

Comparison of current and estimated prefire cover within the burned sample area shows that *O. echinocarpa* has only 27 percent of its former cover. Farther up the alluvial fan, *O. echinocarpa* mortality was nearly complete, probably owing to denser vegetation and more intense fire. In the burned section, *L. tridentata* successfully resprouted and had regained nearly its estimated former cover within five years. *Hymenoclea salsola* generally reseeded and appeared to exceed its former cover. Little difference in ephemeral vegetation ex-
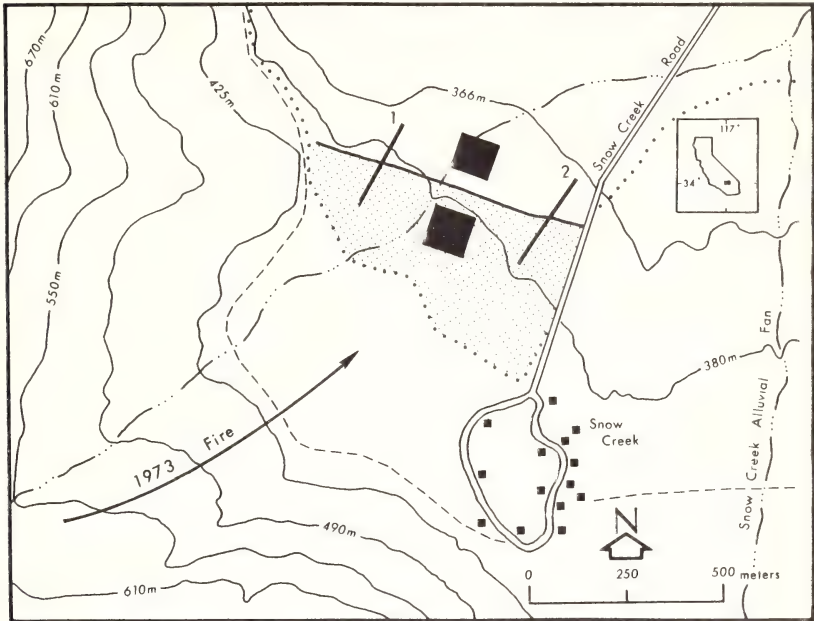
Fig. 1. Location of study area near Snow Creek (Riverside Co.) in southern California. Stippled area denotes burned creosote bush scrub. Dotted line approximates the upper elevational extent of *Larrea tridentata* as does the dashed line for *Opuntia echinocarpa*. Vegetation upslope from dashed line is dominated by coastal sage scrub species admixed with some desert shrubs, and, at higher elevations, chaparral shrubs. Numbered lines straddling fire border represent belt transects; darkened squares indicate line intercept sampling sites. Arrow shows direction in which 1973 fire burned.

isted between the two sites. Species found were *Euphorbia albomarginata* (30 percent cover in unburned area, 30 percent in burned area); *Erodium cicutarium* (6, 10); *Schismus barbatus* (6, 5); *Crassula erecta* (3, 3); and *Bromus rubens* (2, 1). The following species had 0-1 percent cover in both areas: *Malacothrix glabrata, Lupinus bicolor, Cryptantha intermedia, Lotus tomentellus, Lasthenia chrysostoma,* and *Camissonia pallida.* The coefficient of community (0.82) and the percentage similarity (84 percent) between the sites were both fairly high.

DISCUSSION

The portion of the California fire that extended onto the alluvial fan in the Snow Creek area was severe enough to defoliate nearly all creosote bushes, although most resprouted. *Opuntia echinocarpa* survived by directly tolerating the fire. Living individuals bore scorched tissue five years later. No regeneration from fallen unburned joints was apparent. Tratz and Vogl (1977) found that *O. acanthocarpa*, a

TABLE 1.   FREQUENCY OF PERENNIAL PLANTS ACROSS BURN BOUNDARY IN SNOW CREEK DRAINAGE. Data (percents) are based on two belt transects. Percent foliar cover for the dominant shrubs (based on four line intercepts in each study site) is given in parentheses.

Species	Unburned		Burned	
	Living	Dead	Living	Dead
Larrea tridentata	24 (10)	0 (0)	8 (2)	3 (0.4)
Opuntia echinocarpa	6 (4)	1 (0)	6 (2)	11 (4)
Hymenoclea salsola	4 (5)	0 (0)	19 (10)	3 (5)
Encelia farinosa	0.6	0	1.1	0
Prosopis glandulosa	5.1	0	0	0
Mirabilis tenuiloba	0	0	0.8	0
Stillingia linearifolia	0	0	0.5	0
Salvia mellifera	0	0	0.5	0

closely related species, had 25 percent of its individuals resprouting one year after a fire on burned portions of Anza-Borrego Desert State Park, San Diego County. *Opuntia acanthocarpa* displayed the poorest recovery of sampled plants following that fire.

Larrea tridentata and some *H. salsola* plants have resprouting ability comparable to some chaparral plants. The abundance of *H. salsola* in the burned site may reflect an ability for rapid, weedy colonization. Other investigators have tentatively categorized *H. salsola* as a relatively short-lived shrub occurring in naturally disturbed areas in creosote bush scrub. It is also observed as a pioneer in more severely disturbed areas such as those affected by pipeline construction, power transmission lines, and off-road vehicles (Davidson and Fox, 1974; Vasek, Johnson, and Eslinger, 1975; Vasek, Johnson, and Yonkers, 1975).

No fires have occurred on the study area in historic times. In 1911, a fire spread downward from the mountains to the uppermost extent of the alluvial fan, whereas in 1941 the ridge immediately west of the fan burned (U.S. Forest Service, undated). It is of interest that the lower perimeter of the 1911 fire roughly coincides with the upper elevational extent of *O. echinocarpa* on the alluvial fan. Lack of growth rings in *Opuntia* species precludes annular dating, but *O. echinocarpa* specimens taller than about 0.7 m may be 25 years old or more (Park Nobel, pers. comm., 1980). Its average height in our study area was about 1 m, implying that many of the individuals may have been quite old. The decreased survival rate of *O. echinocarpa* associated with increasingly denser vegetation found with elevational increase suggests burning intensity may set additional limits to its distribution.

Data from near Tucson, Arizona, indicate that the survival frequency of *L. tridentata* after controlled burning is directly propor-

tional to fire intensity and season (White, 1968; Cable, 1972). Controlled burns in June of sparse cover of native grasses, augmented by the addition of straw, produced up to 100 percent mortality, whereas lower intensity burns on native grasses are much less damaging. Jumping cholla (*Opuntia fulgida*) and cane cholla (*O. spinosior*) are also susceptible to incineration (Humphrey, 1949, 1974; Reynolds and Bohning, 1956; Cable, 1967, 1972). Cattlemen have long used fire to help control cholla and mesquite.

The intergradation of the creosote bush scrub into the higher elevation shrub communities reflects physiologic tolerance along a topographic moisture gradient. Beatley (1974, p. 260) suggested that the northern boundary and upper elevational limits of *L. tridentata* in southern Nevada "are determined primarily by rainfall in excess of a critical amount, and the rainfall regimes over probably a very long time." She estimated that amount to be 183 mm. The upper elevational distribution of *L. tridentata* and *O. echinocarpa* also may be controlled locally by their susceptibility to periodic and intense fire. Dry fuel values exceeding critical levels could result in large scale mortality. We suggest that in the desert scrub-coastal sage scrub ecotone, the intensity and periodicity of wildfires may be additional factors to physiologic tolerance in limiting the distribution and abundance of some desert perennials.

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ANNOUNCEMENT

PAPERS IN WESTERN PLANT ECOLOGY

A symposium in honor of the retirement of Professor Jack Major will be presented on Friday, 29 May 1981. It will be held at the University of California, Davis, campus in Memorial Union, Room II (upstairs), from 9 a.m. to 5 p.m. Approximately 12 speakers will present research or overview papers on "Western Plant Ecology." There will be no registration fee, but participants must provide their own lunches.

The symposium is being co-sponsored by the California Botanical Society; the UC Davis Institute of Ecology; and the Botany Department, UC Davis.

Speakers and tentative titles are as follows: *G. L. Stebbins,* Floristic affinities of the high Sierra of California; *D. J. Parsons,* Vegetation management and research in Sequoia and Kings Canyon National Parks; *J. L. Vankat,* Vegetation classification and analyses in Sequoia National Park; *P. W. Rundel,* Nutrient cycling and chaparral in Sequoia and Kings Canyon National Parks; *N. Benedict,* Mountain meadows: stability and change; *M. B. Morgan,* Vegetation of the Rae Lakes Basin, southern Sierra Nevada; *D. I. Axelrod,* Age and origin of the Monterrey endemic area; *J. R. Griffin,* Pine seedlings, native herbs, and annual ryegrass on the Marble-Cone burn, Santa Lucia Mountains; *J. A. Neilson,* Distribution, ecology, and proposed revision of the *Streptanthus morrisonii* complex; *R. Macdonald,* Patterns of xylem sap tension and conductance of foothill woodland vegetation types near Lake Berryessa; *R. Gankin,* Ecology and land use planning in San Mateo County; *J. H. Burk,* Phenology, germination, and survival of ephemerals in Deep Canyon; *C. B. Davis,* Seed banks and vegetation history in prairie wetlands.

For further information call the UC Davis Department of Botany: (916) 752-0617.

SEEDLING CHARACTERISTICS AND ELEVATIONAL DISTRIBUTIONS OF PINES (PINACEAE) IN THE SIERRA NEVADA OF CENTRAL CALIFORNIA: A HYPOTHESIS

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ABSTRACT

Seven species of the genus *Pinus* occupy a 3000-m elevational gradient on the western slope of the Sierra Nevada in central California. Three species of 3-needled pines replace each other abruptly over the mountainsides as do three species of 5-needled pines. The seventh species, a 2-needled pine, is found on the upper half of the mountainsides. Observed associations of pines on these slopes consist of a 2- or 3-needled species (or both) with a 5-needled species. A hypothesis is presented that interspecific competition between seedlings, ultimately for water, has led to the distributional patterns observed. This hypothesis is examined in terms of the morphological characteristics of seedlings and their needles that reflect their relative usage of water.

Storer and Usinger (1963) portray seven species of the genus *Pinus* forming a guild over a 3000-m elevational gradient on the western slope of the Sierra Nevada in central California. The distributional pattern of these seven species as described is striking. Three species of 3-needled pines replace each other sequentially over the elevational gradient, as do three species of 5-needled pines. When one species disappears, another appears with the same number of needles per fascicle. The change with elevation is portrayed as abrupt with little or no overlap occurring between species with similar needle numbers. Also, a 2-needled species of pine is found over the upper half of the elevational gradient. Up to about 915 m there is only a 3-needled species (*P. sabiniana*). From 915 m to timberline several associations of pines are found. Each of these higher-elevation groups is composed of a 2-needled or a 3-needled species, or both, associated with a 5-needled pine. At no place on the mountainside are two 3-needled or two 5-needled pines described as occurring together. If the distribution of pines depicted by Storer and Usinger is accurate, the pattern of needle numbers per fascicle requires explanation. I suggest that this distributional pattern represents an example of the competitive exclusion principle in which interspecific competition has led to the elevational separation of species with similar needle number. If so, there must be ecological differences between pine species with different needle numbers because various combinations of these species do occur.

In this paper I demonstrate that the distributional patterns described by Storer and Usinger are accurate. Secondly, I present a hypothesis to explain the associations of pines that are found on the western slopes

of the central Sierra Nevada. Finally, I attempt to examine this hypothesis by a comparison of some of the morphological characteristics of species that either overlap extensively or replace each other abruptly over the elevational gradient.

ELEVATIONAL DISTRIBUTIONS

The elevational distribution of pines on transects of the western slopes of the Sierra Nevada in central California were determined by counting 100 individuals of the genus at stations separated from one another by 77 m altitude along State Highways 4, 88, and 108 (38°16–34'N, 120°0–55'W; Amador, Calaveras, Alpine, and Tuolumne Counties). Trees taller than 15 m were counted on 10-m-wide strips running along the contour of southeastern facing slopes at each station. Sampling was limited to southeastern slope aspects to reduce the variability in species abundance resulting from the different microclimates that exist at the same elevation but on different slope aspects. Only species of *Pinus* were counted and their relative proportions calculated at each station and plotted (Fig. 1a, b, c).

In this area of the Sierra Nevada only seven species of *Pinus* occur: four members of the subgenus *Diploxylon* and three species of the subgenus *Haploxylon*. *Pinus sabiniana* Dougl. (group *Macrocarpa*), *P. ponderosa* Laws., and *P. jeffreyi* Grev. and Balf. (the latter two species members of the group *Australis*) compose the sequence of 3-needled *Diploxylon* pines while *P. contorta* Dougl. (group *Insignis*) is the 2-needled *Diploxylon* species. *Pinus lambertiana* Dougl., *P. monticola* Dougl. (both members of the group *Strobi*) and *P. albicaulis* Engelm. (group *Cembrae*) make up the 5-needled sequence of *Haploxylon* pines (taxa follow Shaw, 1914 and Mirov, 1967). For species of pines with three needles per fascicle abrupt replacements occur at approximately 840 m and 1740 m in this region. The latter replacement involves *P. ponderosa* and *P. jeffreyi,* which hybridize at the interfaces of their distributions (Mirov, 1967). In the region studied the zone of possible hybrids is small (approximately 25 m in elevational range) and falls between sampling sites. Identifications of canopy individuals of these two species are based upon gross characteristics of their barks and cones. For 5-needled species abrupt replacements occur at approximately 1980 m and 2630 m (Fig. 1). For the four possible pairs of replacing species along the mountainsides, in only one instance do two species of *Pinus* with the same needle number occur together in the same sample. This overlap is for the high elevation, low relative abundance situation in which *P. albicaulis* replaces *P. monticola.* Thus the distributional pattern described by Storer and Usinger (1963) is verified.
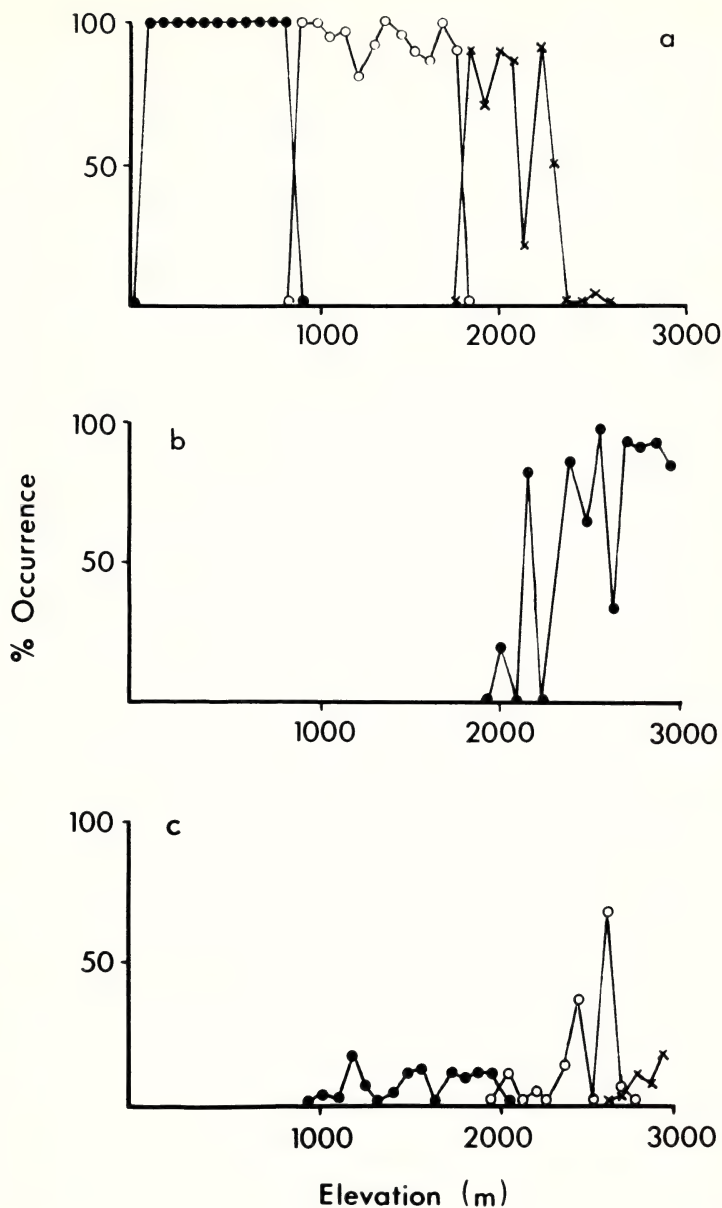
FIG 1.   Percent occurrence of *Pinus* only for the seven species found on southeastern slope aspects on the western slope of the Sierra Nevada in central California. a. 3-needled pines. b. 2-needled pine. c. 5-needled pines.

The Hypothesis

A very precise pattern of replacements is observed among the larger individuals suggesting that their elevational distributions are determined by interspecific competition between seedlings and younger age classes. Seedlings of *Pinus* with different needle numbers per fascicle that are associated elevationally are often found growing together in clumps along with other species of conifers. Likewise, I have found seedlings of species with the same needle number associated in clumps at elevations at which one species replaces another abruptly. Hence the possibility for intense competition exists between seedlings growing in such close proximity within these clumps. Water would seem to be the important limiting factor in this relatively open-canopied community. It has been suggested that water is critical in the early life of pine seedlings (Pearson, 1930). Seedlings are dependent upon the moisture in the upper soil layers, where surface evaporation and transpiration rapidly deplete the available soil moisture (Stone and Jenkinson, 1971). For example, young ponderosa pines suffer intense intraspecific competition for available soil moisture (Weaver, 1961). Further, the smallest individuals of *Pinus* suffer more from decreases in moisture levels than do larger individuals (Turner, 1956; Weaver, 1961; Yeaton, 1978). Seedlings are probably most severely affected by environmental fluctuations because they are small and therefore do not have the benefit of the stabilizing effect provided by reserves accrued from growth in previous years. Hence, adaptive responses in water usage or habitat usage are most likely to be reflected in seedlings (Ledig et al., 1977).

For associated species, clumps of seedlings may be located upon soil patches with varying moisture levels over the course of the growing season. Species of *Pinus* with adaptations to reduce the effects of moisture stress would be expected to outcompete seedlings of species without these adaptations on patches that are relatively dry over the growing season. Adaptations to reduce the effects of drought might appear as a reduction in total needle surface area over which water may be lost, a decrease in the number of stomates to reduce transpirational water loss, or structural differences in needle anatomy to reduce epidermal water loss. In contrast, species of *Pinus* successful in competition on wetter patches may have greater total needle surface areas for increased photosynthetic surface area, increased numbers of stomates for higher rates of gas exchange during photosynthesis, and a reduced necessity for a specialized needle anatomy to reduce epidermal water loss. Their success on these wetter patches may be the result of an increased growth rate and their ability to store reserves to survive periods in which the characteristics of the patch are stressful. Coexistence of species at any one elevation may be maintained by use of patches with differing seasonal moisture regimes ranging from dry to relatively wet.

Species with the same needle number that replace one another abruptly elevationally are also subjected to a wide range of moisture availability. Species occurring at low elevations are faced with a hot dry summer while the species at the highest elevations are faced with the problem of a short growing season and a winter drought. Presumably the central species in each elevational sequence occupies the best available range of conditions for moisture and length of growing season and may outcompete the species above and below it as a result of increased growth rates (Yeaton et al., 1980).

Needle number and total needle length in seedlings

The hypothesis suggests that 2-needled pines should occupy drier sites than associated 3- and 5-needled species and that 3-needled pines should use drier sites than their 5-needled associates because the total needle length per fascicle will increase from 3-needled to 5-needled fascicles. It also suggests that species with the same needle number that replace each other are more similar to one another than are species that form associations. However, these relationships may be complicated when the whole individual is considered due to differences in needle lengths and number of fascicles. The effect of these differences can be studied by measuring the total needle lengths in all fascicles of seedlings of each species and determining if the relationship observed for fascicles holds when the whole seedling is considered.

Needle width may complicate the needle number/needle length relationship. Haller (1962) has stated that needle width is unimportant in comparisons of species with different needle numbers and any width differences would not be great enough to affect these measurements. My analysis of needle widths agrees with Haller's statement. The surface area of a fascicle is approximately 10.28rl for a 2-needled species, 12.28rl for a 3-needled species and 16.28rl for a 5-needled species (where "r" is the radius and "l" is the length of the fascicle). These values result from viewing the fascicle as circular in cross-section. For all fascicles the outer surface area of the fascicle is $2\pi rl$. To this must be added 4rl, 6rl, or 10rl for the inner needle surfaces for 2-, 3-, and 5-needled species. Treating length of fascicle as a constant, to attain the surface area of a 5-needled species, a 3-needled associate must be 33 percent greater and a 2-needled species 58 percent greater in needle width. Similarly, a 2-needled species must be 19 percent greater in needle width to attain the same surface area as a 3-needled associate. Table 1 shows average measurements of needle width for specimens of the seven species of pines in this study. The measurements of needle width are very similar for all seven species.

The pair of associated species with the greatest difference in needle width is that of the 3-needled *Pinus jeffreyi* with the 5-needled *P. monticola* (Table 2). For these species the difference is 33 percent or, in other words, the surface areas per mm of needle length of fascicles

TABLE 1. ELEVATIONAL RANGE AND MEAN NEEDLE WIDTH (± S.E.) FOR THE SEVEN SPECIES OF *Pinus* ON THE WESTERN SLOPES OF THE SIERRA NEVADA. N = 10 for needle-width measurements.

Species	Needles per fascicle	Elevational range (m)	Needle width (mm)
Pinus sabiniana	3	100–915	0.95 ± 0.03
Pinus ponderosa	3	915–1740	0.88 ± 0.04
Pinus jeffreyi	3	1740–2670	0.81 ± 0.04
Pinus lambertiana	5	930–1980	0.70 ± 0.03
Pinus monticola	5	1980–2630	0.61 ± 0.02
Pinus albicaulis	5	2630–3000	0.84 ± 0.03
Pinus contorta	2	1930–3000	0.72 ± 0.03

are equal. For all other pairs of associated species the difference in needle width is smaller than that required for this parameter to have a significant effect on the surface area of species with different numbers of needles per fascicle. Hence, needle width is not a factor in the relationship of needle number per fascicle for associated and elevationally replacing species.

To study the effects of needle length, branching patterns, and spacing of needles along branches, the total needle lengths for seedlings of varying stem diameters were measured. Seedlings of the seven species of pines were found in areas adjacent to California State Highways 4 (through Ebbetts Pass), 88 (through Carson Pass) and 108 (through Sonora Pass). Seedlings were sampled in the centers of the distribution of each respective species. At least 25 seedlings of each species were counted. Seedlings were selected whose stems ranged from 0.5 to 30 mm in diameter as measured by calipers at a point 2.5 cm above the ground and whose diameters were fairly uniformly spaced from one another over this range. Individuals were chosen that had no apparent

TABLE 2. PERCENTAGE DIFFERENCES IN NEEDLE WIDTHS FOR ELEVATIONALLY ASSOCIATED PAIRS OF PINES. Percent difference needed for needle width to be important for measurement of needle surface area for associated species of *Pinus* calculated as (needle width of species with fewer needles per fascicle—needle width of associated species)/(needle width of species with greater number of needles per fascicle) × 100. Negative percent indicates that needle width is greater for species with more needles per fascicle.

Pairs (needles per fascicle)	Expected % difference	Observed % difference
P. albicaulis (5)—P. contorta (2)	58	−14
P. monticola (5)—P. contorta (2)	58	18
P. jeffreyi (3)—P. contorta (2)	19	−11
P. monticola (5)—P. jeffreyi (3)	33	33
P. lambertiana (5)—P. ponderosa (3)	33	26

TABLE 3.   THE RELATIONSHIP BETWEEN SEEDLING STEM DIAMETER AND TOTAL NEEDLE LENGTH FOR SEVEN SPECIES OF THE GENUS *Pinus* OCCURRING ON THE WESTERN SLOPES OF THE SIERRA NEVADA IN CENTRAL CALIFORNIA. Data fit a power curve, $y = cx^E$ where y = total needle length, c = a constant, x = seedling stem diameter, and E = experiment. "r^2" is the coefficient of determination.

Species	Number sampled	Constant	Exponent	r^2
P. sabiniana	25	819	1.83	0.90
P. ponderosa	25	1298	1.76	0.98
P. jeffreyi	27	1187	1.69	0.90
P. lambertiana	25	1656	1.86	0.96
P. monticola	25	679	2.08	0.90
P. albicaulis	25	526	2.16	0.96
P. contorta	25	638	1.82	0.96

damage from grazing herbivores. For each seedling the diameter of each branch off the main stem was measured and all the fascicles of needles on that branch and its sub-branches counted. The length of a typical fascicle of needles on each branch was measured. This needle length was multiplied by the number of needles in the fascicle and that product multiplied by the number of fascicles counted on the branch. The total needle length for each branch on the seedling was then summed. A similar procedure was employed for fascicles growing out of the main stem between branches and these were added to the sum of the branches to give a total needle length per seedling.

The relationship between total needle length per seedling and the diameter of that seedling is best fitted by a power curve. For each species of pine studied, the total needle length per seedling is equal to

TABLE 4.   PAIRWISE COMPARISONS OF ASSOCIATED PINE SPECIES AND ALTITUDINAL REPLACEMENTS. Values in parentheses are mean ratios of the square root of total needle length to stem diameter. Comparisons of the mean ratios were made using the median test.

Species pairs	χ^2	P
Altitudinal Replacements		
P. sabiniana (24.7)—*P. ponderosa* (28.1)	2.88	$0.05 < p < 0.10$
P. ponderosa (28.1)—*P. jeffreyi* (25.3)	2.77	$0.05 < p < 0.10$
P. lambertiana (35.9)—*P. monticola* (29.4)	5.12	$p < 0.05$
P. monticola (29.4)—*P. albicaulis* (27.7)	0	$p \cong 1.00$
Altitudinal Associates		
P. contorta (21.0)—*P. albicaulis* (27.7)	15.68	$p < 0.001$
P. contorta (21.0)—*P. jeffreyi* (25.3)	7.70	$p < 0.01$
P. contorta (21.0)—*P. monticola* (29.4)	11.52	$p < 0.001$
P. jeffreyi (25.3)—*P. monticola* (29.4)	7.70	$p < 0.01$
P. ponderosa (28.1)—*P. lambertiana* (35.9)	8.00	$p < 0.01$

a constant value times the seedling diameter approximately squared. All species fit this model well with correlation coefficients (r) of 0.95 or higher (Table 3).

These data can be used to answer several questions about the species that are either associated or replacing along the western slopes of the Sierra Nevada. Are species that are associated elevationally significantly different from one another in their total needle lengths? Are associated species different such that 5-needled pines have greater total needle lengths than their 3- or 2-needled associates? What relationships exist between total needle lengths for seedlings of species that replace abruptly over the elevational gradient? Are they more similar to one another than seedlings of species that form associations?

To answer these questions the ratio of the square root of total needle length to stem diameter was calculated for each seedling measured in the study. This ratio was used because the total needle length per seedling is approximately equal to the product of stem diameter squared and a species-specific constant (Table 3). Reduction of the data in this fashion reveals the sample value of this constant for each individual measured. Comparisons of these converted data were made using a Median test (Siegel, 1956) for sets of seedlings of elevationally associated or replacing pairs of species. All ratios of square root of total needle length to stem diameter for each species of 3- and 5-needled pine compared with the species replacing them higher on the mountainside have chi-square values with probabilities of occurrence greater than 0.01. Conversely, pairwise comparisons between pines that co-occur on the mountainside all have chi-square values whose probabilities of occurrence are less than 0.01 (Table 4). Furthermore, 5-needled pines attain significantly greater total needle lengths per individual than do their 2- or 3-needled counterparts. Thus, the species that replace one another elevationally have less different total needle lengths than do associated species.

The pattern of needle numbers in adult trees is a reflection of the total needle surface areas of their seedlings. This pattern for seedlings, in which species similar in total needle length per seedling replace one another elevationally and in which species dissimilar in total needle length overlap elevationally is consistent with the hypothesis that water availability for seedlings determines which species can occur together.

DISCUSSION

The data reported here are consistent with the hypothesis that competition between seedlings for soil moisture has led to the distributional patterns observed for the seven species of *Pinus* occupying the western slopes of the Sierra Nevada. Species that are morphologically similar to one another in characters reflecting water use are displaced over

the gradient, while species dissimilar in these characteristics overlap extensively over the same gradient. Additional evidence from the literature supports the hypothesis. Leaf anatomy is one area of possible evidence although morphological differences in their functional sense may not be clearly understood. Harlow (1947) has described the cross-sectional leaf anatomy for most species of North American pines. All *Diploxylon* (2- and 3-needled) species included in this study have well developed dermal regions, particularly in the hypodermal layer. The hypodermal layer is described as either biformed or multiformed with thick-walled cells. In contrast the dermal regions of the three species of *Haploxylon* (5-needled) pines are less well developed with no thickening of the hypodermal cell walls. Thickened cell walls in the dermal region of the *Diploxylon* species may be indicative of greater drought stresses. For example, those *Haploxylon* species of the group *Paracembra* (*Pinus monophylla* and *P. edulis*) occupying habitats at the edge of desert regions in the southwestern United States where moisture stress is high are described by Harlow (1947) as having a hypodermal layer two to four cells thick and the cells with thickened cell walls. It may be that the thickened cell walls and more complex development of the hypodermal layers in the *Diploxylon* species reflect adaptation to moisture stress to reduce epidermal water loss.

A second source of information on the relative water use of associated *Pinus* species is data for photosynthetic and transpiration rates. Unfortunately there is very little direct evidence on rates for associated species of pines. Miscellaneous evidence does exist for two sets of associated species, *P. ponderosa* and *P. lambertiana* in the Sierra Nevada of California and *P. banksiana, P. resinosa,* and *P. strobus* in the Great Lakes region of the United States and Canada. Snow (1924), studying *Pinus ponderosa* (3-needled) and *P. lambertiana* (5-needled), reported that shade was necessary for survivorship of *P. lambertiana* seedlings. In contrast, shade aided but was not necessary for survivorship of *P. ponderosa* seedlings. He concluded that *P. ponderosa* was more drought resistant than *P. lambertiana*. A similar observation about the drought resistance of *P. lambertiana* and *P. ponderosa* was made by Pharis (1966) with a suggestion that associations of these two species optimize water usage by tapping different subsurface zones of the soil.

More extensive work has been done with *Pinus strobus* and its 2- and 3-needled associates. Belyea (1925) reported that *P. strobus* (5-needled) is more susceptible to wind desiccation than its associate *P. resinosa* (long, 2-needled) and attributed the difference to the greater leaf surface area represented by the 5-needled species. Similar studies contrasting *P. strobus* with *P. resinosa, P. banksiana* (short, 2-needled), or *P. rigida* (3-needled) always place *P. strobus* on wetter sites than its 2- or 3-needled associates (Hutchinson, 1918; Cook et al., 1952). In a comparison of water loss in three of these species that

occur together in the vicinity of the Great Lakes, Walter and Kozlow-ski (1964) rank water loss as *P. strobus* > *P. resinosa* > *P. banksiana*. Brown and Curtis (1952), in a gradient analysis of the upland conifer-hardwood forests of northern Wisconsin, ranked these three species relative to the moisture-holding capacity of the soils. *P. banksiana* occurs on dry soils, *P. resinosa* on intermediate soils, and *P. strobus* on soils with greater moisture-holding capacity. While *P. resinosa* and *P. banksiana* are both 2-needled pines, *P. resinosa* has needles four times as long as *P. banksiana*.

Other authors have reported similar patterns in water usage for other pairs of associated species differing in needle number per fascicle [Larson (1927) for *P. monticola* and *P. contorta*; Coile (1933) for *P. taeda* and *P. echinata*; Pessin (1933) for *P. palustris* and *P. clausa*; Wright (1966, 1968, 1970) for *P. lambertiana* and *P. coulteri*]. In all cases the species with the greater needle number occupied what were described as relatively wetter sites.

Despite the observations for the seven species of *Pinus* on the western slope of the central Sierra Nevada reported above, no direct evidence for interspecific competition between seedlings of these species exists. Both Daubenmire (1943) and Haller (1959) have suggested that water stress and/or interspecific competition are critical in determining, at least in part, elevational ranges of species in western mountains. To test the hypothesis that interspecific competition is the organizing mechanism for these seven species of *Pinus,* long term field studies of seedling establishment, growth, and mortality as well as transplant experiments are in progress for the two elevationally replacing species *Pinus sabiniana* and *P. ponderosa,* and for the two elevationally associated species *P. ponderosa* and *P. lambertiana*. In addition, because most pairs of associated species comprise a *Haploxylon* and a *Diploxylon* species, further work on the comparative water requirements of these two subgenera is suggested, particularly with respect to differences in stomatal responses to increasing drought stress. Finally the distributional patterns observed in the central Sierra Nevada must be expanded to other sets of pines to see the generality of the patterns described here.

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PORTULACA JOHNSTONII, A NEW SPECIES OF PORTULACACEAE FROM THE CHIHUAHUAN DESERT

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ABSTRACT

Portulaca johnstonii, distinguished by two radial series of tapering, erect fimbriae around the seeds, is described from the Bolson de Mapimi region of the Chihuahuan Desert, Coahuila, Mexico. It is most closely related to *P. retusa.*

While preparing a treatment of Portulacaceae for Marshall Johnston's Chihuahuan Desert Flora, a distinctive new species of *Portulaca* was encountered and is described below.

Portulaca johnstonii Henrickson sp. nov.

A *Portulaca retusa* siminibus ad marginem trichomatibus subulatis effusis biseriatis differt (Fig. 1).

Glabrous, fleshy, decumbent-ascending annuals 1–2 dm wide. Leaves often subopposite, ovate-spathulate, 2–14 mm long, 1–4 mm wide (to probably larger), obtuse, rounded to truncate at tip, cuneate at base, petioles 1–2 mm long, caniculate, at margins entire, axils with fimbriate white setae 0.2–0.7 mm long. Flower 1–2 at tips of lateral branches, mostly subtended by 1–2 pairs of leaves and a pair of narrowly ovate, acute-acuminate scarious bracts 1.2–3 mm long, pedicels ca. 1 mm long; petals united below, 2–3.5 mm long, yellow, lobes acute; stamens 5–8, filaments united to base of corolla for 0.5–0.7 mm, free filaments 1–1.5 mm long, puberulent above base, anthers 0.3–0.4 mm long; style 1.5 mm long, lobes 3, ca. 0.6 mm high. Fruit 3–4 mm high, circumscissile dehiscent medially, the lid widely conical, 2–3 mm broad at base, usually constricted below tip, overtopped by paired, green sepals 3–4 mm high, these dehiscing circumscissilly with fruit, each with a medial vertically raised, crest-like keel; seeds 2–15, 1.3–1.6 mm in total diameter, body reddish-brown, 0.7–1 mm in diameter, compressed, with 3–4 concentric rows of low, radially elongated tubercules on each side, at margins with 2 rows of rust-colored, conspicuous, subulate, firm fimbriae 0.3–0.4 mm long, base of seed with a small white caruncle 0.1–0.2 mm long.

TYPE: México, Coahuila; Matrimonio Nuevo on road paralleling railroad between Esmeralda and Cuatro Cienegas (near 27°08′N; 103°10′W), locally common in desert flat in gravelly calcareous adobe-clay, 1075 m, 2 Sep 1972, *F. Chiang C., T. L. Wendt, and M. C. Johnston 9125* (Holotype LL; isotype MEXU).

This distinctive species, known only from the type collection, is
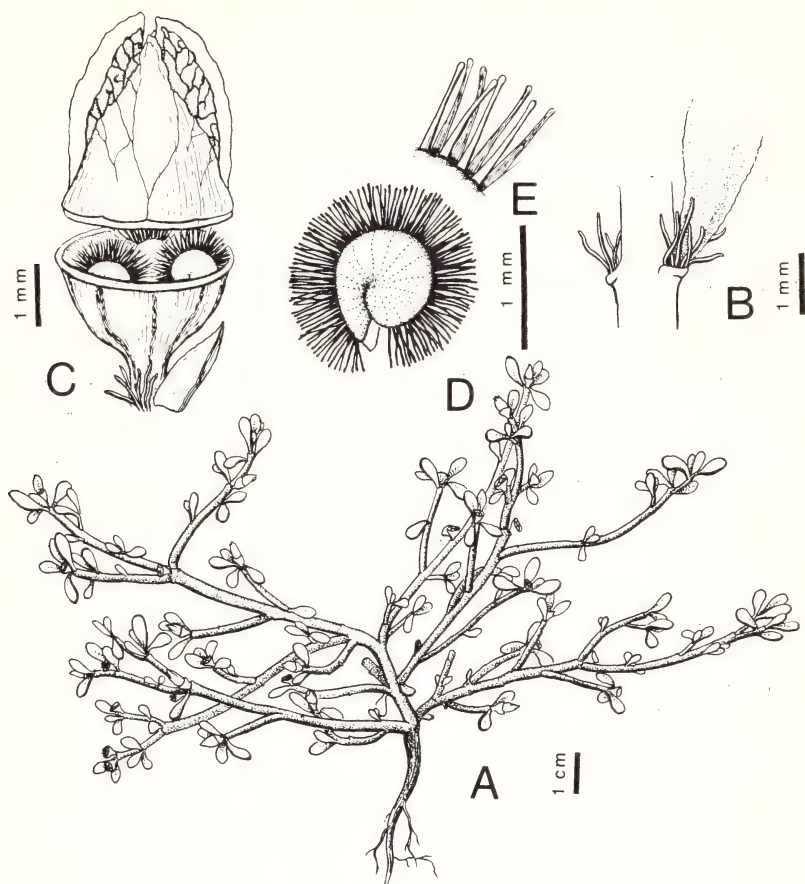
FIG. 1. *Portulaca johnstonii* Henrickson. A. Habit. B. Leaf base showing fimbriate white setae. C. Mature circumscissile capsule showing crested conical lid, seeds, subtending bract, and setae. D. Seed showing radiating fimbriae and small, white, basal caruncle. E. Detail of fimbriae 0.3–0.4 mm long on seed margin, showing their orientation into two rows.

vegetatively very similar to *P. retusa* Engelm. but is immediately distinguishable from this and all other species in the genus by the radiating fimbriae on the seeds. Both species are also very similar vegetatively to the widespread, weedy *P. oleracea* L.

Portulaca johnstonii, named for Marshall C. Johnston, grows in open, clay Tobosa flats with *Hilaria, Sporobolus, Ericameria,* and *Prosopis* in the Bolson de Mapimi region of the Chihuahuan Desert.

MALEPHORA CROCEA (AIZOACEAE)
NATURALIZED IN CALIFORNIA

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ABSTRACT

Malephora crocea, native to Cape Province, South Africa, has been naturalized in southern California at least since 1946, but is not mentioned in California floras. Misidentified specimens have served as the basis for incorrect reports of other species. We document the historical occurrence and current range of *M. crocea* in California and provide a morphological description, illustration, and comparison with other ice plants.

Identification of naturalized plants often is difficult and collections are frequently misidentified. The mesembryanthemums or ice plants (Aizoaceae, sensu Melchior, 1964) are particularly difficult because of the size and complexity of the group and lack of keys to many species. The problem was amplified by the division of *Mesembryanthemum sensu lato* (=Mesembryanthemaceae, Herre and Volk in Schwantes, 1947; Schwantes, 1971) into many genera. Herre (1971) distinguished 125 genera and estimated 2400 species, mostly of xeric habitats in South Africa. Hundreds of species have been cultivated in California; by 1930, Hoffman and coworkers had listed 86 for Santa Barbara. At least 22 have been used as groundcovers in California (Kimnach, 1966). Several persist after cultivation or are naturalized to some degree. Moran (1950) and Munz (1974) considered *Carpobrotus aequilaterus* (Haw.) N. E. Br. [=*Carpobrotus chilensis* (Mol.) N. E. Br.] to be native. Munz listed nine species as naturalized in southern California. This figure is misleading because of misidentifications.

Malephora crocea (Jacq.) Schwant. (Fig. 1) is native to Cape Province, South Africa (Jacobsen, 1960, 1977). It is commonly planted in California in gardens and on streetsides and highway embankments. It is used for erosion control on moderate slopes and is drought tolerant (Anonymous, 1979). Some 15 herbarium specimens show it to be cultivated from Marin and Fresno Counties, California, to Baja California Norte, including Cedros Island, Mexico. A specimen from the James West nursery, San Rafael (*West s.n.,* CAS) shows it was in California by 1933. According to Poindexter (1934), a purple-flowered color form was introduced at about the same time by Kate Sessions, a San Diego

nurserywoman. Also, a specimen was collected in 1938 from E. O. Orpet's Santa Barbara nursery (*Hartwell s.n.*, SBM). *Malephora crocea* was not listed for the Santa Barbara region previously (Hoffman et al., 1930). Orpet later supplied material for freeway plantings to the State of California Division of Highways (Anonymous, 1954).

Malephora crocea is naturalized in western North America mostly along the coast from northern Santa Barbara County to Baja California Norte, Mexico. Some 26 herbarium specimens show it established at Surf, UCSB Campus, Goleta Slough, Santa Barbara, and Carpinteria Salt Marsh, Santa Barbara County; Ventura, Ojai, Pt. Mugu, and East Anacapa Island, Ventura County; Newport Backbay, Dana Point, and Doheny Beach State Park, Orange County; Riverside, Riverside County; and La Mision, Baja California Norte. It occurs as a garden escape in the vicinity of dwellings and along roadsides and has become established on sea bluffs, stream banks, floodplains, coastal sage scrub habitats, and margins of estuaries. Near estuaries *M. crocea* is especially well-established and grows in several situations. It occurs in open sand and silt of disturbed areas above storm tide, usually with *Atriplex patula* L. subsp. *hastata* (L.) Hall & Clem., *A. semibaccata* R. Br., *Carpobrotus edulis* (Haw.) Schwant., *Frankenia grandifolia* Cham. & Schlecht., *Parapholis incurva* (L.) C. E. Hubbs, *Salicornia subterminalis* Parish, *Spergularia marina* (L.) Griseb., and *Suaeda californica* Wats. var. *taxifolia* (Standl.) Munz. It is locally abundant on shell middens exposed in salt marshes at Newport. This is the only habitat where we have observed numerous seedlings. It also occurs in debris at mean high and storm high tide lines where it establishes apparently from stems deposited there. Under these conditions it often grows with *Cakile maritima* Scop., *Carpobrotus edulis*, *Osteospermum fruticosum* (L.) Norl., and other naturalized and native plants dispersed by tides.

Although herbarium specimens show *M. crocea* naturalized at least since 1946, California floras omit it (Munz, 1959, 1968, 1974; Smith, 1976). Most specimens in California herbaria have been misidentified, particularly as *Disphyma crassifolium* (L.) Bol. and *Drosanthemum speciosum* (Haw.) Schwant. Apparently it was from such misidentified specimens that Munz (1959, 1974) reported these two species in southern California. The same plants were included in Shetler and Skog (1978) based on Munz's report and in Kartesz and Kartesz (1980). Although *D. speciosum* is cultivated in California, we have seen no evidence that it is naturalized. Howell et al. (1958) report that *Disphyma crassifolium* occurs in San Francisco. We have seen *Howell 32930* (CAS) from above Point Lobos, San Francisco, and *Walther s.n.* (CAS), which lacks locality data. All other specimens labeled *D. crassifolium* are *M. crocea*.

Other ice plants also have been confused with *M. crocea*. For example, some herbarium sheets of it have been labeled *Carpobrotus*
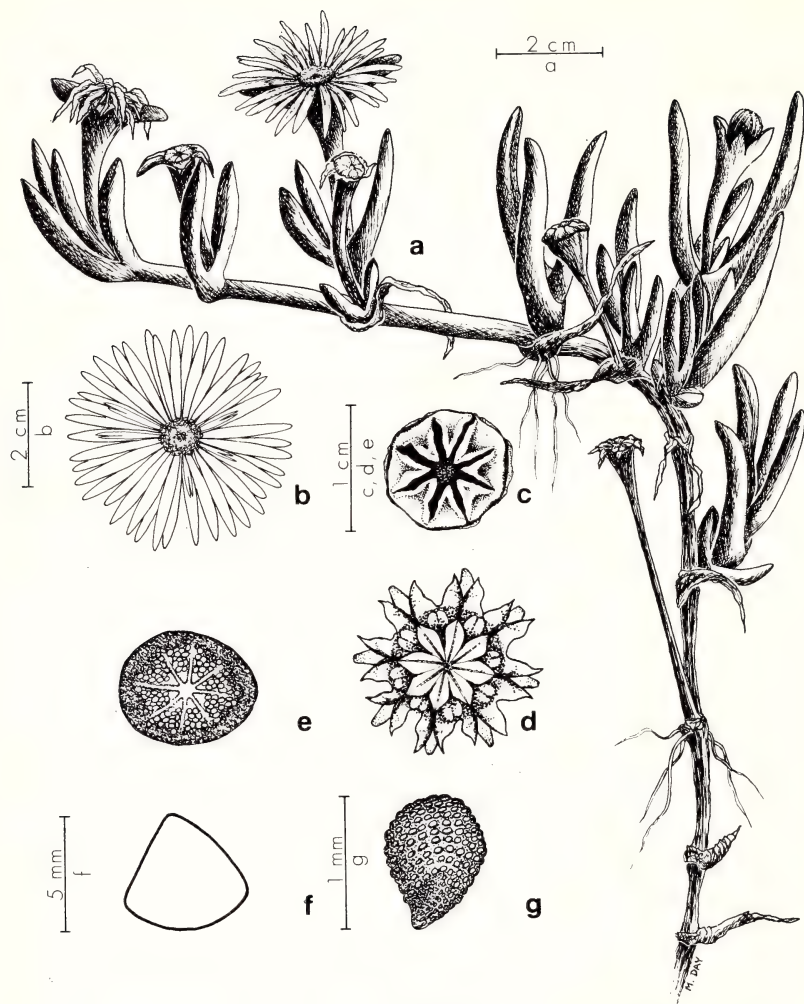
Fig. 1. *Malephora crocea.* a. Habit, showing old and new stem and rooting at nodes. b. Flower, with petals and staminodia. c. Capsule, closed. d. Capsule, open, showing valve wings, seed pockets, and bifid placental tubercles. e. Ovary, cross section. f. Leaf, cross section. g. Seed, showing rows of tubercles.

aequilaterus. This error probably resulted from use of a key to species of *Mesembryanthemum* in Munz (1959) and to genera of the Aizoaceae in Munz (1974). Misidentified specimens of *M. crocea* also occur on a herbarium sheet with a pink form of *Carpobrotus edulis* (a possible hybrid) that is commonly cultivated and naturalized here. *Lampranthus coccineus* (Haw.) N. E. Br. is listed by Munz (1974) as naturalized in coastal environments in southern California. We have not lo-

TABLE 1. CHARACTERISTICS THAT DISTINGUISH *Malephora crocea* FROM FOUR OTHER ICE PLANTS. Species are designated by initials: *C. a.* = *Carpobrotus aequilaterus*; *D. c.* = *Disphyma crassifolium*; *D. s.* = *Drosanthemum speciosum*; *L. c.* = *Lampranthus coccineus*.

		M. c.	*C. a.*	*D. c.*	*D. s.*	*L. c.*
Habit		prostrate, spreading	prostrate, spreading	prostrate, spreading	erect, shrubby	prostrate, spreading
Flower	sepals	4–6, unequal	5, unequal	5, unequal	5–6, unequal	5, equal
	color	orange and/or purple	magenta	pink to magenta	bright orange-red	red
Fruit	type	capsule	berry-like	capsule	capsule	capsule
	locules	8–9 (10)	8–10	5	4–6	5 (4–7)
Seed surface		rough with rows of tubercles	smooth	nearly smooth	rough with ribs and tubercles	rough
Leaf	surface	smooth	smooth	smooth	papillate	smooth
	color	glaucous-blue	green to glaucous-green	dark green	green	green
	cross section	bluntly trigonous	sharply trigonous	bluntly trigonous	terete	narrowly trigonous

cated any naturalized *L. coccineus* nor have we seen any specimens of *M. crocea* bearing that name. However, some specimens of *M. crocea* collected from plants cultivated in California were misidentified as *Lampranthus spectabilis* (Haw.) N. E. Br., a species commonly cultivated but not known to be naturalized in western North America.

Because of the confusion of *Malephora crocea* with other ice plants, we include a description and illustration (Fig. 1), and provide a comparison (Table 1) with other species.

MALEPHORA CROCEA (Jacq.) Schwant., Möller's Deutsch. Gärtn.-Zeitung 43:7. 1928.—*Mesembryanthemum croceum* Jacq., Fragm. Bot. 17. 1800.—*Mesembryanthemum insititum* Willd., Enum. Hort. Berol. 536. 1809.—*Hymenocyclus croceus* (Jacq.) Schwant., Möller's Deutsch. Gärtn.-Zeitung 42:27. 1927.—*Crocanthus croceus* (Jacq.) L. Bol., Fl. Pl. S. Africa 7:255. 1927.

Decumbent or prostrate shrub with pale, corky branches, occasionally rooting at the nodes, forming dense mats to 3 dm high, with stout, gnarled, woody stems in maturity; leaves crowded on short shoots, opposite, connate at base, erect, 2.5–6 cm long, 5–8 mm wide, bluntly trigonous, succulent, smooth, pale bluish-green and glaucous, occasionally reddish; flowers solitary, terminal or axillary, ebracteate, on pedicels 1–6 cm long; calyx 0.8–1.5 cm wide, the lobes 4–6, unequal, at least 2 short, acuminate, with hyaline margins; petals and staminodia usually orange adaxially and purple abaxially; stamens numerous; stigmas 8–9 (–10), plumose; ovaries obcuneiform; placentation parietal; capsule 8–9 (–10) locular, with cell lids, valve wings, adaxial seed pockets with bifid placental tubercles; seeds numerous, lenticular, 1 mm long, 0.8 mm wide, with tubercles arranged in rows (Fig. 1).

Two varieties of *M. crocea* have been designated: var. *crocea* with petals orange adaxially and purple abaxially, and var. *purpureocrocea* (Haw.) Jacobs. and Schwant. with petals purple on both surfaces. Because there is considerable color variation among the populations examined in California, we do not distinguish color forms.

Confusion over the identity of ice plants, as discovered during the investigation of *M. crocea,* suggests that additional taxonomic and nomenclatural problems may exist for other members of the Aizoaceae reported to be naturalized in California. We are continuing to survey the group to contribute to the correct identification of these plants. Because much of the classification of ice plants is based upon fruit characteristics, it would be helpful if collectors prepared herbarium specimens with mature fruits in addition to ample vegetative material, and flowers.

LIST OF SPECIMENS

More than 500 herbarium specimens were examined during this study. Approximately 40 specimens of *M. crocea* have been located

among these and with field observations serve as the basis for this paper. A list of the latter specimens has been distributed to herbaria cited below. Additional copies are available on request from the authors.

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NOTEWORTHY COLLECTIONS

COCHLEARIA OFFICINALIS L. (BRASSICACEAE).—USA, CA, Del Norte Co., Crescent City, 0.1 hectare basaltic sea stack, 1 km offshore from the intersection of Pebble Beach Dr. and Pacific Ave., 20 Jun 1980, *Lester 4829* (HSC). Scattered plants on ne. slope, in crevices of rock in accumulated guano, spread over a 4 × 10-m area. Associated with *Lasthenia minor* subsp. *maritima*.

Previous knowledge. Holarctic, known in Pac. Northw. from AK, B.C., WA, and OR coasts. Alaskan populations are commonly associated with seabird colonies. (Herbaria consulted: CAS, HSC, JEPS and UC (fide Alice Howard), OSC (fide Kenton Chambers), RSA (fide Robert Thorne), and WS (fide Joy Mastrogiuseppe); published sources: Munz, A Calif. fl. 1959; Munz, Suppl. Calif. fl. 1968; Hitchcock et al., Vasc. pls. Pacific Northw. 2. 1964.)

Significance. First record for CA, a 55-km range extension from Cape Sebastian, OR. Locality was breeding ground for Western Gulls, Black Oystercatchers, and Pigeon Guillemots at time of collection. Should be sought on other northcoast offshore rocks that are frequented by seabirds.—GARY S. LESTER, U.S. Fish and Wildlife Service, 791 8th Street, Arcata, CA 95521, MICHAEL C. VASEY, Department of Biology, San Franscisco State University, San Francisco, CA 94132, and WILLIAM E. RODSTROM, P.O. Box 4286, Arcata, CA 95521. (Received and accepted 16 Oct 1980.)

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PEDICULARIS CRENULATA Benth, f. CANDIDA Macbr. (SCROPHULARIACEAE).—USA, CA, Mono Co., Sierra Nevada Aquatic Research Laboratory along n. side of Convict Cr., 1.5 km w. of hwy 395 (T4S R28E S12 se. ¼), 2160 m: 9 Aug 1978, *Howald 952*; 12 Aug 1978, *Orr 337* (UCSB). A small colony (130 plants counted 30 Aug 1980) in moist meadow soil with *Mimulus primuloides, Agoseris glauca, Penstemon oreocharis, Cirsium congdonii* (*C. drummondii*), *Stellaria longipes, Trifolium longipes, Gentiana holopetala, Parnassia palustris* and *Juncus macrandrus*. Plants were mainly in fruit during the 1980 census.

Previous knowledge. Species known from Mono Co. e. to s. WY and CO; the form always rare but scattered throughout range of species. (Herbaria consulted: UC and JEPS kindly checked by Alice Q. Howard, UCSB; published sources: Major and Bamberg, Madroño 17:93–109. 1963); Abrams, Illus. fl. Pac. States. 3. 1951; Munz, A Calif. fl. 1959; MacBride, Contr. Gray Herb. 56:61. 1918; Sprague, Aliso 5:181–209. 1962.)

Significance. Only collections of the sole CA population since 30 Jul 1933 (*Peirson s.n.*, UC). Listed as "presumed extinct" in CA (Smith et al., Inv. rare endang. vasc. pls. Calif. CNPS Spec. Publ. 1, ed. 2. 1980). 400 km w. of the nearest population (Duck Creek, Schell Creek Range, NV). All individuals observed in 1978, 1979, and 1980 had white corollas (f. *candida*), although the typical corolla color is purple. Sprague noted in 1962 (but did not collect) a population of 25–30 white-flowered plants in the same area. The population lies completely within the fenced boundaries of the Sierra Nevada Aquatic Research Laboratory, a unit of the Univ. of Calif. Natural Land and Water Reserves System, and may be the only suitable habitat in the area currently protected from cattle grazing.—ANN M. HOWALD, 419 Ellwood Beach Drive, Apt. 5, Goleta, CA 93117 and BRUCE K. ORR, Department of Biological Sciences, University of California, Santa Barbara 93106. (Received 29 Aug 1980; accepted 3 Sep 1980; final version received 24 Oct 1980.)

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DEDECKERA EUREKENSIS Reveal & Howell (POLYGONACEAE).—USA, CA, Inyo Co., White Mts., 2.4 km ne. of E. Line St., Bishop, between Silver Canyon and Poleta

Canyon (T6S R33E S6 nw.¼ nw.¼), 1460 m, 24 Jun 1980, *Strohm 560* (UC and private collection). Extremely local on a dry gravelly n.-facing slope in Shadscale Scrub. Associated species include *Encelia virginensis* subsp. *actonii, Dalea fremontii, Atriplex confertifolia,* and *Petalonyx nitidus.* Verified by Mary DeDecker.

Previous knowledge. Known from the Last Chance Mts. and the Inyo Mts. of Inyo Co., CA. (M. DeDecker, pers. comm., 1980; Reveal and Howell, Brittonia 28:245–251. 1976).

Significance. First record for the w. side of White-Inyo range and n.-most location, a disjunction of 72 km. Most of the plants were growing on the slope; however, some were found in the wash. Considered "rare and not endangered" (Smith et al., Inv. rare endang. vasc. pls. Calif., CNPS Spec. Publ. 1, ed. 2. 1980).—PATTI J. NOVAK and KATHRYN L. STROHM, Inyo National Forest, Bishop, CA 93514. (Received 18 Aug 1980; accepted 9 Sep 1980.)

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IPOMOEA EGREGIA House (CONVOLVULACEAE).—USA, NM, Grant Co., ca. 11 km nw. of Silver City: T17S R15W center of line between S10 and S11, 2000 m, 6 Sep 1980, *Spellenberg et al. 5864* (NMC). In a wnw.-draining canyon, pinyon-juniper zone, growing on pale, rather barren bedrock outcrop. Very local, ca. 50 plants. Associates included the closely related *I. plummerae (5863),* the rather similar, but annual, *I. costellata,* and the more distantly related *I. hirsutula* among other annuals and hemicryptogams; T17S R15W S11 w-c.¼, 2000+ m, 10 Sep 1980, *Fletcher 4907* (US For. Serv., Albuquerque), 3 plants.

Previous knowledge. Three collections from se. AZ (two in the Huachuca Mts., sw. Cochise Co., the type locality, and one in the Santa Rita Mts., se. Pima Co.), and a fourth from Peru (cited in Macbride, Publ. Field Mus. Nat. Hist. 288. 1931). (Herbaria consulted: ARIZ, ASC, MO, NMC, UNM, Western NM Univ.; published sources: House, Torreya 6:124. 1906; Wooton and Standley, Fl. New Mex. Contr. U.S. Natl. Herb. 19. 1915; Macbride, op. cit.; Kearney and Peebles, Ariz. fl. 1951; Martin and Castetter, Checklist gymnosp. angiosp. New Mex. 1970.

Significance. First record from NM, a ne. range extension of 225 km. Our collection provides further evidence that *I. egregia* is a variant of *I. plummerae,* as first indicated by Macbride, who proposed the former be called *I. plummerae* var. *cuneifolia.* The two taxa are morphologically similar except in leaf form. *I. plummerae,* widespread in AZ, extends to sw. NM and Sonora (Kearney & Peebles, op. cit; McDougal, Seed pls. N. Ariz. 1973), and Peru (Macbride, op. cit.). At all stations known for *I. egregia,* including the disjunct Peruvian site, *I. plummerae* also occurs, but the converse does not hold. *Spellenberg et al. 5863* has six specimens intact with tubers; some of these are *I. plummerae,* others are *I. capillacea* G. Don (*I. muricata* Cav.) as delimited in Kearney and Peebles (op. cit.). *I. capillacea* is said to have elongate tubers, sepals, 5–6 mm long, and the length of the peduncle + pedicel about equal to that of the calyx. *I. plummerae* has globose tubers, sepals 7–9 mm long, and the length of the peduncle + pedicel up to twice the length of the calyx. In *5863* the tubers range from elongate (1.5:1, length:width) to globose (1:1), the sepals range from 6–10 mm in length, and the ratio peduncle + pedicel/calyx ranges from 1:1–1.76:1 (within-plant averages). In addition, in our equally small sample of *I. egregia,* the five tubers ranged from nearly globose to elongate (2.5:1). George Yatskievych, who is working on the *I. egregia-I. plummerae* problem at ARIZ, was most helpful in researching AZ locations for this note and providing comments. Warren L. Wagner assisted us at MO.

STELLARIA NITENS Nutt. (CARYOPHYLLACEAE).—Same location and date as above, *Spellenberg et al. 5869* (NMC, NY). Frequency not recorded, but collection comprises

21 individuals from ca. 0.5 m². Associates included *Drymaria fendleri, D. sperguloides, Bidens leptocephala, Bulbostylis funckii, Euphorbia bilobata,* and *Tagetes micrantha.*

Previous knowledge. B. C. s. to Baja Calif., e. to MT, s. through UT to c. and se. AZ. (Herbaria consulted: ARIZ, ASC, MO, NMC, UNM, Western NM Univ.; published sources; Hitchcock et al., Vasc. pls. Pacific Northw. 2. 1964; Kearney and Peebles, op. cit.; Martin and Castetter, op. cit).

Significance. First record for NM, a ne. range extension of 110 km from the Chiricahua Mts. of AZ. This inconspicuous plant probably occurs elsewhere in NM.—ROB J. SORENG AND RICHARD SPELLENBERG, Biology Department, New Mexico State University, Las Cruces 88003. (Received and accepted 13 Nov 1980; final version received 3 Dec 1980.)

ERIGERON HUMILIS Graham (ASTERACEAE).—USA, ID: Lemhi Co., Lemhi Range, Challis N.F., moist alpine tundra on n. slope Bell Mt., 35° nw. slope on quartzite, 3400 m, 2 Aug 1978, *Henderson et al. 4880* (ID, NY); Custer Co., Lost River Range, Challis N.F., moist alpine tundra on n. slope Leatherman Pass, on limestone, 3300 m, 27 Jul 1979, *Brunsfeld and Brunsfeld 1235* (ID); Butte Co., s. Lost River Range, Challis N.F., moist alpine tundra at head of Elbow Canyon on limestone, 3250 m, 30 Jul 1979, *Brunsfeld and Brunsfeld 1260* (ID). Three additional stations in the Lost River Range have been discovered by the authors, all in habitats similar to those described above. Plants are common in each population but often highly local. *Poa alpina* and *P. rupicola* are common associates on both limestone and quartzite substrates. Populations found on quartzite substrates also are commonly accompanied by *Geum rossii* var. *turbinatum.* Full flower by late Jul. Verified by A. Cronquist (*Henderson et al. 4880*), 1978.

Previous knowledge. Circumpolar but ranging s. in N.A. to s. B.C., n. WY, and nw. MT. (Herbaria consulted: CIC, ID, IDS, MONTU, NY, ORE, OSC, UTC, WS, WTU; published sources: Hitchcock et al., Vasc. pls. Pacific Northw. 5. 1955; Hitchcock and Cronquist, Fl. Pacific Northw. 1973; Dorn, Man. Vasc. pls. Wyo. 1977.)

Significance. First record for ID, an extension s. of 500 km. Although not in jeopardy, it is listed as Rare by the Tech. Comm. on Rare and Endangered Pls., Idaho Natural Areas Council.

HYMENOPAPPUS FILIFOLIUS Hook. var. IDAHOENSIS Turner (ASTERACEAE).—USA, ID: Custer Co., 12 km se. of Challis, Lost River Range, dry canyon bottom, Lime Cr. drainage, on volcanic ash, 2130 m, 18 Jun 1979, *Brunsfeld and Brunsfeld 1010* (ID); Lemhi Co., steep w. slope on e. side Salmon R., 1.6 km ne. of mouth of McKim Cr. on volcanic ash, 1500 m, 14 Jun 1978, *Henderson et al. 4446* (ID); Clark Co., dry, rocky soil near base of Reno Point, s. end Beaverhead Range on limestone, 1760 m, 9 Jul 1975, *Henderson and Jewell 2608* (ID); Custer Co., dry, gravelly sw. slope above road along Challis Cr. at Challis N.F. boundary, 300 m e. of mouth of Pats Cr. on volcanic substrate, 1680 m, 13 Jun 1978, *Henderson et al. 4413* (ID); Butte Co., Lost River Range, open ridge top, Bird Canyon Road 20 km e. of Mackay, on limestone, 2420 m, 1 Aug 1979, *Brunsfeld and Brunsfeld 1301* (ID). Plants in each population generally abundant and associated with *Artemisia tridentata* and often with *Atriplex confertifolia.*

Previous knowledge. This var. known only from the Salmon and Lemhi valleys of Custer and Lemhi cos., ID; a well-marked endemic of e.-c. ID. (Herbaria consulted: ID, IDF, IDS, NY, ORE, OSC, UTC, WS, WTU; published sources: Hitchcock et al., Vasc. pls. Pacific Northw. 5. 1955; Hitchcock and Cronquist, Fl. Pacific Northw. 1973.)

Significance. These collections, 12 additional by the authors, and 16 by Andersen and Davies (ID), have established that this taxon is neither rare nor in jeopardy. Habitats in which the plants are most abundant are severely disturbed by grazing or other

factors. Current land use appears to favor this var. We consider its placement in the Federal Register (1975) as a proposed threatened taxon and similar status offered by Ayensu and Defilipps (Endang. threat pls. U.S. 1978) are unwarrantable.

CAREX RUPESTRIS All. (CYPERACEAE).—USA, ID, Lemhi Co., crest of Lemhi Range, Challis N.F.: dry alpine grassland on quartzite at head of Bruce Canyon, 3000 m, 30 Jun 1977, *Brunsfeld and Brunsfeld 323* (ID, NY); dry rocky limestone outcrop 0.25 km s. of Trail Peak summit, 3200 m, 2 Jul 1977, *Brunsfeld and Brunsfeld 375* (ID). Plants of both populations uncommon with *Poa rupicola, Trisetum spicatum, Carex elynoides,* and *Eritrichium nanum.* Verified by A. Cronquist (*323*), 1978.

Previous knowledge.   Circumboreal but extending s. in USA in Rocky Mts. to the Uinta Mts. of UT. (Herbaria consulted: BOIS, BS, ID, IDF, MONTU, NY, ORE, OSC, WS, WTU; published sources: Hitchcock et al., Vasc. pls. Pacific Northw. 1. 1969; Hitchcock and Cronquist, Fl. Pacific Northw. 1973; Cronquist et al., Interm. fl. 6. 1977; Lackschewitz, Madroño 23:362. 1976.)

Significance.   First records from ID. A w. extension in the USA of ca. 80 km. Although apparently in no jeopardy within ID, it is listed as Rare by the Tech. Comm. on Rare and Endangered Pls., Idaho Natural Areas Council.

ASTRAGALUS AMNIS-AMISSI Barneby (FABACEAE).—USA, ID: Butte Co.: base of limestone cliffs, Middle (Bartell) Canyon, sw. end of Lemhi Range, Challis N.F., 2040 m, 18 Jul 1978, *Henderson et al. 4628* (ID); base of limestone cliffs, East Canyon, sw. end of Lemhi Range, Challis N.F., 1830 m, 5 Jun 1978, *Henderson et al. 4211* (ID); Custer Co.: 6.4 km ne. of Mackay, Lost River Range, base of limestone cliffs, Lower Cedar Cr. Canyon, Challis N.F., 2160 m, 14 Jun 1979, *Brunsfeld and Brunsfeld 956* (ID). Plants uncommon in all locations and nearly confined to stable limestone talus at base of cliffs or ledges and cracks above talus, often in partial shade of *Pseudotsuga menziesii* or *Cercocarpus ledifolius.* Associated closely with *Draba oreibata.* Flowers early to mid-June, fruits Jul. An earlier collection from the type locality (*Henderson 3073,* ID) was verified by C. L. Hitchcock.

Previous knowledge.   Known only from the type locality, Pass Creek Gorge, Custer-Butte Co. line, Lost River Range. Recent examinations of this population by the authors disclose 30–40 readily-observable plants near the base of cliffs, and numerous additional plants on ledges and in cracks of the near-vertical limestone near the upper part of gorge. (Herbaria consulted: BOIS, BS, ID, IDF, MONTU, NY, ORE, OSC, WS, WTU; published sources: Hitchcock et al., Vasc. pls. Pacific Northw. 3. 1961; Hitchcock and Cronquist, Fl. Pacific Northw. 1973.)

Significance.   Until 1978, considered one of Idaho's narrowest endemics. Included on the Federal list as Proposed Endangered (Federal Register, Jun 1976), and is listed as endangered by Ayensu and DeFilipps (op. cit). Collections cited above, 13 additional by the authors, and 3 by Andersen and Davies (all ID), each representing a substantial population in a different canyon in the Lost River and Lemhi ranges, establish the overall abundance of this taxon. There appear to be no immediate or proposed threats to this habitat, and the land managing agencies (USFS and BLM) have no plans for development within these areas. Although reproduction appears to be low, plants of all age classes are present in all populations examined. We believe there is no longer justification for consideration of this taxon as Endangered.

GENTIANA PROPINQUA Richards (GENTIANACEAE).—USA, ID, Custer Co., Lost River Range, Challis N.F., moist alpine meadows: n. slope Leatherman Pass on quartzite, 3120 m, 27 Jul 1979, *Henderson et al. 5448* (ID); lake shore at head of e. Fk. Pahsimeroi River on limestone, 2900 m, 10 Aug 1979, *Brunsfeld and Brunsfeld 1353* (ID, NY). Plants rare in both populations with *Deschampsia caespitosa, Poa alpina, Gentiana tenella, Carex elynoides,* and *Carex subnigricans.* Verified by staff at NY (*Brunsfeld and Brunsfeld 1353*), 1979.

Previous knowledge.   Known from AK e. across Canada to Newfoundland and s.

in Rocky Mts. to Beaverhead Co., MT. (Herbaria consulted: BS, ID, IDF, MONTU, NY, ORE, OSC, WS, WTU; published sources: Hitchcock et al., Vasc. pls. Pac. Northw. 4. 1959; Hitchcock and Cronquist, Fl. Pacific Northw. 1973; Scroggan, Fl. Can. 4. 1978.) Synonym: *Gentianella propinqua* (Richards) Gillett.

Significance. First records for ID, an extension wsw. in USA of 300 km. Listed as Rare for ID by the Tech. Comm. on Rare and Endangered Pls., Idaho Natural Areas Council.

PAPAVER KLUANENSIS D. Löve (PAPAVERACEAE).—USA, ID, Lemhi Co., Lemhi Range, Challis N.F., summit of Bell Mt., 3740 m, Meadow Canyon Res. Nat. Area, 2 Aug 1978, *Henderson et al. 4846* (ID, NY). Extremely rare. Population of 12–15 individuals from the summit to ca. 75 m down the n. and w. faces. No individuals were seen below this elevation or on other aspects. With *Arabis lemmonii* and *Draba lonchocarpa* in full sun among broken quartzite rocks at the summit, and with *Saxifraga debilis* and *Poa rupicola* in partial shade of near-vertical crevices on n. and w. faces. Only a few plants flowering on w. face, those of the summit and n. face still in bud. Verified by B. Ertter (NY), April, 1979.

Previous knowledge. Known from Yukon Terr. s. to NM, mainly along Continental Divide. Apparently restricted to high alpine summits and ridges. Not previously known from ID. (Herbaria consulted: ID, IDS, NY, ORE, OSC, UTC, WS, WTU; published sources: Löve, Brittonia 21:1–10. 1969; Dorn, Man. vasc. pls. Wyo. 1977; listed as *P. radicatum* Rottb. in Rydberg, Fl. Rocky Mts. and adj. plains. 1922; Weber, Rocky Mt. fl. 1976; and Scroggan, Fl. Can. 3. 1978.) *Diagnostic characters.* Fls single, terminal, the petals yellow; fr with brown hairs; pls scapose and densely caespitose, lvs densely hairy; scapes erect at anthesis.

Significance. First record for the Pacific Northwest and for ID, a range extension w. of ca. 480 km. Concentrated floristic studies in this region over the past seven years failed to disclose any other populations. We consider this population to be endangered: although the Bell Mt. site is isolated, there is evidence of considerable foot traffic and the actions of a single, thoughtless individual could eliminate a significant portion of this small population. Listed as endangered for ID by the Tech. Comm. on Rare and Endangered Pls., Idaho Natural Areas Council.

Funding was provided in part by the Challis National Forest and by the C. R. Stillinger Trust, Univ. of Idaho.—DOUGLASS M. HENDERSON, STEVEN BRUNSFELD, AND PAMELA BRUNSFELD, University of Idaho Herbarium, Department of Biological Sciences, University of Idaho, Moscow 83843. (Received 15 May 1980; accepted 7 Jul 1980; final version received 29 Oct 1980.)

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY—GRADUATE STUDENT MEETINGS

The California Botanical Society Graduate Student Meetings will be held at San Francisco State Univ., 24–25 October 1981. The meeting will focus on the presentation of short research papers and reports in progress by graduate students in all botanical and plant related fields. Members and non-members are invited to participate. For further information please contact the Graduate Student Meetings Committee, Dept. of Biology, San Francisco State Univ., San Francisco 94132 or leave a message at (415) 469-1359.

Dr. Harry D. Thiers will present a seminar Saturday evening on his recent work in Australia and the interesting fungal flora of that area.

NOTES AND NEWS

NOTES ON CONES AND VERTEBRATE-MEDIATED SEED DISPERSAL OF *Pinus albicaulis* (PINACEAE).—The literature is unclear as to the events following ripening of *Pinus albicaulis* cones. Sudworth (For. trees Pacific slope. 1908) wrote that cones mature in late August or early September and release their seeds in September or October. "The cones dry out and open slowly . . . ." This information is contradicted by Shaw's classification (The genus *Pinus.* 1914) of *P. albicaulis* in *Cembrae,* a group characterized by inde-hiscent cones. Subsequent authors acknowledged the indehiscence of *P. albicaulis* cones but were confused about dispersal mechansims (e.g., Bowers, Cone-bearing trees Pac. Coast. 1956; Peattie, Nat. hist. w. trees. 1953). Krugman and Jenkinson, who had access to experimental data, suggested that "seeds are dispersed when the detached cone disintegrates" (*In*: Schopmeyer, ed., Seeds woody pls. U.S. 1974). However, informa-tion on cone disintegration and subsequent seed dispersal comes mainly from experi-ments in which cones were protected and does not elucidate the true fate of cones and seeds.

I have gathered cone-fate information from 1973 to 1979 in various locations in Inyo, Mono, Mariposa, and Tuolumne Counties in the eastern Sierra Nevada, California. When *P. albicaulis* cones ripen, the scales separate slightly from the core of the cone (thus, the cones are not completely indehiscent); yet, the scales hold the seeds firmly in place and are not easily dislodged. Cones I collected in 1975 still retain their seeds.

The large, wingless seeds are an attractive food for many birds and rodents. Clark's Nutcracker (*Nucifraga columbiana*) is sympatric with *P. albicaulis* wherever the pine occurs. From midsummer until the cones ripen, nutcrackers forage preferentially on unripe seeds of *P. albicaulis*. Nutcrackers harvest seeds by jabbing their bills repeatedly into the top or sides of cones to loosen and tear off scales. Only rarely do they first detach a cone from a tree before removing seeds. Ripe seeds are taken in quantity and stored in small "caches" consisting of 1 to 15 seeds each (median = 4) in selected "storage slopes" and throughout the forest terrain. I calculated that each nutcracker may store as many as 32,000 *P. albicaulis* seeds each year at subalpine elevations. These seed caches are retrived by nutcrackers in spring and early summer (Tomback, Ph.D. diss., Univ. California, Santa Barbara. 1977a; Tomback, Living Bird 16:123–161. 1977b; Tomback, Condor 82:10–19. 1980). However, many of the seeds are placed in micro-habitats favorable to germination and seedling survival. By mid-October, some seeds have been removed from many *P. albicaulis* cones by Clark's Nutcrackers. These cones are partly or completely hollowed out with little of the cone intact and a shell of closed scales on the underside of the cone (Tomback, 1977a, 1977b, op. cit.).

My studies of Clark's Nutcracker suggest that this bird is an important disperser of *P. albicaulis* seeds. Several kinds of circumstantial evidence, such as seedlings origi-nating in nutcracker seed caches, seedling clusters from caches producing a "multi-trunked" growth form (Clausen, Evolution 19:56–68. 1965; Lüeck, M.A. thesis, Oregon State Univ. 1980), the sites selected by nutcrackers for seed caches, and a consideration of alternative dispersal mechanisms, support the hypothesis that the interaction between the nutcracker and *P. albicaulis* is mutualistic and coevolved. A similar interaction was proposed for the nutcracker and *P. edulis* (Vander Wall and Balda, Ecol. Monogr. 47:89–111. 1977). More direct evidence is required to substantiate both of the proposed interactions.

During late summer and early fall, Douglas squirrels (*Tamiasciurus douglasi*) cut down numbers of *P. albicaulis* cones and bury them in middens. Chipmunks (*Eutamias* spp.) climb into trees and gnaw on the cones to extract seeds. A chipmunk-foraged cone has a distinct appearance: all but the proximal and distal scales are gone, leaving only the core. Chipmunks as well as deer mice (*Peromyscus maniculatus*) are known to cache germinable pine seeds (West, Ecology 49:1009–1011. 1968; Abbott and Quink, Ecology 51:271–278. 1970).

Other mammals and birds take *P. albicaulis* seeds when cones are ripe (Tomback, 1977a, 1977b, op. cit.): e.g., golden-mantled ground squirrel (*Spermophilus lateralis*),

Williamson's Sapsucker (*Sphyrapicus villosus*), White-headed Woodpecker (*Picoides albolarvatus*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), Cassin's Finch (*Carpodacus cassinii*), Red Crossbill (*Loxia curvirostra*), and Pine Grosbeak (*Pinicola enucleator*). With such diverse foraging on *P. albicaulis* cones by vertebrates it is likely that few seed-bearing cones, if any, remain on trees by late fall. Vertebrate foraging has also been observed to "destroy" an entire seed crop of *Pinus lambertiana* (Tevis, J. Wildlife Managem. 17:128–131. 1953) and *P. flexilis* (Clements, Pl. succession. 1916).

To test the hypothesis that most *P. albicaulis* seed dissemination is effected by vertebrates, particularly Clark's Nutcracker, it is necessary to gather information on the condition of old and new cones encountered in the field. Here, I present the results of a preliminary study.

On 9 and 10 August 1979, I surveyed *P. albicaulis* on the east and west slopes of Cathedral Peak, Yosemite National Park, Tuolumne and Mariposa Counties, California. On the east slope I observed the occurrence of old cones in a pure stand between 3050 m and 3250 m (25° slope). For each of the 36 trees along a line transect, I noted the number of old cones visible from my position and tree growth form (following Clausen, 1965, op. cit.). The number of old cones per tree ranged from 0 to 30 [$\bar{x}$ = 4.9 ± 1.5 s.e.]. Proportions of trees encountered in each growth form category are as follows: *erect trunk*: 0.44; *elfinwood*: 0.44; and *intermediate*: 0.11. Fifty percent of the trees had no old cones. One old cone had been nutcracker-foraged, and the remainder were cores, such as those left by chipmunks. A linear regression analysis of number of old cones per tree vs. elevation indicated a significant negative correlation (r = −0.641, p < 0.001), which is probably the consequence of lower cone productivity of the krummholz or "elfinwood" growth form (Tranquillini, Physiol. ecol. alpine timberline. 1979). A One-sample Runs test (Siegel, Nonparametric statistics. 1956) confirmed a significantly greater occurrence of the elfinwood growth form as elevation increased (p = 0.025, one-tailed). On 8 September 1979, I surveyed the east slope of Cathedral Peak for new cones, repeating the same transect. Only 7 trees bore new cones (none of the elfinwood), and all new cones were partly or completely harvested by nutcrackers and chipmunks.

The transect on the steeper (30°) west slope of Cathedral Peak zigzagged over a strip ca. 50 m wide from about 3050 m to 3200 m. Predominantly erect *P. albicaulis* are scattered over the lower regions of the slope, whereas dense elfinwood mats occur in talus above ca. 3200 m. At the very top of the slope where there is some shelter, trees intermediate in growth form occur. For the 44 trees on the transect, I noted the following frequencies of cone occurrence: *no cones*: 0.43; *old cones*: 0.45; *new cones*: 0.39; *old and new cones*: 0.27; *vertebrate-foraged new cones*: 0.23. Thus, by 10 August, vertebrates had opened 59 percent of the new cones. All the old cones observed were either cores or hollow shells.

During September, 1979, I surveyed *P. albicaulis* in other areas to assess the condition of new cones. On 10 September, trees were examined in the vicinity of Budd Lake, Yosemite National Park, Tuolumne Co., California, 3050 m (Table 1). Nutcrackers had foraged 75 percent of the new cones observed. Fifteen trees on each of three different slope aspects were surveyed on 15 September on the west slope of Mammoth Mountain, Mono Co., California (Table 1). Altogether, 78 percent of the new cones were completely or partly destroyed by nutcrackers and chipmunks. (From the data reported, it is apparent that the 1979 *P. albicaulis* cone crop was only fair to moderate in the central Sierra Nevada.)

During 6 to 10 August and 1 to 3 September 1979, I examined 28 old cones found on the forest floor in both the Cathedral Peak and Kearsarge trail-Kearsarge Lakes areas, Mono and Fresno Counties, California. The cones were categorized as follows: *chipmunk cones*—11%, *disintegrating cones* (loose scales)—21% *nutcracker-harvested cones*—21%, *small, closed cones* (ca. 5 cm diameter)—46%. Intact old cones on the ground were rare in all study areas. I pried open the closed cone scales of the small cones encountered and found only white-coated empty seeds. Thus, vertebrate-foraged cones

TABLE 1.   MEAN NUMBER PER TREE AND STANDARD ERROR OF NEW AND VER-
TEBRATE-FORAGED CONES.

Date	Location	Total trees surveyed	New cones per tree	Vertebrate-foraged cones per tree
10 Sep 1979	Budd Lake	10	2.1 ± 0.46	1.6 ± 0.54
15 Sep 1979	Mammoth Mt.	45	2.0 ± 0.47	1.6 ± 0.41

accounted for 32 percent of the cones sampled, and sterile cones accounted for 46 percent.

These data suggest that few if any seeds of *P. albicaulis* remain after vertebrates cease foraging in late fall. It is possible that any remaining cones with a full or partial complement of viable seeds disintegrate and/or abscise soon after this time. Abscission may, in part, be a weight-dependent process, which would explain why only the lighter, vertebrate-harvested old cones remain on the trees. Also, some cones seem more resistant to disintegration, such as those hollowed out by nutcrackers and small, sterile cones.

If so few cones escape vertebrates each year, is cone disintegration the primary seed dispersal mechanism for *P. albicaulis*? Seed-storing vertebrates, particularly Clark's Nutcracker, appear mainly responsible for *P. albicaulis* population recruitment. Not only do nutcrackers and some rodents place a large percent of seeds in sites favorable to germination and seedling survival, nutcrackers transport seeds to storage sites some distance from parent trees (Tomback, 1977a, 1977b, op. cit.). Consequently, nutcracker seed dispersal helps maintain the "pioneering" status of *P. albicaulis*. Seeds released by cone disintegration have lower reproductive value than those stored by nutcrackers and rodents. Because the seeds are large and wingless, many will drop near the parent tree. Thus concentrated, they may be consumed in quantity by seed predators and, because *P. albicaulis* is shade intolerant (Baker, Principles silviculture. 1950), they are less likely to end up in conditions favoring seedling survival. In addition, "pioneering" may be an important reproductive tactic of the species.

Why are *P. albicaulis* cones, as well as cones of other species in Subsection *Cembrae* (classification of Little and Critchfield, Subdiv. genus *Pinus*, U.S.D.A. Misc. Publ. 1144. 1969) indehiscent? All *Cembrae* species are sympatric with one or more subspecies of the Eurasian Nutcracker (*N. caryocatactes*) (Dement'ev, Birds Soviet Union. 5. 1970) or with Clark's Nutcracker. In a nutcracker or rodent dispersal system, natural selection should optimize the number of seeds available to dispersal agents. "Packaged" seeds should attract birds and rodents, increase their foraging efficiency, and thereby maximize the number of seeds stored in favorable sites. Consequently, indehiscent cones should maximize the reproductive success of any pine with vertebrate-dispersed rather than wind-dispersed seeds.

It is interesting to note that the seeds of *Pinus sabiniana* and *P. torreyana* (Subsection *Sabinianae*, Little and Critchfield, 1969, op. cit.) are large and bear non-functional wings, although the cones are dehiscent. The seeds are released over a period of several months (Krugman and Jenkinson, 1974, op. cit.). These pines may be evolving vertebrate seed dispersal. Either they do not have the genetic potential for indehiscent cones, or the seeds may be dispersed by a facultative tactic: seed-storing vertebrates—such as *Peromyscus* (McCabe and Blanchard, Three species *Peromyscus*. 1950) and Scrub Jays (*Aphelocoma coerulescens*), which cannot take seeds from the massive, closed cones—and seed fall. This also applies to *P. flexilis* (Subsection *Strobi*, Little and Critchfield, 1969, op. cit.), which has dehiscent cones. Nutcrackers and rodents, as well as seed fall, may disperse the large, wingless seeds of this species (Vander Wall and Balda, 1977, op. cit.; Tomback, Condor 82, in press. 1980).

AGGREGATION OF *Prunus ilicifolia* (ROSACEAE) DURING DISPERSAL AND ITS EFFECT ON SURVIVAL AND GROWTH.—Dispersing seeds are commonly aggregated at settlement, by vertebrates voiding cohorts of ingested seeds or storing seeds in caches, or by ants collecting and discarding seeds with elaiosomes. Aggregation may have significant consequences for seed and seedling survival and growth. For buried seed, aggregation may increase successful emergence (Linhart, J. Ecol. 64:375–380. 1976.). Seed predation may increase with cohort size (Wilson and Janzen, Ecology 53:954–959. 1972.) or decrease as aggregation lowers seed density over most of the dispersal region. Likewise, later herbivory might be increased or decreased. However, competition among aggregated seedlings surely must be greater than among widely scattered plants. None of these effects has been widely studied, perhaps for technical reasons or for lack of data on post-dispersal seed distributions.

In the California chaparral, seeds of *Prunus ilicifolia* are commonly dispersed by *Canis latrans*, with defecated and vomited cohorts containing 4–66 seeds (mean 23.5 ± 2.4 s.e., n = 34) in the central Santa Monica Mountains (1975, 1977, 1978), and 3–6 seeds at Chalone Peak, San Benito County (n = 4, 1974). This compares with seed cohorts of *Washingtonia filifera* dispersed by *Canis latrans* in eastern San Diego County, of 1–275 seeds (48.7 ± 3.1, n = 252: Bullock, Principles 24:29–32. 1980.). The endocarp/seed units of *Prunus* weighed 1.46 ± .04 g (n = 143), and *Washingtonia* seeds weighed 0.10 g (n = 50).

Experiments were conducted to observe survival and growth of *Prunus ilicifolia*, particularly with reference to aggregation of the seeds. Seeds were collected in the Santa Monica Mountains, and grown at the University of California, Los Angeles, in silty loam 25 cm deep resting on the natural substrate. The plants had only partial morning shade, and were watered only by rain. From December 1973 to November 1974, plants were grown in 1 × 2-m plots with 50 seeds each in four unreplicated conditions of interseed spacing: 20 cm, 10 cm, 5 cm, and 0 cm. Also in this year, cohorts (0 cm seed

TABLE 1. SURVIVAL FROM SEED TO FIRST-YEAR SEEDLING AND MEAN ABOVEGROUND DRY WEIGHT OF SURVIVORS (± s.e).

Aggregation	n	Survival	Biomass (g)
Seed spacing (cm)			
0	50 seeds	0.74	2.9 ± 0.5
5	50	0.64	6.1 ± 1.2
10	50	0.20	6.2 ± 1.5
20	50	0.22	1.4 ± 0.3
Seeds per cohort			
4	7 cohorts	0.79	14.9 ± 2.9
2	7	0.50	12.1 ± 2.3

FIG. 1.   Graft between roots of two three-year-old plants of *Prunus ilicifolia*.

spacing) of 2 and of 4 seeds were grown (7 replicates each), spaced at 50 cm. From November 1974 to November 1977, plants were grown from cohorts of 1, 2, 3, 4, 5, 6, 8, 10 and 12 seeds (at least 9 replicates each), the cohorts spaced at 50 cm.

Both experiments of 1973–1974 showed greatest seedling survival in the most aggregated conditions (Table 1). This may be attributable to decreased desiccation during the summer, due to mutual shading. The mean above-ground biomass of survivors was greatest at intermediate densities in the uniform-spacing plots, but was much greater in the cohorts than in the spaced seedlings (Table 1). Apparently the full survival value of aggregation in these conditions was attained by only 4 seeds and massive aggregation reduced growth but not early survival.

From the 1974 planting, a harvest in November 1977 showed 89 percent survival from seed in cohorts of 1–8 seeds (n = 104 seeds, 32 cohorts), and 88 percent survival in cohorts of 10 and 12 seeds (n = 96 seeds, 9 cohorts). Biomass studies were not feasible but root diameters were measured on a subsample. Comparing cohorts of initial seed numbers of 1, 2–6, and 10 or 12, the total root cross-sectional areas were not significantly different between small, medium and large cohorts. However, the means for individual plants showed a sharp decrease across the three groups (F'_s = 12.34, p < 0.01), and more variability among isolated plants.

Grafting was commonly observed among individuals of a cohort (Fig. 1). Grafting was present in 12 of 30 cohorts with more than one survivor, and joined up to five plants. Grafting was most common near the surface and was distinct from the development of burls with multiple stems.

An interesting consequence of the high survival of cohort seedlings is that any physiognomic shrub may contain several genets, which may have had different female parents. The colonial shrub itself may be a small breeding neighborhood, and present some variety in all aspects of its ecological behavior. Furthermore, some direct physiological interaction among the genets may be possible due to grafting. The fate of individual plants in dispersal cohorts merits wider and closer attention.—STEPHEN H. BULLOCK, Botany Department, San Diego State University, San Diego, CA 92182. (Received and accepted 16 Oct 1980.)

ADVENTITIOUS ROOTING IN COASTAL SAGE SCRUB DOMINANTS.—Adventitious rooting was discovered in *Artemisia californica* Less., *Eriogonum fasciculatum* Benth., *Salvia mellifera* Greene., and *Salvia apiana* Jeps. (voucher specimens in MACF) while collecting plant specimens for a flora of Starr Ranch, a 1600-ha Audubon Sanctuary 11 km east of San Juan Capistrano, Orange Co., CA. There is little information on the occurrence and degree of vegetative spread in common native species (Davis and Heywood, Prin. Angio. Tax. 1973). T. L. Hanes (pers. comm., 1976) indicated that adventitious rooting had not previously been reported in these species of the southern California coastal sage scrub.

A study of these species was initiated from February to October 1976, and during September 1980 to determine a) frequency of occurrence of adventitious rooting; b) environmental factors necessary for root initiation; and c) possible functions of adventitious rooting.

Observations were made by examining a minimum of 50 shrubs of each species in a variety of habitats at Starr Ranch (in the coastal foothills near the southern limit of the Santa Ana Mts.) and along Black Star Road (at the northern end of the Santa Ana Mts.). The dominant species were scored for the presence or absence of adventitious roots.

The results for three habitats are given in Table 1.

Of the four dominants, the highest average occurrence of adventitious rooting across all habitats was *E. fasciculatum* ($\bar{x} = 81$ percent), followed by *S. mellifera* ($\bar{x} = 42$ percent), *S. apiana* ($\bar{x} = 41$ percent), and *A. californica* ($\bar{x} = 10$ percent).

Both *E. fasciculatum* and *S. mellifera* produce many decumbent and vertical stems. Decumbent stems, which form the majority of adventitious roots, arise near the base of a plant and spread horizontally along the ground. Decumbent stems are often inconspicuous when covered with soil and leaf litter. Numerous vertical shoots develop along them; when the shoots are small, they may resemble seedlings.

Eriogonum fasciculatum develops numerous adventitious roots even in the most unfavorable habitats (e.g., on slopes of 80 percent gradient; on dry, south-facing slopes; and on rocky outcrops). Ten percent of the shrubs of this species sampled on level ground showed evidence of an outward circular growth pattern emanating from a single (usually dead) shrub, similar to the "clonal ring" growth of *Larrea tridentata* described by Vasek et al. (Madroño 23:1–13. 1975).

The growth habit of *S. apiana* and *A. californica* differs from *E. fasciculatum* and *S. mellifera* in that the first two species have many erect branches and few decumbent stems. Adventitious roots develop in *S. apiana* and *A. californica* mainly where the basal portions of their vertical stems are covered with soil from erosion or silt deposits. In habitats where soils are packed, there was no evidence of adventitious rooting regardless of slope aspect or amount of shade. Edaphic conditions appear to be an important factor in the formation of adventitious roots in these species.

The environmental factors necessary for the development of adventitious roots appear to be the same as those required in horticultural applications for root development in

TABLE 1. PERCENTAGES OF INDIVIDUALS OF COASTAL SAGE SCRUB DOMINANTS WITH ADVENTITIOUS ROOTS, ARRAYED BY HABITAT. N = total number of individuals sampled in all habitats.

| Species | N | Habitats | | | |
		Slopes	Level	Riparian	Mean
Eriogonum fasciculatum	59	78	75	100	81
Salvia mellifera	72	30	20	75	42
Salvia apiana	51	40	19	80	41
Artemisia californica	98	14	8	0	10

layering, i.e., presence of humus and moisture in close contact with the stem, and elimination of light.

Adventitious rooting may serve several functions, including increasing root surface area. The rate and extent to which roots occupy soil volume is known to be critical to the survival of perennial species. In addition, avoidance of competition by stratification of root systems has been reported in a number of species and habitats (Etherington, Envir. pl. ecol. 1975). Thus, development of adventitious roots may be a means to increase water or nutrient absorption capacity. *Eriogonum fasciculatum* and *S. mellifera* should be investigated further in this regard because their growth habits suggest that their adventitious roots function to enlarge the volume from which soil resources can be absorbed.

Adventitious roots may also help to establish progeny asexually by vegetative reproduction. The growth habits of *E. fasciculatum* and *S. mellifera* suggest such asexual spread, which may be advantageous in harsh environments where seedling establishment is unlikely. However, the coastal sage dominants are all prolific seeders (Hanes, Ecol. Monogr. 41:27–52. 1971) and many seedlings are found in the wild. Additional study is needed to determine the extent of adventitious rooting and its contribution to vegetative reproduction in coastal sage dominants. Once seedlings are established, vegetative growth may give plants a competitive advantage.

Adventitious roots may also provide greater stability for a perennial shrub in a continually or periodically eroding environment. Formation of adventitious roots may be an adaptive response to edaphic conditions that enables the dominants to become reestablished when buried by erosion, as in areas of creep or flood. The geography of much of the coastal sage scrub community is characterized by steep terrain and rocky, sandy soils that are extremely unstable (Hanes, op. cit.). Many shrubs of the dominant species are buried under soil from slides or erosion, and adventitious roots form along the buried portions of their stems. Because many species of plants cannot survive suffocation if their roots are covered too deeply with soil or water (Daubenmire, Pls. Envir. 1974), the capacity to continue growth when buried by soil appears to be the most important function of adventitious rooting in the coastal sage dominants. I thank Drs. T. L. Hanes, C. E. Jones, S. Carlquist, and F. Lang for their comments on the manuscript.—R. JOHN LITTLE, Rancho Santa Ana Botanic Garden, Claremont, CA 91711. (Received 22 Feb 1980; revision received and accepted 16 Oct 1980.)

REVIEWS

Inventory of Rare and Endangered Vascular Plants of California. By JAMES PAYNE SMITH, JR., R. JANE COLE, and JOHN O. SAWYER, JR. in collaboration with W. ROBERT POWELL. viii + 115 p. California Native Plant Society Special Publication 1, Berkeley. ed. 2, 1980. $7.50. Available from CNPS, 2380 Ellsworth, Suite D, Berkeley, CA 94704.

In response to an idea from the fertile mind of its then president, G. Ledyard Stebbins, the California Native Plant Society in 1968 launched its Rare Plant Project to develop information about the rare plants of the state. At the time, intellectual curiosity rather than legal need was the main motivation. That plants had been added to the Endangered Species Act in 1973 came as a surprise to the Society some time after the fact. But by then several versions of a preliminary list had already been developed and circulated to the state's botanical community for comment, initially by Roman Gankin, and, starting in 1971, by W. Robert Powell, who contributed the enormously useful concept of the R-E-V-D coding. While federal efforts were still in developmental stages, the Society in late 1974 published the predecessor of the present edition and it immediately found wide applicability for federal agencies under the National Environmental

Policy Act of 1969 and for various California planning agencies, both local and state-wide, especially in relation to the California Environmental Quality Act of 1970.

New responsibilities of federal land-managing agencies arising from the 1973 federal act made inevitable a surge of field work on rare plants that began to produce much new information. Realizing this, as well as the existence of gaps in information contained in the 1974 inventory, CNPS's new Rare Plant Committee under my chairmanship and working closely with Powell launched revisionary efforts in mid-1976. With the aid of many volunteers, we were able simultaneously to expand the information base by thorough combing of the literature in the course of preparing status reports on 247 rare plants for the U.S. Forest Service in 1977 to 1978, and to net a profit of well over ten thousand dollars from that work. This financed adding voucher information from seven additional California herbaria and reviewing these herbaria and those gleaned for the 1974 edition for information about 187 taxa that were either last-minute additions without data to the 1974 inventory or were later proposed for addition. A further 174 status reports prepared for the State Department of Fish and Game in 1979 under the direction of James P. Smith, Jr., who succeeded me as Rare Plant Committee chairman in February 1979, contributed to the wealth of new information.

The revision resulting from all this activity is most welcome and is indispensable, as was its predecessor, to those with responsibilities toward rare plants. But the 1980 version is marred by numerous inconsistencies and errors, typographical and otherwise. Some, such as misspellings, are easily noticed. Others—ones in taxon codes and numbers signifying rarity, endangerment, vigor, distribution, and county and quadrangle of known occurrence—are not so easily detected. Users should be forewarned and should take advantage of the Society's intent to issue lists of addenda (see Preface).

Arrangement has been changed from the earlier version. Taxa presumed extinct are segregated into List 1, containing 44 plants. Those deemed rare throughout their ranges, whether or not endemic to California, make up the 645 plants of List 2. Taxa considered rare but not endangered throughout their ranges are in List 3 and number 447. The 236 plants of List 4 are taxa rare in California but common elsewhere. The old "main list" of edition 1 thus includes taxa now found in Lists 1, 2, and 4.

I would have preferred the federal way of flagging possibly extinct plants—an asterisk signifying that information is especially desired about them—to listing them separately. Few such plants have been thoroughly searched for and, with good fortune, the situation is likely to change. At least five of the taxa in List 1 were recovered during 1980 field work; one more was recovered in 1978 but not then reported. The heading for this list is misleading in that taxa restricted to California are lumped with taxa found outside the state and not necessarily extinct there. Seven of the 44 are considered widespread outside California.

Primary applicability of the inventory is to the existing legal framework, but discussion of this is lacking. For this reason, inclusion of the purported legal status of various taxa under federal and the new state law (Native Plant Protection Act of 1977, passed at the instigation of CNPS) is especially troublesome. With plants actively under review by both entities, such information can be of only transitory accuracy. Judging from the many queries I receive because of my activity in this area, legal status, or especially lack of it, is information all too likely to be misunderstood and misused by unknowing or unscrupulous persons in attempts to make erroneous points. Lack of legal status seldom indicates a biological judgment; rather it is likely to reflect continuing manpower and political problems.

It is important to know that actual listing is not necessary under either state or federal law to bring to bear certain protective courses of action [see fuller discussions of requirements under state law and of the federal rare plant program in Howard, Fremontia 7(3):18. 1979, and 8(3):14–16. 1980, respectively]. For all the foregoing reasons I should have preferred no mention of legal status, thereby making more likely that inquirers would seek up-to-date information from sources also able to clarify any mistaken ideas.

Ratings assigned by the Smithsonian Institution are included but have no legal significance. Smithsonian and State ratings are broken down dichotomously ("endangered"

and "threatened," and "endangered" and "rare," respectively) but federal ratings (also "endangered" and "threatened") are lumped into merely "listed."

Original plans for the revision were supposed to have included listings of rare taxa by county and by quadrangle of known occurrence. Neither is present. Especially the latter would make many inquiries unnecessary and would be easily producible if the information is still computerized as was the case with the earlier inventory. Perhaps it can be issued with other addenda.

The index is a useful addition. A method of footnoting the plants listed in Appendix 1 so as to distinguish among the various categories lumped therein would have been helpful.—ALICE Q. HOWARD, University Herbarium, Department of Botany, University of California, Berkeley 94720.

A Taxonomic Study of the Ranunculus hispidus *Michaux Complex in the Western Hemisphere.* By THOMAS DUNCAN. Univ. California Publ. Bot. 77:1–125, 70 Figs. Univ. California Press, Berkeley. 1980. ISBN 0-520-09617-7. $7.00.

Past classifications of this widespread group have been plagued by similarities and overlaps of leaf-shapes previously used as primary criteria for identification. As in most other buttercups, not only does leaf-shape in this group vary widely among individuals of the same species but even among leaves on the same plant. Duncan has sought a new classification, widening the range of characters used and applying new statistical techniques aimed at giving a more strictly objective basis for subdividing the complex.

After a brief outline of data-gathering methods, the monograph provides a full discussion of each of the characters to be used, some for the first time. A lucid account ensues of three different computer-assisted approaches that were tried out—cluster analysis, sum-of-fractions analysis, and principal-components analysis. A logical step-by-step procedure shows how a particular "similarity value" was selected to satisfy best Duncan's chosen species distinction (discontinuity in at least three characters). The classification that emerges from application of the first two computer-assisted approaches was tested out to Duncan's satisfaction on many thousands of herbarium specimens. Its superior discriminatory value over more traditional treatments by Benson and by Lourteig appears to be quite clear. The third computer-assisted approach, principal-components analysis, was found in this study to be much less useful than the first two. As to plant characteristics, neither leaf-shape measurements nor leaf-flavonoid compounds turned out to be useful in classifying this group, and even chromosome numbers, falling into only two classes ($2n = 32$ or 64), were found irrelevant taxonomically.

A large section of the monograph is devoted to a standard descriptive revision. Each of the 20 taxa in this new treatment is also illustrated and mapped and provided with an extensive commentary that clarifies many otherwise unanswered questions. The diagnostic key attempts to avoid developmentally- and genetically-labile leaf characters, which tended to weaken previous classifications. Receptacle shape, stolons, and rhizomes are among new features helping discriminate taxa. An extensive appendix of background data contains 20 pages of illustrations of leaf-shape variations in each species, fully vindicating the author's rejection of them as usable taxonomic features.

Although up-to-the-minute numerical methods of data analysis have been used in this revision, its underlying assumptions seem to this reviewer to be curiously old-fashioned. It provides a vital preliminary step to a much more biosystematically comprehensive operation yet to be carried out. Conspicuously missing are the experimental data that for half a century have been recognized as inescapable components of contemporary systematic investigations in both plants and animals. Where are the breeding tests, transplant experiments, mass geographic samplings, and cytogenetic data crucial to evaluation of stages in the evolutionary process?

But even without these other kinds of evidence, Duncan's monograph, as a study using new methods of objective phenetic analysis, is an impressive foundation stone for

more complete studies in the future. Can we dare hope that such efforts, and the funding such extensive studies require, will be sustained for building upon such excellent morphological preliminaries as this?—FULTON FISHER, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada VSA 1S6

Flora Americae Septentrionalis. By FREDERICK PURSH. xxiv + 751 p., illus. 1814 [Dec 1813]. Reprint, 1979, introduced (117 p.) and edited by JOSEPH EWAN. J. Cramer, Vaduz, Liechtenstein. Available from Lubrecht and Cramer, RFD 1, Box 227, Monticello, NY 12701. ISBN 3-7682-1242-4. $60.00.

In his pithy introduction, Ewan provides synopses of the place of Pursh's *Flora* in botanical history, Pursh's collecting activities, other collectors and specimen sources, conditions of publication of the *Flora,* and initial response of the botanical community. In addition, there is a brief chronology of Pursh's life, a gazetteer of localities, and a very welcome annotated list of the 500 to 600 species and varieties that were first published in the *Flora.*

The inventory is alphabetical by genus, then by species, and the annotations provide (so far as known): page in the *Flora,* whereabouts of type or "authentic" specimens, commentary (including references to pertinent publications), and accepted name (if original is generally relegated to synonymy). This invaluable list seems to be as comprehensive as is practicable and represents nearly 30 years of gleanings from American and European libraries and herbaria.

The *Flora* itself treats some 3076 species (fide Ewan). It was the "first account of North American plants to include the Pacific Northwest." Among the "novelties" were plants then known only from the Lewis and Clark collections, including original accounts of *Lewisia rediviva* and *Clarkia pulchella.*—JOHN L. STROTHER, University Herbarium, Department of Botany, University of California, Berkeley 94720.

TRANSITION

FRANK WALTON GOULD

Frank Walton Gould, Distinguished Professor Emeritus of Grass Systematics and former curator of the S. M. Tracy Herbarium at Texas A&M University died on 11 March 1981 in Austin, Texas.

Gould was born in Mayville, North Dakota on 25 July 1913. He earned his bachelor's degree from Northern Illinois University, a master's degree from the University of Wisconsin, and Ph.D. degree in botany from the University of California. He taught biology at Dixie Junior College, St. George, Utah from 1941–1942, and at Compton Junior College, Compton, California from 1942–1944. He then worked as a botanist at the University of Arizona from 1944–1949.

In 1949 Gould moved into a taxonomic position at Texas A&M University. He served as curator of the S. M. Tracy Herbarium until August 1979, when he retired. During his tenure, he built the herbarium into one of the most respected such facilities in the United States. Gould was a world renowned grass systematist and had completed teaching and research assignments in Mexico, Costa Rica, the Dominican Republic, Brazil, Puerto Rico, Sri Lanka, and England. His research projects with leading herbaria resulted in more than 80 definitive treatments of grasses that are recognized world wide.

Frank W. Gould authored the books *Grasses of the Southwestern United States* in 1959, *Grasses of the Texas Coastal Bend* in 1965, *Grass Systematics* in 1968, *The Grasses of Texas* in 1975, and *Common Texas Grasses* in 1978. He also had completed a book on the *Grasses of Baja California* that will be published next year. At the time of his death he was writing a book on the grasses of Mexico.—STEPHAN L. HATCH, Curator of the Tracy Herbarium, Texas A&M University, College Station 77843.

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Contents, continued

CALIFORNIA BOTANICAL SOCIETY

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Contents

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

POLLINATION BIOLOGY OF CALYPSO BULBOSA VAR. OCCIDENTALIS (ORCHIDACEAE): A FOOD-DECEPTION SYSTEM

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ABSTRACT

Calypso bulbosa var. *occidentalis* is a western North American terrestrial orchid. In the northern California populations studied, these plants are allogamous and pollinated by *Bombus* queens and *Psithyrus* females. Bee visitation, however, is infrequent. *Calypso bulbosa* var. *occidentalis* is a generalized food-flower mimic and must rely on exploratory visits of naive bees for pollination. Abrupt rises in the number of flowers pollinated corresponds with sudden increases in available pollinators. Fruit is set low (11–34 percent), and is comparable to that mentioned in reports of other temperate food-deceptive orchids.

A large number of orchids provide no reward to their pollinators. Their visual, olfactory, and sometimes tactile cues are deceitful. Perhaps the most striking examples are the pseudocopulatory orchids, *Ophrys, Trichoceros,* and a variety of Australian species (Kullenberg and Bergstrom, 1976; Pijl and Dodson, 1966; Stoutamire, 1975). The majority of non-rewarding orchids, however, are pollinated by visitors apparently searching for food. Very few such systems have been studied in detail. Recently, much attention has been focused on *Calypso bulbosa* (L.) Oakes, a strikingly beautiful circumboreal orchid, represented by var. *bulbosa* in Eurasia, var. *japonica* Makino in Japan, var. *americana* (R. Br.) Luer in North America from the Rocky Mountains eastward, and var. *occidentalis* (Holz.) Luer in the Pacific Northwest (Luer, 1975). Mosquin (1970) and Stoutamire (1971) found that *C. bulbosa* var. *americana* is nectarless and hypothesized that pollinators are attracted to the flower because of its conspicuous coloration. Furthermore, the flowers appear to rely on newly emerged naive bumblebees to effect pollination.

Two unpublished theses treat some features of the pollination of *C. bulbosa* var. *occidentalis*. Kipping (1971) states that the flowers have nectaries, whereas Krell (1977) and my simultaneous observations indicate that the flowers are nectarless. These conflicting reports did not clarify whether *C. bulbosa* var. *occidentalis* has a fundamentally different pollination ecology from its eastern counterpart. The objective of this study is to elucidate its pollination biology.
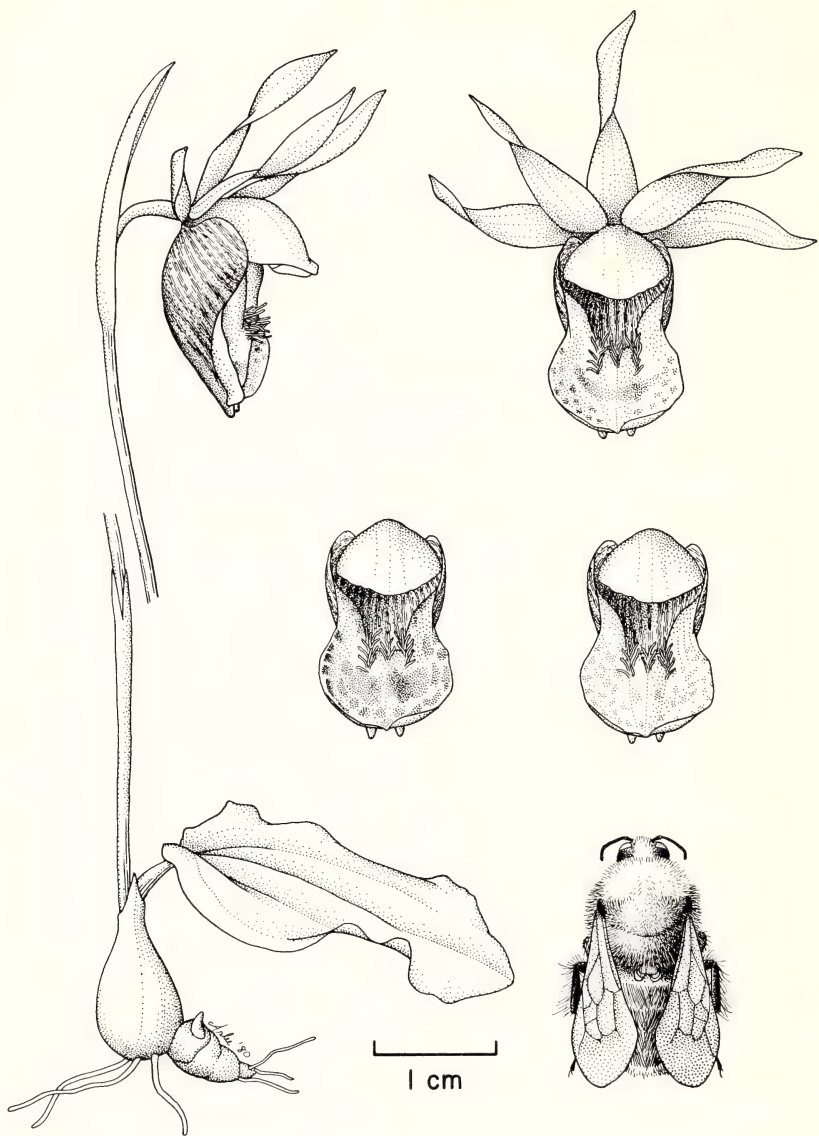
Fig. 1. *Calypso bulbosa* var. *occidentalis* and pollinator. Variation in labellum spot patterns is shown. The *Bombus caliginosus* queen has a pollinarium attached to its scutellum.

TABLE 1.   PERCENT FRUIT SET OF SIX POPULATIONS OF *Calypso bulbosa* VAR. *occidentalis*. All localities are in Humboldt County, California. The number of visited flowers is the number of pollinated flowers plus the number of flowers with pollinaria removed but not pollinated. In 1978, all flowers at the first two sites listed were fortified with 15–45 μl of 10 percent sucrose solution (wt/wt).

Locality	Year	Total number of flowers	Number of flowers visited	Number of pollinated flowers	Percent fruit set
Lanphere-Christensen Dunes	1976	1273	671	141	11
Nature Conservancy, 8 km w. of Arcata: dune forest.	1978	1161	398	82	7
Lord Ellis Summit, Hwy 299: mixed evergreen forest.	1978	57	2	0	0
Korbel, Camp Bauer at entrance: redwood forest.	1978	114	—	34	30
Kneeland, Freshwater Rd., 0.5 km w. of jct. of Greenwood Hgts. Rd.: redwood forest.	1978	349	—	56	16
Kneeland, Maple Cr. Rd., 2 km n. of Freshwater Rd.: mixed evergreen forest.	1978	137	—	47	34
Redwood Valley, Chezem Rd., 1 km e. of hwy 299: mixed evergreen forest.	1978	86	—	28	33

FLOWER MORPHOLOGY AND METHODS

Calypso bulbosa var. *occidentalis* grows in the thick litter of coniferous forests. The plants are perennial and in the fall produce a single ovate leaf from an underground corm. The plants remain in this condition over winter. In early spring a single-flowered inflorescence emerges (Fig. 1). The sole nodding flower has rose-pink sepals and petals. The lamina of the lip is white with reddish-brown spots and is adorned with several rows of hairs. The saccate portion of the lip has numerous dark, reddish-brown stripes. The very broad, slightly arched column is also rose-pink and forms a hood over the lip. During the summer the plants become dormant: the leaf withers, the fruits dehisce, and the many thousands of seeds are dispersed.

Six *C. bulbosa* var. *occidentalis* populations in Humboldt County, California were studied (Table 1). The Lanphere-Christensen Dunes Nature Conservancy population was observed during the spring seasons of 1976 and 1978. The other populations were studied in 1978 only.

At the Lanphere Dunes, I tested *Calypso* for self-compatibility and autogamy. I covered ten plants with insect-exclusion cages and as

these plants flowered, I self-pollinated them. Thirteen other plants were caged and left untouched. Percent seed set was estimated for all capsules developed in these experiments, and also for capsules of ten naturally pollinated flowers collected from the same population. The contents of each capsule were spread on a slide and nine fields were viewed at 40×. I considered a seed viable if it contained a well-developed embryo.

The flowering and fruiting phenologies of the Lanphere Dunes population were assessed in 1976 and 1978. The parameters recorded were the number of unvisited flowers, flowers with pollinia removed, flowers pollinated, withered flowers, and fully developed capsules. For the other populations, I recorded the total number of flowers and pollinations.

During the 1978 season, I added 15–45 μl of 10 percent sucrose solution (wt/wt) to all flowers of two populations, Lanphere Dunes and Lord Ellis Summit (Table 1). The artificial nectar was injected into the spurs with a syringe without damage to the flowers. At least once a week flowers were fortified. All those appearing flaccid due to apparent effects of the sugar solution were removed so that only fresh flowers were present. These manipulations were designed to test the effect of food reward on foraging patterns and visitation frequencies.

At approximately one-week intervals I observed the Lanphere Dunes population for pollinator activity. Bumblebees were captured and examined for pollinaria. Bees that carry orchid pollinaria are considered legitimate pollinators (Dressler, 1976). For the 1976 season, the number of bees seen per hour along a regular transect route, regardless of their activity, was recorded as a measure of bee abundance. These observations lasted 1–4 hours when the bees were most active (mostly 0900–1700 PST).

RESULTS

In these northern California sites, *Calypso* is one of the first-blooming spring flowers. The flowering season generally occurs from March to June in Humboldt County, California (Fig. 2).

Vegetative propagation is not prevalent at any of the *Calypso* populations in northern California with which I am familiar. Plants growing in close proximity were examined for rhizomatous connections. Rarely were these connections found and not one incidence was detected in the exceptionally large population of 2000–3000 plants (including many seedlings) at the Lanphere Dunes.

Calypso bulbosa var. *occidentalis* is self-compatible but not autogamous. All ten flowers self-pollinated by hand set fruit. The mean percent seed set was 81.6 (±10.78 S.D.), which is comparable with that of the ten naturally pollinated flowers (89.4 ± 9.95). All 13 caged flowers failed to set fruit.

Nectar was not detected in flowers in any of the *Calypso* populations studied nor from 30 flowers of potted plants grown in an insect-exclusion cage. Flowers given artificial nectar were adversely affected. Those with 15–45 μl of 10 percent sucrose solution wilted within two weeks, whereas unaltered flowers lasted an average of three. A sugar solution of 30 percent induced wilting within 24 hours.

Fruit set varied from 0–34 percent (Table 1). Two flowers were visited (their pollinaria were removed) at the Lord Ellis Summit population but no pollinations occurred. The Lanphere Dunes population had 11 percent fruit set in 1976 but dropped to 7 percent in 1978 when artificial nectar was added to flowers (G-test, Sokal and Rohlf, 1969: $G = 9.94$, df = 1, $p < 0.005$). There was a substantial decrease in the number of flowers visited (number of flowers with only their pollinarium removed plus the number of pollinated flowers). In 1976, there were 671 flowers visited, whereas in 1978 there were only 398 ($G = 33.25$, df = 1, $p < 0.005$). Pollinator abundance was similar for the two seasons so the difference may be due to short flower life and slight lip sag induced by the artificial nectar.

Insect visits to *C. bulbosa* var. *occidentalis* were infrequent; however, pollinarium-laden bumblebees of three species were caught: *Bombus caliginosus, B. edwardsii* (queens), and *Psithyrus crawfordi* (female). In all cases the pollinaria were attached to the hairless region just under the scutellum (Fig. 1). For attachment to occur there, bees had to enter the flower deeply and back out with arched bodies so that the edge of the scutellum contacted the viscidium, cementing the rest of the pollinarium to the bee. Both pollinium deposition and pollinarium removal occur only as the bee leaves the flower. First the bee passes the stigma where it may deposit pollinia and then the pollinarium is removed.

Pollinium deposition and pollinarium removal are not guaranteed consequences of any given visit by a pollinarium-laden bee. This is because pollinator size is variable, as is the throat of the lip. At the Lanphere Dunes population, the throat gap, measured from the tip of the column to the hairy rim of the lip, ranged from 5–10 mm. Pollinarium loads of bumblebees reflect this imprecise flower-pollinator fit. Each pollinarium has four pollinia and any number of these or none at all may be left on the stigma. At the Lanphere Dunes, approximately one flower was pollinated for every four pollinaria removed. The ratio of pollinated to visited flowers was 0.27 and 0.26 for 1976 and 1978, respectively.

Several bees were observed visiting *C. bulbosa* var. *occidentalis* but failed to effect pollination. On three occasions *B. occidentalis* queens were seen entering flowers at the Lanphere Dunes population. Each bee visited a flower without a pollinarium load and failed to pick one up when it left. *Emphoropsis* cf. *miserabilis* (Anthophoridae), one of the most common bees at Lanphere Dunes, was seen visiting
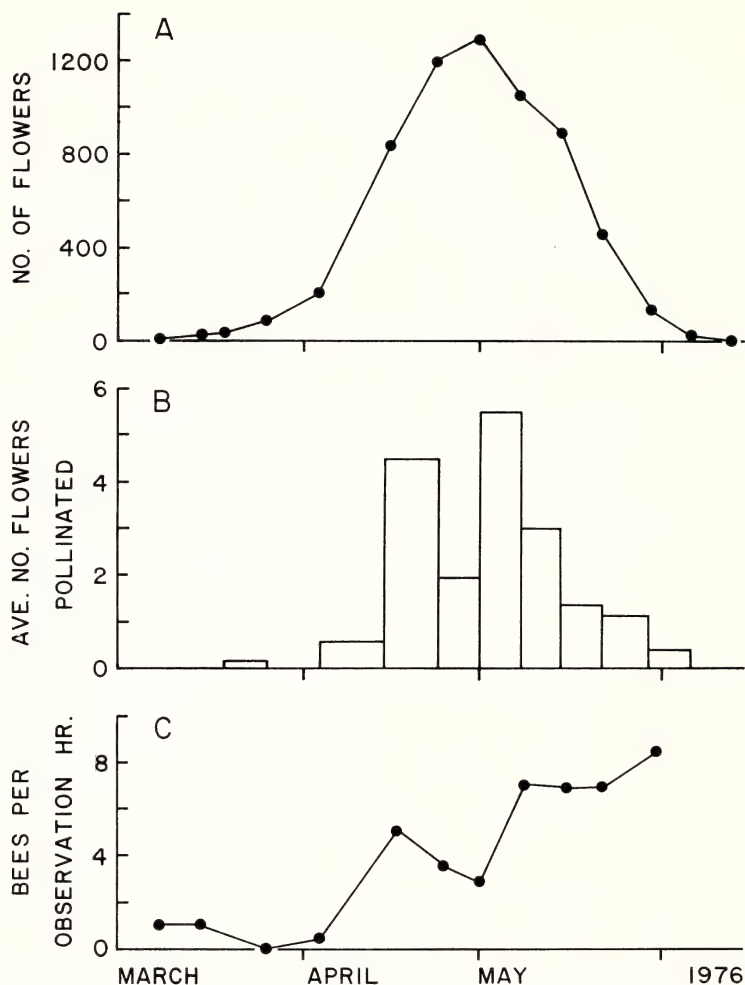
Fig. 2. Phenology of *Calypso bulbosa* var. *occidentalis* and its pollinators. A. Seasonality of flowering. B. Frequency of pollination expressed as the average number of flowers pollinated per day per census interval. C. Availability of potential pollinators. This includes *Bombus* queens and *Psithyrus* females. Data are from the 1976 season at the Lanphere-Christensen Dunes Nature Conservancy.

C. bulbosa var. *occidentalis* six times but was also ineffective in removing pollinaria. This is apparently due to its small size. These bees typically visited 2–3 flowers before leaving the site.

During 1976, the number of *Calypso* flowers pollinated each week at the Lanphere Dunes did not always rise proportionately with an increase in the number of available flowers. A sudden drop in polli-

nations occurred during a week in which the population was at peak flowering (Fig. 2). However, two distinct increases in the relative abundance of bumblebee queens bracketed the peak flowering period of *Calypso* (Fig. 2). These two increases correspond with the two abrupt rises in the number of flowers pollinated.

DISCUSSION

The mechanics of pollinarium removal and deposition clearly indicate that *C. bulbosa* var. *occidentalis* is an outcrossing species. Autogamy did not occur, corroborating the results of Kipping (1971) and Krell (1977). Insect-mediated self-pollination is improbable because bees are not inclined to reenter flowers. Furthermore, geitonogamous pollinations are unlikely because plants produce a single flower each year and, unlike some populations of var. *americana* and var. *bulbosa* (Mosquin, 1970; Mousley, 1925; Wollin, 1975), vegetative propagation is apparently rare.

The western *Calypso,* like the other varieties studied (Mosquin, 1970; Stoutamire, 1971; Wollin, 1975), is pollinated by several species of bumblebees. Five of the ten species caught at the Lanphere Dunes are known pollinators of *C. bulbosa* var. *occidentalis*: queen *B. caliginosus, B. vosnesenskii, B. edwardsii, B. mixtus,* and female *P. crawfordi* (present data; Kipping, 1971; Krell, 1977; R. Thorp, pers. comm., 1977). Queens of seven other species are pollinators of the western *Calypso* at other localities (Krell, 1977; Mosquin, 1970; Thorp, pers. comm., 1977): *B. melanopygus, B. rufocinctus, B. centralis, B. pleuralis, B. bifarius nearcticus, B. flavifrons,* and *B. frigidus.* Two common Lanphere Dunes species, *B. californicus* and *B. occidentalis,* are thus far known to pollinate only *C. bulbosa* var. *americana* (Mosquin, 1970; Thorp, pers. comm., 1977). These and other bumblebee species that are within the appropriate size range to effect pollinarium removal and pollinium deposition might also pollinate the western variety if they encountered it. Bumblebee workers are common during the latter half of the blooming season of *C. bulbosa* var. *occidentalis* and most are apparently too small to be effective pollinators. Because there is variability in the size of the entrance to the lip, it is possible that large workers might pollinate the western variety, as they sometimes pollinate var. *americana* (Mosquin, 1970; Thorp, pers. comm., 1977).

The western *Calypso* is deceptive because it presents no reward to its pollinators. Such orchids generally have low percent fruit set (Ackerman, 1975; Dafni and Ivri, 1979; Thien and Marcks, 1972) and populations of *Calypso* in North America and Europe are no exception (Kipping, 1971; Krell, 1977; Mosquin, 1970; Mousley, 1924; Wollin, pers. comm., 1979; Table 1).

Food deception in the Orchidaceae may involve relatively specific mimicry systems (Nierenberg, 1972; Pijl and Dodson, 1966). There is

no evidence, however, of specific mimicry involving *C. bulbosa* var. *occidentalis* and associated spring-blooming species in northern California. Heinrich (1976) and Jones and Buchmann (1974) noted that bumblebees with established floral preferences may mistake at a distance the flowers of one species for another. The flowers involved are of similar size, coloration, and presentation (height of inflorescences, number of flowers per inflorescence, etc.). Nevertheless, such a mistake is short-lived because the bees veer away upon closer inspection. This behavior was not observed for any bees foraging near or passing through the populations I studied. Mimicry would have to be even more fine-tuned to lure bumblebees for successive complete visits. Those flowers visited by bumblebee queens in the vicinity of the *Calypso* populations I studied cannot be construed on an individual species basis as models for *C. bulbosa* var. *occidentalis*. At least several aspects of associated species differed radically from the orchid (e.g., habit, flower symmetry, shape, color, size, presentation). The western *Calypso* may thus be regarded as a generalized food-flower mimic. The flowers possess a constellation of characteristics typical of the bumblebee-pollinated food-flower syndrome (Heinrich, 1979) and do not necessarily mimic any specific species. This mode of pollination works because bumblebees occasionally explore for new food resources (Heinrich, 1976). Pollination of *C. bulbosa* var. *occidentalis* is dependent on these exploratory visits of uninitiated bumblebees.

Heinrich (1975a, 1975b) noted that bumblebees visited *Calopogon tuberosus* (L.) B. S. P., another non-rewarding orchid, an average of 5.4 times in quick succession. He suggested that the color variation of the flowers enhances the number of visits the pollinators require to learn to avoid the species. The same process may be operating in *C. bulbosa* var. *occidentalis* with its variable and irregularly patterned lip (Fig. 1). In addition, my casual checks of fragrance production indicated that some flowers are quite fragrant, whereas others in the population are scarcely scented. Variability in odor production has been noted elsewhere for both North American *Calypso* varieties (Bradshaw, 1919; Krell, 1977; Mousley, 1924; Stoutamire, 1971).

The phenological data obtained at the Lanphere Dunes during the 1976 season supports the hypothesis of visitation by naive bees. The number of pollinations occurring each week did not correspond proportionately with the number of flowers open and available in the population. This anomalous situation cannot be explained on the basis of weather conditions because that season was relatively mild without any radical weather shifts (U.S. Dept. Commerce, 1976, data for nearby Eureka, California). However, the two pollination peaks did correspond with a jump in abundance of potential pollinators. The abrupt drop in the number of pollinations during the peak flowering period may be attibuted to the phenomenon discussed above: when the first flush of bumblebees occurred, the uninitiated bees visited *Calypso* in

search of food resources. After the first week of emergence most bees either learned that *Calypso* was not a food resource or readily established foraging areas and food preferences (e.g., *Vaccinium ovatum* Pursh and *Arctostaphylos uva-ursi* (L.) Spreng.) without visiting the orchid. The second flush of bumblebees then repeated this process. Despite the drop in pollinations during the peak of flowering, there is synchrony between the blooming season of the orchid and the emergence and availability of its pollinators. Bumblebee queens increase in abundance at the time of peak flower availability. Reliance on newly emerged bumblebee queens for pollination has been suggested for both the eastern North American and Eurasian *Calypso* (Luer, 1975; Mosquin, 1970; Stoutamire, 1971; Wollin, 1975), but until now supportive data have not been published.

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THE HISTORICAL ROLE OF FIRE IN THE FOOTHILL COMMUNITIES OF SEQUOIA NATIONAL PARK

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Abstract

The historical role of fire in the foothill-chaparral and oak-woodland communities of Sequoia National Park must be understood before a management program can be developed that will assure the perpetuation of those community types. Historically, lightning-ignited fires were supplemented by intentional ignitions by Indians and, later, by European settlers. The park fire records since 1920 portray the frequency of both man-caused and lightning fires by year, month, and elevation. Fires have been most common at higher elevations and during summer. This corresponds with the period of maximum drought stress and minimum foliage moisture content. The largest share of the area burned has been within the chaparral community. However, nearly 75 percent of the zone has not burned during this time.

The role fire should be allowed to play in the low-elevation foothill communities of Sequoia National Park poses a management dilemma. Although the objective of fire management programs in national parks is generally to allow fire to play as natural a role as possible in determining vegetation mosaics (Parsons, 1977), the buildup of highly flammable fuels following decades of fire suppression often makes this impossible. Despite evidence that periodic fire has played a vital role in the evolution and maintenance of the foothill-chaparral and oak-woodland communities of the southern Sierra Nevada (Vankat, 1977), current fuel conditions are such that naturally ignited fires cannot safely be allowed to burn. Previous years of fire suppression have resulted in extensive, highly flammable, over-mature fields of brush (Parsons, 1976). In addition to the problems encountered in controlling summer wildfires, such conditions make it difficult to implement a safe, effective program of prescribed burning.

This paper reviews available information on the fire history of the foothill-chaparral and oak-woodland communities of Sequoia National Park. This information provides part of the baseline data necessary for the development of an integrated fire management program for the area. The data were derived primarily from the park's fire atlas, which lists and maps all of the fires that have occurred since 1920. Other accounts of the early fire history of the area in and around Sequoia National Park are reviewed in Vankat (1977) and Kilgore and Taylor (1979).

It is not possible to use standard fire history techniques in brush
and grassland communities. Chaparral fires typically burn all or most
of the above ground biomass. Thus, while it is possible to date the
last fire, there is no accurate way of dating previous ones. Similarly,
fires in grass or woodland areas are commonly of low enough intensity
not to leave scars on the scattered trees. While it is known that fire
plays an important ecological role in chaparral and woodland com-
munities (Biswell, 1974; Griffin, 1977), it is difficult to document fully
the fire history of such areas. Historical accounts and personal recol-
lections must be relied on heavily in such situations.

THE FOOTHILL ZONE

The area encompassed by this study includes more than 28,000
hectares in the southern Sierra Nevada along the western boundary
of Sequoia National Park. Located within the North, Middle, Marble,
East, and South Fork drainages of the Kaweah River, the foothill
zone spans an elevation range between about 460 m and 1830 m. The
topography is generally steep with narrow canyons and cliffs. The
climate of this zone is Mediterranean-type with hot dry summers and
cool moist winters. Annual precipitation averages 65 cm at the lower
elevations and more than 90 cm at the upper elevations. Summer
temperatures frequently exceed 38°C. Soils are primarily sandy loams
of granitic origin. They are often shallow on the steeper hillsides but
attain several meters in depth in more favorable locations.

Following Baker et al. (1981), four major plant communities can be
identified as occurring within the foothill zone: foothill woodland, cha-
mise chaparral, mixed-evergreen woodland, and black-oak forest. The
foothill woodland community is characterized by a grassland under-
story with scattered stands of *Quercus douglassii* and *Aesculus cali-
fornica*. The dominant grasses are primarily introduced annuals that
became established following intensive grazing during the late 1800's
(Vankat and Major, 1978). They are thought to have replaced native
annuals as well as perennial bunchgrasses (Heady, 1977). Chamise
chaparral is widely distributed on the xeric slopes of the foothill zone.
Adenostoma fasciculatum is the dominant and sometimes only species
found in this community. The mixed-evergreen woodland is a highly
variable mixture of shrubs (e.g., *Cercocarpus betuloides*) and trees
(e.g., *Aesculus californica, Quercus chrysolepis*) found primarily on
mesic north slopes and at higher elevations. The black-oak (*Quercus
kelloggii*) forest, with stands of *Chamaebatia foliolosa, Arctostaphylos
viscida,* and *A. patula,* forms a transition between the foothill com-
munities and the mixed-conifer forests. In earlier classification
schemes, the foothill zone was generally divided into oak savanna
(corresponding with foothill woodland), chaparral (including chamise
chaparral and much of the mixed-evergreen woodland), hardwoods

(included in the mixed-evergreen woodland), and black-oak forest. Because these community types were often the basis for past fire records, it has been necessary to use them during much of this report.

FIRE HISTORY

Presettlement.   Fires ignited by lightning are an important element in the dry summer environment of the Sierra Nevada (Komarek, 1967). Unfortunately, the lack of adequate fire dating techniques for the foothill communities has often made it impossible to quantify the frequency or size of lightning fires in presettlement times.

Additional pre-European ignitions came from the local aboriginal populations. For example, it is known that prior to the first coming of Europeans to the area in the late 1850's, the Western Mono Indians used fire to assist in hunting, to promote growth of wild food crops, and to facilitate the collection of seeds in much of the study area (Lewis, 1973; Vankat, 1977). Both Reynolds (1959) and Lewis (1973) present evidence that most Indian burning was carried out in the fall. The influence of aboriginal man on the Kaweah River region was essentially terminated by 1865, when the last Western Mono left the area (Strong, 1964).

Information available for a nearby mixed-conifer forest (Kilgore and Taylor, 1979) documents a decrease in fire frequency after 1870. This corresponds with the end of Indian occupation but is before fire suppression became effective. It establishes the importance of Indian ignitions in the presettlement forest. While it is impossible to document the extent to which the same is true for the lower elevation foothill communities, it is likely that a similar pattern holds. It is thus logical to assume that the pre-aboriginal fire frequency (lightning ignitions only) was less than in the 1800's, but greater than exists today. While it may not be possible to distinguish fully between the relative frequency or ecological significance of Indian versus lightning fires, it is clear that both played an important role in determining the vegetation patterns found in the foothill zone. It is the policy of the National Park Service to include both lightning and Indian ignitions as part of the natural scene.

Post-settlement.   During the 1860's, European settlers first moved into the foothills of the southern Sierra in the area that is now Sequoia National Park. In succeeding years, sheepherders increasingly used the area in moving their flocks to and from the high country. They commonly set fires in the fall while coming out of the mountains in order to clear brush and provide for new, more palatable growth the following spring (Strong, 1964; Vankat, 1977). Vankat (1977) concluded that much of this sheepherder burning can be viewed merely as an extension of aboriginal fires. The two cultures apparently burned "for much the same reasons—to favor certain plant species and to

open the forests". Lightning-ignited fires continued to burn during this period.

Following the establishment of Sequoia National Park in 1890, a policy of suppressing all fires was implemented (Vankat, 1977). Due to limited funding and manpower and poor access to many areas, suppression did not become effective until the 1920's. A policy of fire suppression has remained in effect for the foothill region to the present time. The consequences of this suppression policy are now the cause of considerable concern. The reduction of fire frequency has resulted in an increased fuel density and an abundance of old growth, especially in the chaparral communities (Parsons, 1976; Rundel and Parsons, 1979). Increased fuel accumulations make it increasingly difficult to extinguish fires that do get started. There has also been a loss of typical age-class and community-type mosaics and, in some cases, a change in species composition. For example, Vankat and Major (1978) have documented an increase in cover and density and a decrease in diversity in the chaparral communities as well as an increased cover and density of oak species in the woodland types.

Recent.   Although fire records for the study area before the late 1920's are incomplete, they are sufficient to document the fact that fires caused by both man and lightning were frequent occurrences. For example, early park records show at least 37 lightning fires, 6 man-caused fires, and 22 fires of unknown origin occurring within the foothills of the Kaweah River drainage (an area of 28,366 ha) between 1891 and 1919. The great majority of these fires occurred during the dry summer months when the vegetation is highly flammable. Several (both lightning and man-caused) consumed more than a thousand hectares.

Since the 1920's, nearly complete records have been maintained of all fires occurring within the park. These records provide the only available data base for recent fire history in the foothill zone. Fire frequency and size, of course, have been greatly influenced by suppression activities. Records available for 1920–1929 show at least ten fires of 12 ha or larger, but of undetermined origin, burning a total of 4189 ha within the study area (the records of smaller fires have been lost). In the 49 years from 1930 to 1978 a total of 105 lightning and 107 man-caused fires were recorded for the Kaweah drainage foothill zone. Lightning fires averaged 2.14 ± 2.63 (S.D.; range: 0–10) per year while 2.18 ± 2.00 (range: 0–8) man-caused fires were recorded per year. There were 16 years with no lightning fires, 12 with no man-caused fires, and 4 with no fires at all. Lightning fires burned a total of 592 ha while man-caused fires burned 2811 ha. Most of the fires (91 percent) burned less than 3 ha. It should be noted that the lightning fires reported here represent only those ignitions that resulted in detectable fires. No doubt many lightning strikes are never detected.

TABLE 1.   TOTAL AREA AND NUMBER OF LIGHTNING FIRES BY 305 m (1000 ft)
ELEVATION CONTOURS IN THE ENTIRE KAWEAH RIVER DRAINAGE, SEQUOIA NATION-
AL PARK, 1930–1978.

Elevation (m)	Total area (ha)	No. lightning fires	No. fires per 1000 ha
<610	627	2	3.2
610–914	3134	1	0.3
915–1219	5877	4	0.7
1220–1524	8267	18	2.2
1525–1829	10,461	81	7.7
1830–2134	12,146	99	8.2
2135–2439	12,577	139	11.0
2440–2744	12,538	118	9.4
2745–3049	9795	70	7.1
>3050	7758	10	1.3

Furthermore, the increased efficiency of fire suppression capabilities in recent decades has limited the total area burned to well under the area that would have burned without suppression activities.

Data on the frequency of lightning fires as a function of elevation within the entire Kaweah drainage (Table 1), with the exception of the lowest elevation where the sample area is small, show a steady increase in the number of fires as well as the number of fires per unit area, up to an elevation of 2440 m. This corresponds with the findings of Komarek (1967) and Keeley (1977) for the forest and chaparral regions of California and relates in large part to an increasing frequency of lightning strikes with elevation. The decrease in fires at the highest elevations relates primarily to decreasing fuel supplies. Whereas lightning fires most frequently ignite in the middle elevations, under hot, dry, summer conditions they sometimes burn downslope through the highly flammable brush and grasslands. It should be emphasized that while lightning strikes are relatively rare at the lower elevations, they do occur (Griffin, 1977). It is likely that occasional lightning fires that ignite below the park would burn into the study area were they not suppressed. When ignited under the proper conditions, few ignitions are needed to burn large areas of highly flammable chaparral and oak woodland.

The distribution of lightning fires by month for the study area is presented in Fig. 1. Most of the 32 recorded July fires occurred in the latter part of the month. The late-summer peak in lightning fires corresponds with the onset of maximum flammability as represented by decreasing foliage moisture content (Fig. 1). This timing corresponds with the period of maximum temperatures and minimal precipitation, conditions also favoring maximum burning potential. Thus, the high incidence of lightning fires during the late summer and early fall may
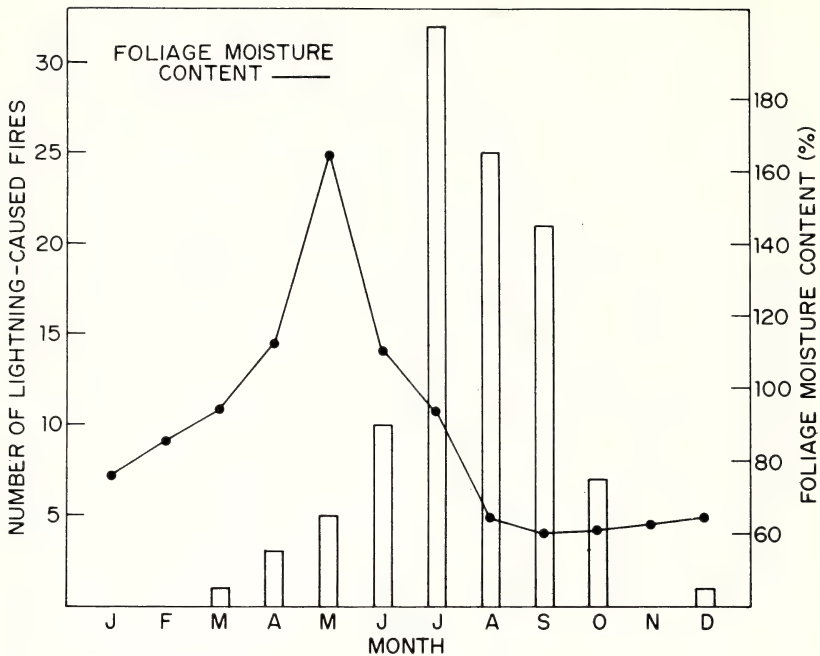
Fig. 1.   Mean number of lightning-caused fires by month for Kaweah River drainage
below 1830 m, 1930–1978, and mean monthly foliage moisture content for *Adenostoma
fasciculatum* within the study area. Foliage moisture determination followed Country-
man and Dean (1979).

be as much a function of weather conditions and vegetation flam-
mability as of lightning-strike frequency.

The monthly distribution of man-caused fires within the study area
corresponds closely with that of lightning fires (Fig. 2). Again, the
peak occurs during the period of hot, dry weather and low foliage
moisture content when the vegetation is most likely to burn. The one
significant difference from the distribution of lightning fires is the rel-
atively large number of man-caused fires in June. This difference may
relate to the fact that electrical storms are rare in June but the period
of high visitor use has already begun (Fig. 2). The strong correlation
between the timing of peak visitor use and the incidence of man-caused
fires emphasizes the potential danger from unwanted wildfires during
the summer months.

The park fire atlas, which maps all fires that burned more than
4 ha in the study area since 1920 (unpublished data), shows that much
of the foothill zone of Sequoia National Park has not burned in at
least 60 years. Biswell (1974) has expressed the opinion that this is
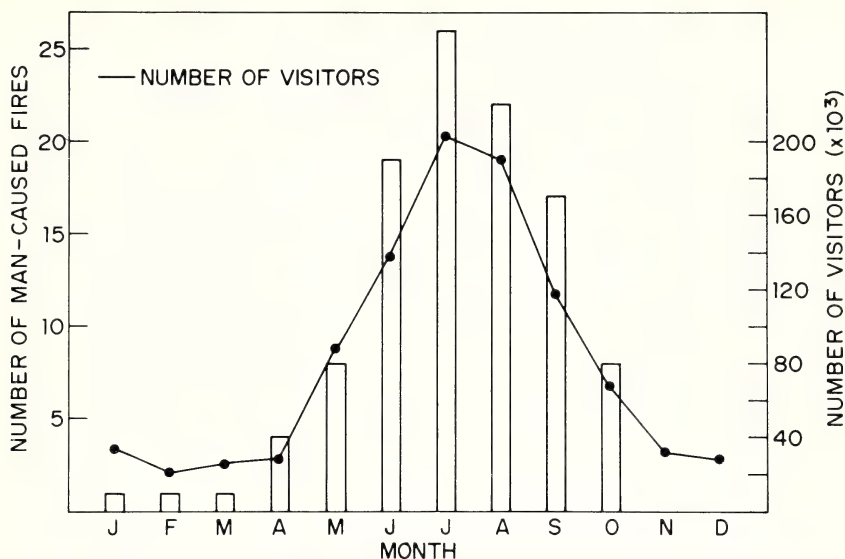
FIG. 2.   Mean number of man-caused fires by month for the Kaweah River drainage below 1830 m, 1930–1978, and monthly 1978 visitation rate for Sequoia National Park.

probably a considerably longer fire-free period than most of these low-elevation communities have experienced for many centuries and perhaps for thousands of years. Together with the evidence for buildup in both live and dead fuels in stands of increasing age, this indicates a serious over-abundance of dense, over-mature, highly flammable brush. It also suggests a lack of distinct age-class boundaries that could be effective fire breaks. Lack of such boundaries can hinder the development of a safe, effective program of prescribed burning (Philpot, 1974).

By superimposing the map of fires larger than 4 ha on a vegetation map of the park we have calculated the area burned since 1920 within each vegetation type (Table 2). The greatest area burned was in chaparral, with the next greatest being in hardwoods. When converted to a percentage of the community type available, the oak savanna and chaparral have had the greatest proportions burned. In all, 8360 ha or slightly less than 30 percent of the foothill zone has been burned at least once by either lightning or man-caused fire since 1920. In addition, 1246 ha, primarily in chaparral, have been burned two or three times during this period (Table 2).

Not included in Table 2 are four prescribed burns which have been ignited as part of the park's fire management program (Parsons, 1977). These fires, which have all occurred since 1969, have burned a total

TABLE 2.   AREA OF EACH FOOTHILL (<1830 m) VEGETATION TYPE BURNED BY
MAN-CAUSED AND LIGHTNING FIRES IN THE KAWEAH RIVER DRAINAGE, 1920–1978.
Percents are based on area of vegetation type within the drainage below 1830 m (study
area) only.

Vegetation type	No. hectares burned	Percent of vegetation type burned	No. hectares reburned
Oak savanna	1073	46.8	194
Chaparral	4271	38.1	673
Hardwoods	1635	20.5	251
Black oak	351	19.3	38
Conifers	1030	13.9	90
Total	8360	25.1	1246

of 1099 ha in the study area. Of this, 48 percent has been in the
chaparral. Most of the area of prescribed burns (557 ha) had previously
burned since 1920.

MANAGEMENT IMPLICATIONS

Together with data on vegetation patterns, age class boundaries,
biomass accumulation, flammability, and an understanding of
fire's role in the reproduction and succession of important plant and
animal species, fire history data provide a basis for predicting the
immediate and long term effects of any fire and so provide an essential
basis for developing a fire-management program. Such information
establishes criteria for simulating the natural fire regime by re-estab-
lishing the seasonal and elevational distribution of historical fires. It
also helps to establish which vegetation types and even which specific
areas have gone the longest without being burned. Such information
is valuable in setting priorities for future management actions.

The foothill zone of Sequoia National Park, like much of the rest
of the foothill zone of the southern Sierra Nevada, contains extensive
areas of over-mature, highly flammable brush. When unplanned fires
ignite, especially at the lower elevations, it is often essential that im-
mediate suppressive action be taken. Otherwise highly destructive,
uncontrollable wildfires may result. This threat is of special concern
due to the location of giant sequoia groves immediately uphill from
the foothill communities and in the path of potential conflagrations.

I conclude that through a carefully planned prescribed burning pro-
gram it will be possible to reduce the accumulated fuels and at the
same time increase the number of distinct age classes and vegetation
boundaries. This will not only restore more natural conditions but will
facilitate suppressive action on future wildfires (Philpot, 1974). While
the first several prescribed burns, for reasons of control, may need to

be in late fall or winter, once a more diverse vegetative and age-class mosaic has been created it should be possible to burn safely at the time of year when natural fires are known to have occurred. In all cases, prescribed burns must be carefully planned to minimize risks while at the same time accomplishing desired objectives. This requires a thorough understanding of the relationship of fire behavior to moisture content of foliage, biomass accumulation, and various weather parameters for each vegetation type. If carefully conducted, such a program should assure the continued survival of healthy foothill woodland and chaparral communities in the southern Sierra Nevada.

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TAXONOMY OF PHACELIA SECT. MILTITZIA (HYDROPHYLLACEAE)

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Abstract

The species of *Phacelia* sect. *Miltitzia* are found in the Great Basin physiographic province of western North America and are distinguished from other members of *Phacelia* by their yellow, marcescent corollas combined with transversely corrugated seeds. An artificial key is provided to the nine species and two varieties of sect. *Miltitzia* recognized in the present taxonomic treatment. One new species, **Phacelia monoensis,** is described and *Phacelia submutica* is reduced to **P. scopulina** var. **submutica.**

Phacelia is the largest genus in the Hydrophyllaceae, consisting of 150–200 species. The genus has a wide distribution, the greatest number and diversity of species being in western North America. Many of the species-groups now included in *Phacelia* were recognized as distinct genera in earlier classifications (Candolle, 1845). Section *Miltitzia* is one such group.

The species belonging to sect. *Miltitzia* are small yellow-flowered annuals found in the arid regions in and around the Great Basin (Fig. 1). These species bloom primarily in the spring and characteristically grow in clay soils having a high pH and relatively high concentrations of soluble salts. They are usually found in the sagebrush-juniper or sagebrush-rabbitbrush communities.

The first species of the *Miltitzia* group to be described was *Eutoca lutea* Hooker and Arnott (1840). However, these authors questioned the plant's affinity with *Eutoca* because it possessed a yellow, marcescent corolla; they excluded it from *Emmenanthe* because of its prostrate growth habit and lack of corolla scales. Candolle (1845) subsequently placed this species in its own new genus, *Miltitzia.* Gray (1857), while describing the second known member of the group (as *Emmenanthe parviflora* Gray), proposed that the plants be treated as the subgenus *Miltitzia* within the genus *Emmenanthe.* Heller (1912) and Brand (1913) raised subgenus *Miltitzia* to the generic rank suggested by Candolle. J. T. Howell (1944a), while preparing a monograph of *Phacelia* sect. *Euglypta,* noted the close morphological similarity between it and *Miltitzia* and, as a result, transferred the *Miltitzia* species to the genus *Phacelia.*

Miltitzia and sect. *Euglypta* have several traits in common. Both have plump, transversely corrugated seeds, and the lateral attachment
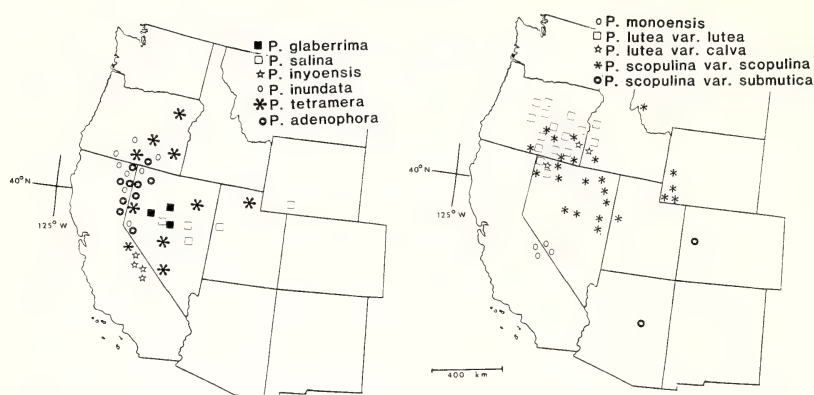
Fig. 1.   Distribution of *Phacelia* sect. *Miltitzia*.

of the ovules to fleshy placentae in *Miltitzia* is characteristic of the entire genus *Phacelia* (Howell, 1944b). The chromosome numbers also indicate the likeness of the two groups (Constance, 1963). In *Miltitzia*, $n = 11$, 12, and 13, whereas in sect. *Euglypta*, $n = 11$, 12, 13, and 23. On the other hand the principal characteristic *Miltitzia* and *Emmenanthe* have in common is the persistent, yellow corolla. In *Emmenanthe* the seeds are compressed and reticulate, the pendent ovules are basally attached to the wing-like margins of membranous placentae, and the chromosome complement of $n = 18$ is unique in the Hydrophyllaceae. *Miltitzia*, as Howell (1944a) concluded, is best treated as a section of the genus *Phacelia*.

METHODS

Field observations and collections were made during the spring months of 1974–1978 throughout the range of the species of sect. *Miltitzia*. More than 600 herbarium specimens were examined during the course of this study. Measurements of vegetative and floral parts were made on herbarium specimens from CAS, CIC, DS, GH, ID, JEPS, K, MO, NY, ORE, OSC, POM, RENO, RM, RSA, UC, US, UTC, WILLU, WS, and WTU. These, together with the field observations, form the basis of the morphological and distributional data.

Floral buds for chromosome number determination were collected in the field and fixed in a modified Carnoy's solution (4 chloroform: 3 ethanol: 1 glacial acetic acid, v/v/v). Acetocarmine squashes of anthers were obtained by using the technique of Snow (1963).

CYTOLOGY

Cave and Constance (1947, 1950, 1959) determined the chromosome numbers for most of the species of sect. *Miltitzia*. Additional counts

TABLE 1. CHROMOSOME COUNTS FOR *Phacelia* SECT. *Miltitzia*. All collection numbers are those of the author. Vouchers are in OSC.

P. adenophora J. T. Howell; $n = 12$
  CA, Lassen Co., Termo, *1198, 1201*.
  NV, Washoe Co., *1195*.
P. lutea (Hooker & Arnott) J. T. Howell var. *lutea*; $n = 12$
  ID, Owyhee Co., Sand Basin, *1014*.
  OR: Harney Co., Stinkingwater Pass, *1018, 1143*; Lake Co., Plush, *1023, 1025*;
    Malheur Co., Succor Creek, *1153, 1154, 1295, 1302*; Sheaville, *1016*; Leslie Gulch,
    1157; Rockville, *1017*.
P. lutea (Hooker & Arnott) J. T. Howell var. *calva* Cronquist; $n = 12$
  ID, Owyhee Co., 43 km sw. of Marsing, *1957*.

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from the present study are presented in Table 1; these confirm the reports by Cave and Constance for the taxa concerned.

The genus *Phacelia* shows great diversity in chromosome numbers and contains both polyploid and aneuploid series (Constance, 1963). One such aneuploid series is found in sect. *Miltitzia*: in *Phacelia tetramera*, $n = 11$; in *P. adenophora*, *P. inundata*, *P. inyoensis*, *P. lutea*, *P. monoensis* (cited as *M. scopulina*, Cave and Constance, 1959), and *P. scopulina*, $n = 12$; in *P. glaberrima*, $n = 13$.

TAXONOMY

PHACELIA Juss. sect. MILTITZIA (DC.) J. T. Howell, Leafl. W. Bot. 4:15. 1944.—*Miltitzia* DC., Prodr. 9:296. 1845.—*Emmenanthe* Bentham subg. *Miltitzia* (DC.) Gray, Proc. Amer. Acad. Arts 10:328. 1875.—TYPE: *Phacelia lutea* (Hooker & Arnott) J. T. Howell.

Low, diffuse, prostrate to decumbent or ascending annuals from slender taproots, usually of alkaline habitats; stems 5–30 cm long; herbage densely hirsutulous to rarely glabrous, usually more or less purplish capitate-glandular; leaves entire to toothed or pinnately lobed, 0.5–4.0 cm long, 0.2–2.5 cm wide; flowers pedicellate, in simple or branched terminal scorpioid cymes; calyx divided nearly to the base, the lobes subequal; corolla yellow to whitish, frequently purplish-tinged with age, marcescent; corolla scales present or lacking; stamens included, subequal to unequal, equally inserted at base of corolla tube; hypogynous disk prominent or inconspicuous; style persistent, 2-cleft or subentire; seeds 7–25, transversely corrugate or striate.

Key to *Phacelia* sect. *Miltitzia*

Corolla tube pubescent within, at least at base; filaments pubescent.
  Corolla 2.0–3.5(–4) mm long; style and branches 0.5–1.5 mm long;

filaments 1.5–2.5 mm long. . . . . 1. *P. monoensis*
Corolla (3.5–)4–8 mm long; style and branches 1.5–3.0 mm long;
    filaments 2.5–4.5 mm long. . . . . 2. *P. adenophora*
Corolla tube glabrous within; filaments glabrous.
    Seeds faintly but definitely transversely striate, 18–25 per capsule;
        style and branches 0.5–1.2 mm long. . . . . 3. *P. inundata*
    Seeds prominently transversely corrugated.
        Corolla 4–10 mm long, usually longer than the calyx; style and
            branches 2–4 mm long.
            Plants densely pubescent. . . . . 4a. *P. lutea* var. *lutea*
            Plants subglabrous, or slightly glandular in the inflores-
               cence. . . . . 4b. *P. lutea* var. *calva*
        Corolla 1.3–4.0 mm long, if longer usually equalling the calyx;
            style and branches 0.2–2.0 mm long.
            Plants glabrous or nearly so; corolla subrotate. . . . .
            . . . . 5. *P. glaberrima*
            Plants densely pubescent; corolla tubular to campanulate.
               Flowers usually 4-merous; corolla 1.3–2.0 mm long. . . . . . .
               . . . . 6. *P. tetramera*
               Flowers 5-merous; corolla 2–4 mm long.
                   Style and branches 1.0–2.0 mm long; capsules with 9–15
                     seeds.
                     Style pubescent ⅓ to all of its length; capsule apic-
                        ulate. . . . . 7a. *P. scopulina* var. *scopulina*
                     Style glabrous except at base; capsule nearly or quite
                        without apiculation. . . . .
                        . . . . 7b. *P. scopulina* var. *submutica*
                   Style and branches 0.5–1.0 mm long; capsules with fewer
                     than 11 or more than 15 seeds.
                     Seeds 18–25 per capsule, corrugations 5–8. . . . .
                        . . . . 8. *P. inyoensis*
                   Seeds 7–10 per capsule, corrugations 9–13. . . . .
                        . . . . 9. *P. salina*

1. **Phacelia monoensis** Halse, sp. nov.

Floribus 5-meris; segmentis calycis per anthesis 2–4 mm longis, ad maturitatem 4–6 mm longis; corolla luteola, 2–4 mm longa, extus et intus pubescenti; filamentis pubescentibus, 1.5–2.5 mm longis; stylo cum ramis 0.5–1.5 mm longo; ovulis 7–10; capsula 2.5–4.0 mm longa; seminibus 1.1–1.7 mm longis, manifeste transverse corrugatis, rugis 8–11.

Annual herb; stems few or several, prostrate; herbage hirsutulous, more or less purplish capitate-glandular; leaves entire toothed or pinnately lobed; flowers 5-merous; calyx segments in flower 2–4 mm long, in fruit 4–6 mm long; corolla tubular to campanulate, yellow, 2–4 mm

long, pubescent externally and internally; corolla scales obsolete; filaments pubescent, 1.5–2.5 mm long; style and branches 0.5–1.5 mm long, style pubescent to midlength; ovules 7–10; hypogynous disk prominent; capsule 2.5–4.0 mm long, apiculate, pubescent; seeds 1.1–1.7 mm long, transversely corrugate, corrugations 8–11; $n = 12$.

TYPE: USA, CA, Mono Co., in red clay, Mormon Ranch, 14 km (8.5 mi) sw. of Bodie, 30 Jun 1945, *Alexander and Kellogg 4346* (Holotype: UC!; isotypes: CAS! DS! NY! POM! RSA! US! UTC! WS! WTU!).

Distribution. Alkaline mountain meadows of central Mono County, California and adjacent Nevada; flowering June–July.

Phacelia monoensis is probably closely related to *P. adenophora* because of the similarity in floral pubescence and possession of a conspicuous hypogynous disk. The two species differ in the size of the floral parts, the presence of corolla scales and the number of ovules; they occupy quite different habitats.

2. PHACELIA ADENOPHORA J. T. Howell, Leafl. W. Bot. 4:15. 1944.—
  Emmenanthe glandulifera Torrey ex Watson, Bot. U.S. Geol.
  Explor. 40th Parallel. 257. 1871.—*Miltitzia glandulifera* (Watson)
  Heller, Muhlenbergia 8:20. 1912.—TYPE: USA, NV, Virginia
  Mts., Jul, *Watson 885* (Holotype: GH!; isotypes: NY! US!). Not
  Phacelia glandulifera Piper, Contr. U.S. Natl. Herb. 11:472.
  1906.
Miltitzia glandulifera var. *californica* Brand, Univ. Calif. Publ. Bot.
  4:224. 1912.—TYPE: USA, CA, Lassen Co., Madeline Plains, Jun
  1898, *Bruce 2135* (Holotype: UC!).

Stems few or several, prostrate to ascending, pubescent, capitate glands present or lacking; leaves pinnately lobed or divided, rarely entire or merely toothed, hirsutulous; flowers 5-merous; calyx segments in flower 2–5 mm long, in fruit 4–7 mm long; corolla campanulate, yellow or the lobes more or less purplish-tinged, (3.5–)4–8 mm long, pubescent externally, corolla tube sparsely to densely pubescent within; corolla scales present; filaments pubescent, unequal, 2.5–4.5 mm long; style and branches 1.5–3.0 mm long, style pubescent ⅓–½ its length; ovules 6–15; hypogynous disk prominent; capsule 2.5–4.5 (–6) mm long, apiculate, pubescent; seeds 1.0–1.6 mm long, transversely corrugate, corrugations 8–12; $n = 12$.

Distribution. Plains and slopes of northeastern California, western Nevada, and southeastern Oregon; flowering April–July.

Phacelia adenophora is a moderately variable species but is well characterized by the conspicuous pubescence on the filaments and within the corolla tube. In central-western Nevada the plant is rather slender and delicate; to the northward it intergrades with a larger, coarser form that Brand (1912) called *Miltitzia glandulifera* var. *cal-*

ifornica. However, var. *californica* is not sufficiently distinct to be recognized taxonomically because the variation between the two forms is continuous and the characters Brand used to distinguish the variant are found throughout the range of the species.

Phacelia adenophora is closely related to *P. lutea* and has been treated as the same species (Jepson, 1943). Some hybridization may occur between these two taxa in northern Nevada and adjacent Oregon. In these areas plants have been found in which the filaments and the inside of the corolla tube range from glabrous to subglabrous to pubescent. Nevertheless, it seems best to retain these taxa as separate species, because in *P. adenophora* usually either the filaments or corolla tube are at least slightly pubescent and plants can therefore be referred readily to one or the other of the two species.

3. PHACELIA INUNDATA J. T. Howell, Leafl. W. Bot. 4:15. 1944.—
   Emmenanthe parviflora Gray, U.S. Pacific R.R. Reports 6:84.
   1857.—*Miltitzia parviflora* (Gray) Brand, Das Pflanzenr. IV.
   251:131. 1913.—TYPE: USA, OR, Klamath Lake, *Newberry s.n.*
   (Holotype: GH!). Not *Phacelia parviflora* Pursh, Fl. Amer. Sept.
   1:140. 1814; nor *Phacelia parviflora* Phil., Anales Univ. Chile
   90:226. 1895.

Stems several, prostrate to ascending, pubescent, glandular; leaves subentire to pinnately lobed, hirsutulous; flowers 5-merous; calyx segments in flower 3–4 mm long, in fruit 5.5–8.0(–10) mm long; corolla tubular to campanulate, yellow, 3–5 mm long, pubescent externally, glabrous internally; corolla scales present or obsolete; filaments glabrous, 1.5–3.0 mm long; style and branches 0.5–1.2 mm long, style pubescent half to all of its length; ovules 18–25(–30); hypogynous disk prominent; capsule 4–7 mm long, apiculate, pubescent; seeds 1.1–1.8 mm long, tending to be flattened, transversely striate, striations 12–14; $n = 12$.

Distribution. Dried edges of alkali lakes and sinks, from south central Oregon to northeast California and adjacent Nevada; flowering May–July.

4. PHACELIA LUTEA (Hooker & Arnott) J. T. Howell, Leafl. W. Bot.
   4:15. 1944.—For synonymy and typifications see the varietal
   headings.

Stems several, prostrate to decumbent, glabrous to hirsutulous, capitate-glandular to eglandular; leaves usually entire or some coarsely toothed to pinnately lobed, glabrous to pubescent; flowers 5-merous; calyx segments in flower 2.5–6.0 mm long, in fruit 4.5–10.0 mm long; corolla tubular to campanulate, yellow, (3.5–)4–10(–11) mm long, glabrous or pubescent externally, glabrous internally; corolla scales pres-

ent or obsolete; filaments glabrous, 2.5–5.0 mm long; style and branches (1.5–)2–4 mm long, style glabrous or pubescent; ovules 7–15(–20); hypogynous disk prominent; capsule 3–7 mm long, apiculate; seeds 1–2 mm long, transversely corrugate, corrugations 9–12; $n = 12$.

4a. PHACELIA LUTEA var. LUTEA—*Eutoca lutea* Hooker & Arnott, Bot. Beech. Voy. 373. 1840.—*Miltitzia lutea* (Hooker & Arnott) DC., Prodr. 9:296. 1845.—*Emmenanthe lutea* (Hooker & Arnott) Gray, Proc. Amer. Acad. Arts 10:328. 1875.—*Phacelia lutea* var. *typica*, Proc. Calif. Acad. Sci. ser. 4, 25:364. 1944.—TYPE: USA, "Snake Fort, Snake Country, California" [Idaho], 1837, *Tolmie s.n.* (Holotype: K!).

Phacelia lutea var. *purpurascens* J. T. Howell, Proc. Calif. Acad. Sci. ser. 4, 25:365. 1944.—TYPE: USA, OR, Grant Co., Humphrey's, 30 Apr 1925, *Henderson 5092* (Holotype: CAS!; isotypes: DS! GH! ORE!).

Herbage densely hirsutulous, from eglandular to densely purplish capitate-glandular, especially in the inflorescence; corolla pubescent externally; style hairy near the base to above the middle.

Distribution. Alkaline areas, usually clay and ash slopes and banks, from central Oregon east to southwestern Idaho and south to northwestern Nevada; flowering April–July.

Phacelia lutea is an extremely variable species. The entire to slightly toothed leaves of typical *P. lutea* in northeastern Malheur County, Oregon, intergrade to the pinnately lobed leaves of *P. lutea* in Lake County. Style pubescence and length are also variable traits, varying as much on an individual plant as between plants. Because Howell (1944b) used these traits to distinguish var. *purpurascens,* it seems best to treat this taxon as part of the variable var. *lutea.*

4b. PHACELIA LUTEA var. CALVA Cronquist, Vasc. pls. Pacific Northw. 4:168. 1959.—TYPE: USA, ID, Owyhee Co., roadside bank alongside U.S. Hwy. 95, 6.4 km (4 mi) ne. of the Idaho–Oregon state line, 12 Jun 1946, *Maguire and Holmgren 26386* (Holotype: NY!; isotypes: CAS! DS! GH! MO! UC! US! WS!).

Herbage essentially wholly glabrous, or slightly purplish-glandular in the inflorescence; corolla glabrous externally; style glabrous.

Distribution. Northern Owyhee County, Idaho, adjacent Malheur County, Oregon, and northwestern Nevada; flowering May–June.

This variety is distinguished from var. *lutea* only by its glabrous condition. Mixed populations of var. *lutea* and var. *calva* have been found and in at least some of these populations there is intergradation in the amount of pubescence, plants ranging from glabrous to subglabrous to moderately pubescent.

5. PHACELIA GLABERRIMA (Torrey ex Watson) J. T. Howell, Leafl. W. Bot. 4:15. 1944.—*Emmenanthe glaberrima* Torrey ex Watson, Bot. U.S. Geol. Explor. 40th Parallel. 257. 1871.—*Miltitzia glaberrima* (Watson) Brand, Das Pflanzenr. IV. 251:131. 1913.— TYPE: USA, NV, Reese Valley, Jul 1868, *Watson 886* (Lectotype: GH!; isolectotypes: NY! US!; syntype: USA, NV, Humboldt Mts., Humboldt Sink, May 1868, *Watson 886* GH! NY! UC!).

Stems several, decumbent, glabrous; leaves entire to subentire to rarely lobed, glabrous or with a few hairs on the margins and apex; flowers 5-merous; calyx segments in flower 2.5–3.0 mm long, in fruit 4–6 mm long, glabrous or with a few hairs at apex; corolla subrotate, glabrous, 2.5–4.0 mm long; corolla scales lacking; filaments 2.5–3.0 mm long, glabrous; style and branches 1–2 mm long, glabrous; ovules (4–)7–10; hypogynous disk prominent; capsule 3–5 mm long, glabrous or with a few scattered hairs at apex, apiculate; seeds 1.1–1.5 mm long, transversely corrugate, corrugations 8–12; $n = 13$.

Distribution. Localized endemic on alkaline clay bluffs or alkaline sinks of central Nevada; flowering May–July.

6. PHACELIA TETRAMERA J. T. Howell, Leafl. W. Bot. 4:16. 1944.— *Emmenanthe pusilla* Gray, Proc. Amer. Acad. Arts 11:87. 1876.—*Miltitzia pusilla* (Gray) Brand, Das Pflanzenr. IV. 251:132. 1913.—TYPE: USA, NV, Steamboat Springs, May, *Watson 878,* in part (Lectotype: GH!; syntype: USA, nw. Nevada, May 1875, *Lemmon s.n.* GH! UC!). Not *Phacelia pusilla* Buckl., Amer. J. Sci. 45:172. 1843; nor *Phacelia pusilla* Torrey ex Watson, Bot. U.S. Geol. Explor. 40th Parallel. 253. 1871.

Miltitzia pusilla var. *flagellaris* Brand, Das Pflanzenr. IV. 251:132. 1913.—TYPE: USA, OR, sterile alkaline soil of the Malheur River, 20 Jun 1898, *Cusick 1946* (Lectotype: US!; isolectotypes: GH! MO! ORE! RM! UC!; syntype: USA, OR, Union Co., dry alkaline soil, 1879, *Cusick 758* GH! NY! US!).

Stems several, prostrate to decumbent, somewhat mat forming, pubescent, glands present or absent; leaves entire to shallowly pinnately lobed, pubescent; flowers 4-merous, rarely 5-merous; calyx segments in flower 1.5–3.0 mm long, in fruit 3.5–4.5 mm long; corolla campanulate, whitish, 1.3–2.0 mm long, pubescent externally, glabrous internally; corolla scales lacking; filaments glabrous, 1.0–1.5 mm long; style 0.2–0.4 mm long, the branches indicated only by an emargination at the apex of the style, glabrous; ovules 12–24; hypogynous disk inconspicuous; capsule 2.5–4.0 mm long, shortly apiculate, pubescent; seeds 0.7–1.0 mm long, transversely corrugate, corrugations 6–9; $2n = 22$.

Distribution. Alkaline flats, washes, and meadows of Nevada, adjacent California, eastern Oregon and north central Utah; flowering May–June.

This species is unique in *Phacelia* in being 4-merous. Howell (1944b) writes that the reduction from the usual 5-merous condition seems to be due to the suppression of one part of the adroecium, calyx, and corolla rather than the union of adjacent parts.

7. PHACELIA SCOPULINA (A. Nelson) J. T. Howell, Leafl. W. Bot. 4:16. 1944.—For synonymy and typifications see the varietal headings.

Stems few to several, prostrate to ascending, hirsutulous, sparsely glandular; leaves entire to toothed to pinnately lobed, pubescent; flowers 5-merous; calyx segments in flower 2.5–4.0 mm long, in fruit 5–8 (–10) mm long; corolla tubular to campanulate, yellow, becoming purplish-tinged, 3–4(–5) mm long, pubescent externally, glabrous internally; corolla scales inconspicuous or obsolete; filaments 2–3 mm long, glabrous; style and branches 1–2 mm long, style pubescent only at base to all of its length; ovules 9–15; hypogynous disk inconspicuous; capsule 3.5–6.0 mm long, pubescent, apiculate or not; seeds 1–2 mm long, transversely corrugate, corrugations 9–12.

7a. PHACELIA SCOPULINA var. SCOPULINA—*Emmenanthe scopulina* A. Nelson, Bull. Torrey Bot. Club 25:380. 1898.—*Miltitzia scopulina* (A. Nelson) Rydberg, Bull. Torrey Bot. Club 40:479. 1913.—*Miltitzia lutea* var. *scopulina* (A. Nelson) Brand, Das Pflanzenr. IV. 251:131. 1913.—*Phacelia lutea* var. *scopulina* (A. Nelson) Cronquist, Vasc. pls. Pacific Northw. 4:168. 1959.— TYPE: USA, WY, Sweetwater Co., Green River, 31 May 1897, *Nelson 3056* (Lectotype: RM!; isolectotypes: GH! MO! NY! US!; syntype: USA, WY, Sweetwater Co., Green River, 30 May 1897, *Nelson 3026* RM! US!).

Fruiting calyx 5–7 mm long; style and branches 1–2 mm long, pubescent ⅓ to all of its length; capsule apiculate; $n = 12$.

Distribution. Alkaline flats and slopes from southwestern Wyoming to central Nevada, north to southeastern Oregon and adjacent Idaho, disjunct in southwest Montana; flowering May–July.

Phacelia scopulina has been considered a variety of *P. lutea* because in eastern Oregon, where their ranges overlap, there are plants which may appear at first to be intermediate. The two species are, however, quite distinct; individual plants can always be referred to one or the other species after examination of the critical characters. No indication of hybridization has been found.

7b. **Phacelia scopulina** var. **submutica** (J. T. Howell) Halse, stat. nov.—*Phacelia submutica* J. T. Howell, Proc. Calif. Acad. Sci. ser. 4, 25:370. 1944.—TYPE: USA, CO, Mesa Co., DeBeque, 19 May 1911, *Osterhout 4458* (Holotype: Accession Number 163032, RM!; isotype: RM!).

Fruiting calyx 6–8(–10) mm long; style and branches 1.0–1.5 mm long, pubescent at the base; capsule not apiculate or insignificantly so.

Distribution. Local endemic on clay knolls in Mesa County, Colorado, near DeBeque, and disjunct along the Little Colorado River near Winslow, Arizona; flowering May–June.

This taxon is not well enough differentiated to deserve species recognition, but it does merit varietal status. The primary characters by which it is separated from var. *scopulina* are the pubescence on the style and the lack of apiculation of the capsule. The amount of pubescence on the style is a variable character. The apiculation of the capsule is the best character distinguishing the two taxa, although some intergradation is indicated; in var. *submutica* the style base on the capsule may be muticous and in var. *scopulina* the apiculation may be very small.

A collection of this variety from Arizona forms the basis for the reported occurrence in Arizona of *P. glaberrima* (Howell, 1944b). When the plant was collected by Newberry on the Ives' Expedition it was misidentified as *Eutoca* (=*Nama*) *aretioides*. When the type description of *P. glaberrima* was written, Newberry's plant was identified as that species. As far as is known this is the only collection from Arizona of any species in sect. *Miltitzia*.

8. PHACELIA INYOENSIS (Macbride) J. T. Howell, Leafl. W. Bot. 4:16. 1944.—*Miltitzia inyoensis* Macbride, Contr. Gray Herb., new series, 49:41. 1917.—TYPE: USA, CA, Inyo Co., foothills w. of Bishop, 23 May 1906, *Heller 8324* (Holotype: GH!; isotypes: DS! MO! NY! US!).

Stems few to several, ascending to erect, pubescent, capitate-glandular; leaves entire to pinnately few-lobed, pubescent, glandular; flowers 5-merous; calyx segments in flower 2–3 mm long, in fruit 3.5–4.5(–6) mm long; corolla tubular to campanulate, pale yellow, 2–3 mm long, pubescent externally, glabrous internally; corolla scales lacking; filaments glabrous, 1.5–2.5 mm long; style and branches 1 mm long, style glabrous, or with a few hairs at base; ovules 16–21(–27); hypogynous disk relatively prominent; capsule 3–4 mm long, apiculate, pubescent; seeds 0.5–1.0 mm long, transversely corrugate, corrugations 5–8; $n = 12$.

Distribution. Alkaline meadows in northern Inyo and adjacent Mono County, California; flowering May–July.

9. PHACELIA SALINA (A. Nelson) J. T. Howell, Leafl. W. Bot. 4:16. 1944.—*Emmenanthe foliosa* M. E. Jones, Zoe 4:278. 1893.—*Miltitzia foliosa* (M. E. Jones) Brand, Das Pflanzenr. IV. 251:131. 1913.—TYPE: USA, UT, Tooele Co., Deep Creek Valley above Furber, 8 Jun 1891, *Jones s.n.* (Holotype: Accession Number

72887, POM!; isotypes:CAS! DS! MO! POM! UC! US!). Not *Phacelia foliosa* Phil., Anales Mus. Nac. Chile. 53. 1891.

Emmenanthe salina A. Nelson, Bull. Torrey Bot. Club 25:381. 1898.—*Miltitzia salina* (A. Nelson) Rydberg, Bull. Torrey Bot. Club 40:479. 1913.—Type: USA, WY, Sweetwater Co., Bitter Creek, 2 Jun 1897, *Nelson 3105* (Holotype: RM!; isotypes: CAS! GH! MO! NY! US!).

Stems few to several, prostrate to ascending, pubescent, capitate-glandular; leaves entire to pinnately lobed, hirsutulous; flowers 5-merous; calyx segments in flower 2–3(–4) mm long, in fruit 4–5(–6) mm long; corolla tubular, yellow 2–3(–4) mm long, pubescent externally, glabrous internally; corolla scales present or absent; filaments glabrous, 1.0–1.5(–2.5) mm long; style and branches 1 mm long, style pubescent at base only or rarely pubescent to midlength; ovules 7–10; hypogynous disk prominent; capsule 3–4 mm long, apiculate, pubescent; seeds 1.1–1.5(–2) mm long, transversely corrugate, corrugations 9–13.

Distribution.   Alkaline flats and clay slopes in southern Wyoming, western Utah, and central and eastern Nevada; flowering May–June.

Phacelia salina has been considered nothing more than a form of *P. scopulina* by Cronquist (1959) and even Howell (1944b) suggested that it might be an ecologically specialized variant of that species with smaller parts, but its characters are quite stable over its entire range and show no overlap with *P. scopulina*. Its nearest relative, however, is undoubtedly *P. scopulina*.

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ALBERT M. VOLLMER: A MEDICAL DOCTOR WHO LOVED LILIES

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Albert M. Vollmer was born May 14, 1896 in San Diego, California, attended Pomona College as a premedical student during the academic year of 1916–17, served in the U.S. Naval Reserves in 1917 and 1918, and returned to Pomona for the academic years 1918 through 1920. He then entered the University of Pennsylvania School of Medicine and received the M.D. degree in 1924. He was an intern at St. Luke's Hospital in San Francisco in 1924–25, was at Sloane Hospital for Women in 1925–26 and took the National Board examinations in 1926 and served as Visiting Obstetrician and Gynecologist at the San Francisco Hospital in 1926–27. Later he was Chief Obstetrician and Gynecologist at St. Luke's Hospital and was on the staff of Franklin Hospital in San Francisco, and Associate Clinical Professor of Obstetrics and Gynecology at the University of California. He was a member of the American Medical Association and of the Pacific Coast Society of Obstetricians and Gynecologists.

By the early 1930's "Mike", as he was known among his friends, had developed a keen interest in the native lilies of California; and he had spent many weekends and vacation periods scouring the state and adjacent Oregon in search of stands of lilies, from which he collected bulbs and seeds to propagate in his San Francisco home garden. I met him through the kind offices of Dr. Philip Leighton, Professor of Chemistry at Stanford, and from 1937 onward for a bit more than a decade accompanied Mike on field trips throughout California, four lengthy trips into Baja California, and one into northern Sonora and southern Arizona.

Mike corresponded with many others who held intense interests in lilies, both in the United States and abroad. Among these correspondents was Dr. Samuel L. Emsweller, who was Principal Horticulturist in Charge of Ornamental Plants in the experimental gardens of the U.S. Department of Agriculture at Beltsville, Maryland. Mike was instrumental in getting Emsweller to visit California in search of lily seeds and bulbs on four or five different occasions. Mike also collected additional seeds and bulbs, which he forwarded to Beltsville in support of research there on propagation and culturing of these plants

and of investigations of the diseases that frequently made it very difficult to grow certain species in gardens and greenhouses.

Mike was very careful to avoid digging large numbers of bulbs and, whenever possible, preferred to collect seed instead of, or in addition to, a small number of bulbs. He was acquainted with Carl Purdy and obtained some material from that dealer, but disapproved of Purdy's practice of digging large numbers of bulbs of various liliaceous plants. More than once Mike made three or four separate trips to a particular locality in order to obtain mature seeds from a threatened stand of lilies rather than dig any bulbs whatever. Furthermore, he took pictures in color with both still and moving picture cameras in order to preserve information about habitats of the plants.

In commenting upon the work Emsweller was carrying forward, Mike wrote, "Anyone who has tried to grow the California lilies has discovered that some are difficult and fail to become established. Dr. Emsweller has had this experience, and for him this was a challenge. The first step in solving this problem was to get firsthand information, resulting in field trips, to see the lilies growing in their native habitats, listing the associated vegetation, and terrain in which they grow, rainfall, variations in temperature, growing season, collections of samples, culturing the soil, digging bulbs, collecting seed and raising them from seed. He is the only person who has seen all the American lilies growing in their native habitat".

Mike was instrumental in helping Emsweller find several rare California lilies growing in the field, and in returning later to collect seed after they had found only plants in bud or with immature capsules. He carried on this field work while serving an active practice from his office on Post Street in San Francisco and attending patients in the hospital!

When my appointment as Scientific Director of the Arctic Research Laboratory took me away from Stanford for several years, Mike assumed active support of the work of a graduate student at Stanford, Mr. Lawrence Beane, who had planned to work beyond his Master's degree, but circumstances made this plan impracticable. However, Larry continued to hold a keen interest in lilies, and he and Mike made a number of extensive field trips to isolated localities in the state so Larry could see the plants under natural conditions and paint them from fresh material.

As an outcome of these expeditions Lawrence Beane published a paper in which he and Vollmer jointly named two new species of *Lilium,* and Larry made three new combinations, supplied a new name for a previously published variety, and recognized a specific name proposed in 1930 by Marcus E. Jones. The last entity had been considered no more than a synonym by most California botanists (Beane, 1955).

Dr. Vollmer also collected herbarium specimens of most California lilies that he had originally collected for propagation, and sent much material to the California Academy of Sciences, the University of California, Stanford University, and to the U.S. National Herbarium in Washington, D.C. He collected and cultivated representatives of such genera as *Calochortus* and *Fritillaria* and of several species within the Amaryllidaceae.

Dr. Vollmer published several papers in the *Lily Yearbook* and in garden journals. In these papers he contributed substantially to knowledge about geographical distribution, soil requirements, and flowering periods of our native lilies (Vollmer, 1954, 1956, 1959). The 1956 paper was presented in person, along with colored moving pictures of many of California's lilies, before the Royal Horticultural Society in London.

It seems appropriate that recognition should be given to the excellent field work carried on by Dr. Vollmer, to the support he gave so generously to professional botanists, and for his devotion to saving the native stands of lilies in our state. I wish that such recognition might have been provided before Mike's death in the spring of 1977, a few weeks before his 82nd birthday. He was a staunch friend who supported my field operations through a decade, and took me to several out-of-the-way lily localities in California.

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FIVE NEW SPECIES OF MEXICAN ERIGERON (ASTERACEAE)

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Abstract

Five new species of *Erigeron* from northern México are described—**E. unguiphyllus,
E. cuatrocienegensis, E. wellsii, E. stanfordii,** and **E. solisaltator.** The first two are
probably obligate gypsophiles; the second two are from the region of Peña Nevada in
southeastern Nuevo León and west-central Tamaulipas; the last is from northeastern
Chihuahua; all are narrow endemics. A new name, **E. gypsoverus,** is proposed for a
previously described gypsophilic *Erigeron*.

Continuing studies of *Erigeron* have brought to light five new
species. Two of them grow in the region to be covered by the Chi-
huahuan Desert Flora, currently in preparation by M. C. Johnston
and J. Henrickson. Two of these (from Coahuila and from San Luis
Potosí) appear to be gypsophilic and are discussed with relation to
other known *Erigeron* gypsophiles from northern Mexico. Two others
apparently are restricted to the relatively small area of Peña Nevada
in west-central Tamaulipas and southeastern Nuevo León and join a
number of other endemics known from there. The distributions of the
new species, as well as of several of their possible close relatives, are
mapped in Fig. 1. A new name is proposed for a previously described
species that may be related to the new gypsophiles.

Erigeron wellsii Nesom, sp. nov.

Erigeron scaposus DC. affinis aliquantum, differt praecipue rhizo-
mate crasso fibris aliquantum carnosus, foliis caulinis non-amplectens,
et corollis radii ligulis latioribus non circinatis ad maturitatem (Fig.
2A).

Perennials with long and thick fibrous roots, from a thick, often
horizontal rhizome 0.5–4.0 cm long; caudex simple, producing 1–3
(–4) upright, monocephalous stems. Stems 15–31 cm tall, simple, mod-
erately pubescent with retrorse, closely to loosely appressed or some-
times spreading, extremely thin, twisted trichomes 0.8–2.2 mm long.
Basal leaves in a persistent rosette, 1.8–6.5 cm long, blades 0.8–2.8
cm wide, obovate, with 2–5 pairs of crenate to crenate-serrate teeth,
attenuate to petiole that is ¼–⅓ as long as leaf, with base usually
purplish; cauline leaves 6–10, alternate, sessile, not clasping, sharply
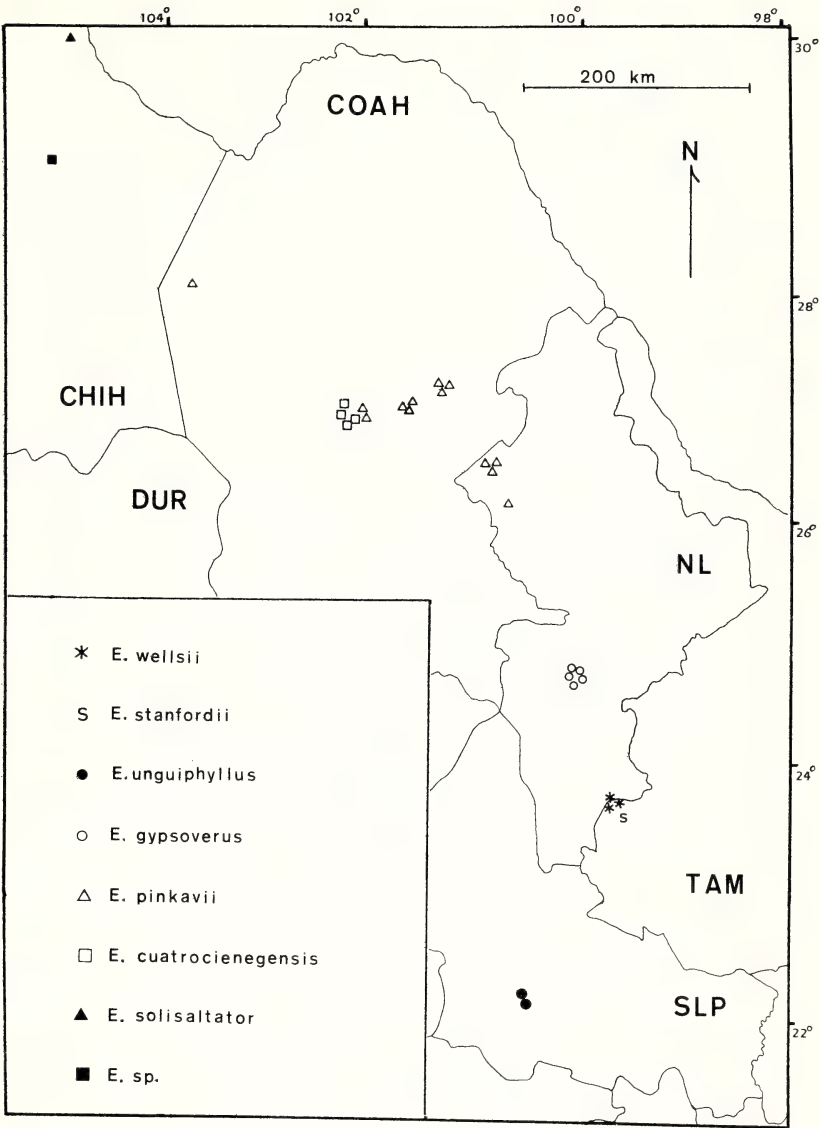
FIG. 1.   Distribution of *Erigeron* species in northeastern Mexico.

reduced in size upward, the lower narrowly oblong to oblanceolate, to 23 mm long and 4 mm wide, the upper linear bracts; leaves moderately pubescent with erect to ascending trichomes, margins eciliate. Heads 1–3(–4) on peduncles 17–85 mm long; involucres hemispheric,
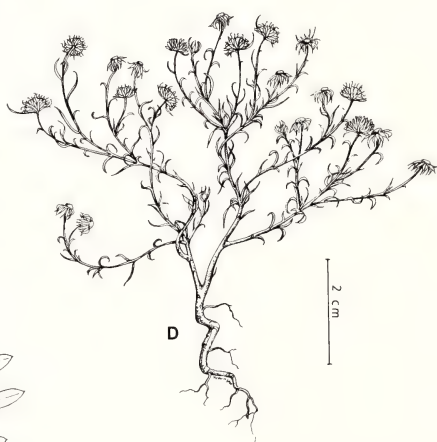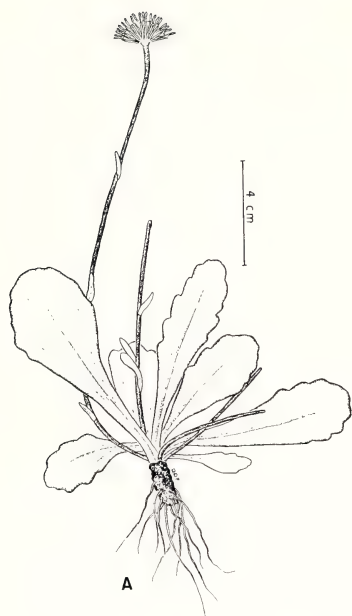
14–19 mm wide (pressed); phyllaries in 3–4 equal to unequal series, probably reflexing after release of achenes, lanceolate to elliptic-lanceolate, often purplish, inner 7.2–9.5 mm long, 0.8–1.2 mm wide, when unequal outermost ½–¾ as long as inner, evenly thin or sometimes with 2 lateral thickenings near base, sparsely pubescent with thin trichomes; receptacles not observed. Ray flowers 70–135 in 2–3 series, corollas white with broad lilac midstripe, drying white to completely lilac, 10.5–14.0 mm long, 0.9–1.5 mm wide, not reflexing or curling with maturity. Disc corollas tubular to narrowly funnelform, constricted in lower ¼–⅓, not indurated, 3.5–4.5 mm long; style branches 0.7–0.9 mm long, including the shallowly triangular to shallowly deltate collecting appendages 0.1–0.3 mm long. Achenes 2.0–2.2 mm long, 0.8 mm wide, with 2 thin, orange ribs, sparsely strigose; carpopodium 5–8 cells high; pappus of ray and disc achenes similar, of (20–)25–30 very slender bristles ca. ⅚ the disc corolla height but somewhat unequal in length, simple or rarely with a few short and inconspicuous outer setae.

TYPE: México, Tamaulipas, in mountains with steep cliffs, 10 km above and w. of Miquihuana, in meadows with pines present, 3110 m, 4 Aug 1941, *L. S. Stanford, K. L. Retherford, and R. D. Northcraft 631* (Holotype: NY!; isotypes: GH!, MO!, OS!).

PARATYPES: Nuevo León: rare, growing in deep moss on ne. slope of Picacho Onofre, 150 m below the summit, ca. 3300 m, small opening in pine woods, Cerro Peña Nevada, ca. 30 km ene. of Doctor Arroyo, 1 Aug 1977, *Nesom R590* with C. Wells (LL, MEXU); in open pine forest, occasional, Peña Nevada, 42 km (26 mi) ne. of Doctor Arroyo, w. side of mt. known locally as Picacho Onofre, 3300 m, 4 Jul 1959, *Beaman 2705* (MSC, US); Tamaulipas, Cerro Peña Nevada, limestone derived soils, exposed open areas, 1 Jun 1974, *Patterson 1518* (LL).

The isotype at MO bears the label data given above, but it is presented on a "correction label". The sheets at GH, NY, and OS have the same collection number, but the locality data are "4 km w. of Miquihuana on limestone ridges in open pine forest". *Erigeron wellsii* was tentatively recognized as an undescribed species by I. M. Johnston, who distributed type sheets as "*E. retherfordii* sp. nov.". However, the herbarium name was never validated by publication. A number of other unvalidated names on collections made by Stanford et al. and distributed by Johnston as "types" also have been found: *Acacia*

←

FIG. 2.   Habit sketches of four new *Erigeron* species. A. *Erigeron wellsii* Nesom. Isotype (MO). B. *Erigeron solisaltator* Nesom. Holotype (LL). C. *Erigeron stanfordii* I. M. Johnston ex Nesom. Holotype (GH). D. *Erigeron unguiphyllus* Nesom. *Hartman and Funk 4098* (OS).

trium, Sphaeralcea oxyloba, Mentzelia retherfordii, Erigeron jimul-cans (=*Erigeron commixtus* Greene), *Erigeron northcraftii* (=*Erigeron pubescens* HBK.), and *Erigeron stanfordii*. The name applied here to the Peña Nevada *Erigeron* recognizes Christopher J. Wells, who is currently a graduate student in botany at Mississippi State University.

The monocephalous stems with very thin, retrorse trichomes, basal rosette with reduced cauline leaves, thin phyllaries, and simple pappus are characters that *Erigeron wellsii* has in common with forms of the *E. scaposus* DC.–*E. longipes* DC. complex. However, the following features of the new species distinguish it from all plants of that complex to which it might appear similar: short, thick rhizome with long, thick, fibrous roots; non-clasping cauline leaves, and relatively broad rays that do not curl upon wilting or maturity. *Erigeron palmeri* A. Gray grows sympatrically with *E. wellsii* and has a similar growth habit, but the former has glabrous or glabrate leaves and stems, leaves with finely serrate or merely mucronulate, ciliate margins, and long petioles. Though plants of *E. palmeri* also are fibrous-rooted, they lack rhizomes.

Pollen grains from several plants of *Erigeron wellsii* average 25 μm in diameter with a range of 22–28 μm. Stainability in cotton blue averages 90 percent; micrograins are uncommon. The relatively large, stainable grains and the presence of micrograins suggest that these plants may be tetraploid.

Erigeron stanfordii I. M. Johnston ex Nesom, sp. nov.

Herbae perennes affinitatis obscurae, rhizomata tenuia, caules monocephales, patenti-pubescentes dense, pars supera caulis fere scaposa, folia strigosa dense et paginis inferis griseo-viridis, phyllaria lineari-triangularia in 4–6 series aequilongas (Fig. 2C).

Perennials from a long, thin, horizontal rhizome; upright caudex branches 0.5–9.0 cm long, produced at short intervals, bare except for dead leaves or petiole bases. Stems 18–24 cm tall, produced singly at tips of caudex branches, simple or with 1–3 short branches on lower ⅓, moderately pubescent with thin, spreading trichomes 0.1–0.6(–0.9) mm long. Leaves on lower ¼–⅓ of stem, 20–45 mm long, blades 5–9 mm wide, elliptic to elliptic-oblanceolate, entire or with 1–3 shallow, serrate teeth, attenuate to petiole ⅓–½ as long as leaf, not clasping, gray-green below, darker green above, moderately to densely pubescent with ascending trichomes, usually more densely below and often nearly pilose, margins eciliate. Heads solitary, peduncles 15–18 cm long with 1–4 linear bracts 3–14 mm long; involucres hemispheric, 10–13 mm wide (pressed); phyllaries in 4–6 imbricated series, reflexing after release of achenes, linear-lanceolate, stramineous with a dark midline, inner 6.0–8.0 mm long, 0.3–0.4 mm wide, mostly glabrous,

outer densely pubescent with vitreous, spreading trichomes, densely and minutely granular–glandular; receptacles shallowly convex. Ray flowers 45–76 in 1–2 series, corollas drying white, lilac-tinged, or yellowish, 11.0–12.7 mm long, 1.5–1.8 mm wide, sometimes curling with maturity. Disc flowers narrowly funnelform, barely or not constricted in lower ¼, 4.0–5.0 mm long; style branches 0.8–0.9 mm long, including the shallowly triangular to shallowly deltate collecting appendages 0.1 mm long. Achenes ca. 2.0 mm long and 0.4 mm wide, with 2 thin, orange ribs, sparsely strigose; carpopodium 5–8 cells high; pappus of ray and disc achenes similar, of 15–21 slender bristles ⁴/₅ the disc corolla height, with a few, inconspicuous, outer setae 0.1–0.3 mm high.

TYPE: México, Tamaulipas, in hills 19 km se. of Miquihuana on road to Palmillas in narrow, deep, and moist arroyo, 2250 m, 11 Aug 1941, *L. S. Stanford, K. L. Retherford, and R. D. Northcraft 838* (Holotype: GH!; isotypes: MO!, NY!, OS!).

I. M. Johnston's name is validated here to commemorate L. S. Stanford, who led collecting trips in 1941 and 1949 to northeastern Mexico. *Erigeron stanfordii* is a very distinctive taxon, but the direction of its affinities within the genus is not clear. It is known only from the type collection, and along with *Erigeron wellsii,* is endemic to the region of Peña Nevada. The most distinctive characters of *E. stanfordii* are the following: slender, creeping rhizomes bearing upright stems; clustered, undifferentiated basal and lower cauline leaves, gray-green and densely pubescent below; peduncles long, leafless, densely pubescent with thin, spreading trichomes, bearing solitary heads; phyllaries very narrowly lanceolate, in 4–6 imbricated series, inner straw-colored with a very conspicuous, narrow, greenish-brown midline. Judging from the relatively large size of the pollen grains, averaging (18–)22(–24) μm in diameter, and high stainability (98 percent), the plants are probably sexual tetraploids.

Erigeron unguiphyllus Nesom, sp. nov.

Habitu *Erigeron gypsoverus* Nesom, sed distinctus phyllariis glandulosis pubescenta patenti, radiis parvioribus numerosibus, pappo setarum pauciorum (Fig. 2D).

Perennials with a woody taproot, highly branched at base from a relatively thick caudex region, producing a low, compact cluster of wiry, crowded-appearing, branched stems. Stems 5–9 cm tall, erect or ascending, moderately pubescent with loosely appressed to ascending or mixed spreading-ascending-appressed trichomes 0.2–0.5 mm long, spreading just under the heads, abundantly but inconspicuously granular-glandular. Basal leaves absent at flowering, cauline 2.5–5.5 mm long, 0.4–0.6 mm wide, not reduced in size upwards except for occasional peduncular bracts, sessile, margins entire, eciliate, apices

apiculate with a distinctive cap of indurated tissue. Heads numerous on peduncles 1–17 mm long; involucres shallowly hemispheric, 3.5–5.0 mm wide (pressed); phyllaries in 2–3 unequal to imbricated series, reflexing after release of achenes, lanceolate to elliptic-lanceolate, yellowish with a brown midregion, inner 2.1–3.0 mm long, 0.5–0.8 mm wide, sparsely to moderately pubescent with spreading trichomes, moderately to densely punctate-glandular; receptacles shallowly to steeply convex. Ray flowers 60–110 in 2–3 series, corollas white, 2.5–3.9 mm long, 0.2–0.5 mm wide, not curling or reflexing. Disc corollas tubular, slightly constricted in lower $^1/_5$, slightly indurated just above, 1.5–2.1 mm long; style branches 0.3–0.4 mm long, including the triangular to deltate collecting appendages 0.1–0.2 mm long. Achenes 0.8–1.0 mm long, 0.2–0.3 mm wide, with 2 thin ribs, sparsely strigose; carpopodium 3–7 cells high; pappus of ray and disc achenes similar, of 6–9 bristles $^3/_5$–$^4/_5$ the disc corolla height, with a conspicuous outer series of setae, squamellae, or scales 0.3–0.8 mm high. $n = 9$.

TYPE: México, San Luis Potosí, Minas de San Rafael, Jul 1911, *C. A. Purpus 5020* (Holotype: US!; isotypes: F, GH 2 sheets!, MEXU!, MO 2 sheets!, NY 2 sheets!, UC!, US!). The number for this collection in Purpus' notebooks at UC is *5120,* although the sheets were distributed as *5020.*

PARATYPES: San Luis Potosí: common on barren, gypseous (?) soil, Hwy 70, 9.6 km (6 mi) e. of Río Verde, 14 Aug 1976, *Hartman and Funk 4098*—voucher for chromosome count, $n = 9$ (ENCB, LL, MEXU, OS, RM); 10 km al e. de Río Verde, sobre el camino a Boquilla, 1000 m, 20 Jan 1959, *Rzedowski 9547* (ENCB); ca. 4 km al n. de Río Verde, sobre el camino a Pastora, 1000 m, 21 Jan 1959, *Rzedowski 9568* (ENCB); ca. 15 km al n. de Río Verde, sobre el camino a Pastora, 1000 m, 21 Jan 1959, *Rzedowski 9588* (ENCB).

Erigeron unguiphyllus is characterized by: a perennial, low, compact habit with wiry stems and tiny, linear leaves that are usually somewhat curved and terminated by a conspicuous, indurated apiculum or mucro; loosely ascending stem pubescence of short hairs; 2–3 series of unequal phyllaries that are spreading-pubescent and minutely punctate- or viscid-glandular; numerous and relatively short ray flowers; and a conspicuously double pappus of 6–9 fragile bristles and an outer series of short setae or scales. The diploid chromosome count of $n = 9$ was made from several cells at diakinesis; meiosis and tetrad formation were regular. Pollen grains are even-sized, averaging about 17.5 μm in diameter and staining 99 percent in cotton blue.

According to Sousa (1969), Purpus collected several times during 1919 and 1911 at Minas de San Rafael (or Minas de San Rafael y Huascama). These mines are located in the vicinity of Río Verde just south of Huascama—22°13′N, 100°15′W, about 96 km due east of San Luis Potosí. *Erigeron unguiphyllus* joins a number of other new species first collected by Purpus in this immediate vicinity. The di-
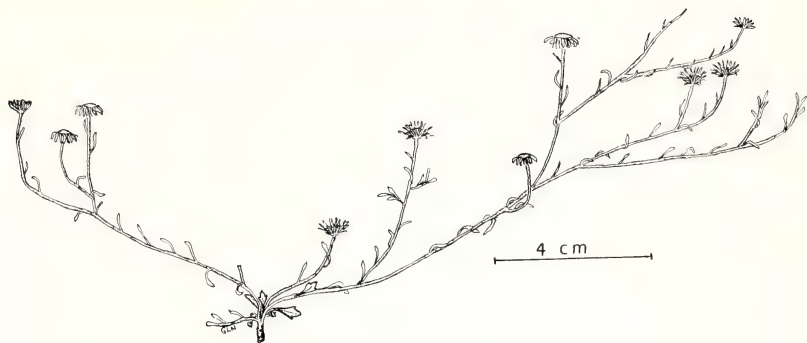
Fig. 3.   Habit sketch of *Erigeron cuatrocienegensis* Nesom. Holotype (ASU).

minutive growth habit of these plants and their resemblance in habit to other known gypsophilic *Erigeron* species suggest that the mines are associated with gypsum outcrops.

Erigeron cuatrocienegensis Nesom, sp. nov.

Habitu *Erigeron pinkavii* Turner affinis, differt imprimis pubescentia brevissima appressa caulium et phyllarorum, foliis caulinis inferis eciliatis, radiis paucioribus, et pappo setarum plus numerosarum (Fig. 3).

Perennials from a woody taproot, producing up to 4 stems at the base from a simple caudex, or the caudex with several very short axes, each bearing erect stems. Stems 6–21 cm high, erect or ascending, simple or usually few-branched, stems and leaves densely strigose with antrorsely appressed, short (0.1–0.6 mm), white trichomes. Basal leaves deciduous after early flowering, ca. 10–18 mm long, blades 1–3 mm wide, entire or with 1–2 pairs of shallow serrations, gradually narrowed to petiolar region; cauline becoming entire, linear, and sessile on upper ⅔ of stem. Heads terminal on peduncles 3–30 mm long, involucres shallowly hemispheric, 5–7 mm wide (pressed); phyllaries in 3 imbricated series, reflexing after release of achenes, innermost widely oblanceolate, 0.6–0.8 mm wide, 2.7–3.0 mm long, with narrow scarious margins, outermost narrower and ca. ½ as long as inner, moderately to densely pubescent with loosely appressed, white trichomes; receptacles slightly convex. Ray flowers 30–55 in 1–2 series, corollas white, sometimes drying lavender-tinged, 4.4–7.1 mm long, 0.6–0.9 mm wide, not curling or reflexing with maturity. Disc corollas tubular, constricted in lower $^{1}/_{5}$, somewhat indurated above, 1.8–2.3 mm long; style branches 0.4 mm long, including the triangular to deltate collecting appendages 0.2 mm long. Achenes 1.0–1.2 mm long, 0.3–0.4 mm wide, with 2(3) thin ribs, sparsely strigose; carpopodium

1–3 cells high; pappus of ray and disc achenes similar, of 18–27 bristles ⅔–⅚ the disc corolla height, usually with a few, inconspicuous, outer setae up to 0.3 mm high.

TYPE: México, Coahuila, Poso de Anteojo (ca. 12 km wsw. of Cuatro Ciénegas), 12 Jun 1968, *E. Lehto, D. J. Keil, and D. J. Pinkava 5511* (Holotype: ASU!).

PARATYPES: Coahuila, desert scrub and bajada, near cave, ne.-facing slope near tip of Sierra de San Marcos, 21 Mar 1972, *Pinkava 10503* (ASU); nw. of Laguna Churince, (ca. 17 km sw. of Cuatro Ciénegas), 13 Aug 1967, *Cole et al. 3766* (ASU); Laguna Chiqueros complex of lakes and streams w. of stabilized dunes of Poso de la Becerra, ca. 16 km (10 mi) sw. of Cuatro Ciénegas, 14 Aug 1967, *Cole et al. 3849* (ASU).

All collections of *Erigeron cuatrocienegensis* have been made within about a 17 km distance wsw. to ssw. of Cuatro Ciénegas (Fig. 1). This narrow endemic is probably an obligate gypsophile, although the occurrence of a gypseous substrate is not mentioned in the collection data. From this immediate locality five other narrowly endemic, gypsophilic Asteraceae of other genera are known, as well as an endemic *Phacelia* (see Atwood and Pinkava, 1977).

Erigeron pinkavii, another narrowly endemic gypsophile, also grows in the Cuatro Ciénegas area and has a growth habit similar to that of *E. cuatrocienegensis,* although this is probably a convergent adaptive complex of characters. Dissimilarities in other characters suggest that their closest relationships are probably not with each other. Their geographic ranges appear to be parapatric or weakly allopatric (Fig. 1); *Erigeron pinkavii* has been collected mostly to the n., ne., and e. of Cuatro Ciénegas. The spreading stem and phyllary pubescence, ciliate leaves, 60–90 ray flowers, and the double pappus of 7–11 bristles and a conspicuous outer series of setae or scales are characters of *E. pinkavii* that mark it as clearly distinct from *E. cuatrocienegensis.*

Judging from the small and even-sized pollen grains, averaging about 18.5 μm in diameter, with a stainability of greater than 99 percent, plants of *Erigeron cuatrocienegensis* are probably diploid. Powell and Powell (1977) reported that *E. pinkavii* is also diploid, and their data suggest that among gypsophilic Asteraceae of the Chihuahuan Desert, diploids are more numerous than polyploids.

Besides *Erigeron pinkavii* and the two new gypsophiles described in this paper, still another gypsophilous, narrowly endemic *Erigeron* has been described from northeastern Mexico, *E. gypsophilus* Turner (Turner, 1975). However, *E.* × *gypsophilus* Beauverd (Beauverd, 1930) holds priority over the 1975 binomial; thus, the plants from south-central Nuevo León are given a new name: **Erigeron gypsoverus** Nesom, nom. nov.—based on *Erigeron gypsophilus* Turner, Wrightia 5:118. 1975. A chromosome count from a recent collection shows this species to be diploid with $n = 9$ (*Nesom R1008:* LL, MEXU).

All four of these gypsophilic endemics apparently are diploid, all have very restricted ranges in northern Mexico (Fig. 1); but each is strongly differentiated morphologically, and the nature of their inter-relationships is not clear. Of great interest would be a knowledge of whether they form a natural group, reflecting a gypsophilous tendency in the ancestral stock from which they radiated, as in examples from several other genera discussed by Turner and Powell (1979), or whether each has independently attained its gypsophily.

From northeastern Chihuahua a collection has been made (Fig. 1) of several plants (*Chiang, Wendt, and Johnston 9851B*, LL) that are very similar to *Erigeron gypsoverus* in growth habit. In addition, the label data indicate that they were growing "above 'Los Morteros' gypsum mine . . . (in) calcareous (and slightly gypseous?) gravel". However, these plants have more herbaceous bases and a pubescence of thicker, widely spreading or ascending below, trichomes on the stems, leaves, and phyllaries. They also have tiny heads with few rays and narrowly oblanceolate, entire leaves, and they produce abortive pollen, indicating that they are probably polyploid. Although these plants are distinctively different from all of the other four known gypsophiles, their probable polyploidy and similarity to some forms in the variable *E. modestus* agamic complex bid circumspection before giving them a formal taxonomic circumscription. Further collections and observations may show that they warrant recognition as a distinctive species.

Erigeron solisaltator Nesom, sp. nov.

A *Erigeron coronarius* Greene affinis, differt phyllariis erectis ad maturitatem receptaculis conicis, et corollis radii ligulis angustis non reflexis ad maturitatem (Fig. 2B).

Annuals from a very slender taproot, producing 1–4 upright stems from a simple caudex. Stems 12–15 cm tall, few-branched near the middle; moderately pubescent with spreading or ascending, whitish trichomes 0.1–0.7 mm long, obscurely granular-glandular. Basal leaves mostly deciduous by flowering, 5–12 mm long, blades obovate to oblanceolate, 2–4 mm wide, entire or shallowly few-toothed, attenuate to narrow petiole ca. ½ as long as leaf; cauline leaves oblanceolate to linear-oblanceolate, sessile to subsessile, entire, lower 6–15 mm long, 2–3 mm wide, gradually reduced in size upwards to linear bracts. Heads few, solitary, peduncles 5–35 mm long, involucres shallowly hemispheric, 5–6 mm wide (pressed); phyllaries in 3 subequal series, remaining erect after release of achenes, oblanceolate, with wide, light or scarious margins, inner 2.8–4.2 mm long, 0.6–0.8 mm wide, outermost ½–⅓ as long as inner, sparsely pubescent with white, spreading trichomes, densely granular-glandular; receptacles hemispheric to very steeply convex. Ray flowers 85–120 in 1–2 series, not reflexing with maturation, corollas white, drying with lavender tips, 3.7–5.5

mm long, 0.2–0.4 mm wide. Disc corollas tubular to narrowly fun-
nelform, constricted in lower $^1/_5$, indurated and inflated above, 1.8–
2.1 mm long; style branches 0.4 mm long, including the shallowly to
very shallowly triangular collecting appendages 0.1–0.2 mm long.
Achenes 0.9–1.0 mm long, 0.5 mm wide, with 2 thin ribs, sparsely
strigose; carpopodium 5–8 cells high; pappus of ray and disc achenes
similar, of 8–9 persistent bristles, with an outer laciniate corona or
series of scales ca. 0.2 mm high.

TYPE: México, Chihuahua, zacatal, *Prosopis glandulosa, Koeber-
linia spinosa,* and *Hilaria mutica,* fine-textured, calcareous alluvium
in flat (bottom of bolson), 1185 m, 0.5 km s. of Rancho El Llano, 14
Jun 1973, *M. C. Johnston, T. Wendt, and F. Chiang 11317F* (Holo-
type: LL!).

Erigeron solisaltator has many similarities with the taxa known as
Achaetogeron linearifolius Watson and *Achaetogeron ascendens*
Greenman and with *Erigeron coronarius* Greene (Nesom, 1980). It
differs from the first two in its annual duration and in its normal
complement of persistent pappus bristles, from the third in having
non-reflexing phyllaries, and from all three in having hemispheric re-
ceptacles and non-reflexing ligules. The location and habitat of *E.
solisaltator* are also distinctive and different from any of its probable
relatives. The single known collection was made in northeastern Chi-
huahua near the Rio Grande (Fig. 1) in the shrubby vegetation of a
small, undrained basin. The epithet means "sun-dancer".

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THE DIANDROUS, HYPOSTOMATIC WILLOWS (SALICACEAE) OF THE CHIHUAHUAN DESERT REGION

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ABSTRACT

A key is provided for the five species of *Salix* in the Chihuahuan Desert Region with two-stamened flowers and leaves with stomates almost confined to the lower surfaces. One species, *S. lasiolepis* Bentham, was previously known and named; three new species are described from the state of Coahuila: **S. pattersonii, S. riskindii,** and **S. wendtii.** The fifth species, also from Coahuila, is discussed but remains nameless because it is known only from two sterile collections.

In the Chihuahuan Desert Region, delineated for floristic purposes by Johnston (1977), willows occur in a few mesic habitats, especially along the Rio Grande and its tributaries and in even more areally restricted and scattered montane canyons and high slopes. Climatic vagaries and logistical difficulties of exploration have so far prevented the gathering of comprehensive material of willows in this region and seem likely to inhibit such gathering for years to come. The challenge of future exploration is to visit each remote population at appropriate seasons in order to collect specimens representing both sexes at various stages of development with a high degree of confidence that the specimens are conspecific. Until such material is forthcoming, treatments of the willows of the Chihuahuan Desert Region must be considered even more preliminary and tentative than treatments of willows in other regions.

Notwithstanding the incompleteness of the herbarium stores, it has been necessary recently to prepare a taxonomic treatment of *Salix* for the *Chihuahuan Desert Flora* being compiled by Dr. James Henrickson and me. I present here some of the results of my study. Because of space limitations I omit further mention of the arboreal, pleiandrous "black" willows, all of which have been fairly well understood by Schneider (1918), Ball (1950, 1961) and Dorn (1976, 1977) and which in this region are found at relatively low altitudes along the Rio Grande and its tributaries. I also exclude from further consideration the species of the very poorly named *Salix* sect. *Longifoliae* Andersson, namely *S. taxifolia* Humboldt, Bonpland & Kunth, *S. exigua* Nuttall and *S. interior* Rowlee. These three species, although diandrous, have relatively loosely flowered catkins and their leaf-blades have almost as many stomates on the upper as on the lower surface. They are also

fairly well understood taxonomically, though far less well than are the "black" willows. With the exception of *S. taxifolia,* the members of sect. *Longifoliae,* like the "black " willows, are nearly restricted to the lower altitudes along rivers and creeks.

The subjects of this paper are the diandrous, multistemmed shrubs or low trees with dense ascending and spreading catkins and spreading leaves with stomates almost entirely absent from their upper surfaces. In the entire region, an area almost as large as California, only a few mountain ranges provide the mesic canyons and slopes suitable for these willows: in Texas, the Davis, Chisos, and Vieja mountains; in Chihuahua, the Sierra Rica; and Coahuila, the Sierra Maderas del Carmen, the Sierra de la Madera, and, at the extreme eastern margin, the Serranías del Burro. From the entire Mexican portion of this region, Johnston (1944) saw only one specimen of this species-group, a sterile specimen from the Sierra de la Madera. Since 1970, mainly through the strenuous and perceptive fieldwork of David H. Riskind, Tom Wendt, Tom Patterson, and Emily J. Lott, several collections have accumulated from northern Coahuila that represent three distinct new species. Study of a recent collection of the Sierra de la Madera population reinforces my suspicion that it represents still another new taxon, but because flowers and fruits are still not available, I refrain from proposing a name for it.

Taxonomic Treatment

Key to species

Lower surfaces of leaves densely canescent-pubescent with antrorse, silky, white hairs, or glabrate.

Aments appearing in February and March, rarely later, on leafless branches of the previous year; leaf-blades oblanceolate to linear-lanceolate; stamen-filaments joined 0.2–0.7 of their length.

Ovaries wholly glabrous; filaments joined only 0.2–0.3 of their lengths . . . . 1. *S. lasiolepis.*

Ovaries hairy at least along lines of dehiscence, sometimes all over; filaments joined more than 0.5 of their length . . . . 2. *S. riskindii.*

Aments appearing in May or August at end of more or less leafy ament-tipped lateral twigs; leaf-blades more or less elliptic; filaments free (unknown in No. 3).

Aments appearing in May with the leaves, much exceeding twig-leaves; leaves entire . . . . 3. *S. pattersonii.*

Aments appearing in August with mature summer leaves; leaves serrulate . . . . 4. *S. wendtii.*

Lower surfaces of leaves with closely appressed, scattered, rufous hairs. . . . . 5. Sp. nov.?

1. *Salix lasiolepis* Bentham, Pl. Hartweg. 335. 1857.—TYPE: USA, CA, banks of the Salinas and Carmel Rivers, near Monterey, *Hartweg 1955* (Holotype: K!).

Salix lasiolepis var. *bracelinae* Ball, J. Wash. Acad. Sci. 40:331. 1950.—TYPE: USA, CA, Contra Costa Co., Antioch, *Eastwood 3729* (Holotype: US!).

Description of material from the Chihuahuan Desert Region: trees or shrubs, usually multi-trunked; one-year-old twigs brownish, rarely pruinose; older twigs olive-green to yellow-brown or commonly orange, internodes 3–8 mm long, with usually ascending-appressed but sometimes spreading, crisp, gray-white hairs 0.3–0.5 mm long when very young, then glabrate; axillary (winter) buds prominent, often 3–6 mm long, hairy like the youngest twigs. Leaf blades linear-lanceolate to linear-oblanceolate, (4–)5–8(–11) cm long, 6–12(–18) mm wide, usually inconspicuously gland-toothed with teeth antrorse-appressed, or nearly entire; abaxial surface with close, white, silky or crisped hairs 0.3–0.8 mm long to quickly glabrate in some specimens, epidermis glaucous to merely pale green; adaxial surface darker green, lustrous and essentially glabrous except on midveins, when very young some leaves with appressed-antrorse silky, white hairs 0.3–0.8 mm long; petioles 2–7 mm long; stipules almost always absent, extremely small when present. Staminate aments: precocious in March or less commonly appearing in July in axils of mature leaves, ascending-appressed, 9–18 mm long, 5–6(–8) mm thick; scales 1.3–1.6 mm long, obovate, blunt, appressed-ascending, abaxial surface with antrorse silky white hairs 0.7–1 mm long; adaxial pubescence similar except glabrous and glandular in lower third; filaments ca. 3–3.5 mm long, joined 1–1.3 mm at base, free 1.7–2.7 mm above; anthers rotundly or narrowly horseshoe-shaped, 0.3–0.4 mm long and wide. Pistillate aments: precocious in March; 1–1.5 cm long, 6–8 mm wide, ca. 50-flowered, dense; scales and flowers at first ascending, later spreading; scales obovate, blunt, 0.6–1 mm long, with antrorse, silky, white hairs 0.6–1 mm long; stipes ca. 0.5 mm long; styles 0.3–0.5 mm long, stigmas 0.2–0.3 mm long. Fruit 2.5–3 mm long, glabrous; seeds ca. 0.7–0.8 mm long.

In this region, *S. lasiolepis* is known from wooded creek-canyons in igneous-rock mountains, principally in the Davis Mountains of trans-Pecos Texas, but with smaller populations in the Chisos and Vieja mountains of trans-Pecos Texas, the Sierra Rica of extreme northern Chihuahua and the Sierra Maderas del Carmen of extreme northwestern Coahuila. The localities are all above 1400 m elevation.

2. **Salix riskindii** M. C. Johnston, sp. nov.

Frutices multicaules vel etiam arbores parvae, ramuli hornotini folioli dense pubescentes; laminae foliorum oblanceolatae 3–7 cm longae

FIG. 1. *Salix riskindii* M. C. Johnston. A. Twig with inflorescences. B. Leafy twig.

9–15 mm latae persistente dense pubescentes (subtus densius) pilis antrorsis adpressis sericeis albis, petioli (1–)2–3 mm longi pubescentes. Amenta praecocia verna adscendentia staminata 15–25 mm longa 8–12 mm crassa; filamenta 2 fere glabra partibus coalescentibus 2–3 mm longis partibus liberis 1–2 mm longis; squamae fructiferes 1–1.5 mm longae ca 1 mm latae pubescentes pilis 1–2 mm longis; ovaria ca 3 mm longa omnino pubescentes vel pubescentes non nisi secus suturas (Fig. 1).

Multi-stemmed shrubs 1–3 m tall or even multi-trunked small slender trees to 7.5 m tall (*Wendt and Lott 126*); leafy twigs of the season brown-gray, densely pubescent with silky, gray-white, somewhat crisped, appressed, spreading hairs; axillary (winter) buds prominent, 5–8.5 mm long, hairy like the youngest twigs. Leaves expanding in April after flowering is completed, apparently ascending or spreading

(not drooping); leaf blades (3–)6–7(–12) cm long, 9–15 (–19) mm wide, oblanceolate, entire, persistently densely pubescent (more densely so beneath) with antrorse, appressed, silky, whitish hairs; stomates present beneath, rare or absent above; petioles (1–)3–11 mm long, pubescent like blades. Flowers appearing in February and March on leafless branches of previous year; aments abundant on twigs but solitary at nodes, dense, sessile, ascending (staminate) or drooping at tip (pistillate), cylindric, 15–25 mm long, 8–12 mm thick, silky-hairy, rounded at tip; winter-bud scales subtending aments buffy brown, pubescent like the leaves, 5–7 mm long. Staminate flowers (*Riskind and Riskind 2052*): scales oblong, 2–3 mm long, blunt, pale brown, dorsally densely pubescent with white, silky, antrorse hairs 1–2 mm long; vestigial ovary slender, conical, yellow-green, gland-like, ca. 0.8 mm long; stamens 2, nearly glabrous, joined part of filaments 2–3 mm long, free parts 1–2 mm long; anthers purple-brown, ca. 0.6–1 mm long, ovate-orbicular. Pistillate flowers at stage of pollen-receptivity not known, present at a later stage with young fruit in *Riskind and Patterson 1944a* and *Wendt 126*: scales brown, more or less oblong-obovate, ca. 1.5 mm long (*1944a*) or 1 mm long (*126*), 1 mm wide, pubescent with antrorse, white, silky hairs 1–2 mm long either equally densely on both surfaces (*126*) or more densely so on back (*1944a*); gland minute, oblong, scale-like, ca. 0.3 mm long; ovary stipe ca. 0.5 mm long with white, silky hairs; ovary ca. 3 mm long, hairy all over (*126*) or only in vertical stripes along lateral sutures (*1944a*); style ca. 1 mm long of which upper 0.2 mm is forked and stigmatic. Seeds (*126* only) numerous, oblanceoloid, ca. 0.9 mm long of which lower 0.2 mm comprises narrowed stipe; hairs numerous, 2–3 mm long attached to disk- or callus-like funicle.

TYPE: México, Coahuila, Sierra Maderas del Carmen, Cañón Carboneras, ca. 1 km s. of El Uno, along perennial stream in pine-oak woodland, 28°59′30″N, 102°33′W, 1500–2100 m, 2 Apr 1974, *Tom Wendt 126* with Emily J. Lott and David Riskind (holotype: TEX).

PARATYPES: México, Coahuila, Municipio de Villa Acuña, Serranías del Burro, Rancho El Bonito, Cañón El Bonito ca. 2.5 km above first dam, 29°1′30″N, 102°7′30″W, 1700 m, 11 Apr 1976, *D. J. Riskind and T. F. Patterson 1944a* (TEX); same locality, 20 Feb 1977, *D. H. Riskind and J. Riskind 2052* (LL); same canyon, 29°0′30″N, 102°7′30″W, 1800 m, 20 Sep 1977, *J. Valdés R. and A. L. Metcalf 2249* (LL).

The label of *Wendt 126* indicates that these willows are shrubs to small trees, sometimes exceeding 7 m in height, abundant in the "main" arroyo, extending from at least 1500 m elevation, where the plants were fully leafed on 2 April, to 2100 m where they were only in bud; the foliage is said to be "silvery light green". The associates are said to be *Quercus* spp., *Cupressus arizonica* Greene, *Pinus arizonica* Engelmann, *P. cembroides* Zuccarini and *Vitis* sp. The label

of *Riskind and Patterson 1944a* notes that these are abundant shrubs to 3 m tall on margins of wet meadow in woodland of *Quercus muehlenbergii* Engelmann in upper reaches of Cañón El Bonito. The label of *Riskind and Riskind 2052* says that these are abundant multistemmed shrubs to 3 m on margins of intermittent stream and ciénega in deciduous woodland in upper reaches of Cañón El Bonito along logging road ca. 2.5 km upstream from first dam, associated with *Quercus gravesii* Sudworth, *Prunus mexicana* Watson, *Quercus muehlenbergii,* and *Pinus arizonica* var. *stormiae* Martínez.

The shorter stature and the slightly different ovary pubescence of the plant of the Serranías del Burro lead to the suspicion that they may deserve recognition as taxonomically distinct from the plants of the Sierra Maderas del Carmen only some 70 km farther west, but the material available is not adequate for a critical evaluation of this point. I await receipt of more adequate specimens from both areas, especially staminate plants from the Sierra Maderas del Carmen.

In Schneider's (1918) treatment of Mexican willows, *S. riskindii* keys to *S. paradoxa* H.B.K. but it differs from *S. paradoxa* in the smaller, sessile aments and much denser, more persistent pubescence of silky hairs as well as the height of joining of the stamen-filaments. *Salix riskindii* may be more closely related to *S. lasiolepis* with which it shares the features of basal filament-joining and over-all habit. But it is quite distinct in a number of other features.

3. **Salix pattersonii** M. C. Johnston, sp. nov.

Frutices multicaules ad 2.25 m alti, ramuli hornotini pilis multis demum glabrati. Laminae foliorum elliptico-oblanceolatae 2–6.5 cm longae 1–2.5 cm latae supra praeter costam glabrae nitidae costis albopubescentibus, subtus persistente dense canescento-pubescentes integrae. Amenta staminata ignota; amenta pisitillata ut videtur inter mensem maii emergentia coetanea in extremitatibus ramulorum ramulis pedunculiformibus 1–2(–3)-nodatis 3–5-mm longis folia ramulorum superantia, in statu fructifera 4–5 cm longa 10–15 mm diametro; capsulae 6–7 mm longae dense pubescentes (Fig. 2).

Multi-stemmed shrubs to 2.25 m tall; twigs of the season slender, dark brown, striate when very young with spreading to retrorse, silky, whitish hairs 0.2–0.3 mm long, older portions glabrate; internodes ca. 2–10 mm long; axillary buds pale brown, sparsely pilose, ca. 3 mm long. Leaves ascending; leaf-blades elliptic-lanceolate, 2–6.5 cm long, 1–2.5 cm wide, with acute tips and cuneate-rounded bases, entiremargined, olive-green, lustrous and essentially glabrous above when nearly mature except for white-pubescent larger veins, on abaxial surface waxy-papillose, glaucous and persistently densely canescent-pubescent with antrorse, silky, white hairs 0.3–0.8 mm long; stomates abundant beneath, absent above; petioles 2–9 mm long, with pubes-

Fig. 2. *Salix pattersonii* M. C. Johnston. Twig with leaves and pistillate inflorescences.

cence like that of the leaves; stipules minute. Staminate aments unknown. Pistillate aments at anthesis not seen, apparently emerging in May with the leaves, terminating 1–3(–3)-noded 3–5-mm-long axillary ascending-spreading twigs, vastly exceeding twig leaves, cylindric, when in fruit 4–5 cm long, 10–15 mm thick; scales 1.5–2 mm long, lanceolate, acute, appressed, with antrorse, silky, white hairs ca. 1 mm long, less densely hairy on adaxial surface; pedicels ca. 1.6–2 mm long; gland absent; capsule 6–7 mm long, densely hairy with antrorse, silky, white hairs ca. 0.5 mm long, after dehiscence with widely recurved valve-beaks; stigmata ca. 0.3–0.4 mm long, deltoid, about as wide as long. Seeds narrowly falcate-ovoid, compressed, nearly black,

at base with numerous, silky, white ascending hairs joined at central whitish easily detached, basal callus-like funicle; embryo green.

Type: México, Coahuila: Municipio de Ocampo, Sierra Maderas del Carmen, 102°33'N, 28°59'W, Campo 4, in cut-over, open, mixed conifer-oak woods, 27 May 1975, *Riskind and Patterson 1809* (Holotype: LL).

The label states that the shrubs are locally common and are associated with *Cupressus arizonica, Pseudotsuga menziesii* (Mirb.) Franco, *Pinus* spp., *Quercus sideroxyla* Humboldt & Bonpland, *Q. rugosa* Née and *Abies durangensis* Martínez var. *coahuilensis* (I. M. Johnston) Martínez. The species is currently known only from the type collection.

On the basis of over-all vegetative similarity and the shape of the bracts, this pistillate material is perhaps related to *Salix oxylepis* Schneider, which was known to Schneider only by material from the region near the Peak of Orizaba. *Riskind and Patterson 1809* also keys to *S. oxylepis* in the more extensive treatment by Espinosa (1979), who reports *S. oxylepis* from six states and the federal district in central Mexico. As compared with *S. oxylepis,* however, *S. pattersonii* has shorter petioles, shorter and narrower leaf blades with persistently pubescent abaxial surfaces, and shorter pistillate aments.

Two sterile collections also from the Sierra Maderas del Carmen are similar enough vegetatively to *Riskind and Patterson 1809* to be placed here tentatively: México, Coahuila, Sierra Maderas del Carmen, rhyolitic s. peaks, nw. side of upper Carboneras Canyon, 28°57'N, 102°34'W, 2400 m, uncommon small tree in mixed conifer-oak forest, 2 Apr 1974, *T. Wendt 124a* (TEX); along road above Catedrales Canyon in nw. part of range due w. of Campo Tres, above 2200 m, common multi-stemmed shrubs along intermittent watercourses with *Pinus, Pseudotsuga, Quercus, Cupressus, Arbutus, Cornus,* 3 Aug 1974, *D. H. Riskind, B. Burleson, and J. T. Baker 1720* (LL). I think that these two collections very likely represent *S. pattersonii.*

4. **Salix wendtii** M. C. Johnston, sp. nov.

Arbores parvissimae fruticoideae ad 3 m altae ad basem multiramosae; ramuli hornotini primitus pilis multis demum glabrati. Laminae foliorum ovato-ellipticae vel ellipticae vel obovato-ellipticae (4.5–)5–7(–8) cm longae 2–3.5 mm latae supra praeter costam glabrae nitidae costis albo-pubescentibus, subtus persistente dense canescento-pubescentes serrulatae dentibus parvis antrorsis glandularibus. Amenta staminata inter mensem Augusti emergentia coetanea cum foliis maturis in extremitatibus ramulorum ramulis pedunculiformibus 2–3 cm longis 2–5-nodatis folia superiora breviora 20–24 mm longa 9–13 mm lata; squamae ovatae 2–2.5 mm longae acutae acuminatae pubescentes; stamina 2, filamenta omnino libera 5–8 mm longa (Fig. 3).

Fig. 3. *Salix wendtii* M. C. Johnston. A. Staminate flower. B. Twig with leaves and one staminate inflorescence.

"Shrubby trees" to 3 m tall, much branched at base; twigs of the season slender, dark brown, striate, when very young with numerous, spreading, silky, whitish hairs 0.5–1 mm long, later glabrate; internodes ca. 1–2 cm long; axillary buds dark brown, glabrous, 4–6 mm long. Leaf blades ovate-elliptic to elliptic to obovate-elliptic, (4.5–)5–7(–8) cm long, 2–3.5 cm wide, firm, membranous, at margins serrulate with small, antrorse gland-tipped teeth (teeth numerous on rapidly growing shoots, less so elsewhere), at tip weakly cuspidate, at base rounded, on upper surfaces olive-green, essentially glabrous and lustrous at maturity except for white-pubescent midvein, on lower surface waxy-papillose, glaucous and persistently densely canescent-pubescent with antrorse, silky, white hairs 0.5–1 mm long; stomates abundant beneath, absent above; petioles (3–)5–8 mm long, with pubescence

like that of leaves; stipules on rapidly growing shoots elliptic-falcate, 4–6 mm long, highly asymmetrical, green, leaf-like in texture, serrulate, lower surface white-hairy especially near base; stipules on slower-growing shoots essentially absent. Staminate aments: appearing in August with mature leaves, terminating 2–5 noded, 2–3-cm-long twigs, ascending, shorter than uppermost twig leaves, subcylindric, 20–24 mm long, 9–13 mm wide (including stamens), with a peduncle 3–4 mm long, silky-hairy. Staminate flowers: subtending bract-scale appressed, ovate, 2–2.5 mm long, acute and acuminate, yellow-brown when dry (said to be green when fresh), pubescent with antrorse, silky, white hairs 0.8–1.3 mm long, less densely hairy above; gland ventral, truncate or even concave at tip, more or less rectangular, ca. 0.3 mm long; stamens 2, filaments wholly free, 5–8 mm long, in basal half with many antrorse silky, white hairs ca. 0.5 mm long; anthers ovoid, 0.7–0.8 mm long, yellow, each with an apical gland. Pistillate aments, flowers, and fruits unknown.

TYPE: México, Coahuila, Sierra Maderas del Carmen, 29°00'N, 102'36'W, near Campo Tres on ridge between camp and "Hell's Kitchen" to the north, common at bases of cliffs of the ridgetop, wsw. slopes, 2600 m, 6 Aug 1974, *T. Wendt and A. Adamcewicz 518* (Holotype: TEX).

Salix wendtii, known only from the type collection, cannot be accommodated in the key or descriptions of Schneider (1918). In Espinosa (1979) it keys to *S. oxylepis* but has longer petioles, shorter, narrower leaf blades, shorter staminate aments and shorter floral scales.

5. **Salix** sp. nov.?

Two sterile specimens represent this entity: México, Coahuila, Municipio de Cuatro Ciénegas, Sierra de la Madera, Cañón del Agua, 27°3' or 27°4'N, 102°24'W, 9 Sep 1934, *C. H. Muller 3242* (GH, LL); same locality, above the canyon on n. slopes, 2450–3100 m, with *Cupressus, Quercus, Pseudotsuga, Pinus,* and *Abies,* 14 Aug 1980, *T. Wendt and E. J. Lott P29* (TEX).

Muller notes on his label that these are trees to 4.5 m tall with smooth, tawny trunks to 10 cm thick. Wendt and Lott (label and pers. comm., 1980) state that these are small trees 2–6(–9) m tall with 5–100 or more stems from the base, with smooth, grayish bark. These willows are not common in the Cañón del Agua at 2450–2900 m, but on the slopes above the canyon, even up to 3100 m on the Pajarito Peak, they are co-dominant with *Cupressus* and other conifers. The lowest, earliest leaves of the newly expanding shoots often have narrowly obovate or oblong blades 2–4 cm long. Somewhat later leaves have longer, narrowly obovate blades usually 4–9 cm long and 2–3 cm wide. The last-formed leaves are broadly lanceolate, 6–10 cm long, 1–2 cm wide and rather regularly serrulate with small, remote teeth.

The upper surfaces are essentially glabrous. The lower surfaces are non-papillate and nearly glabrous but with closely appressed, scattered, pale rufous hairs ca. 0.4 mm long.

According to Johnston (1944), *Muller 3242* "appears to be referable to *S. paradoxa*", but I find that it differs from that species in many features. Because *Muller 3242* and *Wendt & Lott P29* do not correspond with any previously known willows, I suspect that they represent still another local endemic taxon. It is to be hoped that flowers and fruits will be made available for study.

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A NEW SPECIES OF CRYPTANTHA (BORAGINACEAE) FROM WYOMING

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ABSTRACT

A new species, **Cryptantha subcapitata,** is described from Fremont County, Wyoming. It is compared with *C. caespitosa* and *C. spiculifera* which it resembles most closely.

In the course of field collecting in central Wyoming, we came across a mat-forming *Cryptantha* that resembled *C. caespitosa* (A. Nels.) Payson but had a different aspect. Closer examination of these plants revealed several distinct differences from *C. caespitosa,* including longer styles and a different type of pubescence. The longer styles suggested *C. spiculifera* (Piper) Payson but again the pubescence was different as were characteristics of the nutlets and inflorescence. These differences and others support recognition of this mat-forming taxon at the species level.

Cryptantha subcapitata Dorn & Lichvar, sp. nov.

Herba perennis caespitosa, 5–15 cm alta; folia linearia vel lineari-oblanceolata, 8–28 mm longa, 1–3 mm lata, dense strigosa; inflorescentia capitata vel subcapitata; calyx 5–7 mm longus; corolla alba, tubus 3–4 mm longus, limbus 5–6 mm latus; anthera 0.8 mm longa; stylus fructu 1.5–2 mm longior; nuculae 4, ovatae, 2–3 mm longae, dorso tuberculato-rugulosae, pagina ventrali tuberculato-rugulosae, sulco aperto triangulari (Fig. 1).

Mat-forming perennial 5–15 cm high; leaves linear to linear-oblanceolate, 8–28 mm long, 1–3 mm wide, densely appressed strigose and with some slightly larger, spreading, pustulate hairs at least on abaxial surface and margins, the old whitish leaves persisting at base; stems greenish; inflorescence capitate or subcapitate; calyx 5–7 mm long, pubescent like the leaves; corolla white, the tube 3–4 mm long, the limb about 5–6 mm across; anthers about 0.8 mm long; nutlets 2–3 mm long, ovate in outline, dorsal surface rugose at center, mostly tuberculate near margins, the ventral surface rugose and tuberculate,
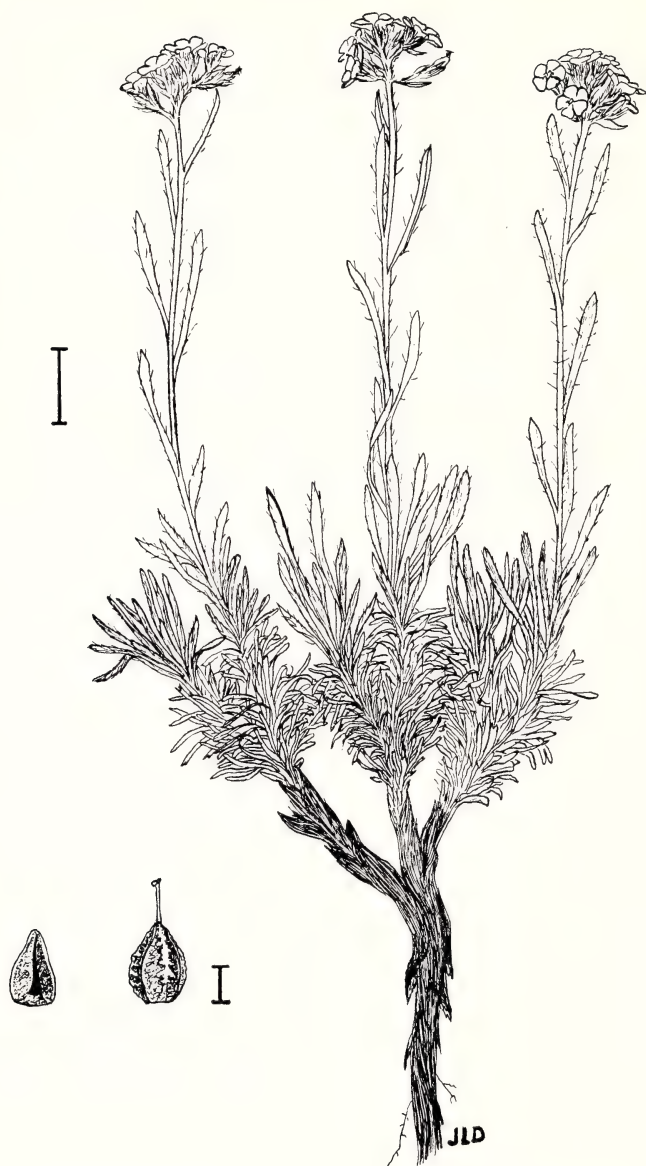
FIG. 1.   *Cryptantha subcapitata* (from *Dorn 3459*). Habit: scale bar = 1 cm. Ventral view of nutlet and four nutlets with protruding style: scale bar = 1.5 mm.

TABLE 1.   SELECTED CHARACTERISTICS OF THREE TAXA OF *Cryptantha*.

Characteristic	*C. caespitosa*	*C. subcapitata*	*C. spiculifera*
Leaf shape	Obovate to oblanceolate	Linear to linear-oblanceolate	Oblanceolate
Leaf pubescence	Uniform, coarse, mostly appressed, not obviously pustulate hairs	Mixture of coarse, appressed, nonpustulate hairs and fewer, spreading, slightly coarser, obviously pustulate hairs	Mixture of fine, somewhat appressed, non-pustulate hairs and fewer, spreading, much coarser, obviously pustulate hairs
Stems	Straw colored	Green	Green or straw colored
Inflorescence	Usually elongate	Capitate or subcapitate	Usually elongate
Styles	Exceed nutlets by <0.5 mm	Exceed nutlets by 1.5–2 mm	Exceed nutlets by 1.5–2 mm
Mature nutlet margins	Usually same as body	Same as body	With narrow, smooth border prominently set off from body by smoothness and color
Nutlet scar	Open	Open	Closed

the scar open for most of length of nutlet, the opening triangular at base; style exceeding nutlets by 1.5–2 mm.

TYPE: USA, WY, Fremont Co., T5N R6E S8, just w. of Boysen Dam, rocky calcareous ridge, 1775 m, 23 Jun 1980, *Dorn 3459*. (Holotype: RM; isotypes: to be distributed).

PARATYPES: same location and date as holotype, *Lichvar 2886* (RM); USA, WY, Fremont Co., 2.4 km se. of Boysen Camp, 1550 m, 3 Jun 1964, *Wight 87* (RM).

Cryptantha subcapitata differs from *C. caespitosa* in that the inflorescence is capitate or subcapitate rather than normally elongate, the styles exceed the nutlets by 1.5–2 mm rather than by less than 0.5 mm, and the pubescence is different. It differs from *C. spiculifera* in that the inflorescence is capitate or subcapitate rather than normally elongate, the pubescence is different, and the nutlet scar is open rather than closed. These and other differences among the three species are summarized in Table 1.

Cryptantha subcapitata is perhaps derived from *C. caespitosa* and thus can be placed in the "caespitosa group" of Higgins (1971). The

pubescence and nutlets of the two are quite similar when compared to other species and the former is on the northern edge of the range of the latter. It is not likely that *C. caespitosa* is derived from *C. subcapitata* because the direction of evolution in this region appears to be from common habitats to rare, more severe habitats. *Cryptantha caespitosa* is found on a variety of relatively common substrates including sandy knolls, rocky slopes, and ridges. *Cryptantha subcapitata* is restricted to relatively uncommon calcareous substrate, a habitat in which many Wyoming endemics or near-endemics are found and in which common species are relatively few.

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ERIOGONUM LIBERTINI (POLYGONACEAE), A NEW SPECIES FROM NORTHERN CALIFORNIA

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ABSTRACT

Eriogonum libertini is a new species of the subgenus *Oligogonum* known only from serpentine outcrops in the California Coast Ranges of Shasta, Tehama and Trinity Counties. It is most closely related to *E. ternatum* Howell, a serpentine species of northernmost California and adjacent Oregon, differing in having a whorl of three foliaceous bracts at midlength along the stem and an inflorescence reduced to a single terminal involucre.

Eriogonum libertini Reveal, sp. nov.

A *E. ternato* Howell foliis brevioribus et semper tomentosis insuper, bracteis 3, foliaceis, inflorescentiis solitaris, floribus majoris (5–8 mm longis nec 3–5 mm longis) cum stipibus longior (1–1.5 mm nec 0.3–0.6 mm longis) differt (Fig. 1).

Low, spreading herbaceous perennial forming a rather dense mat to 4 dm across, with a densely branched, spreading, woody caudex arising from a stoutish, well-defined, woody taproot; leaves in small, well-defined, densely congested rosettes at tips of exposed caudex branches, the leaf-blades numerous, oblong to elliptic or rarely rounded, 0.5–1(–1.5) cm long, 3–5(–7) mm wide, densely white-tomentose below, thinly tomentose and greenish above even at maturity, often drying blackish in age, the apices acute to obtuse, the bases obtuse, with plane, entire margins, on slender petioles 2–6 mm long, thinly tomentose throughout or at least near the leaf-base, otherwise ciliate marginally, the petiole-bases narrowly triangular, 0.5–3 mm long, 0.4–1 mm wide, glabrous or nearly so on both surfaces; flowering stems erect, slender, 5–15 cm long, thinly floccose, with a whorl of three foliaceous bracts about midlength; inflorescences capitate and terminal, 1–1.5 cm across; bracts lacking below involucre, restricted to middle of stem, these narrowly lanceolate to narrowly elliptic, 5–7(–10) mm long, 0.8–2.5 mm wide, tomentose on both surfaces although less so above, greenish-white to white; peduncles (that portion of stem between bracts and involucre) erect, slender, 2–4.5 cm long, thinly floccose; involucres solitary, turbinate-campanulate to campanulate, the involucral tube 4–8 mm long, 5–6(–8) mm wide, densely tomentose without, glabrous within, with 5–8 erect to slightly spreading triangular teeth 0.5–1(–1.5) mm long, the bractlets linear, 4.5–9 mm long, hirsutulous
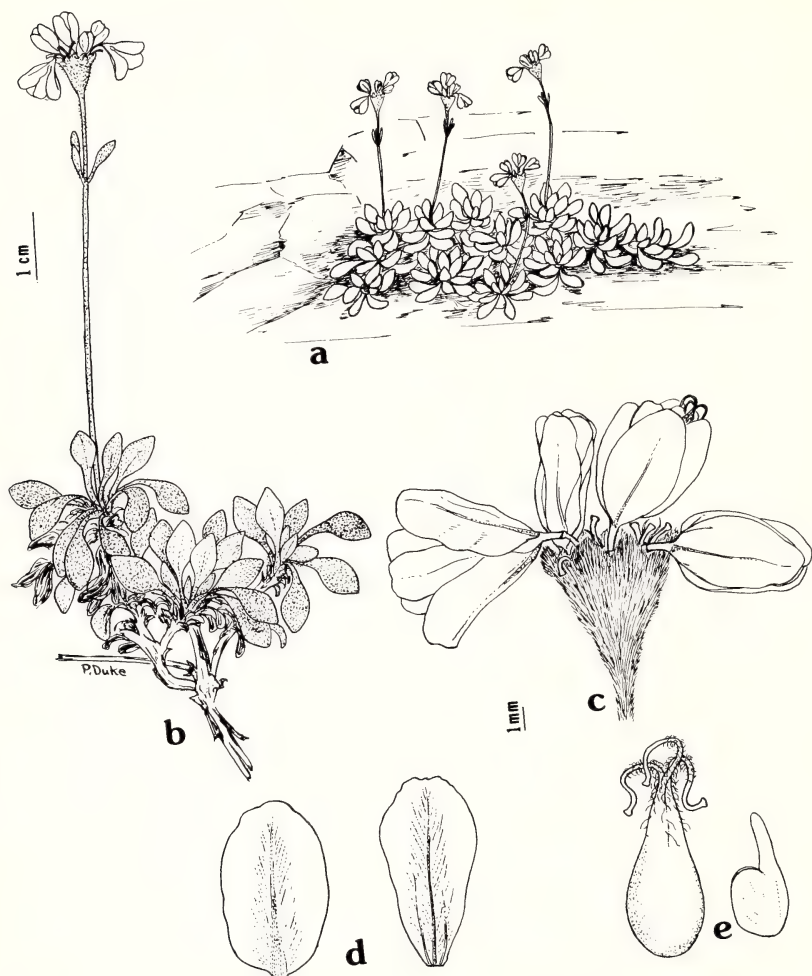
FIG. 1. *Eriogonum libertini* Reveal. a. Habit. b. Detail of leaves and flowering stem. c. Detail of involucre and flowers. d. Outer (left) and inner (right) tepals. e. Achene (left) and embryo (right).

with long, thin cells, the pedicels 4–8 mm long, glabrous; flowers stipitate, sulphur-yellow with a blackish-green midrib, 5–8 mm long including the 1–1.5 mm long stipe, glabrous except for minute glands along midribs of outer tepals and over most of inner surface of inner tepals, the tepals dimorphic, spatulate to oblong with obtuse apices, connate about ¼ of flower length above stipe; stamens slightly exserted to more commonly included, 4–6 mm long, with basally densely pilose fila-

ments and yellowish anthers 0.6–0.8 mm long; style 1.5–2 mm long; achenes light brown, 4–6 mm long, the narrowly globose base tapering gradually to a slightly pubescent, faintly 3-angled beak; embryo curved.

TYPE: USA, CA, Tehama Co., along Tedoc Rd. 18.4 km s. of Hwy 36 (Beegum Rd.) and 1.4 km n. of Tedoc Gap, on a w.-facing serpentine slope in reddish soil associated with pine, oak, and manzanita, 1400 m, 19 Jul 1978, *Reveal 4788* (Holotype: US; isotypes: BRY, CAS, GH, K, MARY, MICH, MO, NY, TEX, UC, UTC).

PARATYPES: USA, CA, Shasta Co.: 1.6 km from Regan Meadow along rd. to Brushy Mt., T28N R11W S1, 27 Jul 1979, *Nelson et al. 5046* (CAS, HSC, MARY, US); Tehama Co.: nw. side of Mt. Tedoc, 1300 m, 17 Jun 1972, *Heckard 2965* (JEPS); near Tedoc Gap, 21 Jul 1949, *Hoffman 3051* (UC); 2.3 km e. of Red Mt. Guard Station on White Rock Rd., 6 Jul 1950, *Hoffman 3693* (UC); rd. from Tedoc Gap to Mt. Tedoc, T28N R9W S28, 1500 m, 25 Jun 1979, *Nelson and Nelson 4888* (MARY); Trinity Co.: 4.3 km nw. of Red Mt., 17 Jul 1949, *Hoffman 3046* (CAS, UC); rd. to Hell-to-Find Lake, T29N R11W S27, 23 Jun 1978, *Nelson and Nelson 4361* (MARY); along Salt Creek Rd. at USFS Rd. 30N24, T30N R11W S33, 950 m, 17 Jun 1980, *Nelson and Nelson 5496* (MARY); 6.4 km (4 mi.) n. of Indian Valley Guard Station, T2N R7E S10, 1340 m, 18 Jun 1980, *Nelson and Nelson 5554* (MARY); 0.8 km (0.5 mi.) s. of Salt Creek Bridge along Hwy 36, T30N R12W S13, 760 m, 19 Jun 1980, *Nelson and Nelson 5626* (MARY); Rattlesnake Ridge, T29N R12W S20, 1220 m, 19 Jun 1980, *Nelson and Nelson 5647* (MARY); Blue Point, T30N R12W S35, 1370 m, *Nelson and Nelson 5690* (MARY); along USFS Rd. 29N28, 11.2 km (7 mi.) s. of Hwy 36, T29N R11W S26, 1370 m, 22 Jun 1980, *Nelson and Nelson 5743* (MARY); Red Mt., T26N R12W S20, 1250 m, 9 Jun 1979, *Nelson and Sawyer 4116* (MARY); rd. from Hayfork Cr. to Hell-to-Find Lake, 1530 m, 30 Jun 1973, *Sawyer 2531* (HSC); sw. of South Dubakella Mt. 1590 m, 3 Jul 1973, *Smith 6991* (HSC); along USFS rd. 30N38 from Hwy 36 to Cold Springs Guard Station, 760 m, 22 Jun 1975, *Smith and Sawyer 8245* (HSC); Blue Point on Blue Point Ridge, T30N R12W S35, 1400 m, 25 Jun 1979, *Smith et al. 10206* (MARY).

The epithet honors Freedom William Hoffman (1880–1959), an amateur botanist interested in plants of serpentine areas in northern California, especially *Streptanthus* (Morrison, 1960).

Eriogonum libertini (from the Latin libertinus = of a freedman) is a local, serpentine endemic mostly restricted to outcrops supporting Jeffrey pine. It forms large mats with occasional rosettes bearing erect flowering stems each with a whorl of three foliaceous bracts about midlength, terminated by a solitary involucre containing numerous, large, glabrous, sulphur-yellow flowers. Outwardly the new species is most similar to *E. ternatum* Howell, which differs in having a

branched, open inflorescence without a whorl of bracts midlength along the flowering stem. Because of the position of the whorled bracts, the new species resembles *E. siskiyouense* Greene, a serpentine endemic restricted to Scott Mountain, Mount Eddy, and associated mountain peaks along the Siskiyou and Trinity County line. It may be distinguished from *E. siskiyouense* by the short, erect to spreading teeth of the involucre, which are not reflexed nor longer than the tube. *Eriogonum ternatum* is more widespread than either *E. libertini* or *E. siskiyouense,* and is found mainly in Del Norte and Siskiyou Counties, California, and in adjacent Josephine County, Oregon. I have seen a recent collection of *E. ternatum* from Trinity County (*Nelson et al. 5062,* CAS, HSC, MARY, NY, US). However, the ranges of *E. ternatum* and *E. libertini* do not overlap.

Eriogonum libertini was indirectly indicated by Lambertson (1980) as a potential candidate for federal listing as an endangered or threatened species. Thanks to the efforts of Thomas W. Nelson who has expanded significantly the known range of the species during his 1980 field work, the plant cannot justifiably be considered for protection.

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DIURNAL ACID METABOLISM IN VERNAL POOL
ISOETES (ISOETACEAE)

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ABSTRACT

Leaves of the vernal pool species *Isoetes howellii* and *I. orcuttii* possess a Crassulacean Acid Metabolism-like pathway while submerged. It is proposed that this was selected because CO_2 availability is greatly reduced during the day in these pools, putting a premium on CO_2-fixation at night. Diurnal changes in physical and chemical characteristics in two vernal pools are compared with diurnal changes in malic acid concentration in *Isoetes* leaves. The data are consistent with the hypothesis.

Isoetes howellii Engelmann (Isoetaceae) is distributed throughout California and other western states in more-or-less temporary vernal pools (Munz, 1959). Because of the mediterranean climate, vernal pools are filled by winter rains and dry out during the summer drought. *Isoetes howellii* prefers deep (20–30 cm) pools (Kopecko and Lathrop, 1975). As a result, it remains submerged longer than most other vernal pool species and is entirely absent from very shallow pools (Zedler and Ebert, 1979). Vernal pools are heavily vegetated and often *I. howellii* will grow in very dense more or less monotypic stands (e.g., Purer, 1939) noted 4000–6000 plants/m² in some pools on mesas near San Diego). By late spring or early summer all species are emergent and as the water table drops most die. Pfeiffer (1922) stated that *Isoetes* corms can survive drought, but she did not mention the species on which she based this conclusion.

Recent evidence has been presented that *Isoetes howellii* has a diurnal acidification/deacidification cycle similar to Crassulacean Acid Metabolism (Keeley, 1981). Submerged leaves of *I. howellii* fix CO_2 at night into malic acid and this product accumulates through the night. During the day malic acid is broken down, resulting in a diurnal fluctuation of 100–200 μequivalents titratable acidity per gram fresh weight. The major difference between *Isoetes howellii* and terrestrial CAM plants lies in stomatal behavior. The prototype CAM plant closes stomates during the day thus restricting CO_2 uptake to the night. Sculthorpe (1967) contends that stomata on submersed aquatics are functionless because of the occlusion of the stomatal apertures by cuticular waxes. Submersed *Isoetes howellii* apparently is no exception as evidenced by the thick wax which lines the stomatal aperture (D. B. Walker, UCLA, pers. comm., 1979). *Isoetes howellii* is capable of CO_2-uptake in both the light and the dark.

The functional significance of CAM-like diurnal acid metabolism in an aquatic plant is unknown. In terrestrial plants Crassulacean Acid Metabolism was selected as a means of increasing water-use efficiency (Kluge and Ting, 1978). This arises from the daytime decarboxylation of malic acid producing an endogenous CO_2 source which maintains C_3-type photosynthesis while stomates are closed. Diurnal acid metabolism in submerged leaves of *Isoetes howellii* undoubtedly is not related to water-use efficiency. However, daytime generation of an internal CO_2 source could have been selected for other reasons. For example, if CO_2 availability were greater at night than during the day CAM could be adaptive in an aquatic environment.

Daytime reduction of CO_2-availability is possible even in pools where the total inorganic carbon is greater than in air. In water, free-CO_2 predominates below pH 6 but is gradually replaced by HCO_3^- and CO_3^{2-} at higher pH. Free CO_2 is the "preferred" substrate for photosynthesis by terrestrial and aquatic plants (Raven, 1970). As free CO_2 is consumed the pH in unbuffered pools rises (Hutchinson, 1957). Above pH 8 free CO_2 is replaced by HCO_3^- and CO_3^{2-}. Although some aquatic plants can take up HCO_3^-, many can not. Preliminary evidence indicates *I. howellii* uses HCO_3^- poorly, if at all. A comparison of C^{14}-fixation (at constant inorganic carbon levels) in the light at pH 5 and pH 8 showed an 80% reduction in C^{14}-fixation at the higher pH (Keeley, unpublished data).

I hypothesize that one selective advantage of "Crassulacean Acid Metabolism" in *Isoetes howellii* is that this pathway provides an internal CO_2 source during the day when externally derived CO_2 becomes limiting to C_3 photosynthesis. The purpose of this study was to compare diurnal changes in malic acid in *Isoetes* leaves with diurnal changes in CO_2 concentration in the pools. *Isoetes orcuttii* A. Eaton is the only other species in the genus commonly found in vernal pools. It is a California endemic, often found in close association with *I. howellii* (Kopecko and Lathrop, 1975), and it was included in this study.

METHODS

Two pools were studied, one in early April 1979 on Miramar Naval Air Station, San Diego Co. and the other in late April 1980 on Mesa de Colorado, Santa Rosa Plateau, Riverside Co. At 0600 hr and 1800 hr (± 30 min) several physical and chemical parameters of the pools were measured and submerged leaf samples were collected from *I. howellii* at the Miramar site and from *I. howellii* and *I. orcuttii* at the Mesa de Colorado site.

Pool parameters were measured as follows: temperature and oxygen concentration with a YSI oxygen meter, pH with a Markson pH meter, and carbon dioxide concentration titrametrically as described by

TABLE 1.   DIURNAL CHANGES IN PHYSICAL AND CHEMICAL PARAMETERS OF TWO
VERNAL POOLS AND MALIC ACID CONCENTRATION OF *Isoetes* LEAVES SUBMERGED IN
THOSE POOLS.

| | | | | | | Malic acid (mg/gm FW) in leaves | | | |
| | Pool parameters | | | | | *I. howellii* | | *I. orcuttii* | |
PST hr	C°	O_2 ppm	pH	Free CO_2 (mg/l)	Total CO_2 (mg/l)	x̄ ± S.D.	N	x̄ ± S.D.	N
				Miramar 8 Apr 1979					
0600	16.0	2.1	6.8	7.5	38.7	7.1 ± 1.5	6	—	—
1800	22.9	12.0	9.0	0	27.2	1.8 ± 0.4	6	—	—
				Mesa de Colorado 26 Apr 1979					
0600	12.5	7.4	6.3	9.5	24.3	12.5 ± 2.8	2	13.1 ± 2.6	2
1800	21.0	11.0	8.5	0	10.6	3.3 ± 0.2	2	3.7 ± 1.4	2

Golterman *et al.* (1978). *Isoetes* leaves were washed in distilled water, blotted dry, weighed, ground in a blender with distilled water, filtered through cheesecloth, and centrifuged at low speed. The supernatant was deproteinized with 1.0 N perchloric acid placed on ice and returned to the lab and assayed for malic acid with an enzymatic end-product assay (Bergmeyer, 1974, pp. 1585–1589).

Isoetes howellii and substrate were transplanted to artificial outdoor pools on campus so they could be sampled every 6 hrs over a two-day period.

RESULTS AND DISCUSSION

Table 1 shows the diurnal changes in physical and chemical parameters of the two vernal pools and malic acid levels in *Isoetes* leaves. During the day the temperature in the pools rose, and associated with this was an increase in oxygen, presumably due to algae and macrophyte photosynthesis. This likely accounts for the decreased free-CO_2 concentration, which in turn would cause the pH of the water to rise (Hutchinson, 1957). Evening pH values of 8.5 and 9.0, coupled with daytime total-CO_2 losses greater than the free-CO_2 losses, suggest that some species in the pools may be using HCO_3^- to some extent. Both *Isoetes howellii* and *I. orcuttii* have substantial malic acid pools in their leaves in the morning, and these are greatly depleted by the end of the day.

Some of these parameters were followed more closely over a time course of two days in artificial pools in May 1979 (Fig. 1). The fluctuation patterns of free-CO_2 in the pool (as indicated by pH) and malic acid in the leaves are reversed. Free-CO_2 in the water was largely depleted by noon and the bulk of the malic acid in the leaves was
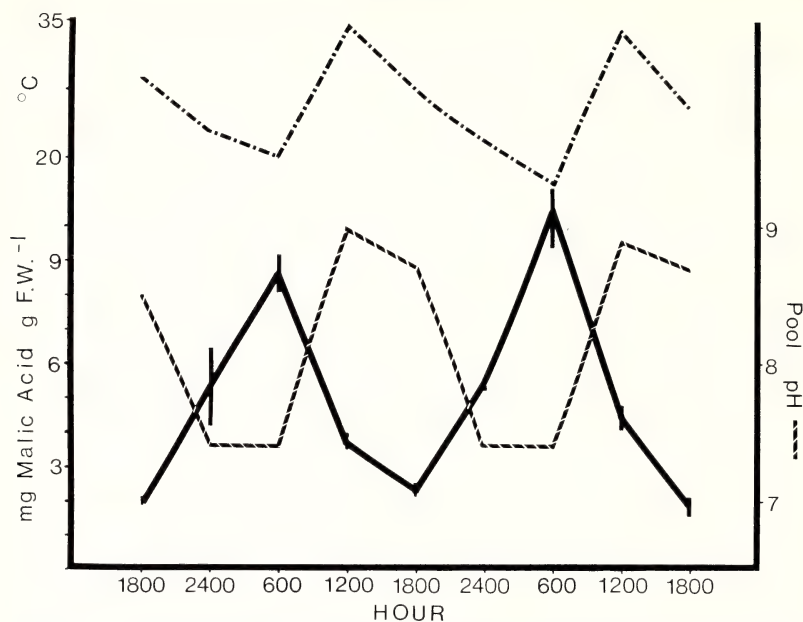
Fig. 1. Diurnal fluctuations in pool temperature and pool pH (dashed lines) in artificial pools and malic acid concentration in submerged *Isoetes howellii* leaves. Each
point is the mean of two replicates, vertical bars represent ±1 S.D.

broken down by this time. Between 1800 hr and 2400 hr the pool pH
dropped to a range where free-CO_2 was once again present. Through
the night the pH did not drop below 7.3, indicating that free-CO_2 did
not account for much more than 10 percent of the total CO_2 in the
water. Malic acid accumulated in the leaves throughout the night.

One other experiment done in the artificial pools was a comparison
of diurnal changes in malic aid concentration in submerged and
emergent leaves. Submerged leaves had a 6-fold increase in malic acid
overnight, whereas approximately adjacent emergent leaves showed
less than a 2-fold increase. This pattern was the same whether expressed as a fraction of fresh weight or chlorophyll. Thus this pathway
appears to be facultative and of lesser importance as the pools dry.

The data presented here are consistent with the hypothesis that CO_2
availability is greatly reduced during the day in these pools and that
this puts a premium on CO_2-fixation at night in *Isoetes*. Recent gas
exchange studies indicate that at the free CO_2 levels present at night
in these pools, *Isoetes howellii* is capable of substantial *net* CO_2 uptake at night (Keeley and Bowes unpublished data). Further studies
are needed to elaborate the relative contribution of dark and light CO_2
fixation.

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THE ECOLOGICAL STATUS OF STIPA PULCHRA (POACEAE) IN CALIFORNIA

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ABSTRACT

We present information clarifying the past and present role of the native perennial grass *Stipa pulchra* in the California grassland. *Stipa pulchra* occupies a diverse array of habitats in northern and central California, as shown from information collected on more than 1500 plots by the State Cooperative Soil–Vegetation Survey. *Stipa pulchra* did not increase in density over a 20-year period in ungrazed areas on the Hopland Field Station in northern California and was replaced by other perennial grasses and annuals on some plots. *Stipa pulchra* germinated more slowly than associated annual plants and *S. pulchra* seedlings apparently did not survive the period of rapid spring growth in annual grassland. In pot trials fewer *S. pulchra* germinated and plants grew poorly when grown with high densities of *Bromus mollis* and *Festuca megalura*. High densities of *B. mollis* limited *S. pulchra* growth more dramatically than high densities of *F. megalura*. We suggest that *S. pulchra* is the most common California native grass not because the species dominated the original California grassland, but because it is favored by disturbances common now. Disturbances that reduce associated annuals are important for colonization by *S. pulchra*.

Stipa pulchra Hitchc. has long been regarded as the most important perennial species of the California grassland. Because *S. pulchra* is the most common native grass now, it has often been assumed to have dominated the pristine grassland. Yet progress towards understanding the historical role of native species has been slow, primarily due to the lack of overlap between the destruction of California's grasslands and the arrival of scientific observers of vegetation. The introduction of domestic livestock and alien plant species of Mediterranean origin beginning in 1769 completely changed the grassland flora (Burcham, 1957). Early records do not document the change adequately, but today few grassland areas are dominated by native plants (Barry, 1972) and even locations with numerous native species contain large numbers of alien plants (Heady, 1977).

Because of the complete alteration of the vegetation, with introduction of essentially a new flora, ecologists must rely on circumstantial evidence and inference to a large degree when reconstructing the original grassland. Early explorers occasionally referred to the presence of bunchgrasses (Burcham, 1957), and the distribution of native

species of perennial grasses follows closely the extent of the present grassland (Beetle, 1947), although stands are widely scattered.

Clements (1920) called the *Stipa setigera* (synonym for *S. pulchra*) consociation a part of the *Agropyrum* (sic)-*Stipa* Association. Clements based his classification on stands of bunchgrasses along fenced railroad rights of way. Although *S. pulchra* is favored by frequent fires, such as would have occurred along railroad tracks (Biswell, 1956), Clements' designation of the climax California prairie as a perennial grassland has been accepted with little modification (Munz and Keck, 1949; Barry, 1972; Baker, 1976; Küchler, 1977; Heady, 1977) and surprisingly little additional evidence.

Observations of vegetational change in protected California grassland yield inconsistent results. Succession after elimination of livestock grazing often shows the return of perennial grasses, particularly near the coast (Heady, 1977). Yet many areas have not returned to perennials even after decades of protection (White, 1967). Disturbance such as fire and some seasonal grazing patterns favor *S. pulchra*.

Experimental work with *S. pulchra* has yielded limited results applicable to observed patterns of vegetation. Robinson (1968) concluded that clay soils and abundant soil nitrogen favored *S. pulchra* in the central coast. Yet most areas remained dominated by annual grasses. Hull and Muller (1977) investigated the causes of the replacement of *Avena* grassland by *S. pulchra* following a change from cattle to horses and an alteration of grazing patterns in the south coast. Hull and Muller strongly implicated an allelopathic component that altered the associated annual flora when *S. pulchra* became dominant. Savelle (1977) found that stands of *S. pulchra* in northern California included an understory of *Festuca megalura*, whereas adjacent areas with similar soil were dominated by *Bromus* spp. Savelle found striking differences in decomposition and productivity in adjacent perennial and annual grasslands.

Arthur Sampson, California's first range plant ecologist, intensively investigated *S. pulchra* in the late 1920's and 1930's (Sampson and McCarty, 1930). His objectives centered around evaluation of native perennial grasses as forage for livestock. Unfortunately, the native bunchgrasses proved not only difficult to manage but less productive under grazing than the introduced annuals which had replaced them (Green and Bentley, 1957). Thus range improvement research shifted to non-native perennial species. Yet rangeland management has matured from a narrow, livestock centered discipline, into a broader science concerned less with a single product than a class of land. Restoration of native vegetation, including grasses, is now again a logical goal on many rangelands such as nature preserves and areas needing low-maintenance landscaping.

Heady (1977) summarizes the current attitude of vegetation ecologists towards this species: "*Stipa pulchra,* beyond all doubt, dominated

the valley grassland." *Stipa pulchra* is found on a wide variety of soil types, slopes and habitats (Barry, 1972), often with a different group of associated annuals than adjacent grassland without perennial grasses. Although grazing contributed to the decline of the native perennials, removal of grazing does not necessarily result in the return of perennial species, and never in the elimination of introduced annuals.

In this article we examine the present occurrence of *S. pulchra* in northern California and present information collected over a period of 20 years in a protected area. We next look at field patterns of establishment and mortality, and finally report results of studies investigating the interactions of seedlings of *S. pulchra* and introduced annuals. Our objective is to use these diverse data to help clarify the past and present role of *S. pulchra* in the California grassland.

Methods and Results

Soil-vegetation survey plots. The State Cooperative Soil–Vegetation Survey has mapped soils and associated vegetation in California since 1947. Shortly after the establishment of the survey, personnel began inventorying understory vegetation. Acre plots were established in selected locations for intensive sampling. More than 1500 plots have now been located, primarily in the North Coast and the foothills of the Sacramento Valley. Of primary interest are data from a listing of all herbaceous species present on the plot and from a step-point sample taken if herbaceous cover exceeded 5 percent. In conjunction with the sampled soils and other environmental information, this set of plots forms a valuable resource for examining plant distribution.

Of the 1517 total type-acre plots available, 51 recorded the presence of *S. pulchra* (Fig. 1). These plots were examined to establish the types of habitat favoring *S. pulchra*. Because of the very large number of plots involved, the sample forms an extensive survey of the types of habitat occupied by *S. pulchra* in the North Coast and the Sacramento Valley. Rather than being restricted, *S. pulchra* occupies a wide diversity of habitats, particularly in the Sacramento Valley. On the 51 plots, *S. pulchra* varied in density from a trace to 8 percent cover and occurred on 33 different soil series at elevations from 30 to 890 m. It was found on plots with annual precipitation ranging from 56 to 127 cm with a single stand at 190 cm rainfall. Although more common on southerly slopes than on northerly slopes (73 versus 27 percent), all slope aspects were represented. *Stipa pulchra* most commonly occurred on plots with less than 5 percent woody cover. Plots with more than 50 percent canopy cover contained little *S. pulchra,* and no plants appeared on plots with more than 80 percent woody cover.

Permanent transects. Shortly following the establishment of the Hopland Field Station in Mendocino County 180 km north of San
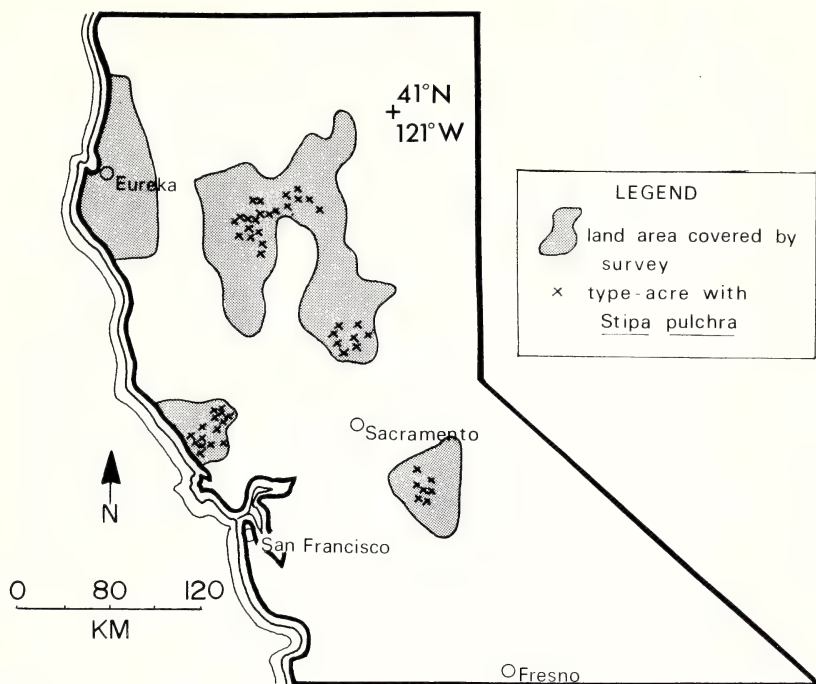
FIG. 1.   Location of type-acre plots containing *Stipa pulchra*. Of 1517 acre-square plots established by the Soil-Vegetation Survey, 51 contained identified *S. pulchra* between trace and 8 percent cover.

Francisco, the University of California designated two "Biological Areas" to be excluded from grazing by domestic livestock. The areas were set aside in 1956 in pastures formerly heavily used by sheep. Biological areas on the Hopland Field Station are located in oak woodland/grass vegetation typical of the valleys of the North Coast Ranges. With a Mediterranean climate, the area has dry and warm summers, cool and wet winters. The Foster Biological Area is located at an elevation of about 300 m and receives an average of 95 cm annual precipitation. The Riley Biological Area averages 700 m in elevation, with 120 cm mean annual precipitation.

In 1958, two years after the establishment of the Biological Areas, 24 permanently marked, 30-m transects were established to monitor changes in perennial grass density. The transects formed four clusters composed of three transects each, replicated in each Biological Area. Within each Biological Area two clusters were located within woodland canopy cover, and two in open grassland. Transects were all on similar soils. Along the transect within a belt extending 0.76 m on either side, all perennial grasses were tallied by species. Sampling of
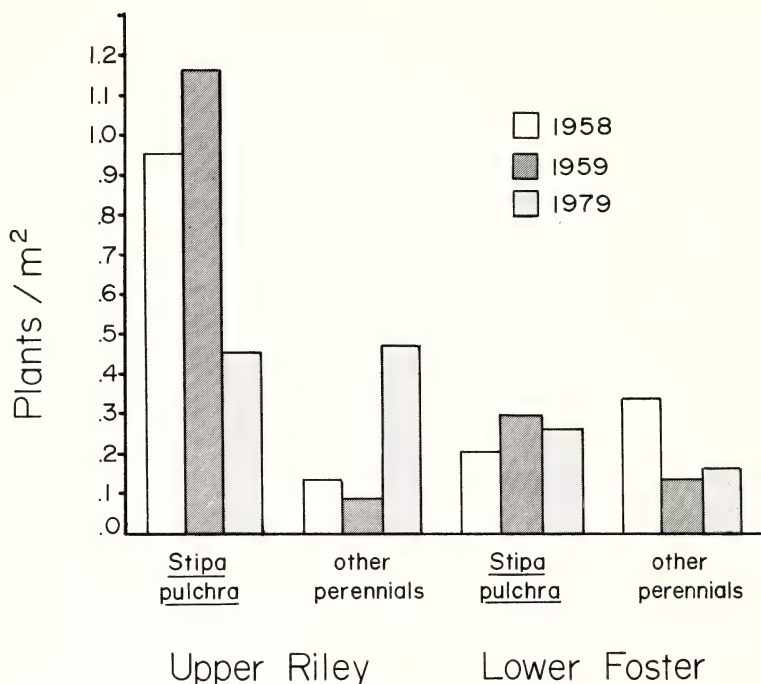
Fig. 2. Perennial grass species density on permanent transects on three sample dates. Transects were located at Hopland Field Station, Mendocino County in two "Biological Areas" ungrazed by livestock since 1956.

the transects was repeated in late summer of 1959 and 1979. An intensive search failed to relocate one transect cluster in the Foster area in 1979.

Numbers of perennial grasses varied widely between transects and even between clusters. This variability, coupled with systematic arrangement of the plots, precludes statistically supported conclusions concerning the differences between sample dates. However, because the plots are permanent, and thus represent repeated measures of the same spot, conclusions still have validity.

The higher-elevation plots in the Riley area contained greater densities of *S. pulchra* and other perennial species than the lower-elevation Foster plots (Fig. 2). Densities averaged 1.07 plants/m² on the upper transects and 0.37 plants/m² on the lower.

The differences between 1958 and 1959 are generally minor with the exception of a decrease in perennial species other than *S. pulchra* on the lower area. *Melica* spp. decreased from 0.17 to 0.09 plants/m² and *Danthonia californica* decreased from 0.07 to zero plants/m² on

the lower area. *Stipa pulchra* remained at nearly the same density. Between 1959 and 1979, density of *S. pulchra* changed little on the lower Foster area, even after more than 20 years without livestock.

On the upper Riley area *S. pulchra* declined in density between 1959 and 1979 (Fig. 2), while other perennial grasses, most notably *Elymus glaucus,* increased. Total perennial density changed little, with the exception of one cluster. On that cluster, in the absence of sheep grazing, the formerly abundant *S. pulchra* plants have been reduced from 2.18 to 0.05 plants/m^2, and have been replaced by the annuals *Carduus pycnocephalus* and *Taeniatherum asperum*.

Stipa pulchra was found both within the woodland zone and in the open grassland, although open areas contained more abundant *S. pulchra. Elymus glaucus* tended to occur more frequently under oak canopy, although it was also found in small numbers in open grassland. The perennial grass vegetation has changed little between 1959 and 1979, without a consistent increase of *S. pulchra*. In the Riley area other perennial grasses replaced *S. pulchra* between 1959 and 1979.

Germination, establishment, and mortality in the field.   In conjunction with a study of the population dynamics of annual grassland reported elsewhere (Bartolome, 1979), field observations were made of the behavior of *S. pulchra* seedlings at the Hopland Field Station. At weekly intervals through the fall and biweekly throughout the 1974–1975 growing season, the composition of the grassland was determined. Sampling consisted of 125 6.45-cm^2 samples of soil taken on each sample date with attached plants on which all species were counted. Germinable seed in soil samples was also determined before the fall rains, during the first six weeks of the fall, and twice in spring. The plot had been ungrazed by livestock since 1958 and used for evaluation of the effects of removal of varying amounts of natural mulch. Initially dominated by introduced annuals, *S. pulchra* increased on the plot in the first few years following the initiation of treatment, then remained stable.

Although *S. pulchra* seedlings were relatively few, several conclusions may be drawn. First, *S. pulchra* may germinate more slowly than the associated annual species and did not reach a peak density until well into the fall growing season (Fig. 3). However, the absence of germinable seed after the second week of the season precludes a definitive conclusion. Introduced annuals reach near-maximum density within the first six weeks of the season (Bartolome, 1979). *Stipa pulchra* densities fall rapidly as a result of mortality during the initiation of rapid spring growth by the associated annuals. The drop in *S. pulchra* density in the spring contrasts to the annual species which suffer little mortality during the rapid growth period (Heady, 1958). No *S. pulchra* seedlings occurred in samples after April.
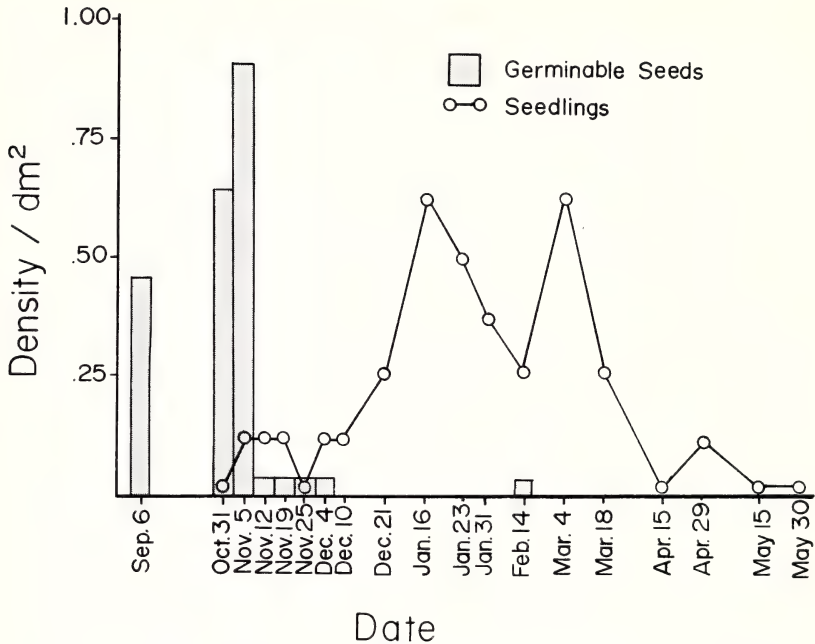
FIG. 3. Number of *Stipa pulchra* seedlings and germinable seeds in a sample of 125 6.45 cm² plots at the Hopland Field Station, Mendocino County during the 1974–1975 growing season.

Species interactions. Because annual plant density was high on the study plot, as it generally is wherever *Stipa* is observed, further investigation of the interaction of *S. pulchra* with annual species was initiated. Regardless of the historical role of *S. pulchra* in the pristine native grassland, today a major factor in its persistence is the nature of interactions with the introduced annual grasses. The key period for observing such interactions would be during germination and seedling establishment. Poor early germination or growth would precipitate later spring mortality. We examined *S. pulchra* in two pot experiments, one growing *S. pulchra* alone and the second in combination with annual grasses.

In both experiments, *S. pulchra* seeds were sown in plastic pots 14.6 cm in diameter. Pots were divided into blocks consisting of seeds gathered from three different locations (two coastal and one inland valley site). Cultures were grown at Oxford Tract at the University of California, Berkeley. The first experiment was conducted indoors in a greenhouse from 30 January to 30 March 1978. The interspecific experiment matured outdoors on benches from 30 May to 30 July 1978. In both experiments, observations were taken most frequently

FIG. 4. Cumulative average number of *Stipa pulchra* seeds germinating out of 25 under four moisture regimes and three mulch levels in pots.

toward the beginning, during the initial rapid growth period, and less frequently later as growth rates leveled off.

In order to follow plant growth through time, nondestructive measures of growth (number of germinated seeds, length of the longes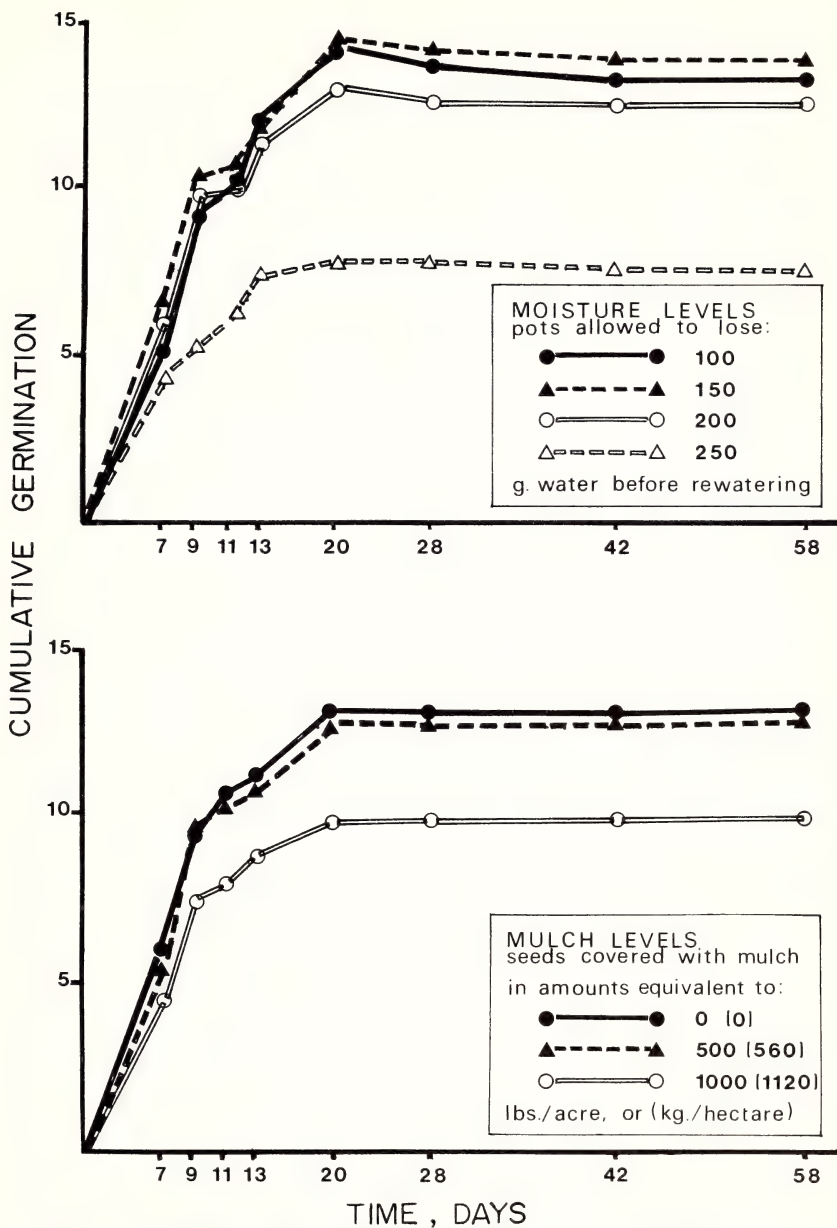t leaf, number of leaves and number of tillers) were recorded in the above experiments. A separate height–weight experiment was conducted to determine the relationship of these parameters to early-growth plant biomass. Length of longest leaf and number of leaves correlated best with biomass ($r^2 = 0.84044$, $p < 0.001$ and $r^2 = 0.83716$, $p < 0.001$, respectively) confirming the validity of using these measures to describe plant growth.

For the first experiment, *S. pulchra* seeds were sown alone at densities of 25 seeds per pot, and were subjected to three different levels of mulch cover and four different treatments of moisture stress. Mulch treatments consisted of leached and dried annual grass straw placed on top of the pots in weights corresponding to 0, 560, and 1120 kg/ha. For the moisture treatments, an alteration of wet and dry periods was induced, because it corresponds more closely to actual field conditions than does maintaining moisture at a constant level. With a soil tensiometer, the approximate relationship of pot weight to four soil water potentials (-3, -6, -12, and -15 bars) was established. Pots were allowed to dry down to established weights, then were rewatered. Instrumentation, and the fact that measurements were taken in relatively shallow pots compared to field soil depths, render only very approximate estimates of actual potential; thus the treatments should be thought of in terms of a gradation from constantly moist to infrequently moist.

Results of the above experiment showed that the final number of germinated seeds per pot differed significantly between seed sources, suggesting that there may be considerable genetic variability in natural populations. Of the 25 seeds per pot, an average of 12.75, 12.0, and 6.85 seeds germinated from Mendocino, Marin, and San Joaquin County sources, respectively.

Germination patterns were much more strongly impeded by treatments throughout the experiment than was growth of established seedlings. Germination was highly significantly suppressed both by the highest levels of moisture stress and the highest levels of mulch (Fig. 4).

In the second experiment, constant densities of perennial grass seeds were sown in pots in combination with varying densities and species of annual grasses. Encircling five *S. pulchra* seeds in plastic pots 14.6 cm in diameter were annual seeds at densities of 1, 3, 9, 18, and 54 seeds per *Stipa* seed. These numbers of annuals correspond to field densities of 300, 900, 2700, 5100, and 16,000 seeds/m², typical of low to moderate densities observed in the field (Bartolome, 1979).

To reduce genetic variation in the annual grasses, we used commercial strains of *Bromus mollis* and *Festuca megalura*. *Festuca megalura,* often mistakenly referred to as a native species (Lonard and Gould, 1974), commonly occurs in *S. pulchra* stands. *Bromus mollis* is the most widely distributed annual grass species in California (Janes, 1969).

Results from pot trials support field observations reported above. *Stipa pulchra* seeds germinated more slowly and attained a lower density after 40 days with high densities of both *Festuca megalura* and *Bromus mollis* (Fig. 5) compared to control. Seedlings grew more slowly as represented by fewer leaves at high density (Fig. 5). Of particular interest, however, is the different effect of the two annual species. *Bromus mollis* appeared to have a much more detrimental effect on perennial seedlings than *Festuca megalura.* This effect shows up particularly well when comparisons are made between the two species averaging overall values for density versus both number of seeds germinating and leaf number per seedling. *Bromus mollis* showed a significant negative correlation with density and number (r = −0.7554, p < 0.01) and size (r = −0.5979, p < 0.01) of perennial seedlings at 40 days, whereas the relationship for *Festuca,* although present, is not significant at the 5 percent level. Values for length of the longest leaf and number of tillers show the same results as for number of leaves, and thus are not presented graphically.

Conclusions

Evidence presented helps clarify the ecological role of *Stipa pulchra* in California grasslands. Although *S. pulchra* has often been described as the dominant and even the equivalent of undisturbed California prairie, the results and observations above suggest a lesser role.

Permanent transects at the Hopland Field Station failed to show an increase of *S. pulchra* over twenty years of protection from grazing by livestock. Indeed, *S. pulchra* decreased with protection on the Riley area, was replaced by other perennial grasses in one cluster, and by annuals in another. This lack of directional change is supported by similar *Stipa* stands examined at the Hastings Reservation by White (1967). The Soil–Vegetation Survey shows that *S. pulchra* occurs on a wide variety of sites, with broad distribution in the northern part of the state, and probably similar distribution throughout its range. *S. pulchra* is far from a rare or endangered species.

Experimental results also support the idea that *S. pulchra* is opportunistic, with few of the characteristics of typical climax species. *S. pulchra* germinates readily under all but severe moisture stress. It appears to establish most readily on bare ground, rather than under a cover of mulch. One might anticipate a climax species to prefer a
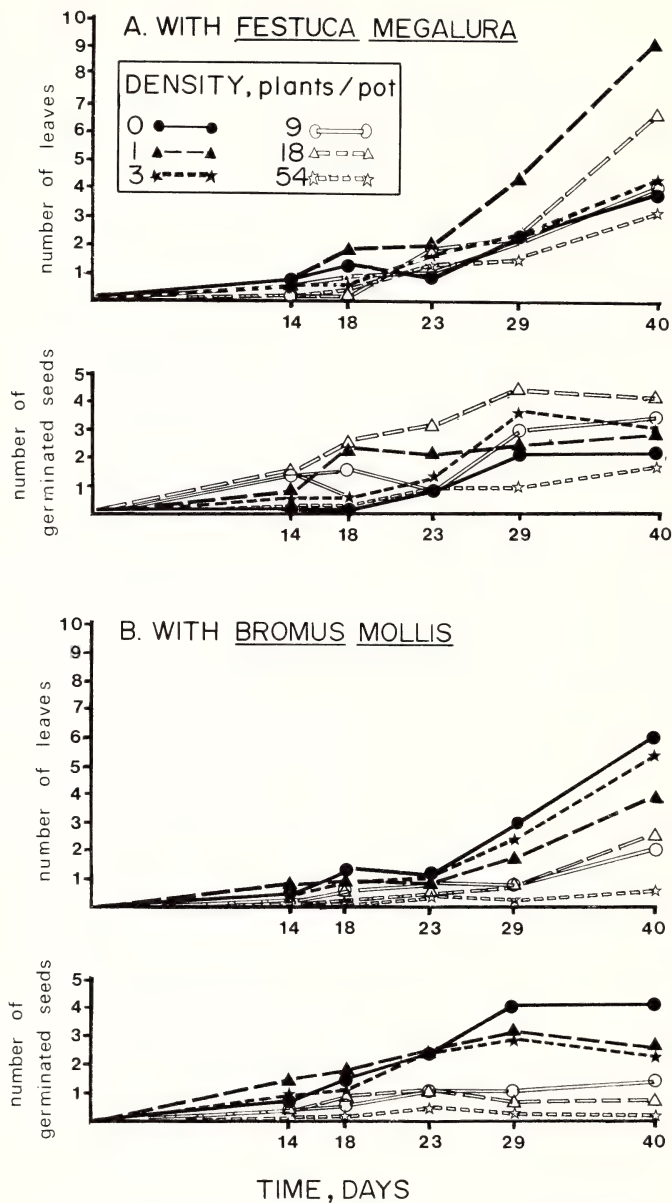
Fig. 5. Cumulative number of leaves per plant and number of germinated seeds of *Stipa pulchra* germinated in pots with six densities of A. *Festuca megalura* and B *Bromus mollis*.

higher litter cover or at least be adapted to such conditions. It cannot compete successfully against a rapidly-growing, robust annual such as *Bromus mollis,* yet *S. pulchra* possesses some similar germination features (rapid germination, germination on bare sites) to those of the annuals with which it now grows. Where the annual cover is dense, *S. pulchra* seedlings often do not survive. Where the annual cover is reduced either by fire, grazing, or disturbance, *S. pulchra* seedlings thrive. Once established, a *S. pulchra* plant can persist under moderately heavy grazing.

Its vigorous seeding habit and substantial quantities of viable seed place *S. pulchra* in a position to occupy suitable sites rapidly following disturbance of the annual cover. *Stipa pulchra* may have occupied a similar status in the pristine grassland, occupying areas of disturbance such as land slips and burned areas. Thus when the first ecologists observed relicts of the grassland they saw *S. pulchra,* not as the remnant climax species, but the native perennial species best able to thrive under disturbance. Far from being the dominant of the California prairie, it was a survivor because it is adapted to disturbance and does well when not grazed heavily in the spring. The dominants of the original prairie remain undetermined.

The major questions remain: What was the nature of the pristine grassland, and did the new annuals from the Mediterranean replace native annuals or native perennials? What were the dominants of the pristine vegetation? These questions may be answerable through an expanded application, i.e., more native species, of the methods used in this study. Clearly, the evidence to date points to a role for *S. pulchra* not necessarily as the dominant pristine grass of California, but a native species adapted to disturbance. *Stipa pulchra* is clearly not in danger of elimination, having survived under 200 years of heavy grazing and frequent burning.

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NOTEWORTHY COLLECTIONS

LUPINUS CITRINUS Kell. (FABACEAE).—USA, CA, Madera Co., Indian Lakes Estates, Rd. 417, 3.1 km e. of jct. with Hwy 41 (T8S R21E S28 ne.¼), 685 m; 8 May 1974, *Wells s.n.* (CAS); 11 May 1980, *Hamon 8042A* and *8042B* (UC); 8 Jun 1980, *Bartel 1019* (UC). Open decomposing granite outcrops in digger pine/oak woodland. Associated with *Calyptridium pulchellum, Cryptantha flaccida, Mimulus bicolor, M. dudleyi, Parvisedum congdonii,* and *Pectocarya penicillata*.

Previous knowledge. Reported from Fresno and Mariposa Cos. (Munz, A Calif. fl. 1959) and also as Fresno Co. endemic (Jepson, Fl. Calif. 2:277. 1936; Abrams, Ill. fl. Pacific states 2:494. 1944). Mariposa Co. reports erroneous and probably based on either incorrect county notation on label [28 May 1903, *Congdon s.n.* (UC)] or label data transposed during remounting [11 May 1902, *Congdon s.n.* (MIN)].

Significance. First record for Madera Co., a range extension wnw. of 29 km. Considered rare and endangered by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980). Under review as endangered species by the U.S. Fish & Wildlife Service (Fed. Reg. 45:82520. 1980).

STREPTANTHUS FARNSWORTHIANUS J. T. Howell. (BRASSICACEAE).—USA, CA: Madera Co., Mammoth Pool Rd., 3.5 km e. of jct. with Italian Bar Rd. (T9S R23E

S2 ne.¼ nw.¼), 1000 m: 29 May 1977, *Hemphill s.n.* (PUA); 8 Jun 1980, *Bartel 1020* (UC), scattered on exposed slate slope in *Quercus douglasii* woodland, associated with *Avena barbata, Lupinus benthamii, Mimulus guttatus, Pellaea mucronata,* and *Trifolium tridentata*; Fresno Co., Petersen Mill Rd., 0.4 km e. of jct. with old Tollhouse Rd. (T10S R24E S17 sw.¼ sw.¼), 1220 m, 21 Jun 1980, *Bartel 1022* (UC), open granite slope in *Pinus ponderosa-Quercus chrysolepis* mosaic, associated with *Arctostaphylos viscida, Brodiaea elegans, Bromus carinatus, Lupinus stiversii, Pellaea mucronata,* and *Penstemon laetus.*

Previous knowledge. Known from Kern, Tulare, and Fresno Cos. from metamorphic slate substrate (Howell, Leafl. W. Bot. 10:182–183. 1965).

Significance. First record for Madera Co., a range extension nw. of 28 km. First collection from granite. Recently numerous other Fresno Co. stands have been noted by the author and officers of the Sierra Natl. For. on granite in the Tollhouse area and on slate near Pine Flat Reservoir. Voucher specimens are not yet deposited. Many colonies on granite appear to be new invasions of open rock outcrops and roadcuts, suggesting a recently evolved ecotype. Considered rare but not endangered by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980). Dropped from review as potentially endangered by the U.S. Fish and Wildlife Service (Fed. Reg. 45:82559. 1980).—JIM A. BARTEL, U.S. Fish and Wildlife Service, Endangered Species Office, 1230 "N" Street, Sacramento, CA 95814. (Received 27 Oct 1980; accepted 13 Nov 1980; revised version received 5 Jan 1981.)

THELYPODIOPSIS PURPUSII (Brandegee) Rollins (BRASSICACEAE).—USA, NM, Socorro Co.: Sevilleta Wildlife Refuge, Los Pinos Mts., canyon directly e. of Nunn-Burris Ranch site, ca. 1825 m: 19 Apr 1975, *Manthey 27* (UNM); 2 May 1980, *Spellenberg and Ward 5484* (NMC); Sepultura Canyon, ca 1800 m, 19 Apr 1975, *Manthey 55* (UNM); Doña Ana Co., s. end of San Andres Mts., ne. side of Black Mt. (T20S R5E S31 s.-center), 1700–1800 m, 7 May 1980, *Spellenberg and Todsen 5497* (GH, NMC); Otero Co., 5.8 km e. of Hwy 70 e. of Alamogordo in Marble Canyon (T16S R10E S22 se.¼), 1850 m, 11 May 1980, *Spellenberg 5501* (GH). At each site the *Thelypodiopsis* was associated with *Juniperus monosperma* and various shrubs and perennial grasses that commonly occur with this tree. Plants were rare at all sites in 1980, possibly due to a "poor" year. Manthey's collections are much more robust; the winter of 1974–75 was considerably wetter. In 1980, plants grew on steep slopes in shelter of rocks or at the protected bases of cliffs and gully banks in relatively inaccessible areas. The species probably is more frequent than collections indicate because spring in NM is often dry and collecting, therefore, not very rewarding.

Previous knowledge. The species has been known for about 75 years from Coahuila, and within the last 20 has been found in w. TX, s. NM, and n. AZ. Its existence in NM was known from a single collection in Luna Co., *Spellenberg 3002,* made in 1973. (Herbaria consulted: GH, NMC, UNM; published sources: Rollins, Contr. Gray Herb. 206:1–18; Wooton and Standley, Fl. New Mex., Contr. U.S. Natl. Herb. 19. 1915. R. Rollins, pers. comm.).

Significance. Besides the new county records and the indication that this species is not especially rare in NM, our 1980 collections clarify the nature of *Thelypodium vernale* Wooton & Standley. That species is known only from the type collection made in 1908 in "low mountains west of San Antonio", Socorro Co., NM (Wooton & Standley, 1915). This collection apparently is lost, as noted in a revision of *Thelypodium,* in which *T. vernale* is excluded from *Thelypodium* and tentatively referred to *Sisymbrium* (Al-Shehbaz, Contr. Gray Herb. 204:1–148. 1973.). We easily "keyed" our collections to *T. vernale,* and the plants match well Wooton and Standley's description. Rollins, after viewing our material, agreed that *T. vernale* and our material are apparently the same,

but stated that they are properly placed in *Thelypodiopsis purpusii*, based on the earlier published *Thelypodium purpusii* Brandegee (Brandegee, Zoe 5:232, 1906).

NEMACLADUS GLANDULIFERUS Jepson var. ORIENTALIS McVaugh (CAMPANULACEAE). —USA, NM, Hidalgo Co., in the s. end of the Sierra Rica, ca. 0.4 km w. of the Mexico border and 3.2 km s. of the upper corner of the NM "boot-heel" (T29S R14W S36 ne. ¼), 1440 m, 14 May 1980, *Spellenberg and Ward 5520* (NMC, TEX). Gravelly limestone in an arroyo, very local, only 4 plants, with *Larrea tridentata, Calliandra eriophylla,* and other shrubs of the Chihuahuan and Sonoran deserts.

Previous knowledge. Widespread from s. CA and sw. UT to s. AZ and nw. MEX, and known from a number of collections made during activities of the Mexican Boundary Survey in 1852 in the vicinity of present-day El Paso, TX (McVaugh, Amer. Midl. Naturalist 22:521–550. 1939). (Herbaria consulted: ARIZ, ASC, MO, NMC, TEX, UNM, Western NM Univ.; published sources: Correll and Johnston, Man. vasc. pl. Tex. 1970; Martin and Castetter, Checklist gymnosp. angiosp. New Mex. 1970; McVaugh, 1939; Wooton and Standley, Fl. New Mex., Contr. U.S. Natl. Herb. 19. 1915).

Significance. This is the only collection of *Nemacladus* that unequivocally originates in NM, although "stony hills near Frontera" as cited by McVaugh for Sonoran records of this species by Charles Wright in 1852 refers to a low range of hills in extreme s. Doña Ana Co., NM, and adjacent CHIH, just w. of present-day El Paso, TX (Gray, Pl. Wrightianae, Tex.–NM, II. 1852; Torrey, Rep. Mex. Bndy. Surv., II, Botany. 1858). Localities of collections stated to be from NM, "in the valley of the Rio Grande below Donana" (McVaugh, 1939) are also indefinite. Doña Ana is the point in NM at which the border turned west from the Rio Grande prior to the Gadsden Purchase. Our collection is the first to be made in the general region in nearly 130 years. It is ca. 165 km se. of the nearest site in AZ in Graham Co. and about that far w. of the early record from near El Paso, TX. The plants are inconspicuous, and though probably not frequent, they simply might have been overlooked in the intervening years.—DARRELL WARD and RICHARD SPELLENBERG, Department of Biology, New Mexico State University, Las Cruces, 88003. (Received 4 Dec 1980; revised version received and accepted 17 Feb 1981.)

CAREX DEWEYANA Schwein. subsp. DEWEYANA (CYPERACEAE).—Mexico, Edo. de Hidalgo, Real del Monte, near Pachuca, *Cupressus* forest, 2850 m, 27 Aug 1944 (in fruit), *E. Hernández X. 462* (MSC). Verified by F. J. Hermann, Feb 1979.

Previous knowledge. Range: Lab. and Newf. to sw. Mack. and AK, s. to PA, OH, n. IA, CO, UT and B.C. The weakly differentiated subsp. *leptopoda* (Mack.) Calder & Taylor (incl. *C. deweyana* var. *bolanderi* [Olney] Boott), the characteristic phase of the cordilleran region, extends from B.C. to nw. MT, s. to s. CA, AZ and NM; also in e. Asia. (Herbaria consulted: F, MICH *ex herb.* F. J. Hermann, MSC, WIS; published sources: Braun, Monocotyledoneae [of Ohio]. 1967; Calder and Taylor, Canad. J. Bot. 43:1389–1391. 1965; Great Plains Fl. Assoc., Atlas fl. Great Plains. 1977; Harrington, Man. pl. Colorado, ed. 2. 1964; Hermann, Man. Carices Rocky Mts. and Colorado Basin. 1970; Hermann, Man. Genus *Carex* in Mexico and Central Amer. 1974; Hitchcock et al., Vasc. pl. Pacific Northw., pt. 1. 1969; Johnston, J. Arnold Arb. 25:49–50. 1944; Mackenzie, *in* N. Amer. Fl. 18, pt. 3:114–117. 1931; Matuda, Las Ciperaceas Edo. Mexico. 1959; Sánchez, Fl. Valle Mexico. 1978.)

Diagnostic characters. Keys to *Carex bromoides* Willd. in Hermann (1974), but clearly set off from that species by its thick, oblong-lanceolate, broader (1.2–1.6 versus 0.8–1.2 mm wide, ca. 3–3.5 instead of 4–5 times as long as wide) perigynia, the dorsal faces of which are nerveless or faintly nerved at base rather than conspicuously several-

nerved; by its paler, usually wider (2–5 rather than 1–2.5 mm wide) leaves; by its thinner and, except for the green central zone, whitish-translucent (instead of often orangish-tinged) pistillate scales; and by its oblong-ovate, broader (1.2–1.6 mm wide, ca. 1.5 times as long as wide) achenes. In *C. bromoides* the achenes are 0.8–1.1 mm wide and ca. 2–2.5 times as long as wide.

Significance. New to Mexico; 2030 km disjunction from nearest known populations in Las Animas and Larimer Cos., CO. One other very wide-ranging temperate species, *Carex interior* Bailey, has a similar range, but it extends farther s. on the Great Plains and reappears in Chihuahua and Distrito Federal, Mexico.—THEODORE S. COCHRANE, Department of Botany, University of Wisconsin, Madison 53706. (Received 10 Dec 1980; accepted 23 Feb. 1981.)

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WOLFFIA COLUMBIANA Karst. (LEMNACEAE).—USA, CA, San Diego Co., San Dieguito River, 1.5 km sw. of Lake Hodges Dam, s. side of Hwy S-6 (33°2′N, 117°8′W), 76 m, 26 Sep 1980, *Armstrong s.n.* (SD 106362). Forming dense populations at surface of quiet ponds, mixed with *W. punctata* with combined density of 100–150 per cm^2 of water surface. Associated with *Lemna gibba, Azolla filiculoides, Cyperus erythrorhizos, Pluchea purpurascens, Echinodorus berteroi, Paspalum distichum, Eclipta alba,* and *Scirpus acutus.*

Previous knowledge. Known from Canada, e. US, Mexico, s. to Colombia. A minute, free-floating rootless angiosperm, barely visible without magnification. Often associated with *Lemna, Spirodela,* and *Azolla.* The genus has undoubtedly been overlooked many times because of its small size. (Herbaria consulted: RSA, SD; published sources: Daubs, Ill. Biol. Monogr. 34. 1965; Mason, A fl. marshes Calif. 1957.)
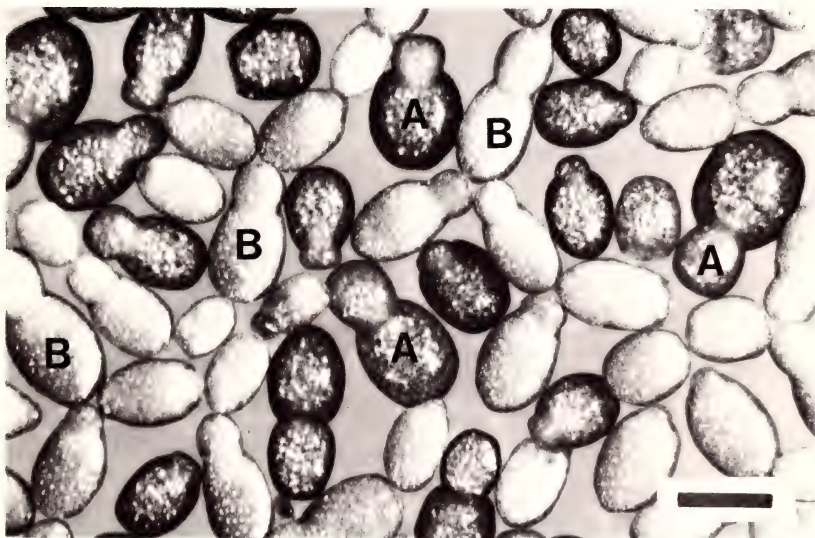

FIG. 1.   Dense population of *Wolffia* from the San Dieguito River, San Diego Co., CA. A. *Wolffia columbiana.* B. *W. punctata.* Scale bar is 1 mm.

Significance.   First record of *W. columbiana* in s. CA, a se. extension of 387 km from Oso Flaco Lake, San Luis Obispo Co. This species is clearly distinguished from *W. punctata* by its globose frond which is minutely roughened, but not flattened, on the dorsal surface (Fig. 1).—WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069. (Received 26 Nov 1980; accepted 23 Feb 1981.)

CALYPTRIDIUM PULCHELLUM (Eastw.) Hoov. (PORTULACACEAE).— USA, CA: Mariposa Co.: three small, widely separated populations on ridge e. of Ben Hur Rd. (T6S R18E S14 e.½ se.¼ and S24 nw.¼ nw.¼), 592 m, 1 May 1980, *Hamon 8019* (UC, FSC): this site is thought to be Pea Ridge, the type locality, found with *Lupinus deflexus* and a pale color form of *Lupinus stiversii*; granite dome 100 m w. of Mariposa Cr. and 400 m n. of Buckeye Rd. on the Jack Kirk Ranch (T6S R18E S11 se.¼ nw.¼), 460 m, 11 May 1980, *Hamon 8064* (UC, FSC, HSC), with *Lupinus deflexus* and *Streptanthus diversifolius*; Madera Co.: s. slope of small hill, 400 m w. of Ahwahnee (T6S R20E S36 ne. ¼), 730 m, 26 May 1980, Hamon, pers. obs. (no collection made because of extremely small, impacted population), associated with *Lupinus stiversii*; Indian Lakes Estates, 3 km e. of SH41 on Road 417 (Picyune Rd.) two populations 400 m apart (T8S R21E S28), 610 m: 11 May 1980, *Hamon 8049* (UC, FSC); 17 May 1980, *Hamon 8067* (UC): these are the largest populations noted, associated with *Lupinus citrinus, Mimulus layneae, Streptanthus diversifolius*; Fresno Co., decomposed granite outcrop on e.-facing slope 2 km sw. of Sugarloaf Hill, Sierra Natl. For. (T9S R24E S30 sw.¼ sw.¼), 1097 m, 20 May 1980, *Hamon 8078* (UC) associated with *Lupinus citrinus* and *Camissonia hirtella*.

Previous knowledge.   Collected only twice; originally at "Pea Ridge" by J. W. Congdon on 19 April 1901 (Eastwood, Bull. Torrey Bot. Club 29:79. 1902) and then by R. F. Hoover in 1938 (Hoover, Leafl. W. Bot. 2:222–225. 1940). Thought to occur only in the type locality (Hinton, Brittonia 27:197–208. 1975) and categorized as possibly extinct (CNPS Spec. Publ. 1. 1980).

Diagnostic characteristics.   Diminutive annual with sparsely fibrous root system. Inflorescence terminal and paniculate, stigma not sessile, inserted anthers a pale, rose-red that fades to yellow on drying.

Significance.   Rediscovery of species presumed extinct, with new records for Fresno and Madera Counties. Only one population found on public land (Sierra Natl. For.) with all others endangered by foothill real estate development. All populations were only a few meters in diameter with few individual plants.—DAN HAMON, 2823 E. Lansing Way, Fresno, CA 93726. (Received 9 Jan 1981; accepted 18 Feb 1981.)

NOTES AND NEWS

SPECIFIC STATUS FOR *Trifolium haydenii* VAR. *barnebyi* (FABACEAE).—In 1947 H. Dwight Ripley and Rupert Barneby collected an unusual *Trifolium* in the foothills of the Wind River Mountains in Wyoming. This collection was referred by Gillett (Canad. J. Bot. 50:1975–2007. 1972) to *T. gymnocarpon* Nuttall, with the comment that, forwardly directed hairs on the ovary "eliminates the possibility of its being *T. haydenii* as originally identified. The leaflets, too, which are quite glabrous, fit the shape of those of *T. gymnocarpon.*" More recently Isely (Brittonia 32: 55–57. 1980) described *T. haydenii* Porter var. *barnebyi* from the same collection. Both Gillett and Isely had only the original material to work with. This past summer we revisited the original locality, made extensive observations on the population, and collected more material. It was

TABLE 1.   SELECTED CHARACTERISTICS OF THREE TAXA OF *Trifolium*.

Characteristic	*T. gymnocarpon*	*T. barnebyi*	*T. haydenii*
Distribution	OR, ID, & c. WY to CA, AZ, & NM	c. WY	ID, MT, extreme nw. WY
Habitat	Desert to low montane	Sagebrush-juniper zone	Alpine to high montane
Habit	Cespitose	Densely matted	Loosely matted
Petioles	Pubescent	Pubescent	Glabrous
Leaflets	Pubescent dorsally	Glabrous mostly	Glabrous
Leaflet shape	1–2 times as long as wide	Twice as long as wide	1–1.5 times as long as wide
Leaflet veins	Wide spaced 5–10 pairs primary	Narrow spaced 12–18 pairs primary	Wide spaced 5–10 pairs primary
Peduncles	Pubescent	Pubescent	Glabrous
Pedicels	Pubescent	Pubescent	Glabrous
Calyx	Pubescent	Pubescent usually	Glabrous
Calyx teeth	About as long as tube	1.5–2 times as long as tube	1–2 times as long as tube
Banner	2.5–4 times as long as wide	1.5–2 times as long as wide	1.5–2 times as long as wide
Ovary	Pubescent	Pubescent	Glabrous

immediately apparent that this was not *T. haydenii* nor any other *Trifolium* known from this region. Superficially, the plants resembled *T. haydenii* because of the mat-forming habit and lack of an involucre. The habitat, in the sagebrush-juniper zone, was inappropriate for *T. haydenii*, which is found mostly in alpine areas but descends occasionally into high montane forests. Furthermore, this location was considerably south of any known station for *T. haydenii*. On closer examination the plants appeared much closer to *T. gymnocarpon* than to *T. haydenii* except for the mat-forming habit.

Table 1 summarizes characteristics of the three taxa, and reveals that the "barnebyi" material is unique only in the venation pattern of the leaflets. This pattern, with veins more numerous and more closely spaced than in the other two species, is easily observed as different. There are four additional differences from *T. gymnocarpon* and eight additional differences from *T. haydenii*. These combined with field observations of the three taxa make it exceedingly difficult to consider the "barnebyi" material as conspecific with either of the other two species. We therefore elevate *T. haydenii* var. *barnebyi* to specific status.

Trifolium barnebyi (Isely) Dorn & Lichvar, stat. nov.—*Trifolium haydenii* Porter var. *barnebyi* Isely, Brittonia 32:56. 1980.

Mat-forming perennial to 5 cm high; petioles pubescent, 3–18 mm long; leaflets 3, 3–11 mm long, glabrous, or rarely pubescent on dorsal midrib, mostly oblanceolate, usually toothed at least above, closely veined with mostly 12–18 pair of primary veins on larger leaflets, the veins usually much less than 0.5 mm apart; peduncles and pedicels pubescent; involucre lacking; flowers 8–18, 8–13 mm long; calyx 4–6 mm long, pubes-

cent at least in sinuses between teeth (rarely glabrous), the teeth mostly 1.5–2 times as long as tube; corolla whitish, drying brownish; ovary pubescent at least on dorsal suture; ovules mostly 1–4. Locally common on ledges of pale red sandstone and on sand pockets at base of sandstone outcrops at about 1950 m. elev. about 25 km sse. of Lander, Fremont Co., WY. TYPE: USA, WY, Fremont Co., 16 km (10 mi) s. of Perrin, 1950 m, 30 Jun 1947, *Ripley and Barneby 8924* (Holotype: NY; isotypes: NY, ISC, RM!). Other collections studied: USA, WY, Fremont Co., T3lN R99W S25 sw.¼, 1950 m, crevices of pale red sandstone, 27 Jun 1980, *Dorn 3483* (RM); *Lichvar 2955* (RM).

The three species can be distinguished easily using the following key.

1. Plants glabrous throughout. . . . . *T. haydenii*
1. Plants pubescent at least on peduncles, pedicels, and ovaries.
   2. Plants mat-forming; leaflets glabrous except rarely on dorsal midrib. . . . .
      . . . .*T. barnebyi*
   2. Plants not mat-forming; leaflets obviously pubescent, at least dorsally. . . . .
      . . . .*T. gymnocarpon*

Trifolium barnebyi is likely derived from *T. gymnocarpon,* even though the growth habits of the two are quite different. This view is supported by morphological similarities and by the dispersal and habitat. It is unlikely that *T. haydenii* was ever as far south as the type locality of *T. barnebyi,* for if it was, relict populations would likely have been found in the Wind River Mountains. *Trifolium barnebyi* is apparently adjusted to a specialized sandstone habitat and is presumably endemic there. The few similar habitats, all within 30 km of the known population, have yet to be investigated.—ROBERT D. DORN, Box 1471, Cheyenne, WY 82001 and ROBERT W. LICHVAR, The Nature Conservancy, Wyoming Natural Heritage Program, 1603 Capitol Ave., #325, Cheyenne 82001. (Received 10 Nov 1980; accepted 30 Jan 1981; revised version received 10 Feb 1981.)

Carex whitneyi OLNEY (CYPERACEAE): NOT ENDANGERED.—A survey was conducted from May through August 1980 to locate, document, and describe undiscovered populations of *Carex whitneyi* within its previously known range. The species is currently on List 2 of the CNPS Inventory of Rare and Endangered Vascular Plants of California (Smith et al., 1980) and the previous known range was limited to Mariposa, Tuolumne and Fresno Cos., CA.

Individual plants were identified and enumerated and culms were collected and verified by J. T. Howell (Curator Emeritus, CAS). All specimens are deposited at CAS and FSC. The survey identified 35 populations (with a total of 4667 plants) in Fresno Co., 9 populations (2932 plants) in Madera Co., 10 populations (4444 plants) in Tuolumne Co., 8 populations (432 plants) in Alpine Co., and 2 populations (42 plants) in Calaveras Co.

Based on our review of available literature and herbarium and field investigations of morphological and habitat characteristics we conclude that the species should be described as: *Carex whitneyi* Olney.—Densely cespitose; culms 2.5–9 dm tall; blades flat or ± revolute, 2–6 mm wide; spikelets 3 or 4; the terminal male, linear, 0.5–2.5 cm long, the lateral spikelets female, oblong or linear-oblong 1–3 cm long, 5–10 mm wide; female scales ovate, appressed-ascending, or ± spreading at maturity, hyaline-margined, 3–5 nerved; perigynia ovate, obovate, or elliptic-ovate, 3.5–5 mm long, 1.5–2.5 mm wide, tapering or contracted into a bidentulate or oblique beak 0.25–1.0 mm long, the beak somewhat hyaline. Habitat: dry to moist, often sandy; flat or moderate slopes; on the edge of meadows, in open to dense forests; often in disturbed soils where the surface litter has been removed; 1158 to 3658 m; Yellow Pine Forest to Subalpine Forest; Sierra Nevada from Tulare Co. to s. OR and w. NV.

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY—GRADUATE STUDENT MEETINGS

The California Botanical Society Graduate Student Meetings will be held at SAN FRANCISCO STATE UNIV., 24–25 October 1981. The meeting will focus on the presentation of short research papers and reports in progress by graduate students in all botanical and plant related fields. Members and non-members are invited to participate. For further information please contact the Graduate Student Meetings Committee, Dept. of Biology, San Francisco State Univ., San Francisco 94132, or leave a message at (415) 469-1359.

Dr. Harry D. Thiers will present a seminar Saturday evening on his recent work in Australia and the interesting fungal flora of that area.

Information for Contributors

Manuscripts submitted for publication in Madroño should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All 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, 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, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the Madroño page, and designed for reduction to ⅔ original size. 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 latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in Madroño 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in Madroño over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 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 @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

Contents, continued

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LOCAL FLORAS OF ARIZONA: AN ANNOTATED BIBLIOGRAPHY

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ABSTRACT

There are more than 80 local floras for Arizona that provide information on current and past plant distributions. They are briefly summarized. Although many areas in Arizona have been intensively botanized, floras are still lacking for some important regions.

Local floras, that is, relatively complete plant lists from defined areas, have value beyond simply cataloging the plants of an area. Local floras provide 1) valuable historical information, descriptions of new species, and documented range extensions; 2) data about the distribution of plants, condensing locations from hundreds of herbarium specimens into a line or two of print; and 3) a baseline for following immigration and extinction of species in an area. Local floras also provide the data needed for floristic comparisons of areas (as in Raven, 1963; Schaak, 1970; Lane, 1976) and for creating and testing ecological models such as island biogeography (Harper et al., 1978), patterns of species diversity (Richerson and Lum, 1980), or species migration rates (Meyer, 1978).

This bibliography is the first to concentrate on local floras of Arizona. Ewan (1936) lists and briefly summarizes a broad array of botanical papers dating as far back as 1848. Schmutz (1978) published an extensive bibliography on native Arizona plants in which references are classified and cross-referenced according to subject, but not annotated. Although both sources provided references for this paper, most are not cited in either bibliography.

I have attempted to include all published and unpublished Arizona plant lists that appear to be reasonably complete. Incomplete lists are included when they are the only lists available for a particular area or when they are one of a series of plant lists for an area. Some very old floras, although obviously incomplete, are included because of their historical value. I also include a few plant lists from ecological studies, but omit popular guides to wildflowers or single life forms (e.g., cacti). Manuals covering large regions such as the Sonoran desert, Arizona or the southwest are not considered.

Floristic work is continuing in Arizona. Although floras have been a frequent topic for masters' theses (Lane, 1976; Lehto, 1970; Reeves, 1976; Schaak, 1970; Halse, 1973; and others), more and more floras

are being compiled at the direction of state and federal agencies and conservation groups.

Several areas of Arizona have been neglected floristically (Fig. 1). For example, the dry mountain ranges of the lower Colorado River valley, although floristically distinct and containing a number of endemic species, have not been treated as a single unit in any flora. Only part of this interesting region is covered by Simmons (1966). The White Mountains have been enthusiastically botanized by professional and amateur biologists for many years, but no comprehensive plant list has been compiled for this area. Floras have yet to be written for many major mountain ranges, including the Baboquivari, Pinaleño and Santa Rita Mountains. Still other areas (e.g., Grand Canyon) have been studied many times.

The flora of an area is dynamic; some species immigrate and establish, others disappear as their habitats are removed or changed. Any list is at best a static record of a continuously changing assemblage of plant species.

Northern Arizona

1. Grand Canyon

McKee, E. D. 1934. Flora of Grand Canyon National Monument. Grand Canyon Nature Notes 9:316–321. Lists 87 taxa; classifies conspicuous plants by association; compares floras of Grand Canyon National Park and Grand Canyon National Monument. Incomplete.

Patraw, P. M. 1936. Check-list of plants of Grand Canyon National Park. Grand Canyon Nat. Hist. Assoc. Bull. 6 [Grand Canyon]. Lists 635 taxa for 272,798 ha. Annotations include habitat, associations, common names, local and regional distribution. Small-scale map shows collection localities.

Clover, E. U. and L. Jotter. 1944. Floristic studies in the canyon of the Colorado and tributaries. Amer. Midl. Naturalist 32:591–642. Lists 490 taxa; study area was the Green and Colorado Rivers from Greenriver, Utah to Boulder Dam, Nevada. Correlates plant associations with habitat, elevation and latitude; annotations include collection locations, collection numbers, relative abundance, and habitat.

McDougall, W. B. 1947. Plants of Grand Canyon National Park. Grand Canyon Nat. Hist. Assoc. Bull. 10 [Grand Canyon]. Lists 882 taxa for 272,798 ha; updates Patraw (1936). Annotations include common names, collection locality, relative abundance, and elevational ranges.

Deaver, C. F. and H. S. Haskell. 1955. Ferns and flowering plants of Havasu Canyon. Plateau 28:11–23. Lists 382 taxa for 210 ha.

115°　　　　　　　　　　　　　　　　　　　　　　　　　109°

37°　　　　　　　　　　　　　Glen Canyon　　　　　　　　37°
　　　　　　　　　　　　　　　　Navajo Mt.

3

1a
Boysag Point　　　　　　●4●

2　　　　　1　　　　　　　　　　　5
Rampart　Havasu Canyon　●Roaring Springs
Cave　　　　　●Grandview　　　　　　6●

N O R T H E R N　　　A R I Z O N A
7
9 ○ ●8
10 ○
11 ● ●12
13a
13
14　　　　13b
17 ○　18●

C E N T R A L　A R I Z O N A
Carnero
Lake
McNary ● ●Phelps
15　16　19●　25　27 ●Cabin
21 ○ 24
20　　26
22●
23

SOUTHWESTERN
ARIZONA　SOUTHEASTERN ARIZONA　32
33
30　31
34　48
37 ○ 35
28　29 Dripping　　Tumamoc Hill　45
Springs
Quitobaquito　36　38
40　44
39　46
47
41
43 42

N

0　　100 km

32°　　　　　　　　　　　　　　　　　　　　　　　32°
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FIG. 1.　Location of local floras in Arizona. *Northern Arizona:* 1. Grand Canyon; 1a. Arizona Strip; 2. Lake Mead National Recreation Area; 3. Kaiparowits Basin; 4. Navajo National Monument; 5. Canyon de Chelly National Monument; 6. Window Rock; 7. Wupatki National Monument; 8. Sunset Crater National Monument; 9. San Francisco Mountain; 10. Bill Williams Mountain; 11. Flagstaff; 12. Walnut Canyon National Monument; 13. Oak Creek Canyon; 13a. Volunteer and Sycamore Canyons; 13b. Chevelon Canyon. *Central Arizona:* 14. Hualapai-Aquarius Planning Units; 15. Harcuvar Mountains; 16. Vulture Mountains; 17. Skull Valley; 18. Montezuma Castle National Monument; 19. Lake Pleasant Regional Park; 20. White Tank Mountains Regional Park; 21. McDowell Mountain Regional Park; 22. Phoenix; 23. Sierra Estrella Regional Park; 24. Three-Bar Wildlife Area; 25. Sierra Ancha; 26. Tonto National Monument; 27. White Mountains. *Southwestern Arizona:* 28. Cabeza Prieta Game Range; 29. Organ Pipe Cactus National Monument. *Southeastern Arizona:* 30. San Pedro River; 31. Aravaipa Creek; 32. Clifton; 33. Gila River; 34. Santa Catalina Mountains; 35. Rillito River; 36. Baboquivari Mountains; 37. Tucson Mountains; 38. Rosemont; 39. Santa Cruz County; 40. Tumacacori Mission National Monument; 41. Sycamore Canyon; 42. Canelo Hills; 43. Patagonia-Sonoita Creek Sanctuary; 44. Whetstone Mountains; 45. Chiricahua Mountains; 46. Huachuca Mountains; 47. Mule Mountains; 48. Hooker Cienega.

Incomplete list, emphasizing spring and fall flora; discusses geology and vegetation; lists crops grown by Havasupai Indians.

McDougall, W. B. 1964. Grand Canyon Wildflowers. Mus. N. Arizona Bull. 43, Flagstaff. Lists 975 taxa for 272,798 ha; popular guide, relatively complete. About 120 species illustrated with photographs; includes short species descriptions, glossary of botanical terms, keys to families and species.

Schmutz, E. M., C. C. Michaels, and B. I. Judd. 1967. Boysag Point: a relict area on the North Rim of Grand Canyon in Arizona. J. Range Managem. 20:363–369. Ecological study; lists 88 taxa for 28 ha; discusses climate and physiography; compares floras and plant communities of Boysag Point with those of nearby mainland area.

Bennett, P. S. 1968. Inventory of plants found near Hearst Tanks, South Rim, Grand Canyon. *In* Teachers Manual: Environmental Awareness, p. 77–83. Grand Canyon National Park, Grand Canyon, Arizona 86023. Unpubl. report. Lists 185 taxa for Grandview Natural Area; incomplete list based on one month of collection; indicates introduced species.

Phillips, B. G. and A. M. Phillips, III. 1974. Spring wildflowers of the Inner Gorge, Grand Canyon, Arizona. Plateau 46:149–157. Lists 186 taxa; emphasizes spring-flowering ephemerals; covers the Inner Gorge from Lee's Ferry to Rampart Cave. Annotations include collection localities, common names, habitat, and elevation. Notes new county records.

Smith, E. L. 1974. The Grandview Natural Area. *In* Established Natural Areas in Arizona: a guidebook for scientists and educators, p. 207–217. Office of Economic Planning and Development, Phoenix. Lists 104 taxa for 166 ha; partial checklist based on Bennett (1968); describes climate, topography, and plant communities. Vertebrates also listed.

Phillips, A. M., III. 1975. Flora of the Rampart Cave area, lower Grand Canyon, Arizona. J. Arizona Acad. Sci. 10:148–159. Lists 270 taxa; annotations include common names, growth form, habitat, local distribution, and relative abundance; discusses habitats, lists characteristic species of each habitat.

Bennett, P. S. 1978. Vascular plants, Grand Canyon National Park. Grand Canyon Computer Center. Unpubl. [computer printout] available from Western Archaeological Center, 1415 N. 6th Ave., Tucson, Arizona. Lists 1574 taxa for 493,000 ha; annotations include relative abundance, nativity, and special status (threatened, endangered, or sensitive); recently revised (B. G. Phillips, pers. comm.).

Phillips, B. G., R. R. Johnson, A. M. Phillips, III, and J. E. Bowers. 1979. Resource values of the aquatic and riparian vegetation of Roaring Springs, Grand Canyon. Proc. Second Conf. Sci. Res.

Nat. Parks, San Francisco, 1979. 4:141–155. Natl. Techn. Inform. Serv., 5285 Port Royal Rd., Springfield, Virginia 22161. Lists 68 taxa; annotations include relative abundance, habit, and common names; discusses hydrology and plant associations; compares flora of Roaring Springs with that of three other springs in the Grand Canyon.

1a. Arizona Strip

Gierisch, R. 1981. Herbarium list, Arizona Strip District. Unpublished list, USDI, BLM, Arizona Strip District, P.O. Box 250, St. George, Utah 84770. Lists 863 taxa for region north of Grand Canyon and south of Utah; incomplete list compiled from herbarium specimens at BLM, St. George. Plant collection in the Arizona Strip by BLM personnel is continuing.

2. Lake Mead National Recreation Area

Holland, J. S., W. E. Niles, and P. J. Leary. 1979. Vascular plants of the Lake Mead National Recreation Area. Lake Mead Techn. Rep. 3. Biological Sciences, Univ. Nevada, Las Vegas. Lists 823 taxa for 607,500 ha. Discusses history of botanical collecting around Lake Mead; describes physiography and vegetation types. Annotations include habit, elevational range, local distribution, common names, collection locations, location of voucher specimens, relative abundance, threatened or endangered status, and synonymy.

3. Kaiparowits Basin

Clute, W. N. 1919. A trip to Navajo Mountain. Amer. Bot. (Binghamton) 25:81–87; ———. 1920. Notes on the Navago [sic] region. Amer. Bot. (Binghamton) 26:39–47. Clute (1919) described journey from Flagstaff to Navajo Mountain; mentioned changes in vegetation with increasing elevation. Clute (1920) described location and habitat for collections in Nelson (1920).

Nelson, A. 1920. Flora of the Navajo Reservation. Amer. Bot. (Binghamton) 26:48–56; 87–89; ———. 1922. Flora of the Navajo Reservation II. Amer. Bot. (Binghamton) 28:20–25. Lists 152 taxa. Incomplete list with historical interest; five new species are described. Annotations include relative abundance, habitat, species descriptions, and local distribution.

Lindsay, D. A. 1959. Vascular plants collected in Glen Canyon, 1958. *In* Ecological Studies of the Flora and Fauna in Glen Canyon, p. 63–72. Univ. Utah Anthropological Papers 40, Glen Canyon Ser. 7. Lists 115 taxa for Glen Canyon between Hite, Utah and Lee's Ferry, Arizona; annotations include common names, habitat, relative abundance, and collection location; based on a four-week collecting trip.

McDougall, W. B. 1959. Plants of the Glen Canyon area in the herbarium of the Museum of Northern Arizona. Unpublished. Museum of Northern Arizona, Flagstaff. Lists 304 taxa; compiled from collections made between 1936 and 1958; annotations include collection location, number, and date, collector, relative abundance, and habitat.

Gaines, X. M. 1960. An annotated catalogue of Glen Canyon plants. Mus. N. Arizona Tech. Ser. 4, Flagstaff. Lists 199 taxa. Based on a four-week collecting trip from Hite, Utah to the mouth of Kane Creek. Annotations include common names, collection localities and numbers.

Welsh, S. L., N. D. Atwood, and J. R. Murdock. 1978. Kaiparowits flora. Great Basin Naturalist 38:125–179. Lists 851 taxa for 1,400,000 ha; annotations include common names, collection locations, collectors and collection numbers, habitat, elevational range, relative abundance, and local distribution. Lists threatened and endangered plants; discusses physiography.

4. Navajo National Monument

Brotherson, J. D., G. Nebeker, M. Skougard, and J. Fairchild. 1978. Plants of Navajo National Monument. Great Basin Naturalist 38:19–30. Lists 293 taxa; annotations include habit, nativity, local distribution, collector, and collection date and number. Compares flora with that of Kaiparowits Basin, Arches National Park, and Uintah Basin; discusses species diversity within the Monument; describes climate, geology, and plant communities.

5. Canyon de Chelly National Monument

Halse, R. R. 1973. The flora of Canyon de Chelly National Monument. M.S. thesis, Univ. Arizona, Tucson. Lists 474 taxa for 33,955 ha. Includes keys to species, short species descriptions, and ethnobotanical information. Other annotations include collection numbers, local distribution, common names, and relative abundance. Discusses history and geology.

Harlan, A. and A. E. Dennis. 1976. A preliminary plant geography of Canyon de Chelly National Monument. J. Arizona Acad. Sci. 11:69–78. Adds 44 taxa to flora; annotations include habit, relative abundance, plant community, and local distribution for 112 perennials. Describes major plant communities.

Schmutz, E. M., A. E. Dennis, A. Harlan, D. Hendricks, and J. Zauderer. 1976. An ecological survey of Wide Rock Butte in Canyon de Chelly National Monument. J. Arizona Acad. Sci. 11:114–125. Lists 76 taxa for 12 ha; annotations include abundance, frequency, and cover. Lists plant macrofossils from packrat midden dated at 6210 ± 90 years B.P., concludes no important

local changes in vegetation or climate have occurred for 6000 years.

6. Window Rock

Bohrer, V. L. and M. Bergseng. 1963. An annotated catalogue of plants from Window Rock, Arizona. Navajo Tribal Museum, Window Rock. Lists 181 taxa within 16-km radius of Window Rock. Annotations include collection date, collection location, common name, habitat, elevation, plant association, and habit.

7, 8. Wupatki and Sunset Crater National Monuments

McDougall, W. B. 1962. Seed plants of Wupatki and Sunset Crater National Monuments. Mus. N. Arizona Bull. 37, Flagstaff. Lists 268 taxa for 15,390 ha. Annotations include common names and short species descriptions; notes local distribution of species in the two Monuments. Includes keys to species, glossary of botanical terms.

9. San Francisco Mountain

Little, E. L., Jr. 1941. Alpine flora of San Francisco Mountain, Arizona. Madroño 6:65–81. Lists 49 taxa for 518 ha; annotations include geographic range, habitat, relative abundance, and phenology. Describes plant associations and growth forms of alpine plants; discusses biogeography of some alpine species. Mentions endemics, lists 24 additional timberline species.

Schaak, C. G. 1970. A flora of the arctic-alpine vascular plants of the San Francisco Mountain, Arizona. M.S. thesis, N. Arizona Univ., Flagstaff. Lists 82 taxa for 518 ha. Annotations include common names, elevational range, relative abundance, habitat, and distribution. Provides keys to species and short species descriptions. Discusses plant adaptations to alpine environments, krummholz, and slope effect. Compares local arctic-alpine flora with that of the Rocky Mountains; describes plant communities.

Paulik, L. A. 1979. A vascular flora of the subalpine spruce-fir forest of the San Francisco Peaks, Arizona. M.S. thesis, Northern Arizona Univ., Flagstaff. Lists 189 taxa for 3600 ha; discusses history of plant collection and ecological study on San Francisco Peaks; describes plant communities and lists characteristic species of each. Altitudinal extensions or records and plants of disturbed areas are listed separately. Distributions of two endemic species are shown on small-scale maps.

10. Bill Williams Mountain

Hazen, J. M. 1978. The flora of Bill Williams Mountain. M.S. thesis, N. Arizona Univ., Flagstaff. Lists 221 taxa for 5180 ha. Discusses

life zones; lists dominant plants in each zone; notes introduced plants and altitudinal records. Describes geology and climate.

11. Flagstaff

Read, A. D. 1915. Flora of the Williams Division of Tusayan National Forest, Arizona. Plant World 18:112–123. Lists 284 taxa; covers the region west of Flagstaff and south of the Grand Canyon to the edge of the Colorado Plateau. Incomplete list with historical interest; notes introduced, new, or recently-described species; describes vegetation of elevational zones.

McDougall, W. B. 1959. Typical seed plants of the ponderosa pine zone. Mus. N. Arizona Bull. 32, Flagstaff. Lists 293 taxa for 172 ha. Includes keys to species, glossary of botanical terms, common names, and short species descriptions. Covers the area around the Museum of Northern Arizona near Flagstaff.

12. Walnut Canyon National Monument

Arnberger, L. P. 1947. Flowering plants and ferns of Walnut Canyon. Plateau 20:29–36. Lists 151 taxa for 761 ha. Incomplete list. Discusses plant communities in relation to soil moisture on north- and south-facing slopes.

Spangle, P. F. 1953. A revised checklist of the flora of Walnut Canyon National Monument. Plateau 26:86–88. Adds 82 taxa collected between 1947 and 1953 to the flora of Walnut Canyon.

Joyce, J. F. 1976. Vegetational analysis of Walnut Canyon, Arizona. J. Arizona Acad. Sci. 11:127–135. Ecological study; lists 93 additions to flora of Walnut Canyon. Discusses microclimates, plant communities.

13. Oak Creek Canyon

Deaver, C. F. 1930. Floristic studies in Oak Creek Canyon. M.S. thesis, Univ. Arizona, Tucson. Lists 194 taxa from upper Oak Creek Canyon. Incomplete list, based on collections from three representative areas. Annotations include relative abundance and habit. Includes photographs of some plants and vegetation types.

Sutton, M. 1952. A botanical reconnaissance in Oak Creek Canyon. Plateau 25:30–42. Lists 446 taxa for a 35-km stretch of Oak Creek Canyon. Road log with mileages and elevations notes interesting plants and plant associations; discusses vegetation changes with decreasing elevation. List annotated with common names.

Aitchison, S. W. 1978. Oak Creek Canyon and the Red Rock Country of Arizona: a Natural History and Trail Guide. Stillwater Canyon Press, Flagstaff. Appendix lists 590 taxa for 200 ha; annotated with common names. Mammals, birds, amphibians, and reptiles are listed separately. Vegetation, fauna and geology are discussed; a road log notes features of interest.

13a. Volunteer and Sycamore Canyons

Schilling, M. A. 1980. A vegetational survey of the Volunteer and Sycamore Canyon region. M.S. thesis, Northern Arizona Univ., Flagstaff. Lists 376 taxa by plant community; discusses plant communities, climate, history, physiography, and geology. Plants of disturbed areas, introduced plants, and elevational extensions are listed separately. The flora is compared with the floras of Oak Creek Canyon, Walnut Canyon, Bill Williams Mountain, and the San Francisco Peaks.

13b. Chevelon Canyon

Aitchison, S. W. and M. E. Theroux. 1974. A biotic inventory of Chevelon Canyon, Coconino and Navajo Counties, Arizona. Unpublished report, submitted to U.S. Soil Conservation Service and USDA, Sitgreaves National Forest. For information on availability contact S. W. Aitchison, Museum of Northern Arizona, Flagstaff. Lists 195 taxa; annotated with common names. Discusses plant communities, slope aspect, rare or endangered species. Lists vertebrates, provides small-scale vegetation map.

Central Arizona

14. Hualapai-Aquarius Planning Units

Butterwick, M., D. Hillyard, and B. Parfitt. 1979. Annotated list of taxa of vascular plants collected in the Hualapai-Aquarius environmental impact statement area. Unpubl. report, USDI, Bur. Land Management, Phoenix District Office, 2929 W. Clarendon Ave., Phoenix. Lists 865 taxa for 698,220 ha. Annotations include common name, habitat, habit, nativity, relative abundance, vegetation type, and collectors.

15, 16, 17. Harcuvar, Vulture, and Skull Valley Planning Units

Butterwick, M., P. Fischer, D. Hillyard, and D. Ducote. 1980. Annotated list of taxa of vascular plants collected in the Harcuvar, Vulture and Skull Valley Planning Units. Unpubl. report, USDI, BLM, Phoenix District Office, 2929 W. Clarendon Ave., Phoenix. Lists 559 taxa for the Harcuvar Planning Unit, 482 taxa for the Vulture Planning Unit, and 558 for the Skull Valley Planning Unit. Annotations include common names, habit, relative abundance, habitat, local distribution, collector and collection number.

18. Montezuma Castle National Monument

Spangle, P. and M. Sutton. 1949. The botany of Montezuma Well. Plateau 22:11–19. Lists 189 taxa. Incomplete list with no anno-

tations. Discusses geomorphology and origin of the well (a sink-hole). Describes climate and plant communities.

McDougall, W. B. and H. S. Haskell. 1960. Seed plants of Monte-zuma Castle National Monument. Mus. N. Arizona Bull. 35, Flagstaff. Lists 308 taxa for 423 ha. Includes keys to species, glossary of botanical terms, and short species descriptions.

19. Lake Pleasant Regional Park

Lehto, E. 1970. A floristic study of Lake Pleasant Regional Park, Maricopa County, Arizona. M.S. thesis, Arizona State Univ., Tempe. Lists 364 taxa for 5827 ha. Discusses phenology of plants in disturbed habitats. Annotations include common names, hab-itat, collectors and collection numbers. Discusses history, geology, and climate. Lists plants for each habitat, includes photographs of vegetation types.

20. White Tank Mountains Regional Park

Keil, D. J. 1973. Vegetation and flora of the White Tank Mountains Regional Park, Maricopa County, Arizona. J. Arizona Acad. Sci. 8: 35–48. Lists 332 taxa for 11,564 ha; annotations include relative abundance, habitat, and growth form. Discusses vegetation zones, includes vegetation map at 1:63,000.

21. McDowell Mountain Regional Park

Lane, M. A. 1976. Vegetation and flora of McDowell Mountain Re-gional Park, Maricopa County, Arizona. M.S. thesis, Arizona State Univ., Tempe. Lists 286 taxa for 8475 ha; annotations in-clude plant community, habitat, collector and collection number, and relative abundance. Shows distribution of species among six Maricopa County regional parks. Discusses history, climate, and soils. Includes photographs and vegetation map.

22. Phoenix

Hamilton, F. L. 1933. The desert garden: native plants of Phoenix and vicinity. Frances L. Hamilton, Phoenix. Deposited at Univ. Arizona Science Library, Tucson 85721. Lists 138 taxa for desert ranges near Phoenix, including Phoenix Mountain Park, Camel-back Mountain, Papago Park, and Squaw Peak. Incomplete. Pro-vides keys to families and species, line drawings of plants. An-notations include common names, habitat, short species descriptions, relative abundance, and phenology.

23. Sierra Estrella Regional Park

Sundell, E. G. 1974. Vegetation and flora of the Sierra Estrella Re-gional Park, Maricopa County, Arizona. M.S. thesis, Arizona State Univ., Tempe. Lists 330 taxa for 7533 ha; annotations in-

clude common names, collector and collection number, relative abundance, vegetation zone, plant community, elevation, and phenology. Describes history, geology, and climate; reviews past botanical work. Discusses plant communities and floristic differences between Sierra Estrella and South Mountains. Includes photographs and a topographic map.

24. Three Bar Wildlife Area (Mazatzal Mountains)

Dickerman, R. W. 1954. An ecological survey of the Three-Bar Game Management Unit located near Roosevelt, Arizona. M.S. thesis, Univ. Arizona, Tucson. Lists 286 taxa for 15,753 ha. Ecological study; incomplete list. Annotations include habitat, collection locations and numbers, relative abundance, phenology, and vegetation type. Discusses forage value for deer; describes vegetation types and effect of fire on chaparral. Includes photographs of vegetation types and map of burned areas.

McCulloch, C. Y. and C. P. Pase. 1968. Checklist of plants of the Three Bar Wildlife Area. *In* Wildlife Research in Arizona 1967, p. 77–88. Arizona Game and Fish Dept., Phoenix. Lists 521 taxa for 15,753 ha; annotated with common names; notes artificially-seeded species. About 20 taxa are identified only to genus.

25. Sierra Ancha

Johnson, R. R. 1960. The biota of Sierra Ancha, Gila County, Arizona. M.S. thesis, Univ. Arizona, Tucson. Lists 449 taxa for 5192 ha. Lists plants, birds, and mammals; plant list annotated with collection localities. Discusses life zones, analyzes distribution of plants reaching northern or southern limit in Sierra Ancha. Includes photographs of vegetation types.

Pase, C. P. and R. R. Johnson. 1968. Flora and vegetation of the Sierra Ancha Experimental Forest, Arizona. USDA For. Serv. Res. Paper RM-41. Lists 735 taxa for 5192 ha; relatively complete list based on 35 years of botanical exploration. Discusses floristic affinities; describes vegetation types. Includes photographs and vegetation map.

26. Tonto National Monument

Burgess, R. L. 1965. A checklist of the vascular flora of Tonto National Monument. J. Arizona Acad. Sci. 3:213–223. Lists 270 taxa for 454 ha; annotations include common name, life form, relative abundance, and habitat. Compares flora with that of Montezuma Castle National Monument.

27. White Mountains

Judd, B. I. 1972. Vegetation zones around a small pond in the White Mountains of Arizona. Great Basin Naturalist 32:91–96. Lists 32

taxa. Describes vegetation zones around Carnero Lake; lists common name, percent protein, relative abundance, and vegetation zone for each species; discusses succession from pond to forest.

Smith, E. L. 1974. Phelps Cabin Research Natural Area. *In* Established Natural Areas in Arizona: a guidebook for scientists and educators, p. 127–133. Office of Economic Planning and Development, Phoenix. Lists 195 taxa for 126 ha; summarizes 25 years of botanizing; annotated with common names. Includes vegetation map at 1:10,500, acreage of each vegetation type.

McLaughlin, S. P. 1978. Productivity of the understory community in an Arizona ponderosa pine forest. Ph.D. dissertation, Univ. Arizona, Tucson. Lists 180 taxa for 50 ha; complete list, no annotations; an interesting area with a species-rich understory.

Southwestern Arizona

28. Cabeza Prieta Game Range

Simmons, N. M. 1966. Flora of the Cabeza Prieta Game Range. J. Arizona Acad. Sci. 4:93–104. Lists 238 taxa for 380,700 ha; annotations include common names, elevation, collection localities, ethnobotanical information, and use by wildlife. Illustrates plant replacement with matched photographs.

Lehto, E. 1979. Plants of Cabeza Prieta Game Range. Unpubl. list. For information on availability contact the Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson 85719. Lists 304 taxa for 380,700 ha; no annotations.

29. Organ Pipe Cactus National Monument

Phillips, J. W. 1967. A checklist of the plants of Organ Pipe Cactus National Monument. Unpubl. ms. deposited at Organ Pipe Cactus National Monument. Lists 456 taxa for 133,898 ha; annotations include local distribution, common names, and comments on identification.

Adams, W. B. 1971. A checklist of the plants of Organ Pipe Cactus National Monument. Unpubl. ms. deposited at Organ Pipe Cactus National Monument. Lists 520 taxa for 133,898 ha; annotations include collection locality, common names.

Adams, W. B. 1971. A flora of Quitobaquito. Unpubl. ms. deposited at Organ Pipe Cactus National Monument. Lists 93 taxa for Quitobaquito pond and vicinity.

Phillips, J. W. 1971. Preliminary flora of Dripping Springs. Unpubl. ms. deposited at Organ Pipe Cactus National Monument. Lists 91 taxa for Dripping Springs in the Puerto Blanco Mountains.

Jordan, E. H. 1975. A checklist of the plants of Organ Pipe Cactus National Monument. Unpubl. list deposited at Organ Pipe Cactus National Monument. Lists 521 taxa for 133,898 ha; compiled

from herbarium specimens at the Monument and University of
Arizona; annotations include common names and location of
voucher specimens.

Bowers, J. E. 1980. Flora of Organ Pipe Cactus National Monument.
  J. Arizona-Nevada Acad. Sci. 15:1–11; 33–47. Lists 522 taxa for
  133,898 ha; annotations include elevational range, collection lo-
  cations, local distribution, relative abundance, common names,
  phenology, and habit. Small-scale map shows collection localities.
  Discusses species richness, distributional limits, paleobotany, and
  mesic habitats.

SOUTHEASTERN ARIZONA

30. San Pedro River

Gavin, T. A. 1973. An ecological study of a mesquite bosque. M.S.
  thesis, Univ. Arizona, Tucson. Lists 43 taxa for 137 ha; anno-
  tations include common names and relative abundance. Study
  area was along the San Pedro River near Mammoth. Birds, mam-
  mals, amphibians, and reptiles also listed. Discusses historic vege-
  tation change, examines conservation of riparian habitat. Dis-
  cusses seasonal aspects of flora. Includes vegetation map.

31. Aravaipa Creek

Kepner, W. G. 1978. Vegetation and flora of the Aravaipa Creek
  Primitive Area, Graham and Pinal Counties, Arizona. Unpubl.
  report, USDI, BLM, Safford District Office, 425 E. 4th St., Saf-
  ford, Arizona. Lists 150 taxa for 3238 ha; annotated with common
  names. Describes vegetation types, riparian habitats; discusses
  hydrology, geology, and climate.

Warren, P. L. and L. S. Anderson. 1980. Annotated checklist of
  plants of the George Whittell Wildlife Preserve. *In* T. B. John-
  son, ed., 1980 Progress Report for the Biological Survey of the
  George Whittell Wildlife Preserve, Graham and Pinal Counties,
  Arizona, p. 80–124. For information on availability contact the
  Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson
  85719. Lists 320 taxa; complete list to follow in final report. An-
  notations include common name, habit, elevational range, habi-
  tat, local distribution, relative abundance, and brief species de-
  scriptions.

32. Clifton

Davidson, A. 1904. Flora of the Clifton district, Arizona. Bull. S.
  Calif. Acad. Sci. 3:110–111; 4:18–19, 35–36, 130–131; 5:67–70;
  6:34–36. Lists 348 taxa; annotations include collection localities,
  relative abundance, habitat, and phenology. Compiled from col-

lections within a 40-km radius of Clifton. Incomplete list with historical interest.

33. Gila River

McGill, L. A. 1979. Vascular flora. *In* Resource inventory for the Gila River Complex, eastern Arizona, p. 56–83. Unpubl. report, USDI, BLM, Safford District Office, 425 E. 4th St., Safford, Arizona. Lists 394 taxa; annotations include common names and taxonomic citations; notes established exotics. Discusses species diversity, riparian habitats.

34. Santa Catalina Mountains

Whittaker, R. H. and W. A. Niering. 1964. Vegetation of the Santa Catalina Mountains, Arizona. I. Ecological classification and distribution of species. J. Arizona Acad. Sci. 3:9–34; ——. 1968. Vegetation of the Santa Catalina Mountains. III. Species distribution and floristic relations on the north slope. J. Arizona Acad. Sci. 5:3–21. Lists 1210 taxa; annotations include growth form, Raunkaier life form, floristic affinity, distribution, elevational range, and relation to topographic moisture gradients. Ecological study that analyzes vegetation along moisture and elevational gradients.

35. Rillito River

Willis, E. L. 1939. Plant associations of the Rillito floodplain in Pima County, Arizona. M.S. thesis, Univ. Arizona, Tucson. Lists 201 taxa, notes habit of each. Ecological study; discusses riparian plant communities in relation to water table; describes vegetation types.

36. Thomas Canyon (Baboquivari Mountains)

Toolin, L. J. 1979. A floral survey of Thomas Canyon, Baboquivari Mountains, Pima County, Arizona. Unpubl. For information on availability contact the Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson 85719. Lists 183 taxa. Briefly discusses major plant communities and lists noteworthy collections.

37. Tucson Mountains

Thornber, J. J. 1909. Vegetation groups of the Desert Laboratory domain. *In* V. M. Spalding. Distribution and movements of desert plants, p. 103–112. Publ. Carnegie Inst. Wash. 113. Lists 442 taxa for 1036 ha. Classifies plants by habitat and growth form; lists introduced species. Discusses growth form in relation to climate and habitat.

Wadleigh, R. 1969. Plant list for Tucson Mountain District of Saguaro National Monument. Unpubl. Available from Unit Man-

ager, Saguaro National Monument, Box 595, Tucson, Arizona 85704. Lists 430 taxa for 8499 ha. Notes whether plant was observed or collected, location of voucher specimens.

Turner, R. M. 1977. Plant species list: Tumamoc Hill. Unpubl. Available from USGS Research Project Office, 301 W. Congress, Tucson, Arizona 85701. Lists 438 taxa for 1036 ha. Updates Thornber (1909). Annotations include synonymy, habitat.

38. Rosemont (Santa Rita Mountains)

McLaughlin, S. P. and W. Van Asdall. 1977. Flora and vegetation of the Rosemont area. *In* An environmental inventory of the Rosemont area in southern Arizona. 1:64–98. Deposited at the Univ. Arizona Science Library, Tucson 85721. Lists 416 taxa for 6475 ha. Discusses vegetation change, floristic affinities. Analyzes plant communities, includes interesting discussion of plant communities on limestone. Provides photographs of vegetation types, vegetation map at 1:63,000.

39. Santa Cruz County

Kaiser, J. M. 1980. Vegetation of Santa Cruz County. Unpublished manuscript. USDA Plant Protection and Quarantine Program, Nogales, Arizona. Lists 957 taxa for 322,589 ha; based on 32 years of plant collection; excludes grasses, sedges, and ferns. Annotations include species descriptions, collection localities, distribution in Arizona and Santa Cruz County. Profusely illustrated with color photographs.

40. Tumacacori Mission National Monument

Mouat, D. A., S. J. Walker, and B. D. Treadwell. 1977. The Tumacacori Mission National Monument floral inventory and vegetation map project. Office of Arid Lands Studies, Univ. Arizona, Tucson. Lists 130 taxa for 4 ha: annotated with common names. Includes map of perennial species at 1:250.

41. Sycamore Canyon (Pajarito Mountains)

Toolin, L., T. R. Van Devender, and J. M. Kaiser. 1980. The flora of Sycamore Canyon, Pajarito Mountains, Santa Cruz County, Arizona. J. Arizona-Nevada Acad. Sci. 14:66–74. Lists 625 taxa for 932 ha; complete list based on 35 years of collection. Discusses species with disjunct distributions, species known in U.S. only from Sycamore Canyon. Describes geographic affinities of flora. Annotations include location of voucher specimens.

42. O'Donnell Canyon (Canelo Hills)

Yatskievych, G. A. 1980. Plant list for O'Donnell Canyon, Canelo Hills, Santa Cruz County, Arizona. Unpubl. For information on

availability contact the Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson 85719. Lists 251 taxa. Annotations include habitat, collector and collection dates. Notes rare or endemic species.

43. Patagonia-Sonoita Creek Sanctuary

Fay, J. M. 1978. Vegetation and flora of the Patagonia-Sonoita Creek Sanctuary, Patagonia, Arizona. Unpubl. For information on availability contact the Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson 85719. Lists 287 taxa for 125 ha; annotations include brief species descriptions, phenology, relative abundance, habitat, local distribution, common names, ethnobotanical information, and use of plants by wildlife. Provides keys to the species. Discusses conservation of cottonwood gallery forests. Describes local history, plant associations, floristic affinities, patterns of disturbance. Includes vegetation map.

44, 47. Whetstone and Mule Mountains

Wentworth, T. R. 1976. The vegetation of limestone and granite soils in the mountains of southeastern Arizona. Ph.D. dissertation, Cornell Univ., Ithaca. Lists 515 taxa for the study area, which included parts of the Mule, Whetstone, and Huachuca Mountains. Ecological study; annotations include substrate, growth form, floristic affinity, Raunkaier life form, and distribution. Discusses substrate relations and species diversity in southeastern Arizona.

45. Chiricahua Mountains

Clark, O. M. 1939. Chiricahua summer flora. Southwestern Monuments Monthly Reports (Oct):318–329; ———. 1940. Check list of the flora of Chiricahua National Monument. Southwestern Monuments Monthly Reports (Sep):201–215. Lists 601 taxa for 4308 ha. Incomplete; annotated with common names.

Robinson, M. D. 1968. Summer aspect of a high coniferous forest in the Chiricahua Mountains, Arizona. M.S. thesis, Univ. Arizona, Tucson. Lists 71 taxa for the Fly's Peak area. Ecological study; discusses relationship between slope aspect, climate, elevation, and vegetation. Describes plant communities.

Reeves, T. 1976. Vegetation and flora of Chiricahua National Monument, Cochise County, Arizona. M.S. thesis, Arizona State Univ., Tempe. Lists 687 taxa for 4308 ha; annotations include common names, phenology, relative abundance, habitat, elevational range, and vegetation association. Describes plant communities; provides topographic, geologic, and vegetation maps; illustrated with photographs of vegetation types.

46. Huachuca Mountains

Wallmo, C. O. 1950. Vegetation mapping of Fort Huachuca Wildlife Area. *In* Fort Huachuca Wildlife Area surveys 1950–1951, p. 1–43. Arizona Game and Fish Commission, Phoenix. Lists 482 taxa for 18,063 ha. Collections and species lists made by L. N. Goodding; grasses extensively annotated. Other annotations include browse and forage value, use by wildlife, and relative abundance. Discusses vegetation types; provides vegetation map at 1:75,000. Goodding's list was updated (to 554 taxa) in 1963.

Wentworth, T. R. 1976. See 44, 47. Whetstone and Mule Mountains.

Toolin, L. J. 1980. Final report on the flora of Ramsey Canyon. Unpubl. For information on availability contact the Arizona Natural Heritage Program, 30 N. Tucson Blvd., Tucson 85719. Lists 343 taxa. Discusses physiography and climate; notes plants of special interest. Annotations include habit, local distribution, relative abundance, phenology, common names, and habitat.

48. Hooker Cienega

Yatskievych, G. and C. E. Jenkins. 1981. Fall vegetation and zonation of Hooker Cienega, Graham County, Arizona. J. Arizona-Nevada Acad. Sci. In press. Lists 113 taxa; study area is 8 km long. Annotations include habitat, location of voucher specimens, common names, and state and county records. Discusses vegetational zonation and hydrology.

LITERATURE CITED

EWAN, J. 1936. Bibliography of the botany of Arizona. Amer. Midl. Naturalist 17:430–454.

HARPER, K. T., D. C. FREEMAN, W. K. OSTLER, and L. G. KLIKOFF. 1978. The flora of Great Basin mountain ranges: diversity, sources, and dispersal ecology. Great Basin Naturalist Memoirs 2:81–103.

MEYER, S. E. 1978. Some factors governing plant distributions in the Mojave-Intermountain transition zone. Great Basin Naturalist Memoirs 2:197–207.

RAVEN, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289–317.

RICHERSON, P. J. and K. LUM. 1980. Pattern of plant species diversity in California: relation to weather and topography. Amer. Naturalist 116:504–536.

A NEW SPECIES OF QUERCUS (FAGACEAE) FROM SOUTHERN CALIFORNIA

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ABSTRACT

Quercus cornelius-mulleri Nixon & Steele is described from southern California, U.S.A., and Baja California Norte, Mexico. Fused-stellate trichomes, which were previously known in *Quercus* only in the series *Virentes,* are reported for the new species.

The scrub oaks of the subgenus *Quercus* (*Lepidobalanus* Endl. ex Oersted) in southern California have been a source of confusion to botanists since the earliest botanical expeditions (for a complete discussion of the nomenclatural history of the California scrub white oaks, see Tucker, 1952a). Trelease (1924) included all of the southern California scrub white oaks in *Quercus dumosa* Nutt., recognizing some varieties (such as var. *turbinella* (Greene) Trel.). Tucker (1952a, 1952b) established *Q. turbinella* Greene subsp. *californica* Tucker as a taxon distinct from *Q. dumosa,* with a range from the western edge of the Mojave Desert northward through the inner coast ranges to San Benito County. Tucker (1952a, 1953) did not include material from the desert border mountains of San Diego and Riverside Counties in his concept of *Q. turbinella* subsp. *californica*; this material, he felt, was "best referred to *Q. dumosa,* rather than *Q. turbinella.*" Recent investigations indicate that these latter populations are representative of an undescribed species, distinct in fundamental morphological characters, distribution, and ecology from *Q. dumosa, Q. turbinella* subsp. *turbinella,* and *Q. turbinella* subsp. *californica*. It is a pleasure to name the species in honor of Professor Emeritus Cornelius H. Muller, both for his great contributions to oak taxonomy, and for his devotion to those fortunate enough to be his students.

Quercus cornelius-mulleri Nixon & Steele sp. nov.
Frutices sempervirentes multiramosi 1–2(–3) m alti; rami hornotini 1–1.5 mm diametro dense tomentulosi trichomatibus sessilibus stellatis breviradiatis; gemmae 2.5–3 mm longae ovoideae glabrae. Folia crassa coriacea ovata vel oblonga vel obovata vel subrotundata ad marginem dentata dentibus saepe minus quam 2 mm longis vel integra, supra obscure viridia, trichomatibus sparsis stellatis, subtus dense tomen-

tulosa trichomatibus sessilibus superpositis minutis radiis (8–)12(–16) ad basem coalescentibus usque ad 0.1 mm longis adpressis; petioli 2– 5 mm longi tomentulosi. Amenta fructifera subsessilia; cupula fructi- fera hemisphaerica vel profunde cyathiformes; glans annua saepe fu- siformis vel late conica sed variabilis.

Multi-stemmed rounded shrubs 1–2 or 3 m tall, the crowns densely branched; twigs of the season 1–1.5 mm in diameter, terete, densely short-stellate tomentulose (individual rays less than 0.2 mm long), persisting tomentulose the second year, occasionally only sparsely pu- berulent and brown; buds 2.5–3 mm long, ovoid, obtuse, glabrous and dull brown, the younger scales ciliate-hairy; stipules ca. 4 mm long, subulate, strigose, caducous; leaves evergreen, rather thick and coriaceous, ovate to oblong or narrowly obovate, or subrotund, api- cally acute or rounded, basally rounded to cuneate, the margins spar- ingly toothed throughout or entire, flat or sometimes undulate, car- tilaginously thickened, the teeth sclerenchymatously tipped, the spines usually shorter than 2 mm; upper surface dull green, sparsely pubes- cent with minute stellate hairs, 0.15–0.17 mm in diameter, about 1 mm distant or much more sparse or occasionally deciduous; lower surface appearing glaucous because of a dense tomentulum of over- lapping minute stellate hairs, to 0.2 mm in diameter, closely ap- pressed, consisting usually of 12 (from 8 to 16) rays fused at their bases and forming a flattened rotate cluster; glandular trichomes absent on mature leaves; the midrib yellow against the white or ivory tomen- tulum; veins 6 or 7 on each side, slightly raised above, more prominent (even under tomentulum) beneath, irregularly branched and anasto- mosing; petioles 2–5 mm long, tomentulose similarly to the twigs or less so on the abaxial side; staminate catkins 25–55 mm long on slender sparsely pubescent rachises, the flowers distant except for the con- gested distal quarter, calyx lobes ciliate, the filaments markedly exsert- ed, anthers glabrous; pistillate catkins subsessile with clusters of 2–3 flowers or sometimes solitary; fruit annual, solitary, paired, or in clus- ters of 3, subsessile; cups hemispheric to cup-shaped, or sometimes deeply cupped, basally rounded, as much as 20 mm broad and 13 mm high, scales somewhat thickened basally, gray-tomentulose throughout or the short thin apices glabrous and brown; acorns variable, usually fusiform or broadly conical to ellipsoid, 20–30 mm long and 10–13 mm broad or smaller, glabrous except at the puberulent apices, the basal one-third enclosed in the cups.

Type: USA, California, San Diego Co., ca. 24.7 km on McCain Valley Road n. from its junction with Interstate 8 (32°45′N, 116°20′W), 1335 m elevation, July 24, 1980, *Nixon and Steele 2765* (Holotype: UCSB; isotypes: DAV, NY, RSA, SD, TEX, UC).

Paratypes: México, Baja California Norte: Cantu Grade, 9.7 km e. of La Rumorosa, *Moran 13147* (RSA, SD); 6 km e. of La Rumorosa,

then n. 0.8 km, *Steele 374C, 374E* (UCSB); 6.4 km s. of La Rumorosa, *Steele and Nixon 383* (UCSB); 32 km s. of La Rumorosa, *Nixon and Hendon 2335A* (UCSB); USA, CA, San Diego Co.: McCain's Ranch, Manzanita Indian Reservation, *Gander 8880* (SD); Montezuma Valley, *Muller 4040* (CHM); *Dubbers, Harbison and Higgins 44.129* (SD); 1.5 km e. of Burnt Rancheria Campground, Laguna Mountains, *Cox s.n.* (SD); 11.2 km e. on County Rd. S22 from its junction with County Rd. S2, Culp Valley, *Steele and Hendon 391* (UCSB); Riverside Co.: Hidden Valley Campground, Joshua Tree Natl. Monument, *Wilken 7552* (UCSB); 21 km s. of Palm Desert on CA Highway 74, *Nixon and Hendon 2547* (UCSB); San Bernardino Co.: Dry Morongo Creek, *Dunkle 3378* (LAM); 19 km s. on CA Highway 18 from its junction with CA Highway 247, *Nixon and Hendon 2553* (UCSB, TEX).

Quercus cornelius-mulleri occurs on the northeastern side of the San Bernardino Mountains, eastward to the granitic mountains of Joshua Tree National Monument, southward along the desert margin of the San Jacinto Mountains to the Laguna Mountains in San Diego County, and extends into Baja California Norte, Mexico, along the eastern escarpment of the Sierra Juarez. The southernmost known population is aproximately 40 km south of the international border, but it is likely that the species is found further to the south, possibly along the east side of the Sierra San Pedro Martir.

The species usually occurs on granitic soils in association with *Pinus monophylla* Torr. & Frem., between elevations of 1000 m and 1800 m. Additional associates include *Juniperus californica* Carr., *Adenostoma sparsifolium* Torr., *Rhus ovata* Wats., and at the lower elevational limits, such desert species as *Larrea tridentata* (Sessé & Moc. ex DC.) Cov.

Morphological and distributional differences among the four taxa of scrub oak (subgenus *Lepidobalanus*) that are found south of the Tranverse Ranges are outlined in Table 1.

The Baja California populations lie in the single-needle piñon belt (*Pinus monophylla*), at an elevation below those of *Q. turbinella* subsp. *turbinella*. *Quercus turbinella* is associated commonly with four-needle piñon (*P. quadrifolia* Parl. ex Sudw.) in this area. The two oak species are readily distinguished by differences in leaf spination, leaf color, peduncle length, and trichome characters (see Table 1). In their zone of contact, hybrids occur sporadically, but there is little indication of introgression away from the contact area into the main populations of either species.

Quercus cornelius-mulleri is not in contact with either *Q. turbinella* subsp. *turbinella* or *Q. turbinella* subsp. *californica* in San Diego and Riverside Counties. However, *Q. engelmannii* Greene, and to a lesser extent, *Q. dumosa,* enter its range in this area. Hybridization between

Q. cornelius-mulleri and *Q. engelmannii* has been confused often with hybridization between the latter and either *Q. turbinella* subsp. *californica* (not in the area) or *Q. dumosa.* The type of *Q. acutidens* Torr., collected by Parry (NY!) is such an intermediate and was probably collected along the trail inland from San Luis Rey. In this vicinity (near Warner Springs), "pure" populations of both species come to within 8 km of each other, with intervening populations showing indications of hybridization. Some hybridization between *Q. dumosa* and *Q. cornelius-mulleri* occurs where coastal elements mix with desert elements in the areas of relatively low mountain passes. This situation occurs sporadically, such as in the vicinity of Garner Valley and Santa Rosa Summit, Riverside County, and Montezuma Valley, San Diego County.

From Cajon Pass (San Bernardino County) westward, *Q. cornelius-mulleri* is replaced by *Q. turbinella* subsp. *californica* in the interior and *Q. dumosa* in the coastal areas. There does not appear to be contact between *Q. cornelius-mulleri* and the former, although this might be expected east of Cajon Pass on the north side of the San Bernardino Mountains. *Quercus cornelius-mulleri* is also the common scrub oak in the granitic ranges from Morongo Valley eastward into Joshua Tree National Monument. The desert scrub oak of the New York Mountains of eastern San Bernardino County is *Quercus turbinella* subsp. *turbinella,* which also occurs commonly to the east in the desert ranges of Arizona, New Mexico, west Texas, and northern Mexico (see Tucker, 1952a).

Characters of leaf trichomes have been used to distinguish species of *Quercus* in previous studies (Dyal, 1936; Tucker, 1952b; Tucker and Muller, 1957). More recently, Hardin (1976, 1979) has shown the value of scanning electron microscopy (SEM) in the study of *Quercus* leaf trichomes. Scanning electron microscopy indicates that *Q. cornelius-mulleri* is unique among the California oaks in its possession of fused-stellate trichomes on the lower leaf surface (see Figs. 1–4). Hardin (1976) defined the fused-stellate trichome as "a 'non-glandular' trichome with fusion of the rays beyond the base to a maximum of two-thirds the length of the rays." Although the foliar trichomes of *Q. cornelius-mulleri* are typically highly fused, the degree of fusion varies both on individual plants and within populations. No geographic patterns of trichome variability are apparent within the species. Hardin (1979) reported fused-stellate trichomes only for the series *Virentes* Trel., a small, closely related group of white oaks from the Southeastern United States, Mexico, and Central America. Since *Q. cornelius-mulleri* shares no other important diagnostic features with the *Virentes* (which possess connate cotyledons, pubescent anthers, and thick pubescent acorn cup-bases) there is no reason to assume any close relationship between *Q. cornelius-mulleri* and the latter group.

TABLE 1.   MORPHOLOGICAL AND DISTRIBUTIONAL CHARACTERS OF THE SOUTHERN CALIFORNIA SCRUB WHITE OAKS.

Character	Q. cornelius-mulleri	Q. dumosa	Q. turbinella subsp. turbinella	Q. turbinella subsp. californica
Leaf base	oblique to rounded	oblique to rounded	cordate to rounded	variable, often slightly decurrent
Leaf color	bicolored, upper surface gray or yellow green, lower surface white to ivory	± unicolored, upper surface green, lower surface dull green	± unicolored, both surfaces yellow-green to gray-green	± unicolored, both surfaces gray-green
Leaf margins	sparingly toothed or entire to spinescent	mucronate-dentate to entire, rarely spinose	regularly spinescent-toothed	irregularly spinescent-toothed
Leaf pubescence—upper surface	sparsely to moderately stellate-pubescent	glabrous to sparsely stellate-pubescent	± uniformly stellate-pubescent	± uniformly stellate-pubescent
Leaf pubescence—lower surface	very dense, ± covering entire lower surface and obscuring the 2° veins	sparse, concentrated near the midrib and not obscuring the 2° veins	moderate, uniformly scattered over the surface but not obscuring the 2° veins	sparse to moderate not obscuring the 2° veins
Pubescence type	stellate and fused-stellate hairs only	stellate hairs and some uniseriate glandular hairs	stellate hairs and many uniseriate glandular hairs	stellate hairs and some uniseriate glandular hairs
Diameter of stellate hairs	0.16–0.26 mm	0.18–0.26 mm	0.21–0.36 mm	0.18–0.24 mm

TABLE 1. CONTINUED.

Character	Q. cornelius-mulleri	Q. dumosa	Q. turbinella subsp. turbinella	Q. turbinella Subsp. californica
Ray number	(8–)12(–16)	(6–)8(–10)	(8–)10(–14)	(6–)8(–12)
Ray fusion (visible with SEM)	yes	no	no	no
Acorn attachment	sessile or subsessile	sessile or subsessile	pedunculate	sessile or subsessile
Acorn cup scales	thin to tuberculate	tuberculate	thin	usually thin
Distribution	desert margins of San Bernadino Mts. of southern California south through the San Jacinto Mts. and the Laguna Mts. to the Sierra Juarez of Baja California Norte	coastal (mostly) slopes from northern Baja California to Tehama Co. and the north coast ranges of California	eastern California (New York Mts.) east to Arizona and Texas; Baja California Norte	inner coast ranges from Cajon Pass (San Bernadino Co., CA) north to San Benito Co., California
Elevation	1000 m–1800 m	30 m–1600 m	1400 m–2000 m	300 m–2000 m
Habitats	desert margin in the lower piñon belt and/or desert chapparal	chapparal, southern oak woodland	desert chapparal, upper piñon, (Baja California) piñon-juniper woodland (Arizona)	interior chapparal, piñon-juniper woodland, foothill woodland
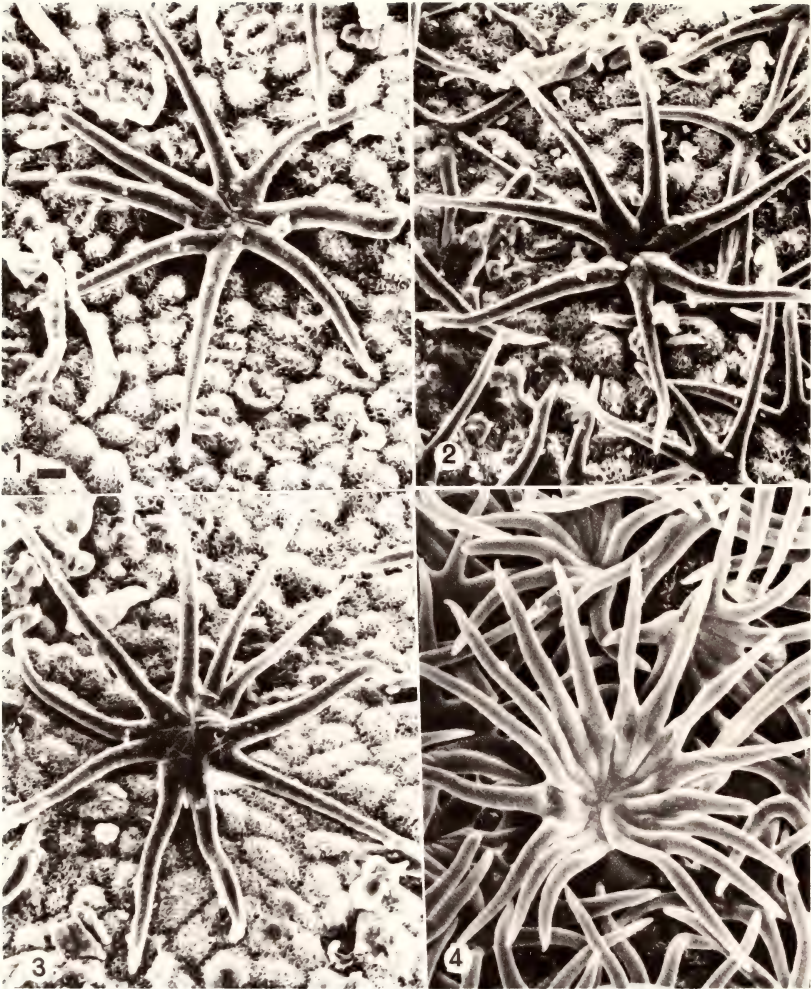
FIGS. 1–4. Scanning electron micrographs of abaxial leaf surfaces of southern California scrub white oaks. FIG. 1. *Quercus dumosa* Nutt. (Ventura Co., *Muller 5220* (Muller Private Herbarium)). FIG. 2. *Quercus turbinella* Greene subsp. *californica* Tucker (Santa Barbara Co., *Tucker 1885-4* (Muller Private Herbarium)). FIG. 3. *Quercus turbinella* Greene subsp. *turbinella* (Baja California Norte, *Steele and Nixon 386* (UCSB)). FIG. 4. *Quercus cornelius-mulleri* Nixon & Steele (Baja California Norte, *Moran 13147* (SD)). Scale (FIG. 1) 10 μm. All figures to the same scale.

Further study is needed before the relationships of *Q. cornelius-mulleri* can be determined.

In addition to ray-fusion in the stellate trichomes of *Q. cornelius-mulleri,* the high ray number, usually around twelve per trichome but

FIG. 5. Typical fruiting specimen of *Quercus cornelius-mulleri* Nixon & Steele. (San Diego Co., 3.2 km w. of Jucumba on old Highway 80 (UCSB). The bar is equal to 1 cm. Fruit and twig to same scale.

often up to sixteen, amply separates it from all other California white oaks. *Quercus dumosa* and *Q. turbinella* subsp. *californica* possess typically eight rays per foliar trichome. The mean ray number of foliar trichomes of *Q. turbinella* subsp. *turbinella* is aproximately ten. The density of trichome cover in *Q. cornelius-mulleri* is also unique among the California scrub oaks. The lower leaf epidermis is typically occluded by the densely packed, appressed, minute trichomes. The stellate trichomes of the other three scrub oaks are never so dense as to obscure totally the lower leaf surface. Glandular trichomes (simple
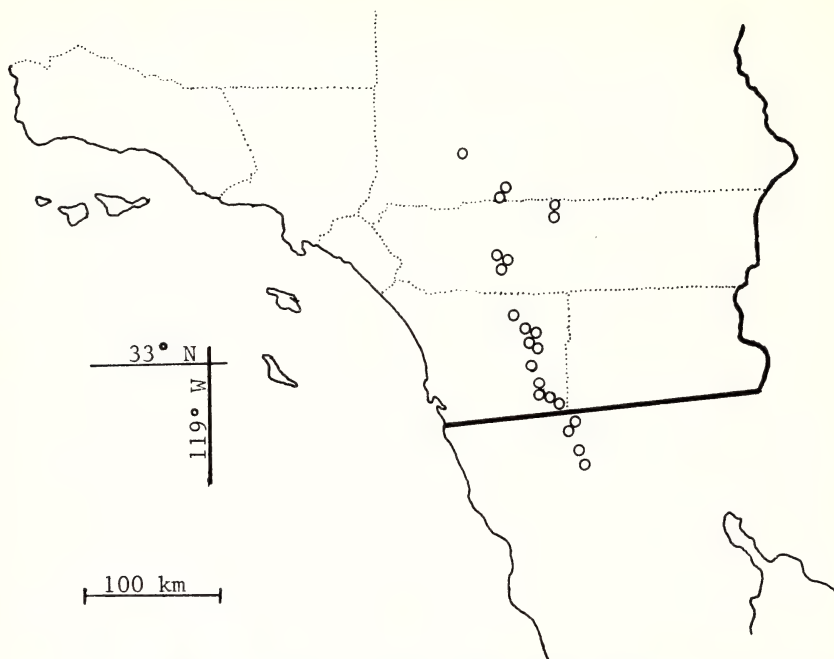
Fig. 6.   Distribution of *Quercus cornelius-mulleri* Nixon & Steele in California and Baja California Norte, Mexico.

uniseriate trichomes, as defined by Hardin, 1976) are lacking on the mature leaves of *Q. cornelius-mulleri,* but are consistently found on the mature leaves of the other California white oaks.

These fundamental differences between *Q. cornelius-mulleri* and the other scrub white oaks of southern California preclude its inclusion as a subspecific taxon within any of those species. Similarly, there is no evidence that the populations which constitute *Q. cornelius-mulleri* were derived by hybridization from any of the extant California species. It is not intermediate morphologically or ecologically between any known species. On the contrary, it is unique among California oaks morphologically; and based upon its distribution, it appears to be more xeromorphically adapted than the other California scrub oaks.

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A NEW SPECIES OF ACACIA (LEGUMINOSAE: MIMOSOIDEAE) FROM BAJA CALIFORNIA SUR, MEXICO

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Abstract

Acacia kelloggiana Carter & Rudd is described from Baja California Sur, Mexico. To date it is known only from Cerro Giganta at the northern end of Sierra de la Giganta and from Sierra de las Palmas, the next range to the north, a distribution from 26°08' to 27°N.

The genus *Acacia* is well represented in Baja California, Mexico. Eleven species are included in Wiggins' (1980) Flora of Baja California, four of which are considered endemic to the peninsula. We here propose another species currently known only from Cerro Giganta in the northern Sierra de la Giganta and from Sierra de las Palmas, the next range to the north.

This new species, known locally as "garabatilla de espina negra", appears most closely related to *Acacia peninsularis* (Britton & Rose) Standley from southern Baja California, and *A. occidentalis* Rose from Sonora and Sinaloa. On the basis of a sterile collection from the vicinity of Bahía Escondido (*Wiggins 17529*, DS), *A. occidentalis* was considered by Wiggins (1980) to occur in the peninsula. On examination, we believe this to be a specimen of *Mimosa purpurascens* B. L. Robinson, "garabatilla", a common shrub in the area. As indicated in the following key, the most conspicuous differences are in characters of leaves, spines and fruit.

Key to *Acacia kelloggiana* and Related Species

Leaves with 1–2(–3) pairs of pinnae; leaflets 3–8 pairs, spatulate-obovate, often emarginate, 5–10 mm long, 2.5–6 mm wide, glabrous or puberulent (Baja California Sur, 27°N southward) .... *A. peninsularis*
Leaves with 1–18 pairs of pinnae; leaflets 5–23 pairs, linear, 3–8 mm long, 0.6–1.8 mm wide, glabrous or puberulent, sometimes minutely glandular-ciliate along margins.
    Branches pubescent (sparsely pilose); spines unguiculate, internodal,

irregularly dispersed; leaves 1.5–4 cm long with 2–4 pairs of pinnae; leaflets 5–12 pairs, puberulent to glabrescent, about 3–5 mm long, 0.6–1.0 mm wide; flowers in heads about 1.5 cm in diameter, the calyx about 1.5 mm long, the petals 2.5 mm long; legume 2–2.5 cm wide, tortuous, chartaceous, contracted between seeds (Sonora, Sinaloa) .... *A. occidentalis*

Branches glabrous; spines, when present, strongly unguiculate, stipular, paired (or occasionally subopposite); leaves 5–15 cm long with 1–13(–18) pairs of pinnae; leaflets 9–23 pairs, essentially glabrous, minutely ciliate and glandular along margin, about 5–8 mm long, 0.6–1.8 mm wide; flowers in heads about 2 cm in diameter, the calyx 2.5–3 mm long, the petals 3–4 mm long; legume 1.5–2 cm wide, falcate, subcoriaceous, slightly contracted between the seeds (Baja California Sur, ca. 26°08′ to 27°N .... *A. kelloggiana*

Acacia kelloggiana Carter & Rudd, sp. nov.

Frutices vel arbores ca. 2–7 m alti, maximam partem spinis stipularibus recurvatis armati; folia 5–15 cm longa, pinnarum paribus 1–13(–18); foliolarum paribus 9–23, foliolis linearibus, glabris, 5–8 mm longis, 0.6–0.8 mm latis, nervo medio excentrico, submarginali; inflorescentiae ex pedunculis axillaribus 1(–3) constantes, floribus albidis in capitulis globosis diam. 2 cm dispositis; legumina subfalcata, 8–15 cm longa, 1.5–2 cm lata, subcoriacea, glabra, seminibus 2–8 (Fig. 1).

Acaciae peninsulari atque *A. occidentali* affinis sed foliolis minoribus pluribusque, leguminibus subcoriaceis haud torulosis discedit.

Shrubs or small trees 2–7 m tall, crown spreading; bark glabrous, smooth except for a few low, narrow ridges, the lenticels conspicuous; spines stipular, paired or occasionally subopposite (sometimes lacking), broad-based laterally compressed, strongly recurved, to ca. 9 mm long, dark brown to black; stipules 4–8 mm long, narrowly linear, 1 mm wide or less, early caducous; leaves bipinnate, rarely fascicled, 5–15 cm long; petioles minutely glandular, 1–2 cm long with a sessile cupulate gland often occurring at the mid-point, or occasionally on the lower or upper third (cupulate gland is also frequently present on the rachis at the base of the terminal pair of leaflets and occasionally between the base of the three or four subterminal pairs of leaflets); pinnae opposite or subopposite, 1–13(–18) pairs; leaflets 9–23 pairs, glabrous, but often with minute marginal glands, linear, obtuse, mucronulate, 5–8 mm long, 0.6–1.8 mm wide, the midrib strongly eccentric; inflorescence of 1(–3) axillary peduncles (sometimes peduncles terminal on short axillary stems) 1–2.5 cm long, the receptacle ovoid to oblong, 1.4–3(–5) mm long, 0.8–2 mm broad; flowers in globose heads 2 cm in diameter, 25 or more per head, but only one or two developing pods, whitish, pedicellate, the inconspicuously glandular

FIG. 1. Holotype of *Acacia kelloggiana* Carter & Rudd. *Carter & Sousa 5152*.
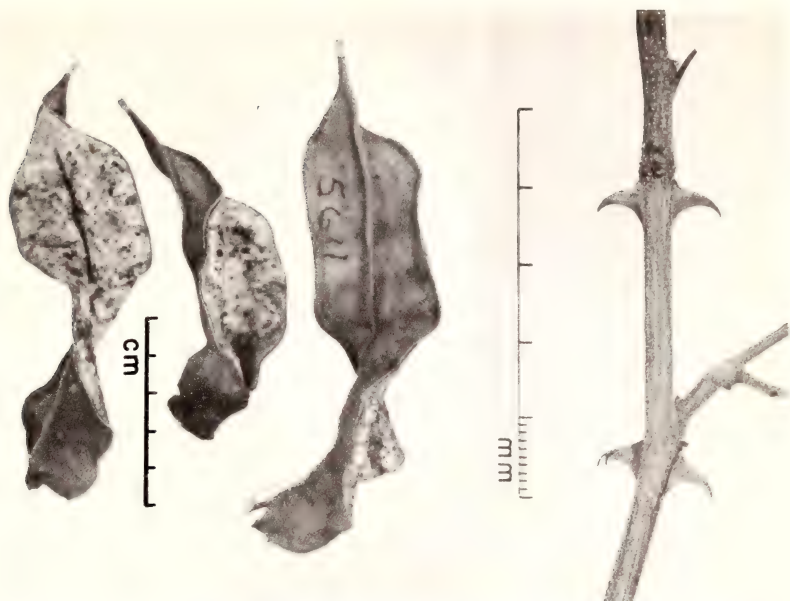
FIG. 2. *Acacia kelloggiana.* Left: Unilaterally dehisced legumes. *Carter 5611*; Right: Strongly recurved spines. *Carter 5241.*

pedicels 2–3 mm long; calyx glabrous (or nearly so), valvate, 2.5–3 mm long, about two thirds the petal length; petals 3–4 mm long with narrow white-membranous glandular margins; stamens exserted, ca. 8 mm long; legume 8–15 cm long, 1.5–2 cm wide, 2–8-seeded, compressed, somewhat falcate, sinuate-margined, slightly constricted between the seeds, subcoriaceous, margin slightly thickened, tan to black in age, usually unilaterally dehiscent, the stipe ca. 5–15 mm long; seeds subovate to ovate, compressed, 7–9 mm long, 6 mm wide, 1.5–3 mm thick, uniformly dark brown, the pleurogram inconspicuous.

TYPE: Mexico, Baja California Sur, Sierra de la Giganta: vicinity of La Matancita, Arroyo Hondo, north side of Cerro Giganta, ca. 26°08′N, 111°34′W, 750 m, 13 Oct. 1966, *Annetta Carter & Mario Sousa 5152* (Holotype: UC 1472700; isotypes: MEXU, US, BM).

PARATYPES: All Arroyo Hondo collections are from Cerro Giganta (1766 m) nw. of Loreto, Baja California Sur, Mexico, the principal peak of the Sierra de la Giganta, a mountain range that extends along the Gulf of California side of the peninsula from 24°30′ to 26°30′N. Arroyo Hondo heads into the n. and ne. side of the peak and forms a huge basin at the base of high basaltic cliffs. La Matancita (750 m) is a permanent water spring high in the nw. side of Arroyo Hondo
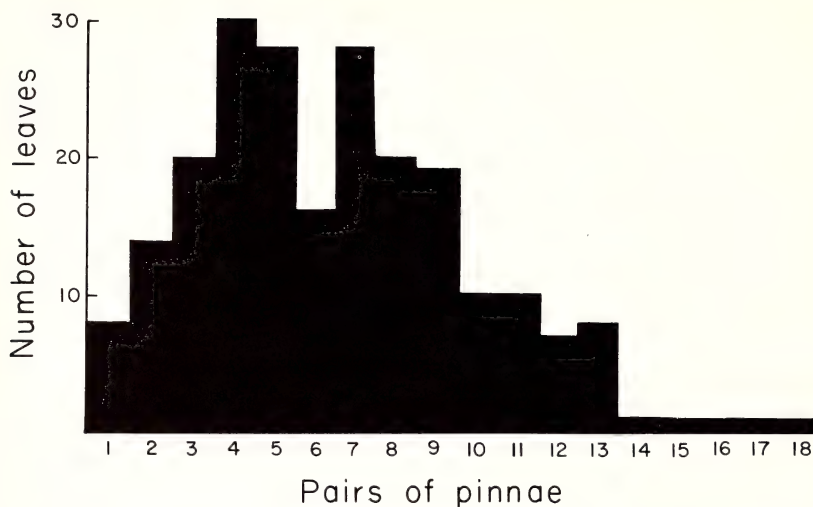
FIG. 3. *Acacia kelloggiana*. Histogram representing frequency distribution of pairs of pinnae (based on 222 leaves of 14 individuals).

basin. (Except as otherwise noted, all collections are at UC. Duplicates will be distributed.) Alt. 690–820 m. Arroyo Hondo: 12 Dec 1938, *H. S. Gentry 4110* (DS, DES, K, UC); 24 Nov 1947, *Carter, Alexander & Kellogg 2007*; 14 Oct 1966, *Carter & Sousa 5170, 5176*; 29 Aug 1971, *Carter 5622, 5623, 5623a, 5624*. Vicinity of La Matancita, Arroyo Hondo: 13 Oct 1966, *Carter & Sousa 5156*; 3 June 1967, *Carter 5241*; 28 Aug 1971, *Carter 5611* (previous season's dehisced legumes from under shrub), *5612*. With scattered *Nolina beldingii* and leguminous shrubs, ridge nw. of main peak (Cerro Giganta), 1400–1500 m, abundant at this elevation and some distance below, 26 Nov 1947, *Carter, Alexander & Kellogg 2039*. Sierra de las Palmas: La Champagna, s. of Santa Rosalía, 1440–1600 m, 27–29 Apr 1952, *Fox & Gentry 11805* (DES).

At the height of the dry season the shrubs are leafless (e.g., *Carter 5241*, June); they come into leaf and bloom with the advent of the summer rains, and by November and December only the dehisced legumes are found.

During the course of his 1930 field trip to Baja California Marcus Jones (1933) did some collecting in the Sierra de la Giganta. From Loreto he went by animal to Arroyo Hondo (his Arroyo "Undo"). In his field journal (p. 107) Jones says, "There is an *Acacia* here with white flowers and hooked spines that is very annoying and at all elevations, rarely 10 ft. high, but have seen little fruit of it." We have

been unable to locate any Jones specimens of this *Acacia* in various herbaria, but he is undoubtedly referring to our *A. kelloggiana*.

Vegetation in the basin of Arroyo Hondo is dense, with *Quercus tuberculata* the dominant in the several steep canyons fingering up to the basalt cliffs of the Comondú Formation (Beal, 1948, pp. 74–77). Other common species at the higher elevations (750–850 m) are *Lysiloma divaricata, Mimosa purpurascens, Erythrina flabelliformis, Croton magdalenae, Jatropha vernicosa, Karwinskia humboldtiana, Pachycormus discolor, Alvordia glomerata* and *Franseria arborescens*. On exposed slopes and at lower elevations (600–700 m) are *Lysiloma candida, Jatropha cuneata, Fouquieria diguetii* and *Lemaireocereus thurberi*. *Acacia kelloggiana* is abundant in the above two associations. On the lower slopes and flats of Arroyo Hondo basin *Prosopis palmeri, Jatropha cinerea* and *Ruellia peninsularis* are common. *Ficus palmeri* and *Pachycereus pringlei* are scattered throughout. Local ranchers say that this is the only locality where they have seen "garabatilla de espina negra". The Gentry and Fox collection from Sierra de las Palmas was growing in *Nolina*-grassland on undulating, broken terrain of a volcanic mountain top. Such a habitat and association occurs also on the crest of Cerro Giganta.

The common name "garabatilla de espina negra" serves to differentiate *Acacia kelloggiana* from "garabatilla", *Mimosa purpurascens,* a common shrub in the Sierra de la Giganta. The spines of the latter are also broad-based and strongly recurved, but they are light-colored and internodal.

Acacia kelloggiana is named in memory of Louise Kellogg, with whom, in company of Annie M. Alexander, the senior author made her first trip to Baja California in 1947, as well as a number of subsequent memorable trips following Miss Alexander's death in 1950. Alexander and Kellogg botanical specimens were collected in many remote parts of California and Nevada, and their collection numbers reached almost 6000. Many of their specimens serve as the bases for new taxa; duplicates have been distributed widely by UC, where the first set is deposited.

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RE-ESTABLISHMENT OF ANGELICA CALIFORNICA (UMBELLIFERAE)

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Abstract

Angelica californica Jepson emend. DiTomaso, previously included within *Angelica tomentosa* Watson, is re-established as a distinct species from the Sierra Nevada foothills and the Coast Ranges of northern California. Illustrations, a distribution map, and several distinguishing characters are provided.

Nine species of *Angelica* are believed to occur in California, the eight recognized by Munz (1959) and the recently described *A. callii* Math. & Const. (1977). Four of these are found along the Sierra Nevada–Cascades axis from Shasta County to Tulare County. The remainder occur in the western, coastal portion of the state from Siskiyou and Del Norte Counties to San Diego County.

Jepson (1893) described *Angelica californica* on the basis of a single collection from the Vaca Mountains of Solano County and noted its similarity to *Angelica tomentosa* Watson. In 1901, Jepson emended his treatment and demoted *A. californica* to a variety of *A. tomentosa*. Since that time, there has been a great deal of confusion about the identity of coastal foothill *Angelica*. As in *A. arguta* Nutt. ex Torrey & Gray, the ovaries of *A. californica* are glabrous, or nearly so, in contrast to the densely pubescent ovaries of *A. tomentosa*. Based on this character, specimens of *A. californica* sensu Jepson key to *A. arguta* in Munz (1959). However, most herbarium sheets of *A. californica* have been annotated as *A. tomentosa,* presumably because *A. arguta* is a more northern taxon.

After visiting many populations and studying numerous herbarium specimens, I have found several additional differences between *A. tomentosa* and *A. californica* (Table 1). Judged on the basis of these criteria, *A. californica* extends as far north as Shasta County and as far east as Butte and Tehama Counties (Fig. 1). Jepson's (1893) description of *A. californica* was not only incomplete with respect to important morphological characters, but it also failed to indicate the range of variability within the species. The present study more accurately describes *A. californica,* defines its range, and proposes its re-establishment as a distinct species.

Angelica californica Jepson emend. DiTomaso.—*Angelica californica* Jepson, Erythea 1:8. 1893. *Angelica tomentosa* S. Wats. var. *californica* Jepson, Fl. W. Middle Calif. 356. 1901.

TABLE 1.   CONTRASTING CHARACTERS OF *Angelica californica* AND *A. tomentosa*.

Character	*A. californica*	*A. tomentosa*
Umbel shape in mature fruit	Flat-topped or bowl-shaped	Spherical
Ray orientation	Ascending	Spreading
Fruit pubescence	Glabrous (pubescent in Tehama Co.)	Scabrous to tomentose (glabrous in Siskiyou Co.)
Leaflet color	Abaxial surface light green; adaxial surface green	Both adaxial and abaxial surfaces glaucous
Leaflet length/width ratio	2:1 to slightly less	Usually 3:1, occasionally 2:1 or 5:1
Oil tubes (vittae)		
Interval	1–3	1 (rarely 2)
Commissure	2–6	2 (occasionally 4)
Total vittae	6–20	6 (occasionally 8 or 10)
Soil type	Sandstone, shale, or volcanic	Usually serpentine
Flowering time	May to early July	July to October

Plants stout, 1–2.5 m tall, the stem and foliage glabrous to pubescent, strongly scented; leaves deltoid, bipinnate to three times pinnately divided, to 12 dm in length, 8 dm in width; leaflets lanceolate to ovate or oval, (2–)4–8(–14) cm long, (1–)2–4(–8) cm broad, acute to obtuse, the larger petiolulate and with 1 or 2 narrow lobes or leaflets at base, the others sessile, length/width ratio 2:1 or less, excluding petiolule, sharply serrate, the teeth acute to acuminate, irregularly spaced, the abaxial surface glabrous to pubescent and slightly lighter in color than adaxial surface, both surfaces scabrous on veins; petiole stout, 1–6 dm long, sheathing at base; cauline leaves reduced upward, pinnate, the uppermost sheaths bladeless; inflorescence usually glabrous, the umbels flat-topped in flower, becoming concave and bowl-shaped in fruit; involucre wanting, or rarely present; rays 15–50, 2–13 cm long, usually glabrous, or occasionally hispidulous at base and apex, ascending or curved upward, unequal, usually webbed; involucel of 1–10 inconspicuous filiform bractlets, or lacking; pedicels 1–15 mm long, spreading-ascending, usually glabrous, occasionally webbed; flowers white or rarely pinkish, the petals oval to obovate, glabrous to sparsely puberulent or rarely pubescent; styles slender, much longer than the conical stylopodium; ovaries glabrous, or rarely pubescent; fruit green to purple, oval to oblong, 6–7(–10) mm long, 4–6(–7) mm broad, the dorsal ribs low, rounded, the lateral ribs broader than the dorsal but narrower than to equal to the body; vittae irregular in size and variable in number (6–20), 1–3 under the intervals, often appearing continuous about the seed, 2–6 on commissure (Fig. 2).
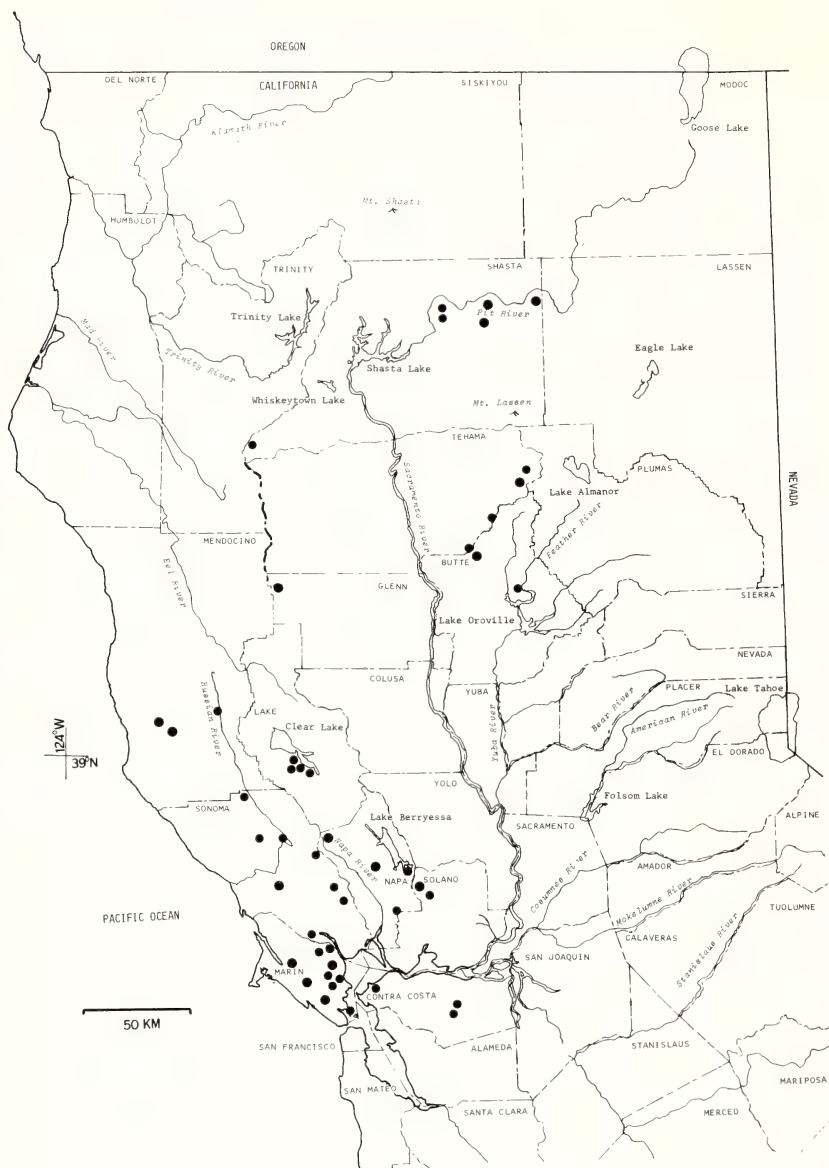
Fig. 1. Distribution of *Angelica californica*.

TYPE: USA, CA, Solano Co.: Gates Cañon, Vaca Mountains, 20 June 1892, *W. L. Jepson 14246* (Holotype: JEPS!. Topotype: *Di Tomaso 1744*, HSC).

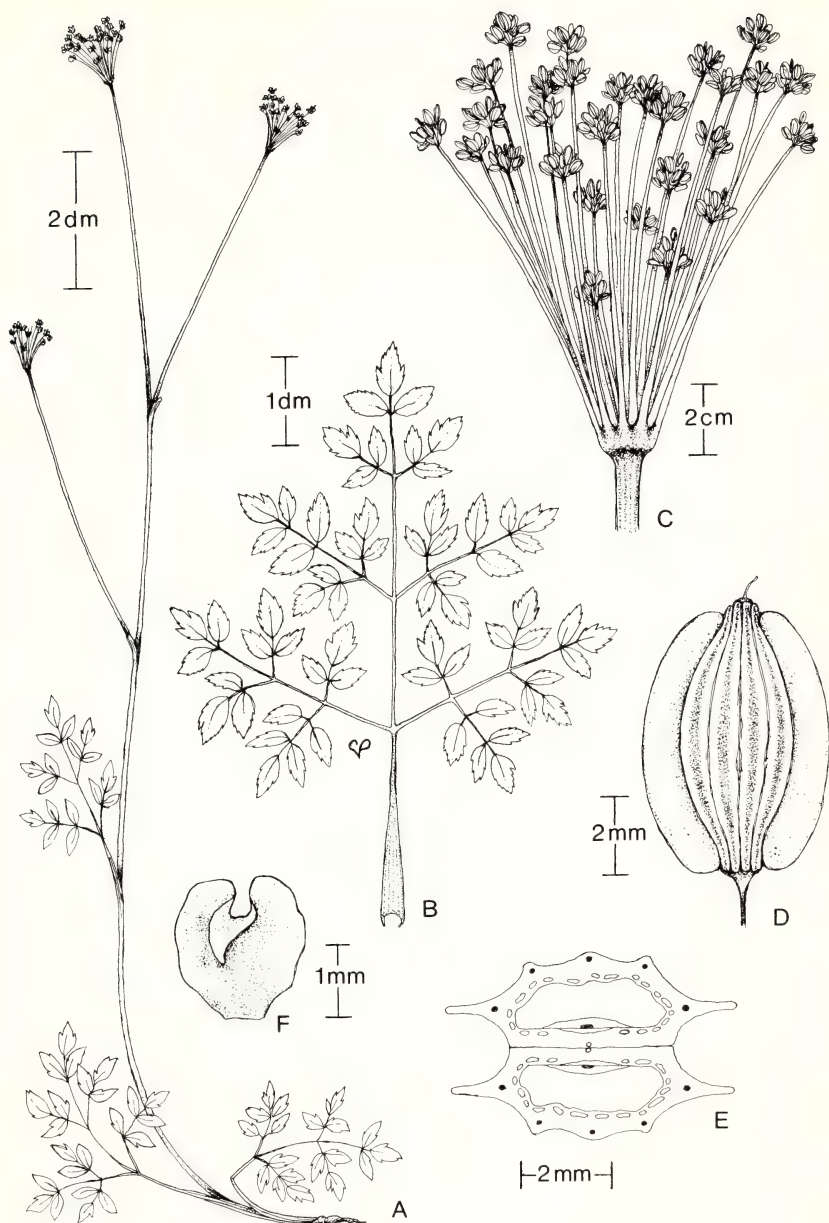*Habitat and Distribution.* Dry volcanic, shale, or sandstone slopes

FIG. 2. *Angelica californica.* A, habit. B, basal leaf. C, mature inflorescence. D, dorsal view of entire fruit. E, transection of fruit. F, petal. All from *DiTomaso 1595, 1732,* and *1736.*

between 20 and 1600 m, from Shasta County to Butte County in the foothills of the Sierra Nevada and to Contra Costa County in the Coast Ranges.

Jepson's description of *A. californica* states that "the leaflets are always smaller and usually much thinner" than in *A. tomentosa*. In addition, he notes that *A. tomentosa* is "hoary-tomentose, has equal rays, and solitary depressed oil-tubes in the intervals", as compared to "3 oil-tubes in the intervals" of *A. californica*. It is puzzling that Jepson neglected to consider ovary pubescence, ray orientation, and glaucousness of leaflets in his comparison of the two taxa. I have found these characters to be very effective in separating *A. californica* and *A. tomentosa* in the field. However, several of the important field characters, e.g., glaucousness, ray orientation, umbel shape, and orientation of the mature fruiting stem, are not always evident in herbarium material. This, and the presumed restriction of *A. californica* to the Vaca Mountains, may have contributed to Jepson's later decision, in 1901, and that of Mathias and Constance (1944–45) to include *A. californica* in *A. tomentosa*.

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COMPOSITION OF NATIVE GRASSLANDS IN THE SAN JOAQUIN VALLEY, CALIFORNIA

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Abstract

The native grasslands of California have undergone great change since European contact but early accounts of Spanish and Anglo-Americans provide some information about their former condition. They suggest that the dry alluvial fans of the San Joaquin Valley, which account for 60 percent by area of California grasslands, were dominated by annual species and xerophytic shrubs. Perennial bunchgrasses were common only on certain well-watered floodplains.

Alterations in the grasslands of California as a result of European contact and settlement were great and began so early in the historic period that the former condition of these grasslands will always be open to question. Evidence from written documents and contemporary field observations supports the view that perennial bunchgrasses were abundant in communities now composed largely of exotic annuals. This had led to the conclusion, now widely accepted, that all native grasslands were dominated by perennial species (Munz and Keck, 1949; Clark, 1956; Oosting, 1956; Benson, 1957; Burcham, 1957; Munz, 1959; Muller and Muller, 1964; Wells, 1964; Dasmann, 1966; McCown and Williams, 1968; Crampton, 1974; Ornduff, 1974; Heady, 1977; Küchler, 1977). Some of the interpretations of fact have been questioned and doubt has been expressed that the bunch grasslands were as extensive as has been assumed (Biswell, 1956; Twisselmann, 1963, 1967; Klapp, 1964; Naveh, 1967; McNaughton, 1968). The objective of this paper is to review the evidence on the nature of the prehistoric grasslands, giving emphasis to documentary information from the southern Central Valley. It was here on the dry alluvial fans that the largest tracts of native grassland occurred (Fig. 1), yet most of the evidence that has been used to reconstruct the former condition of the community is derived from much more humid sites either along the coast or at higher elevations.

Documentary Evidence

Perennial bunchgrasses. Toward the end of the nineteenth century the deterioration of the quality of California rangelands was investigated in several important surveys reviewed by Talbot and Cronemiller (1961). Of particular concern was the invasion by annuals and
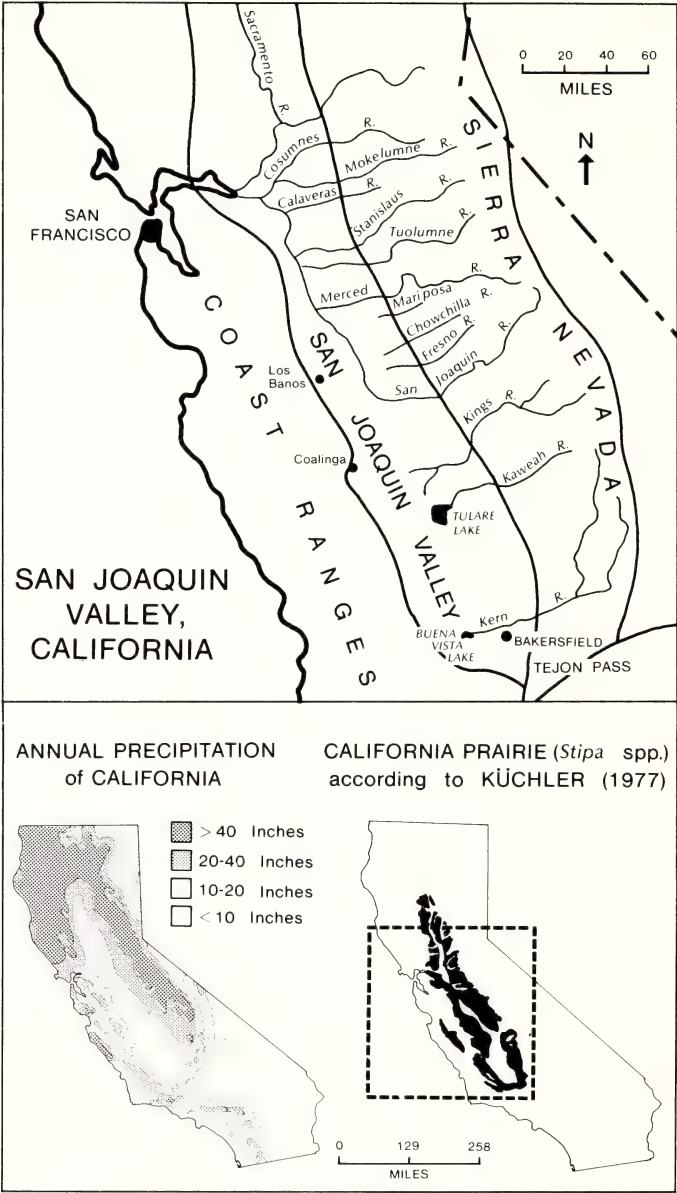
FIG. 1. The natural setting of native grasslands in California. Upper: The San Joaquin Valley. Lower: California precipitation (left); California prairie (right), after Küchler, 1977.

replacement of perennial grasses that reduced the carrying capacity of the range. In a study of a portion of northwestern California Davy (1902) carefully documented reports of residents who observed the decline of bunchgrasses over many years. More recently Burcham (1957), in his detailed history of California rangeland, collected further early written descriptions of bunchgrass where annual grasslands stand today. Almost all of these sites are in northern coastal locations (Mendocino, Humboldt, and Monterey Counties) where mild, humid conditions prevail all year. One exception is an account from Bryant (1848, p. 309) which was made during a journey from the San Joaquin Valley to San Jose in 1847.

> From this plain we entered a hilly country, covered to the summits of the elevations with wild oats and tufts or bunches of a species of grass, which remains green throughout the whole season.

The reference is unmistakably to the hills of the Coast Range where pockets of bunchgrasses may still be found. Yet this description stands in strong contrast to the scene in the San Joaquin described by the same person at another point along the way. The more arid Valley plains which stood above the river bottoms were characterized as "dry and crisp" with "large tracts of wild oats" (Bryant, 1848, p. 300). No mention was made of bunchgrasses at these locations.

The absence of information about natural conditions in the San Joaquin Valley is often attributed to the lack of detail in the first accounts by the Spanish and the disruption of the ecosystem by feral herbivores before Anglo-Americans made more accurate descriptions. It is true that feral horses were present in the Valley at least by 1807 (Cook, 1960) and extremely large herds were noted after 1830, when hunting by Indians ceased as a result of decline in human populations (Bryant, 1848; Fremont, 1848; Leonard, 1904; Farquhar, 1937). However, there are instructive Spanish accounts, made even before feral livestock could have had significant effect, which leave no doubt about the scanty natural plant cover at least during certain times of the year. Zalvidea described the area around Buena Vista Lake in July 1806 in the following manner:

> The area covered in the morning consisted of extensive plains. In quality the land is alkaline. The shore of the lake is completely covered with a great deal of tule. Elsewhere, and in the hills bordering the plains, I saw neither pasturage nor watering places. (Cook, 1960, p. 245)

Muñoz, diarist on the Moraga expedition, in October of the same year judged the country he saw in present day Merced and Madera Counties to be equally barren.

All the country traversed today has very poor grass and is very
stony . . . . All the country we observed between the Tecolate
[Chowchilla River] . . . and the Santa Ana [Fresno River] is
worse than bad. From the Santa Ana to the San Joaquin there
is a little pasturage, although it is sparse and spread out widely.
(Cook, 1960, p. 251)

The Martinez expedition in 1816 saw the same region in May and
even reported a bunchgrass growth form that almost certainly referred
to *Sporobolus airoides*, a plant tolerant of high salinity and common
in the marshes of the Valley even now. Otherwise the herbaceous
vegetation was very poor.

In all our trip we did not see a good tree, nor wood enough to
cook a meal, nor a stone, nor even grass enough for the horses,
more than bunchgrass, or what grows in the swamps. (Cook, 1960,
p. 271)

Similarly in June, 1824, Portilla said: "The road was flat and the land
quite poor, with no grass" (Cook, 1962, p. 155).

Similar observations were made by early Anglo-American travellers
after 1840 and, quoted alone, they are often cited as evidence of en-
vironmental degradation caused by feral cattle and horses. In fact
barrenness may have been a natural condition of the landscape. Se-
rious overgrazing may not have occurred until the droughts of 1861
and 1864, the first since stock had been brought to the Valley in large
numbers in response to the demand for meat created by the gold rush.

When Fremont passed over the land between the Kings and Kern
Rivers in April 1844 he noted:

To-day we made another long journey of about forty miles,
through a country uninteresting and flat, with very little grass
and a sandy soil. (Fremont, 1845, p. 253)

Others reported similar conditions in the 1850's.

The Tularé Valley, from the mouth of the Mariposa to the Tejon
pass at its head, is about one hundred and twenty miles in extent,
and varies from eight to one hundred miles in width. With the
exception of a strip of fertile land upon the rivers emptying into
the lakes from the east, it is little better than a desert. The soil
is generally dry, decomposed and incapable of cultivation, and
the vegetation, consisting of artemisias and wild sage, is ex-
tremely sparse. (Farquhar, 1937, p. 262)

The plains between the streams are destitute of foliage, and the
soil generally gravelly and poor. (Williamson, 1855, p. 13)

There was but little or no vegetation, and the surface was dry and
gravelly. (Blake, 1855, p. 41)

After leaving the grove by the [Kern] river, we entered at once among the most desolate hills. Not a sign of herbage was seen on them—not enough to attract a bee. (Kip, 1954, p. 92)

One might expect that had bunchgrasses been present at least the basal tussock would have been obvious throughout the year and might have attracted some attention. In fact, Fremont, whose descriptions are the most detailed of any explorer, does mention bunchgrasses on two occasions. Both of these were in exceptionally well-watered sites east of the delta in the Sierra Nevada foothills. Those sites receive runoff from the mountains in addition to the local precipitation.

Leaving the Mo-Kel-um-ne, . . . we travelled about twenty miles through open woods of white oak, crossing in the way several stream beds—among them the Calaveras creek. These have abundant water, with good land above; and the Calaveras makes some remarkably handsome bottoms. Issuing from the woods, we rode about sixteen miles over an open prairie, partly covered with bunch grass, the timber reappearing on the rolling hills of the river Stanislaus in the usual belt of evergreen oaks (Fremont, 1848, p. 16). Emerging from the woods, we travelled in a south-easterly direction, over a prairie of rolling land, the ground becoming somewhat more broken as we approached the To-wal-um-ne river, one of the finest tributaries of the San Joaquin. The hills were generally covered with a species of geranium, (*erodium cicutarium*), a valuable plant for stock, considered very nutritious. With this was frequently interspersed good and green bunch grass, . . . (Fremont, 1848, p. 17)

Fremont makes it clear that this verdant condition was confined to the northeast portion of the San Joaquin Valley, because only a little farther south, beyond the Merced River, he noted:

. . . the country had lost its character of extreme fertility, the soil having become more sandy and light . . . . (Fremont, 1845, p. 250)

Annual herbs. If perennial bunchgrasses were not common the question arises what were the dominant herbaceous species. Other accounts from the more typical dry plains of the Valley make no mention of bunchgrasses but describe in some detail the annual herbs that grew abundantly, at least in wet years, and appeared to be the dominants in the community. For example, in the spring of 1850 a traveller making his way through the Coast Ranges at the latitude of Los Banos observed the change in aspect of vegetation as he approached the Valley.

By this time we could see what had caused the mass of color so noticeable from the mountain the day before. The entire plain,

as far as we could see, was covered with wild flowers. Almost all of the flowers were new to us. . . .

As we passed below the hills the whole plain was covered with great patches of rose, yellow, scarlet, orange and blue. The colors did not seem to mix to any great extent. Each kind of flower liked a certain kind of soil best and some of the patches of one color were a mile or more across. (Mayfield, 1929, p. 9)

A few years later Muir described a similar phenomenon:

The Great Central Plain of California, during the months of March, April, and May, was one smooth, continuous bed of honey-bloom, so marvelously rich that, in walking from one end of it to the other, a distance of more than 400 miles, your foot would press about a hundred flowers at every step. Mints, gilias, nemophilas, castilleias, and innumerable compositae were so crowded together that, had ninety-nine per cent of them been taken away, the plain would still have seemed to any but Californians extravagantly flowery . . . . Because so long a period of extreme drought succeeds the rainy season, most of the vegetation is composed of annuals, which spring up simultaneously, and bloom together at about the same height above the ground, the general surface being slightly ruffled by the taller phacelias, pentstemons and groups of *Salvia carduacea,* the king of the mints. (Muir, 1894, p. 342)

Fremont also mentioned fields of wildflowers during his 1845 expedition even though it was early in the season (January and February).

The California poppy, (*Eschscholtzia Californica,*) the characteristic plant of the California spring; *memophila insignis* [*sic*], one of the earliest flowers, growing in beautiful fields of a delicate blue, and *erodium cicutarium,* were beginning to show scattered bloom. (Fremont, 1848, p. 19)

Descriptions of spring wildflower blooms have not been found in the Spanish records because most expeditions were made in summer months. However, in July, 1806, Zalvidea reported flowering of a summer growing herb, probably *Hemizonia pungens,* in the southern San Joaquin Valley.

All this territory is covered with a species of herb which has a little stem with a yellow flower, the stalk being no more than a quarter [of a yard] high. (Cook, 1960, p. 246)

The occurrence of *Erodium* as a component of herbaceous cover at an early date is of special interest because the common species (including *E. cicutarium*) are generally considered to be native of Mediterranean Europe (Robbins, 1951; Clark, 1956; Munz, 1974).

Fremont mentioned it on a number of occasions during both his 1844 and 1845 expeditions (Fremont, 1845, 1848) and leaves no doubt about its abundance in the Central Valley, and the fact that Indians made use of the plant.

> Instead of grass, the whole face of the country is closely covered with *erodium cicutarium,* here only two or three inches high. Its height and beauty varied . . . being, in many low places which we passed during the day, around streams and springs, two and three feet in height. (Fremont, 1845, p. 253)

Other accounts from the first ranchers to settle a portion of the West Side plains near present day Coalinga emphasize how *Erodium* appeared to dominate the ground cover presumably in the absence of tall growing perennial grasses.

> This valley was covered with the finest possible stand of dry alfileria, remaining from the extremely wet winter of 1852. (Latta, 1949, p. 333)

Erodium cicutarium was apparently common throughout the Southwest at the time of the first scientific explorations (Torrey, 1859) and was so widely naturalized in California even early in the nineteenth century that Brewer and Watson (Calif. Geol. Survey, Bot., 1880) doubted that it was an exotic. The discovery of the species in the earliest known adobe bricks made by the Spanish suggested to Hendry (1931) that it spread into California before European settlement, a possibility that Jepson (1933) also accepted. The plant has very effective dispersal mechanisms and others of the genus are native to North America and Australia. It is possible that *E. cicutarium* itself may have reached the New World without human assistance. If the species was either indigenous to California or spread ahead of settlement, then its presence, especially in more arid sites, cannot be used as an indication of environmental degradation.

Hoover (1935) felt grasses were relatively unimportant in the "primitive" flora of the San Joaquin Valley. References to them in the written records are rarely specific enough to allow identifications to be made with confidence. Several early references to 'wild oats' have been found (Bryant, 1848; Perkins, 1863; Leonard, 1904; Latta, 1949), but the name may have been applied to many annual grasses in the same way that 'sage brush' was used to describe any grey-green shrub and not specifically species of *Artemisia.* It is less likely that *Avena* could be mistaken for a bunchgrass that possesses a quite different life-form.

RELICT ANALYSIS

Observations by Davy (1902) in northwestern California strongly suggested that sites protected from grazing tended to contain more

abundant native perennial bunchgrasses. In 1917 and 1918 Clements found the bunchgrass *Stipa pulchra* (probably including *S. cernua*) common in fenced railroad rights-of-way in the Central Valley and, believing them protected from grazing and burning, concluded that this drought-tolerant perennial must have dominated the grassland before grazing caused its replacement (Clements, 1934; Clements and Shelford, 1939). However, Biswell (1956) has pointed out that these sites were burned almost annually to prevent accidental fires and this *Stipa,* which is favored by burning, probably became established only as a result.

In the southwestern San Joaquin Valley other relict sites protected from grazing, such as fenced road sides, oil fields, quarries, and arroyos were searched but no perennial grasses were seen. Instead, xerophytic shrubs, particularly of *Atriplex polycarpa,* were often found growing more prolifically than on adjacent grazed rangeland. This saltbush is rated highly as a browse (Piemeisel and Lawson, 1937; Chatterton, 1970) and its decline under grazing has been noted (Love and McKell, 1966). It is quite possible that in the drier portion of the Central Valley, especially the West Side, this community of low shrubs was once more extensive than at present.

Present Distribution Patterns

It is often stated that *Stipa pulchra* and *S. cernua* were dominants in the grasslands and occupied more space than all the other species combined. *Poa scabrella, Aristida divaricata, Koeleria macrantha, Melica imperfecta,* and *M. californica* may have been generally widespread whereas *Danthonia, Festuca, Deschampsia, Agrostis,* and *Muhlenbergia* species may have had more restricted distributions (Shantz and Zon, 1924; Clements, 1934; Clements and Shelford, 1939; Beetle, 1947; Munz and Keck, 1949; Burcham, 1961; Crampton, 1974; Ornduff, 1974). Twisselmann (1963, 1967) observed *Stipa* to be uncommon where annual precipitation falls below 245 mm and does not occur at all in places receiving less than 200 mm. The distribution map of *Stipa* published by Stebbins and Love (1941) supports Twisselman's observation by showing *Stipa* to be absent from the dry western San Joaquin Valley and elsewhere confined largely to riparian or foothill sites. Furthermore, this is in close agreement with an early report by Brewer to Watson when the former made collections for the first flora of the State in 1863.

> *Stipa setigera* [*S. pulchra, S. cernua*]. It is common on the Coast Ranges and on the foothills of the Sierra Nevada and according to Prof. Brewer, is the most common and, valuable "Bunchgrass" of the dry hills. (Calif. Geol. Survey, Bot., 1880, vol. 2, p. 286)

Botanical reconnaissance made in conjunction with the railroad surveys of the Central Valley indicates that 75 grass species were collected, of which only one or perhaps two, *Poa douglasii* and *Elymus* sp., are perennials (Durand and Hilgard, 1855). Had bunchgrasses been as abundant as supposed, one would expect them to be better represented in the collections made before significant settlement occurred in the region.

Areas of bunchgrass identified by Crampton (1974) in the delta region occupy relatively moist sites influenced by the cool, humid, maritime air able to penetrate to this part of the Central Valley through the San Francisco Bay gap. These conditions are not typical over the remainder of the Valley.

In California, variable and unpredictable moisture, temperature, and light at the time of germination and the cool winter months cause extraordinary variation in productivity and floristic composition from year to year (Heady, 1956; Naveh, 1967). Klapp (1964) has concluded that ephemeral annuals are best adapted to this unpredictable and inconsistent climate. In its drier phases the climate is unsuitable for most perennial herbs, and the grasslands of this region are composed mainly of annual species, standing in marked contrast to communities in other temperate areas.

Conclusions

Evidence for the former importance of perennial bunchgrasses in the grasslands of California, and their subsequent decline as a result of grazing, exists for many places in the Coast Ranges, the Sierra foothills and in some localized, well-watered floodplains in the interior. However, the San Joaquin Valley, which contained much of California's native grasslands, was either wetland of fluctuating extent or dry alluvial fan. The degree of its natural aridity may not have been appreciated because earliest settlement was concentrated along the riparian oases and later large scale irrigation schemes caused almost all of the thin natural vegetation cover of the plains to be replaced by highly productive agriculture. Observations used to reconstruct the former composition of grassland communities comes from humid parts of the State that were settled first. This information cannot be extrapolated to explain conditions in drier locations such as the San Joaquin Valley.

Accounts of the San Joaquin Valley by Anglo-Americans are said to represent descriptions of an environment already degraded by the grazing of feral livestock, yet observations made by the Spanish before any significant impact of European civilization are quite consistent with those of the middle of the nineteenth century. Neither indicate the existence of perennial bunchgrasses but instead emphasize the lack of vegetation cover during the dry months and the abundance of bril-

liantly flowering herbs in the spring. This leads to the conclusion that, except for riparian and wetland sites, much of the southern Central Valley supported a grassland of annual species or, in the most arid parts on some soils, a community of xerophytic shrubs with an understory of annuals.

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POST-ERUPTION SUCCESSION ON ISLA FERNANDINA, GALÁPAGOS

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Abstract

In 1968 the mixed shrub forest on the western caldera rim of Isla Fernandina, Ga-lápagos, was buried by a major eruption of tephra. In June, 1971; July, 1973; and August, 1977, vegetation on the western rim was quantitatively sampled in plots along a transect extending 1.5 km from deep, barren tephra to the undestroyed original vege-tation. In the 9 years following the eruption, only a few species of weedy composites and grasses became sparsely established in gullies on the deep tephra. By contrast, where the original plants were shallowly buried, vigorous vegetative sprouting of shrubs and of rhizomatous perennial herbs resulted in nearly complete cover by 1977. Species apparently reproducing only by seed returned more slowly than those species with vegetative reproduction. Land iguana activity and precipitation appear to influence the rate and patterns of revegetation. The shrub forest is composed of weedy species able to survive volcanic disturbance and revegetate newly created open habitats.

Rarely is the opportunity available to begin a study of plant succes-sion immediately following volcanic activity. The studies that have been done were usually on lava substrate, often in moist climates (Smathers and Mueller-Dombois, 1974). This paper reports six years of plant succession on tephra (fine-grained ash and coarser particles of pyroclastic origin) of arid Isla Fernandina, westernmost island of the Galápagos archipelago. These islands are one of the most active volcanic fields on earth, and their biology is closely related to their volcanic history.

In May, 1968, Fernandina, a basaltic shield volcano, experienced a violent summit eruption and caldera collapse (Simkin and Howard, 1970). One feature of this activity was a ground-level surge of tephra from the caldera floor up on to the rim of the caldera and 10 km downslope to the sea. This was a cool, wet, sticky, high density, and high velocity flow (B. Nolf, pers. comm., 1977). Vegetation was oblit-erated in an area of approximately 25 km^2 on the western slope of the volcano and variously damaged in an area three times that. A few patches escaped in the lee of topographic shelters. Destruction was by burial under as much as 8 m of tephra toward the center of the flow (B. Nolf, pers. comm., 1977) and by uprooting, breaking, debarking, and partial burial toward the shallower edges.

On the Galápagos Islands lava flows are the major alternative sub-strate to tephra. Lava flows present a most inhospitable habitat for plant colonization, and most are barren for long periods. For example,

one 1825 flow south of Punta Espinosa, Fernandina (B. Morrell, 1825, cited in Brower, 1968) had almost no plants growing on its surface after 150 years. By contrast, revegetation of the tephra on the rim of Fernandina was easily visible within nine years.

The pre-eruption vegetation on the northeast caldera rim of Fernandina was a dense tangle of shrubs and herbs described qualitatively by Eliasson (1972) and Colinvaux (1968) as 2–3 m tall shrub forest dominated by *Scalesia microcephala* Robins. Similarly, on the northwest section of the rim *Scalesia microcephala* was a dominant shrub, but of nearly equal size and numbers were *Zanthoxylum fagara* (L.) Sarg., *Tournefortia rufo-sericea* Hook. f., and *Solanum erianthum* D. Don. Also present were *Darwiniothamnus tenuifolius* var. *glandulosus* (Harling) Cronq., *Lippia rosmarinifolia* Anderss. var. *rosmarinifolia, Baccharis gnidiifolia* HBK., *Alternanthera filifolia* (Hook. f.) Howell, and a number of smaller shrubs and herbs. This shrub forest still existed apparently undisturbed around half of the rim and was, therefore, available as a source of plants for recolonization of the tephra.

METHODS

Reestablishment of rim vegetation on the tephra was studied 3, 5, and 9 years after the eruption (June, 1971; July, 1973; and August, 1977). A transect was established beginning on deep tephra at a permanent metal post marking the high point (1494 m) of the west rim and running 18° east of due north. The transect extended north approximately 1.2 km across deep barren tephra (Fig. 1) and continued ¼ km across sparsely vegetated shallow tephra (Fig. 2) to the boundary of the original forest. In the barren area a circular plot of 9.1 m radius was established every 91 m and a count made of all plants encountered. In the sparsely vegetated area, circular plots of 1.5 m radius were established every 15 m for count of herbaceous species; in addition, a plot of 9.1 m radius was established at each third site (46 m intervals) for a count of shrub species. The same plots were resampled each year of the study, except that in 1977 the solitary 1.5 m radius plots were omitted.

In 1973 additional sampling was done (3.1 m radius circular plots at 91 m intervals) along a ⅓ km line extending south from the southern edge of the barren tephra.

In 1977 land iguana (*Conolophus* sp.) feces found in the plots were collected and the seeds they contained brought back to the laboratory. The seeds were tested for germination ability to determine if iguanas provide a possible means of seed dispersal to and across the tephra. Samples from 11 sites along the transect were put on moist paper in petri plates and placed in light.

Fig. 1. View north from about meter 500 of the rim transect, 1977. Here the tephra layer was deep enough to destroy the vegetation entirely. Gullies interrupt the hard, smooth surface evident at the left foreground. Grass clumps visible at right are 0.2–0.3 m tall.

RESULTS

Distribution and density of dominant species encountered along the transect are shown in Fig. 3. The transect crossed three communities—barren, shrub, and the ecotone between them. These are discussed separately below.

Barren area. Toward the center of the tephra, where the deposit was thickest and the destruction of vegetation complete, little revegetation occurred in the nine years following eruption. Approximately 3 km of the rim along the west side of the caldera were still practically barren, another 3 km to the south only sparsely vegetated. The surface of the tephra was a hard crust of fine-grained material, broken in places by gullies centimeters to meters deep exposing coarser textured layers (Fig. 1). Hardening of the surface apparently occurred soon after deposit, as photos taken in successive years show essentially no change in gully pattern or size.

Even the hardiest plants rarely were found growing on the hardened tephra surface. Colonization occurred almost exclusively where the surface was broken. Most plants grew in gullies, in the lines where the wall of the gully met the floor. Here seeds blown from the surrounding area could accumulate; the broken surface and occasional shade increased the seedlings' chances of success. A second site of

FIG. 2.   View north along the northern ¼ km of the rim transect, 1971. Here at the tapering edge of the tephra layer, vegetation was only partially destroyed. Most vegetation visible is 0.5–1.5 m tall.
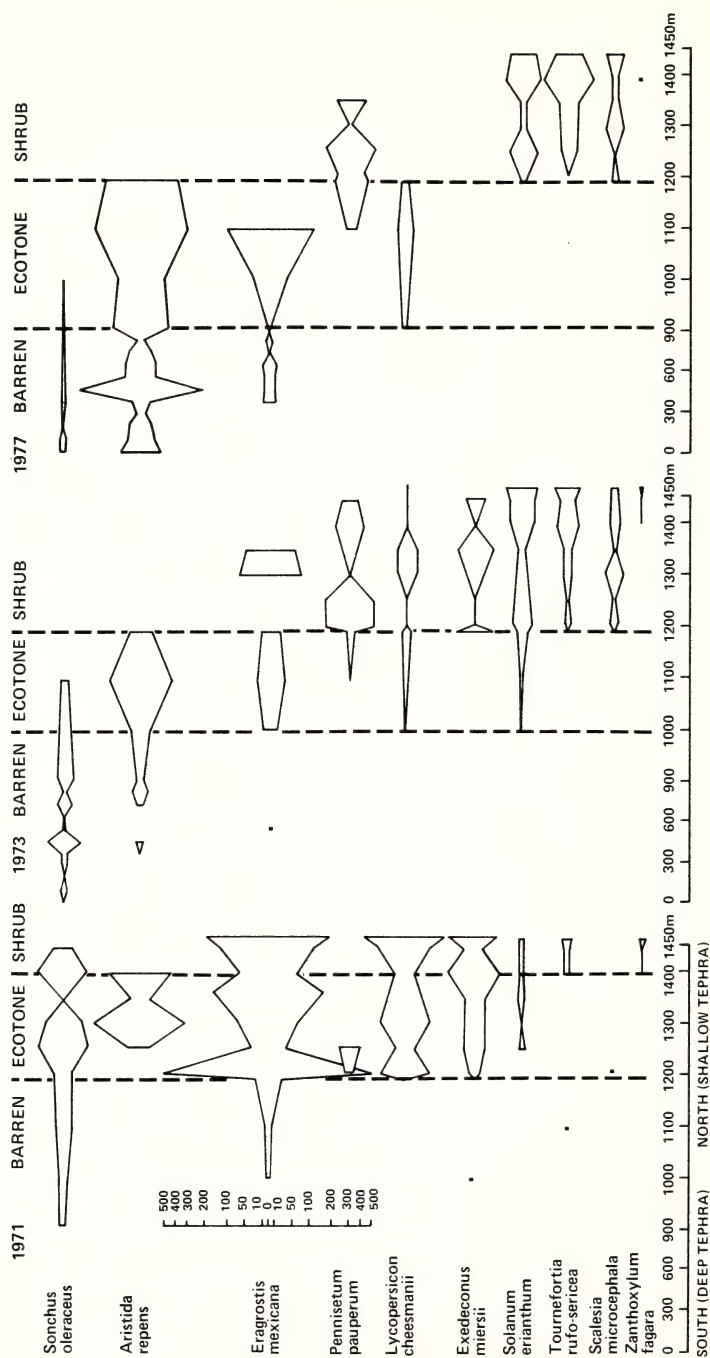
FIG. 3. Distribution and density of dominant species by year. The horizontal axis represents location along transect. Note change of scale at 900 m. The vertical scales represent number of plants per 0.025 ha (log scale).

colonization was at the base of rocks where morning fog condensing on the cool rock face could run to the ground. A third site was provided by scattered depressions that appeared to contain water at some time during the year. In the highlands of Santa Cruz, vegetation is most lush during a cool season from July to December (Van der Werff, 1979). No precipitation records are available for the rim of Fernandina; the few days observed in this study (June, July, and August) were dry. The limiting factors for plant growth on the tephra appeared to be lack of moisture and of appropriate establishment sites.

Few species were able to grow at all in these conditions. Only three were found with any regularity: *Sonchus oleraceus* L., an annual, cosmopolitan, weedy composite; *Aristida repens* Trin., an annual, endemic, weedy grass; and *Eragrostis mexicana* (Hornem.) Link, a widespread, tropical, weedy grass. Other species found less frequently were *Eragrostis ciliaris* (L.) R. Br., *Cyperus ligularis* L., and *Muhlenbergia microsperma* (DC.) Kunth, widespread tropical weedy species, and *Cyperus anderssonii* Boeck. and *Verbena townsendii* Svens, Galápagos endemics. Between 1971 and 1977 these species became less abundant at the north of the transect as shrubs grew and more abundant to the south as gradual breakup of the hard surface occurred (Fig. 3).

Ecotone.   This community is defined by the scarcity of any shrubs except *Solanum erianthum* and *Baccharis gnidiifolia* and the presence of three herbaceous species not found in the "barren" community: *Pennisetum pauperum* Steud. is a large perennial grass, endemic to Fernandina and Isabela high-elevation lava and cinder beds. *Lycopersicon cheesmanii* Riley, a short-lived perennial endemic to the Galápagos, and *Exedeconus miersii* (Hook. f.) D'Arcy, an annual common in the Galápagos at sea level on sandy substrata and found also in Peru, are sprawling vines of the Solanaceae. All three are found only sparsely in the undisturbed original forest but are highly successful pioneer species on the edge of the tephra. No *Exedeconus* was found anywhere at the rim in 1977. The moisture-retaining surface layer of tangled vegetation and litter resulting from growth of these species provides a habitat in which other plants can grow.

In 1977 the tiny moss *Bryum argenteum* Hedw. was found growing in extensive patches in this area. The capsules are only 8–9 mm high, and in August the entire plant appeared simply as a darker crust on the hard tephra surface. Interestingly, this species was also a post-eruption pioneer on the island of Surtsey in the North Atlantic (Fridriksson, 1975).

In 1971 much of the northern ¼ km of the transect could be defined as "ecotone." In 1973 and 1977 the ecotone community was a distinct band moving onto the tephra. This band was about 180 m wide in 1973 and 270 m wide in 1977. Figure 3 indicates the sharp demarcation

of the advancing edge of vegetation that was evident in the field. This edge between "barren" and "ecotone" communities was defined by the sharp increase in both vegetative cover and number of species. The total number of species encountered in summed samples north of the barren/ecotone line (all "ecotone" plus all "shrub") was 17–19 each year, contrasted with 8–9 species to the south ("barren" samples). This edge advanced approximately 180 m south onto the tephra between 1971 and 1973 and an additional 90 m between 1973 and 1977.

Shrub area.   In contrast to the still barren area at the center of the tephra, the ¼ km at the northernmost edge experienced vigorous revegetation in the nine years following the eruption. Here tephra deposits were thinner and destruction of vegetation less complete than in the km sampled across the barren tephra to the south. A sparse cover of scattered shrubs and herbs in 1971 grew by 1977 to a nearly-impenetrable tangle 2–4 m tall (Figs. 4 and 5). Densities of shrub species by year are given in Table 1.

The major shrub species found in the shrub area were the same that dominated the undisturbed forest to the north, where four species were about equally dense and dominant. During revegetation, however, these four were present in strikingly different proportions. In 1977, *Solanum erianthum* and *Tournefortia rufo-sericea* were twice as numerous as *Scalesia microcephala*. Excavations showed that these two species, especially *Tournefortia rufo-sericea,* were sending up abundant vegetative shoots. Nevertheless, each apparently separate plant that arose without evident aboveground connection to another was counted as an individual. Thus much of the apparent increase in numbers of *Solanum erianthum* and *Tournefortia rufo-sericea* was from a few genets that survived burial under tephra and sprouted vegetatively. In *Solanum erianthum* reproduction by seed also appeared to be vigorous, and it was the only shrub found as occasional pioneer individuals on the deeper tephra.

Scalesia microcephala apparently reproduced by seed only, and individuals of all sizes were present in 1973. By 1977, the majority of *Scalesia* were 2–3 m tall.

Zanthoxylum fagara, common in the original forest, was practically nonexistent in the disturbed area. Nowhere were any small *Zanthoxylum* seen. It appears that new plants become established with difficulty in this habitat but, once established at a later seral stage, persist, as *Zanthoxylum* was well represented in the original forest.

Seed germinability.   Seeds collected from iguana droppings in August, 1977, were tested for germination in December, 1977. In eight of 11 petri plates of seeds, including half of those from the most barren area, seeds germinated after two weeks (22 dicot seeds of at least two species and four grass seeds of two species). None survived long enough for identification.

FIG. 4.   (Upper) view north along the northern ¼ km of the rim transect, 1973. Most shrubs are 1 to 2 m tall.

FIG. 5.   (Lower) view north along the northern ¼ km of the rim transect, 1977. Shrubs are a solid cover 2 to 4 m tall. Compare with Figs. 2 and 4, the same view in 1971 and 1973

TABLE 1. SHRUB DENSITY AVERAGED OVER NORTHERN ¼ KM OF TRANSECT, AREA OF RAPID REVEGETATION ("SHRUB AREA"). Numbers are individuals per 0.1 ha.

	1971	1973	1977
Solanum erianthum	3.8	107	121
Tournefortia rufo-sericea	4.9	52	130
Scalesia microcephala	1.0	41	60
Total shrub density	8.7	200	311

South of barren tephra. Vegetation to the south of the thickest tephra existed in a somewhat different pattern from that at the northern edge. The rim topography to the south was more varied, with more ridges and hollows, and corresponding irregularity in tephra depth and other features of the physical environment. Vegetation here grew not in a distinct advancing front as at the north edge, but in irregular patches. Some of these patches were clearly survivors from the pre-eruption forest; notable were a few sparse stands of *Opuntia insularis* Stewart and several stands of rim shrub forest. In other patches *Solanum erianthum* dominated. Over much of this area grew a sparse grass community, unlike anything to the north. Here grass cover in 1973 ranged from 10–50 percent composed of three species in the following proportions: 4 *Aristida repens* : 2 *Eragrostis mexicana* : 1 *Muhlenbergia microsperma.* Also present were occasional individuals of *Sonchus oleraceus, Cyperus anderssonii, Verbena townsendii, Lycopersicon cheesmanii,* and *Solanum erianthum.*

DISCUSSION

Reproductive strategies. The species found growing on the tephra in the nine years since eruption may be characterized as being to some degree weedy. "Weedy" here denotes possession of some combination of the following characteristics: (1) The plant has the potential for rapid growth in perhaps temporarily favorable conditions and the tolerance to survive harsh environmental conditions. (2) Reproductive potential by seed is high, or, alternatively, ability to grow by root or stem sprouting is well developed. (3) Ability to compete with other plants is poor.

Three reproductive strategies were evident in successful colonizers of the tephra: weedy annuals, rhizomatous perennial herbs, and root-sprouting shrubs.

In the harshest sites of deepest tephra, opportunistic annual herbs were the most effective colonizers. The habitats offering any possibility of success for seedlings were scattered, thus those plants producing a large number of easily dispersed seeds had the greatest chance of successful establishment. Both *Sonchus oleraceus* and *Aristida repens,*

found commonly on the tephra, have fruits with hairs or awns that would facilitate their dispersal by wind across the smooth tephra.

Some species spread after initial establishment by rhizome growth. Although all the grasses on the more barren tephra are cited as annuals by Reeder and Reeder in Wiggins and Porter (1971), my observations suggest that some may behave as perennials. *Eragrostis mexicana* in particular grew in stout-based clumps that appeared to be perennial. Several groups were dug up and found to be connected by rhizomes over a distance of a meter or more. This anomalous behavior is another example of the well-documented plasticity of weed species (Baker, 1965; Mayr, 1965). Because barren tephra is so inhospitable to even the most vigorous colonizers, extensive revegetation must await the slow breakup of the surface.

Vigorous ramet production can be an important mode of growth and monopolization of resources for weedy perennials (Bunting, 1960; Baker, 1965). *Solanum erianthum* and *Tournefortia rufo-sericea,* the two shrub species most successful in early establishment on the tephra, had abundant stem and root sprouting. The apparent predominance of this form of growth in these shrubs helps explain the very rapid revegetation of the edge of the tephra. Shrubs surviving intact and roots or branches shallowly buried may all have sprouted. These shrubs show bursts of increased stem density and size resulting in rapid filling of space. Such a burst made *Solanum* the dominant species by 1973; by 1977 *Tournefortia* had attained equal density (Table 1). This rapid growth is characteristic of early successional stages (Odum, 1969) and frequently accounts for rapid revegetation after volcanic eruption (Sands, 1912; Gates, 1914; Aston, 1916; Griggs, 1918).

Extensive ramet production maintains existing genotypes and present fitness. Its importance in this community supports Pickett's (1976, p. 111) suggestion that "genetic systems favoring reduced recombination are selected for in relatively severe early successional habitats."

Scalesia microcephala showed no evidence of vegetative propagation and was slower to become reestablished. Seedlings were apparently able to compete successfully with earlier shrubs and with each other. Continual recruitment of seedlings (Table 1) suggests that *Scalesia* may eventually regain its original density.

Rate of revegetation.   The rate and pattern of revegetation is influenced not only by differing reproductive and growth strategies but also by rainfall and by land iguanas. The Galápagos are notorious for their year-to-year fluctuations in rainfall. A 12-year record from San Cristóbal (Chatham) Island, for example, shows a range in annual rainfall of 3.6–142 cm (Palmer and Pyle, 1966). It is considerably drier on Fernandina than on San Cristóbal, but fluctuations are extreme here as well. Although no precipitation data are available for the rim

of Fernandina, Boersma (1977), working at Punta Espinosa on the northeast corner of the island, observed no precipitation during June and August, 1971, but frequent cloud cover and precipitation more than 15 times between June and August, 1972. The weed strategies of the rim flora are those to be expected in a harsh and fluctuating environment. Climatic variation over the coming years will play a major role in determining the rate at which revegetation of the tephra will continue.

Land iguanas, found throughout the area, may facilitate revegetation in two ways. They appear to play a role in seed disperal to and across the tephra, as they and their often seed-filled droppings were found on even the most barren areas. They also may influence soil development. Their droppings consists of plant material in various stages of decomposition and during the wet season may provide an excellent germination site for seeds contained within or blown to the droppings. Several workers have suggested that such addition of organic matter, particularly nitrogen, to volcanic tephra is prerequisite to revegetation (Griggs, 1933; Eggler, 1963). In addition, extensive iguana tunnels help break up the solid surface of the tephra. A number of collapsed burrows were observed in the barren and ecotone areas. Plants were growing in each, usually in marked contrast to the surrounding unbroken and barren surface.

Vulcanism and plant communities. Persistence of the shrub forest on the rim of Fernandina must be considered in the long-term context of volcanic activity. In the western Galápagos there have been at least 29 eruptions in the last 50 years, 40 eruptions in the last 150 years, and 50 eruptions since the first known eruption 183 years ago in 1797 (T. Simkin, pers. comm., 1981). Periodic disturbances must always have been a feature of Fernandina's environment. Indeed, if "vulcanism" is substituted for "competition", Hutchinson's (1951, p. 575) definition of fugitive species seems a singularly apt description of Fernandina's shrub forest: "They are forever on the move, always becoming extinct in one locality as they succumb to competition and always surviving by reestablishing themselves in some other locality as a new niche opens. The temporary opening of a niche need not involve a full formal successional process." One trend usually expected in succession is an increase in species number (Odum, 1969). This was not true of the first nine years of rim revegetation on Fernandina. There was, instead, rapid recolonization by most of the same few species found in the original climax forest. Whittaker (1965, p. 257) pointed out that "severe, unstable, and recent environments limit the numbers of species which have evolved to maintain themselves in these environments." Earlier workers on Fernandina tephra (Colinvaux et al., 1968; Eliasson, 1972) reported species not represented in these samples; these may well become established here in the future.

Revegetation of the Fernandina tephra supports Porter's (1976, 1979) description of the Galápagos flora as basically weedy. In this arid and periodically disturbed environment, it appears that selection has been for weedy species able to enter new terrain quickly and persist in or at the edges of mature shrub communities. Root and stem sprouting by shrubs is one means of maintaining populations in the face of periodic moderate disturbance. Classic herbaceous weed strategies predominate in areas of the most serious disturbance. Thus in the unstable environment of this active volcano, communities are composed of variously resilient species able to recover from disturbance and revegetate newly created open habitats.

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A LATE PLEISTOCENE AND HOLOCENE POLLEN RECORD FROM LAGUNA DE LAS TRANCAS, NORTHERN COASTAL SANTA CRUZ COUNTY, CALIFORNIA

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Abstract

A 2.1-m core from Laguna de las Trancas, a marsh atop a landslide in northern Santa Cruz County, California, has yielded a pollen record for the period between about 30,000 B.P. and roughly 5000 B.P. Three pollen zones are recognized. The earliest is characterized by high frequencies of pine pollen and is correlated with a mid-Wisconsinan interstade of the mid-continent. The middle zone contains high frequencies of both pine and fir (*Abies,* probably *A. grandis*) pollen and is correlated with the last full glacial interval (upper Wisconsinan). The upper zone is dominated by redwood (*Sequoia*) pollen and represents latest Pleistocene to middle Holocene. The past few thousand years are not represented in the core. The pollen evidence indicates that during the full glacial period the mean annual temperature at the site was about 2°C to 3°C lower than it is today. We attribute this small difference to the stabilizing effect of marine upwelling on the temperature regime in the immediate vicinity of the coast. Precipitation may have been about 20 percent higher as a result of longer winter wet seasons.

Introduction

The Quaternary vegetation history of coastal California is not well understood. Several fossil floras have been published (Chaney and Mason, 1930; Mason, 1934; Warter, 1976; see Johnson, 1977 for a review), but the detailed history of vegetation change is not yet known. In large part, this uncertainty reflects the limitations of the pollen record. Only four pollen diagrams have been published (Heusser, 1960; Adam, 1975); none covers more than the past 8000 years. In this paper, we report on a pollen analysis of a 210-cm core from Laguna de las Trancas in northern Santa Cruz County (Fig. 1) that covers the period 30,000 B.P. to roughly 5000 B.P. Its pollen content indicates marked changes in vegetation.

STUDY SITE

The general environmental setting of the study area has been described by Hecht and Rusmore (1973). Laguna de las Trancas lies in a small depression at the head of a landslide about 7 km southeast of Point Año Nuevo (Fig. 1). It is situated on a marine terrace (170 m above sea level) 1 km inland from the present coastline. A radiocarbon date of 29,500 ± 560 years (USGS-153) on a piece of pine wood from a depth of 312 cm near the base of the marsh deposits indicates that the marsh was formed approximately 30,000 years ago. The landslide event may have been associated with movement along the nearby Ben Lomond or San Gregorio faults. The bedrock in the immediate vicinity of the marsh is the Santa Cruz Mudstone of Clark (1966, 1970), a siliceous organic marine mudstone of late Miocene and early Pliocene age (Greene, 1977).

The topography of the coastal area is rugged, especially to the north, where the coastline intersects the San Gregorio fault, and where steep cliffs rise from the beach to an elevation of 180 m. The marsh itself is located on a narrow interfluve between Waddell and Scott Creeks, two small but perennial streams that rise in the Santa Cruz Mountains about 20 km from the coast. They occupy steep-walled valleys, the mouths of which have been drowned by the postglacial rise in sea level.

The area has a Mediterranean-type climate that is characterized by winter rain and summer drought. Mean annual rainfall is about 77 cm, mostly falling between November and April (Rantz, 1971). Temperature extremes are rare, and seasonal averages range from 17°C in September to 9°C in January. Coastal fog is common in summer (U.S. Dept. Commerce, 1977).

The present vegetation of the area forms a complex mosaic of plant communities. The general distribution of some of the more important taxa is shown in Fig. 1. Locally important along the coast is a shrub community (Type 50, Fig. 1) in which the dominant species locally are coastal sage (*Artemisia californica* Less.) and coyote bush (*Baccharis pilularis* DC.). Farther inland the coastal shrub gives way to a coniferous woodland (Type 9, Fig. 1) in which the local dominant is Monterey pine (*Pinus radiata* D. Don). This species has a very restricted natural distribution and is found at only three localities along the California coast. Here at Point Año Nuevo, *Pinus radiata* is at the northernmost limit of its natural range; its total range covers an area of less than 60 km² (Fowells, 1965, p. 390).

There has been considerable discussion as to the causes for the very localized distribution of Monterey pine (Moulds, 1950; McDonald, 1959; Stebbins, 1965), but is is generally agreed that summer drought is an important limiting factor. Evidence of this was apparent on the eastern margins of the Año Nuevo population during the early fall of
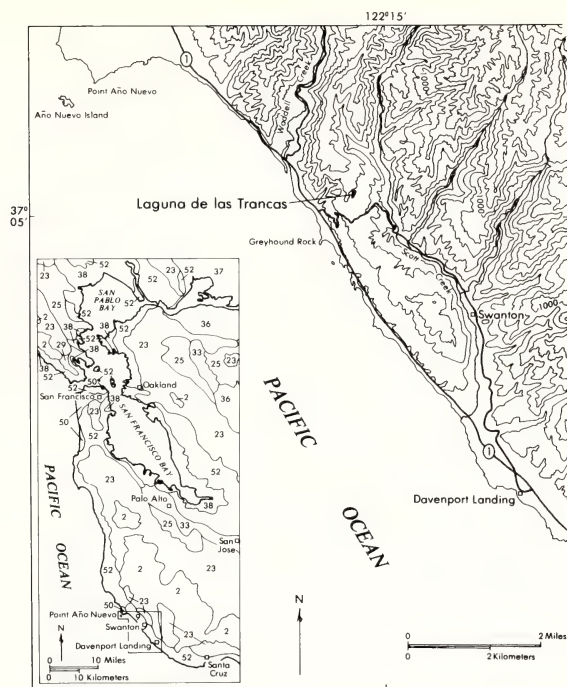
FIG. 1.   Map showing the locations of Laguna de las Trancas. Inset map shows the location relative to San Francisco Bay; numbered regions indicate vegetation types, and are taken from the vegetation map of California by Küchler (1977; reproduced by permission). Vegetation types are: 2, Redwood forest (*Pseudotsuga-Sequoia*); 9, Coastal cypress and pine forests (*Cupressus, Pinus*); 23, Mixed hardwood forest (*Arbutus-Quercus*); 25, Blue oak-digger pine forest (*Pinus-Quercus*); 29, Chaparral (*Adenostoma-Arctostaphylos-Ceanothus*); 33, Valley oak savanna (*Quercus-Stipa*); 36, California prairie (*Stipa* spp.); 37, Tule marsh (*Scirpus-Typha*); 38, Coastal saltmarsh (*Salicornia-Spartina*); 50, Northern seashore communities (*Elymus, Baccharis*); and 52, Coastal prairie-scrub mosaic (*Baccharis, Dantonia-Festuca*). Base for large map is taken from USGS Davenport and Año Nuevo 7.5-minute quadrangles.

1977. Several trees showed signs of stress in the form of yellow needles and premature needle fall, probably in response to the unusually severe drought of the two preceding years. In the main part of the stand, however, there was no evidence of drought stress; furthermore, there is no indication that the Monterey pine is a species that is doomed to an early extinction (cf. Ornduff, 1974). Reproduction is everywhere evident, and no other tree species appears to be better adapted to this particular environment. Occasional Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and live oaks (*Quercus agrifolia* Neé) are found among the pines, and in some places a mixed hardwood forest has developed (Type 23, Fig. 1); neither appears to have any consistent

competitive advantage. Beneath the pines there is a discontinuous shrub layer that consists largely of California lilac (*Ceanothus thyrsiflorus* Esch.), California holly (*Heteromeles arbutifolia* M. Roem.), hazelnut (*Corylus cornuta* var. *californica* (A. DC.) Sharp), and poison oak (*Toxicodendron diversilobum* (T. & G.) Greene).

Farther inland, floristic composition is largely a function of slope, aspect, and available moisture. On the more mesic sites, redwood (*Sequoia sempervirens* (D. Don) Endl.) is the dominant species (Type 2, Fig. 1); it is often found in association with madrone (*Arbutus menziesii* Pursh), tanbark oak (*Lithocarpus densiflora* (H. & A.) Rehd.), and the California bay (*Umbellularia californica* (H. & A.) Nutt.). On drier sites, Douglas fir (*Pseudotsuga menziesii*) and knobcone pine (*Pinus attenuata* Lemmon) are locally common, as are several species of oak (*Quercus agrifolia, Q. chrysolepis* Liebm., *Q. wislizenii* A. DC.). Natural hybrids between *Pinus radiata* and *P. attenuata* have been reported from near Point Año Nuevo (Fowells, 1965, p. 394). On very dry sites, chaparral species are dominant, including chamise (*Adenostoma fasciculatum* H. & A.), coyote bush (*Baccharis pilularis*) and manzanita (*Arctostaphylos* spp.). Chaparral species are also locally common in abandoned pastures and in areas that have recently been cleared by logging or fire.

The two permanent streams that run through the area, Scott and Waddell Creeks, are fringed by a riparian woodland that includes broadleafed maple (*Acer macrophyllum* Pursh), California buckeye (*Aesculus californica* (Spach) Nutt.), red alder (*Alnus oregona* Nutt.), cottonwood (*Populus trichocarpa* T. & G.), box elder (*Acer negundo* L. ssp. *californicum* (T. & G.) Wesmael), willows (*Salix* spp.), and the California nutmeg (*Torreya californica* Torr.).

Since the beginning of European settlement, the vegetation of the area has been drastically modified by human disturbance. Large areas on the marine terraces and in the valley bottoms have been cleared for agriculture. In other areas the vegetation has been variously affected by logging, grazing, and changes in fire frequency.

METHODS

A core was taken from the central part of the marsh with a 10-cm-diameter piston corer. The marsh normally consists of a floating mat of *Typha* and *Scirpus* approximately 75 cm thick. Of this, the upper half is living roots and the lower portion coarse peat. Because the mat as a whole was too loosely consolidated to be successfully cored with our equipment, we began coring at a depth of 105 cm below the water surface. Below this depth the sediments were reasonably compact, and a 210-cm core was recovered in five sections. By the fall of 1977, after 2 years of severe drought, the marsh had dried out completely, and the water table was about a meter below the ground surface. The

upper part of the sediments was sampled at that time, but no analyses of the top part of the section have been completed.

The core shows marked changes in lithology (Fig. 2). The upper 90 cm (105 to 195 cm) consists largely of silt with an increasing proportion of coarse plant debris toward the surface. Between 195 and 210 cm there is a sand layer with some clay lenses. This material is loosely consolidated and was successfully recovered only after several coring attempts. Below the sand layer is almost a meter of brown clay and a basal 10 cm of silt. Bedrock was not encountered, but the sediments below 315 cm were too compact to be recovered with our equipment.

The core was split and sampled at 5-cm intervals for pollen analysis. Constant volume samples of 2.5 cm^3 were taken from the undisturbed central portion of the core, and tablets containing a total of approximately 25,000 *Lycopodium* spores were added to each sample as a control (Stockmarr, 1971). The extraction procedures followed were basically those described by Faegri and Iverson (1975); in brief, samples were treated with HCl (10 percent), HNO$_3$ (10 percent) and acetolysis. The pollen-rich residue was then stained with 1 percent safranin and mounted in silicone oil. In general, pollen preservation was good, although at certain levels, particularly the sandy levels, there was a high proportion of broken grains.

A least 250 fossil grains were counted at each level. Because of the large numbers of certain pollen types present, a ratio method of counting was followed. For most levels, the count was made up to a total of 100 control grains. For some levels, however, the ratio of pollen grains to controls was too large to make this count feasible, in which case only 50 or, more rarely, 25 controls were counted. For very abundant types, such as pine, the count was stopped at 100 pine grains; the number of controls was recorded, and the count continued excluding pine. When the count for a level was complete, the pine/control ratio was then used to estimate the pine total. This method has the advantage of allowing for a better representation of minor taxa.

Pollen Types

In this analysis, 26 pollen or spore types are assigned to known genera, 18 to family or subfamily, and 3 to groups of families. In addition, 15 unknown but distinctive pollen types were observed; none of them, however, accounted for more than one percent of the total count at any level.

Perhaps the most frustrating feature of fossil pollen analysis in California is the problem posed by the Taxaceae, Cupressaceae, and Taxodiaceae. Their pollen grains are very similar and are often lumped together as TCT pollen (for example, see Helley, Adam, and Burke, 1972). In this study, however, we distinguish between *Sequoia* and other TCT pollen on the basis of the thicker exine in *Sequoia* grains.

DEPTH IN CM	LITHOLOGY	POLLEN ZONE
105	PEAT & BLACK SILT	REDWOOD ZONE
150	INCREASING SILT	
160	BLACK SILT	
	BLACK SILT	
195	SAND & CLAY	PINE-FIR ZONE
210	LOOSE SAND	
	BROWN SILTY CLAY	PINE ZONE
250	DISCONTINUITY	
	BROWN SILTY CLAY	
280	PINE FOSSILS	
	BROWN SILTY CLAY	
305		
315	BROWN SILT	

FIG. 2.   Generalized lithology of the Laguna de las Trancas core.

Our TCT category probably includes *Cupressus, Juniperus,* and *Torreya,* and possibly *Calocedrus,* which has been found as macrofossils in deposits at Mountain View in San Mateo County dated at 21,000 to 24,000 years B.P. (Helley et al., 1972).

We did not attempt to make any distinctions within the genus *Pinus.* Ting (1966) has proposed that statistical analyses of morphological characters can be used to identify California pine pollen to the species level. Even when using reference material, however, we were unable to distinguish the pollen of several of the pines now growing in the vicinity of the marsh (*Pinus radiata, Pinus attenuata, Pinus ponderosa* Dougl. ex P. & C. Lawson), and we therefore did not attempt to identify fossil material below the generic level. As we indicate later, this taxonomic problem complicates the interpretation of the pollen diagram.

Several different sizes of grass pollen were present, and three size classes were arbitrarily established (Gramineae A, grains <25 μm; Gramineae B, 25–40 μm; and Gramineae C, grains >40 μm). Because of the wide range of possibilities no attempt is made in this paper to relate them to particular genera. The Compositae are a floristically diverse group in coastal California, and this diversity is reflected in the pollen record. Here we follow tradition (for example, Martin, 1963) in recognizing only four types: "High-spine" Compositae, Liguliflorae, "Low-spine" Compositae or *Ambrosia*-type, and *Artemisia.*

Typha latifolia L. pollen is distinctive insofar as it retains the tetrad arrangement and is therefore listed as a separate type. Unfortunately, *Typha angustifolia* L. pollen cannot be distinguished from *Sparganium* pollen or from some broken *Typha latifolia* tetrads, and we therefore include all *Typha*-like monads in the *Typha/Sparganium* category.

The curves in the pollen diagram represent changes in percentages rather than "absolute" values. The pollen sum includes all arboreal types but excludes herbs and aquatics. Unknown and indeterminate pollen and spores are included in the diagram under "unknowns."

Results and Discussion

Pollen diagrams derived from small marshes such as Laguna de las Trancas are more difficult to interpret than diagrams from lacustrine or marine environments. Marsh diagrams reflect two kinds of vegetation change: changes in the upland vegetation and changes in the marsh itself. In order to avoid confusing local and regional effects, we excluded aquatic pollen types from the pollen sum and calculated their values as percentages of the total nonaquatic pollen. In the discussion that follows, we consider the upland record first. The diagram (Fig. 3) can be divided into the three zones shown in Fig. 2: a pine zone (levels 315–235) at the base, a pine-fir zone (levels 225–185), and a
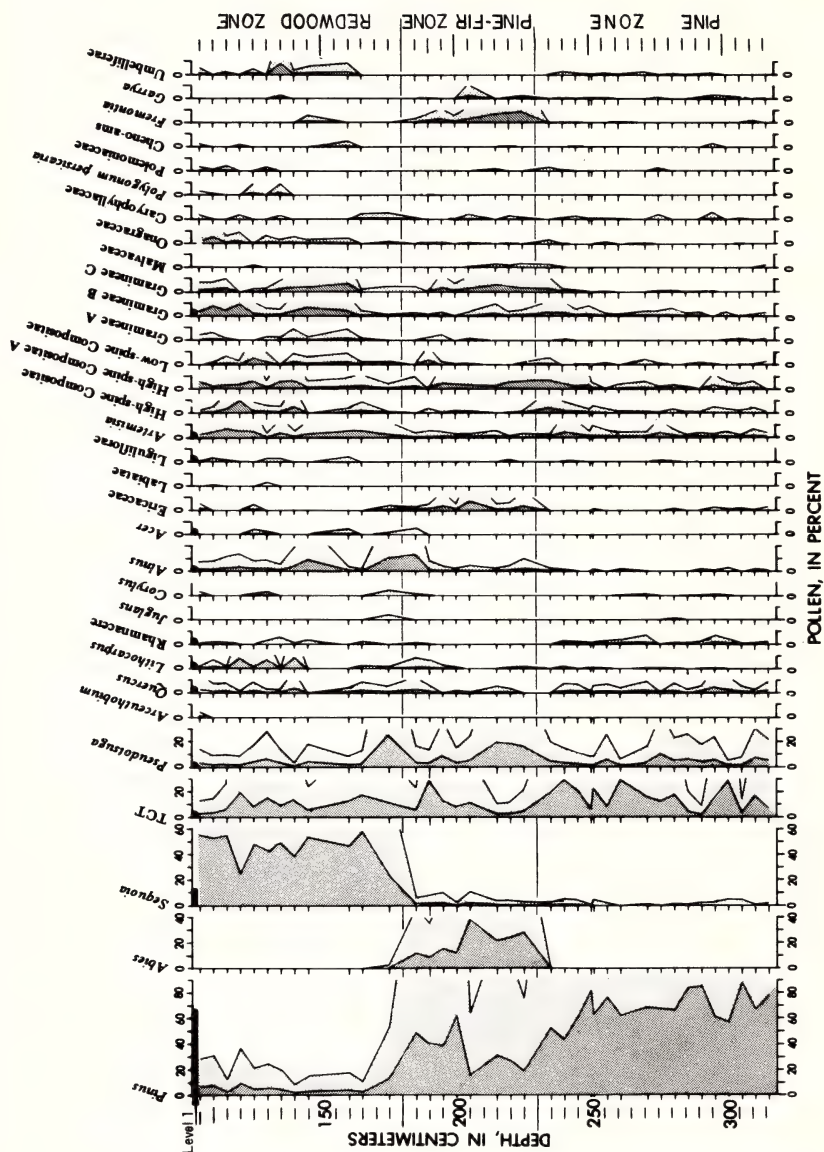
redwood zone (levels 175–105). We do not have radiocarbon dates for the critical zone boundaries, but we tentatively suggest the following chronology: 1) The pine zone = 30,000–24,000 B.P., corresponding to an interstade of the mid-Wisconsinan; 2) The pine-fir zone = 24,000–12,000 B.P., corresponding to the main glacial advance of the upper Wisconsinan in the mid-continent (full glacial): and 3) The redwood zone = latest Pleistocene to Mid-Holocene (12,000 to perhaps 5000 B.P.)

Because the core does not include the peat mat that at present covers the marsh, the past several thousand years are not represented in the diagram. Level 1 represents a composite surface sample taken to allow comparison of the present pollen accumulation with the fossil record.

Basal pine zone. Pine pollen percentages in the lowest meter of the core are persistently high. We do not feel that it is possible to distinguish among the closed cone pines (*Pinus radiata, P. attenuata, P. muricata* D. Don) on pollen morphology alone; theoretically, therefore, any combination of these species, and perhaps hybrids between them, could have been present in the area at this time, as could other species such as *Pinus ponderosa, P. sabiniana* Dougl., and perhaps even *P. contorta* Dougl. ex Loud. Fortunately, however, we can be reasonably certain that one of the pines present was the knobcone pine (*Pinus attenuata*). During the coring operation, an incomplete cone was recovered at 280 cm with cone scales that show the minutely spinose tip characteristic of the species (H. Schorn, oral commun., 1975).

TCT pollen was encountered at all levels in this zone but never accounted for more than 5 percent of the total. As stated, several genera could be represented, including *Juniperus, Cupressus, Calocedrus* and *Torreya*. The only other pollen type of importance in this zone is *Pseudotsuga*. Several pollen types are conspicuously rare or absent, including *Sequoia, Quercus,* Gramineae, and Compositae.

Taken as a whole, the pollen record indicates that during this time period, the upland vegetation in the vicinity of the site was coniferous forest dominated by pine and Douglas fir. The Douglas fir may have been a more important component of the vegetation than the pollen

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FIG. 3. Pollen diagram for the major nonaquatic pollen types in the Laguna de las Trancas core. The horizontal scale is the same for all curves, and is for the darkly-shaded curve; the lightly-shaded curve is a 3× exaggeration of the dark curve. Depth is shown in centimeters below the water surface at the time the core was taken. The depth scale does not apply to the top sample plotted in bar-histogram form (level 1). That sample is a composite modern soil-surface sample. Frequencies less than 1 percent in level 1 are represented by a dot. The pollen sum for the modern sample excluded pollen of *Plantago,* which did not occur in the fossil samples.

diagram indicates because its pollen is large and is commonly under-represented on pollen diagrams (Baker, 1976). Similarly, chaparral species such as *Arctostaphylos manzanita* Parry and *Adenostoma fasciculatum* may have been present on drier sites, but we have not observed any pollen from these insect-pollinated species in our samples.

Detailed paleoecological interpretation of the pine zone is precluded by the taxonomic imprecision concerning the pine and TCT pollen. In view of the limited importance of *Sequoia, Quercus,* Gramineae, and Compositae, we would tentatively suggest that the climate of the area at that time was cool and dry, possibly analogous to the interior valleys of the Coast Ranges of Oregon and northern California. Another possibility is that there may be no modern analog for the pine zone at Laguna de las Trancas.

Pine-fir zone. At the 210-cm level, there is a marked change in pollen frequencies. Pine declines in importance, and fir and ericaceous pollen suddenly increase. The discovery of fir pollen was unexpected. Fir is not now native to the Santa Cruz Mountains, and the nearest natural stand is 100 km to the south in the Santa Lucia Mountains. We do not believe, however, that the fir pollen found at Laguna de las Trancas represents the Santa Lucia fir (*Abies bracteata* D. Don ex Poiteau). Comparison with modern reference materials suggest that the Laguna de las Trancas fir is more likely to be *Abies grandis,* the grand fir. This species has a wide distribution in the Pacific Northwest and ranges down the California coast to the Russian River, a distance of 150 km north of Laguna de las Trancas. In northern California, the grand fir is largely restricted to the coast. It is found in association with redwood below elevations of about 600 meters, and with Bishop pine (*Pinus muricata*) in the immediate vicinity of the coast (Griffin and Critchfield, 1972).

Unfortunately, the ericaceous pollen cannot be identified to species. In view of the similarity between the fir and Ericaceae curves, we suggest that the following are likely possibilities: Labrador tea (*Ledum glandulosum* Nutt. ssp. *columbianum* (Piper) C. L. Hitchc.), huckleberry (*Vaccinium* spp.) and salal (*Gaultheria shallon* Pursh). All are locally common along the northern California coast, especially in sandy, low-pH environments. The Ericaceae are primarily insect pollinated, and whatever species produced the ericaceous pollen at Laguna de las Trancas must have been growing in close proximity to the marsh. In our experience, chaparral ericads such as manzanita (*Arctostaphylos* spp.) are not well recorded in the fossil pollen record.

As in the basal pine zone, Douglas fir pollen was encountered at all levels; in one sample, it accounts for 32 percent of the total tree pollen. It can be safely assumed, therefore, that Douglas fir was an important component of the vegetation. Also of interest is the increase in grass
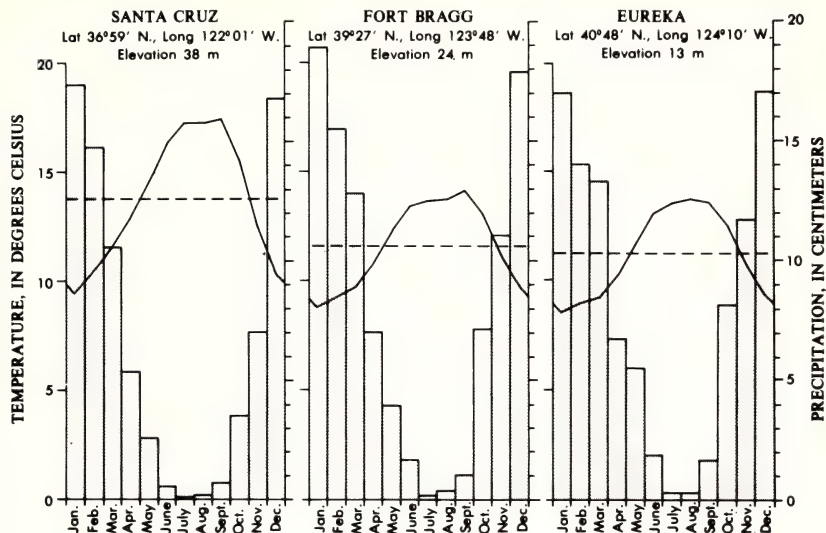
F IG. 4.   Comparison of climatic data for Santa Cruz, Fort Bragg, and Eureka, Calif. Data are from U.S. Department of Commerce (1964); values used are climatic normal values, with the exception of the Fort Bragg temperature data, which are for a period of 25 years. Shaded vertical bars are mean monthly precipitation, solid curve displays mean monthly temperatures, and dotted lines show mean annual temperatures.

and high-spine Compositae pollen; we take this as clear evidence that the vegetation around the marsh was not completely closed forest.

Taken as a whole, the pine-fir assemblage suggests that during the last full glacial interval the vegetation of the Laguna de las Trancas area was very similar to that which is found today about 2.5° farther north, along the northern coast of California. The fir pollen is the most convincing evidence of climatic change, and suggests that the full glacial climate in the vicinity of the marsh was on average at least 2° to 3°C cooler than at present. This estimate is based on a simple comparison between the mean monthly temperature curves for Fort Bragg and Santa Cruz (Fig. 4), and is only a minimum value. Fort Bragg is located directly on the coast, whereas during the last glaciation the Laguna de las Trancas site was several kilometers inland, and the moderating effect of the ocean upon the climate may have been less than at Fort Bragg.

The lithology of the core also provides evidence of environmental change during the last full glacial interval. The high sand concentration in the pine-fir zone can be interpreted in several ways. If it is fluvial in origin, it could indicate changes in rainfall in the watershed and more effective erosion and transport of sand-sized sediment. It could also be attributed to a lowering of the water level in the marsh

and an increase in the transport of sand into the central area of the marsh. A third possibility is that the sand is aeolian in origin. No sedimentological studies have been carried out on the Laguna de las Trancas core, and we are not able to state definitively how the sand was deposited in the marsh. We suggest, however, that it was blown in. The watershed area of the marsh is very small (<10 ha) and it seems unlikely that, even with a significantly different precipitation regime, there would be a marked increase in the amount of surface runoff and erosion. A more plausible explanation is that during the last full glacial interval, active sand dunes were more extensive along the central California coast than they are today. During the period 30,000 B.P. to 10,000 B.P., the combined Sacramento and San Joaquin drainage reached sea level west of the Golden Gate. The sand supply to the coast must have been considerably greater then than it is today. In this respect, the central California coast during the last full glacial interval may have been similar to the present day Oregon and Washington coast, where massive dune systems are fed by the Columbia River. At present, there is a small dune field on Año Nuevo Point, 7 km northwest of the marsh. Conceivably, during the full glacial much of the now-submerged coastal plain was covered by active dunes, and some sand may have blown up as far as the 170-m terrace. *Abies grandis* currently grows on coastal dunes on the far northern California coast (Barbour and Johnson, 1977) and probably occupied the same sort of habitat near Laguna de las Trancas. Fir trees must have been growing near the marsh, because fir pollen is large and is not blown long distances.

One puzzling aspect of the pine-fir zone is the absence of *Sequoia* pollen. It seems unlikely that the full glacial climate was severe enough to eliminate redwoods from the Santa Cruz Mountains as a whole. A more plausible explanation is that stronger winds restricted this salt-sensitive species to more sheltered, inland locations. It is generally agreed that circulation of the atmosphere was intensified during the full glacial (see, for example, Wilson and Hendy, 1971; Lamb and Woodroffe, 1970), and average wind speeds were probably higher then along the California coast than they are today, particularly in summer. The absence of redwood pollen in the pine zone may also be a reflection of stronger onshore winds.

Spruce (*Picea*) is absent from the pine-fir zone. Mason (1934) reported Sitka spruce (*Picea sitchensis* (Bong.) Carr.) needles and twigs in his Tomales flora but failed to find cones, and suggested therefore that at that location the species might have been at the southern limit of its Pleistocene range. Tomales Bay is 140 km north of Laguna de las Trancas and the flora has since been dated at 29,050 ± 1100 B.P. (Berger and Libby, 1966). Spruce pollen has recently been discovered in early Holocene sediments from Bolinas Lagoon (Byrne and Bergquist, unpublished data).

A present, Sitka spruce and grand fir grow together in coastal Or-
egon (Fowells, 1965), but spruce does not extend as far south along
the coast as fir in California (Griffin and Critchfield, 1976). A similar
distributional relation may have existed during the full glacial.

Considered as a whole, the pine-fir assemblage indicates a south-
ward displacement of species ranges of at least 150 km during the last
glaciation. This estimate is significantly less than Warter's (1976) 320
km estimate based on paleobotanical evidence from La Brea and Car-
pinteria. If both grand fir and Sitka spruce were displaced comparable
distances along the coast, however, the coastal temperature change
was probably not much greater than our estimate. The climatic dif-
ference between Fort Bragg and Eureka is rather small (Fig. 4), and
the main southern limit of Sitka spruce lies between those two sites
(Griffin and Critchfield, 1976). Because Sitka spruce did not reach
Laguna de las Trancas during the last full glacial, we suggest that the
full-glacial climate at Laguna de las Trancas was milder than the
present climate at Eureka. The implication is that average monthly
temperatures were depressed by 2° to 3°C along the coast, and that
precipitation was about 20 percent higher, with the increase occurring
primarily in the form of longer winter rainy seasons (cf. Fig. 4). This
estimate is significantly less than the CLIMAP full glacial temperature
depression estimate for the California coast of 9° to 11°C (Gates, 1976).
If our 2° to 3°C estimate is correct, it suggests that coastal California,
unlike most other areas of North America, experienced a full glacial
climate that was not very different from that of the present. Presum-
ably, then as now, the Pacific Ocean had an important moderating
influence. One important reason why the temperature depression may
not have been great is that sea-surface temperatures close to the Cal-
ifornia coast are strongly influenced by coastal upwelling, and the
upwelling water undoubtedly changed temperature much less between
interglacial and glacial intervals than did the normal ocean mixed
surface layer farther offshore.

In the same context, we emphasize that the Laguna de las Trancas
pollen diagram records primarily changes in coastal climate and should
not be extrapolated inland. The presence of fir at Laguna de las Tran-
cas, for example, does not mean that boreal forest species or com-
munity distributions migrated southward through California as a
whole during the full glacial. In fact, the available evidence shows
that they did not. A recently analyzed core from Clear Lake contains
very little spruce or fir pollen in the levels of full-glacial age (Adam,
1979). Similarly, spruce pollen is absent from late Pleistocene sections
of a core from Osgood Swamp, near Lake Tahoe (Adam, 1967).

There is an interesting parallel here with the late-Pleistocene vege-
tation history of eastern North America. The discovery of spruce cones
and pollen in Pleistocene sediments in Louisiana was formerly thought
to be evidence of a southward, en masse migration of the Boreal Forest

(Deevey, 1949). More recently, it has been interpreted as the result of a more localized migration down the Mississippi Valley where cold-air drainage coming from the Laurentide Ice Sheet would have provided climatically favorable conditions (Delcourt and Delcourt, 1975). In a similar but more persistent way, the cool-summer climate of the California coast allows for a southward extension of "northern" species.

Redwood zone.   Above 180 cm the importance of both pine and fir drops sharply and redwood increases. Also the lithology of the core indicates a shift from the high sand concentrations of the pine-fir zone to an increasing proportion of silt.

Redwood clearly dominated the vegetation of the area at this time; pine, Douglas fir, and oak are rare. On the other hand, both grass and Compositae pollen reach consistently high values. We infer that redwood was dominant on the more mesic sites and that drier sites were open grassland. Chaparral species were probably also present, but unfortunately this vegetation type is not clearly recognizable in the fossil record.

The two most significant aspects of the redwood zone are the high redwood percentage and the virtual absence of pine. The redwood rise can be logically explained as simply the response to an amelioration of climate during the early Holocene. If the previous discussion regarding the absence of redwoods during the full glacial is correct, it follows that a reduction in the strength of onshore winds would allow the redwoods to move out of the more protected locations and expand westward toward the coast. The absence of pine is less easily accounted for.

At present, Monterey pine is the dominant tree in the immediate vicinity of the site, accounting for 80 percent of the modern pollen rain (Level 1 in Fig. 3). During the early and middle Holocene, however, the situation was clearly different. The low pine percentages in the redwood zone are conclusive evidence that pines were not present in the immediate vicinity of the marsh at this time. Pines produce abundant wind-dispersed pollen and are usually overrepresented in pollen diagrams.

Axelrod (1967) has hypothesized that the present restricted distribution of the closed-cone pine forest is a result of postglacial climatic change. More specifically, he suggested that during the cooler full glacial, the closed-cone pines were widely distributed along the coast, and that as the climate became hotter and drier during the mid-postglacial period (the xerothermic), they were restricted to the areas of their present disjunct distributions. The Laguna de las Trancas record supports this hypothesis in part, but not entirely.

The main problem with the xerothermic hypothesis is that the high redwood percentages in the Holocene argue against persistent drought

along the coast during this period. By this we do not mean to say that the middle Holocene climate was not different from that of the present, but rather that it was not different enough to account for the disappearance of the pines.

A more plausible explanation is that the change from glacial to postglacial climate caused the pine decline. With the exception of *Pinus attenuata,* all the closed-cone pines are adapted to cool-summer climates. They are found today along the coast, where summer fogs ameliorate the effects of summer drought. During the interstadial conditions of the mid-Wisconsinan and the full glacial conditions of the upper Wisconsinan, a cool-summer climate probably was characteristic of most of the California coastline. During the early postglacial, however, summer droughts must have become more severe, and the closed-cone pines would have been restricted to especially favorable sites. At this time sea level was still well below its present level, and the ancestors of the Monterey pines that are now found at Laguna de las Trancas could have been 10 to 20 km to the west. At sea level rose during the Holocene, the pines could have migrated eastward to assume their present distribution. In other words, the pine curve in Fig. 3 is probably best explained as being a reflection of changes in climate and related changes in sea level.

Aquatic sequence. The aquatic diagram (Fig. 5) shows marked changes in pollen and spore frequencies, which we interpret to be primarily a reflection of hydroseral succession. For purposes of discussion, two stages can be recognized.

The first stage coincides with the basal pine zone (levels 315–235) and represents open-water conditions. The pond was probably not very deep at this time but it was deep enough to prevent the establishment of marsh plants such as *Scirpus* and *Typha.* The only aquatics consistently present were *Equisetum* and *Myriophyllum.* The lithology of the core also indicates that the marsh had not yet formed. Except for a silty layer below 305 cm, the sediments are fine-grained and contain little organic matter.

The second stage includes both the pine-fir and redwood zones and is characterized by an expanding area of marsh around the edges of the pond. This is well shown in the diagram by the *Typha latifolia* and Cyperaceae curves. Cyperaceae in this case almost certainly represents the tules (*Scirpus acutus* Muhl. and possibly *S. validus* Vahl.). The irregular increase in *Alnus* also reflects the process of hydroseral succession.

A similar successional trend is evident in the *Azolla* curve. The species represented here is *Azolla filiculoides* Lam., the water fern. *Azolla* is a floating aquatic, but needs shallow water for successful reproduction (Bonnet, 1957). The frequent changes in *Azolla* percentages probably reflect short-term changes in water depth.
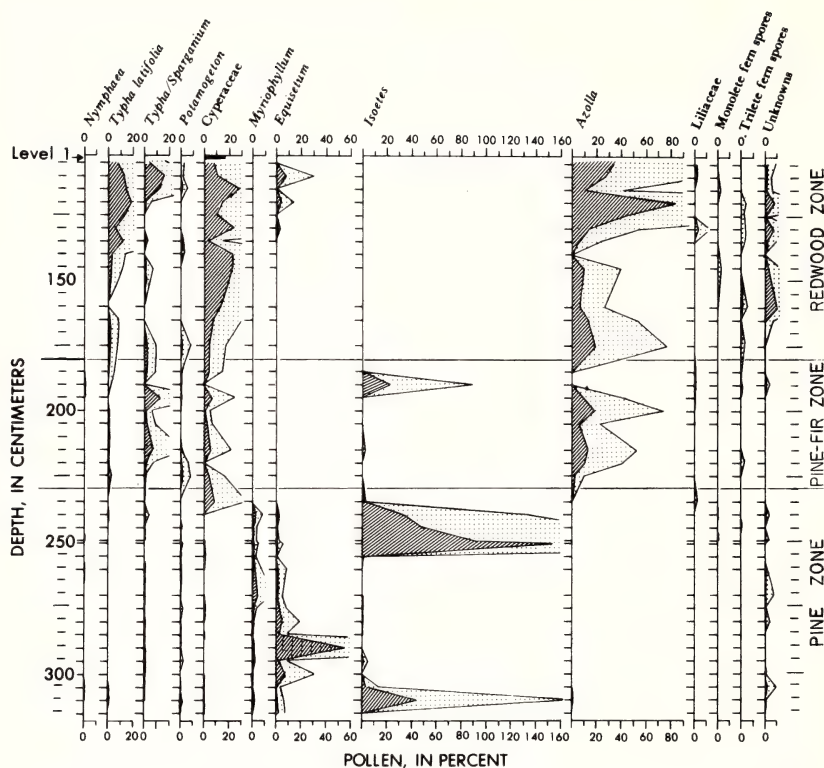
Fig. 5. Diagram for the aquatic types in the Laguna de las Trancas core. Depth and percentage scales are the same as for Fig. 3.

The lithology of this section of the core is more complicated than that of the basal zone. As suggested, the sand layer is probably the result of increased dune activity along the coast, in which case it does not reflect any hydrological changes within the marsh itself. Above the sand layer, however, the sediments are predominantly silty and contain an increasing amount of organic material toward the top of the core. This can probably be attributed to the gradual shallowing of the pond and increased extent of the marsh. Today, the peat mat covers all but a small part of the pond.

In brief, both the lithology of the core and the aquatic pollen record reflect the progressive filling of the pond and the expansion of the marsh. At the same time, this process of hydroseral succession was complicated by regional changes in climate. We recognize the danger of circular reasoning here, but suggest that at least one of the curves in Fig. 5 shows changes in frequency that are best interpreted as resulting from climatic change rather than hydroseral succession.

The *Isoetes* curve is irregular and shows three major peaks. The peaks in themselves may or may not be meaningful, but it is probably significant that *Isoetes* is restricted to the basal pine and pine-fir zones. In the eastern United States *Isoetes* is reported as being important in lake deposits that date to the last full glacial (Frey, 1953). Unfortunately, the climatic tolerance of *Isoetes* is not yet well understood, and we therefore cannot draw any specific conclusions from its occurrence at Laguna de las Trancas.

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NOTES AND NEWS

VARIATION IN IMMATURE CONE COLOR OF PONDEROSA PINE (PINACEAE) IN NORTHERN CALIFORNIA AND SOUTHERN OREGON.—Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) has been the subject of much research, possibly as much or more than any other forest tree in North America. There are now more than 3500 articles that report on some feature or relationship of ponderosa pine; possibly one third of these deal exclusively with the tree (Axelton, USDA For. Ser. Res. Pap. INT-40. 1967; Gen. Tech. Rep. INT-12. 1974; Gen. Tech. Rep. INT-33. 1978). Yet only three of these make note

of immature cone color. For the cone color of 20 trees in Idaho, Maki (J. For. 38:55–60. 1940) reported 15 percent light (green to yellow-green), 50 percent dark (purple), and 35 percent medium (between green and purple). Krugman and Jenkinson (USDA Handb. 450. 1974) record vars. *arizonica* (Engelm.) Shaw and *scopulorum* Engelm. as green and var. *ponderosa* as green to yellow-green, rarely purple. Critchfield and Allenbaugh (Madroño 18:63–64. 1965) record only green-colored cones from the Sierra Nevada, but I observed trees with purple cones in northern California and southern Oregon. In 1976, in the South Warner Mountains of Modoc County, California, I noticed a decided increase in the frequency of purple cones with increased elevation.

A good crop on ponderosa pine in northern California and southern Oregon in 1978 provided the opportunity to study immature cone color more carefully. This was undertaken: (1) to test for correlations of cone color with other characteristics of ponderosa that vary in this region; (2) to determine whether cone color could be a marker for some economic criterion; (3) to understand better the relationship of ponderosa to other pines.

In 1978, cone color was recorded in mid-August for 33 locations (Fig. 1). Roadside positions that gave a view of a number of cone-bearing trees with front-lighting by the sun were selected. The crowns were scanned with binoculars and the cone color of each tree was classified into three categories. The color classification and nomenclature system of Kornerup and Wanscher was used (Politiken Forlag, Copenhagen. 1974) as follows—light (green to yellow-green, 28 and 29 A&B 6–8), medium (red to pale red, 8 and 9 B&C 6–8), dark (purple, 11 and 12 E&F 7–8). All cones on a tree were of one color class. Cones attacked by insects or that will abort are more nearly true pink and lack green pigment. Such cones are smaller and scattered throughout a tree among cones falling into one of the three basic classes. Any tree with cones not distinctly purple or green to yellow-green was placed in the intermediate category.

A series of viewing sites was used until 100 cone-bearing trees had been classified. This usually was accomplished in less than 1.5 km. At three sites only 50–75 trees could be viewed and classified easily because of the scattered location of cone-bearing trees. Each series was considered a plot. Though ponderosa pines have irregular cone crops, most trees in many locations had maturing cones in 1978; and it was assumed that the cone-bearing trees were representative of the area.

Each plot was placed into one of five groups on the basis of the frequency of trees in each of the three classes of cone color (Fig. 1). Virtually all trees in Group 1 plots had trees with only light-colored cones; less than 50 percent of the trees in Group 5 plots had light colored cones. Groups 2, 3, and 4 were gradations between 1 and 5.

The frequency of trees with medium and dark cones increased from south to northeast in the study area (Fig. 1). Group 1 and Group 2 plots were nearly all west of the Sierra Nevada-Cascade crest; Group 3, 4, and 5 plots were found only east of the crest.

Elevation may be associated with the shift in cone color in parts of the region. This possibility is shown best by the three plots in the South Warner Mts. at the headwaters of the Pit River (Fig. 1:A). The Group 3 plot there was at about 1800 m; the Group 4 plot at about 2100 m; and a Group 5 plot at about 2400 m. The next three plots along the Pit River (Fig. 1:B) reinforce the relationship of cone color to elevation. A Group 4 plot was at about 1500 m; two Group 3 plots to either side were between 1200 and 1500 m. Ponderosa pine is not abundant above 1800 m in this region, but I hypothesize that higher elevation stands generally will have higher frequencies of darker cones.

An elevational shift from green to purple was found by Sturgeon and Mitton (Amer. J. Bot. 67:1040–1045. 1980) for immature cones of white fir (*Abies concolor* [G. and G.] Lindl.) in southern Colorado. They reported only two colors, green and purple, and did not report geographical variation. They conclude that purple pigment functions in thermoregulation at high elevations.

Xylem monoterpene composition is associated with shift in cone color in that it changes abruptly in the general area of the study; 3-carene increased significantly while β-pinene, limonene, and α-pinene decreased significantly from south to north and east in northern California and southern Oregon (Smith, USDA Tech. Bull. 1532. 1977).

Sturgeon (Evolution 33:803–814. 1979), in an intensive study in the area, found the shift
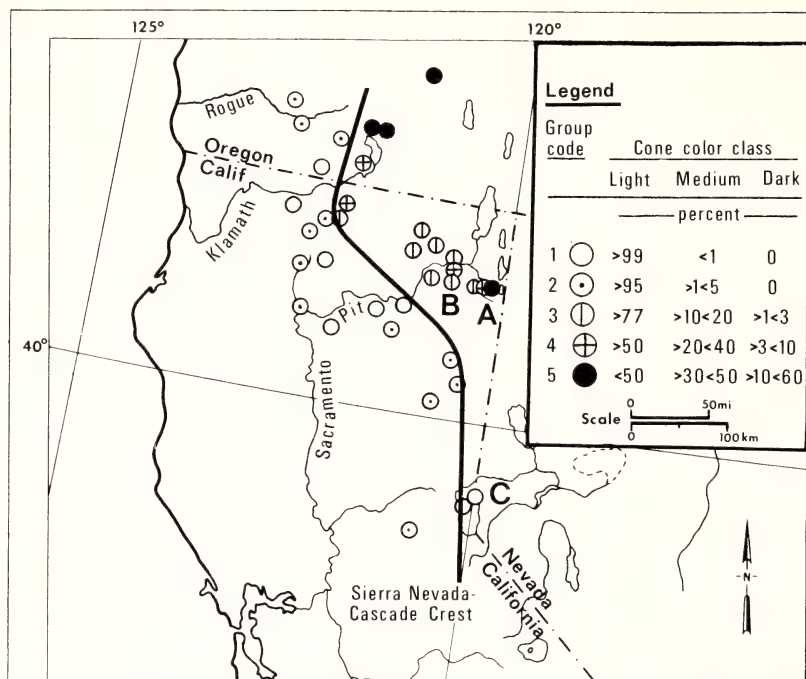
Fig. 1. Stand classification of ponderosa pine in northern California and southern Oregon for immature cone color. A. Three sites near headwaters. B. Three sites along the Pit River. C. Localized epidemic of mountain pine beetle in 1957–1959.

to occur generally at the Cascade Crest. Because data suggest that changes in resin composition are associated with cone color, three plots at the headwaters of the Pit River (Fig. 1:A) were analyzed for both characteristics simultaneously. The average monoterpene composition was essentially the same as that reported earlier (Smith, Madroño 21:26–32. 1971) but there was no consistent association with cone color. Trees with light-colored cones at the lowest elevation had the same approximate composition as trees with dark colored cones at the highest elevation and conversely. Resin composition and cone color appeared to be independent.

The susceptibility of ponderosa pine to the attack of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) appears to shift in this same general region of California and Oregon. This insect historically has had a greater tendency to be epidemic in ponderosa pine east of the crest line (Miller, USDA For. Ser. File Rep. 1920; Eaton, J. For. 39:710–713. 1941). There have been no epidemics in ponderosa pine west of the crest line. This association probably does not imply causality because many variables other than monoterpene composition can influence the severity of bark beetle epidemics.

Speculations on the evolutionary relationships of ponderosa, particularly with Jeffrey pine (*P. jeffreyi* Grev. and Balf.) and Washoe pine (*P. washoensis* Mason and Stockwell), have been discussed by Haller (Madroño 16:126–132. 1961) and Wang (USDA For. Serv. Res. Pap. WO-24. 1977). Haller (1961) first concluded that Washoe pine arose through hybridization between Jeffrey pine and the Rocky Mountain variety of ponderosa pine (var. *scopulorum*). Later (Haller, Proc. Amer. Bot. Soc. 52:646. 1965), he suggested that Washoe pine arose from hybridization of var. *ponderosa* with var. *scopulorum*.

Both dark cone color and high proportions of 3-carene are characteristic of Washoe pine (Smith, 1971). I therefore conclude tentatively that at one time Washoe pine occupied many higher-elevation sites throughout northeastern California and southern Oregon. It has been replaced slowly by ponderosa pine. The process of hybridization between the two has produced ponderosa pines with dark- and medium-colored cones and with high 3-carene resin.

Color of immature cones may have more than one cause. It is possible that the hybridization of ponderosa and Washoe pine may have been the cause in northeastern California while having been selected for independently in southern Oregon. Sturgeon and Mitton's similar cone-color results with *Abies* (1980), however, suggest that dark-colored cones are somehow adaptive at higher elevations and may be selected for independently in different lineages. Haller's (1965) views of the ancient range and origin of Washoe pine are nevertheless consistent with the hybridization hypothesis.—RICHARD H. SMITH, Pacific Southwest Forest and Range Experiment Station, P.O. Box 245, Berkeley, CA 94701. (Received 17 Mar 1980; accepted 12 Jan 1981; final revision received 17 Feb 1981.)

REVIEWERS OF MANUSCRIPTS

Many people have contributed to the preparation of volume 28, in particular James C. Hickman, who served as associate editor during my initiation, and the editorial board members. Dr. Sterling Keeley, my colleague at the Natural History Museum in Los Angeles, has been particularly helpful. Reviewers of manuscripts are essential in maintaining the quality of any scientific journals, and the thoughtful, constructive criticisms of those listed below is gratefully acknowledged.

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EDITOR'S REPORT FOR VOLUME 28

Between 1 Jul 1980 and 30 Jun 1981, 66 manuscripts were received. Sixty-one percent of the submissions were articles; 23 percent were noteworthy collections; and 16 percent were notes and news. Their current statuses are as follows: in review (19 articles, 3 noteworthy collections, 4 notes and news); being revised by authors (6, 3, 1); accepted and awaiting publication (9, 4, 2); published in volume 28 (10, 11, 3). In addition, 17 articles, 4 noteworthy collections, and 6 notes received before 1 Jul 1980 were published in volume 28. Of the material appearing in volume 28, 54 percent represented articles, 33 percent noteworthy collections, and 12 percent notes and news. Only two papers were rejected.

A smooth transition between editors was possible because of the carefully organized procedures of the former editor, Dr. James C. Hickman. Madroño conventions are somewhat complicated, and because of Jim's meticulous attention to detail and his typed guidelines, the assumption of these duties was a pleasure rather than a task. On behalf of the Society, I want to express here my deep appreciation to Jim for this help.

Manuscript submissions have been slightly behind those of 1980, but time from submission to publication is now about one year. This appears to be a fortuitous compromise between the need for quick publication and the editor's need for a slight backlog. Most reviewers have been inordinately prompt in returning manuscripts, and authors have been very good about returning their revisions. Thus, there is a slight decrease over the 1980 season in the number of manuscripts out for revision. However my six-week absence this spring allowed a manuscript build-up so that the number of manuscripts now in review is larger.

Noteworthy collections continue to be popular items to submit, but increasing press costs are forcing a change in the format for the appearance of this sort of data. Specifications will appear in a future issue of Madroño.

As was the case with Jim, I shall continue to welcome suggestions and criticisms from members.

C.D.   8 Jul 1981

Dates of Publication of MADROÑO, volume 28

No. 1, pp.	1–48:	12 February	1981
No. 2, pp.	49–100:	3 June	1981
No. 3, pp.	101–192:	31 July	1981
No. 4, pp.	193–279:	8 December	1981

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Classified entries: major subjects, key words, and results; botanical names and plant families (new names are in **boldface**); geographical areas; reviews. Incidental references to taxa (including lists and tables) are not indexed separately. Species appearing in Noteworthy Collections appear under plant family and state or country. Authors and articles are listed alphabetically in the Table of Contents.

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Adventitious rooting in Coastal Sage Scrub dominants, 96.

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CALIFORNIA BOTANICAL SOCIETY

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PECCATA, ERRATA, ET CONFUSIONES

In addition to the phenomenally small number of typographical errors in Volume 29, most of which were of utterly no significance, the "received—accepted" data were omitted from all the articles in issue no. 1, for Jan 1982. No one has complained about this, but my apologies anyway.

Benedict and Major: received 18 May 1980; revision accepted 11 Nov 1980.

Meinke and Constance: received 6 Jan 1981; revision accepted 23 Mar 1981.

Wendt and Todsen: received 17 Feb 1981; revision accepted 26 Mar 1981.

Minnich: received 25 Feb 1981; revision accepted 1 May 1981.

Cook: received 27 Mar 1980; revision accepted 29 Jul 1980.

Conard and Radosevich: received 11 Jul 1980; revision accepted 27 Dec 1980.

John Strother also informs me that he would have preferred the illustration in his paper (*Dicoria,* Fig. 1, 29(2)) to have been rotated 90° counterclockwise. He is right. It would have been better and would have taken less space.

We also apologize for the collating error that resulted in a number of deletions in Madroño copies sent to the Bay area.

MADROÑO

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A WEST AMERICAN JOURNAL OF BOTANY

Contents

A PHYSIOGRAPHIC CLASSIFICATION OF SUBALPINE MEADOWS OF THE SIERRA NEVADA, CALIFORNIA

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Abstract

Sierran subalpine meadows in the upper Kern River drainage are classified based on their physiographic characteristics. Two main divisions are recognized: meadows with predominantly vegetated margins (Type I), and meadows with predominantly sandy margins (Type II). Meadows of both types occur in a variety of topographic positions. Geographic distribution, sandy margins, hydrology, and geologic stability of the various meadow types are discussed.

Meadows constitute an important element of the subalpine zone of the Sierra Nevada of California. Previous research on Sierran subalpine meadows has concentrated primarily on an assessment of their condition and trend in a range management context (Armstrong 1942, Bennett 1965, Sharsmith 1959, Strand 1972, Sumner 1948). In the 1960's an ecosystem analysis was undertaken that compiled detailed data on various components of the meadow ecosystems in the Rock Creek drainage, Sequoia National Park (Hubbard et al. 1965, Hubbard et al. 1966, Harkin and Schultz 1966, Leonard et al. 1967, Leonard and Johnson 1969, Griffen et al. 1970). Without a meadow classification this information is difficult to synthesize, and cannot readily be used outside of the area where it was generated. Other data on Sierran meadows are scattered through the literature (Klickoff 1965, Pemble 1970, Beguin and Major 1975, Burke 1980, Ratliff 1979).

Our research aims at understanding the dynamics of Sierran subalpine meadow ecosystems through plant community analysis. The objectives are: 1) description and classification of subalpine meadow vegetation; 2) correlation of vegetation types and species distribution with environmental factors; 3) study of the origins and successional sequences of meadow ecosystems; and 4) effects of meadow origins on meadow ecosystems (Benedict and Major 1979). To meet these objectives we have developed two meadow classifications: a physiographic classification of whole meadows, and a vegetation classification within meadows. This paper presents the physiographic classification of subalpine meadows. A descriptive classification of an ecosystem is an

important first step in understanding an ecosystem because it provides an organizing structure for future information.

Field work was carried out during the summers of 1977, 1978, and 1979. Observations and descriptions of the physiographic character- istics of subalpine meadows seen during this period were recorded (i.e., meadow location in relation to water source, presence and lo- cation of springs and seeps, drainage patterns, glacial deposits, bed- rock outcrops, etc.). Vegetation sampling, environmental measure- ments, and soil coring were done concurrently for other aspects of this project. Field work was concentrated in the southern part of Sequoia National Park and adjacent U.S. Forest Service lands, although var- ious meadows throughout the southern Sierra were examined (Fig. 1).

Description of Study Area

The Sierra Nevada is a tilted fault block with a gradual slope to the west and a steep escarpment on the east. The crest runs in a north- south direction and includes Mt. Whitney (4418 m), the highest peak in the contiguous United States. In the southern Sierra, the Kern River runs north-south roughly parallel to and west of the main crest (Fig. 1). On the west side of the Kern River basin is the Great Western Divide with peaks to 4165 m (Midway Mountain). The river follows a fault in its upper portions (Lawson 1904, Webb 1946) forming a canyon 730 m deep opposite Whitney Creek.

The meadows examined for this study occur between 2800 m and 3530 m primarily along the Whitney Creek and Rock Creek drainages. At these elevations the forest vegetation consists primarily of lodgepole pine (*Pinus contorta* subsp. *murrayana*) stands and foxtail pine (*Pinus balfouriana*) stands. The lodgepole pine forests are generally open with sparse understory vegetation. They occur along river bottoms, in gla- ciated valleys, and on some slopes. The foxtail pine forests are very open with little understory vegetation. They occur on steep slopes (both bedrock and morainal), and on many of the ancient erosion surfaces described by Lawson (1904) and Matthes (1950, 1962).

Physiographic Classification

In the Kern River drainage, within and just south of Sequoia Na- tional Park, there are two broad types of subalpine meadows: those with predominantly vegetated margins and continuous vegetation (Type I, Fig. 2); and those with predominantly sandy margins and sparse vegetation (Type II, Fig. 3). Type I meadows typically have dense meadow vegetation bordering directly on forest vegetation (al- though there can be distinct differences in the species composition along the forest-meadow ecotone), occur in areas glaciated relatively recently (probably late Wisconsin), and are surrounded by a forest composed mainly of *Pinus contorta* subsp. *murrayana,* at least
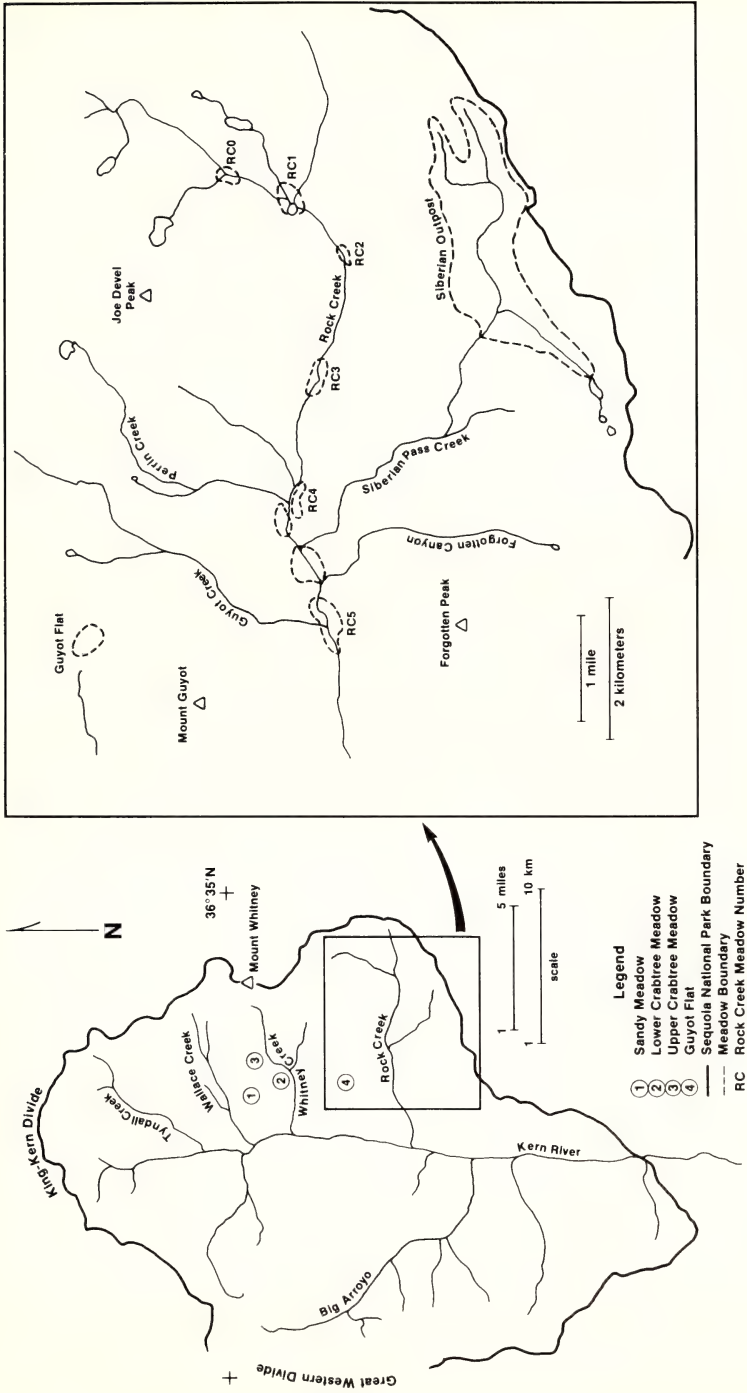
Fig. 1.   Location of study sites in Sequoia National Park.
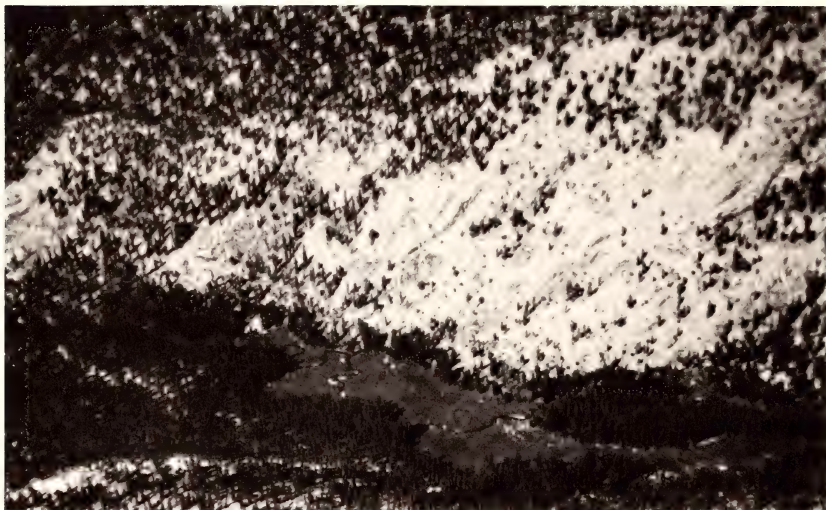
Fig. 2. Rock Creek Meadow 3. Example of a Type I subalpine meadow with vegetated margins.

immediately adjacent to the meadow. Type II meadows typically have an area of granitic sand between the forest and the dense meadow vegetation, and vegetation of the sandy margins is composed of distinctive plant communities that usually are not associated with Type I meadows. The sandy margins are surrounded by forest composed of
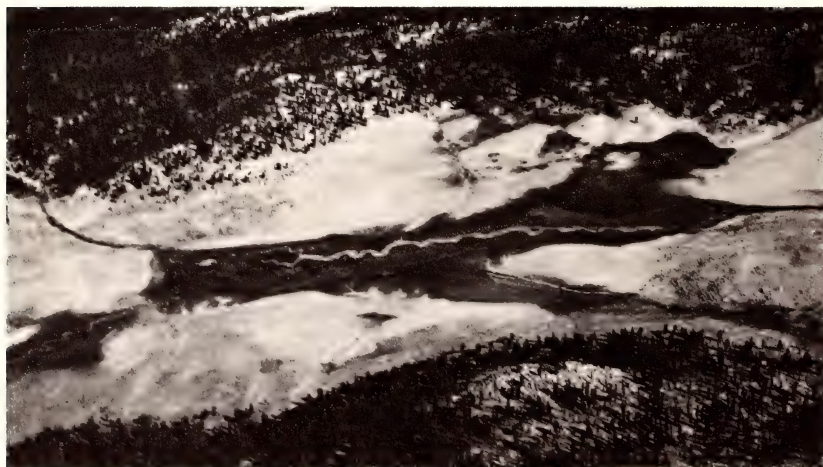
Fig. 3. Siberian Outpost. Example of a Type II subalpine meadow with sandy margins.

TABLE 1. PHYSIOGRAPHIC CLASSIFICATION OF SELECTED MEADOWS SHOWN ON MT. WHITNEY QUADRANGLE (15′) AND KERN PEAK QUADRANGLE (15′).

Code		Description	Example	Elev. (m)
I		Predominantly vegetated margins		
	A	Topographic basin		
	1	Bedrock	Lower Crabtree Meadow	3148
			Rock Creek Meadow #1	3185
			Rock Creek Meadow #2	3145
	2	Moraine	Upper Crabtree Meadow	3184
			Rock Creek Meadow #3	3048
			Wright Creek Meadows	3292–3353
	B	Slope		
	1	Lateral moraine	Rock Creek Meadow #4	2426
			Lower Rock Creek	2804–2426
	2	Bedrock	Trail Crew Stringer, Rock Creek	3185
	C	Stream	Army Pass Creek Meadows	3292–3414
II		Predominantly sandy margins		
	A	Basin	Siberian Outpost	3292
			Big Whitney Meadow	2450
			Guyot Flat	3243
	B	Stream	Sandy Meadow	3200–3231

either pure foxtail pine (*Pinus balfouriana*) or a mixture of foxtail and lodgepole pine and occur in areas of relatively more ancient glaciation (early Wisconsin and/or pre-Wisconsin) or in areas that have not been glaciated.

Type I meadows are found in several different physiographic positions (Table 1, Fig. 4). They occur in topographic basins (Type IA) that result from either bedrock configuration (Type IA1) or from damming by a recessional or lateral moraine (Type IA2). In these situations water accumulates in the area occupied by the meadow. Type I meadows can also occur on slopes where ground water comes to the surface as springs or seeps (Type IB). This can result from water emerging near the base of a lateral moraine (Type IB1) or from water forced to the surface by the bedrock configuration (Type IB2). It is often difficult to determine in the field which of these alternatives has contributed to the formation of a particular meadow because the bedrock may not have a surficial outcrop and/or the bedrock configuration might force water to the surface beneath a lateral moraine. Type IB meadows were described by Muir (1894) as hanging meadows. Type I meadows also occur along streams and have been called stringer meadows (Type IC). These narrow meadows are found in forested areas and amidst
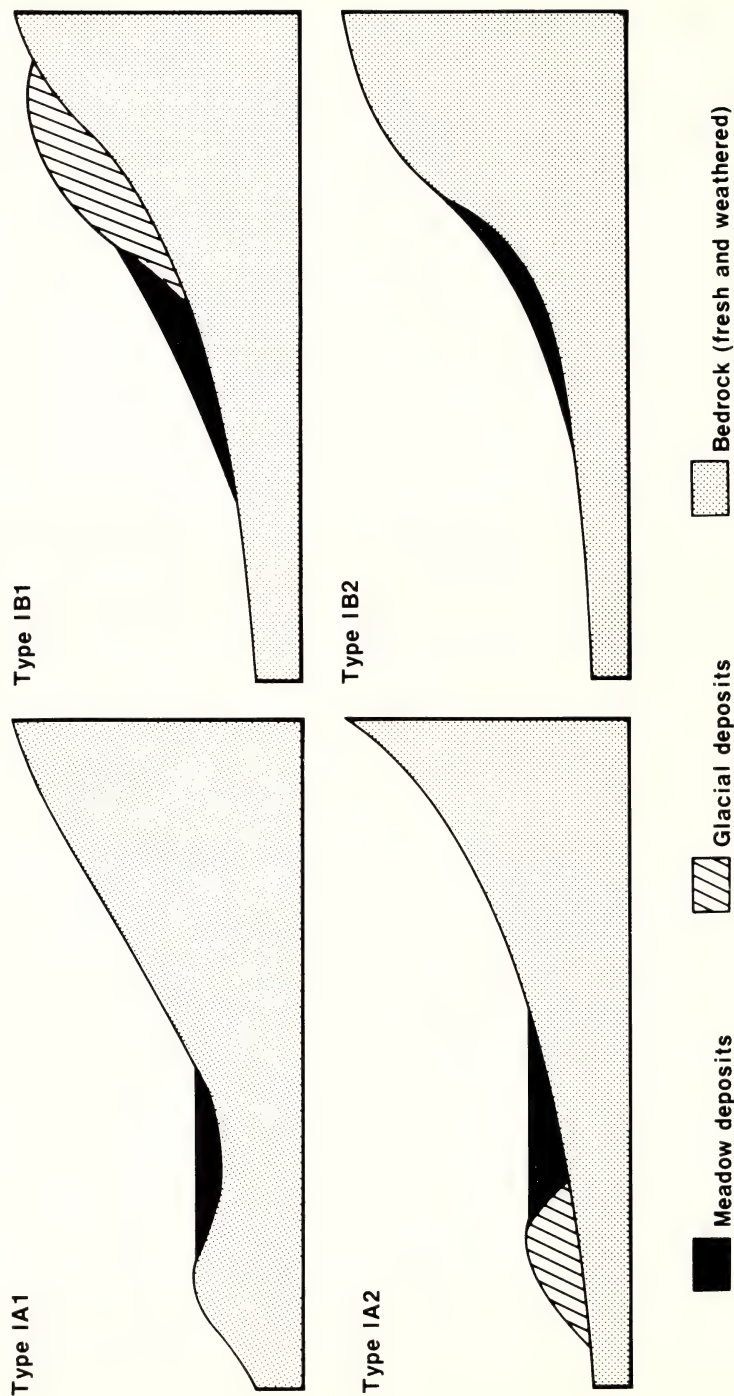
FIG. 4. Diagrammatic examples of selected meadow types.

boulders. Type IC meadows result from a variety of conditions, all of which have in common that the stream is the main source of water although springs and/or seeps may also contribute. At Sagehen Creek in the northern Sierra, bogs result from logs damming the stream (Rae 1970).

Type II meadows occur in large basins (Type IIA) or along stream courses (Type IIB). Meadows in large basins are more common than meadows along stream courses. Type II meadows have not been described in detail previously. Webb (1952) briefly mentions their existence in the southern Sierra. As with Type I meadows, water is present in areas of dense meadow vegetation. The sandy margins, though, are arid.

DISCUSSION

Geographic distribution. So far, Type II meadows have been found only in the extreme southern high Sierra. Their distribution is positively correlated with the southern limits of glaciation in the Sierra, which corresponds roughly with the southern boundary of Sequoia National Park (Webb 1952, Clague et al. 1973). At these southerly latitudes, the various Wisconsin and pre-Wisconsin glacial stages are spatially separated. Farther north, areas glaciated in pre-Wisconsin glacial periods are rare in the subalpine zone, and the areas glaciated by the various Wisconsin stages often overlap completely except at their lower boundaries (which are often outside of the subalpine zone). Type II meadows are also correlated with the almost pure, mature foxtail pine forests that occur in the southern Sierra (Rundel et al. 1977).

Type I meadows are common throughout the Sierra at different latitudes and elevations. They are the dominant and most diverse physiographic meadow type in the Sierra. The distribution of the subtypes of Type I meadows has not yet been investigated.

Sandy margins. The origins of the sandy margins of Type II meadows are unclear at present. One hypothesis is shown diagrammatically in Fig. 5. If this hypothesis is correct, the sand and gravel deposits should show bedding, and the ancient meadow surface should be identifiable under the sand deposit. In Big Whitney Meadow (Type II) bedded sand deposits have been found in a highly eroded area with gully formation, suggesting a fluvial origin for the deposits. In Siberian Outpost (also Type II), there are several stream channels cutting down through the sand deposits on the north side of the meadow. At the floor of one of these is a meadow surface that has a stream gully forming in it. This gully enlarges downstream until it joins with the main part of the meadow. The meadow surface, which is being eroded, may represent the old meadow surface that was buried, uncovered by the stream, and is now being eroded. An alternative explanation
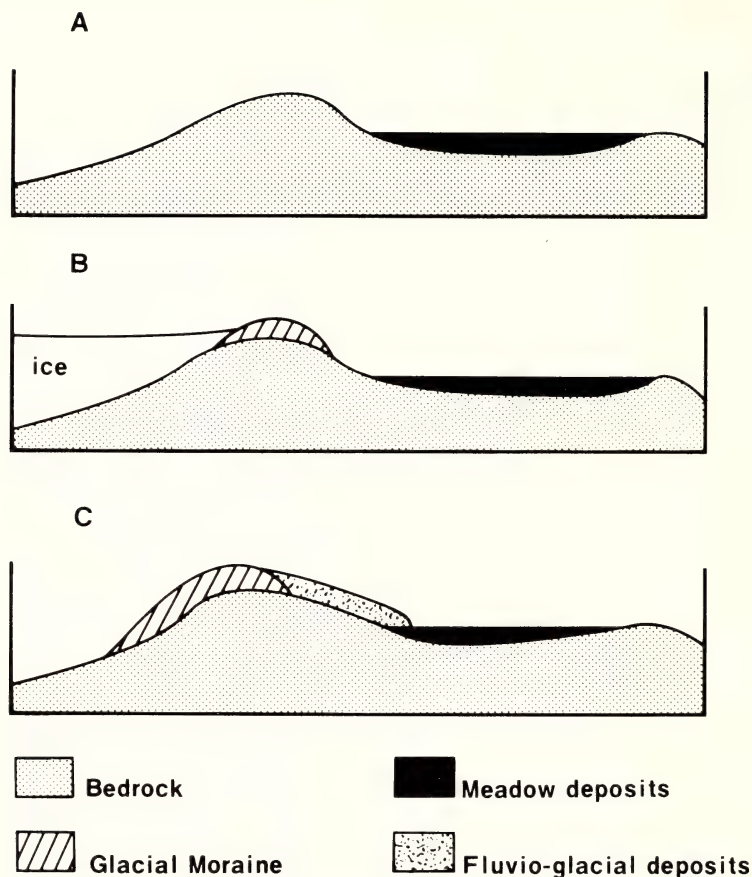
Fig. 5. Origin of sandy margins in Type II meadows. Sandy margins were deposited during late Wisconsin glaciation by debris-laden water from valley glaciers. A. Before early Wisconsin or pre-Wisconsin glaciation, meadow forms in shallow basin on high plateau between drainages. B. Late Wisconsin ice is predominantly in valleys. Lateral movement of debris-laden water from glacier deposits sand, gravel and boulders on meadow surface. Meadow basins may have flooded because of ice blockage at lower end. C. Present state. Areas glaciated in late-Wisconsin time are delineated by moraines, sand deposits, and meadow surface. Diagrams represent Rock Creek drainage (left side), left lateral moraine of Rock Creek Glacier, and Siberian Outpost (right side), Sequoia National Park.

is that it represents renewed erosion of the meadow surface caused by either natural events (e.g., changes in the stream gradient) or over-grazing of the area by sheep and cattle in the late 1800's (DeBenedetti and Parsons 1979) resulting in a second, lower surface. Another hypothesis for the origin of the sandy margins is that the sand was deposited in late Pleistocene lakes that may have occurred in these basins.

Another enigma is the maintenance of these sandy margins as barren areas without forest cover or typical meadow vegetation. As will be shown in a future paper on Sierran subalpine meadow vegetation, these sandy margins have a distinct plant community not found associated with Type I meadows. It is dominated by *Calyptridium umbellatum, Eriogonum incanum,* and *Stipa occidentalis.* Why these sandy margins are not covered by forest trees is not known. One possibility is that these areas are too dry. Another is that they have too high a frequency of nights when needle-ice formation churns the soil, possibly due to radiative cooling and/or cold air drainage. Needle-ice formation was observed in Siberian Outpost throughout the summer of 1979.

Hydrology.   Type I and Type II meadows are correlated with different hydrologic patterns that result from the age and weathering characteristics of the different surfaces. In areas with Type II meadows, the surface is highly weathered (usually to granitic sands). As a result most precipitation percolates deeply into the weathered substrate and becomes available at the surface only in basin centers or at the bottom of slopes. In areas with Type I meadows the surface is less weathered and has much exposed bedrock. Precipitation does not percolate as deeply; there is more overland flow (e.g., streams); and ground water emerges frequently at the surface.

Geological stability.   Meadow stability is a nebulous concept that is best divided into two categories based on the time scale involved, biological and geological. Biological stability refers to the persistence and recovery of the biological component of a meadow ecosystem (Pickford and Reid 1942), and is beyond the scope of this paper. Geological stability refers to the persistence of the geological conditions that create an environment favorable for meadow formation. Geological stability is directly related to the different physiographic meadow types.

The geological stability of Type I meadows varies in the following ways. Bedrock basin meadows (Type IA1) are very stable because of the slow rate of stream erosion and the low probability of breaching the bedrock dams. In addition it is virtually impossible for the bedrock dam to be destroyed by natural catastrophic events (e.g., massive floods). In contrast, meadows in basins formed by morainal materials (Type IA2) are less stable. Streams constantly erode the moraine and catastrophic events increase erosion rates. Once the dam is breached, the meadow progressively dries out and may be replaced by forest vegetation. Invasion by forest can be rapid, as evidenced by the rate at which lodgepole pines have colonized Osgood Swamp near Lake Tahoe after the morainal dam was artificially breached. As opposed to Type IA (basin meadows), the long-term stability of Type IB (slope meadows) is controlled by other factors. Because these meadows are

maintained by water from springs and seeps, one way to destroy or disrupt them is to alter the position of or flow from the source. This would happen only if the landscape were altered by man or glacial activity, or if climatic changes altered the precipitation and hydrologic patterns of the region (e.g., Wood 1975).

The stability of Type II meadows is poorly understood. It is partly dependent on factors similar to those important in Type I meadows, such as spring/seep patterns, stream dams, and erosion rates. Because the dynamics of the sandy margins are not known, it is difficult to understand how these margins affect meadow stability. Further research is needed to answer these questions.

An excellent example of contrasting types of stability is provided by comparing Upper and Lower Crabtree Meadows in the Whitney Creek drainage. Upper Crabtree Meadow is enclosed by glacial moraines and consists of three distinct sections. The eastern section is relatively flat, very wet, and has vegetation characteristic of wet areas. The southern section is raised above the main part of the meadow by approximately 1 m and is separated from it by a medial moraine. This section is extremely wet with numerous small ponds and is characterized by *Carex rostrata*. The western section is dryer and slopes downstream to the moraine dam. In this section there is a definite meandering stream channel. The stream has cut through the moraine to the extent that the western or lower section of the meadow is drying out. The geological conditions causing the formation of the meadow are therefore not stable over a long period of time.

In contrast to this, Lower Crabtree Meadow is formed by a bedrock bar across the downstream side of the meadow. Species such as *Carex rostrata* and *C. scopulorum* dominate the vegetation. There are two breach points, one of which is currently occupied by Whitney Creek. The stream is cutting into the bedrock at a much slower rate than into the moraine at the lower end of Upper Crabtree Meadow. As a result this meadow is geologically more stable than Upper Crabtree Meadow.

Further research is needed to explore and document these ideas. This will greatly increase our knowledge of and provide useful information for the management of Sierran meadow ecosystems.

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LOMATIUM OREGANUM AND L. GREENMANII (UMBELLIFERAE), TWO LITTLE KNOWN ALPINE ENDEMICS FROM NORTHEASTERN OREGON

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ABSTRACT

Lomatium oreganum and *L. greenmanii,* two rare species endemic to the higher Wallowa and Blue Mountains of Oregon, are morphologically and ecologically separate and behave as distinct taxa. The taxonomic affinities of these plants are not well known, but we speculate that they include ties to several *Lomatium* species of the Basin and Range province of Utah, Nevada, and eastern California.

In the lengthy list of potentially threatened or endangered Oregon vascular plants (Siddall et al. 1979) are seventeen members of the large genus *Lomatium*. Two of these, *L. oreganum* Coult. & Rose and *L. greenmanii* Mathias, are of particular interest. *Lomatium oreganum* occupies a few small, scattered sites in the Wallowa Mountains and the nearby Elkhorn Ridge of the Blue Mountains. *Lomatium greenmanii* is endemic to the Wallowas and is known only from the type collection of 1900 and from a single recently discovered locality. Information about the type locality is scant, and speculations concerning its precise location have never been resolved. Both taxa are restricted to the alpine summits of these ranges (Mason 1975); this may have saved them from extinction, but it has also prevented them from becoming adequately known.

The two species were first collected by William Conklin Cusick, pioneer plant explorer of the region, in 1886 and 1900, respectively. *Lomatium greenmanii* was not recognized as a distinct entity until much later (Mathias 1938) and was not rediscovered until 1975. Cronquist (1961, p. 555) suggested that "further collecting may well show *L. greenmanii* to be merely a glabrous form of *L. oreganum.* One does not expect to find two species as similar as these in the same habitat and local area."

Vegetatively, these species are very reminiscent of certain members of the largely cordilleran genera *Aletes, Cymopterus, Oreoxis, Podistera,* and *Musineon,* a number of which are essentially indistinguishable in the (frequent) absence of ripe fruits. The junior author was

struck by the strong similarity in foliage between flowering specimens of *Cymopterus nivalis* S. Wats. and *Lomatium greenmanii* and, in seeking to obtain mature fruits for comparison, unintentionally spread the suggestion that the two might even be conspecific. They are not.

The senior author has been successful in securing adequate material of both *L. oreganum* (Fig. 1) and *L. greenmanii* (Fig. 2), which now permits a reassessment. By their possession of dorsally compressed fruits with prominently winged lateral (marginal) ribs and filiform, unwinged or scarcely winged dorsal ribs, both species are properly assigned to *Lomatium*. The two are similar in habit—caespitose development from a fibrous multicipital caudex surmounting a deep taproot, oblong to lanceolate pinnately dissected leaves, reduction of the inflorescence to a solitary terminal umbel with only 1–3 fertile umbellets, each bearing 1–6(–8) short-pedicellate fruits, yellow flowers, and dorsally flattened fruits. Additionally, they are phenologically equivalent, blooming in July and fruiting in August.

Despite the overall resemblances, which are heightened by the rare occurrence of glabrous individuals of *L. oreganum* among the "normal" pubescent ones, a significant number of differences exist, as indicated in Table 1. Unfortunately, no cytological data are available and presumably would be difficult to obtain in view of the general infrequency of flowering and the rugged, remote nature of the few known localities.

Although both species may be broadly characterized as alpine, there are habitat dissimilarities that merit comparison and discussion.

Lomatium oreganum frequents harsh, formerly glaciated sites in scoured cirques and on ridges of timberless zones where ice and snow lie late in the season. Its altitudinal range is ca. 2400–2950 m. The substrate is a coarse, decomposed granitic "sand" or often (especially in the Blue Mountains) a loose granodiorite talus. The majority of closely associated species are circumboreal or exhibit wide distributions in the western cordillera. These include *Selaginella watsonii, Oxyria digyna, Arenaria capillaris, Silene acaulis* var. *exscapa, Draba densifolia, D. paysonii* var. *treleasii, Smelowskia calycina, Sedum roseum, Saxifraga bronchialis* var. *austromontana, Ivesia gordonii, Sibbaldia procumbens, Luzula parviflora*, and *Carex* spp. It is worth noting that in the Blue Mountains *L. oreganum* is consistently found with *Geum rossii* and *Bupleurum americanum*, species quite rare outside their primary ranges in the Rocky Mountains. The latter taxon is not known elsewhere in the Pacific States.

Lomatium greenmanii must be interpreted from its single known population, which sporadically covers several acres at the summit of Mount Howard (2500 m) in the Wallowa Range. The physiography here is a mosaic of windswept knolls and ridges, with sparse subalpine forest interspersed by moist meadows. *Lomatium greenmanii* occupies the gentle, open slopes in thin, fine-textured soil often overlying pro-
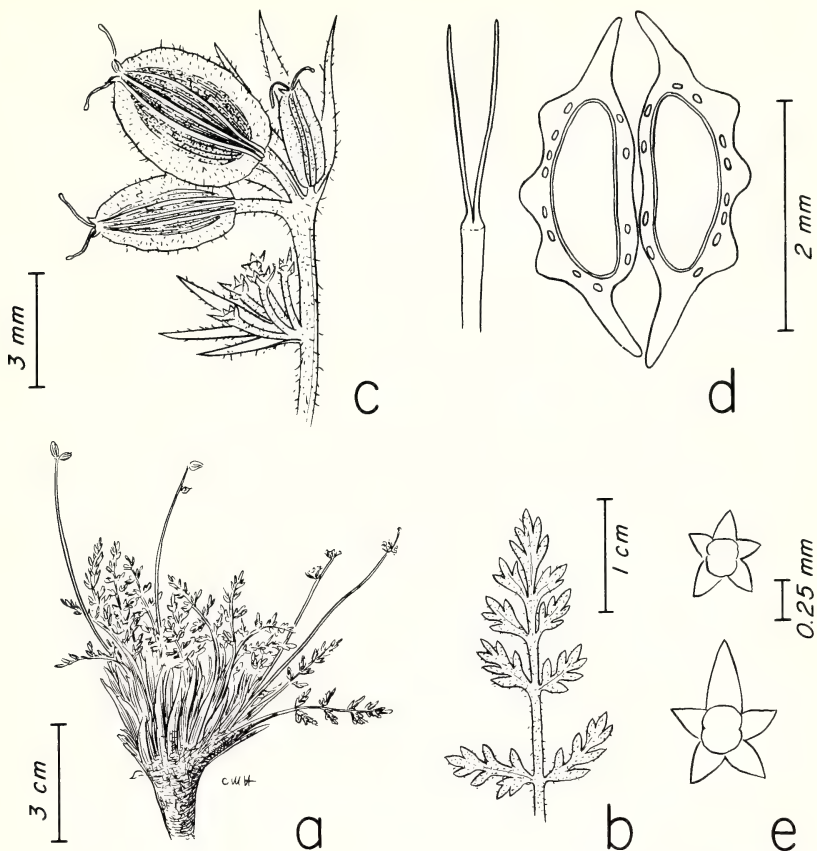
FIG. 1. *Lomatium oreganum.* a. Flowering and fruiting habit. b. Leaflet dissection.
c. Fruit. d. Carpophore and fruit transection. e. Calyx teeth.

truding granite fragments. Rarely, it is found in deeper soils at the
edges of subalpine meadows, although it appears unable to cope with
rigorous competition. Collectively, the plant associations here take on
a less boreal aspect than those inhabited by *L. oreganum.* Community
associates include widespread taxa such as *Spraguea umbellata, Eri-
ogonum ovalifolium, Arabis lyallii, Draba paysonii* var. *treleasii,* and
Ribes montigenum, as well as some of more regional distribution, such
as *Heuchera cylindrica* var. *alpina, Lomatium cusickii,* and *Aster
alpigenus.* Also associated are *Castilleja chrysantha* and *Erigeron
chrysopsidis* var. *brevifolius,* which are themselves localized, north-
east Oregon endemics.

   In summarizing the field data, some interesting comparisons can be
drawn. *Lomatium oreganum* is an inhabitant of glacial debris, accom-
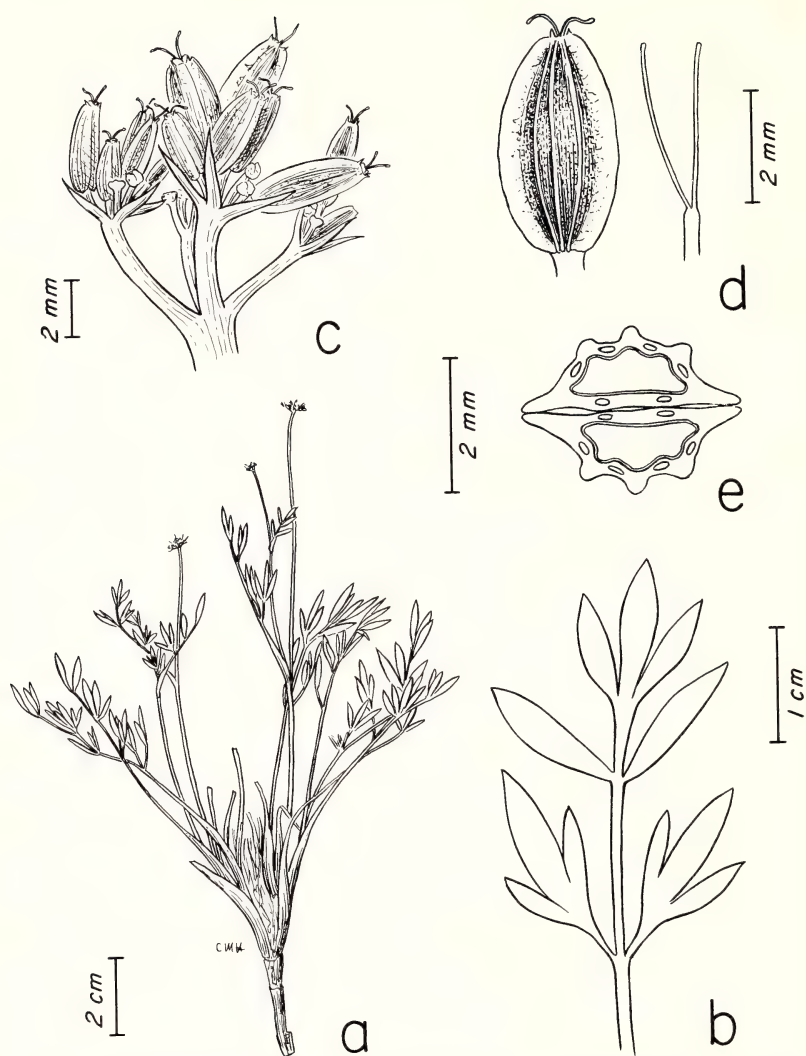
FIG. 2. *Lomatium greenmanii.* a. Flowering habit. b. Leaflet dissection. c. Fruiting umbellets. d. Mature fruit, with carpophore. e. Fruit transection.

panied by a congruous assemblage of familiar circumboreal as well as typically northern or Rocky Mountain taxa. This association is rare in Oregon and is considered a glacial relict. *Lomatium greenmanii* is found in a less severe alpine or subalpine situation, on a substrate displaying fewer traces of evident glacial scarring. Its associates com-

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *Lomatium oreganum* AND *Lomatium greenmanii*. (See also Figs. 1 & 2.)

Character	*L. oreganum*	*L. greenmanii*
Habit	Strictly acaulescent, plants usually matted	Distinctly caulescent, with 1 or 2 stem leaves; plants not matted
Vesture	Softly short-pubescent (rarely glabrous) throughout	Glabrous, except slightly scaberulous on leaf margins and veins
Leaves	Oblong, the divisions obtuse to acutish, often crowded	Lanceolate, the divisions lanceolate-ovate, acuminate, usually remote
Calyx teeth	Evident, often unequal	Minute and inconspicuous, subequal
Vesture of ovaries and fruit	Short-puberulent (rarely glabrous)	Completely glabrous
Fruit dimensions	Oval-elliptic, 4.5–6 mm long, 2–3 mm broad	Ovate, 3–3.5(–5) mm long, 2–2.5(–3.2) mm broad
Oil tubes	Small, 1–3 in the intervals, usually 4 on the commissure	Large, solitary in the intervals, 2 on the commissure

prise a more heterogeneous mix, including boreal, Northwest regional, and locally endemic elements. Together these form a vegetation type not uncommon in this area at this elevation.

While these ecological observations shed little light on the degree of relationship of these *Lomatium* species, they do suggest that the times of their respective appearances in northeast Oregon and the events that led to the perpetuation of each may have been different. The Blue and Wallowa Mountains, although separated by less than 50 km at their nearest point, possess very dissimilar endemic floras. The existence of *L. oreganum* in both ranges, coupled with its particular habitat specificity, indicate that it is likely a relict itself. Its origin is unknown, as is the extent to which its hypothetical migratory route paralleled those of the known relicts with which it so closely associates today. The history of *L. greenmanii* is even less clear, and it will doubtless remain obscure until additional populations can be located and studied.

In addition to their resemblance to and possible affinity with each other, these two Oregon lomatiums are very similar to *L. minimum* Mathias of the Cedar Breaks and Bryce Canyon area in southwestern Utah. Perhaps this means only that most alpine Umbelliferae tend to resemble one another. Mathias (1932, p. 498) attributed to *L. minimum* a close relationship "to those species . . . referred by Coulter and

Rose to the genus *Cynomarathrum* . . . ." Although *Cynomarathrum* was regarded by Coulter and Rose (1900, p. 245) as "much nearer *Pteryxia* and *Pseudocymopterus*" by virtue of its evident calyx teeth, acaulescent habit, fibrous multicipital caudex, and mostly narrow and pinnately divided leaves, its species are now customarily referred to *Lomatium*. It is not difficult to believe that the Great Basin species *L. eastwoodae* (Coult. & Rose) F. Macbr., *L. latilobum* (Rydb.) Mathias, *L. megarrhizum* (A. Nels.) Mathias, *L. nuttallii* (A. Gray) F. Macbr., *L. parryi* (S. Wats.) F. Macbr., and *L. scabrum* (Coult. & Rose) Mathias may be evolutionarily allied with the two Oregon taxa. High-altitude forms of *L. nuttallii* (some of which have been regarded as specifically or varietally distinct under the epithet "alpinum"), *L. parryi,* and *L. scabrum* appear to illustrate how such dwarfs as *L. minimum, L. oreganum,* and *L. greenmanii* could have developed from inhabitants of the Basin and Range province of Utah, Nevada, and eastern California.

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A NEW VARIETY OF POLYGALA RIMULICOLA (POLYGALACEAE) FROM DOÑA ANA COUNTY, NEW MEXICO

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Abstract

Polygala rimulicola Steyermark var. **mescalerorum** Wendt and Todsen (Polygalaceae) is described from the San Andres Mountains in Doña Ana County, New Mexico.

The cliff-dwelling species *Polygala rimulicola* Steyerm. was long thought to be endemic to the Guadalupe Mountains of Texas and adjacent Eddy County, New Mexico (Hershey 1940, Correll and Johnston 1970). Todsen's (1973) report of the species from the San Andres Mountains of Doña Ana County, New Mexico, extended its known range 180 km to the wnw. Study of the species throughout its range shows the disjunct Doña Ana County populations to be differentiated sufficiently from the other known populations to be considered a distinct variety, separable from the typical variety by the following key (refer also to Figs. 1 and 2).

Keel-beak deltate or rounded in outline, often obscure, 0.1–0.3(–0.5) mm long, its length equal to or less than its diameter in the vertical plane at its junction with the keel-sac; seed-body (1.0–)1.1–1.5(–1.7) mm long . . . . var. *rimulicola*
Keel-beak linear or oblong in outline, 0.3–0.7 mm long, its length usually more than 1.5 times as great as its basal diameter; seed-body (1.4–)1.7–1.9 mm long . . . . var. *mescalerorum*

Polygala rimulicola Steyermark var. *rimulicola,* Ann. Missouri Bot. Gard. 19:390. 1932.
    Type: USA, TX, Culberson Co., Guadalupe Mts., Smith Canyon, exposed rock crevices, 1900 m, 20 Jul 1931, *Moore & Steyermark 3515* (Holotype: GH!; isotypes: CAS!, NY!, UC!, US!).
    The typical variety (Fig. 2) is known outside of the Guadalupe Mountains only from the Sierra Diablo, Culberson Co., Texas, where it was discovered by Samuel Sikes and Jackie Smith (now Poole) in 1973 (*Sikes & Smith 535* (LL)).
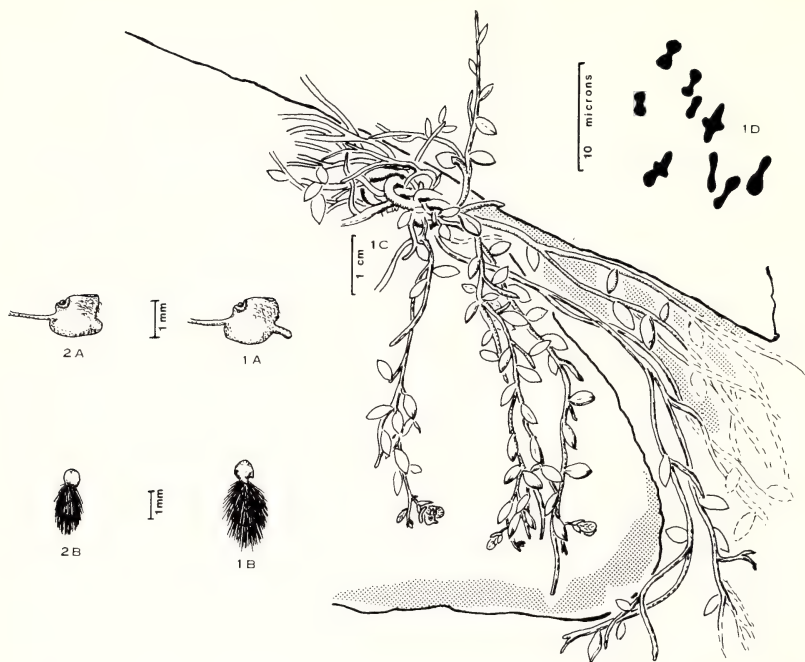
FIGS. 1–2.   FIG. 1. *Polygala rimulicola* var. *mescalerorum*. A. Keel-petal, showing
(left to right) basal claw (adnate to staminal sheath in situ), keel-sac, and cylindrical
keel-beak; B. Seed, showing aril (above) and pubescent seed-body; C. Habit, in lime-
stone crevices (from a photograph of the type population); D. Chromosomes (*Wendt &*
Todsen 370). FIG. 2. var. *rimulicola*. A. Keel-petal (note rounded beak); B. Seed.

Polygala rimulicola var. **mescalerorum** Wendt & Todsen, var. nov.

A var. typica rostro carinae lineari vel oblongo 0.3–0.7 mm longo,
vagina staminum ventraliter ad centrum et ad marginum pubescenti,
seminibus 2.8–3.2 mm longis, corpore seminis (1.4–)1.7–1.9 mm longo
recedit. Fig. 1.

Flowers 2.9–4.5 mm long; outer sepals lightly ciliate on lower half;
keel-beak linear to oblong in outline, 0.3–0.7 mm long, its length
usually more than 1.5 times as great as its basal diameter; staminal
sheath adaxially pubescent medially and near the margins; seeds (in-
cluding aril and pubescence) 2.8–3.2 mm long, body (1.4–)1.7–1.9 mm
long. $n = 9$. TYPE: USA, NM, Doña Ana Co., White Sands Missile
Range, on w. side of Tularosa Basin in San Andres Mts., e. slopes of
Black Mt., 32°31′N, 106°28′W, ca. 1600 m, in cracks of w.-facing
cliffs of sandy limestone, locally common, 4 Jul 1974, *Wendt & Todsen*
370 (Holotype: LL; isotypes: LL, NMC).

PARATYPE: USA, NM, Doña Ana Co., San Andres Mts., on ne.-facing limestone cliffs, ca. 1700 m, 18 Jun 1972, *Todsen 2258* (NMC).

A single individual of the type population yielded a chromosome count of $n = 9$ (Fig. 1D). The same number characterizes the typical variety (Wendt, unpub. data) and is the base number for sect. *Rhinotropis* (Wendt, unpub. data), to which *P. rimulicola* belongs.

Although Steyermark (1932), in his description of the species, and Correll and Johnston (1970) describe *P. rimulicola* as lacking a beak on the keel-petal, abundant material shows a small beak generally to be present in var. *rimulicola* (Fig. 2A). However, this structure is well developed only in the new variety.

Polygala rimulicola var. *mescalerorum* is known from only two very small populations on Black Mountain: the type population, and a second population ca. 0.5–1 km to the north. The new variety certainly should be considered rare and endangered. The name honors the Mescalero Apaches, who inhabited this area of New Mexico at the time of the coming of the Spaniards and who figure so prominently in its history and past and present culture.

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PSEUDOTSUGA MACROCARPA IN BAJA CALIFORNIA?

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ABSTRACT

A southern California endemic, *Pseudotsuga macrocarpa,* has been reported by many authors to occur in the Sierra San Pedro Mártir of northwest Baja California. This report started with Sudworth, who perhaps confused the San Felipe Valley east of the Sierra San Pedro Mártir with that east of the type locality in San Diego County. Despite review of old records, study of aerial photographs, and visits to most likely sites, no authentic records are known. In fact, although the higher mountains south of the International Border are quite mesic, habitats suitable for *Pseudotsuga macrocarpa* appear to be wanting.

Data from herbaria and aerial photographs show that *Pseudotsuga macrocarpa* (Vasey) Mayr. has a fragmented range in southern California from the Figueroa and San Emigdio Mountains southward to its type locality in Banner Canyon at the south end of the Volcan Mountains in San Diego County (Fig. 1). It occurs in all ranges between except for the Hot Springs (San Ysidro), Santa Rosa, and northern San Jacinto Mountains, which are relatively arid owing partly to rain shadows of the Cuyumaca, Palomar, and Santa Ana Mountains to the west. Between 500 and 1500 m elevation in the chaparral belt, it grows on active slopes overlying shattered bedrock in deep canyons, on cliffs, and on steep northern exposures invariably as mixed evergreen forest (see Sawyer et al. 1977) mostly with *Quercus chrysolepis.* At higher elevations, especially in the San Gabriel and San Bernardino Mountains, more continuous *P. macrocarpa* forests grade into mixed conifer forest between 1500 and 2200 m, still on steep slopes with abundant *Quercus chrysolepis* understory (Bolton and Vogl 1969, McDonald and Littrell 1976, Thorne 1977, Minnich 1978). A map by Griffin and Critchfield (1972) accurately shows the gross range of *P. macrocarpa,* but the small scale suggests a more continuous distribution than actually exists. The long pendulous branches make this tree easy to identify in aerial photographs (Minnich 1978). A comprehensive large scale map for *P. macrocarpa* (1:250,000), interpreted from 1:60,000 color infrared aerial photographs, is on file at the Earth Sciences Department, University of California, Riverside. Fig. 1 shows a generalized rendition of this map.

It appears that the type locality in Banner Canyon is almost the southern limit of documented occurrence. The only plausible records
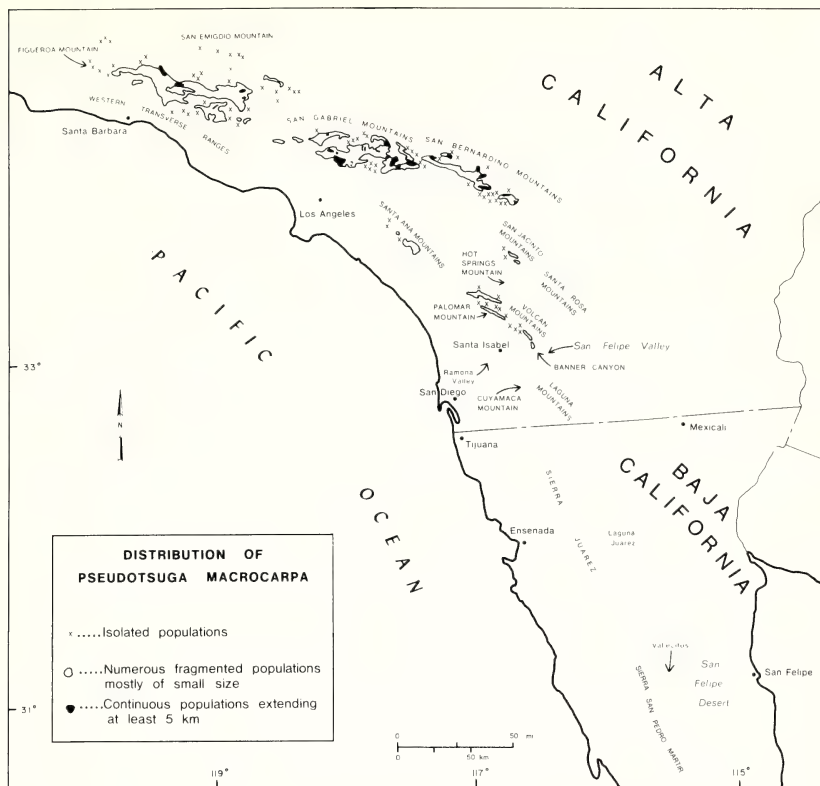
FIG. 1.   Distribution of *Pseudotsuga macrocarpa*.

south of there are Vegetation Type Map survey of California (VTM) plots on work maps of several individuals along three tributaries of Chariot Canyon, a few km south of Banner Canyon (Griffin and Critchfield 1972). These were field checked in January 1981 and no conifers were observed except for juvenile *Pinus coulteri* in one gully. No. *P. macrocarpa* snags, which may stand for 50 to 70 years (Minnich 1978), were seen, nor was any evidence seen of fire in surrounding vegetation or fire perimeter records (on file, Cleveland National Forest) that possibly could have been responsible for this tree's disappearance since the VTM survey. It is believed that VTM workers never saw *P. macrocarpa*. Their symbolization for *P. macrocarpa* on the Ramona quadrangle field maps is at variance with plots for it on other quadrangles of the survey (manuscript map on file with William B. Critchfield, Pacific Southwest Forest and Range Experiment Station, Berkeley, California). Therefore, I believe they mislabeled these populations

for *Quercus chrysolepis* found in all three gullys. VTM workers recorded no other populations in comprehensive mapping from there to the Mexican border, a span of 50 km that includes the mesic Cuyumaca and Laguna Mountains.

The subject of this paper is the actual southern limit of *P. macrocarpa*—whether this tree occurs in Baja California as often reported.

Reports for Baja California

Without citing sources, Sudworth (1908) noted that *P. macrocarpa* was "sparingly represented at altitudes of 5000 to 7000 feet [1500–2100 m] on Mount San Pedro Mártir." Others indicating its presence in this range include Jepson (1909), Abrams (1910), Standley (1920–26), and Peattie (1953). References to *P. macrocarpa* in "lower California" include Dallimore and Jackson (1923), Davidson and Moxley (1923), and Bowers (1942). Munns (1938) mapped a continuous narrow strip along the Sierras Juárez and San Pedro Mártir south to latitude 31°N. More recently, Gause (1966), citing many of these early references also mapped *P. macrocarpa* in both the Sierras Juárez and the San Pedro Mártir. Finally, in an inventory of the forests of Baja California (Secretaria de Agricultura y Ganaderia, 1968), "*Pseudotsuga* sp." is said to occur in the arroyos in the eastern zone of the San Pedro Mártir between 2000 and 2100 m. Moreover, a table showing diameter class relationships with wood volume for "*Abies, Pseudotsuga,* and *Calocedrus*" (Table 2, p. 39) seems to imply actual field measurement of the tree. No specific location for *Pseudotsuga* was given in the report.

Doubt about a Mexican distribution began early and has persisted ever since. Jepson (1910, 1923) quickly revised his southern limit to Banner Canyon. Abrams (1940) followed suit. Little (1952) noted that Sudworth's San Pedro Mártir occurrence was not supported by specimens and concluded that his observation resulted from an error in compiling data. He also felt that later records were probably based upon Sudworth. Martínez (1953) was apparently unaware of any collections of *Pseudotsuga* in Baja California. Referring to Gause's article, Bolton and Vogl (1969) stated that Wiggins doubted these sources; and indeed Wiggins (1980) did not list the tree in his flora of Baja California. Bolton and Vogl hypothesized that such an error might be due to a "specimen with a misinterpreted locality." The reference to "*Pseudotsuga* sp." in the San Pedro Mártir in the S.A.G. inventory (1968) appears untrustworthy, in view of a glaring inconsistency between their observations and the floristic composition of forests there. The report states that although Martínez (1953) listed the presence of *Abies concolor* in Baja California, this tree was not observed anywhere in the inventory of the National Forests.

"Maximo Martínez (1953) consigna la presencia de *Abies concolor* en el estado de Baja California; sin embargo, no se observó ningún ejemplar en los trabajos que el Inventorio Nacional Forestal efectuó en es entidad."

Many researchers have seen or collected *Abies concolor* in the San Pedro Mártir; and it is so abundant at Vallecitos that it is incomprehensible that anyone could miss it. Clearly, of the two genera, *Abies* and *Pseudotsuga,* the Inventorio Forestal saw only one and that was probably *Abies*. This is supported by the listing of *Abies* in several of their field data tables.

Despite the various reports, there seem to be no authentic records of *P. macrocarpa* in Baja California. Brandegee (1893), who summarized the state of knowledge in northern Baja California, including the studies of the interior mountains by Orcutt, does not list the tree. A 1905–1906 Bureau of Biological Survey (USDA) sponsored expedition, trekked across the San Pedro Mártir for several weeks from Rio San Rafael through Vallecitos and La Grulla to Misión San Pedro Mártir without seeing it (Nelson 1921, Goldman 1916). Reid Moran (pers. comm. 1980) has visited many areas of the San Pedro Mártir (Observatorio to Cerro Venado Blanco and Cañon Copal; Valle Picacho southward; Rancho San Pedro Mártir to Los Llanitos, to La Encantada, to Santa Rosa, to La Grulla, to La Joya; Vallecitos to El Picacho del Diablo and down Cañon del Diablo; and Rancho La Suerte to the south end of *Pinus jeffreyi* forests on Rio Santa Eulalia), and has not seen it in these areas. As stated previously, Wiggins (1944, 1980) after extensive collecting in northern Baja California does not list *P. macrocarpa*.

Basis of Sudworth's report. Most reports of *P. macrocarpa* in Baja California probably go back to Sudworth. Would Sudworth make up a story? Not intentionally, of course, but authors of floras covering large areas are dependent on second-hand information for geographic ranges of species. It seems that Sudworth, or a source of his, may have erred with a common place name San Felipe. The type specimen of *P. macrocarpa* was collected near San Felipe during the Ives Colorado River expedition of 1857–1858. This is an old place name given by Pedro Fages of the Anza Expedition of 1782 for the valley east of the Laguna Mountains near Julian, San Diego County, California (Gudde 1959). The San Pedro Mártir is near the San Felipe Desert, the Bay of San Felipe, and the town of San Felipe. This is also an old place name which dates to the expedition of Jesuit Fray Fernando Consag in 1746 and later used during the expeditions of José Joaquín Arrillaga of 1796 (Arrillaga 1969) and José Longinos Martínez of 1790 (Simpson 1938, p. 27), both of which trekked from the San Pedro Mártir to the port of San Felipe de Jesús. The following perhaps tortuous scenario may be worth hearing out.

In 1857, J. S. Newberry of the Ives expedition, which followed the old Butterfield Stage Coach road through San Felipe Valley, collected a five inch cone recognized as *"Abies douglasii* var. *macrocarpa"* by Torrey (Ives 1861, pt. 4, p. 28). Because Banner Canyon was probably unnamed at that time, the Ives report states somewhat ambiguously that the specimen was found in the "mountains near San Felipe." During the 1869–1874 Julian gold strike, local newspaper accounts began referring to this drainage as "San Felipe Canyon" (Ellsberg 1972). Botanical accounts of *P. macrocarpa* in ensuing decades used this place name in describing this southern population (Vasey 1876a, 1876b; Watson 1880).

Sudworth had much information at his disposal by the time he wrote his book. He had enormous field experience in California (see forward by Metcalf in Sudworth 1967). He also had access to geographic information in local floras, unpublished silvical studies, field reports, and boundary surveys of the Forest Service, the Biological Survey, and field notes of C. Hart Merriam. Indeed, the accuracy of his distribution of *P. macrocarpa* in southern California attests to the quality of these sources. Data from Baja California, however, were lacking. There is no evidence he ever visited Baja California (see bibliography in Nelson 1921). Merriam published some articles on the Cape region but none on northwest Baja California (Nelson 1921). The only possible source of Sudworth was an ambiguous report by North (1907), who lists "spruce" in addition to fir and other conifers known from the Sierra San Pedro Mártir. Moreover, the name "San Felipe" was losing ground in the literature by the turn of the century. San Felipe Canyon was renamed Banner Canyon on 1901 U.S. Geological Survey topographic sheets (Ramona quadrangle, scale 1:125,000). San Felipe Valley, which contained no permanent settlement, failed to appear on the early Survey General Maps of the State of California (U.S. Dept. of the Interior 1907). Collections or observations of *P. macrocarpa* in this area were no longer associated with the name San Felipe. It is possible, therefore, that Sudworth may have misread the comment "mountains near San Felipe" in the Ives report to mean near the fishing village and desert east of the San Pedro Mártir. This interpretation is made more appealing if Sudworth did read North's (1907) account of "spruce" in the San Pedro Mártir, which stands side by side with consistent references to the San Felipe Desert. It is also possible, of course, that Sudworth relied solely on North. He seems to have set off a chain reaction of references.

Search in most likely sites.   Many people, including myself, have searched for *P. macrocarpa* in Baja California. I have seen most Baja California forests either on field trips or through aerial photography but have never found this tree. There is, of course, no way of absolutely disproving its occurrence in such inaccessible country.

Conifer forests occur in Baja California only at the crests of the relatively undissected Sierras Juárez and San Pedro Mártir (Goldman 1916, Nelson 1921, Wiggins 1960), mostly along gentle plateau surfaces, basins, and watercourses, where *P. macrocarpa* is unlikely. The lower Sierra Juárez (elev. 1900 m) supports *Pinus jeffreyi* forest along the highest part of the plateau, concentrating around Laguna Juárez (Hanson). *Pinus coulteri,* several thousand trees, also occurs in association with *Quercus chrysolepis* on Cerro Guadalupe (or Cerro Blanco) near the village of Guadalupe. The higher Sierra San Pedro Mártir, especially around Vallecitos (2500 m), is covered by mixed conifer forest resembling those in California, dominated by *Pinus jeffreyi,* with *P. lambertiana, Abies concolor, Calocedrus decurrens,* and a few alpine trees including *P. contorta, Populus tremuloides,* and the endemic *Cupresses montana* in the vicinity of the east rim and on Picacho del Diablo (3100 m).

Forests on elevated plateaus, in valleys, and on old erosion surfaces in southern California also lack *P. macrocarpa,* although significant stands invariably occur in nearby steep canyons. Vallecitos forests in the Sierra San Pedro Mártir descend short distances off the northwest and eastern edges of the plateau on steep north facing slopes and in canyons, often in association with *Quercus chrysolepis.* These stands seem to be the closest analogies to *Pseudotsuga macrocarpa* forests of southern California in habitat and physiognomy. Using Cetenal vertical aerial photographs (Mexico: 1:40,000, black and white), I examined the flanks of the Vallecitos plateau stereoscopically for populations of long branched (stellate) trees. I mapped canyons with an abundance of such trees and field checked them during trips to Diablo Canyon, the Observatorio, and the north end of Sierra Corona at Rio San Rafael. These trees consistently proved to be *Pinus lambertiana,* which also has long branches, though less exaggerated than in *P. macrocarpa.* Analysis of Cetenal aerial photographs elsewhere in the range showed no apparent *Pseudotsuga macrocarpa.* I also saw no trees in two trips along the plateau (Vallecitos to La Grulla, Alcatraz, Santa Rosa meadow, Rio Santa Eulalia, Santo Tomás and San Ramón; Vallecitos to Los Llanitos, La Encantada, La Grulla, and La Tasajera).

ECOLOGY

The apparent absence of *P. macrocarpa* in Baja California is paralleled by the absence or infrequence of many companion trees found at middle elevations of southern California. This is seen in the differences in vegetation zonation there and Sierra San Pedro Mártir. In southern California, mixed conifer forest grades downslope into mixed evergreen forest dominated by robust spreading oaks (*Quercus chrysolepis, Q. agrifolia*), *Umbellularia californica,* and *Pinus coulteri,* as

well as *Pseudotsuga macrocarpa.* These also form multilayered stands
with mesic shrubs such as *Quercus dumosa, Q. wislizenii,* and *Cea-
nothus integerrimus* extending upslope from the chaparral belt (Saw-
yer et al. 1977, p. 377; Thorne 1977; Minnich 1976). On the Pacific
slope of the Sierra San Pedro Mártir, mixed conifer forest gives place
abruptly to a strikingly xeric chaparral dominated by *Arctostaphylos
peninsularis, Adenostoma fasciculatum,* and *A. sparsifolium,* even on
shady northern exposures and in canyons. Many mixed evergreen for-
est species, growing with or near *P. macrocarpa* in southern Califor-
nia, are absent from the Sierra San Pedro Mártir. *Umbellularia cali-
fornica, Arbutus menziesii, Lithocarpus densiflora* along with
deciduous *Quercus kelloggii* and *Acer macrophyllum,* for example, do
not reach Baja California (Griffin and Critchfield 1972). (*Umbellularia
californica* is reported by Wiggins (1980) although Moran (pers.
comm., March 31, 1981) has found no specimen of it from Baja Cal-
ifornia; I have not seen it there.) Only a few populations of *Quercus
agrifolia* may be seen along watercourses, springs, and fault seeps.
Most *Q. chrysolepis* is a small-leaved shrubby ecotype (Myatt 1975),
sympatric with mixed conifer forest on the plateau, with only local
stands entering into the chaparral belt to as low as 1800 m. Among
conifers, the southern limit of *Pinus ponderosa,* which is more com-
monly associated with mesic mixed conifer forests at lower elevations
(Thorne 1977, Minnich 1978), is known to be at Pine Valley, San
Diego County, 25 km north of the Mexican Border (Griffin and Critch-
field 1972). *Pinus coulteri* is either absent (Nelson 1921, Wiggins 1980)
or rare in the San Pedro Mártir. Three plots of *P. coulteri* there in
Critchfield and Little (1971) based on observations by Sleeper (letter:
E. L. Sleeper to W. B. Critchfield, February 26, 1964) are not sup-
ported by specimens or by the field observations I made at two of the
sites (see also Griffin and Critchfield 1972). Its documented southern
occurence is at Cañada El Rincón in the southern Sierra Juárez, east
of Santa Catarina; overall, it is rare in the Sierra Juárez (Moran 1977).
Below the mixed conifer forest belt are only xeric *Pinus quadrifolia,
Juniperus californica,* and an occasional *P. jeffreyi* in a basin or wa-
tercourse.

Why do *Pseudotsuga macrocarpa* and other elements of mixed ev-
ergreen forest decline or disappear while more mesic mixed conifer
forest trees continue southward into increasingly arid Baja Califor-
nia? Snow appears to play an important role in the seasonal rhythm
of available soil moisture in the root zone in mixed conifer forest and
other high elevation communities along the Pacific coast. An accu-
mulating snow pack in winter is effectively water storage that may be
sufficient to carry tall trees through the long summer drought. Mixed
evergreen forest in southern California and northward is elevationally
stratified below the snow zone (Major 1977), but annual rainfall is still
large enough to support tree growth. Because the Sierra San Pedro

Mártir is at the very southernmost limit of reliable winter cyclonic storms, however, the success of forest there is more strongly tied to snow accumulation. In mixed conifer forest on the plateau, moisture is almost certain during the summer growing season irrespective of annual precipitation load because snow persists until late spring. Snow preservation is enhanced by low temperatures due to strong ground inversions on clear windless nights. Vegetation below the forest belt of the plateau is vulnerable to the irregular, unreliable rainy season. Habitats suitable for trees such as *Pseudotsuga macrocarpa* are wanting because mesic conditions are correlated with cold, continental climate. Instead, drought-adapted chaparral prevails at temperate middle elevations, with stands extending as high as 2300 m on the west face of the San Pedro Mártir plateau. The physical environment of northern Baja California, therefore, appears to be unsuitable for mixed evergreen forest trees with mesic temperature requirements, such as *Pseudotsuga macrocarpa*.

Moreover, *P. macrocarpa* occupies fire-resistant habitats with relatively non-flammable tree-sized *Quercus chrysolepis,* which buffers it from lethal chaparral fires. Because *P. macrocarpa* directly survives frequent fire, the interval between partially lethal defoliating disturbances is long enough for some of the slow growing saplings to mature. Such a trend is unlikely in the San Pedro Mártir because *Quercus chrysolepis* grows there mostly as a shrub. Its fuel geometry is like that of chaparral (horizontally and vertically contiguous), which carries fire with sufficient intensity to immolate conifer overstory regularly. Throughout its range *P. macrocarpa* almost never occurs with chaparral understory (Minnich 1980).

Thus, it may not be surprising that the range of *P. macrocarpa* stops at Banner Canyon, because mesic, temperate habitats on unstable surfaces are rare south from there. The eastern scarp of the Laguna Mountains becomes increasingly arid south of the type locality because of the greater distance from the Pacific Ocean and the rain shadows of the Cuyumaca Mountains. Cuyumaca Mountain and most of San Diego County westward are geomorphically undissected. Steep eroding surfaces of the Sierra Juárez and the San Pedro Mártir are mostly confined to their faulted eastern scarps which are much too dry for *P. macrocarpa*.

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UNILATERAL INFERTILITY IN PARAPATRIC SPECIES OF ESCHSCHOLZIA (PAPAVERACEAE): SELECTION FOR ISOLATION?

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Abstract

Natural populations exist of the hybrids *Eschscholzia californica* × *E. caespitosa* and *E. californica* × *E. lobbii*. Crossing and backcrossing experiments demonstrate pronounced unilateral fertility between *E. californica* and *E. caespitosa* (the former more often fertile). Growth of con- and interspecific pollen on excised styles and pollination with interspecific and later conspecific pollen show that the cause of this unilateral fertility is mainly seed abortion. Similar tests show a nearly complete bilateral fertility barrier between *E. lobbii* and *E. californica* that is based on seed abortion and unilateral stylar incompatibility; and they show that complete bilateral infertility exists between *E. lobbii* and *E. caespitosa* and is caused by seed abortion. An explanation of the patterns of fertility and their physiological bases is offered in terms of breeding system, chromosome number and repatterning, selection for barriers to gene flow, and reproductive life spans of the species. A consequence of unilateral fertility is unilateral introgression.

The genus *Eschscholzia* comprises 13 species of annual and perennial herbs native to the western United States and to northwest Mexico. The three northernmost, *E. californica* Cham., *E. caespitosa* Benth. and *E. lobbii* Greene, were studied; all are obligate outbreeders with a diploid chromosome number of 12 (Ernst 1958). *Eschscholzia californica* is most widely distributed, occurring in diverse, open habitats from Oregon south to Baja California. Commonly it occurs in sandy or gravelly soils of stream-side deposits, alluvial fans, sand dunes, rocky hillsides where soil is shallow, and disturbed areas such as road cuts. It grows on soils derived from diverse parent materials and occurs from sea level to 2000 m (Cook 1962, 1965; Munz 1959). Its range within California includes that of the other two species. However, its populations are only occasionally in reproductive contact and rarely interact competitively with the others because they occur in distinct habitats.

Eschscholzia caespitosa grows mainly in the mountain arc around the Central Valley of California, chiefly at intermediate altitudes (120–1050 m) in shaley soils alongside brush species such as *Adenostoma fasciculatum* H. & A. of the Foothill Woodland and Chaparral communities (Munz 1959).

Eschscholzia lobbii occurs around the margins of the Sacramento Valley and on the east side of the San Joaquin Valley, but mainly at
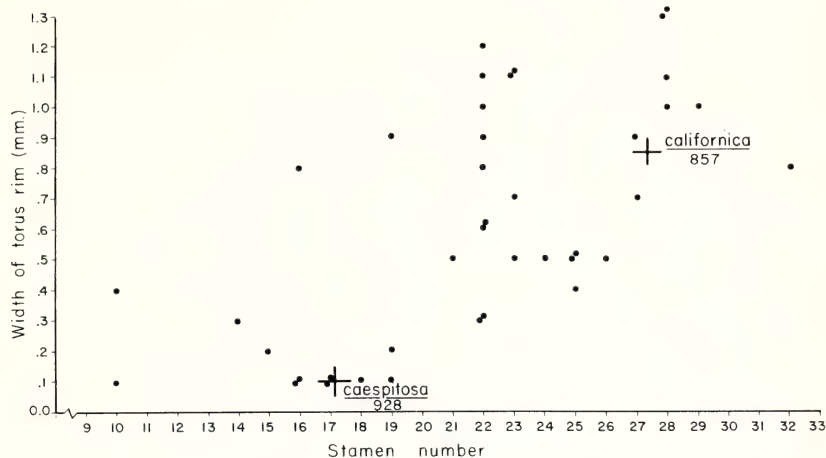
FIG. 1.   Scatter diagram of 40 individuals of hybrid population 854. Mean values of pure populations of *E. caespitosa* and *E. californica* have been indicated by crosses.

altitudes below *E. californica* and *E. caespitosa* (30–600 m). It grows in hard clay or gravelly clay, occasionally in gravel, in the Valley Grassland and in meadows within the Foothill Woodland communities (Munz 1959).

I encountered two aberrant populations: one included intermediates between *E. californica* and *E. caespitosa* (*Cook 854*, ORE; Fig. 1) and grew beside a road that was cut between adjacent habitats of the two species. The other included *E. californica* plants with *E. lobbii*-like leaves (*Cook 940, 941*, ORE). It occurred in a fallow field, where individuals typical of both species cohabited.

In this paper I attempt to determine whether these aberrant populations could have arisen by hybridization rather than by differentiation from the highly heterogeneous *E. californica* gene pool, to explore the nature of physiological isolation between the species, and to draw inferences concerning its evolution.

EXPERIMENTAL METHODS AND RESULTS

Interpopulation crosses.   To test for the possibility of hybridization between the species, we pollinated emasculated flowers of greenhouse-grown plants. Plants from only one population of each species were chosen for the test. All came from the inner North Coast Range or adjacent Sacramento Valley: *E. californica* (*Cook 940*, ORE) and *E. lobbii* (*Cook 941*, ORE) from where they grew together on red gravelly clay at 102 m 4.8 km west of Red Bluff, Tehama County and *E.*

TABLE 1.   RESULTS OF RECIPROCAL INTERSPECIFIC POLLINATIONS AND VERIFI-
CATION OF HYBRIDITY OF PROGENY. Numbers in parentheses are: parental plants/total
combinations of parents; total flowers pollinated.

	Carpels not elongated %	Carpels elongated %	Total matured F_1 seeds	Total F_1 plants matured	Number of F_1 hybrids matured
♀ ♂					
cal. × *cae.* (21/14; 181; 253)	21	79	1952	10	8
cae. × *cal.* (11/12; 49; 202)	77	23	14	3	0
cal. × *lob.* (21/16; 249; 316)	18	82	113	9	0
lob. × *cal.* (16/15; 46; 155)	84	16	58	33	0
lob. × *cae.* (13/10; 27; 92)	93	7	91	30	0
cae. × *lob.* (11/10; 45; 153)	93	7	5	3	0

caespitosa (*Cook 928,* ORE) from a steep south-facing slope at 300 m
in Mix Canyon, Solano County, about 190 km south of the Red Bluff
site. Pollinated flowers from reciprocal crosses were scored for carpel
elongation, aborted seeds and plump, presumably viable seeds (Table
1).

There are pronounced differences depending on which species
served as ovulate parent. Carpels of *E. californica* elongated and
produced either aborted or plump seeds when pollinated by *E. caes-
pitosa,* but the reciprocal cross was much less successful. The same
general relationship held between *E. californica* and *E. lobbii.* No
appreciable reciprocal difference occurred in the predominantly un-
successful crosses between *E. caespitosa* and *E. lobbii.*

Progeny of all these crosses were grown to maturity to reveal the
extent to which the seed was produced by hybridization or contami-
nation. In fact, only seed from *E. californica* plants produced hybrids
(for methods see below); those seeds of the other species that did de-
velop to maturity grew into non-hybrid individuals (Table 1).

Authenticity of hybrids.   Because *E. californica* and *E. caespitosa*
are difficult to differentiate, a hybrid index was developed and used
to classify putative hybrids. The characteristics used in the index were
stamen number, torus rim width, ratio of maximum width of petal to
length of petal extending beyond its widest point, and width of widest
stamen filament. For each character state pure *E. californica* was
given a value of 2 and pure *E. caespitosa* a value of 0. Next I estimated

the fertility and shape of parental and putative hybrid pollen after staining with aceto-orcein.

The average pollen fertilities of the pure species are *E. californica* 83, *E. caespitosa* 39, and *E. lobbii* 98 percent (I do not know why the fertility of *E. caespitosa* is so low; it may have been due to conditions in the greenhouse or to intrinsic factors). Eight individuals had hybrid indices between 3 and 5. The mean of their pollen fertilities was 46. More significantly, their pollen grains were of irregular shapes and various sizes, whereas the pollen of the pure species fell into two discrete groups: large fertile and small sterile grains. This irregularity of pollen grains of the hybrids between *E. californica* and *E. caespitosa* is due to formation of micro- and macro-nuclei at microsporogenesis, which in turn is due to failure in hybrids of one of the short pairs of chromosomes to synapse or attain the metaphase plate in anaphase I and to occurrence of chromosomal bridges. Forty-eight percent of 21 anaphase cells were normal in one hybrid studied. This value corresponds closely to the 45 percent fertility that it was estimated to have by the method of pollen staining.

Evidently genic and structural differences between chromosomes of *E. californica* and *E. caespitosa* cause reduced fertility in their hybrids.

Unilateral infertility between species.   Two possibilities were explored as the mechanism for the observed infertilities: (1) that an incompatibility reaction occurred between styles and pollen, and (2) that although syngamy might occur, ovule development might be arrested in one of the two parents.

I used Straub's method of culturing styles (Straub 1947) to study pollen tube growth. Flowers were emasculated; 1–3 days later styles ca. 1.5 cm long were excised, pollinated at their tips with the desired pollen, and placed base down in a solution of 10 percent sucrose and 50 ppm boric acid in the well of a cylindrical depression slide. After 24 hours I counted the tubes that emerged from the basal end of each style and measured their emerged lengths with an ocular micrometer. The results are given as indices that are the arithmetical means, for each treatment, of the products of the mean lengths of tubes and number of tubes emerging (Table 2).

Although self-pollinations are somewhat effective, growth of pollen tubes in them is less in all cases than in intraspecific outcrosses. This accords with knowledge of self-incompatibility based on self-pollination and seed harvest.

A more important result is that *E. californica* pollen grows better in the styles of the other species than in its own. Pollen of *E. caespitosa* does not show this, growing about as well on styles of the other species as on its own. Pollen of *E. lobbii* grows poorly on *E. californica* but well on *E. caespitosa* styles. Hence there are no pronounced unilateral stylar incompatibilities between *E. californica* and *E. caespitosa* or

TABLE 2. COMPATIBILITY INDICES FOR SELF- AND CROSS-POLLINATIONS WITH THREE SPECIES OF *Eschscholzia*. Tabulated values are arithmetical means of (n) values, which are products of the average lengths (micrometer units) of tubes emerging from a style and an index to the number of tubes emerging from that style (0 for none, 1 for 1–9, 2 for 10–20 and 3 for 21 or more tubes).

Pollen	On own style (n)	On other *E. californica* style (n)	On other *E. caespitosa* style (n)	On other *E. lobbii* style (n)
E. californica	2.60 (29)	2.99 (34)	3.60 (27)	3.70 (15)
E. caespitosa	0.53 (12)	2.25 (18)	2.44 (30)	2.45 (18)
E. lobbii	0.70 (7)	0.75 (18)	2.68 (20)	2.31 (10)

between *E. caespitosa* and *E. lobbii*. There is, however, a unilateral stylar incompatibility involving *E. lobbii* and *E. californica*.

The data on carpel elongation and seed growth in Table 1 are consistent with the hypothesis of zygotic death: ovules of *E. lobbii* might abort early when fertilized by *E. californica*, precluding carpel elongation. Abortion might occur later in *E. caespitosa* with greater attendant carpel elongation and production of obviously aborted seeds. When *E. californica* is the ovulate parent numerous seeds might begin development and stimulate carpel elongation. Subsequently many seeds might abort but many others would mature to produce hybrid individuals.

To test for zygotic death, plants of each species were first pollinated with pollen from another species and then after 24 hours with compatible pollen from another member of its own species. This technique distinguishes whether there is pre- or postzygotic death in two ways. First, if the foreign pollen were to cause zygotic death, we should expect no seed set; if interspecific pollination does not lead to zygote formation, then the second pollination should bring about normal seed set. Second, hybridization occurring without early zygotic death can be detected by studying development of the seeds produced.

Greatest seed set was obtained when no foreign pollen was used (Table 3). Fewest seeds occurred in combinations between *E. lobbii* and *E. caespitosa*. Of these two, *E. lobbii* has the larger sterilizing effect on *E. californica*. These results are similar to those of the initial crosses (Table 1). Again, *E. californica* and *E. caespitosa* are more interfertile than *E. californica* and *E. lobbii*, which in turn are more interfertile than *E. caespitosa* and *E. lobbii*.

Hybridity was estimated from the following characters: seed length, width, and viability (by germination in 5000 ppm, 10 percent active gibberellic acid); seedling abnormalities (green hypocotyl, radical death, chlorosis); cotyledon color and shape; adult morphology; and pollen form and stainability. Ungerminated seeds were preserved, dissected and examined for presence of embryo and endosperm. Seeds of

TABLE 3.   RESULTS OF INTERSPECIFIC CROSSES THAT WERE FOLLOWED 24 HR LATER BY INTRASPECIFIC CROSSES. The outcome of raising seeds from these crosses.

Combination			n	Crosses % fertile pollinations	x̄ seeds per carpel	n	% normal adults	% normal dormant seeds	% abnormal seeds and seedlings	% hybrids
♀	♂	♂								
cal.	× cal.	× cal.	21	81	20	23	78	9	13	0
cae.	× cae.	× cae.	24	79	7	19	84	5	11	0
lob.	× lob.	× lob.	34	91	25	10	70	30	0	0
cal.	× cae.	× cal.	22	32	6	18	0	6	44	50
cae.	× cal.	× cae.	25	48	5	19	63	21	16	0
cal.	× lob.	× cal.	22	18	9	17	65	23	12	0
lob.	× cal.	× lob.	31	35	7	19	63	16	16	5
cae.	× lob.	× cae.	23	26	3	26	50	8	42	0
lob.	× cae.	× lob.	31	12	4	0				

proven hybrids were smaller and scarcely overlapped in length and width those of normal *E. californica*. Seeds with abnormal embryos were intermediate in size.

Intraspecific crosses result in a higher proportion of normal individuals than interspecific crosses (Table 3). Hybrids are produced between *E. californica* and *E. caespitosa* only when the former is the ovulate parent. The interspecific crosses between these species differ significantly (Chi-square test) from their intraspecific controls. The results of first pollinating *E. californica* by *E. lobbii* do not differ significantly (Chi-square test) from the pure *E. californica* control cross, although they are in the direction of fewer normal adults. The reciprocal cross, except for producing a single, totally sterile hybrid and a few abnormal seeds, is similar. This was the first such hybrid obtained in 529 attempts.

Results are incomplete involving *E. caespitosa* and *E. lobbii* crosses; however, a significant increase of abnormal seeds is indicated.

There are also differences between the intraspecific crosses (e.g., *E. lobbii* shows no abnormal seedlings and more dormancy). Apparently *E. californica* and *E. caespitosa* carry a greater load of abnormal seedlings in intraspecific crosses. The dormancy of *E. lobbii* may be due to slight inhibition of germination by gibberellin at the concentration used.

In conclusion, interspecific crosses are characterized by zygotic death; however, when *E. californica* is the ovule parent there is ap-

TABLE 4.   RECIPROCAL CROSSES BETWEEN *E. californica* × *E. caespitosa* HYBRIDS AND THEIR PARENTAL SPECIES.

Species combination	Combinations of individuals		Flowers pollinated		Total seed produced	Seeds/ total flowers
♀ ♂	Total	Fertile	Total	Fertile		
cal. × hybrid	7	6	55	46	444	8.1
hybrid × *cal.*	2	1	32	3	5	0.2
cae. × hybrid	7	4	24	17	42	1.8
hybrid × *cae.*	6	6	131	45	197	1.5
hybrid × hybrid outcross	3	3	112	51	110	1.0

preciable probability of its hybrids with *E. caespitosa* reaching maturity.

Fertility of interspecific hybrids in backcrosses.   To test for introgression and fertility, two series of pollinations were performed on *E. californica-E. caespitosa* hybrids. The first made use of hybrids derived from the initial simple crosses. Plants were selfed, crossed amongst themselves, and backcrossed reciprocally to both parents. Backcrosses were successful only with *E. californica* as the ovulate parent. Neither hybrids nor *E. caespitosa* set seed when pollinated by hybrids.

The second series of backcrosses involved the hybrids obtained from the experiment with repeated pollinations and was performed in another year, under more favorable conditions. Hybrids and *E. caespitosa* set seed in this trial, yet the average seed set of *E. californica* when crossed by a hybrid is 4.5 times greater than that of *E. caespitosa* when so crossed, and the seed set of *E. californica* when crossed by a hybrid is 40 times greater than that of the reciprocal cross (Table 4). Indeed, it is easier for hybrids or *E. caespitosa* to pollinate hybrids than it is for *E. californica*.

DISCUSSION

The aberrant populations could have arisen by hybridization because stylar incompatibility does not exist between the species and they have overlapping flowering periods and morphologically similar flowers. Furthermore, *E. californica* is promiscuously pollinated (Cook 1962).

The rareness of wild hybrid populations results from the infrequency with which these ecologically differentiated species come into reproductive contact and the strength of postzygotic barriers between them. The postzygotic barrier between *E. caespitosa* and *E. lobbii* is evi-

dently complete. That between *E. lobbii* and *E. californica* is strong. And that between *E. caespitosa* and *E. californica* is weak. However, it is weak unilaterally, because mainly *E. californica* plants set seed in reciprocal crosses among the species and their hybrids. Thus introgression will occur into *E. californica,* whereas *E. caespitosa* will remain pure, for physiological reasons alone. *Eschscholzia californica* thus has access to a greater store of variability than *E. caespitosa,* which will remain more clearly defined taxonomically but with less evolutionary flexibility.

How may these reproductive relationships have arisen? Of course I can only answer speculatively. *Eschscholzia lobbii* and *E. californica,* although parapatric in the Central Valley, are remote genetically: they differ sharply in seed morphology; there is a partial unilateral stylar incompatibility between them; and zygotic death is bilaterally highly probable and early acting. *Eschscholzia caespitosa* and *E. californica,* by contrast, appear closely related. They are similar morphologically, lack stylar incompatibility altogether and produce hybrids relatively easily. I will argue in what follows that *E. caespitosa* has diverged from *E. californica* and that, as it has, selection has favored unilateral infertility to enhance reproductive isolation of the emerging *E. caespitosa* populations.

Perennial *E. californica* plants occupy the most mesic habitats of any *Eschscholzia* species. *Eschscholzia caespitosa* lives on rocky shallow soils in association with chaparral—under conditions that are geoclimatically more recent (Axelrod 1950, 1967). The earliest stage of evolution of *E. caespitosa* from *E. californica* would have occurred at the ecogeographic margin of *E. californica.* I suggest a parallel with *Clarkia* in the southern Sierra Nevada, where evolution has occurred under conditions of extreme selection by drought (Lewis 1962). The likelihood of reproductive contact between the emerging *E. caespitosa* population and *E. californica* would have been greatest at the earliest stage in divergence, when the number of diverging genotypes would have been small; and they would have had the least spatial isolation. Under such conditions there would have been strong selection for a gene flow barrier that would protect the integrity of the adaptive gene complexes and thereby increase the reproductive capacity of the divergent plants. Numerically dominant *E. californica* plants would have experienced less selective pressure for a barrier against hybridization with the incipient species. In this way unilateral infertility may have evolved.

It might be expected that a prezygotic barrier should have evolved, for it would have been more efficient than a postzygotic barrier in preventing waste of parental gametes. In the species under consideration evolution of prezygotic barriers has been inhibited, it seems, by continued dependence on similar pollinators. Lengths of styles have not diverged, so style length difference has erected no barrier to pollen

tube growth. Furthermore, conservatism of the gametophytic self-incompatibility system may have hindered evolution of interspecific incompatibility responses.

Grant (1966) has argued that postzygotic barriers are not effective and not likely to be advantageous selectively. They are usually considered a consequence of evolutionary divergence of spatially remote populations (Muller 1942). On the contrary, postzygotic barriers can be selectively advantageous: if two differentially adapted populations interbreed and their hybrids are less fit, individuals suffer reduction in fitness in varying degrees from several causes. First, the fitness of hybrid offspring is relatively low. Second, if hybrids develop vegetatively but not reproductively they may reduce the fecundity of near relatives by competing with them for resources. Third, even if they do not germinate they may compete with normal seeds for parental nutrients "in utero." Fourth, hybrid seed development may terminate or foreshorten parental flowering even though inviable seeds are produced. Thus the earlier in ontogeny that abortion occurs the higher is the reproductive potential of adapted parental individuals.

Another factor may have caused more intense selection for an isolating mechanism in *E. caespitosa* than in *E. californica,* namely, longevity and its related temporal distribution of reproductive effort. *Eschscholzia caespitosa* is monocarpic (semelparous) whereas *E. californica* is polycarpic (iteroparous). Stebbins (1950, p. 238) implied that partial sterility would occasion a greater selective disadvantage to annuals than to perennials because the latter produce an "excess of seeds." Grant (1958) noted that autogamous annuals are more completely separated by hybrid sterility than are perennials. Perhaps this characteristic applies as well to allogamous annuals. (One could test this hypothesis that monocarpy is correlated with more effective isolation by comparing annual and perennial races of *E. californica.*)

These speculations indicate a possible course of evolution of *E. caespitosa* from *E. californica* and seek to show that the unilateral postzygotic infertility could have been of selective advantage. They accord with a growing theory of the possibility of sympatric or parapatric divergence and the selective origin of isolating mechanisms (Jain and Bradshaw 1966, Maynard Smith 1966, White 1968, Dickinson and Antonovics 1973, Udovic 1980). Unfortunately, ex post facto study of our flora can rarely provide convincing evidence of how it arose. Yet in seeking to interpret its diversity and distribution it is essential that we know what the possible courses of evolution are.

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POST-FIRE SUCCESSION IN WHITE FIR
(ABIES CONCOLOR) VEGETATION OF
THE NORTHERN SIERRA NEVADA

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Abstract

Post-fire seral changes in the structure and composition of *Abies concolor*-dominated vegetation were studied in the northern Sierra Nevada. The major change observed was a shift in dominance from montane chaparral shrubs to *Abies concolor*. Despite large changes in the dominance of individual species, most species encountered can occur at any point in the sere. Regeneration of shrub species was episodic, occurring only after fire or other disturbance. *Abies concolor* reproduction was continuous throughout the succession. However, tree density decreased with time as basal area increased to a maximum of 100 to 125 m²/ha. All stages of the seral sequence were characterized by greater than 75 percent canopy coverage and a predominantly mono-layered structure. On older sites, openings in the canopy caused by tree mortality allowed patchy understory development. Two species groups were detected in association analysis. One group, which contained *A. concolor* and three montane chaparral shrubs, characterized the early stages of succession. The second group, primarily herbaceous and sub-shrub root parasites, characterized mature *A. concolor* forests. Polar ordination also revealed two major clusters of stands characteristic of the montane chaparral and forest-dominated phases of succession.

White fir [*Abies concolor* (Gord. and Glend.) Lindl.] occurs in montane areas throughout much of the western United States. The white fir type (SAF 211) forms extensive, nearly pure stands in parts of the Siskiyou, Cascade, and Sierra Nevada ranges of Oregon and California (Gordon 1980). In the northern Sierra Nevada, as elevation and moisture availability increase, there is a gradual transition from *Pinus ponderosa* forests, through mixed conifer forests, to more or less pure *A. concolor* stands, and finally to *Abies magnifica* forests. *Abies concolor* is frequently the dominant species on mesic sites between 1500 and 2000 m (Gray 1979, Rundel et al. 1977, Waring 1972, Griffin 1967, Fowells 1965).

Natural fires in the mixed conifer forest of the Sierra Nevada are believed to occur about every eight years (Wagener 1961). Such frequent fires maintain open forest with little understory and prevent the invasion of shade-tolerant and fire-intolerant species such as *A. concolor* while favoring fire-tolerant species such as *Pinus ponderosa*

(Kilgore 1973, Vankat and Major 1978). Exclusion of natural fires in the mixed conifer zone is leading to increasing dominance by *A. concolor* in many areas (Gordon 1980, Rundel et al. 1977). However, the resulting increase in fire hazard may cause many of these stands to burn before *A. concolor* attains canopy dominance. The restriction of nearly pure *A. concolor* stands to mesic sites within the geographic range of the species suggests that natural fires are less frequent on these sites. The lengthy branch retention and high tree densities typical of white fir forests increase the tendency for fires to crown when they do occur. After a crown fire, sites are occupied rapidly by montane chaparral shrubs. In the white fir type, early conifer reproduction in these brushfields is primarily of *A. concolor*. In the continued absence of fire, shrubs are eventually overtopped by emergent conifers and a forest dominated by *A. concolor* will form.

Studies that discuss some aspects of structure and composition of *A. concolor* stands (Gray 1979, Vankat and Major 1978) or of montane chaparral succession (Bock and Bock 1977, Wilken 1967, Skau et al. 1970) have either been lacking in detail or have emphasized the drier-site mixed-conifer type. The most detailed vegetation research in the Sierra Nevada mixed-conifer zone has concentrated on the *Sequoiadendron* groves that are scattered along the west slope of the southern Sierra. Although densities of *A. concolor* are high, basal area in these groves is dominated by *Sequoiadendron*. Soil moisture and plant water potentials are higher in the groves than in adjacent *A. concolor*-dominated areas (Rundel 1972), suggesting that *Sequoiadendron* groves are not representative of the white fir type. In addition, information from mixed-conifer forests in the southern Sierra should be supplemented with data from the white fir type more typical of the northern Sierra to provide a more balanced view of the full range of white fir-dominated vegetation in the Sierra Nevada.

The objective of this paper is to describe changes in floristic composition and vegetation structure during the post-fire seral sequence that leads to *Abies concolor*-dominated vegetation in the northern Sierra Nevada.

METHODS

Study sites. The study was conducted during 1976 and 1977 in the northern Sierra Nevada in Sierra County, California. All study locations were characterized by high white fir densities either on the site or in nearby vegetation. Stands with diverse post-fire successional histories were identified and 12 were selected for intensive study. Location, aspect, slope, elevation, and approximate date of the last major fire are shown for each study site in Table 1.

The date of the most recent crown fire was determined for sites 1, 3, 4, 5, and 10 from local fire records (U.S. Forest Service, Sierraville,

TABLE 1. DESCRIPTION OF STUDY SITES. All sites were located in Sierra County, California. Sites are arranged from youngest to oldest in terms of relative successional age.

Study area	Site number	Location	Elevation (m)	Aspect	Slope	Approximate date of last crown fire
Webber Lake Rd	4	Sec 15, T19N, R15E	2010	N	25°	1972
Rice Canyon	1	Sec 4, T19N, R15E	1800	N60°E	20°	1939
Rice Canyon	3	Sec 33, T20N, R15E	1830	N30°E	20°	1918
Strang Ranch	5	Sec 16, T20N, R15E	2010	N110°E	25°	1915
Strang Ranch	10	Sec 16, T20N, R15E	1700	N45°E	20° to 25°	1915
Webber Lake Rd	2	Sec 8–9, T19N, R15E	2010	N40°E	20°	1890
Strang Ranch	9	Sec 16, T20N, R15E	1770	N30°E	25°	1850
Haypress Creek	11	Sec 30, T20N, R13E	1740	N180°E	20°	1870
Haypress Creek	12	Sec 30, T20N, R13E	1740	N180° to 220°E	20°	1870
Haypress Creek	7	Sec 30, T20N, R13E	1800	N220°E	20°	1880
Haypress Creek	6	Sec 30, T20N, R13E	1750	N200°E	10°	1780
Haypress Creek	8	Sec 30, T20N, R13E	1830	N230°E	20°	1700

CA). This was not possible for the remaining sites. On sites 2, 7, and 8, times of most recent fires were estimated from increment cores taken at the edge of fire scars on residual trees. On the remaining sites (6, 9, 11, 12) where residual trees did not have fire scars, 2 to 3 dominant trees were cored with an increment borer at 0.5-m height. Twenty years were added to core ages to compensate for early suppressed growth. Elevation, aspect, seed source, and site quality should influence rates of succession on different sites. Therefore, stands dominated by trees were ranked according to the mean basal area per tree (for trees >0.1 m DBH) to obtain relative successional ages of the stands.

Vegetation transects. The large structural differences between montane chaparral and forest sites necessitated the adaptation of sampling methods to vegetation structure. Sites dominated by shrubs were sampled by line intercept (Canfield 1941) to determine canopy coverage, species composition, and vertical structure of the vegetation. Six 25-m tape transects each were established at random on sites 1, 3, 4, 5, and 10. Horizontal canopy interception and canopy height (nearest 0.2 m) were recorded by species at 0.1-m intervals. Percent cover and mean canopy height were determined for each species on each transect. Total canopy coverage was calculated as 100 percent minus the percentage of ground surface with no canopy cover. Tree density was evaluated by counting all saplings, by species, in a 1 × 25-m belt transect adjacent to each line transect. All transects were perpendicular to slope contours.

On sites where trees formed the dominant canopy (2, 6, 7, 8, 9, 10, 11) vegetation was sampled by the point-centered quarter (PCQ) method (Cottam and Curtis 1956). Twenty points were established per site, except on site 8 where space permitted only eight points. Points (7–30 m apart depending on vegetation density) were placed along 3–5 randomly located transects across the slope contours. The number of transects per site was determined by the maximum transect length that was possible within each stand. Species and trunk diameter were recorded for four trees (>0.1 m DBH) at each point.

Diameters were measured with a diameter tape. Determination of total density followed Morisita (1960). Density, relative density, mean basal area, total basal area, and relative basal area were determined for each species. Overstory canopy cover of each species was estimated visually at each point and mean canopy cover was determined by species for all points on each study site. Site 10 was sampled by both line transect and PCQ because trees had emerged above the brush but shrub cover was still high.

Association analysis. To characterize further the vegetation and flora, relevés (Braun-Blanquet 1932) were taken along each PCQ and line transect. A seven-class cover-density scale was used in which R = single individual; + = <1 percent; 1 = 1–5 percent; 2 = 6–25 per-

cent; 3 = 26–50 percent; 4 = 51–75 percent; and 5 = 76–100 percent cover. Relevé data were subjected to association analysis (Ceska and Roemer 1971) on a Burroughs 6700 computer. The program identified groups of species that tended to occur together. Each group of species had a corresponding group of stands, such that each of the species occurred in at least 40 percent of the stands and each stand contained at least 40 percent of the species. In addition, none of the species could occur in more than 25 percent of the stands outside the group. Each stand was identified in the association table by a three-digit number. The first two digits are the number for the study site (Table 1) and the third digit represents a stand number within the study site.

Polar ordination. A polar ordination (Bray and Curtis 1957) was performed on relevé cover data. Log transformation of mean cover values for each class increased the relative importance of indicator species with low cover values. Interstand similarity was calculated using Sorensen's community coefficient (Sorensen 1948). The maximum similarity between samples in functionally identical vegetation was assumed to be 0.9 in calculations of interstand distance. For each of three axes, pole stands were selected that maximized an index of efficiency and reliability for the ordination. Stands were positioned along ordination axes using the Pythagorean method described by Beals (1960).

Diameter-class distributions. Trees sampled on the PCQ transects were aggregated into 0.1-m diameter classes to generate frequency distributions of diameter classes for sites 2, 6, 7, 8, 9, 10 and 11. Frequency was expressed as a percentage of the total number of trees sampled on each site.

Flora. A complete list of the 146 species in 35 families encountered in the field investigations is available in Conard (1980).

Results and Discussion

Montane chaparral sites. At sites where most of the conifers were beneath the shrub canopy (1, 3, 4, 5) the average shrub cover was 81 percent (Table 2). However, low shrub cover (35 percent) and large numbers of dead and dying shrubs were noted on site 10. Sixty percent of the coniferous saplings encountered there had overtopped the shrub canopy, and *A. concolor* canopy coverage was 47 percent. Shrubs on site 10 were apparently being replaced by *Abies concolor.*

Ceanothus velutinus was the dominant shrub species on sites 1, 3, 4, and 5. However, in the older stands (sites 3 and 5), cover of *Arctostaphylos patula* increased to approximately 25 percent (Table 2). *Chrysolepis sempervirens* was also an important species on many montane chaparral sites. It was usually present in small numbers beneath the canopies of the *Ceanothus velutinus* and *Arctostaphylos patula.*

TABLE 2. CANOPY COVERAGE AND HEIGHTS OF SHRUBS AND CONIFEROUS SAPLINGS ON SITES DOMINATED BY MONTANE CHAPARRAL. *Indicates less than 1 percent cover. Study sites are arranged according to the estimated time from the last crown fire (Table 1). Site 10 is the oldest whereas site 4 is the youngest. Means are presented ± one standard error.

| | Study site | | | | | | | | | |
Species	10 Cover (%)	10 Height (m)	5 Cover (%)	5 Height (m)	3 Cover (%)	3 Height (m)	1 Cover (%)	1 Height (m)	4 Cover (%)	4 Height (m)
Shrubs										
Ceanothus velutinus	5 ± 2	1.5 ± 0.3	27 ± 3	1.4 ± 0.1	41 ± 7	0.8 ± 0.1	59 ± 2	1.0 ± 0.1	66 ± 3	1.1 ± 0.04
Arctostaphylos patula	2 ± 1	1.1 ± 0.1	24 ± 5	1.3 ± 0.05	25 ± 8	1.2 ± 0.2	8 ± 3	1.3 ± 0.05	3 ± 2	0.4 ± 0.06
Chrysolepis sempervirens	28 ± 11	0.9 ± 0.1	6 ± 2	0.7 ± 0.1	15 ± 5	0.8 ± 0.1	*		7.3	0.5
Salix scouleriana					*		*			
Prunus emarginata			1 ± 0.7	1.3 ± 0.3	*					
Quercus vacciniifolia			39 ± 11	1.1 ± 0.5						
Ribes viscosissimum									*	
R. roezlii									*	
Dead brush	7 ± 4									
Total living shrub cover	35		86		75		68		74	
Trees										
Abies concolor	47 ± 8		9 ± 5		6 ± 2		7 ± 2			
A. magnifica			1.3 ± 1.3							
Pinus lambertiana	1.5 ± 1.5									
Total tree cover	48.5		10.3		6.0		7.0		0	
Total cover	84 ± 3		96 ± 1		81 ± 3		72 ± 3		74 ± 3	

At site 10, where the tree canopy was beginning to close, *C. semper-virens* was the dominant shrub. These observations suggest that *C. sempervirens* is more shade tolerant than *C. velutinus* or *A. patula*. Other common shrub associates that had locally high cover on some sites but rarely attained a high percentage of the total vegetation cover included *Salix scouleriana, Prunus emarginata, Quercus vaccinifolia, Ribes roezlii*, and *R. viscosissimum* (Table 2).

High densities of seedling and sapling *Abies concolor* (1100 to 11,000 st/ha) were observed on all montane chaparral sites except site 4, which had experienced the most recent burn. The high density (533 st/ha) of dead *A. concolor* present on that site five years after the fire indicated that it had supported an *A. concolor* forest in the past. The presence of several mature trees that had escaped the fire indicated that a seed source was available. The absence of *A. concolor* reproduction suggests that several years may be required on some sites before conditions are favorable for *A. concolor* establishment.

Forest sites.   The mean relative density and relative basal area of *Abies concolor* on forest sites were 93 and 94 percent, respectively (Table 3). Total stand basal areas increased from 13 m²/ha on site 10 to 127 m²/ha on the oldest site studied (site 8). Only on site 2 were the relative densities of *Abies magnifica* and *Pinus jeffreyi* greater than 10 percent. Other occasional associates were *Calocedrus decurrens* and *Pinus lambertiana*. A clump of large *Salix scouleriana* occurred on site 9, although the species is more typical of montane chaparral sites.

Shrub cover on forested sites was less than 5 percent except on site 10. The cover of *A. concolor* saplings (trees <0.1 m DBH) ranged from 1.3 percent (site 7) to 13.6 percent (site 2). Cover of *A. magnifica* saplings was 6.4 percent on site 6. In addition the mean basal area per tree of *A. magnifica* was only 28, 45, and 46 percent of that for *A. concolor* on sites 6, 9, and 2, respectively (Table 3). This suggests that *A. magnifica* is seral to *A. concolor* on some sites. Perhaps the cool understory microclimate at the upper elevation range of *A. concolor* forests favors *A. magnifica* reproduction.

Reproduction and size-class distributions.   The range in tree densities of the younger stands (2, 7, 9, 10, 11) was comparable with that observed by Schumacher (1926) for even-aged stands of *A. concolor* (>0.1 m DBH) in the Sierra Nevada. Schumacher (1926) also noted a decrease in density with increasing stand age. A negative relationship between relative age, expressed as basal area/tree (A), and tree density (d) was also observed in our study (ln d = -0.073 ln A + 5.04; r^2 = 0.86, p < 0.01). This relationship suggests that the amount of *A. concolor* seedling establishment decreases with increasing stand age, even though some establishment does occur in stands of all ages.

The diameter class distributions of *A. concolor* in stands of different

TABLE 3. DENSITY (d), BASAL AREA (BA), AND MEAN BASAL AREA PER TREE (A) OF TREES GREATER THAN ONE dm DBH ON FORESTED SITES. A total of 456 trees were measured. Study sites are arranged according to the estimated time from the last fire. Site 8 is the oldest site whereas site 10 is the youngest. AC, AM, CD, PJ, PL, and SS refer to *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, *Pinus jeffreyii*, *Pinus lambertiana*, and *Salix scouleriana*. Overall means are shown ± one standard error.

Species	Study site 8			Study site 6			Study site 7			Study site 11		
	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (st/ha)	BA (m²/ha)	A (m²/tree)
AC	199	127	0.64	315	99.4	0.32	862	108.9	0.13	1494	101.1	0.068
AM				30	2.8	0.09	15	3.6	0.25	19	0.3	0.017
CD				10	0.8	0.08						
PJ				5	3.2							
PL												
SS												
Total	199 ± 6	127	0.64	360 ± 5	106.1	0.30	977 ± 15	112.6	0.13	1513 ± 19	101.4	0.067

Species	Study site 9			Study site 2			Study site 10			Mean over all sites	
	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (st/ha)	BA (m²/ha)	A (m²/tree)	d (%)	BA (%)
AC	614	40.9	0.067	1241	51.4	0.041	778	13.2	0.017	92.6 ± 3.5	94.3 ± 2.9
AM	8	0.2	0.030	253	4.9	0.019				3.5 ± 2.3	1.5 ± 1.0
CD										0.8 ± 0.4	0.6 ± 0.4
PJ	16	0.4	0.023	187	9.6	0.051	27	0.4	0.013	2.1 ± 1.5	2.7 ± 2.0
PL	8	0.1	0.012							0.7 ± 0.5	0.3 ± 0.3
SS	8	0.2	0.020							0.2 ± 0.2	0.1 ± 0.1
Total	655 ± 8	41.8	0.064	1686 ± 24	65.8	0.039	805 ± 14	13.6	0.017	99.9	100
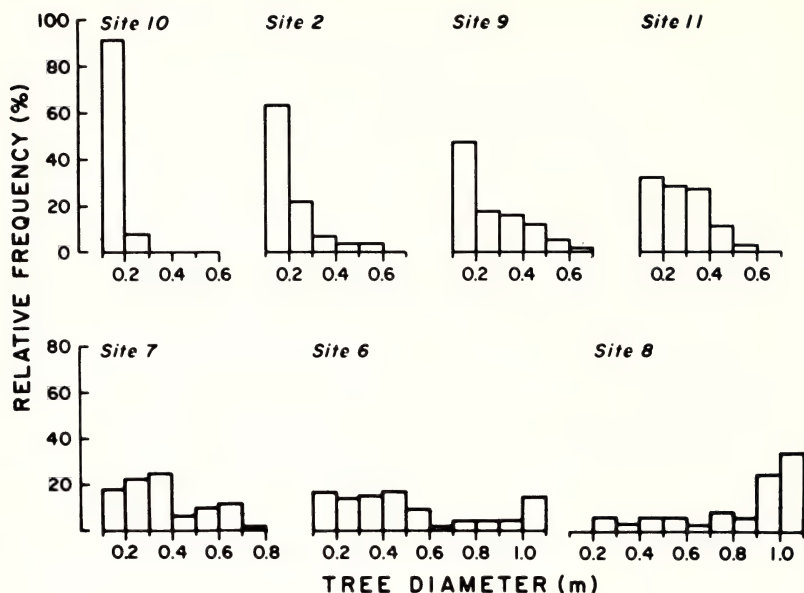
FIG. 1.   Frequency distributions of diameter classes (0.1-m intervals) for trees >0.1 m DBH on sites dominated by trees. Study sites are arranged according to the estimated time from the last fire. Site 10 is the most recent whereas site 8 is the oldest.

ages also indicate a decrease in seedling establishment as stands mature (Fig. 1). However, both the wide range of diameters observed in old stands and the ability of *A. concolor* to become established under low light levels suggest that growth suppression of trees in the populations is combined with a certain level of continued reproduction. Schumacher (1926) observed similar shifts in size-class distributions for *A. concolor* stands that he considered to be even-aged. However, as stand ages in his studies were determined only from dominant trees, an evaluation of the entire age class distribution for his stands is impossible.

In an even-aged stand, height and growth rate of individual trees should be strongly correlated. A comparison of heights and growth rates of white fir saplings on two montane chaparral sites did not support such a relationship (Conard 1980). Rather, variations in height for trees of similar growth rates encompassed nearly the entire range of values expected for a continuously reproducing population. Although detailed age-class information is lacking, the evidence presented suggests that most *A. concolor* stands are not even-aged.

Association analysis.   Despite the wide range in age and structure of the sites selected for study, only two species groups were detected
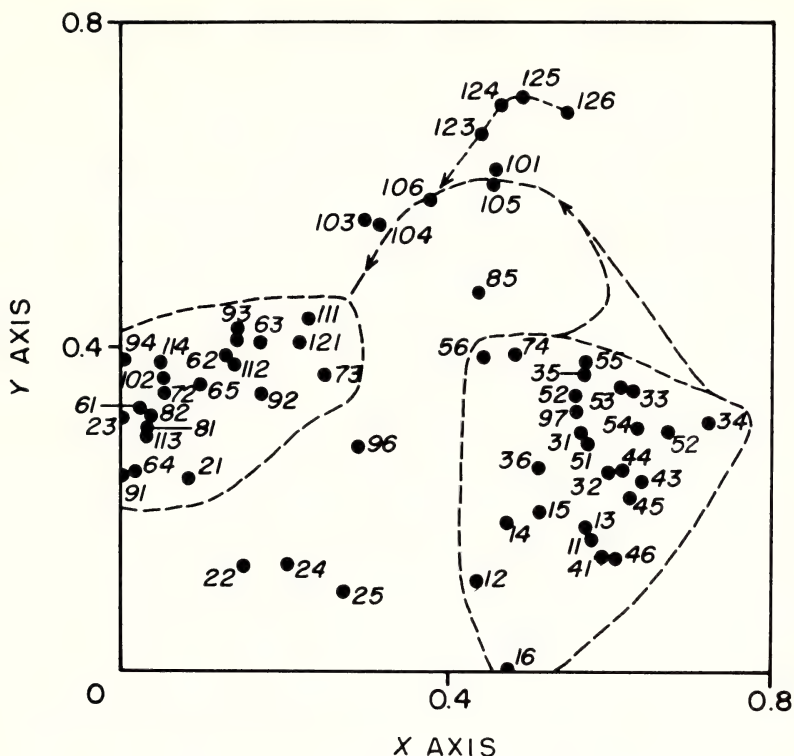
Fig. 2.   Polar ordination of stands. Stands are identified by site number. The last digit of each number identifies individual stands within study sites. Arrows indicate the direction of post-fire succession.

by association analysis (Table 4). The most widespread group, which occurred in 77 percent of the stands, included *Abies concolor, Ceanothus velutinus, Arctostaphylos patula,* and *Chrysolepis sempervirens.* The stands in which this group did not occur were generally those with such a high *A. concolor* canopy coverage that very few shrubs were present.

The other species group, which occurred in 18 percent of the stands, contained *Pyrola picta, Pteridium aquilinum, Chimaphila menziesii, Corallorhiza striata,* and *Kelloggia galioides.* Other species restricted to relevés in which this group occurred were *Pterospora andromedea, Sarcodes sanguinea, Hieracium albiflorum,* and *Pleuricospora fimbriolata.* This group of nine high fidelity species includes representatives of five of the ten genera of Pyrolaceae in California, most of which are probably root parasites. The nearly exclusive occurrence of this group in the late phases of the seral sequence is probably in re-

TABLE 4. ASSOCIATION TABLE FOR RELEVÉ DATA FROM INDIVIDUAL STANDS. Species-stand groupings are indicated by heavy horizontal lines. Symbols in the table are cover classes described in the text.

Species name / Stand number	Montane chaparral 041	042	043	044	045	046	011	012	013	014	015	016	031	032	033	034	035	036	051	052	053	054	055
Abies concolor							1	2	1	2	2	1	2	1	1	+	2	2	1	2	1	1	2
Ceanothus velutinus	5	4	5	4	4	4	3	4	4	4	4	4	4	3	2	4	3	4	3	3	2	2	2
Arctostaphylos patula	+	2	1		1	+	2		2	1	2		2	+	3	2	3	3		3	2	3	2
Chrysolepis sempervirens			+	3			+						2	3	2	2	2			1	1	2	2
Pyrola picta		R																					
Pteridium aquilinum																						+	
Chimaphila menziesii																							
Corallorhiza striata																							
Kelloggia galioides																1							
Pterospora andromedea																							
Sarcodes sanguinea																							
Pleuricospora fimbriolata																							
Hieracium albiflorum																							
Abies magnifica																							
Pinus ponderosa																			+		+		
Pinus monticola																							
Pinus lambertiana																							
Pinus jeffreyi																							
Calocedrus decurrens																	R						
Stephanomeria lactucina																							
Sitanion hystrix					R	+			+														
Gayophytum diffusum parviflorum	R		R		R	R										+							
Purshia tridentata									1														
Ceanothus cordulatus			+																			R	
Quercus vaccinifolia																			4	3	4	3	4
Ribes viscosissimum hallii	1	+		+	R																		
Ribes roezlii			+	+	+																		
Salix scouleriana									1					+									
Prunus emarginata													+	+		+	+	1		+			1
Alnus tenuifolia																							
Apocynum pumilum					+		+																
Symphoricarpos acutus					+				+	1	+												1

sponse to the low light intensities common on the forest floor (often 1 percent of full sunlight). This species group is remarkably similar to the *"Pirola-Corallorhiza"* union in *Abies magnifica* forests described by Oosting and Billings (1943), who speculated that the same union should also occur in the mixed conifer forests in the Sierra Nevada.

Breaches in the canopy caused by windthrow or death of canopy trees became more common in older forests. Such openings were patchy in their distribution and lent a locally heterogeneous appearance to the vegetation (Bonnicksen 1975). Increased light penetration to the forest floor permitted development of some understory vegetation in these areas. Stands 025, 095, 096, 097, and 074 represent local patches of low canopy coverage (Table 4). These areas are characterized by an increased cover of *Abies concolor* saplings and montane chaparral shrubs, especially *Chrysolepis*. Where openings are large

TABLE 4. CONTINUED.

Transition											Abies concolor forest																					
												Young												Mature								
0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
5	9	0	0	0	0	0	2	2	9	9	0	2	2	2	9	9	1	1	9	9	1	1	7	7	6	6	7	6	6	6	8	8
6	7	3	4	1	5	6	5	4	5	6	2	1	2	3	2	3	1	2	1	4	3	4	1	2	2	3	3	1	4	5	1	2
3	2	4	3	3	2	3	2	4	1	+	4	5	4	4	4	5	5	5	4	4	4	5	5	4	5	5	5	5	5	5	3	4
3	4						5	2							+	1																
2	2							2	1	+																						
2	2	2	2	2	4	4					3				+	+	1	+					R	+	+							
		+																					+	+	R	R	+	+	+	+	R	
																+							+	+	2	2	1	1		2		R
															R								+	+	R	+	+	R	+	+	R	+
															R								R			R			R	R	+	
																							+	+	+				+			
																																R
																							R		+							
																							R									
																							R		+	R						
1											2	2			1	1	1		R		1	1	2	1			1	+	2			
+													+						R													
					2	+	+								R	R					1											
R											+				R			R					R					1				R
											+				+	+	R						R	R	1	+	+					
																		+											+			
																								+								
+		2	2	2	2	2									2	2	+				1	1					+	+			
		+																														
													+	+									1	1					+		
											3																+					
																						R										
																								+				+				
																							+				+					
															+								+	+	+	+						

and overstory canopy cover is low, *Ceanothus velutinus, Prunus emarginata,* and *Salix scouleriana* may also occur.

Polar ordination. Shrub-dominated stands (montane chaparral) (1, 3, 4, 5) and tree-dominated stands (*Abies concolor* forest) (2, 6, 7, 8, 9, 11) separate into two distinct groups by polar ordination (Fig. 2). The two clusters of stands are connected by a bridge of intermediate stands, represented by site 10, in which tree canopy closure caused a decrease in shrub cover (Table 2).

A. concolor canopy coverage greater than 75 percent occurred in 82 percent of the 22 stands in the forest group. In an additional two stands, cover of *A. concolor* plus *A. magnifica* was greater than 75 percent. The forested stands that fell outside this group in the ordination (tree canopy coverage less than 75 percent), had greater than

TABLE 5. RELEVÉS OBTAINED ALONG A 250-m TRANSECT AROUND THE FLANK OF RIDGE ALONG THE 1750-m CONTOUR. All stands represent seral stages after the same fire. The environment became less "mesic" as the canyon in which the transect was taken widened and the slope became less protected (study site 12). Stands are arranged according to maturity and environment. Site 121 was most mature and most mesic whereas Site 126 was less mature and most xeric.

| | Stand number | | | | | | | | | | | |
| | 121 % cover | | 122 % cover | | 123 % cover | | 124 % cover | | 125 % cover | | 126 % cover | |
Species	Canopy	DBH <1 dm	Canopy	DBH <1 dm	Canopy	DBH <1 dm	Canopy	DBH <1 dm	Canopy	DBH <1 dm	Canopy	DBH <1 dm
Trees												
Abies concolor	75	15	60	2.5	50	7.5	24	15	8		1.5	
Pinus ponderosa							3		4		6	
Calocedrus decurrens				+		1	3		16	5	6	2.5
Pinus lambertiana					+				4		+	
Quercus kelloggii									8		+	
Total	75	15	60	3	50	8.5	30	15	40	5	14	2.5
Shrubs												
Chrysolepis sempervirens	1		+		5		5		15	15		
Garrya fremontii					15		5		30	25		
Arctostaphylos patula					10		40		30	55		
Ceanothus integerrimus							5			2.5		
Ceanothus cordulatus							5		5			
Prunus emarginata										+		
Quercus chrysolepis										+		
Total living brush	1		0		30		60		80	98		
Total dead brush	25		80		50		25		5	0		
Dead and alive shrubs	26		80		80		85		85	98		

5 percent cover of montane chaparral shrubs (Table 4). The importance of including information on canopy coverage, as well as species presence, in the ordination is illustrated by the high correlation coefficient for this ordination (r = 0.80) when compared with an ordination based solely on species presence (r = 0.64).

Stands 121 through 126 illustrate the potential influence of environmental conditions on the absolute time scale of the seral sequence (Table 5). These stands represent a transect from montane chaparral (125, 126) into a closed canopy *Abies concolor* forest (121, 122). The transect paralleled a gradient in aspect and exposure along a slope that had been burned uniformly, but where succession had proceeded more rapidly at the mesic end of the gradient. The changes in structure observed on the transect were similar to those discussed previously for other sites (Tables 2–4). A decrease in shrub canopy coverage from 98 to 1 percent between the xeric and mesic ends of the transect was associated with an increase in tree canopy coverage from 14 to 75 percent. Increased tree canopy density also corresponded with increasing cover by dead shrub canopies. In stand 122, where few living shrubs were observed, dead shrub canopy coverage was 80 percent.

The mesic end of the gradient supported *Abies concolor*-dominated forest. However, due to the xeric nature of the shrub-dominated end of this gradient, species composition of these stands was more typical of that at lower elevations. This resulted in a separation of the xeric stands (123 to 126) from other montane chaparral stands in the polar ordination (Fig. 2). Despite these large differences in species composition, the transect demonstrates a directional sequence in the polar ordination that parallels the sequence observed for the other stands.

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NOTEWORTHY COLLECTIONS

Readers and contributors will notice a change in the format of Noteworthy Collections beginning with this issue. Increased page charges are part of the reason for this change, but also there are available many local natural history and biology journals in which such contributions are just as appropriate, if not more so, than in the pages of Madroño. Herbarium label data and extensive lists of previous localities are here no longer considered publishable forms of information within the Noteworthy Collection format. Madroño's function will be to bring new records to the attention of floristic workers, who can then either write to collectors or borrow the cited specimens. Information submitted under the former heading of "previous knowledge" and complete information on "noteworthiness" will still be useful in judging the significance of the collections but will not necessarily appear in print.

Arizona

HYPOXIS MEXICANA Schult. (AMARYLLIDACEAE).—Cochise Co., Garden Canyon, Huachuca Mts. (T23S R11E S1), 1905 m; 7 Aug 1979, *McLaughlin and Bowers 1790* (ARIZ).

Significance. First collection in AZ since the late 1800's (*Lemmon 2891*).

LINUM SUBTERES (Trelease) Winkler. (LINACEAE).—Coconino Co., 5.5 km sw. of Pipe Springs National Monument (T40N R6W S25), 1520 m; 12 Aug 1979 *McLaughlin and Bowers 1813* (ARIZ).

Significance. Second collection in AZ. Collected in the same area in 1946 (*Parker 6243*) but not included in Ariz. fl. (Kearney & Peebles 1960).—JANICE E. BOWERS and STEVEN P. McLAUGHLIN, Office of Arid Lands Studies, Univ. Arizona, Tucson 85721. (Received 6 Jul 1981; accepted 26 Aug. 1981.)

California

ASPLENIUM TRICHOMANES L. (ASPLENIACEAE).—Del Norte Co.: ca. 36 m s. of 18 m falls on Myrtle Cr., Middle Fork of the Smith River, 3.5 km nne. of Hiouchi (T17N R1E in the se. corner of the nw.¼ of S33), 183 m, 30 Jun 1980, *Lang 1400* (SOC).

Significance. The first record for California. This collection extends the known range of the species s. and w. ca. 295 km of its nearest known location near McKenzie Pass, OR (*Cole 54,* OSC).—FRANK A. LANG, Dept. Biology, Southern Oregon State College, Ashland 97520 and VEVA STANSELL, Box 959, Gold Beach, OR 97444. (Received 29 May 1981; accepted 17 Aug 1981.)

ASTRAGALUS TEGETARIOIDES M. E. Jones (FABACEAE).—Lassen Co., Ash Valley, along Adin-Madeline Rd., 26 km e. of Adin (T38N, R11W, Sec. 32), 1500 m, 6 Jul 1980, *Nelson & Nelson* 5988 (HSC, NY). (Determined by Rupert C. Barneby.)

Significance. First known collection in CA, extending the range 325 km s. of its previously only known locations. This taxon is considered rare and endangered in OR and should be considered as such in CA. According to Barneby, the CA plants differ slightly from the OR ones, in that the calyx teeth are slightly longer, the banner is ca. 1 mm longer, and the corolla is purplish instead of white suffused with lilac. The habitat is also different. The CA population is growing in a sage brush steppe, whereas in OR they grow in a ponderosa pine forest.—THOMAS W. NELSON and JANE P. NELSON, Department of Biological Sciences, Humboldt State University, Arcata, CA. (Received 5 Dec 1980; accepted 23 Feb 1981.)

Montana

ANTENNARIA MONOCEPHALA D.C. (ASTERACEAE).—Deer Lodge Co., Anaconda-Pintlar Wilderness, E-Goat Pk. (T2N R14W S5), 2835 m, 10 Aug 1975, *Lackschewitz 6266* (MONTU, WTU).

Significance. First report for MT and contiguous USA.

GENTIANA TENELLA Rottb. (GENTIANACEAE).—Madison Co., Gravelly Range, n. flank of Cave Mt. (T10S R1W S32), 2890 m, 7 Sep 1977, *Stickney 3699,* MRC; Carbon Co., Beartooth Mts., 0.5 km s. of Moon Lake (T9S R18E S20), 3040 m, 15 Aug 1979, *Rosentreter 1535* (MONTU).

Significance. First records for MT, a range extension of 50 km e. from Yellowstone Natl. Park.

JUNCUS TRIGLUMIS L. (CYPERACEAE).—Carbon Co., Beartooth Mts., 1 km n. of WY border, 0.5 km n. of Glacier Lake (T9S R18E S29), 3000 m, 15 Sep 1976, *Lackschewitz 7033* (MONTU, MONT, COLO, NY, WTU); Hell Roaring Plateau, 3 km n. of WY border (T9S R18E S22), 3020 m, 11 Aug 1977, *Lackschewitz 7782* (MONTU, COLO, NY, WTU).

Significance. First records for MT, range extensions of 11 and 13 km from Park Co., WY.

KOENIGIA ISLANDICA L. (POLYGONACEAE).—Carbon Co., Beartooth Mts., just along WY border off Hwy 212 (T9S R19E S32), 2960 m, 13 Aug 1977, *Lackschewitz 7859* (MONTU); shallow pond, 1.5 km s. of Moon Lake (T9S R18E S29), 3040 m, 15 Aug 1979, *Lackschewitz 9150* (MONTU, MONT, COLO, WTU); 0.5 km s. of Albino Lake (T9S R17E S25), 3050 m, 30 Aug 1980, *Lesica 1027* (MONTU).

Significance. First reports for MT, all occurrences less than 12 km from nearest known populations in Park Co., WY.

LOMATIUM BICOLOR (Wats.) Coult. & Rose (APIACEAE).—Ravalli Co., Bitterroot Mts., e. slope off St. Josephs Rd. (T10N R20W S20 w.¼), 1730 m, 10 Jul 1974, *Lackschewitz 5153* (MONTU, NY). (Det. by A. Conquist, NY, 1976); Selway-Bitterroot Wilderness, divide w. above Tin Cup Lake (T2N R23W S1), 1980 m, 19 Jun 1971, *Lackschewitz 2728* (MONTU).

Significance. First report for MT.

MUSINEON VAGINATUM Rydb. (APIACEAE).—Missoula Co., ne. foothills of Bitterroot Mts., 19 km sw. of Missoula (T11N R20W S16 w.½), summit of "McClay Mt.", 1730 m, 29 May 1976, *Lackschewitz 6477* (MONTU, WTU); 8 Jul 1976, *Lackschewitz 6612* (MONTU, MONT, RM); Sapphire Mts., 9 km s. of Missoula (T12N R19W S30 nw.¼),

1310 m, 27 Apr 1978, *Lackschewitz 79320* (MONTU, MONT, WTU); 0.66 km e. above previous location, 1460 m, *Lackschewitz 7933* (MONTU); Granite Co., Garnet Range near Rattler Gulch Rd., 8 km w. of Drummond (T11N R13W S9 w.½), 1410 m, 13 May 1977, *Lackschewitz 7170* (MONTU, WTU, NY). (Collections confirmed by Ronald L. Hartman, RM, 1980.)
Significance. Range extension in MT of 270 km to the nw. from previously known occurrence in Gallatin Co.

PHACELIA THERMALIS Greene (HYDROPHYLLACEAE).—Phillips Co., C. M. Russell Natl. Wildlife Range, near Slippery Anne Ranger Station (T22N R23E S19), ca. 700 m, 12 Jun 1978, *Lackschewitz 8125* (MONTU, MONT, NY); Garfield Co., York Island in Fort Peck Reservoir (T25N R41E S82 w.¼), ca. 690 m, 28 Jun 1978, *Lackschewitz 8248* (MONTU).
Significance. First record for MT, ca. 800 km ne. of known range.

PLANTAGO HIRTELLA H.B.K. (PLANTAGINACEAE).—Ravalli Co., Sapphire Mt. (T4N R19W S7), Sleeping Child Hot Springs Resort, 1370 m, 3 Jun 1978, *Cory 1769* (MONTU, NY). (Det. by A. Cronquist, NY, 1980.)
Significance. First record for MT, more than 750 km from Grays Harbor, WA and first report of an occurrence this far inland in USA.

RIBES TRISTE Pall. (GROSSULARIACEAE).—Granite Co., Anaconda-Pintlar Wilderness, near Falls Fork of Rock Cr. (T3N R15W S29 se.¼), 2140 m, 25 Sep 1974, *Lackschewitz 5888* (MONTU); Falls Fork Rock Cr. (T3N R15W S19), 1980 m, 20 Jul 1975, *Lackschewitz 6076* (MONTU, NY, WTU).
Significance. First report for MT, about 300 km e. of occurrences in the Blue Mts. OR and WA.

RORIPPA SYLVESTRIS (L.) Besser (BRASSICACEAE).—Missoula Co., town of Missoula, Clark Fork island adjacent to U. of Montana campus, 970 m, 30 Jun 1979, *Lackschewitz 8940* (MONTU, WTU); Konah Ranch, Clark Fork island (T13N R2W S8 se.¼), 13 km w. of first collection, 940 m, 7 Aug 1979, *Lackschewitz 9127* (MONTU).
Significance. First report for MT, at least 280 km from nearest known occurrence.

SATUREJA DOUGLASII (Benth.) Briq. (LAMIACEAE).—Sanders Co., Cabinet Gorge (T27N R34W S20), 670 m, 13 Aug 1970, *Stickney 2197* (MRC, MONTU); Ravalli Co., Trapper Cr. Trail (T2N R21W S20), 1520 m, 18 Jul 1975, *Cory 1494* (MONTU).
Significance. First report for MT, 70 km e. of nearest known populations in Bonner and Idaho Cos., ID.

SAUSSUREA DENSA (Hook) Rydb. (ASTERACEAE).—Lewis & Clark Co., Bob Marshall Wilderness, n. part of "Chinese Wall", Cont. Divide (T24N R11W S31), 2470 m, 26 Jul 1979, *Lackschewitz 9113* (MONTU, COLO, WTU).
Significance. Second record for MT, 20 km w. of the occurrence in Teton Co.

VERONICA VERNA L. (SCROPHULARIACEAE).—Mineral Co., near Gold Cr. (T18N R21W S31 sw.¼) 3 km se. of St. Regis, 270 m, 19 May 1960, *Stickney 354* (MRC); Missoula Co., 10 km w. of Missoula near Butler Cr. (T14N R20W S24), 1100 m, 8 May 1968, *Stickney 1640* (MRC); Flathead Co., Hog Heaven Mining District (T25N R23W S16), 1190 m, 9 Jun 1977, *Lackschewitz 7283* (MONTU, NY, WTU); Missoula Co., Waterworks Hill n. of the town of Missoula (T13N R19W S15), 1070 m, 11 May 1978, *Lackschewitz 7941* (MONTU, MONT, WTU); Ravalli Co., Bitterroot Mts., Medicine Hot Springs, 1370 m, 21 May 1978, *Lackschewitz 7952* (MONTU, WTU); Missoula Co., bare hills n. of Missoula (T14N R19W S35), 1220 m, 28 May 1978,

Lackschewitz 7960 (MONTU, COLO, NY). (Verified by N. H. Holmgren, NY; W. A. Weber, COLO, 1980.)

Significance. First report for MT and N. America.—KLAUS H. LACKSCHEWITZ, PETER LESICA, ROGER ROSENTRETER, Dept. Botany, Univ. Montana, Missoula 59812, JACULYN K. CORY, SW581 Westside Rd., Hamilton, MT 59840 and PETER F. STICKNEY, Associate Plant Ecologist, For. Sci. Lab., Drawer C, Missoula, MT 59806. (Received 4 Mar 1981; accepted 7 Aug 1981.)

New Mexico

PLUMMERA AMBIGENS Blake (ASTERACEAE).—Hidalgo Co.: Maverick Spring Canyon, Peloncillo Mts. (T30S R21W S1 and S11), 1650 m, 15 Sep 1980, *Todsen 800815-1* (NMC).

Significance. The second locality in NM for this rare (proposed threatened) species, between the previously-known locations in NM and AZ.

EYSENHARDTIA POLYSTACHYA (Ortega) Sarg. (FABACEAE).—Hidalgo Co.: Beehive Canyon, Peloncillo Mts. (T29S R21W S33), 1800 m, 4 Sep 1979, *Todsen 790804-1* (NMC).

Significance. Confirmation of occurrence in NM and extension n. 60 km.

CUPHEA WRIGHTII Gray (LYTHRACEAE).—Hidalgo Co.: Skull Canyon, Peloncillo Mts. (T30S R21W S10), 1700 m, 3 Sep 1979, *Todsen 790803-1* (NMC).

Significance. First record from NM.

ASPICARPA HIRTELLA Rich. *sensu latu* (MALPIGHIACEAE).—Hidalgo Co.: Peloncillo Mts., Skull Canyon (T30S R21W S10), 1800 m, 3 Sep 1979, *Todsen 790803-2* (NMC), and Maverick Spring Canyon (T30S R21W S11), 1650 m, 6 Sep 1979, *Todsen 790806-1* (NMC). Verified by William Anderson.

Significance. First records for NM.

HEUCHERA GLOMERULATA Rosendahl, Butters, and Lakela (SAXIFRAGACEAE).—Hidalgo Co.: Animas Peak (T31S R19W S28), 2100–2500 m, 28 May 1977, *Todsen 770528-1* (NMC).

Significance. First record for NM. A range extension of 50 km se.—THOMAS K. TODSEN, Dept. Biology, New Mexico State Univ., Las Cruces 88003. (Received 23 Mar 1981; accepted 28 May 1981.)

Utah

CAREX MICROGLOCHIN Wahl. (CYPERACEAE).—Duchesne Co., Ashley Natl. For., Uinta Mts., S. Fork Rock Cr. 50 km nw. of Duchesne (T2N R8W nw.¼ USM), 2805 m, 26 Aug 1980, *S. Goodrich 15061* (BRY, NY, OGDF).

Significance. First record for UT, a w. range extension from c. CO.

CAREX PARRYANA Dewey (CYPERACEAE).—Just below Joe's Valley Dam (T18S R6E 24), 2190 m, s. facing slope, 25 Jun 1977, *M. E. Lewis 4765* (OGDF); head of Rilda Canyon (Big East Mt.) (T16S R6E S17), 3110 m, 8 Aug 1977, *M. E. Lewis 5125* (BRY, OGDF); San Rafael Swell, Old Smiths Cabin (T21S R14E S5), 1390 m, 5 Jun 1979, *J. Harris 326* (BRY).

Significance. Range extension of 300 km from Cache Co. UT.

EPILOBIUM NEVADENSE Munz. (ONAGRACEAE).—Millard Co., Fishlake Natl. For., Canyon Mts., Eightmile Cr. 11 km w. of Scipio (T18S R3W S32 sw.¼), 2347 m, 12 Aug 1980, *S. Goodrich 14918* (BRY, MO); above the head of John Williams Canyon, 11 km nw. of Scipio (T17S R3W S29 e.¼), 2710 m, 2 Sep 1980, *S. Goodrich 15144* (BRY, MO).

Significance. A range extension of 230 km from s. UT.

KOBRESIA SIMPLICIUSCULA (Wahl.) Mack. (CYPERACEAE).—Duchesne Co., Ashley

Nat. For., Uinta Mts., S. Fork Rock Cr. 50 km nw. of Duchesne (T2N R8W S24 nw.¼ USM), 2805 m, 26 Aug 1980, *S. Goodrich, 15068* (BRY, NY, OGDF). Emery Co., Scad Valley Meadow (T16S R6E S27), 2590 m, 24 Jul 1980, *M. E. Lewis 6620* (OGDF).

Significance. First records for UT, a s. range extension of 370 km from Driggs, ID, and a w. range extension of about equal distance from CO.—SHEREL GOODRICH, Shrub Sciences Laboratory, Intermt. For. and Range Exp. Sta., USDA For. Serv., Provo, UT 84601, and MONT E. LEWIS, R-4 USDA For. Serv., Ogden, UT 84401. (Received 10 Jul 1981; accepted 26 Aug 1981.)

NOTES AND NEWS

WOOD ANATOMY OF *Actinocheita* (ANACARDIACEAE).—*Actinocheita* is a monotypic genus (*A. potentillifolia* (Turcz.) Bullock) of anacards occurring in the states of Guerrero, Oaxaca and Puebla, Mexico. Although originally included in *Rhus,* Barkely (Ann. Missouri Bot. Gard. 24:1–10. 1937) removed the species from *Rhus* and placed it in its own segregate genus (*Actinocheita*), primarily on the basis of its axillary panicles, ovary on a gynobase, and long-villous trichomes covering the fruit. (It should be mentioned that there has been some disagreement regarding the correct specific epithet for this taxon. It appears that *A. potentillifolia* should be used instead of *A. filicina* (DC.) Barkley; see Barkley and Reed, Amer. Midl. Nat. 21:368–377. 1939; Barkley, The Biologist 28:9–23. 1945; Bullock, [Kew] Bull. Misc. Inform. 440–441. 1937; 337–339. 1939.) The purpose of this note is to present data on the wood anatomy of *A. potentillifolia* and to compare these data with those of species of *Rhus* and other Anacardiaceae.

Wood of *A. potentillifolia* was collected by the author south of Oaxaca, Mexico and voucher specimens (*Young 106, 107*) were deposited in RSA and duplicates in ILL. Wood samples were prepared and analyzed as described elsewhere (Young, Aliso 8:133–146. 1974), and reference slides are available from the author.

The wood of *A. potentillifolia* is distinctly diffuse porous, and the mean vessel member diameter was 76 μm (range = 30–115 μm, s^2 = 283). Vessels were mostly solitary or in short multiples, and the mean number of vessels/mm² was 33 (range = 26–40). All vessel members had simple perforation plates and were somewhat angular in outline, with alternate pitting on the lateral vessel walls (pits more or less elliptical). Mean vessel member length was 489 μm (range = 280–650 μm), and mean libriform fiber length was 942 μm (range = 570–1100 μm). Tracheids were not detected. Vessel members also lacked helical sculpturing on their walls. Only uniseriate and biseriate rays were present, and the former predominated. Mean uniseriate ray height was 528 μm (range = 280–1150 μm). The rays were heterogeneous with upright, procumbent (predominated) and square cells. Crystals were present in the rays, but resin canals were not detected. Axial parenchyma was scanty paratracheal.

In its wood anatomy, *A. potentillifolia* is similar to *Rhus* as well as many other genera of tribe Rhoeae in possessing the following features: (1) simple perforation plates; (2) libriform fibers (no tracheids); (3) alternate, elliptical pitting on lateral vessel walls; and (4) heterogeneous, mostly uniseriate rays. The most distinctive feature distinguishing the wood of *A. potentillifolia* from that of species of *Rhus* is that the wood of *Actinocheita* is diffuse porous (with few vessels/mm²), whereas that of all *Rhus* taxa studied to date is ring porous (with many vessels/mm²) (Young, Aliso 8:133–146. 1974). In this regard, *Actinocheita* is similar to *Malosma, Metopium, Amphipterygium* and most other genera of Rhoeae. Only four genera of Rhoeae (*Cotinus, Pistacia, Rhus* and

Toxicodendron) have ring porous wood (Heimsch, Lilloa 8:84–198. 1942). *Actinocheita* also differs from *Rhus* in having much longer vessel members (x̄ = 489 μm in *Actinocheita*; x̄ = 275 μm in *Rhus* subgen. *Rhus* and 208 μm in *R.* subgen. *Lobadium*) and libriform fibers, and in lacking helical sculpturing of vessel walls. Again, in these features *Actinocheita* more closely resembles *Malosma* and *Metopium* than it does *Rhus*. *Actinocheita* differs from *Malosma* and *Metopium* in lacking resin canals in its rays.

In my opinion, the data presented here support Barkley's contention, based upon vegetative features, that *A. potentillifolia* should be segregated from *Rhus* proper. In terms of its wood anatomy, *Actinocheita* is as distinct from *Rhus* as are *Malosma* and *Metopium,* and even more so than *Cotinus*.—DAVID A. YOUNG, Department of Botany, University of Illinois, Urbana 61801. (Received 6 Feb 1981; accepted 12 Mar 1981.)

MISCELLANEOUS CHROMOSOME NUMBERS IN ASTERACEAE.—Vouchers for the following chromosome counts are deposited at MO unless otherwise indicated. Both meiotic and mitotic counts were made in material fixed in 3 parts absolute ethanol to 1 part glacial acetic acid and stained in acetocarmine.

Anthemis cotula L. $2n = 9$ bivalents. San Luis Obispo Co., CA, *Raven 20160*.

Arnica longifolia D. C. Eat. ssp. *myriadenia* (Piper) Maguire. $2n$ = ca. 50. Mono Co., CA, *Raven 20802*.

Chrysanthemum coronatum L. $2n = 6$ bivalents + ring of 6. San Diego Co., CA, *Raven 20168*.

Erigeron peregrinus (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. $2n = 9$ bivalents. Tuolumne Co., CA, *Raven 20803*.

Gnaphalium chilense Spreng. $2n = 14$ bivalents. Tuolumne Co., CA, *Raven 20822*.

Grindelia hirsutula H. & A. $2n = 12$ bivalents. Napa Co., CA, *Raven 20200*.

Leucanthemum vulgare Lam. (*Chrysanthemum leucanthemum* L.). $2n = 9$ bivalents. Tuolumne Co., CA, *Raven 20804*.

Santolina chamaecyparissus L. $2n$ = ca. 45, up to 9 bivalents, the rest univalents. Cultivated, Los Angeles Co., CA, *Raven 20164*.

Santolina virens Mill. $2n = 9$ bivalents. Cultivated, Los Angeles Co., CA, *Kyhos 64-087*.

Sonchus asper (L.) Garsault. $2n = 9$ bivalents. Napa Co., CA, *Raven 20201*.

Tanacetum douglasii DC. $2n = 27$ bivalents. Humboldt Co., CA, *Munz 19869* (progeny, RSA *8726*), *Everett & Balls 18636* (progeny, RSA *8537*).

Tanacetum huronense Nutt. $2n = 54$. Ca. 3.5 mi. sw. of Mackinaw City, Cheboygan Co., MI, *Voss* (MICH).

Studies made by Raven of populations along the coast of northern California and in cultivation at Rancho Santa Ana Botanic Garden, Claremont, in 1961–1962, convinced him that the entities that have been called *Tanacetum camphoratum* Less. and *T. douglasii* DC. cannot be distinguished by any constant set of characteristics and should not be regarded as taxonomically distinct at any level. Populations that occur on the coastal dunes of Mendocino and Humboldt Counties are highly variable. This western entity is closely related to *T. huronense* Nutt., and probably should not be regarded as specifically distinct either from it or from the circumpolar *Tanacetum bipinnatum* (L.) Schultz Bip., the first-named species in the complex, which also has $2n = 54$. The whole entity is thus evidently hexaploid. A map of the ranges of the included "species" in North America has been given by Mickelson and Iltis (Proc. Wisconsin Acad. Sci. 55:200–203. 1966; see also Hultén, Fl. Alaska, p. 892.)—DONALD W. KYHOS, University of California, Davis 95616 and PETER H. RAVEN, Missouri Botanical Garden, P.O. Box 299, St. Louis 63166. (Received 23 Feb 1981; accepted 2 Mar 1981.)

REVIEWS

Plants of Deep Canyon and the Central Coachella Valley, California. By JAN G. ZA-
BRISKE. x + 174 p. Univ. of California, Riverside. 1979. Hardbound $14.95; softbound
$8.95.

Deep Canyon, draining into the western Colorado Desert from the north slope of the
Santa Rosa Mountains, is the site of the Philip L. Boyd Deep Canyon Research Center
of the University of California, Riverside. This large drainage, from 2657-m Toro Peak
to the desert floor, is diverse in topography and vegetation: it is divided here into nine
habitat areas, as shown on a foldout contour map in color. After an introduction and
a short chapter on the climate, the book discusses the physical setting and the vegetation
for each habitat area, giving much interesting information. The appearance of the
vegetation is shown by 20 clear photographs. These also help identify a few prominent
plants, and individual drawings show a dozen others. An appendix gives more detailed
information: a checklist of 619 plants, with altitudinal ranges shown graphically; and
data from 22 surveys of perennial plants, at 122-m elevational intervals, each along a
400-m horizontal line.

This attractive book will be a useful introduction to the plants for visiting biologists
working at the Research Center. And because representative parts of the drainage are
crossed by or easily reached from Highway 84 and the Toro Peak road, it will have a
wider usefulness, helping and encouraging the botanical public to learn about this
interesting broad transect of vegetation.—REID MORAN, Natural History Museum, San
Diego, CA 92112.

Flora Silvestre de Chile. Zona Central. By ADRIANA HOFFMANN J. 255 p. Ediciones
Fundación Claudio Gay, Santiago, Chile. 1980. (Price not given.)

This paperback guide to the wildflowers, vines, shrubs, and trees of the central zone
of Chile is a welcome addition to the sparse literature on the interesting flora of that
country. The area covered is between Los Vilos at ca. 32° in the north and Constitución
at about 35° in the south, a distance of 400 km. This area, which includes the capital
city of Santiago, is referred to as the Matorral Mediterranean Zone. Within this zone
there are three floristic regions: the coastal strip (including the coastal ranges), the
central valley (mostly cultivated), and an Andean area.

This attractive handbook illustrates and describes approximately 450 species of woody
and herbaceous plants that occur in this region. The guide is color-coded, a practice
that is a familiar one in the North American popular-guide literature. The first part of
the book is devoted to woody plants; subsequent sections cover herbaceous plants with
white, blue to purple, red or rose, and yellow or orange flowers respectively. The brief
descriptions of the species are given on even-numbered pages, and watercolor illustra-
tions are grouped opposite these on odd-numbered pages. Though there are no keys,
the quality of the illustrations is excellent and should make identifications of unknowns
quite easy.

In view of the climatic similarities between central Chile and cismontane California,
it is not surprising that the two regions share a number of plant introductions from the
Old World. Wild radish, scarlet pimpernel, Bermuda buttercup, mullein, cichory, hem-
lock, sweet clover, and other exotics abound in both regions. California has contributed
Lupinus arboreus and *Eschscholzia californica* to the Chilean flora; both are extremely
common there. Other familiar genera are native to this central zone: there are indigenous
Chilean members of *Lepechinia, Ribes, Baccharis, Salix, Haplopappus, Collomia,
Clarkia, Calandrinia, Phacelia,* and other genera also represented in western North
America. In addition to these are genera with a Latin American flavor such as *Mutisia,
Lapageria, Puya, Alstroemeria, Azara, Escallonia, Nolana,* and *Tropaeolum.*

The book presents a general discussion of ecological characteristics of the central

zone, origins of common names, an introduction to classification and nomenclature, hints on photographing and pressing plants, a brief history of Chilean botany, and a partially illustrated glossary of terms. Interestingly, "How to use this field guide" appears in English as well as Spanish, and English common names are given for the exotics. The nomenclature used seems to be up to date, though the author still recognizes *Godetia* and *Jussiaea*. This guide is thoroughly professional in all respects, and I trust it will prove to be a forerunner of others in Chile and elsewhere in South America.— ROBERT ORNDUFF, Department of Botany, University of California, Berkeley, CA 94720.

The California Islands: Proceedings of a Multidisciplinary Symposium. Edited by DENNIS M. POWER. vii + 787 p. Santa Barbara Museum of Natural History, Santa Barbara, CA. 1980. $20.00, paper.

The task of organizing and preparing for publication papers presented in any symposium is tremendous; but when the symposium is multidisciplinary, as was that on the California Islands held at Santa Barbara Museum of Natural History, Santa Barbara, California, from 27 February to 1 March 1978, the accomplishment deserves highest praise. Dennis M. Power is to be congratulated. Over 400 people attended the symposium and 69 papers were on the program. Of these, 43 are included in this published record. The California Islands are delimited as extending from Isla Cedros and Islas San Benitos, Baja California, Mexico (ca. Lat. 28°N) on the south to the Farallon Islands, California (ca. Lat. 38°N) on the north.

The papers included in the Proceedings are grouped under the following headings: Geologic History and Paleontology (3 papers); Prehispanic Man (2 papers); Vegetation Changes and the Impact of Feral Animals (5 papers); Evolution and Ecology of Land Plants (5 papers); Biogeography, Evolution, and Ecology of Marine Organisms (14 papers); Biogeography, Evolution, and Ecology of Land Animals (14 papers); Summary. Many of the papers present summaries of early work in addition to treating results of investigations carried on since the Symposium on the Biology of the California Islands organized in 1965 by the Santa Barbara Botanic Garden.

Berger's paper on early man on Santa Rosa Island indicates the presence of man on this island in association with dwarf mammoth remains, a discovery which may push the dates of man on the island, and even in the Americas, back 40,000 years. The impact of man, both prehistoric and modern, and his introductions (fire, goats, cattle, sheep, pigs) on the vegetation is an inter-relationship that is discussed not only in the second and third sections, but also in many papers of other groups.

Discussions of the relatively recent plate tectonics theories are tucked into such papers as those by Wenner and Johnson and by Yanev. It would have been useful to have had a paper devoted to this subject alone.

In comparison with the number of papers devoted to marine and land animals, those treating plants are disappointingly few. The Baja California islands and the northern islands received comparatively little attention in the Symposium—even less in the zoological papers than in the botanical ones. The majority of the papers are concerned with the Channel Islands.

An important part of the volume is the inclusion of references for each paper. Many of the bibliographies are extensive and will be most helpful to future workers. Even though quality of the contributions varies, the Proceedings will serve as a valuable reference work for those interested in the biology of the California Islands.

An excellent summary by Dennis Power unifies the volume. He speaks of new research tools that have been brought into play in the work represented by the papers presented. He also discusses the distribution and biology of species under such subsections as aboriginal man, recent landscape changes, and conservation. ANNETTA M. CARTER, Herbarium, Department of Botany, University of California, Berkeley, CA 94720.

The Road I Came. The Memoirs of a Russian-American Forester. By N. T. MIROV. An autobiography. 227 p. The Limestone Press, Kingston, Ontario. 1980. ISBN 0-919642-84-5.

This book was authored by Dr. Mirov at the request of his family. It was written in such an interesting fashion that it was felt by the family that it should be shared with the botanical community. It was published in 1978 and is available through Joan Mirov, 453 Tahos Road, Orinda, CA 94563. The first printing was small and the second printing will be priced around $15.00.

It is comprised of three parts: The Old World—his early years 1893–1912, college days 1912–1916, war and the revolution 1916–1922, life in China 1920–1923; The New World—dealing in how he became interested in forestry, early experiences in San Francisco, Florida, the Scott Mountains and journeys to Europe and Asia; The Remaining Years—lecture tours, Canada, USSR, New Zealand, and Australia.

This book is enhanced by 35 good quality pictures and two maps. It is exciting, amusing, and the reader will find himself experiencing a range of emotions as the vicissitudes of Mirov's life are encountered. Two memorable anecdotes relate to his introduction to the concept of species while a student in Russia and the beginning of his botanical career as a naturalist on the island of Baikal.—WALTER KNIGHT, Field Associate, California Academy of Sciences, San Francisco, CA 94118.

Edward Stuhl's Wildflowers of Mount Shasta. By Edward Stuhl and Marilyn Clement Ford. Clementine Publishing Co., 123 N. Spring St., Klamath Falls, OR 97601. 1981.

This book is oriented to the general public although it will be of interest to professional botanists. The introduction is written by Dr. Wm. Bridge Cooke, author of *Flora of Mount Shasta.* Of the 650 species of vascular plants in the area, 204 are depicted in full color paintings by Stuhl. The book's 134 pages include beautiful black and white photographs of the mountain, an account of its plant communities, a descriptive index of the flora, the history of the area, and an account of the botanical explorations there. Hard cover $33.00, soft cover $27.00.—WALTER KNIGHT, Field Associate, California Academy of Sciences, San Francisco, CA 94118.

ANNOUNCEMENT

On Saturday 24 Oct 1981, Southern California Botanists and the Department of Biological Sciences, California State University, Fullerton, will co-sponsor a symposium on "Cacti and Succulents" in honor of Dr. Lyman Benson. It will be held in the University Center Multipurpose Room, California State University, 800 N. State College Blvd., Fullerton. General admission is $10.00, students and Southern California Botanists members, $5.00. One unit of college credit is available through CSU Extended Education. For further information, call (714) 773–2611.

Program: Ecology and evolution of the Galápagos opuntias (Dr. E. F. Anderson, Whitman College); Cactus alkaloids: chemotaxonomy (Dr. Jerry McLaughlin, Purdue Univ.); Innovative structural designs of cacti (Dr. A. C. Gibson, UCLA); Responses of cacti and succulents to water stress: shifts in metabolism from C_3 to CAM (Dr. I. P. Ting, UC, Riverside); Cactus chromosomes and hybridization (Dr. D. Pinkava, Arizona St. Univ.); Stonecrop family: variations on a pattern (Dr. Reid Moran, Nat. Hist. Museum, San Diego). Followed by a reception hosted by CSUF.

HERBARIUM NEWS

The Herbarium staff of the University of California, Santa Barbara, has initiated a publication series which serves as a vehicle for UCSB students, faculty and staff and other associated investigators. Manuscripts accepted for publication include primarily those with floristics emphasis and those for which voucher specimens are deposited at UCSB. Papers published in this series might not be available otherwise to the general scientific community. This endeavor is consistent with the goals of the UCSB Herbarium, summarized as follows: (1) to maintain a collections repository; (2) to provide botanical services; (3) to function as a research facility within the Department of Biological Sciences; and (4) to provide educational programs.

UCSB Herbarium Publication Number I, A Flora of Valentine Eastern Sierra Reserve, is a product of floristic research conducted by UCSB students, and consists of two parts (97 pages): Part I, Valentine Camp, by Ann Howald; and Part II, Sierra Nevada Aquatic Research Station, by Bruce Orr. Valentine Eastern Sierra Reserve (VESR) is managed by the University of California, Santa Barbara, as part of the University of California's Natural Land and Water Reserves System (NLWRS). Mrs. Edward L. Valentine donated one portion of VESR, Valentine Camp, to the University in 1973. The property consists of 136 acres immediately below the Mammoth Lakes Basin at an elevation of about 8000 ft. (2667 m). This parcel provides an unusually diverse sample of Eastern Sierra habitats on the ecotone between the sagebrush desert of the Great Basin and the coniferous forests of the higher Eastern Sierra.

The Sierra Nevada Aquatic Research Station (SNARL) was originally established in 1935 by the Bureau of Sports Fisheries and Wildlife. The SNARL facilities were turned over to the University in 1973. Situated eight miles southeast of the community of Mammoth Lakes, at an elevation of about 2333 m, SNARL's 53 acres lie just below the steep eastern slope of the Sierra Nevada. High Desert Riparian Woodland, Great Basin Sagebrush and Riparian Meadow Vegetation are plant communities found within the boundaries of SNARL.

A limited number of copies of this publication have been made available through a grant from the Valentine Endowment Fund. Requests for complimentary copies should be sent to Wayne R. Ferren, Jr., Senior Museum Scientist, UCSB Herbarium, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

The 1981 Jesse M. Greenman Award

The 1981 Jesse M. Greenman Award has been won by William R. Buck for his publication "A generic revision of the Entodontaceae" (Journ. Hattori Bot. Lab. 48:71–159. Aug. 1980). This monographic study is based on a Ph.D. dissertation from the Department of Botany, University of Michigan, Ann Arbor.

The Greenman Award, a cash prize of $250, is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation which was published during the *previous* year. Papers published during *1981* are now being considered for the 15th annual award, which will be presented in the summer of 1982. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, USA. In order to be considered for the 1982 award, reprints must be received by 1 July 1982.

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POPULUS × INOPINA HYBR. NOV. (SALICACEAE), A NATURAL HYBRID BETWEEN THE NATIVE NORTH AMERICAN P. FREMONTII S. WATSON AND THE INTRODUCED EURASIAN P. NIGRA L.

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ABSTRACT

Populus × **inopina** Eckenwalder is a putative natural hybrid between *P. fremontii* S. Watson and *P. nigra* L., species of distinct subsections of sect. *Aigeiros* Duby. It has been found in association with both parents along Coyote Creek, Santa Clara County, California. Morphological features and chromatographic profiles of leaf flavonoids of trees growing at this site support a hybrid interpretation of the type tree and suggest possible backcrossing to both parents. Apparent absence of similar hybrids at other localities at which *P. nigra* has been planted may reflect the unisexuality of the introduced trees. While most specimens of *P. nigra* planted in the range of *P. fremontii* are staminate individuals, the trees planted at Coyote Creek are pistillate, creating a situation favoring hybridization.

Populus fremontii S. Watson (sect. *Aigeiros* Duby) is a southwestern tree that frequently hybridizes with *P. deltoides* Marshall (sect. *Aigeiros*) and with *P. angustifolia* James and *P. trichocarpa* Torrey & A. Gray (both sect. *Tacamahaca* Spach) in their regions of sympatry (Eckenwalder 1977b, in press). No other natural hybrids of this species have previously been reported. Although *P. deltoides* and *P. trichocarpa* are often used as parents in interspecific poplar breeding programs, the small size and poor form of *P. fremontii* have usually excluded it from such programs (Zsuffa 1975). Stout and Schreiner (1933) reported crossing *P. fremontii* as female parent with *P. deltoides* (also the reciprocal cross), *P. trichocarpa, P. nigra* L. (sect. *Aigeiros*), and *P. × berolinensis* Dippel (*P. nigra* × *P. laurifolia* Ledebour (sect. *Tacamahaca*)), but they apparently considered the hybrids unsuitable for cultivation, presumably discarded them, and did not describe them. Thus hybrids of *P. fremontii* with sympatric native species have been described, but not those with any exotic species. I found a single locality in California at which *P. fremontii* has apparently hybridized successfully with the introduced black poplar, *P. nigra*.

MATERIALS AND METHODS

The population of cottonwoods containing the putative hybrid lines Coyote Creek in the Hellyer Unit of Coyote Creek County Parkway, San Jose, Santa Clara County, California. The site is developed for recreation but the vicinity of the creek retains its riparian woodland. Some poplar trees are planted in this area (including a row of *P. nigra*)

but most are apparently spontaneous (including *P. fremontii* and the hybrids). Presence of saplings as well as mature trees confirms the existence of conditions favoring regeneration. I first visited the site in November 1975 and sampled shoots bearing early and late leaves (Critchfield 1960, Eckenwalder 1977a) and mature winter buds. Shoot cuttings were also made, rooted in sand, and grown in a greenhouse at the University of California, Berkeley. Swelling, staminate flower buds for chromosome counts were collected in March 1976 and preserved in 3:1 (v/v) ethanol/acetic acid. Shoots bearing male and female flowering catkins were also collected in March and fruiting specimens in April. Reproductive specimens only partly duplicated the original vegetative specimens. Vegetative and reproductive specimens were assessed for characteristics distinguishing *P. fremontii* from *P. nigra* and used to construct a hybrid index. Description of the hybrid was based on specimens from two individuals. Quantitative features of the description bracket the normal range and include outlying extremes in parentheses. Following these figures are means and coefficients of variation (mean divided by standard deviation × 100%) determined by measurement of ten randomly selected organs of each type.

Chromosome counts were made from pollen mother cell squashes stained in acetocarmine and from aceto-orcein-stained root tip squashes from plants cultivated in the greenhouse (Smith 1974). The small size of the chromosomes precluded analysis of meiotic pairing behavior in presumptive hybrids. Pollen fertility was assessed using percent stainability of 200 grains per sample by aniline blue in lactophenol, a method that may overestimate fertility (Hauser and Morrison 1964). Diameters of 10 unacetolyzed grains per sample were measured in glycerine jelly mounts.

Single leaves of each individual sampled from the population were crushed and extracted in enough acidified (5% HCl) methanol to cover the fragments. Two-dimensional paper chromatograms of each extract were developed on 46 by 57 cm sheets of Whatman 3MM paper in TBA (3:1:1 (v/v) tert-butanol/acetic acid/water) and in 15% aquaeous acetic acid according to the methods of Mabry et al. (1970), which emphasize flavonoids and other polyphenolics. The resulting chromatographic profiles were compared with reference profiles for *P. fremontii* and *P. nigra* obtained by exhaustive extraction of bulk samples (Eckenwalder 1977b). Some compounds of the reference profiles were tentatively identified using chromatographic techniques and by reference to previous studies of flavonoids in the genus (Hegnauer 1973, Crawford 1974, Jones and Seigler 1975). Similarities of chromatographic profiles to standard *P. nigra,* ranging from 12 to 58%, were scaled for the individuals of the local population from 0 (*P. fremontii*) to 100 (*P. nigra*) to construct a chemical index.

Voucher specimens will be deposited at TRT and UC.

TABLE 1.   COMPONENTS OF A HYBRID INDEX SEPARATING *P. fremontii* FROM *P. nigra* USING TEN VEGETATIVE CHARACTERS. Scores of 0 for each character identify character states of *P. fremontii*, whereas scores of 2 identify those of *P. nigra*. Intermediate states score 1. Typical *P. fremontii* would total 0 on the hybrid index while typical *P. nigra* would total 20.

Character	States characteristic of		
	P. fremontii	Intermediates	*P. nigra*
	Score 0	Score 1	Score 2
Terminal twig thickness	>5.0	4.5–5.0	<4.5
Winter bud color	greenish tan	brown	red brown
Vesture of bud scales	dense	thin	glabrous
Terminal bud scale number	10–12	9–10	7–9
Flowering bud scale number	5–6	4	3–4
Flowering bud curvature	straight	hooked at tip	curved
Early leaf tooth number	8–14	15–19	20–25
Lamina width/length ratio	>1.1	1.0–1.1	<1.0
Apex length/width ratio	<1.0	1.0–1.6	>1.6
Lamina base shape	cordate	W-shaped	cuneate
Total index value	0	10	20

RESULTS

A hybrid index based on ten vegetative characters known to separate *P. fremontii* from *P. nigra* (Table 1; Eckenwalder 1977b) clearly groups most sampled individuals with one or the other of the two species (Fig. 1). The putative F_1 hybrid (*Eckenwalder 1132*) is the only tree with an intermediate hybrid index score. This individual is intermediate between the presumptive parents in leaf form (Fig. 2) as well as in many other features. It has a reduced pollen fertility of 56.5% (Table 2, Fig. 1), close to the 55% average for the comparable Eu-

TABLE 2.   POLLEN CHARACTERISTICS OF *P. fremontii* AND *P. × inopina* FROM COYOTE CREEK AND OF SPECIMENS OF *P. nigra* 'ITALICA' CULTIVATED ON THE UNIVERSITY OF CALIFORNIA, BERKELEY CAMPUS. Average diameter and standard deviation in μm of 10 grains of each sample mounted in glycerine jelly. Percent stainability of 200 grains of each sample mounted in aniline blue in lactophenol (lcb). Collection column includes Eckenwalder collection number.

Taxon	Collection	Diameter	Stainability
P. nigra 'Italica'	*1180*	23.0 ± 1.95	91.0
P. nigra 'Italica'	*1182*	21.2 ± 1.48	96.0
P. × inopina	*1172 (=1132)*	31.9 ± 5.69	56.5
P. fremontii subsp. *fremontii*	*1171 (=1127)*	23.6 ± 2.31	87.5
P. fremontii subsp. *fremontii*	*1173*	23.6 ± 1.26	98.5
P. fremontii subsp. *fremontii*	*1174*	24.5 ± 1.68	96.5
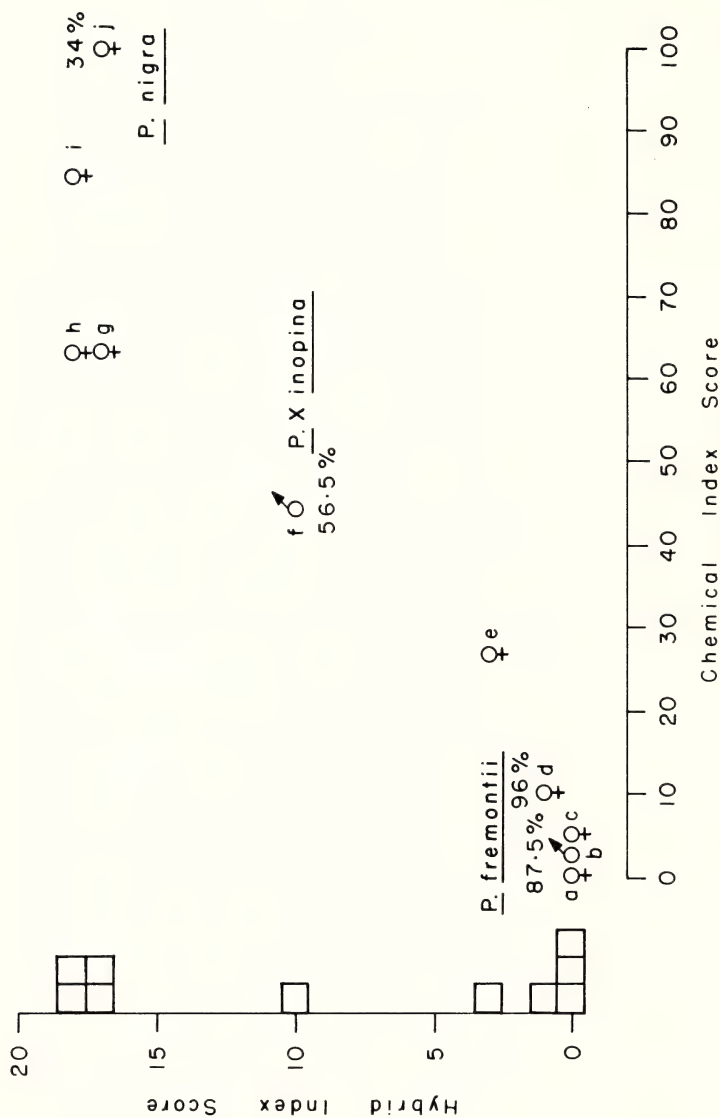
Fig. 1. Hybrid index score (ordinate) versus chemical index score (abscissa) of poplars from Coyote Creek. Scores of individuals localized by conventional sex symbols. Eckenwalder collection numbers: *P. fremontii:* a—*1125*, b—*1127* (=*1171*, pollen fertility 87.5%), c—*1126*, d—*1128* (=*1186*; *1200*, capsule maturation 96% based on 8 catkins with 25–35 flowers), e—*1131*; *P.* × *inopina:* f—*1132* (=*1172*; *1185*, pollen fertility 56.5%); *P. nigra:* g—*1130*, h—*1134*, i—*1133*, j—*1129* (=*1199*, capsule maturation 34% based on 7 catkins with 35–45 flowers).
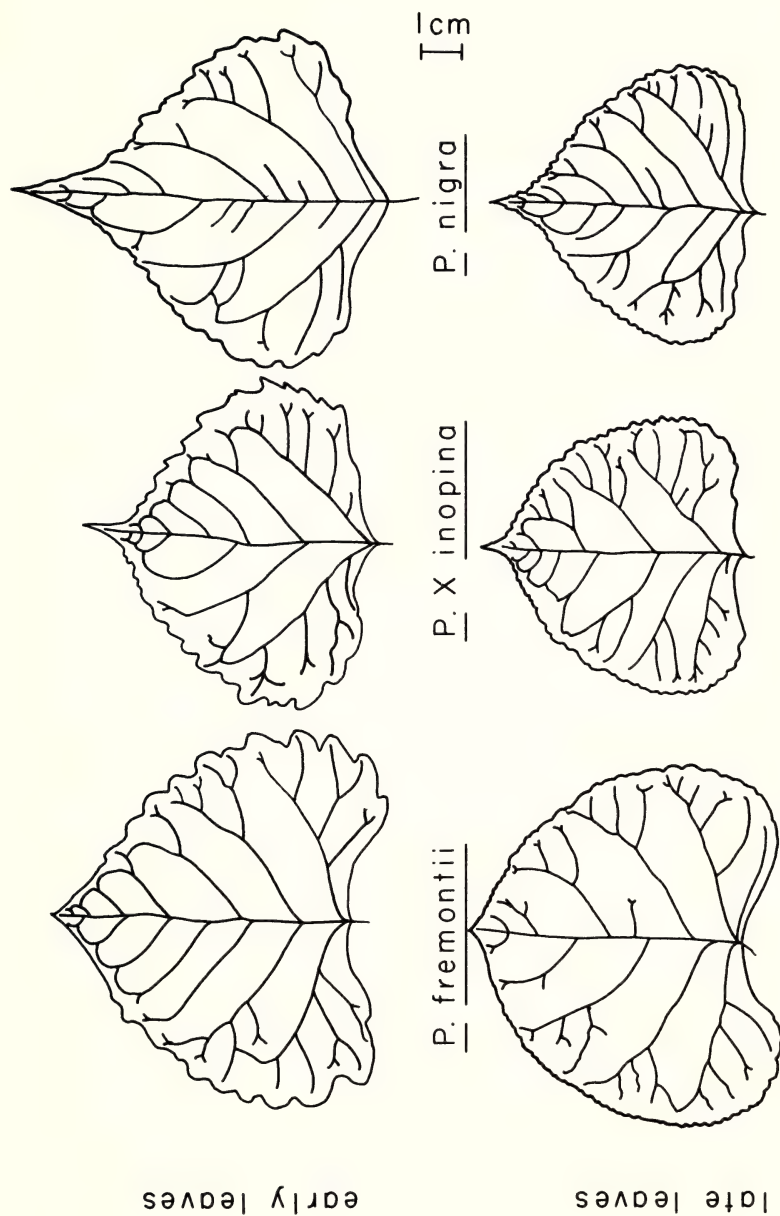
Fig. 2.   Tracings of early and late leaves of *P. fremontii*, *P.* × *inopina*, and *P. nigra* with major venation. Eckenwalder collection numbers: *P. fremontii*: early leaf—1127, late leaf—1125; *P.* × *inopina*: 1132; *P. nigra*: 1129. Scale bar = 1 cm.

roamerican hybrid, *P.* × *canadensis* Moench (*P. deltoides* × *P. nigra*; Smith 1943, Eckenwalder 1977b). Its pollen grains are larger than those of either parent, but are also much more variable in size (Table 2), probably reflecting meiotic irregularities (Smith 1943).

In contrast to the sharp delineation of the two species and their hybrid by the hybrid index scores, chemical index scores (Fig. 1) are more variable. Although *P.* × *inopina* is still nearly intermediate (chemical index 44), the remaining individuals are not as tightly clumped by their chemical index scores as they were by the hybrid index. The scoring of the hybrid index, however, was biased to include most variation in states assigned to the parent species and the appearance of the plants suggested more intergradation than is indicated by their index scores. Morphologically, some individuals of the Coyote Creek population seem like typical representatives of *P. fremontii* or *P. nigra,* but chromatographic profiles (Table 3, Fig. 3) show that these individuals contain compounds more typical of the other species than of their own species elsewhere (e.g., compounds 1–12, 42, 43 in *P. fremontii* and 15–24 in *P. nigra*). Individuals in this population have only 21 of the 37 compounds known from the reference profiles of *P. fremontii* (31 compounds) and *P. nigra* (18 compounds; Eckenwalder 1977b). The individual of *P.* × *inopina* has an additive chromatographic profile typical of interspecific hybrids (Alston and Turner 1962). The predominant flavones of *P. fremontii* (compounds 23 and 24) are combined in *P.* × *inopina* with the flavonols that dominate the profile of *P. nigra* (compounds 27, 41–43, 51 and 53). This additive profile parallels those found in intersectional hybrids between North American species of sections *Aigeiros* and *Tacamahaca* (Crawford 1974, Jones and Seigler 1975, Eckenwalder, in press).

Individuals identified as hybrids between *P. fremontii* and *P. nigra* at Coyote Creek are intermediate between these species in morphological and chemical features. They may be described as:

Populus × **inopina** Eckenwalder, hybr. nov.

Arbor verosimiliter ex hybridatione inter *P. nigra* L. et *P. fremontii* S. Wats. orta. Inter his species intermedium est in ramulis, gemmibus hyemales colore et formis, staminibus numero, formis laminorumque.

Deciduous, presumably dioecious tree of low stature (to 20 m), dividing near base into separate trunks that ascend to a relatively narrow, rounded crown. First year twigs coarse, the dominant twigs 4–6 mm thick ($\bar{x}$ = 5.0 mm, CV = 13%), the lateral twigs 2.5–3.5 mm thick ($\bar{x}$ = 2.9 mm, CV = 11%), tan tinged with orange, turning grayish-tan by the third year. Winter buds brown, resinous, sparsely pubescent on some scales; terminal buds lance-ovate, (13–)15–17 mm long ($\bar{x}$ = 15.7 mm, CV = 8%), 4–7 mm thick ($\bar{x}$ = 5.4 mm, CV = 21%), with (7–)8(–10) bud scales ($\bar{x}$ = 8.1, CV = 11%); male flowering
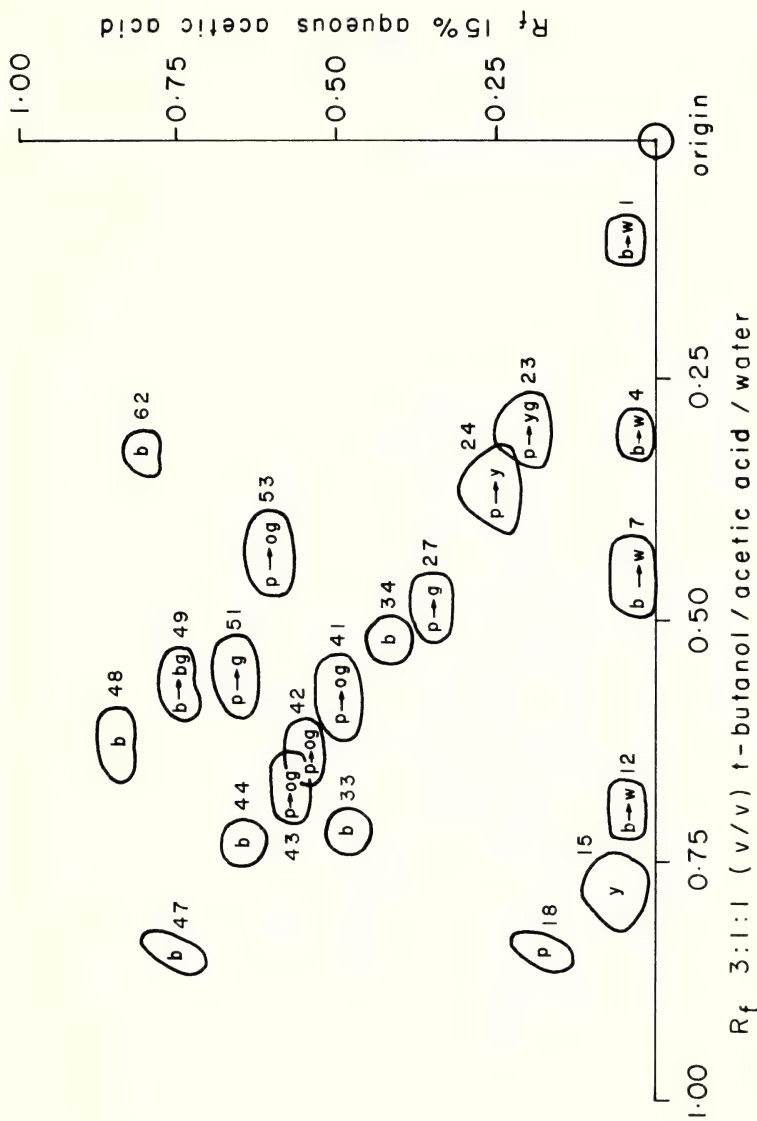
FIG. 3. Composite chromatogram of *P. fremontii*, *P.* × *inopina*, and *P. nigra* from Coyote Creek. Spots numbered as in Table 3. Designations of colors in ultraviolet light and changes after fuming with ammonia: b—light blue, bg—bluegreen, g—green, o—orange, p—uvl absorbing, y—yellow.

TABLE 3. CHROMATOGRAPHIC PROFILES OF *P. fremontii*, *P.* × *inopina*, AND *P. nigra* FROM COYOTE CREEK COMPARED TO REFERENCE PROFILES FOR THE TWO PARENT SPECIES ELSEWHERE. + compound regularly present; (+) compound infrequent. Compounds 27, 48, and 49 are present in all individuals of the population, all others vary.

Spots	Tentative identification	Reference P. fremontii	P. fremontii	P. × inopina	P. nigra	Reference P. nigra
1, 4, 7, 12	unidentified		(+)	+	+	+
15	flavonol aglycone	+	+	+	(+)	
18	chrysin	+	+	+	(+)	
23	orientin	+	+	+	(+)	
24	vitexin	+	+	+	(+)	
27, 41	quercetin monoglycosides	+	+	+	+	+
42, 43	kaempferol monoglycosides		(+)	+	+	+
51	kaempferol diglycoside				+	+
53	quercetin diglycoside			+	+	+
33, 34, 62	unidentified phenylpropanoids	+	+	+		
44, 47	unidentified phenylpropanoids	+	(+)	+	+	+
48, 49	unidentified phenylpropanoids	+	+	+	+	+
Individuals examined		112	5	1	4	2

buds narrowly ovate, asymmetric, spreading from the first year shoots, bent at the tip, (19–)20–25(–27) mm long (x̄ = 22.6 mm, CV = 12%), (4.5–)6–7(–9) mm thick (x̄ = 6.4 mm, CV = 20%), with 4 bud scales (invariant in 25 buds); female flowering buds unknown. Leaves (Fig. 2) grayish green above, slightly whitened beneath, lacking basilaminar glands; early leaves deltoid-ovate with a toothless, acuminate, sometimes slightly falcate apex and a distinct flexure in the base in the form of an inverted W, (4–)6.5–8.5(–10) cm long (x̄ = 7.2 cm, CV = 24%), (2.5–)6.5–9(–10) cm wide (x̄ = 7.0 cm, CV = 32%), with (12–)15–19 rounded serrations on each side (x̄ = 16.9, CV = 14%), the largest of these in the lower third of the margin, 3–4.5(–5) mm deep (x̄ = 3.9 mm, CV = 18%), grading to 0.2 mm near the apex; late leaves more rounded, the apex shorter and the flexure of the base less pronounced, (2.5–)5–8.5 cm long (x̄ = 5.9 cm, CV = 32%), (2.5–)5.5–7.5(–9) cm wide (x̄ = 6.0 cm, CV = 33%), with (17–)22–26(–37) crenate teeth on each side (x̄ = 24.0, CV = 23%), of irregular size distribution, the largest (0.4–)0.6–0.8(–1.2) mm deep (x̄ = 0.7 mm, CV = 33%), grading down to 0.1 mm between the larger teeth; the petiole slightly longer than the blade. Male catkins 3–4(–5) cm long (x̄ = 3.7 cm, CV = 19%), with 35–50 flowers (x̄ = 39, CV = 18%); bracts obovate, laciniate, clawed, brown or tan with a brown fringe, (4–)5–7(–7.5) mm long overall (x̄ = 6.0 mm, CV = 18%), (2.5–)3–4.5(–6) mm wide (x̄ = 4.0 mm, CV = 26%), the claw (0.8–)1.5–2(–3) mm long (x̄ = 1.7 mm, CV = 35%); pedicels longer at the base of the catkin than towards its apex, 0.5–1 mm long (x̄ = 0.8 mm, CV = 33%), elongating to 1–2.5 mm after anthesis (x̄ = 1.7 mm, CV = 36%); floral disc oblique, shallowly conical, 2–2.5(–4) mm across (x̄ = 2.5 mm, CV = 24%); stamens inserted evenly across the disc, 25–50 (x̄ = 37.9, CV = 24%), anthers red at anthesis; pollen spherical, psilate, inaperturate, diameter 31.9 μm ± 5.69 μm. Female catkins and flowers unknown. Flowering in March. Chromosome number $2n$ = ca. 38 (*Eckenwalder 1172*). Known only from type locality; trees of this parentage produced artificially by Stout and Schreiner (1933) apparently destroyed.

TYPE: USA, CA, Santa Clara Co.: along creek, Hellyer Unit of Coyote Creek County Parkway, San Jose, 6 Nov 1975, *Eckenwalder 1132* (Holotype: UC; isotypes: TRT, and to be distributed.)

PARATYPES: Male flowering specimens from type tree: 4 Mar 1976, *Eckenwalder 1172*; 13 Mar 1976, *Eckenwalder 1184*; male flowering specimen from another tree: 13 Mar 1976, *Eckenwalder 1185*.

The epithet reflects my surprise at finding this hybrid combination here, when, based on crossing the creek by freeway and seeing the trees from adistance at 90 km/hr, I expected to find a population of *P. fremontii, P. trichocarpa,* and their hybrid, *P. × parryi* Sargent.

These hybrids are intermediate between their putative parents in many characteristics including growth habit (*P. nigra* is more erect

than *P. fremontii*); twig thickness and color (thicker than *P. nigra,* more orange than *P. fremontii*); bud shape and color (thicker and not as red as *P. nigra,* without the green cast of *P. fremontii*); early leaf blade shape (broader, with a more cordate base than *P. nigra,* apex more elongate than *P. fremontii*) and teeth (larger than *P. nigra,* more numerous than *P. fremontii*); time of autumn coloration (far more advanced in early November in *P. nigra* than in *P. fremontii*); and stamen number (15–20 in *P. nigra,* 30–70 in *P. fremontii*). If female trees are found, they should also be intermediate in carpel number (2 in *P. nigra,* 3–4 in *P. fremontii*) and disc width (2–3 mm in *P. nigra,* 5–8 mm in *P. fremontii*).

DISCUSSION

Natural and artificial interspecific hybridization are well known in *Populus* (Zsuffa 1975), whose species are all diploid with $n = 19$ (Smith 1943). Hybrid poplars, whether found in nature or produced artificially, are traditionally given binomial hybrid designations (Rehder 1940, Wagner 1970). This convention, which is also common in other woody plant genera, e.g., *Quercus* (Tucker 1968), is followed here for consistency and in anticipation of the discovery and possible cultivation of additional individuals of the new hybrid.

The parents of the hybrid described here are both members of sect. *Aigeiros,* but they are assigned to distinct subsections (Bugała 1967). The American cottonwoods, *P. fremontii* and *P. deltoides,* of subsect. *Americanae* Bugała are easily distinguished by twig, bud, leaf, flower, and fruit characters from the black poplar, *P. nigra,* of subsect. *Euroasiaticae* Bugała (Eckenwalder 1977a). They have probably had a separate evolutionary history for at least 10 million years, the age of the earliest known record of subsect. *Americanae* (Eckenwalder 1977b). There is no evidence of pre-Columbian contact between trees of the two subsections, but they were brought together following European settlement of North America. Spontaneous hybridization between *P. deltoides* and *P. nigra* occurred in Europe during the eighteenth century, giving rise to the widely cultivated *P.* × *canadensis* (Boom 1957). *Populus fremontii* was discovered much later than *P. deltoides* (Eckenwalder 1977a) and has not apparently hybridized with *P. nigra* in Europe, where it is rarely planted (Houtzagers 1937).

Populus nigra is widely planted in North America but this is the first report of local hybridization between this species and either of the native cottonwoods, *P. deltoides* or *P. fremontii,* with which it frequently occurs. This paucity of hybrids may be attributed to the sex of the introduced trees. Almost all black poplars planted in North America are from a single staminate clone, the Lombardy poplar (*P. nigra* 'Italica'), and its pollen may not be able to compete with pollen of *P. deltoides* or *P. fremontii* in fertilizing ovules of these species in

natural populations (Baker 1951). At Coyote Creek, the trees of *P. nigra* are pistillate and, without nearby Lombardy poplars, the only seed they can set is from hybridization with *P. fremontii* (Eckenwalder 1977b). Hybridization would also be promoted by disturbance of the habitat at this site (Anderson 1948). Even so, difficulty in hybridization is reflected in the low percentage of capsules maturing on *P. nigra* here (34%; Fig. 2 j) and in the low pollen fertility of *P. × inopina* (56.5%; Fig. 2 f). These figures are comparable to those for male *P. × canadensis* (55% average pollen fertility for four trees of different cultivars; Smith 1943; Eckenwalder 1977b). All three species and both hybrids are diploids with $n = 19$ (Smith 1943, Eckenwalder 1977b, 1978) so barriers to crossing are not a product of differences in chromosome numbers (Willing and Pryor 1976).

The new hybrid may be distinguished from the related *P. × canadensis* by its ovate, brown, less resinous winter buds (lanceolate, reddish, and very resinous in *P. × canadensis*) and by its early leaves. These are more deltoid than ovate, with coarser teeth, lacking even the sporadic single basilaminar glands of *P. × canadensis,* with a shorter apex, and without a distinct shoulder in the outline of the lamina base. Overall, *P. × canadensis* is closer to *P. nigra* in appearance than is *P. × inopina,* which more closely resembles its American parent in many respects. Collectors should search for this hybrid and others that may arise between native and introduced trees. As with all poplar studies, collections are most valuable when they are gathered from a single tree over its phenological cycle: flowering shoots in early spring, fruiting branches in late spring, and leafy shoots with early and late leaves and mature winter buds in late summer.

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TAXONOMY OF THE ALLIUM LACUNOSUM COMPLEX (LILIACEAE)

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ABSTRACT

A new variety of *Allium lacunosum* from California, var. **kernensis,** is described and reduction of *A. davisiae* to varietal status under *A. lacunosum* is proposed. A key to and discussion of the four varieties of the species is presented along with a distribution map and chromosome numbers for each, all $n = 7$.

Frequently in western North America, species limits have been confused by lack of representative collections that would allow accurate appraisal of geographic variation. This situation is well illustrated by the *Allium lacunosum* complex.

Allium lacunosum Wats. consists of four distinct geographic varieties extending from just north of San Francisco Bay south through the Coast Ranges and east across the Tehachapi Mountains and southern Sierra Nevada on to the western Mojave Desert. As described by Watson (1879) the species is restricted to serpentine soils on high ridges and peaks in the Coast Ranges from San Francisco Bay to Santa Barbara County, California.

In 1908 Jones described a similar species, *A. davisiae,* from the western Mojave Desert. Following its original publication this latter taxon was treated as a synonym of *A. lacunosum* in many floristic treatments of California (Abrams 1923, Jepson 1923, Munz 1935). Ownbey (1959) resurrected *A. davisiae,* recognizing quantitative and distributional differences from *A. lacunosum.*

Additional taxa with affinities to these two include material described by Eastwood (1938) as *A. lacunosum* var. *micranthum* from the inner South Coast Range and a few anomalous populations, vaguely referred to by Ownbey (1959) and here described as *A. lacunosum* var. *kernensis* McNeal and Ownbey, occurring at the southern tip of the Sierra Nevada.

As part of a revision of the *Allium acuminatum* alliance, of which *A. lacunosum* and *A. davisiae* are members (Saghir et al. 1966), we were able to survey a large number of collections of these taxa through the courtesy of the following herbaria: CAS, DS, GH, JEPS, MO, ND, NY, OSC, POM, RSA, UC, US, WS and WTU. Voucher specimens and bulbs of the putative taxa were collected over a period of several years. Bulbs were grown in Pullman, Washington and Stock-

ton, California for determination of chromosome numbers. All counts were made on pollen mother cells from fresh buds using aceto-orcein squashes. In addition bulb coats were removed, vapor-coated with silver and examined on an ETEC SEM. The data from these investigations support the conclusion that *A. lacunosum* consists of four well-defined but closely related geographic varieties.

Discussion

The varieties of *Allium lacunosum* closely resemble one another in a series of characteristics that are unique in the *Allium acuminatum* alliance. We have elected to take a conservative view of these taxa because of this combination of characteristics rather than to separate them at the specific level on the basis of characters that are quantitative in nature.

Allium lacunosum has a characteristic bulb coat reticulum with square, polygonal, or ± transversely elongate meshes (Figs. 1–4). The walls of these meshes are distinctly sinuous (Fig. 5). Only one other North American species, *A. acuminatum* Hook., is even superficially similar to *A. lacunosum* in this regard, and here the walls of the meshes are much thicker and not sinuous (Fig. 6).

Presumably, owing to the dry conditions under which all varieties of *Allium lacunosum* grow, the bulb coats do not disintegrate rapidly. They persist and accumulate, investing the bulb with a thick cover.

The leaves of *Allium lacunosum* var. *lacunosum* are narrow, concave-convex and ± falcate, a condition found only rarely in the *A. acuminatum* alliance. *Allium lacunosum* var. *davisiae* is distinctive in having leaves that are falcate and up to 3 mm wide. *Allium lacunosum* var. *micranthum* and var. *kernensis* have leaves that are narrow and straight. In all four varieties the leaves wither from the tip by anthesis; because of this, few herbarium specimens show the differences in shape that have been noted.

All four varieties have portions of the ovary densely covered with minute rounded protuberances, a characteristic that is unique in the alliance.

Chromosome counts show that all varieties are $n = 7$ (Table 1), the usual number in North American species of *Allium*.

Taxonomic Treatment

The following treatment is given to emend the circumscription of *Allium lacunosum* and to delimit its varietal elements.

Allium lacunosum Wats. Proc. Amer. Acad. Sci. 14:231. 1879. For synonymy and typification see the varietal headings.

Bulbs ovoid, 1–2 cm long, coats brown to yellow brown, a new coat developing annually, old coats accumulating and investing the bulb
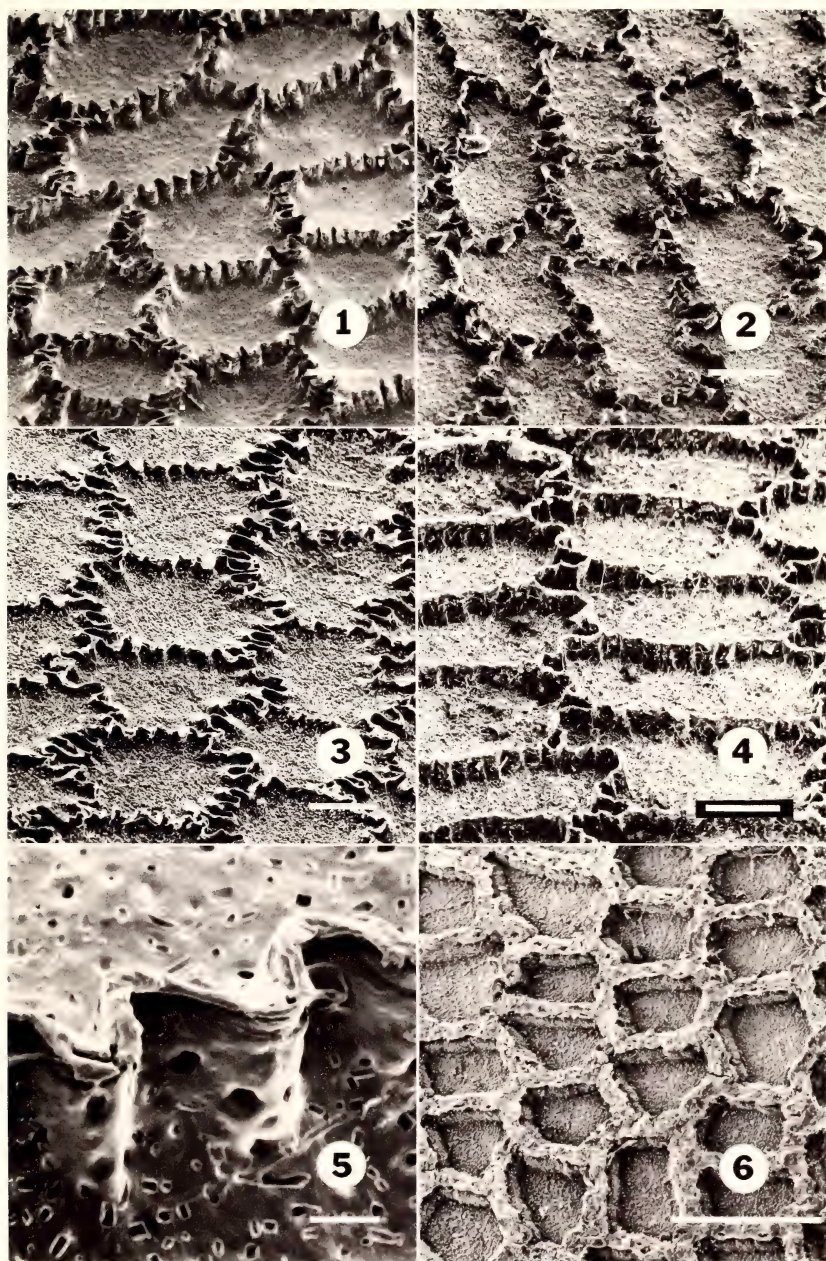
FIGS. 1–6.   Scanning electron micrographs of *Allium* bulb coat reticulations. 1. *Allium lacunosum* var. *lacunosum*. 2. Var. *micranthum*. 3. Var. *kernensis*. 4. Var. *davisiae*. 5. Detail of sinuous cell wall in var. *lacunosum*. 6. *A. acuminatum*. (Scale: Figs. 1–4 & 6 = 100 μm; Fig. 5 = 10 μm)

TABLE 1.   CHROMOSOME NUMBERS FOR *Allium lacunosum* VARIETIES. All collections are from California; vouchers are in WS unless otherwise indicated in parentheses. Our counts were all made on microsporocytes during first meiotic metaphase. * Indicates previously unpublished counts by Dr. Hannah C. Aase.

Variety	n	Collection
lacunosum	7*	Tiburon Hills, Marin Co., 22 Apr 1947, *Hoffman s.n.*
	7*	0.5 mi e. of Belvedere, Tiburon Peninsula, Marin Co., 13 Oct 1947, *Kruckeberg s.n.*
micranthum	7	Above the entrance station e. side of Pinnacles Natl. Mon., San Benito Co., 20 Apr 1970, *McNeal 496* (CPH).
kernensis	7	Bodfish-Havilah Rd., 5.2 km se. of Hwy 178, Kern Co., 18 Apr 1970, *McNeal 492* (CPH).
	7*	Road from Kernville to Glennville, e. slope of Greenhorn Mts., Kern Co., 12 May 1949, *Munz 13158.*
davisiae	7	5.5 km s. of Mojave on Hwy 14, Kern Co., 6 Apr 1973, *McNeal 1243* (CPH).
	7*	3.2 km w. of Palmdale, Los Angeles Co., 10 Aug 1947, *Epling s.n.*
	7	Stoddard Wells Rd., 28.1 km s. of Barstow, San Bernardino Co., 7 Apr 1973, *McNeal 1247* (CPH).

with a thick cover, coats distinctly cellular-reticulate, the meshes square, polygonal or ± transversely elongate with sinuous walls; leaves 2, 0.75–2 times as long as the scape, withering from the tip by anthesis; scape terete, 10–35 cm tall; bracts 2 or 3, lance-ovate to ovate, 5–15 mm long, becoming papery; umbel 5–45 (or more)-flowered, pedicels 1–3.5 times as long as the flowers, each pedicel with its flower deciduous as a unit at maturity; perianth segments white or pale pink with darker mid-nerves, spreading, lance-ovate to ovate, obtuse, acute or short acuminate, 4–9 mm long and 1–4 mm wide; stamens 0.7–0.8 as long as the perianth, anthers yellow, rounded at the apex; ovary 3-lobed, 3-grooved with a ridge on either side, the ridges prolonged above into a crest with 3 minute, 2-lobed central processes, ridges and crest densely covered with minute rounded protuberances; stigma capitate, scarcely thickened, obscurely 3-lobed; seeds black, alveoli minutely roughened; $n = 7$.

Key to the varieties of *Allium lacunosum*

a. Umbels compact, pedicels 0.75–1.5 times as long as the flowers, scapes 10–25 cm tall

      b. Leaves 1–2 times as long as the scape; scape 10–20 cm tall; flowers 7–9 mm long. Coast Ranges from Marin to Santa Barbara Co. and on Santa Rosa and Santa Cruz Islands . . . .
. . . . 1. var. *lacunosum*

     bb. Leaves equalling the scape or shorter; scape 15–25 cm tall; flowers 6–8 (usually less than 7) mm long. East of the Greenhorn Mts. in the vicinity of Lake Isabella, Kern Co. . . . . . .
. . . . 2. var. *kernensis*

aa. Umbels loose, pedicels spreading 1.5–3.5 times as long as the flowers; scapes 15–35 cm tall.

      c. Bracts 3, obtuse or acute; leaves subterete, 1 mm or less wide, straight; flowers 4–6 mm long. Inner Coast Ranges in San Benito, southern Monterey and northern San Luis Obispo Cos. . . . . 3. var. *micranthum*

     cc. Bracts 2 acuminate; leaves flattened, up to 3 mm wide, ± falcate; flowers 6–8 mm long. Carriso Plains, San Luis Obispo Co. and sporadic southward to San Bernardino and San Diego Cos. . . . . 4. var. *davisiae*

1. ALLIUM LACUNOSUM Watson var. LACUNOSUM. Proc. Amer. Acad. Sci. 14:231. 1879.—TYPE: USA, CA, Santa Clara Co., summit of Mariposa Peak. 20 Jun 1862. *Brewer 1284*. (Holotype: GH!; isotypes: MO! UC! US!).

Distribution. Tiburon Peninsula in Marin Co., south through the Coast Ranges to Santa Barbara Co. and Santa Rosa and Santa Cruz Islands, CA (Fig. 7). Apparently restricted to serpentine soil on ridges and peaks at 300–1000 m. Flowering late Apr–early Jun.

This taxon has a smaller stature than any of the other varieties, its scapes varying from 10(–7) to 20(–25) cm tall. The leaves are narrow and ± falcate. Umbels are compact and the ratio between flower length and pedicel length ranges from 0.75 to 1.5. The perianth segments are white with deep pink or purple mid-nerves.

Allium lacunosum var. *lacunosum* intergrades with var. *davisiae* in the Tehachapi Mountains, the closest point of contact between the two.

2. **Allium lacunosum** Watson var. **kernensis** McNeal and Ownbey, var. nov.

Scapo 15–25 cm longo; umbella 10–45 (vel pluribus) floribus; segmentis perianthii 5–7(–8) mm longis, albis vel roseis, nervo medio viridi vel purpureo-viridi.

TYPE: USA, CA, Kern Co., 1.5 km w. of Kernville Rd. on the rd. to Glennville, e. slope of the Greenhorn Mts., 12 May 1949, *Munz 13158*. (Holotype: POM!).

36°N

122°W

o **var. davisiae**
■ **var. kernensis**
● **var. lacunosum**
+ **var. micranthum**
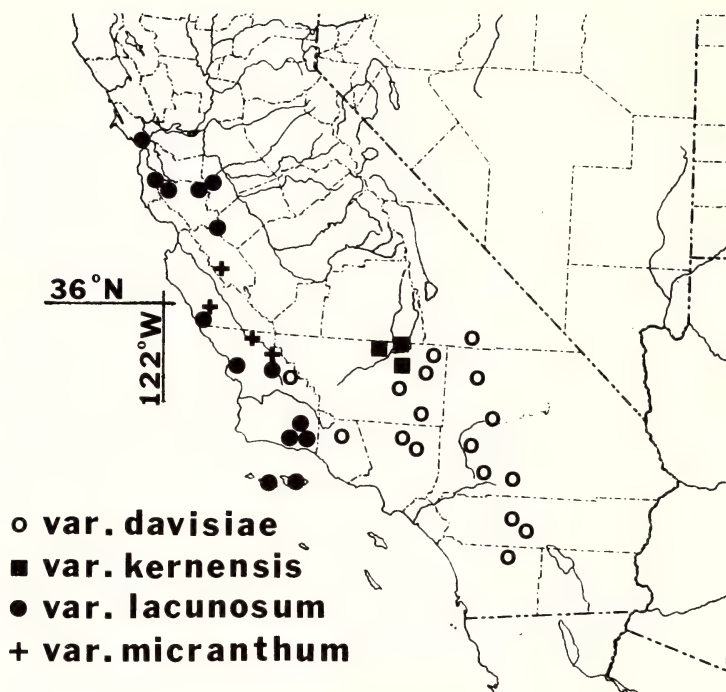
Fig. 7.   Distribution of the varieties of *Allium lacunosum*.

Distribution. Rocky, sandy or clay soils, southern tip of the Sierra Nevada from Kernville and Pilot Knob south to Piute Mt., Kern Co., CA (Fig. 7). Flowering May–Jun.

Variety *kernensis* is a well marked geographic variant. Specimens of this taxon are, on the average, taller than the typical variety and their leaves are narrow and straight. The flowers are somewhat smaller and usually more numerous, the ratio of flower length to pedicel length ranges from 1 to 2, and the umbels are compact. The midnerve of the perianth segments is commonly green in contrast to the deep pink or purple of var. *lacunosum*.

3. ALLIUM LACUNOSUM Watson var. MICRANTHUM Eastwood, Leafl. W. Bot. 2:101. 1938.—TYPE: USA, CA, San Benito Co., The Pinnacles. 3 May 1937. *Eastwood & Howell 4231*. (Holotype: CAS!; isotypes: GH! POM! US!).

Distribution. Rocky clay and serpentine soils, Inner Coast Range of California in San Benito, southern Monterey and northern San Luis Obispo Cos. (Fig. 7). Flowering late Apr to May.

Variety *micranthum* differs from typical *Allium lacunosum* in being taller with straight, narrow leaves. The involucre commonly has three bracts, whereas two is the usual number in the other varieties. The flowers are the smallest in the complex, and the ratio of flower length to pedicel length ranges from 1.5 to 3.5. The umbels are loose.

4. **Allium lacunosum** Wats. var. **davisiae** (Jones) McNeal & Ownbey, comb. nov.—*Allium davisiae* Jones, Contr. W. Bot. 12:78. 1908.—TYPE: In his protologue Jones states that this species "grows in gravelly soil and among rocks at Victor [now Victorville], California." 8 May 1903 at 2900 ft (880 m). No specimens with data exactly conforming to this statement were found; however, specimens bearing slightly different data seem to be the collections he had in mind inasmuch as he annotated three of them as types. Two of these specimens are: California, San Bernardino Co., Victor, 2600 ft (790 m). 17 May 1903 *Jones s.n.* (US! MO!). The third bears the same label data but is dated 18 May 1903 (US!). We assume that the differences may be accounted for as mental lapses or carelessness on Jones' part and have concluded that the material dated 17 May and annotated as types by Jones should be interpreted as type material. Hence, we designate the US sheet #855767 as lectotype. Several herbaria have duplicates of it (CAS! DS! GH! MO! POM! WS! WTU!) which, with the exception of MO, are identified by Jones as various other species.

Allium pseudobulbiferum Davidson, Bull. So. Calif. Acad. Sci. 20:49. 1921.—TYPE: *Davidson 3410,* collected by Kessler from elevated ground east of the river at Victorville, San Bernardino Co., CA, 1 May 1921 (LAM!). This is an immature and fragmentary specimen consisting of a partial scape and an umbel. It corresponds closely with specimens of var. *davisiae* at the same stage of development.

Distribution. Rocky, sandy, or clay soil, Mohave Desert, south to the San Jacinto Mts., Riverside Co. and northern San Diego Co., extending northwest to the Carriso Plains, San Luis Obispo Co. (Fig. 7). Flowering Apr–Jun.

Variety *davisiae* differs from typical *A. lacunosum* in being, on the average, considerably taller. Specimens usually bear a larger number of somewhat smaller flowers, the ratio of flower length to pedicel length ranges from 2 to 3, and the umbels are loose. Collections from northeast Ventura Co. and from the San Jacinto Mts. appear to be intermediate between var. *davisiae* and the typical variety. The flowers in these are slightly larger than var. *davisiae*; however, because of the stature of the plants and the length of the pedicels, both of which considerably exceed var. *lacunosum,* the specimens are placed here.

List of Exsiccata

More than 100 herbarium specimens were examined during this study. Along with field observations these form the basis for our morphological and distributional data. Lists of these specimens are available from the senior author.

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FLORAL VARIATION IN CHLOROGALUM ANGUSTIFOLIUM (LILIACEAE)

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ABSTRACT

Four northern California field populations of *Chlorogalum angustifolium* consist of plants of two floral types: short-styled and long-styled. In short-styled plants the stigma level is below the tier of anthers; in the long-styled plants it is above the anthers. In the Butte County population studied in greatest detail, long-styled plants are twice as numerous as short-styled plants. The two forms do not differ significantly in anther size, number of pollen grains per anther, filament length, number of flowers per inflorescence, or height and degree of branching of the inflorescence. The two forms do differ significantly in ovary and tepal lengths. Approximately 36 percent of both forms bore fruit in the field, although the average number of fruits per plant was 60 percent higher on short-styled plants ($\bar{x} = 1.60$) than on long-styled ($\bar{x} = 0.99$). No incompatibility exists within or between the two forms; however, seed-set was significantly lower for selfed long-styled plants than for selfed short-styled ones. No long-styled plants set seed without mechanical transfer of pollen, whereas up to 30 percent of flowers of short-styled plants did so. It is suggested that the presence of short-styled plants in populations of *C. angustifolium* insures some degree of seed production during times when pollinators are scarce.

The five species and three varieties of *Chlorogalum* Kunth. (Liliaceae) are remarkably uniform in most floral and vegetative characters, e.g., flower size, anther color, bulb coat morphology, and inflorescence size (Hoover 1940). However, several populations of *C. angustifolium,* the second most widespread species, were found to consist of plants having two readily distinguishable floral types: short-styled and long-styled. This study investigated selected morphological characters of long- and short-styled plants of *C. angustifolium* Kell. from field-collected samples, including experimental pollinations to determine incompatibility between and within the two forms. Preliminary studies were made of degree of autogamy and floral senescence in this species.

MATERIALS AND METHODS

Four field populations (Palermo and Chico, Butte County, and Freeman School and Corning Rd., Tehama County) of *Chlorogalum angustifolium* in northern California were observed to consist of long- and short-styled plants. Bulbs collected from two of these populations (Palermo and Freeman School) were cultivated and brought to flower in the greenhouse. Artificial crosses between 288 flowers on 27 plants were made using fine forceps which were cleaned with 95 percent ethanol between pollinations. To avoid contamination of stigmatic

surfaces during emasculation, only newly opened flowers with unde-hisced anthers were used in pollinations. Within an hour after anthe-sis, masses of pollen were placed on the three minute stigmatic lobes. No distinction was made between the two whorls of stamens, which occur at the same level in both long- and short-styled forms of this species. Seeds from the crosses were harvested, counted and weighed at the time of capsule dehiscence, about 6 weeks after pollination.

Flowers and buds were collected at random from the Freeman School population and preserved in 50 percent formalin-acetic acid-ethanol (FAA). Floral parts were measured using Mitutoyo dial cali-pers at 15× magnification under a dissecting microscope. Pollen pro-duction of long- and short-styled forms was compared by suspending pollen from two adjacent undehisced anthers of preserved flowers in measured volumes of 50 percent ethanol. After thorough mixing, 10 μl samples of the suspension were placed in an "Ultra-Plane Spot Lite" counting chamber and allowed to settle for 60 seconds. Sixty-five grids were counted for each of 10 long-styled and 10 short-styled sample dilutions.

At the peak of the flowering season, a 50-m line transect was run through the center of the Palermo population, and adjacent inflores-cence axes were collected every 1 m along the line. These axes were measured and the number of flowers, fruits, and seeds per axis deter-mined.

Differences between the two means of measurements of various parameters of the two forms (tepal length, height to first branch, num-ber of seeds per fruit, etc.) were compared using the Student's t test (Mendenhall 1971).

Surface features of pollen and stigmas were examined using a Cam-bridge Stereoscan S-4 scanning electron microscope after the tissues were fixed in FAA, dehydrated through a graded ethanol series, crit-ical point dried in amyl acetate, and coated with gold.

Results

Inter- and intrapopulation crosses using plants from two hetero-morphic populations of *Chlorogalum angustifolium* indicate that no incompatibility exists between long- and short-styled plants of this species. The percentage of seed-set was not significantly different in the classes $S \times S$, $S \times L$, $L \times S$, $L \times L$, and *S-selfed* (Table 1). Non-emasculated flowers of the long-styled form that did not have pollen mechanically transferred to the stigmas (class *L-unpollinated*) failed to produce seeds, whereas 30 percent of unpollinated, non-emasculat-ed flowers of short-styled plants (*S-unpollinated*) set seeds. The av-erage number of seeds per fruit in cross classes $S \times S$, $S \times L$, $L \times S$, $L \times L$, *S-selfed*, and *S-unpollinated* did not differ significantly (Table 1). Only 6.3 percent of crosses of the class *L-selfed* resulted in seed

TABLE 1.   RESULTS OF POLLINATIONS IN *Chlorogalum angustifolium*.

Cross class (female parent × male parent)	Total number of crosses	Number of crosses resulting in seed		Seed weight (mg)		Number of seeds per fruit		
		n	%	x̄	n	x̄	s	n
S × S	44	30	68.2	4.2	95	3.80	1.27	30
S × L	49	34	69.4	4.6	118	3.47	1.48	34
L × S	19	13	68.4	4.6	41	3.23	1.09	13
L × L	33	18	54.5	4.5	57	3.41	1.28	17
S-selfed	14	10	71.4	4.4	39	3.90	1.10	10
L-selfed	16	1	6.3	3.6	2	2.00	—	1
S-unpollinated	60	18	30.0	4.3	69	3.83	1.04	18
L-unpollinated	53	0	0	—	0	0	—	0

production, with only two seeds produced in that single successful cross. Average weights per seed in the classes $S \times S$, $S \times L$, $L \times L$, *S-selfed,* and *S-unpollinated* were nearly identical, and the departure of seeds from *L-selfed* from this value may be a result of the small number of seeds available for measurement.

Of 109 plants of *C. angustifolium* sampled along a 50-m transect through the Palermo population, 36 were short-styled and 73, long-styled. Mean measurements of overall inflorescence height, height to first branch of the inflorescence, number of inflorescence branches, number of flowers, number of fruits, and number of seeds of the two forms are shown in Table 2. Long-styled and short-styled plants differ significantly ($p < 0.05$) only in average number of fruits per plant. In the field, 35.7 percent of long-styled plants and 37.1 percent of short-styled plants bore fruit at the time of sampling.

Mean measurements of selected floral characters of the two forms from plants of the Freeman School population are shown in Table 3. Long-styled and short-styled plants differ significantly ($p < 0.01$) in ovary, style, and tepal lengths.

Scanning electron microscope studies of pollen and stigmatic surfaces of long- and short-styled plants revealed no differences between the two forms. Size and surface ornamentation of pollen grains were identical in long- and short-styled plants, and stigmatic surfaces of both forms are wrinkled at the margins and covered with a smooth layer of unornamented cuticular material along the center of the three minute lobes.

DISCUSSION

Four natural populations of *Chlorogalum angustifolium* in northern California consist of plants of two floral types: short-styled and long-

TABLE 2. MEASUREMENTS OF SELECTED PARAMETERS OF BOTH FLORAL FORMS FROM A HETEROMORPHIC POPULATION OF *Chlorogalum angustifolium*, PALERMO, BUTTE CO., CALIFORNIA. Paired means followed by superscript a differ at the .05 level.

Floral form	Overall height (cm)			Height to first branch (cm)			Number branches			Number flowers			Number fruits per plant			Number seeds per fruit		
	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n
Long-styled	46.88	8.09	70	24.60	5.37	70	4.07	1.12	70	53.54	25.52	70	0.99[a]	1.89	70	2.03	0.89	62
Short-styled	50.24	9.03	35	27.42	5.30	35	4.03	1.27	35	54.77	27.78	35	1.60[a]	2.67	35	1.83	0.89	63

TABLE 3. MEASUREMENTS OF SELECTED PARAMETERS OF BOTH FLORAL FORMS FROM A HETEROMORPHIC POPULATION OF *Chlorogalum angustifolium*, FREEMAN SCHOOL, TEHAMA CO., CALIFORNIA. Paired means followed by superscript b differ at the .01 level.

Floral form	Tepal length (mm)			Anther length (mm)			Filament length (mm)			Number pollen grains per anther in 10 µl sample dilution			Ovary length (mm)			Style length (mm)		
	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s	n
Long-styled	9.96[b]	0.61	60	2.64	0.51	60	5.97	0.28	60	29.5	7.32	10	2.08[b]	0.38	10	5.59[b]	1.17	10
Short-styled	8.71[b]	1.12	60	2.82	0.51	60	5.46	0.64	60	32.3	10.90	10	1.47[b]	0.23	10	2.08[b]	0.53	10
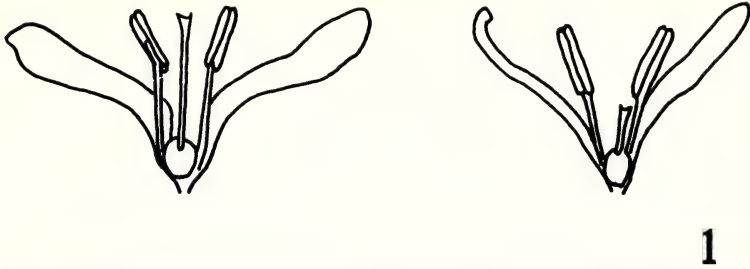
FIG. 1.   *Chlorogalum angustifolium*. Long- and short-styled forms, with parts drawn to scale; see Table 3 for mean measurements. ×2.

styled (Fig. 1). In short-styled plants the stigma level is below the tier of anthers. In the long-styled form, it is above the height of the anthers. No further differences exist between the two forms in terms of pollen size and shape, stamen height, stigma surface characters or pollen production. Furthermore, plants of the two forms do not differ significantly in the average overall height of the inflorescence, the degree of branching of inflorescence, number of flowers per inflorescence, or number of seeds per fruit (Table 2). In addition to the difference in style lengths between the two forms, tepal and ovary lengths are greater in long-styled flowers than in short-styled. However, while the measured differences in these two characters are statistically significant, in the author's experience it has not been possible to distinguish between long- and short-styled plants on the basis of tepal and/or ovary lengths alone.

The results of crossing experiments (Table 1) do not indicate the presence of incompatibility in this species within or between the two forms. The decreased seed-set in the cross class *L-selfed* suggests some degree of self-incompatibility in this form, which appears to be lacking in short-styled plants. Alternatively, the low seed-set for *L-selfed* crosses could be a result of inbreeding depression (Lloyd 1968). The *S-selfed* crosses do not show a similar reduction in seed-set. If inbreeding depression is in fact present in long-styled individuals, these results may be indirect evidence that in the field long-styled plants are more outcrossed than short-styled.

The results of experiments in which long- and short-styled flowers of *C. angustifolium* were allowed to self spontaneously provide insight into the possible function of different style lengths in this species. Without artificial transfer of pollen from anthers to stigma, long-styled plants of *C. angustifolium* were never able to produce seeds, whereas 30 percent of flowers of greenhouse-grown short-styled plants set seeds (Table 1). This ability would insure some degree of seed production by short-styled plants in the event of pollinator failure, and could

perpetuate the short-styled form. In light of this, however, it is somewhat difficult to explain why long-styled plants predominate in the Palermo population by a 2:1 ratio. On the other hand, short-styled plants along the Palermo transect average approximately 60 percent more fruits per plant than the long-styled plants (Table 2). This difference in fecundity could result from self-pollination of short-styled plants, although there is no evidence that the short-styled plants are self-pollinated in the natural habitat and no reason to suspect that pollination rates limit fruit-set in the field. Interestingly, the same percentage of long- and short-styled plants along the transect bore fruit at the time of sampling (35.7 percent and 37.1 percent, respectively).

The mechanics of flower closing in this species suggest a means by which self-pollination may be accomplished. Floral senescence in *C. angustifolium,* which is similar to that reported for *C. pomeridianum* (Jernstedt 1980), occurs 6–8 hours following anthesis. As senescence progresses, the tepals uncurl and come together to close the flower. The filaments also collapse downward toward the ovary. This positions the anther sacs directly on the stigmas of the short-styled plants, potentially resulting in self-pollination. A similar sequence of events occurs in long-styled flowers. However, because in this form the stigma already projects above the anther sacs, collapse of filaments of long-styled plants serves to remove anthers farther from the stigmatic surface, seemingly precluding the possibility of pollen transfer and self-pollination in this form.

Results of crossing experiments suggest, however, that additional factors may be involved in the regulation of cross- and self-pollination in this species. If the collapse of anthers upon senescence were sufficient to cause selfing in short-styled plants of *C. angustifolium,* it seems likely that greater than 30 percent of *S-unpollinated* crosses would have resulted in seed production (Table 1). Likewise, the percentage of seed-set in all cross classes is far from 100 percent, despite the liberal coating of stigmatic surfaces with pollen at the time of pollination. Pollen viability, style-stigma interactions, time of gamete maturation, and resource limitation could be involved, and further work is necessary to understand the control of seed-set in this species.

The floral variation described here for *Chlorogalum angustifolium* has a superficial resemblance to the phenomenon of heterostyly, although a close examination shows them to differ significantly. Heterostyly is a genetically controlled floral polymorphism in which the two or three forms of a heterostylous species produce flowers that differ reciprocally in style and stamen lengths (Baker 1964, Mulcahy 1965, Vuilleumier 1967, Ganders 1979). The floral polymorphism is usually genetically linked with a sporophytic self-incompatibility system (Ganders 1979), and the syndrome of morphological and physiological features is thought to be governed by a supergene (Barrett

1979). In its typical forms, heterostyly is clearly a breeding system that evolved to enforce outcrossing (Baker 1964, Mulcahy 1965, Vuilleumier 1967, Barrett 1977, 1978; Ganders 1979). In contrast, differences in style lengths in long- and short-styled forms of *C. angustifolium* are not accompanied by stamen length variation, nor is an incompatibility system found. Instead of increasing the efficiency of cross-pollination, as in classic heterostyly, the opposite seems to be the case in *C. angustifolium,* with the presence of short-styled individuals perhaps increasing the likelihood of selfing in the field. An understanding of the genetic basis for this floral variation must await data on seed germination, seedling vigor, and floral morphology of progeny from the experimental crosses.

An analogy perhaps more appropriate than that of heterostyly may be found in the development of modern tomato varieties (Rick and Dempsey 1969, Rick 1976). Although cultural conditions are known to affect style length in tomatoes (Howlett 1939), modern cultivars have come to possess very short styles, included within the anther tube, as a result of artificial selection in breeding programs. This change in stigma position has increased self-pollination and consequently, fruit-set, and has resulted in very low rates of outcrossing (Rick 1976, Rick et al. 1977, 1978). It may be that natural selection has resulted in a similar situation in *Chlorogalum angustifolium*. Further studies of the breeding sytem in this species could shed light on this process, and comparison with other species in the genus, which are not known to exhibit such floral variation, might prove instructive.

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TAXONOMY AND DISTRIBUTION OF OROBANCHE VALIDA (OROBANCHACEAE)

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Abstract

The name **Orobanche valida** subsp. **howellii** is proposed for populations in the central North Coast Ranges of California, some 600 km from the known range of *O. valida* subsp. *valida*. *Orobanche valida* subsp. *valida,* heretofore known from two collections of the 1920s in the San Gabriel Mountains of southern California, has been recollected from two populations in these mountains. An overlooked specimen collected in 1908 in the Topatopa Mountains of Ventura County is morphologically intermediate between the two subspecies.

Orobanche valida Jepson [Section *Nothaphyllon* (=Sect. *Myzorrhiza*)] has been known from two early collections from the San Gabriel Mountains of southern California (Munz 1959, 1974). W. A. Armstrong collected plants of the taxon near both earlier sites in 1979. Meanwhile, orobanches of uncertain relationships were collected in north-central California by J. T. Howell in 1926, D. Hemphill in 1951, and later by others. We have since recognized their affinity to *O. valida* (Collins 1973, Heckard and Chuang 1975). Armstrong's material allows us to augment earlier morphological and ecological descriptions and to document consistent differences from the northern plants, for which subspecific status is proposed here.

Orobanche valida Jepson, Madroño 1:255. 1929.—Type: USA, CA, Los Angeles Co., San Gabriel Mts., South Fork of Rock Creek, 6250 ft, 2 Jun 1928, *Frank B. and Mabel B. Peirson 7937* (Holotype: JEPS; isotype: RSA).—*Orobanche ludoviciana* Nutt. var. *valida* (Jeps.) Munz, Bull. Torrey Bot. Club 57:621. 1930 [1931]. Pl. 39, Fig. 16.

Stem fleshy, mostly underground, terminated by elongated, subspicate, blackish purple inflorescence, simple or with a few subordinate spikes at base of inflorescence, the entire axis (10–)15–30(–35) cm long, weakly pilose below, becoming densely so in inflorescence; scales few, narrow to broadly ovate. Inflorescence subspicate with flowers short-pedicelled (rarely to 1 cm long) below to sessile above, ⅓ as long as to equaling the non-floriferous portion of stem, dense throughout or with lower flowers widely spaced; bracts lance-acuminate to lanceolate

or subulate, to ca. 1 cm long, mostly shorter than the calyx, exceeding
the bud before anthesis; flowers subtended by paired linear-subulate
bracteoles nearly as long as the calyx. Bracts, bracteoles, and calyces
blackish purple, puberulent to short-pilose with mostly glandular
hairs. Calyx (4.5–)7–10(–11) mm long, deeply 5-cleft into narrow lin-
ear-subulate lobes usually 1 mm broad at base, the tube 2–3 mm deep.
Corolla 12–16(–18) mm long with lips 4–5 mm long, the tube strongly
constricted above ovary and arching forward at constriction, sparsely
to densely short-pilose or puberulent; lips short-pilose to puberulent
(some hairs gland-tipped) on both upper and lower surfaces; upper lip
erect to spreading and recurved, 3–5 mm long, divided 1–2 mm into
2 triangular-acute dark purple divisions; lower lip spreading, 4–5 mm
long, divided ca. 3 mm into 3 triangular to triangular-lanceolate di-
visions, usually exceeding upper lip ca. 0.5 mm, each lobe with whitish
margins and centrally marked with a dark purplish band along mid-
vein extending into the paler tube; palatal folds evident, pale yellow
to whitish, puberulent or glabrous within throat of corolla. Stamens
included, the upper pair ca. 5 mm long, the lower ca. 6 mm; filaments
glabrous or with a few hairs at base; anthers white, almost round, ca.
1.5 mm long, each theca with apiculate base, glabrous or pilose. Ovary
narrowly ovoid, the nectary not evident; placentae 2, cleft by a groove
running their length; stigma peltate, crateriform, slightly bilobed with
the lower lobe larger; capsule narrowly ovoid, 2–3 mm broad, 6–7
mm long. Seeds irregularly ovoid to rhombic, 0.3–0.4 mm long, light
tannish brown, favose.

Key to subspecies of *Orobanche valida*

Corolla puberulent externally, weakly so or glabrous at constriction,
　　　the trichomes ca. 0.1 mm long; palatal folds of throat glabrous;
　　　anthers glabrous; filaments glabrous at base .. 1. subsp. *valida*
Corolla short-pilose externally, densely so at constriction, the tri-
　　　chomes 0.2–0.4 mm long; palatal folds of throat puberulent; an-
　　　thers pilose, the anther pairs held together by hairs; filaments
　　　sparsely pilose at base .... 2. subsp. *howellii*

1. OROBANCHE VALIDA subsp. VALIDA. Fig. 1, F–L.

Axis (10–)15–30(–35) cm long, 5–10 mm broad at mid-point, usually
not enlarged basally. Bracts, bracteoles, and calyx glandular-puber-
ulent, the trichome stalks 2(–3)-celled, ca. 0.1 mm long. Corolla
12–14(–16) mm long, the lips and upper tube puberulent (with tri-
chomes 0.2–0.3 mm long), becoming weakly so or glabrous at con-
striction and below; palatal folds of throat glabrous. Anthers and base
of filaments glabrous. $n = 24$ (count courtesy of T. I. Chuang, based
on *Armstrong s.n.*, 12 Jul 1979, JEPS).
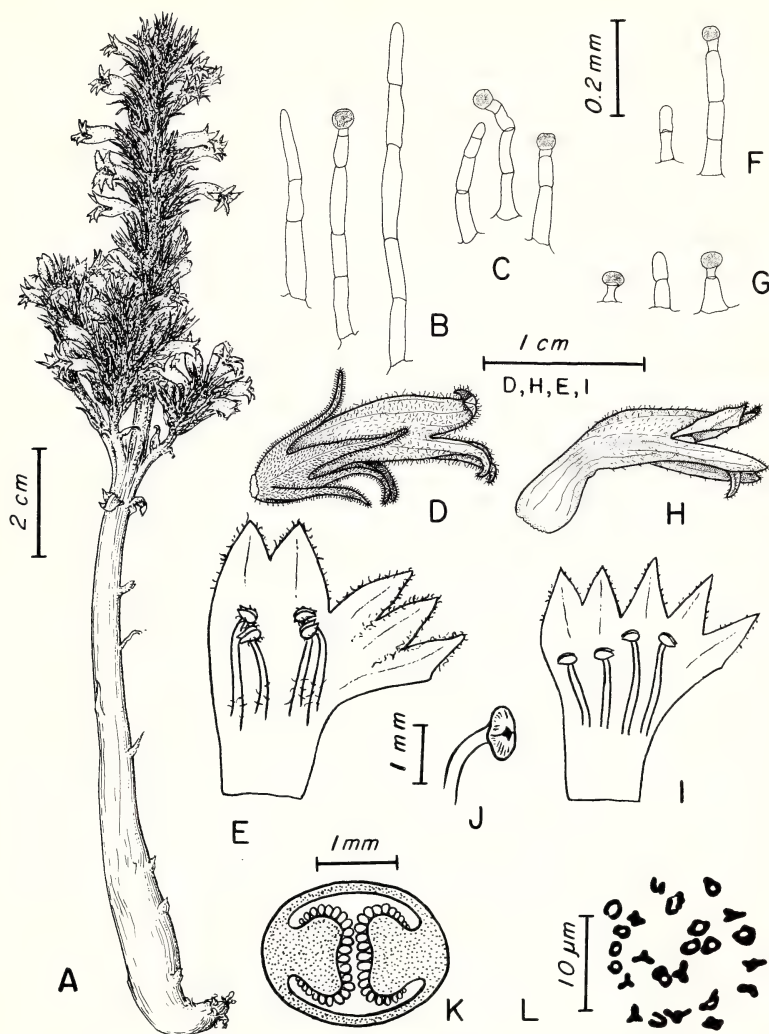
FIG. 1. *Orobanche valida*. A–E. subsp. *howellii*, drawn from *Hemphill s.n.*, 14 Jul 1951. A. Habit. B. Trichomes of corolla. C. Trichomes of calyx. D. Flower. E. Corolla (open). F–L. subsp. *valida*, drawn from *Armstrong s.n.*, 12 Jul 1979. F. Trichomes of corolla. G. Trichomes of calyx. H. Corolla. I. Corolla (open). J. Stigma. K. Ovary (XS). L. Meiotic chromosomes, $n = 24$.

Hosts. Earlier reports on *Garrya* and *Eriodictyon* verified by Armstrong specifically as *Garrya veatchii* (*Armstrong s.n.*, 15 Aug 1979) and *Eriodictyon trichocalyx* var. *trichocalyx* (*Armstrong s.n.*, 1 Aug 1979).

Habitat and distribution. On slopes of loose, decomposed granite with chaparral shrubs such as *Quercus chrysolepis, Q. wislizenii* var. *frutescens, Ceanothus leucodermis, Garrya flavescens, Cercocarpus betuloides,* and *Eriogonum fasciculatum* subsp. *polifolium.* San Gabriel Mountains, CA, 1250–2000 m. Jun–Aug.

Known localities. CA: Los Angeles Co., San Gabriel Mountains: San Gabriel Divide, 1250 m, collector not specified, 5 Jul 1940 (UCSB); trail up s. fork Big Rock Creek, 2.4 km sw. of South Fork Campground, 34°23′N, 117°50′W, *Armstrong s.n.,* 12 Jul 1979, topotype (JEPS, RSA). San Bernardino Co.: San Gabriel Mountains, s. trail to Baldy Lookout, 1770 m, *Johnston 5290* (POM); se. firebreak ridge of Lookout Mt., 1800 m, w. side of ridge near 34°14.6′N, 117°40.3′W, *Armstrong s.n.,* 1 Aug 1979, 15 Aug 1979 (JEPS).

The specimen (Mt. Islip, *Burlew,* LAM) that Jepson suggested as a likely paratype of *Orobanche valida* is *O. parishii* (Jepson) Heckard.

Orobanche valida subsp. **howellii** Heckard and Collins, subsp. nov. Fig. 1, A–E.

A *Orobanche valida* subsp. *valida* bracteis, bracteolis, calycis pilorum stipitibus 3-cellulis ca. 0.2–0.4 mm longis obsitis, corollae tubo dense usque ad eius stricturam brevipilosa, plicis corollae interius puberulentis, atque antheris filamentorum basibusque pubescentibus discedit.

Axis (6–)10–20 cm long, ca. 3–5 mm broad at mid-point, usually enlarging basally to ca. 1 cm. Bracts, bracteoles, and calyx densely glandular short-pilose, the trichome stalks mostly 3-celled, ca. 0.2–0.4 mm long. Corolla 14–16(–18) mm long, the lips and tube densely short-pilose (with trichomes 0.4–0.7 mm long) to below constriction; palatal folds of throat puberulent. Anthers and base of filaments pilose. $2n =$ 48.

TYPE: USA, CA, Mendocino Co., Impassable Rock [nw. of summit of Mt. Sanhedrin], 5600 ft, 14 Jul 1951, *Donald V. Hemphill s.n.* (Holotype: UC; isotype: OSC).

Hosts. Reported to be parasitic on *Garrya fremontii* (*Heckard 2331*; *Hemphill s.n.,* 21 Sep 1963) and on *Quercus chrysolepis* (*Hemphill s.n.,* 14 Jul 1951).

Habitat and distribution. On rocky (volcanic and ultramafic) slopes in open chaparral. Mountains, central North Coast Range, CA, 1215–1700 m. Jun–Sep.

Known localities. CA: Glenn Co., Red Mt. lookout station, on serpentine, *Hoffman 2495* (UC); Lake Co.: skyline fire trail, sw. slope Cobb Mt., *Hamann s.n.,* Jun 1968 (CAS); Sonoma Co., head of Jacket Cr., Mt. St. Helena, *Hemphill s.n.,* 21 Sep 1963 (CAS); *Heckard 2331*

(JEPS); Napa Co., Mt. St. Helena, 1220 m, *Howell 2203* (CAS). The plants have been sighted by Glenn Clifton in two other localities in Napa Co.: Hunting Creek (T11N, R4W, Sec 13) and near Lake Berryessa (T9N, R4W, Sec 21).

The new subspecies is named in honor of John Thomas Howell, Curator Emeritus of the California Academy of Sciences, who has made significant contributions to our knowledge of California plants and who first collected *O. valida* subsp. *howellii*.

The most striking features distinguishing *Orobanche valida* subsp. *valida* from subsp. *howellii* are the differences in indument on floral parts. On the microscopic level there is a difference in trichome size on the corolla and on the bracts, bracteoles, and calyx (Fig. 1, B, C, F, G): those of subsp. *howellii* are about twice as long as those of subsp. *valida*. Available collections indicate that the two subspecies differ in other features: subsp. *howellii* has a slightly larger corolla and the plants in general are smaller than subsp. *valida*; stems of subsp. *howellii* are narrow below the spike but enlarged gradually toward the base while those of subsp. *valida* are broader throughout.

The earliest collection of *O. valida,* two specimens recently detected on a sheet with *O. bulbosa* Beck, adds complexity to the morphological distinction of the subspecies. The specimens (*Dudley & McGregor 121,* 4–6 Jun 1908), from the Topatopa Mountains of Ventura County in southern California, appear to be intermediate in indument of the corolla and in trichome size of the bracts and calyx. The anthers are pilose as in subsp. *howellii,* but the stem is similar to subsp. *valida* in being broad and not enlarged basally. Additional collections of *O. valida* in the Topatopa Mts. and other localities are needed to assess morphological constancy. It is likely that the plants will be found in other areas. Their summer flowering and the habitat in rocky chaparral areas in remote regions have doubtlessly contributed to their infrequent collection.

The relationship of *Orobanche valida* to other species of section *Nothophyllon* is difficult to assess owing to the limited number of morphological features available for comparative purposes and to lack of knowledge of evolutionary trends in these features. Seemingly the closest relatives of *O. valida* are the huskier, desert-dwelling plants of *O. cooperi* (Gray) Heller, which share such features as purplish black herbage and corolla with deep purplish markings and copious, relatively long trichomes. The two are, in our opinion, certainly specifically distinct, with *O. valida* having narrower spikes (2–3 cm vs. ca. 4 cm broad in *O. cooperi*), narrower bracts (lanceolate to lanceovate vs. lance-ovate to ovate), and smaller corollas (11–14 mm vs. 16–30 mm). Also distinguishing the two are the desert habitat of *O. cooperi* and its nearly complete host-restriction to the tribe Heliantheae subtribe Ambrosiinae of Compositae. *Orobanche valida* is morphologically closer to the small-flowered race ($n = 48$) of *O. cooperi* (Heckard

and Chuang 1975) than to the large-flowered race ($n = 24$). This raises the possibility that *O. valida* subsp. *valida* may be ancestral, along with the large-flowered race, in an amphidiploid origin of the higher polyploid. This aspect needs further study.

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DICORIA ARGENTEA (COMPOSITAE: AMBROSIINAE), A NEW SPECIES FROM SONORA, MEXICO

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ABSTRACT

Dicoria argentea Strother from southern coastal Sonora is allopatric to and has larger fruits with relatively smaller bracts than its congeners.

Ann Johnson noted populations of this species on beach dunes at Isla Lobos, Isla Huivulai, and the type locality, all on Sonoran coast south of Guaymas. The plants are apparently restricted geographically (reported sought but not found by Dr. Johnson, e.g., at Guaymas, Sonora, and Topolobampo, Sinaloa). According to the collector, the plants are locally dominant on the dunes and are associated with *Asclepias subaphylla* Woodson, *Croton californicus* Muell.-Arg., and *Palafoxia linearis* (Cav.) Lag.

Dicoria argentea Strother, sp. nov.

Suffrutices procumbentes ad ca. 2 dm alti et ca. 3 m diam.; folia lanceolata vel ovata 8–25 mm longa 3–12 mm lata integra sericeo-cana; bracteae flosculorum pistillatorum orbiculares vel reniformes postremo ca. 5 mm longae; flosculi pistillati 1–2; flosculi staminati 6–18+ corollis 3–4 mm longis; achenia includentia alae 9–12 mm longa 10–13 mm lata; corpora acheniorum 6–8 mm longa 4–6 mm lata; alae acheniorum 3–4 mm latae (Fig. 1).

Sprawling, procument suffrutices to ca. 2 dm high, to ca. 3 m diam.; stems appressed sericeo-canescent, less so in age; leaves sometimes opposite, mostly alternate, petioles mostly 2–10 mm long, blades lanceolate to lance-elliptic or ovate, 8–25 mm long, 3–12 mm wide, 3-nerved from near base, basally cuneate, apically acute, entire, both faces sericeo-canescent; heads solitary or 2–3 loosely aggregated; peduncles mostly 1–3 cm long; involucres roughly campanulate at anthesis; phyllaries proper 5, free, herbaceous, ovate to lanceolate, 2–4 mm long, abaxially sericeo-canescent; "paleae" or inner phyllaries 1–2, each subtending a pistillate floret, membranous, becoming scarious, ovate to orbicular or subreniform, somewhat cupped, ca. 2 mm long, 3 mm wide at anthesis, ultimately to 5 mm long, sparsely to densely appressed-pilose abaxially; receptacles very small, slightly convex, apparently without paleae subtending the staminate florets; pistillate florets 1–2, corollas none, style branches rather stout, ca. 1 mm long; staminate florets 6–18+, corollas pale yellow or ochroleucous, tube 0.3–0.5 mm long, grading gradually into cylindro-campanulate throat 2.5–3.0 mm long, lobes 5, equal, deltoid, erect or incurved, 0.5–0.8
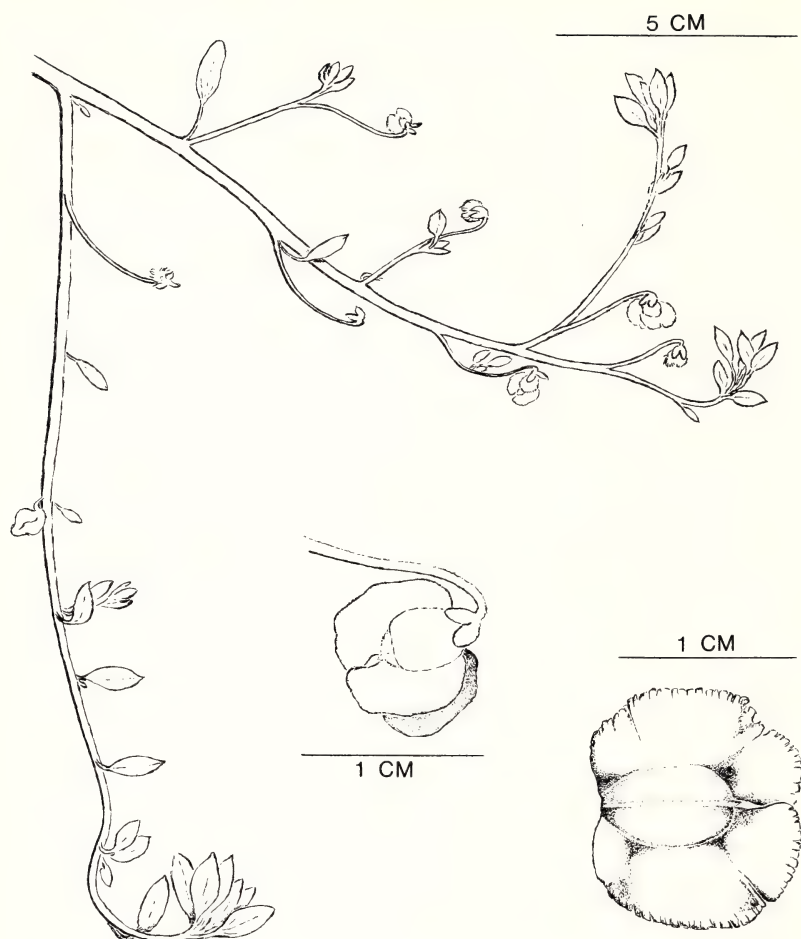
FIG. 1. Habit, immature head, and achene of *Dicoria argentea*.

mm long, throat and lobes abaxially strigillose, stamens united by dilated filament bases, anthers free, 1.2–1.5 mm long, styles reduced, unbranched; achenes dorsi-ventrally flattened, the body black/brown, sometimes buffy-mottled on abaxial face, ovate-elliptic, 6–8 mm long, 4–6 mm wide, weakly keeled or ridged medially on one or both faces, subglabrous or sparsely puberulent and with scattered resinous globules, wings stramineous, cartilaginous, 3–4 mm wide, sparsely puberulent, glabrescent, pectinate-erose or fimbriate; pappus none, but apex of achene may be minutely bidentate and crowned with a tuft of hairs that are soon lost.

TYPE: México, Sonora, Huatabampito (10 km s. of Huatabampo), ca. 26°38′N, 109°40′W, forming dunes just back from beach, 9 Jan 1981, *Ann F. Johnson 8001*. (Holotype: DAV; isotypes: to be sent to ARIZ, C, ENCB, G, K, MEXU, NY, SD, UC, US).

Consistently small entire leaves plus mostly solitary heads and large fruits (9–12 mm long and 10–13 mm wide, including wings) with relatively small subtending bracts readily distinguish *D. argentea* from its congeners, all of which range farther north in Sonora, Baja California, western Arizona, southern California, southwestern Colorado, southern Nevada, northwestern New Mexico, and southern Utah (records in CAS, DS, JEPS, and UC and in standard floras of the area). Rydberg (N. Amer. Fl. 33:11–13. 1922) recognized 7 species of *Dicoria*; I suspect that number might be reduced to 4–6 were the genus critically reviewed. *Dicoria argentea* seems to be morphologically isolated within its genus.

ON THE RECOGNITION OF TRICHOSTEMA
MEXICANUM EPLING (LAMIACEAE)

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ABSTRACT

Additional collections of *Trichostema mexicanum* Epling from the Chihuahuan Desert indicate it can be consistently separated from the more wide-ranging *T. arizonicum* of the mountains of Chihuahua, Sonora and adjacent Arizona and New Mexico. The former has smaller, completely blue-violet flowers and recognizable differences in inflorescence development and vesture.

Epling (1940) described *Trichostema mexicanum* (Fig. 1 A–E) from a single collection of C. H. Muller (*3053*) from Puerto de San Lazaro in west-central Coahuila, Mexico (ca. 63 km south of Monclova). The new taxon was considered most closely related to *T. arizonicum* Gray (Fig. 2 A–D), which occurs mainly in southeastern Arizona and adjacent northern Sonora with scattered collections in southwestern New Mexico, northern Chihuahua and southern Sonora, Mexico (Lewis 1945, Lewis and Rzedowski 1978). Epling noted that *T. mexicanum* differs from *T. arizonicum* in certain reduced features, mainly vesture, smaller flowers and unbranched inflorescences. Lewis (1945) submerged *T. mexicanum* in *T. arizonicum,* placed in his new section *Paniculatum,* noting that the characteristics of Muller's collection fell just within the range of variation in *T. arizonicum.* He also noted the similarity of the Muller specimen with one from the Mustang Mountains in Arizona collected in 1884 by Pringle. Since that time two additional collections referable to *T. mexicanum,* one reported by Lewis and Rzedowski (1978) from northern San Luis Potosí (*Rzedowski 6352,* MEXU) and one from northern Zacatecas (113 air km northeast of Cuidad Zacatecas along highway 54 at K115; *Henrickson 6675,* LL), indicate a geographical and character continuity supporting the distinctness of the species.

The character differences between *T. arizonicum* and *T. mexicanum* are indicated in Table 1 and Figs. 1 and 2. The strongest, most consistent differences are found in corolla size as indicated from total corolla and filament lengths measured in dried specimens. Corolla color also appears to be consistently different (Table 1). According to label data, color of the four posterior corolla lobes of *T. arizonicum* varies within a population. The lavender color of these lobes apparently fades to white upon drying except when the petals dry rapidly in certain herbarium specimens.

More variation is found in inflorescence development. *Trichostema arizonicum* typically has paired dichasia at the upper nodes but oc-
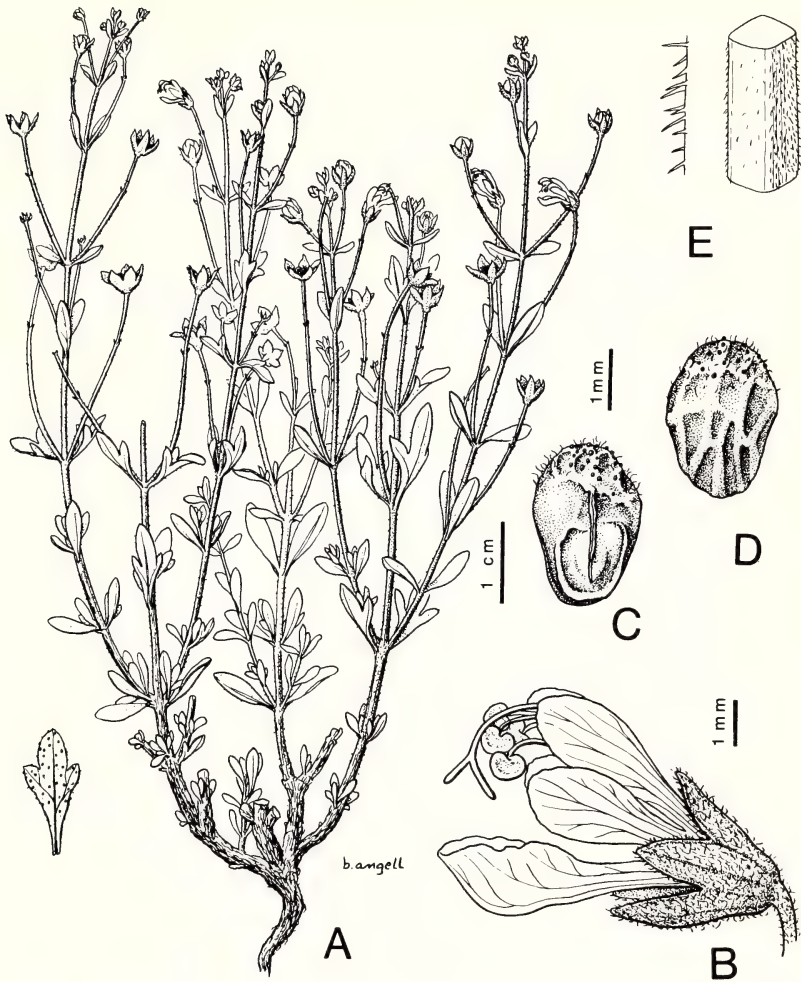
FIG. 1. *Trichostema mexicanum*. A. Habit showing paired flowers on long peduncles and pedicels at upper nodes. Larger leaves are commonly lobed (*Henrickson 6675*, LL). B. Flower, side view with slightly exserted anthers. C–D. Mature mericarp. C. Adaxial view showing conspicuous attachment scar and sessile glands, trichomes on top. D. Abaxial view showing coarse, alveolate sculpturing. E. Stem vestiture showing straight declined hairs. Magnifications as indicated.

casional individuals have only two flowers per paired node. This can vary from plant to plant within a single gathering as exemplified by two collections by F. W. Gould (*3695*) from the Santa Catalina Mountains in Arizona. One sheet at LA has only racemose inflorescences with paired flowers at the nodes, whereas a sheet at ARIZ shows the

TABLE 1. CHARACTER DIFFERENCES BETWEEN *Trichostema arizonicum* AND *T. mexicanum*.

	T. arizonicum	*T. mexicanum*
Inflorescence	Flowers borne in paired, axillary 3(–5)-flowered dichasia.	Flowers paired at upper nodes.
Corolla length	9.0–13.5 mm.	4.0–5.0 mm.
Filament length	15–25 mm.	5–6 mm.
Corolla color	Four posterior lobes light lavender to white, anterior lobe blue-violet marked with white or lavender.	Dark blue-violet throughout with lighter markings on anterior lobe.
Stem vesture	Trichomes decurved, to 0.1(–0.2) mm long [to 0.3(–0.4) mm long in s. Sonoran populations], mixed with stipitate glands.	Trichomes declined (rarely some decurved), mostly 0.13 mm long, mixed with stipitate glands.
Pedicel vesture	Obscurely stipitate-glandular.	Strongly stipitate-glandular.
Nutlet vesture	Mostly few scattered, sessile to short-stipitate glands to 0.1 mm long. (Longer non-glandular trichomes in s. Sonora populations).	Mostly longer, straight to curved, non-glandular trichomes 0.1–0.2 mm mixed with more numerous, longer stipitate glands.
Nutlet ornamentation	Reticulate pattern obscure.	Reticulate pattern bolder, more distinct.
Range	Southern Arizona, New Mexico to s. Sonora, w. Chihuahua	Central Coahuila, n. Zacatecas to central San Luis Potosí.
Habitats	Oak woodland, grassland, streamsides; 1200–1800 m.	Xeric habitats, *Larrea* grasslands to arid scrub; 1200–2300 m.

characteristic paired dichasia. Variation in inflorescence development was also noted in *T. mexicanum*. The Rzedowski (*6352*) specimen exhibits a few three-flowered dichasia.

Vesture differences between the two species hold for most specimens, but variation does exist. The typically decurved stem trichomes of *T. arizonicum* (Fig. 1 E) are usually mixed with scattered sessile to short-stipitate, yellow-tipped glands. In some specimens pedicels have longer, coarser, decurved trichomes or more strongly developed stipitate glands. Some specimens from southern Sonora have much longer, decurved trichomes 0.3(–0.4) mm long on stems and leaves. The may also have longer stipitate glands on the inflorescence and longer hairs on nutlets. Vesture of *T. mexicanum* also shows some variation. Stem trichomes are mostly declined (Fig. 1 E) but they may be mixed with some decurved trichomes. Stipitate glands are more abundant on ped-
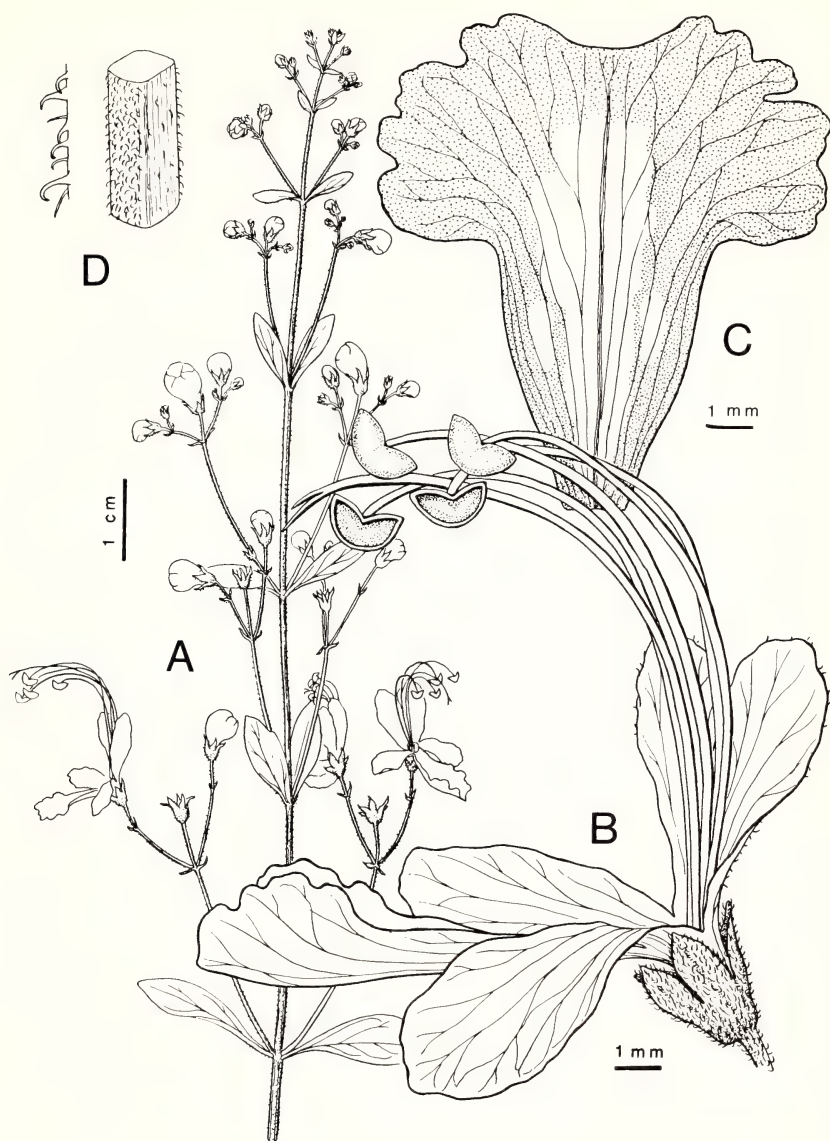
FIG. 2. *Trichostema arizonicum*. A. Habit showing paired lateral dichasia at upper nodes (*Kearney & Peebles 14878*, ARIZ). B. Flower, oblique lateral view showing long-exserted anthers. C. Anterior corolla lobe showing outline and pattern of white on surface. D. Stem vestiture showing characteristic decurved trichomes. Magnifications as indicated.

icels in this species as well. Leaves and calyces of both species have upcurved trichomes mixed with sessile to short-stipitate glands.

Of the 76 collections of *T. arizonicum* studied from ARIZ, LA, LA in UC, NY, RSA-POM, TEX-LL, and UC, very few exhibited any intermediate characteristics with *T. mexicanum*. None exhibited floral similarities; only two specimens of *T. arizonicum* were characterized by simple racemose, instead of paniculate, inflorescences; and only a few plants were more strongly stipitate-glandular in inflorescences, a characteristic of *T. mexicanum*. The above noted Pringle 1884 collection from the Mustang Mountains in Arizona was similar to *T. mexicanum* only in the reduced inflorescence. All other characteristics were typical of *T. arizonicum*.

In my opinion, the data presented above supports the recognition of *T. mexicanum* as a distinct species. The following key can be used to separate the taxa.

a. Corollas 4–5 mm long; dark blue-violet throughout except for white markings on the anterior lobe; filaments 5–6 mm long; flowers paired at nodes; stem trichomes mostly straight, declined but not decurved; pedicels usually strongly stipitate-glandular; central Coahuila to northern Zacatecas, San Luis Potosí, Mexico ......
....*T. mexicanum*
aa. Corollas 9–13.5 mm long, the anterior lobe blue-violet with white markings, the other lobes white to lavender; filaments 15–25 mm long; flowers borne in paired, 3–5-flowered dichasia; stem trichomes decurved; peduncles mostly obscurely glandular; southern Arizona, southern New Mexico to Sonora, western Chihuahua, Mexico ....*T. arizonicum*

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ENVIRONMENTAL AND COMPOSITIONAL ORDINATIONS OF CONIFER FORESTS IN YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT

Quantitative phytosociological data from thirty stands sampled along an elevational gradient (1220–2440 m) in Yosemite National Park are used to generate a direct environmental ordination (elevation vs. a scalar-index integrating site topographic parameters) and two compositional ordinations (Bray-Curtis technique and reciprocal averaging). In each case, elevation emerged as the principal factor controlling forest pattern. Environmental scaling revealed that lower elevation forests (1220–1900 m) in Yosemite consist of a ponderosa pine/incense-cedar type on xeric topographic settings and a white fir/incense-cedar type on mesic topographic settings. Higher elevation forest (1900–2400 m) are generally dominated by a mixture of red fir and white fir, although neither the environmental nor the compositional arrangement of stands adequately accounts for patterns of species dominance in these forests. In this study, integrated use of environmental and compositional techniques reinforce interpretations as well as provide insights which are not directly apparent from independent use of either approach.

Both environmental and compositional ordination techniques have proven to be valuable means of analyzing patterns of plant and animal communities in "natural" settings (Whittaker 1956, Curtis 1959, Bond 1957). While Whittaker (1967) argued that the use of environmental measures (e.g., elevation, aspect, topographic position) is a more direct approach to analyzing plant-environment relationships, McIntosh (1967) and others from the "Wisconsin" school contended that it is preferable to avoid presupposing any necessary environmental control of vegetation pattern; rather, they defend the compositional approach to ordination because it allows the unforced emergence of significant environmental controls from vegetation data. From a biogeographic perspective, the evolution of these two ordination techniques is strongly tied to the character of respective study sites. Environmental ordination techniques were developed for use in midlatitude mountainous regions, where elevation plays a dominant role in controlling local climate and hence vegetation patterns. Moreover, topographic conditions modify the effects of elevation or climate and must be incorporated in any quantitative assessment of vegetation patterns in areas of complex relief. Compositional ordination techniques, on the other hand, were created to analyze vegetation patterns over broad geographic areas of reduced local variability, in which environmental gradients are only subtly expressed in the landscape, if at all (Curtis and McIntosh 1951). Furthermore, compositional ordination was used to impose an organizational framework on a set of geographically discontinuous sites. Although neither ordination method exhibits a

universal superiority, both approaches to vegetation study may be integrated to enhance the analysis of ecological patterns in a region (Loucks 1962). The present study provides a comparison of the results of environmental and compositional ordinations of forest stands in Yosemite National Park, California. In addition, although descriptive treatments of forest patterns in the Sierra Nevada are readily available (Klyver 1931, Munz and Keck 1949, Storer and Usinger 1963), this study represents one of the rare attempts to quantify these phytosociological patterns (Rundel et al. 1977) and is the first such effort in Yosemite National Park.

Thirty stands were selected for sampling in the conifer forests of the montane and lower subalpine zone (1220–2440 m) on the western flank of the Sierra Nevada in Yosemite National Park, California—twenty-five stands between South Entrance and Glacier Point, plus five stands within a 10 km radius of Crane Flat. This area possesses a relatively mild climate with a pronounced summer dry period (the period from June through August receives less than 3 percent of the total annual precipitation). Mean annual precipitation increases with increasing elevation within the sampled zone, from 850 mm at 1220 m to 1500 mm at 1830 m and above. At 1200 m (Yosemite Village), maximum/minimum temperatures range from 30°/12°C in July to 10°/−2°C in January. Mean temperatures are presumed to decline with elevation at a rate of approximately 0.5°C per 100 m (National Oceanic and Atmospheric Administration 1978).

Most stands are on weakly developed soils (Xerochrepts) derived from the Cretaceous granodiorite of which the Sierra Nevada batholith is composed. The exceptions are two stands near Glacier Point, which are on Quaternary glacial till derived from the granodiorite, and two stands near Crane Flat, which are on Paleozoic metasedimentary carbonates flanking the batholith (Matthes 1930, Matthews and Burnett 1966). The initial material for soils on many sites appears to be derived from colluvial processes.

Methods

The thirty stands sampled were stratified so that six stands occurred in each of five elevation belts, each belt 244 m in vertical extent, between 1220 and 2440 m. Each stand was judged to be homogeneous, in the sense that no environmental or vegetational discontinuities were apparent. Vegetation sampling was restricted to forests that had apparently been free from wholesale disturbance for extended periods. Riparian sites were excluded from consideration. Each stand was composed of twenty 1/100 ha circular quadrats, located by a stratified systematic unaligned technique (Berry and Baker 1968) within a 4 by 5 unit grid pattern, each grid unit being 15 m on a side. In the center of each stand topographic position (ridgetop to lower slope), cross-

slope and down-slope configuration (convex to concave), aspect, slope steepness, and elevation were recorded. Within each quadrat, the species and basal area at breast height (1.4 m) of each individual in the tree layer were recorded. The tree layer was considered to include all stems exceeding 0.8 dm^2 (10 cm dbh) at breast height. Saplings (stems exceeding breast height but smaller than 0.8 cm^2) and seedlings were also recorded by species. Inclusion of this information in ordinations, however, yielded patterns similar to those reported below, which are based on tree layer data only, and, thus are not presented.

Environmental ordering of stands consisted of establishing a bivariate space with elevation on one axis and a synthetic index of site topographic condition on the second axis. Unlike Whittaker (1956, 1967) who quantified the topographic complex gradient with a weighted average technique dependent on the vegetal cover (Ellenberg 1947), I have assigned positions along the topographic axis by using a modification of the Topographic Potential Moisture Index (TPMI) (Parker 1980). This is a synthetic scalar index based on the sum of assigned values for the following set of slope characteristics: topographic position, slope configuration, aspect, and steepness. TPMI values may range from 0 (driest sites) to 60 (wet sites). For each stand, between 0 and 20 TPMI units are assigned for topographic position (ranging from 0 on ridgetops to 20 in valley bottoms) and aspect (ranging from 0 at ssw. to 20 at nne.). For each stand, between 0 and 10 TPMI units are assigned for steepness (ranging from 0 on slopes >30° to 10 on slopes <3°), and configuration (ranging from 10 for concave, or water collecting, slopes to 0 for convex, or water dispersing, slopes). Topographic position and slope aspect are weighted twice as heavily as the other factors because both factors were judged to have more influence on vegetation distribution, as inferred from field observation and previous literature (Whittaker 1956, Hack and Goodlett 1961). The following modifications in the use of TPMI from Parker (1980) were made: soil depth was omitted as a factor in determining the TPMI because it rarely affects moisture availability patterns during the growing season in Sierran montane conifer forests (Arkley 1981), slope configuration was refined to include both cross-slope (transverse) and down-slope (longitudinal) components, and riparian sites were not sampled so as to alleviate the confounding influence of locally high groundwater.

Compositional ordination of tree species was performed by two different techniques, Bray-Curtis ordination (Bray and Curtis 1956) and reciprocal averaging (Bakuzis and Hansen 1959, Hill 1973). In each case, importance values for all tree species (after Curtis and McIntosh 1951) were used to provide a data matrix for statistical treatment. For the Bray-Curtis ordination the measure of dissimilarity used to generate an ecological distance matrix among stands was the Manhattan metric [$c = 1 - 2w/(a + b)$]. The endpoint selection method used to

generate the Bray-Curtis ordination was the regression method of Beals (pers. comm.). Reciprocal averaging, which is an iterative technique that successively refines weighting values, or "scores," for both species and stands along a single compositional gradient, was adopted for use after examining the Bray-Curtis ordination and identifying the prominence of a single environmental gradient (elevation) in the vegetation data. The exclusion of groundcover composition from these ordinations may limit the interpretation of patterns within dominant cover types (Peet 1981), but should have little influence on the interpretation of environmental patterns among overstory species.

Results

Three forest types are recognized in the direct environmental ordination: ponderosa pine (*Pinus ponderosa*)/incense-cedar (*Calocedrus decurrens*) forest, white fir (*Abies concolor*)/incense-cedar forest, and red fir (*Abies magnifica*)/white fir forests (all taxonomy after Munz 1959, 1968) (Fig. 1). Most stands are readily assigned to one of these three types. However, two stands represent transitional elements between types (Stands 8 and 17), a predictable result given the continuous variation of vegetation (Whittaker 1967), whereas three of the red fir/white fir forest stands are compositional variants that include locally important Jeffrey pine (*Pinus jeffreyi*; Stands 20 and 24) or lodgepole pine (*Pinus contorta* subsp. *murrayana*; Stand 28) populations.

The distribution of stands and forest types indicates the significance of both elevation and topographic conditions in controlling vegetation patterns (Fig. 1). The ponderosa pine/incense-cedar forest type and the white fir/incense-cedar forest type occur at elevations from 1200 to 1900 m, and are differentiated topographically. Ponderosa pine is more common at lower elevations, on south-facing slopes, and on upper slope positions, where solar radiation and potential evapotranspiration are high and runoff is dispersed. Compensation for macroclimatic changes along the elevational gradient is reflected in the progressive restriction of ponderosa pine to drier sites associated with steep, south-facing, and convex slopes above 1600 m. White fir, which is present on mesic sites in the lower elevation forests of Yosemite National Park, also displays the interplay of elevation and topographic setting. White fir is a common dominant in forests above 1600 m, but below this elevation white fir is dominant only on north-facing, concave slopes characterized by reduced solar radiation, reduced potential evapotranspiration, and concentrated surface runoff and soil throughflow. Stand 8, a dry mesic site at 1600 m, is considered transitional because of the equivalent importance value (25.7 percent) of both white fir and ponderosa pine. This quantification of the relative importance of ponderosa pine and white fir along a topographic sequence
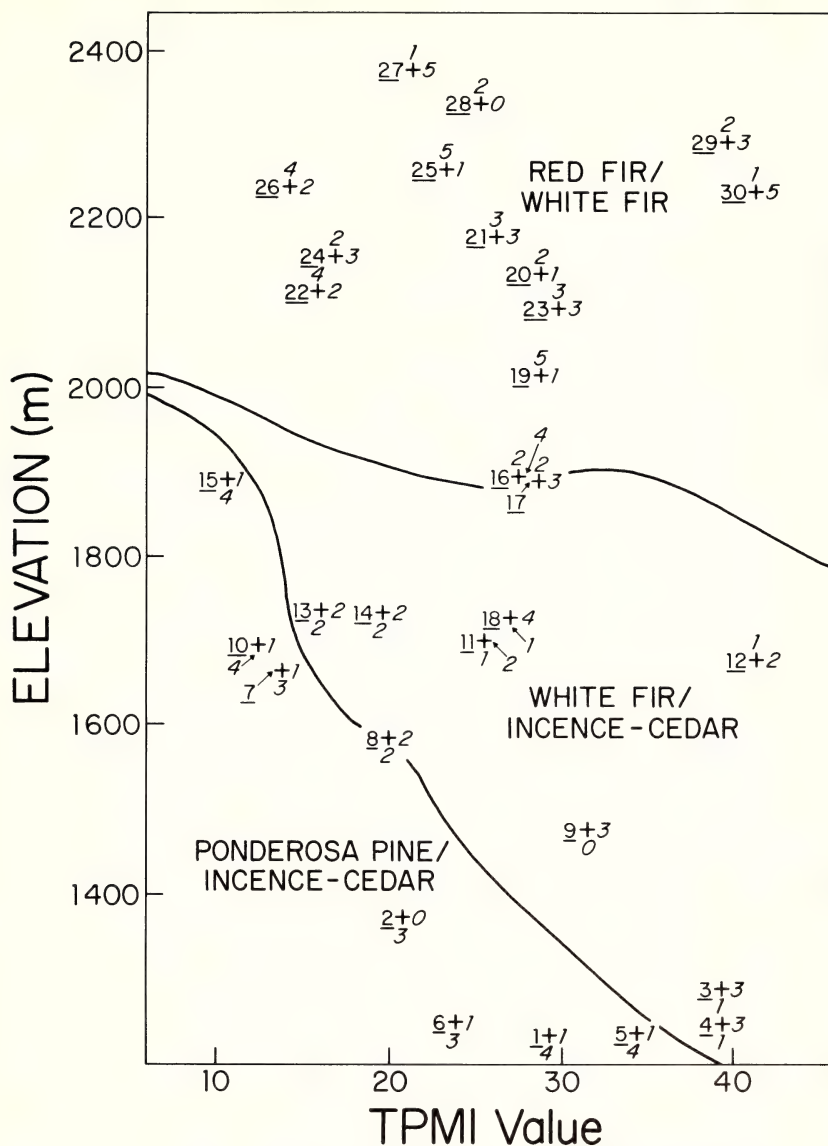
FIG. 1.   Environmental ordination of Yosemite stands. Using a scale of importance values, with 5—80.1–100.0, 4—60.1–80.0, 3—40.1–60.0, 2—20.1–40.0, and 1—0.1–20.0, the importance of ponderosa pine (below), white fir (right), and red fir (above) is indicated next to stand positions. Stand numbers are underscored to the left of plotted position.

enumerated by the TPMI in lower elevation Yosemite forests corrob-orates the descriptive treatments of tree distribution patterns in the central Sierra that have been published during the last half-century (cf. Rundel et al. 1977).

The zone between lower and higher elevation forests (ca. 1900 m) is under-represented in this study. I considered the occurrence of in-cense-cedar to be crucial in making this elevational distinction. All stands classified as red fir/white fir lack incense-cedar and are clearly removed from white fir/incense-cedar forests in the compositional or-dination. The compositional ordination does suggest that Stand 17 is somewhat transitional in nature, with similar importance values for red fir (26.0) and incense-cedar (24.8). Clearly, Stands 12 and 18 might also be classed as compositionally transitional. All three of these tran-sitional stands occupy a continuous portion of the mesic side of the environmental space, between 1700 and 1900 m.

Red fir/white fir forests occur in a wide variety of topographic set-tings between 1900 and 2400 m in Yosemite National Park. In this elevation zone, the TPMI is not effective in differentiating habitats where red fir reaches highest dominance from those where white fir is most important (Fig. 1). There is little indication that red fir is more abundant than white fir on more mesic sites, or at higher elevations, although the regional zonal relationship of these two species suggests that red fir is better adapted to cooler, moister settings than white fir. The forests of this zone appear to be ecotonal mixtures of white fir and red fir located in the lower portion of a broad elevation zone dominated solely by red fir (Oosting and Billings 1943). The inability of the TPMI to identify habitat preferences of red and white fir on these transitional sites may be related to the confounding influence of unusual microclimatic conditions. For example, Stands 29 and 30 ap-pear on the figures to be cool, moist sites, occuring at high elevations (2200–2300 m) and on protected exposures (north-facing, lower slopes). Therefore, the dominance of white fir in these forests is puzzling until it is noticed that these stands are located immediately above Glacier Point. Because of their location on the rim of Yosemite Valley, they may experience the warming and drying influence of an upslope day-time breeze (as described for the North Rim of the Grand Canyon by Halvorson 1972), resulting in the enhancement of evapotranspiration rates. This example illustrates the need for exercising caution in in-terpreting the interaction of elevation and TPMI values, because local wind conditions can override the influence of topographic parameters in controlling water availability and demand on certain sites. The strong dominance of Stand 28 by lodgepole pine is also apparently related to wind. Here, extreme exposure on the flank of a granite outcrop induces physiological drought and locally alters winter snow-pack depth and persistence.

Bray-Curtis ordination (Fig. 2) verifies the existence of the forest
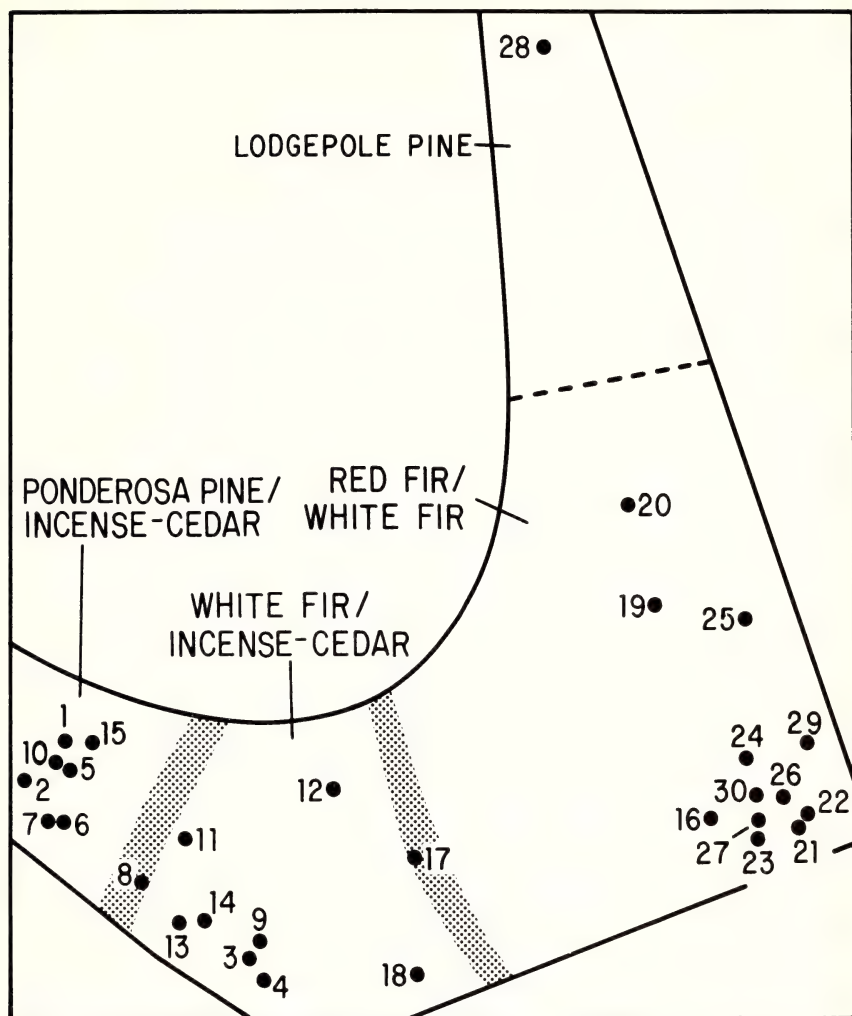
FIG. 2. Bray-Curtis ordination of Yosemite stands. Stands are located with respect to the first two synthetic axes of a Bray-Curtis type ordination.

types recognized above. In this ordination, however, the composition of Stand 28 (dominated by lodgepole pine) is unique and warrants separate recognition from red fir/white fir forests. As was the case in the environmental space, the ordination identifies two transitional stands (8 and 17). The first axis of the compositional ordination correlates well with elevation ($r = 0.847$, $p < 0.01$).

The emergence of elevation as the factor most strongly correlated

with forest composition prompted the use of the first axis of a recip-
rocal averaging ordination as an alternative means of arranging the
stands because this technique generates an arrangement of species
optima, as well as stand locations, along a single ecological gradient.
Like the Bray-Curtis ordination, reciprocal averaging values for stands
emphasize the elevational gradient ($r = 0.814$, $p < 0.01$). The three
forest types are clearly distinguished by reciprocal averaging (ponder-
osa pine/incense-cedar stand scores range from 0.0 to 7.2, white fir/
incense-cedar stand scores range from 21.0 to 37.5, and red fir/white
fir stand scores (except Stand 28) range from 53.7 to 79.3). Moreover,
the transitional nature of Stands 8 (18.1) and 17 (46.2) and the unique-
ness of Stand 28 (100.0) are underscored. Of particular ecological in-
terest is the arrangement of species optima along the elevational gra-
dient, with reciprocal averaging scores increasing with increasing
elevation: ponderosa pine (0.0), California black oak (*Quercus kellogg-
ii*) (9.0), incense-cedar (14.1), sugar pine (*Pinus lambertiana*) (21.6),
white fir (43.7), red fir (66.6), Jeffrey pine (72.4), and lodgepole pine
(92.4). This quantitative arrangement of species optima by reciprocal
averaging parallels the descriptive treatments of vegetation zonation
published by previous workers (Rundel et al. 1977).

DISCUSSION

Both the environmental and compositional ordinations presented
for Yosemite National Park indicate the significance of elevation in
controlling forest community patterns and document quantitatively
the zonal sequence of forest types as well as the associated sequence
of species optima along an elevational gradient.

Among the two lower elevation forest types, the environmental or-
dination clearly differentiates the role played by topographic features.
In this regard, the Topographic Potential Moisture Index provides an
integration of slope-related hydrologic factors that is useful for seg-
regating dominance patterns of ponderosa pine and white fir. By con-
trast, although both of the compositional ordination techniques (Bray-
Curtis and reciprocal averaging) support the recognition of two lower
elevation forest types (ponderosa pine/incense-cedar and white fir/in-
cense-cedar), these techniques fail to indicate the importance of mois-
ture regime as influenced by topographic parameters in controlling
dominance by white fir and ponderosa pine. Thus, by failing to dis-
tinguish between elevation and topographic modifications of available
moisture, the use of compositional ordination alone results in the loss
of valuable interpretive information.

Patterns of tree species occurrence in high elevation forests are not
adequately explained by either environmental or compositional meth-
ods. Local peculiarities in wind, snowpack, and substrate conditions
obscure the expression of elevation and topographic influence on the

distribution of forest types, rendering the TPMI ineffective in segregating habitats. The separation of one lodgepole pine dominated stand in both compositional ordinations underscores the need to consider factors in addition to elevation and topographic condition in examining environmental relationships among higher elevation forest types in Yosemite.

If a choice between environmental and compositional ordination is necessary, direct analysis of environmental gradients may be preferable in situations where the complex of environmental factors influencing vegetation patterns is obvious, such as in landscapes of high relief. At the same time, care must be taken to avoid misinterpreting species patterns on sites modified by specific extenuating factors, such as edaphic constraints. However, in landscapes where direct environmental control of vegetation is not apparent, either because of subtle expression of environmental gradients or marked temporal heterogeneity among stands, compositional ordination may help identify the most important environmental factors. I found that union of the two techniques yielded a mutual reinforcement of the interpretive pattern and provided some unique insights. Environmental, or direct gradient analysis, techniques allow direct assessment of the influence of site factors on patterns of dominance, whereas compositional ordination identifies both stand clusters and transitional stands and thus facilitates the placement of forest types within an environmental framework.

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NOTES AND NEWS

Taxonomy of *Lomatium bicolor* (Umbelliferae).—*Lomatium bicolor* (Watson) Coulter and Rose belongs to the group of diminutive, usually acaulescent root-tuber geophytes known as tuberous lomatiums (sect. *Cous* of M. E. Jones, Contr. W. Bot. 12:1–81. 1908). Recent systematic studies of this group have shown that *L. bicolor* consists of two morphologically and geographically intergrading varieties (Schlessman, Systematics of the tuberous species of *Lomatium* (Umbelliferae), Ph.D. dissertation, Univ. Washington. 1980). Variety *bicolor* is a regional endemic of northern Utah, southeastern Idaho and southwestern Wyoming. The range of the more common var.

leptocarpum extends from northeastern California through eastern Oregon and south-eastern Washington to Idaho, Wyoming, Colorado, and the Grand Canyon of Arizona.

Representative specimens of var. *bicolor* tend to have irregularly thickened roots, numerous (80–250) filiform leaf segments, and relatively broad (1.5–4.5 mm), elliptic fruits with long (1–10 mm) pedicels. Variety *leptocarpum* is characterized by a more or less globose-thickened root, leaves with relatively few (20–130), linear segments, and narrow (1.5–3 mm), narrowly elliptic to linear fruits with short (0.1–2 mm) pedicels. Certain specimens from central and eastern Idaho and northeastern Oregon have the numerous filiform leaf segments characteristic of var. *bicolor* and fruits characteristic of var. *leptocarpum*.

Marcus E. Jones (1908) recognized *Lomatium bicolor* (Watson) Coulter and Rose as the closest congener of *L. leptocarpum* (Nuttall ex Torrey and Gray) Coulter and Rose. Mathias and Constance (North American Flora 28:161–295. 1945; Constance, pers. comm.) saw no clear discontinuity between the two taxa and treated them as a single species, *L. leptocarpum*. However, the epithet *bicolor* has priority at specific rank and recognition of two varieties requires the new combination presented here. A complete revision of the tuberous lomatiums is in preparation.

Lomatium bicolor (Watson) Coulter & Rose var. *bicolor,* Contr. U.S. Natl. Herb. 7:237. 1900.—*Peucedanum bicolor* Watson, Bot. King Surv. 129. 1871.—TYPE: USA, UT, Salt Lake Co., Parley's Park, *Watson 467* (Lectotype: US!; Isolectoptype: GH!; Paratypes: GH!, US!).—*Cogswellia bicolor* M. E. Jones, Contr. W. Bot. 12:33. 1908.

Lomatium bicolor var. **leptocarpum** (Nuttall ex Torrey & Gray) Schlessman, comb. nov.—*Peucedanum triternatum β leptocarpum* Nuttall ex Torrey & Gray, Fl. N. Am. 1:626. 1840.—TYPE: USA, Oregon (?), Wahlamet (sic) and Columbia Plains, *Nuttall s.n.* (Lectotype: PH!).—*Peucedanum ambiguum* var. *leptocarpum* (Nuttall ex Torrey & Gray) Coulter & Rose, Rev. N. Am. Umbell. 59. 1888.—*Lomatium leptocarpum* Coulter & Rose, Contr. U.S. Natl. Herb. 7:213. 1900.—*Cogswellia leptocarpa* M. E. Jones, Contr. W. Bot. 12:33. 1908.—*Lomatium ambiguum* var. *leptocarpum* Jepson, Madroño 1:159. 1924.

Peucedanum bicolor var. *gumbonis* M. E. Jones, Contr. W. Bot. 10:55. 1902.—TYPE: USA, ID, Indian Valley, 15 Jul 1889, *M. E. Jones s.n.* (Lectotype: US!); Monroe Creek, 20 Apr 1900, *M. E. Jones s.n.* (Paratypes: BM!, NY!).

————————

SPREAD OF *Filago arvensis* L. (COMPOSITAE) IN THE UNITED STATES.—*Filago arvensis* is an annual Eurasian weed, typical of sandy pastureland and streamsides. It has been introduced into the USA and Canada, and it is spreading at an exponential rate. This may constitute some cause for alarm because the plant forms dense colonies and has been reported to be unpalatable to livestock by several stockmen who have sent specimens to MONT. Moreover, *F. arvensis* may be adapting to the diverse environmental conditions of northwestern USA; we have found the plant growing not only in well-used pastures, but forest clear-cuts, rangelands and grainfields as well.
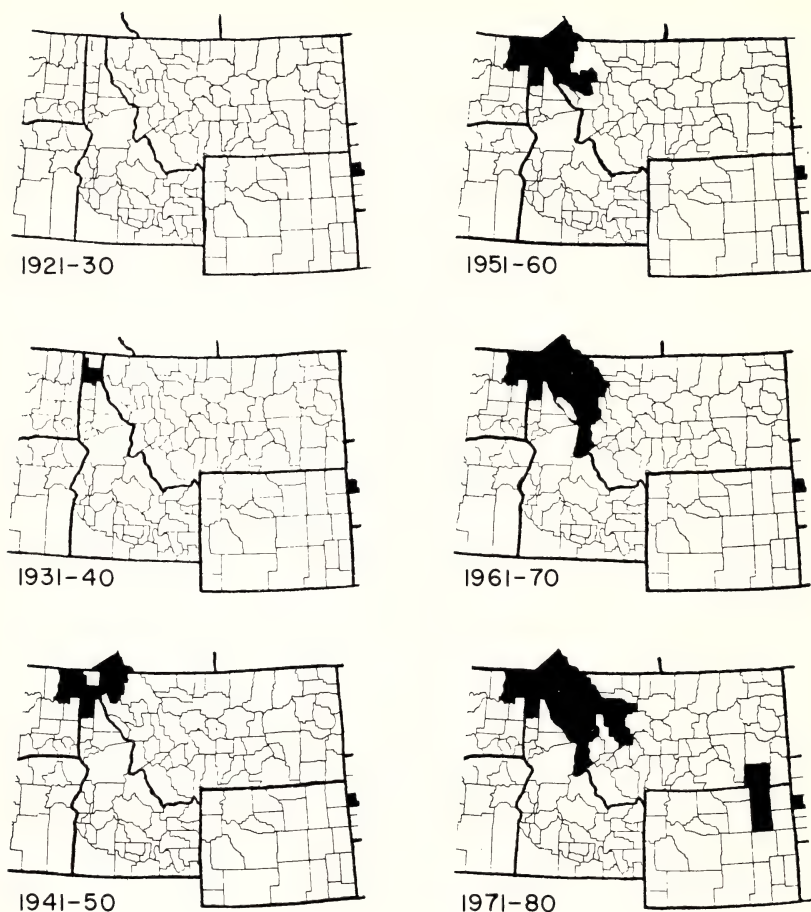
FIG. 1.   Spread of *Filago arvensis* by counties during the six decades from 1921–80 in Idaho, Montana, South Dakota, Washington and Wyoming. (In the 1940s *F. arvensis* also spread into southeastern British Columbia.)

To document the spread and current distribution of *F. arvensis* we surveyed nine herbaria (ID, IDS, MONT, MONTU, NY, RM, UCB, WSP and WTU) for preserved specimens and identification records of the plant. Additionally, in conjunction with a general weed survey in Montana, we searched for the plant throughout the western half of that state.

The migration of *F. arvensis* is depicted on a county basis in Fig. 1. The species was first collected in North America by A. C. McIntosh in 1926 in Lawrence Co., South Dakota, but was misidentified as *Gnaphalium palustre*. The specimen was deposited in RM, where R. Hartman correctly identified it in 1979. Because *F. arvensis* is not listed in The Vascular Plants of South Dakota (T. Van Bruggen, Iowa State Univ. Press. 1976), McIntosh's collection also represents a state record for South Dakota. A second introduction seems to have been made in the 1930s in the northern Idaho region.
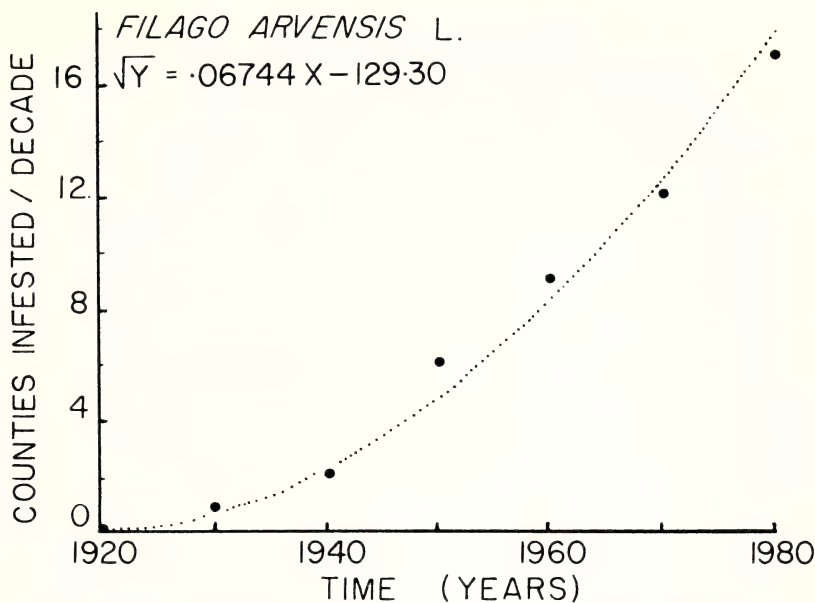
FIG. 2. Rate of spread of *F. arvensis* by counties in the past six decades in Idaho, Montana, South Dakota, Washington and Wyoming. Y = number of counties, X = date.

This latter arrival quickly spread in all directions (including into British Columbia), but particularly east- and southeastward into Montana. By slowly spreading westward, the original South Dakota population probably gave rise to the specimens collected in northeastern Wyoming and southeastern Montana. Evidence for a distant third introduction is the NY specimen collected in Cheboygan Co., Michigan in 1956 (A. Cronquist, in litt.). No mention of *F. arvensis* was made in several state and regional North American floras that we checked, thus we believe this species to be restricted in the USA to the boundaries shown in Fig. 1 for 1980 (plus northern Michigan).

So far, *F. arvensis* has spread into at least 17 northwestern US counties. Its spread into new counties in the past six decades (1921–80) has occurred at an exponential rate (Fig. 2). From our preliminary analysis of migration rates for 250 alien weed species in the northwestern USA (Forcella and Harvey, New and exotic Weeds of Montana, I and II. Montana Dept. of Agriculture, Helena. 1981) we have concluded that exponential migration rates are characteristic of noxious weeds, whereas ruderals typically spread at approximately linear rates. Thus in the not too distant future we suspect that *Filago arvensis* may become a problem weed.

CLIMATE DIAGRAM FOR THE UNIVERSITY OF CALIFORNIA SAGEHEN CREEK FIELD
STATION.—The Sagehen Creek drainage basin, e. of the Sierra crest in ne. Nevada and
se. Sierra Counties, contains a mixture of forest, scrub, bog, and stream habitats and
is the site of various biological research projects (see Madroño 22:115–139. 1973). The
climate diagram for Sagehen Creek (Fig. 1) is drawn according to the scheme devised
by Heinrich Walter (Vegetation of the earth and ecological systems of the geo-biosphere.
Second edition. New York, Springer-Verlag. 1979). Monthly averages for temperature
and precipitation are plotted above an abscissa representing the year from Jan (left)
through Dec (right). These averages are based on data compiled by E. Alan Cranston
(University of California Sagehen Creek Station weather records. Manuscript in field
station library. 1970.) for temperatures collected over 16 years (Nov 1952–Mar 1954, Jan
1955–Dec 1969) and for precipitation collected over 10 years (1957, 1961–1969).

Several climatological benchmarks are shown on the figure. For the period of obser-
vation, mean annual temperature was 4.7°C, and mean annual precipitation was 912
mm (mostly as snow). The highest temperature recorded was 34.4°C (1 Aug 1954), and
the mean daily maximum for the warmest month (Jul) was 26.7°C. The mean daily
minimum for the coldest month (Jan) was −11.8°C, and the lowest temperature recorded
was −33.9°C (24 Feb 1962). The mean daily minimum falls below freezing (0°C) in Sep
through May (indicated by black bars below abscissa), and the actual daily minimum
may fall below freezing in the remaining months Jun through Aug (diagonal stripes).
The dotted area where the precipitation curve falls below the temperature curve indi-
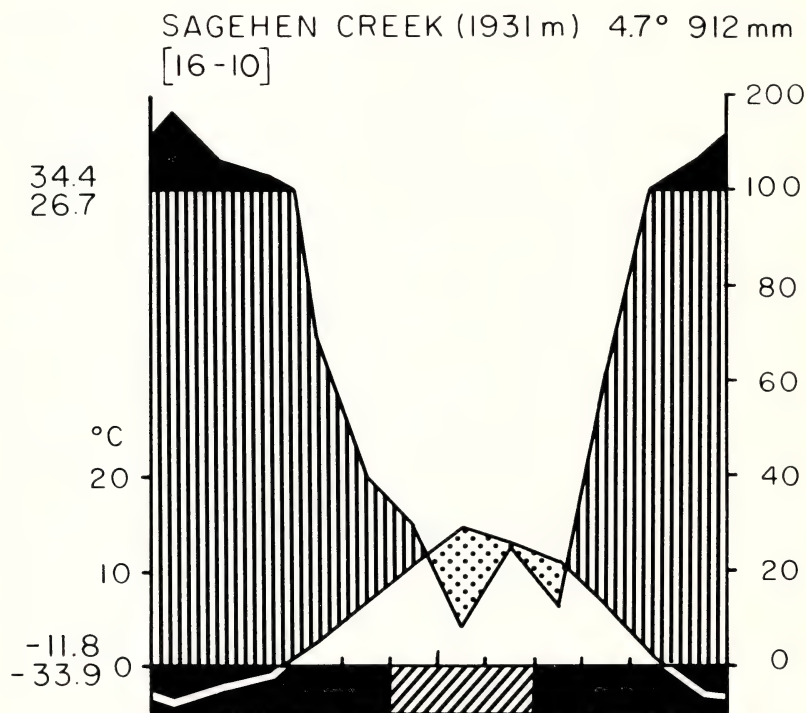
FIG. 1.   Climate diagram for Sagehen Creek Field Station, elevation 1931 m, average
annual temperature 4.7°C, average annual precipitation 912 mm. (See text for expla-
nation of scales and other data.)

cates the approximate period of water stress to plants (late Jun–late Sep, with the slight drought sometimes broken by summer thundershowers).

Sagehen Creek drainage basin ranges in elevation from ca. 1860 m to 2672 m. The weather station itself (located ca. 120°14′30″W and 39°25′45″N according to U.S. Geol. Surv. Truckee 15′ quadrangle. 1955) lies at 1931 m. Thus, the climate diagram is representative more of conditions in the lower part of the basin. Though but one of several methods for representing climate (see, e.g., Barbour, M. G., et al. 1980. Terrestrial plant ecology. Menlo Park, Benjamin/Cummings Publishing Co., Inc.), this climate diagram for Sagehen Creek may be compared to more than 8000 such diagrams for stations throughout the world (Walter, Heinrich, and Helmut Lieth. 1960–1967. Klimadiagramm-Weltatlas. 3 parts. Jena, VEB Gustav Fischer Verlag).—DALE E. JOHNSON, 12283 Ranch House Rd, San Diego, CA 92128. (Received 24 Aug 1981; accepted 28 Sep 1981.)

NOTEWORTHY COLLECTIONS

California

ERIOPHYLLUM NUBIGENUM Green ex. Gray (ASTERACEAE).—Mariposa Co., Yosemite Natl. Park, near the top of Chilnualna Falls, 1890 m, 2 Jun 1980, *Botti 26* (YNP). *Previous knowledge.* Three locations in Yosemite National Park. *Significance.* The last recorded sighting or collection of this taxon was 4 Jun 1897 by J. W. Congdon at Chilnualna Falls in Yosemite. Its rediscovery at the same site after 83 years ended a lengthy search for this taxon, which was believed to be "possibly extinct" according to a CNPS Plant Status Report, 1977. Subsequently the site of the collection by Mrs. Dodd, 1891 (UC) in Little Yosemite Valley and three other previously unknown sites were located.—STEPHEN J. BOTTI, Resources Management Specialist, Yosemite Natl. Park, CA 95389. (Received 23 Feb 1981; accepted 12 Mar 1981.)

MIRABILIS LAEVIS (Benth.) Curran (NYCTAGINACEAE).—Alameda Co., rocky slope on the nw. ridge of Mission Pk, Fremont, ca. 775 m. Colony appears to be fairly extensive. *N. Havlik 929* (UC); *N. Havlik 930* (CAS). *Significance.* First record for Alameda Co., range extension some 200 km n.—NEIL HAVLIK, E. Bay Reg. Park Distr., 11500 Skyline Blvd, Oakland, CA 94619. (Received 3 Jul 1981; accepted 16 Dec 1981.)

Montana

HOWELLIA AQUATILIS Gray (CAMPANULACEAE).—Missoula Co., sw. side of Lindbergh Lake Rd. 0.8 km nw. of Swan River crossing (NE¼ S7 T19N R16W), 1240 m, 29 Jul 1978, *McCune 2287* (MONTU, MONTU at Yellow Bay, PH). (Determined by A. E. Schuyler, Jul 1978.) *Significance.*—First record of *Howellia* in MT and its easternmost record. *Howellia*

is listed as rare and endangered in CA, ID, OR, and WA.—BRUCE MCCUNE, Dept. Botany, Univ. Wisconsin, Madison 53706. (Received 30 Apr 1981; accepted 20 Aug 1981.)

Wyoming

CAREX BIPARTITA All. (CYPERACEAE).—Park Co., Beartooth Plateau, head of Wyoming Cr. (T58N R104W S21 SE¼), 3172 m, 21 Jul and 22 Aug 1980, *Evert 2088* and *2428* (RM); Absaroka Range, at head of West Blackwater Cr. (T51N R107W S30 NW¼), 3175 m, 13 Aug 1980, *Evert 2384* (RM); Absaroka Range, 0.8 km se. of Chaos Mtn. (T50N R108N S30 NW¼), 3111 m, 28 Jul 1980, *Evert 2250* (RM). Occasional on tundra in wet soil along streamlets.

Previous knowledge. Wet places at high altitudes, CO, UT, and MT n. to AK, circumpolar; also in New Zealand.

Significance. First reports for WY. The three WY localities are 6 km, 77 km and 85 km respectively from the nearest known population in Carbon Co., MT.

CAREX DEWEYANA Schwein. (CYPERACEAE).—Park Co., 0.4 km e. of East Entrance of Yellowstone Natl. Park (T52N R109W S8 SW¼), 2104 m, 2 Jul 1976, *Evert 1083* (RM); along Grinnell Cr., 2.4 km n. of Hwy 14 (T52N R108N S6 NW¼), 2287 m, 9 Aug 1980, *Evert 2343* (RM). Occasional in moist meadow and open woodland.

Previous knowledge. Open woods and stream banks, Labrador to B.C. and s. and w. to PA, IA, SD, NM, AZ and CA.

Significance. First reports for WY. About 247 km from the nearest known population in Rosebud Co., MT.

CAREX INCURVIFORMIS Mack. (CYPERACEAE).—Park Co., Absaroka Range ne. end of Wapiti Ridge (T51N R105W S19 NE¼), 3355 m, 29 Jul 1979, *Evert 1538* (RM). On tundra, among boulders near the edge of a vernal pool.

Previous knowledge. Alpine ledges and turf, CA, CO and MT, n. to Alta. and AK, circumpolar; also in S. America.

Significance. First report for WY. About 350 km from the nearest known population in Deer Lodge Co., MT.

DIANTHUS BARBATUS L. (CARYOPHYLLACEAE).—Park Co., Aspen Cr. and Hwy 14, ca. 48 km w. of Cody (T52N R107W S23 NE¼), 1860 m, 18 Jul 1980, *Evert 2129* (RM). Several colonies have been observed for eight years in woods near cabin and appear to be spreading.

Previous knowledge. Native of Europe, cultivated and spreading to roadsides and groves; locally established from s. Que. to s. B.C., s. to DE and w. to ND, w. MT, w. OR, w. WA and n. CA.

Significance. First report for WY. About 432 km from the nearest known population in Missoula Co., MT.

GENTIANELLA PROPINQUA (Rich.) Gillett GENTIANACEAE).—Park Co., Absaroka Range, near Flora Lake (T51N R109N S25 NW¼), 2958 m, 20 Aug 1972 and 17 Aug 1980, *Evert 178* and *2404* (RM). In moist subalpine meadow and spruce-fir groves.

Previous knowledge. Meadowlands, streambanks and woods, AK s. to B.C., Alta., OR and MT, e. to Que. and Labrador.

Significance. First report for WY. About 257 km from the nearest known population in Beaverhead Co., MT. This is apparently the most southerly station for this species in N. Amer.

MYOSOTIS ARVENSIS (L.) Hill (BORAGINACEAE).—Park Co., along Fishhawk Cr., ca. 0.4 km s. of Hwy 14 (T52N R108W S27 SW¼), 1952 m, 5 Jul 1980, *Evert 2015* (RM). In disturbed area along trail.
Previous knowledge. Eurasian, established in fields and roadsides, Nfld. to Ont. and MN and s. and w. to NJ, WV and PA, local in MT, OR, WA, B.C., Man. and Sask.
Significance. First report for WY. A range extension of ca. 422 km from the nearest known population in Missoula Co., MT.

MYOSOTIS MICRANTHA Pall. (BORAGINACEAE).—Park Co., along Hwy 14, at Fire Fighter's Memorial ca. 51 km w. of Cody (T52N R107W S21 SW¼), 1891 m, 29 Jun 1978, *Evert 1258* (RM). In Moist disturbed area. (Synonym: *M. stricta* Link.)
Previous knowledge. Road sides and old fields naturalized from Europe, s. Que. to s. B.C. and s. and w. to VA, IA, MT, ID, OR and CA.
Significance. First report for WY. A range extension of about 400 km from the nearest known population in Ravalli Co., MT.

POTENTILLA RECTA L. (ROSACEAE).—Park Co., 0.4 km w. of Wapiti Ranger Station, Shoshone Natl. For. (T52N R106W S21 NE¼), 1800 m, 21 Jul 1980, *Evert 2134* (RM). Common in irrigated pasture. Fremont Co. (T31N R10W S24), 2165 m, 1 Sep 1977, *Roth 27* (Central Wyoming Community College).
Previous knowledge. Eurasian, naturalized in fields and roadsides, widespread in e. U.S. and Can., locally w. and s. to NE, SD, n. CO, TX, MT, ID and e. WA.
Significance. First reports for WY. About 390 km from the nearest known population in Ravalli Co., MT.—ERWIN F. EVERT, 1476 Tyrell Ave., Park Ridge, IL 60068. (Received 2 Apr 1981; accepted 24 Aug 1981.)

ANNOUNCEMENT

CBS GRADUATE STUDENT AWARD, 1981

The award for the outstanding paper presented at the 1981 California Botanical Society Graduate Student Meetings, held at San Francisco State University on 24 Oct, was won by Luann Z. Wright, Department of Botany, San Diego State University. The title of her presentation was SHOOT GEOTROPISM: ITS RELATIONSHIP TO THE ACID-GROWTH THEORY.

ANNOUNCEMENT

The Society for Economic Botany will hold its 23rd annual meeting at the University of Alabama in University, Alabama, 14–17 June 1982. Featured will be a symposium entitled "U.S. OILSEEDS INDUSTRY–GERMPLASM TO UTILIZATION." Further information can be obtained from C. Earle Smith, Jr., Anthropology, Box 6135, University of Alabama, University, AL 35486.

Information for Contributors

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All 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, 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, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. 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 latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted eight pages in MADROÑO over a two year period. Joint authors are each assessed the full page number. Beyond that number of pages a required editorial fee of $40.00 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 @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

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AGE AND ORIGIN OF THE MONTEREY ENDEMIC AREA

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Davis 95616

Abstract

The Monterey endemic area originated during late Wisconsin and Holocene times. Widespread sandy substrates afforded sites for the origination, by various modes, of new species following population movements into the region. Their sources included taxa *a*) from forest communities that earlier were in the lowlands under cooler, moister Pleistocene climates, *b*) from widespread species along the central coastal strip, and *c*) from interior and southern alliances that probably invaded the area during the Xerothermic. In addition, paleoendemics of wider Quaternary distribution found a haven here under the influence of the Monterey submarine canyon on land climate; it provided an effective local foggy shield from Xerothermic conditions. The paleoendemics include two cypresses and a *Pinus radiata* population with relatively small cones. By contrast, the *P. radiata* populations at Año Nuevo and Cambria, farther removed from a more persistent foggy shield, apparently developed larger cones in response to Xerothermic aridity.

Of the diverse endemic regions in California (Stebbins and Major 1965), the Monterey area poses a unique problem. Although it is much smaller than the mountainous Santa Cruz and Santa Lucia endemic areas directly north and south, it is richer in endemics even though those areas are far more diverse in relief, climate, and rock-soil type. Furthermore, there are no serpentine exposures in the Monterey area to help account for its high endemism, as in the Santa Cruz or Mt. Tamalpais areas. In addition, whereas the larger endemic areas in the northern (Siskiyou) and southern (Diegan) parts of the state have a relatively high incidence of warm season precipitation that appears to account for the persistence of paleoendemics there (Raven and Axelrod 1978), this is not true of the Monterey area. This low-lying region not only has a much lower total rainfall than endemic areas to the north and south in the outer Coast Ranges, it receives less warm season precipitation than those areas. Furthermore, the occurrence of quartz diorite at Monterey-Carmel can scarcely explain the high endemism there. The same rock makes up the northern half of Inverness Ridge and Montara Mountain, north and south of San Francisco. Both are nearly equal in size to Monterey-Carmel endemic area yet few endemics occur there. Clearly, other factors must account for the occurrence in this local region of the highest number of endemics in the outer central Coast Ranges. To provide a basis for interpreting its history, some of the general features of its flora and vegetation are recalled briefly (Howitt and Howell 1963, 1973; Stebbins and Major 1965). All specific names are those in Munz (1973).

Flora and Vegetation

Monterey County is a meeting place for plants from the north and south. Howitt and Howell (1963, 1973) report that of the 1400-odd native species, about 150 and 160 reach their northern and southern limits there, respectively, excluding the flora of the higher Santa Lucia Mountains. In the Monterey endemic area members of the closed-cone pine forest include the notable paleoendemics *Cupressus goveniana* and *C. macrocarpa* with very restricted ranges (see Griffin and Critchfield 1972) and *Pinus radiata,* apparently a relict, ancestral population (see below). In addition, the area has six endemic species of *Arctostaphylos* as well as other taxa listed in the Appendix. Inland from the coast, the Salinas and Carmel Valleys are covered with coastal sage on drier slopes that alternates with a *Quercus agrifolia* woodland-grassland on moister flats and north-facing slopes. Farther up Carmel Valley climate rapidly becomes more continental and *Quercus agrifolia* woodland-grassland gives way to *Quercus lobata-Q. douglasii* woodland-grassland, with *Pinus sabiniana* joining them farther inland. In this interior area, commencing about 20–25 km southeast of Monterey, there are numerous additional species that have a wider distribution in the inner Coast Ranges but do not extend into the coastal strip. Among these are (for others, see Howitt and Howell 1963, 1973; Linsdale 1955):

Aesclepias eriocarpa	*Orthocarpus attenuatus*
Amorpha californica	*Pectocarya penicillata*
Baccharis viminea	*Penstemon centranthifolius*
Calochortus splendens	*Penstemon heterophyllus*
Camissonia graciliflora	*Phacelia brachyloba*
Cercocarpus betuloides	*Phacelia douglasii*
Cirsium proteanum	*Plagiobothrys canescens*
Cryptantha microstachys	*Plagiobothrys nothofulvus*
Emmenanthe penduliflora	*Prunus ilicifolia*
Eriodictyon californicum	*Quercus douglasii*
Gilia achilleifolia	*Quercus dumosa*
Gilia tenuiflora	*Quercus lobata*
Lasthenia chrysostoma	*Rhamnus ilicifolia*
Linanthus bicolor	*Salvia columbariae*
Malacothrix clevelandii	*Sanicula bipinnata*
Microseris elegans	*Senecio douglasii*
Microseris heterocarpa	*Trichostema lanatum*

Howitt and Howell (1963, p. 17) note that a number of these species, as well as those in the flora a few km southeast in Salinas Valley and adjoining interior valleys, have affinities with the Mohave Desert flora, a relationship also displayed by the floras of the inner Santa Cruz Mountains (Thomas 1961) and the Mt. Hamilton Range (Shar-

smith 1945). This interior aspect of the flora, so evident in middle and upper Carmel Valley, is reflected also by the large, relict stand of *Pinus sabiniana* in Pine Canyon eight miles south of Salinas. It suggests that the community probably had a wider occurrence on the seaward slopes of the outer Coast Ranges in the Xerothermic, of which the stand near Gorda also appears to be a relict (Axelrod 1966, p. 50).

A number of taxa in the coastal Monterey region extend into the drier, inner Coast Ranges, where they are prominent members of the flora. Among these are (for others, see Howitt and Howell 1963, 1973):

Aesculus californicus	*Lepidium nitidum*
Allium hickmanii	*Lupinus albifrons*
Athysanus pusillus	*Lupinus nanus*
Calochortus luteus	*Mahonia pinnata*
Chorizanthe coriacea	*Malacothamnus fasciculatus*
Clarkia cylindrica	*Orthocarpus purpurascens*
Clarkia lewisii (=bottae)	*Platystemon californicus*
Collinsia heterophylla	*Potentilla glandulosa*
Convolvulus subacaulis	*Ranunculus californicus*
Datisca glomerata	*Ribes malvaceum*
Delphinium patens	*Solanum umbelliferum*
Eriastrum densifolium	*Trifolium gracilentum*
Eschscholzia californica	*Viola pendunculata*

This summary suggests that the Monterey endemic area recently has accumulated its unique taxa from diverse sources. Clearly, the area is a haven for conifers that had a wider distribution along the coast in the past. The Appendix shows that other endemics are allied to species now in mixed conifer forests to the north that probably invaded the lowlands of the area during the Pleistocene when rainfall was higher and temperature lower than they are now in the Monterey area. These endemics occur chiefly on sandy substrates, notably old dunes, elevated floodplains, and old coastal terraces. Also in similar sites are taxa allied to species that are widespread along the central California coast. In addition, another group has affinities with presently interior and southern species that imply that a warmer, drier climate affected the area following the last major glacial-pluvial stage.

Endemic Taxa with Forest Affinities

Some Monterey endemics are allied to taxa in the mixed conifer and Douglas fir forests to the north, including species of *Allium, Arctostaphylos* (4 spp.), *Lupinus, Ribes,* and *Trifolium* (Fig. 1). Although these forests occur chiefly at elevations above 750 m in the Coast Ranges to the north, they were at sea level in the San Francisco Bay region during the late Pleistocene. This is shown by the San Bruno flora (Potbury 1932), dated at 10,000 BP. It represents a *Pseudotsuga*

forest like that now near Inverness, 60 km north in Marin County, where rainfall is 800 mm or more as compared with half that at the fossil site today. In addition, a small flora near Mountain View at the southwest corner of San Francisco Bay, dated at 20,000 to 23,000 BP, contains *Calocedrus, Cupressus, Pinus,* and *Pseudotsuga,* indicating that mixed conifer forest was then at sealevel (Helley et al. 1972), and that a much cooler, moister climate was then in the area (for estimate, see Axelrod 1981). There was a similar climate there in the late Pliocene-early Pleistocene, as shown by the Santa Clara flora near Saratoga, with *Calocedrus, Pseudotsuga,* and *Pinus* cf. *lambertiana* (Dorf 1930). Under the cooler, moister climate of the late Pliocene and early Pleistocene, mixed conifer forest ranged far to the south, occupying the lowlands of interior southern California (Axelrod 1966). The present forest patches in the central and south Coast Ranges, including the higher Santa Lucia Mountains, probably are remnants of that time. Inasmuch as the ranges were largely elevated during the late Pliocene and Pleistocene (Christensen 1966), it would appear that the mixed conifer forests that formerly blanketed the lowlands were, in essence, elevated bodily to their present moister, cooler sites where they persisted as climate became drier and warmer over the lowlands. Climatic-topographic differences over the area during the later Pleistocene, especially in the Xerothermic, probably account for the discontinuous distributions of the forest taxa in the higher Coast Ranges today.

Many taxa in the Monterey area that evidently originated from older, mesic forest species occur in an area of lower rainfall than that in which their presumed ancestors lived. Whereas the Monterey area receives 450–500 mm yearly, rainfall is two and three times that amount in areas where the inferred ancestral, or closely related, taxa now live. The high incidence of summer fog compensates for low rainfall to some degree. However, it appears that the usual habitat of many of the endemics on dunes and sandy areas may account for their persistence. Contrary to popular notion, dunes and old elevated terraces are not dry. Even dunes do hold water (Bagnold 1941, p. 245–246), the amount depending on the internal structure (bedding) of the dune, the degree of compaction, and the size of the grains, which determines porosity. The dunes in Clatsop County near Seaside in the northwest corner of Oregon are capable of storing 80 percent of the annual precipitation, which there averages 2000 mm annually (Frank 1968). In the desert of southeastern California, subsurface sands of the Eureka Dunes (Pavlik 1979, 1980), Kelso Dunes (Sharp 1966), and Algodones Dunes (Norris and Norris 1961) are moist well into summer. Pavlik showed that endemics on Eureka Dunes are in fact mesophytes as compared with nearby desert plants bordering the Eureka Dunes, situated in the lee of the Inyo-White Mountains. He also reported

Monterey Endemics allied to forest taxa

Allium   hickmanii

Arcto.   edmundsii

Arcto.   montereyensis

Arcto.   pajaroensis

Arcto.   pumila

Ceanothus rigidus

Chorizanthe pungens

Ribes menziesii v. hystrix
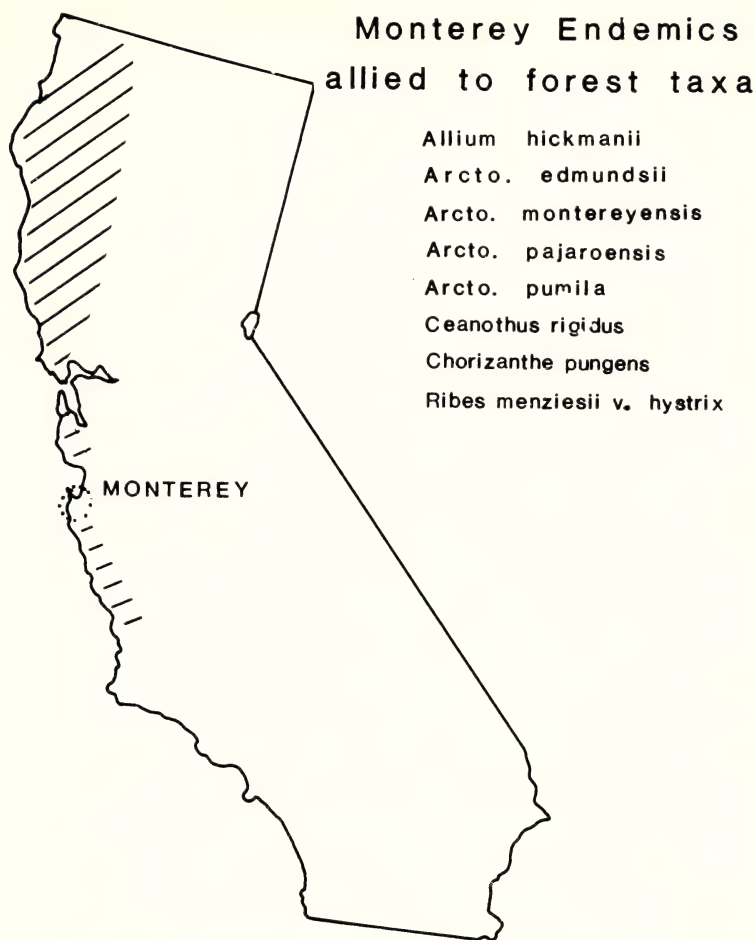
MONTEREY

FIG. 1.   Monterey endemics allied to forest taxa occur chiefly in the mountains to the north, under wetter and cooler climate.

(pers. comm., Dec 1980) that in summer moist sand occurs in Eureka Dunes fully 150 m above the desert floor. Clearly, while the Monterey endemics derived from forest taxa are in an area of low precipitation, they persist on sandy sites presumably because they are relatively mesic. Moisture comes from winter rainfall, from drainage from bordering hills where precipitation is higher, and from the dense, wet fog that commonly hugs the ground during summer. In addition, nonmarine terrace deposits regularly have silty or clayey lenses that act as water tables.

The Monterey occurrence of numerous endemics on sandy sub-strates is not unique. *Pinus torreyana*, situated between Del Mar and La Jolla, is confined to the Linda Vista Terrace and Eocene Torrey Sandstone. Road cuts and the walls of gulches in these formations are wet and seep water late in the year. The population of *P. torreyana* on Santa Rosa Island is confined to the predominantly sandy Santa Margarita Formation which also retains ample moisture through the year. The elevated terraces between Nipomo and Lompoc have several woody endemics, including *Arctostaphylos purissima*, *A. rudis*, *A. viridissima*, *Ceanothus impressus*, *Eriodictyon capitatum*, and *Malvastrum gracile*. In addition, *Arctostaphylos morroensis* is confined to sandy hills south of Morro Bay. Other woody taxa on elevated terraces include the following that have wider distributions: *Arctostaphylos cruzensis*—San Luis Obispo Co. north to southern Monterey Co.; *Arctostaphylos tomentosa* var. *crassifolia*—Oceanside to San Diego; *Baccharis pilularis*—Russian River to Pt. Sur, Monterey Co.; *Ceanothus dentatus*—Monterey south to San Simeon; *Ceanothus gloriosus*—Marin Co. north to Pt. Arena; *Ceanothus ramulosus*—Burton Mesa, Nipomo Mesa, and north to Monterey Co.; *Ceanothus verrucosus*—San Diego Co. and southward; *Eriogonum parvifolium*—Monterey to San Diego Co.; *Haplopappus ericoides*—Bolinas, Marin Co., south to Los Angeles Co.; *Helianthemum scoparium*—Mendocino Co. south to Santa Barbara Co.; *Lupinus arboreus*—Del Norte Co. south to Santa Barbara Co.; *Lupinus chamissonis*—San Francisco south to Los Angeles Co.; *Lupinus variicolor*—Humboldt Co. south to San Luis Obispo Co.

The preceding lists are not intended to be complete, and annuals and herbaceous perennials have not been considered. The data do indicate that sandy substrates, especially stabilized dunes and elevated terraces, probably support endemic taxa because of the adequate moisture provided by these environments. Apart from the moisture factor, it is apparent that plants in these sites may be removed from competition. This may be due in part to greater moisture as compared with bordering environments, and also to the problem of moving sand and hence establishment and continued growth on a relatively unstable substrate. It is also likely that they can tolerate better the nutrient-poor sands and thereby escape competition.

Endemic Taxa with Coastal Affinities

Some of the endemic taxa (Appendix) appear to be members of closely related species groups that occur along the coast, as exemplified by *Chorizanthe*, *Eriogonum*, *Erysimum*, *Haplopappus*, and *Mimulus* (Fig. 2). The endemics may have originated by geographic isolation, or other means, in the later Quaternary chiefly. The two varieties of *Arctostaphylos tomentosa*, as well as *Ceanothus griseus* var. *horizontalis*, probably belong to this group with coastal affinities.

Monterey Endemics

allied to coastal taxa

Arcto. tomentosa f. trichoclada
    ''   ''   f. hebeclada

Ceanothus griseus v. horizontalis

Eriogonum parvifolium ssp. lucidum

Erysimum ammophilum

Haplopappus eastwoodiae

Lupinus tidestromii

Malacothrix saxitilis v. arachnoidea

Mimulus guttatus v. arenicola

Trifolium polydon
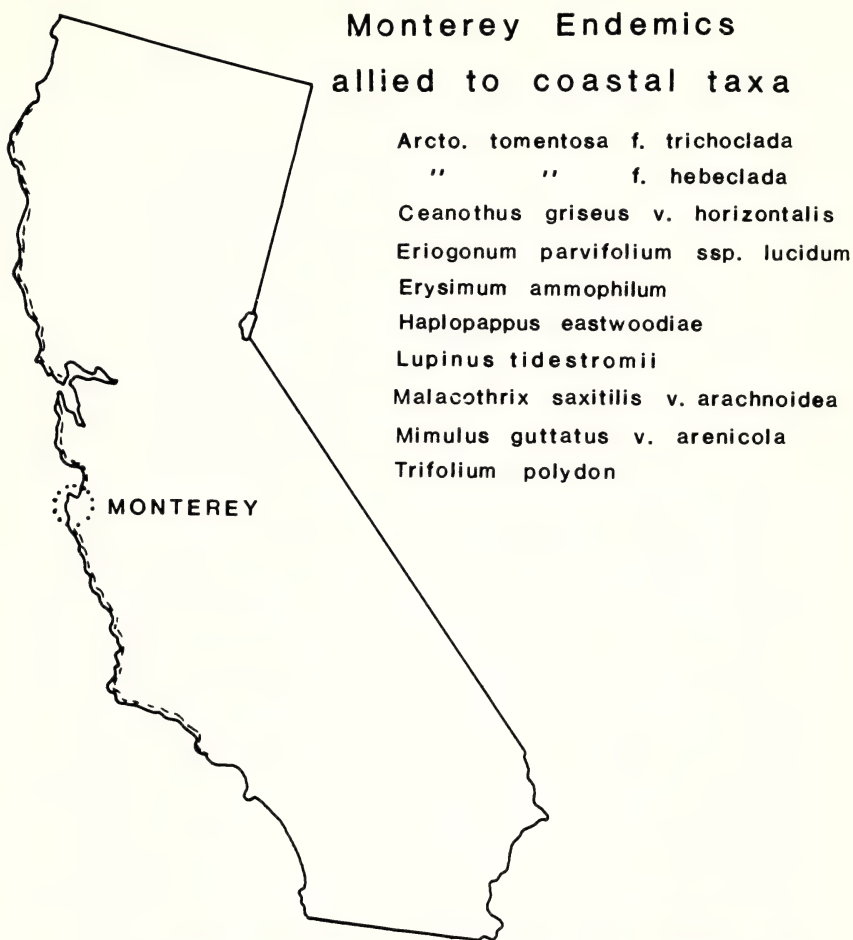
MONTEREY

FIG. 2. A number of Monterey endemics are related to species of primarily coastal occurrence.

ENDEMIC TAXA WITH INTERIOR AND SOUTHERN AFFINITIES

Some Monterey endemics (*Allium hickmanii, Arctostaphylos montereyensis*) have isolated occurrences in the interior. Whether they are invading that area, or retreating from it, is not presently clear. A number, however, do have affinities with taxa that are in the interior or to the south in warmer regions, as *Cordylanthus, Corythrogyne, Delphinium, Eriastrum, Gilia, Malacothrix,* and *Triteleia* (Fig. 3). As with the group above, they differ from their presumed ancestral, or allied, taxa in only minor ways, often of subspecies or varietal nature.

Monterey Endemics
allied to interior taxa

Arctostaphylos hookeri
Corethrogyne filaginifolia
v. viscidula
Cordylanthus littoralis
Delphinum hutchinsoniae
Eriastrum virgatum
Gilia tenuiflora ssp. arenaria
Triteleia versicolor
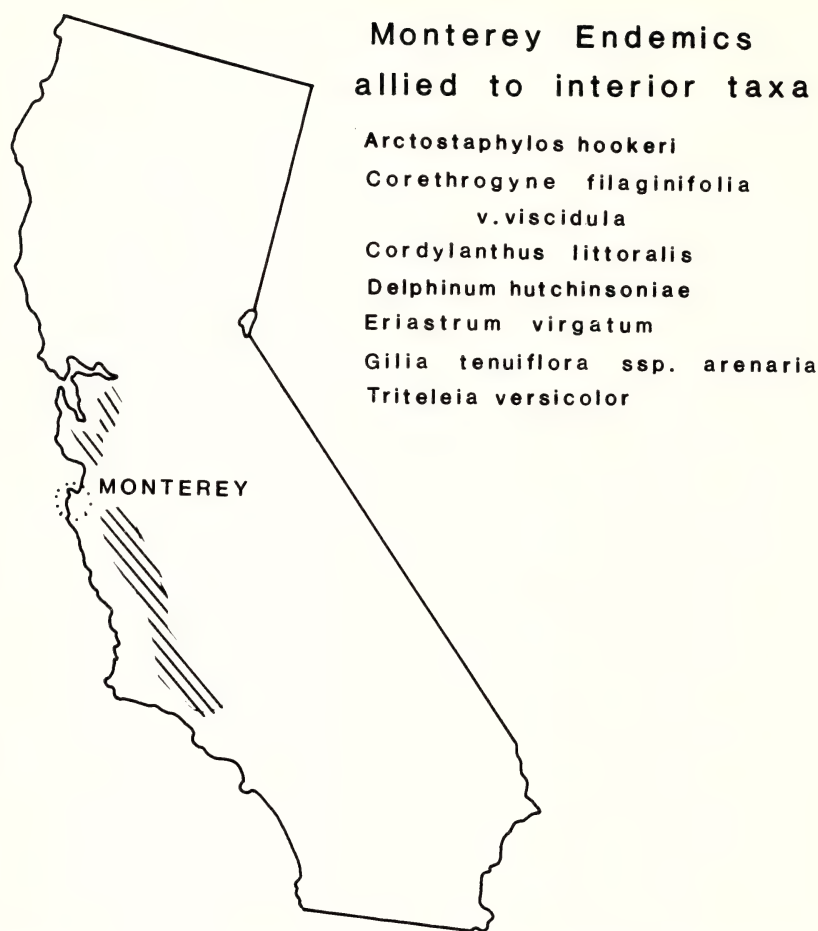
Fig. 3.   Some Monterey endemics are allied to taxa that occur chiefly in the interior and to the south.

They probably were derived from interior and southern taxa that invaded the coastal strip during the Xerothermic. The effect of this warmer drier climate of 8000 to 4000 years ago (see Axelrod 1966; 1981, p. 851) also appears to clarify the puzzling relationships displayed by the *Pinus radiata* populations at Año Nuevo and Cambria north and south of Monterey, respectively, as well as the reason for the persistence of the narrow endemics *Cupressus macrocarpa* and *C. goveniana* in the area.

PALEOENDEMICS AT MONTEREY

Three conifers are restricted to the Monterey area. *Cupressus go-veniana* and *C. macrocarpa* have very limited ranges (see Griffin and Critchfield 1972) and *Pinus radiata* does not extend beyond the near-coastal sector around Monterey-Carmel. All of them have fossil records north and south of Monterey (Fig. 4). As outlined elsewhere (Axelrod, MS), the pine and cypresses were restricted southward by colder Wisconsin-age climate and were confined northward as drier, warmer climate spread during the Holocene. That their survival in the Monterey area probably can be ascribed to local environment is suggested by the interrelationships of the central California populations of *Pinus radiata*.

EVOLUTION OF *PINUS RADIATA* POPULATIONS

The *Pinus radiata* population at Monterey has a smaller mean cone size than those at Año Nuevo and Cambria, which are in wetter and drier areas to the north and south (Axelrod 1980, pl. 1 and fig. 2). Cones the size of the Monterey population have been recovered at Drakes Bay to the north and near Pt. Sal to the south (Axelrod 1980). In addition, smaller-coned *P. radiata* populations like those of the Guadalupe Island stands have been found at a number of sites of various ages (5 m.y. to 20,000 years) in the coastal region (Fig. 4). However, the larger-coned *P. radiata* populations at Año Nuevo and Cambria are not now known to have a fossil record. Cone-size of the fossil Carpinteria population (radiocarbon age older than 40,000 years) is intermediate between those produced by the Monterey and Año Nuevo stands (Axelrod 1980, fig. 2). This probably reflects the warmer climate in that very different floristic-climatic province. An earlier increase in cone size is expectable there in view of the semiarid taxa (*Arctostaphylos glauca, Juniperus californica, Pinus sabiniana*) that covered steep dip-slopes of Eocene and Oligocene sandstones directly east of the pine forest that inhabited the floodplain, taxa that indicate a climate warmer than that now in the region.

The trend to larger-coned *P. radiata* populations in central California probably was an adaptation to increasing summer drought (Axelrod 1980), for the larger seeds would favor seedling establishment (see Baker 1972), especially under the progressively more extreme mediterranean-type climate that was emerging during the later Pleistocene. This suggests that the Cambria population may have originated in or near its present area during the Xerothermic. It now inhabits the driest area of the three California populations, an area that presumably was warmer and drier during the Xerothermic as judged from other evidence in California (Axelrod 1966, 1981). This is implied also by the occurrence of the typically interior *Pinus sabiniana* in the
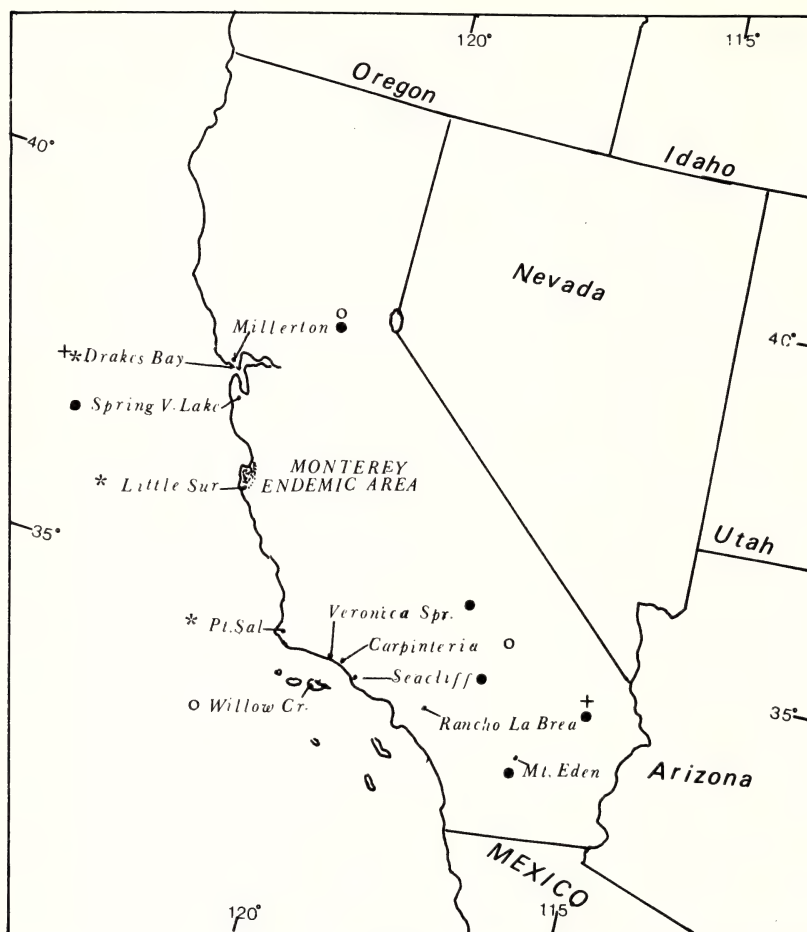
FIG. 4. Fossil occurrences of paleoendemics. *Pinus radiata*, * Monterey population, ● Guadalupe Island population cone size; + *Cupressus macrocarpa*; ○ *Cupressus goveniana*. Ages of localities are Mt. Eden, 5 m.y.; Seacliff, 1 m.y.; Veronica Springs Quarry, 1 m.y.; Drakes Bay, ? 0.75–1.0 m.y.; Carpinteria older than 40,000 BP; Rancho La Brea, 30,000 BP; Millerton, 28,000 BP; Pt. Sal, 28,000 BP; Willow Creek, 15,000 BP; Little Sur, 10,000 BP.

nearby region, and of shrubs in the adjacent South Coast Ranges that are disjunct from Los Angeles and Riverside Counties (*Adenostoma sparsifolium, Quercus dunnii*), or which occur elsewhere in the coastal strip from Santa Barbara County southeastward (*Ceanothus spinosus*).

The Año Nuevo population may also have originated locally in response to the spread of drier, warmer Xerothermic climate. Its in-
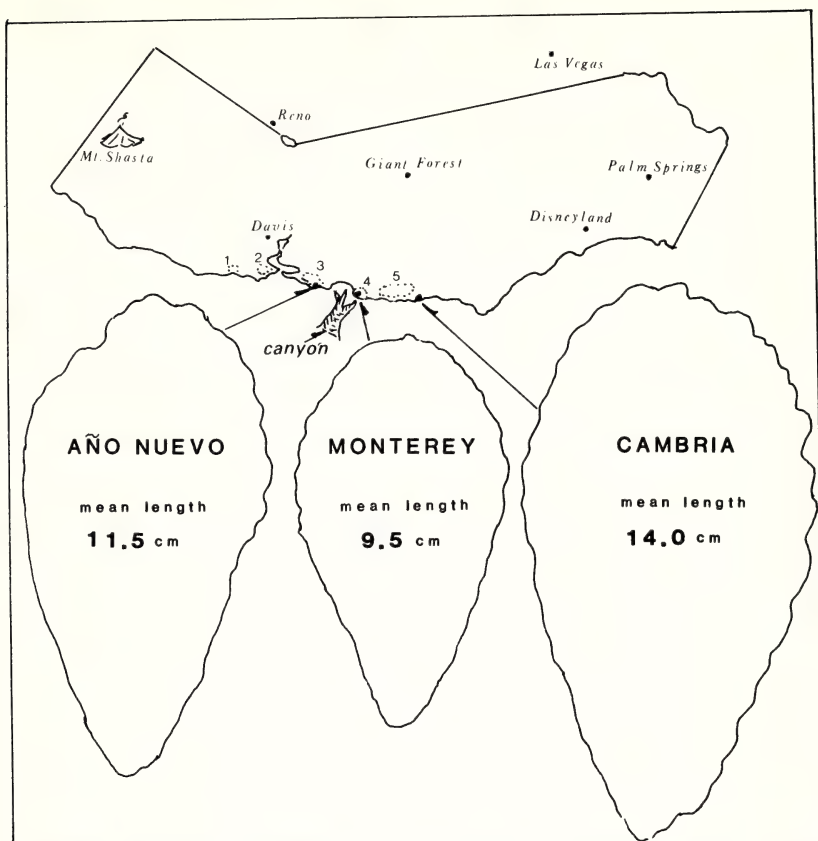
FIG. 5.   Illustrating mean cone size of the California populations of *Pinus radiata* (from Axelrod 1980). Size of Monterey submarine canyon greatly exaggerated; see Fig. 6. Endemic areas in the outer central Coast Ranges are: 1. Pitkin-Bodega, 2. Tamalpais, 3. Santa Cruz, 4. Monterey, 5. Santa Lucia (see Stebbins and Major 1965, fig. 5).

fluence may be judged from the flora of the inner Santa Cruz Mountains, 25 to 30 km east. Some 60-odd taxa from the inner south Coast Ranges reach their northern limit of distribution there (Thomas 1961). Since Pliocene and late Pleistocene floras from the inner Santa Cruz Mountains show that mesic, mixed conifer forest and Douglas fir forest occupied the adjacent lowlands under a climate much wetter and cooler than that now there (Dorf 1930, Potbury 1932, Helley et al. 1972; see above), the xeric southern taxa must have entered the inner Santa Cruz Mountains following the last glacial-pluvial, that is, during the Xerothermic (Axelrod 1981). Because the Año Nuevo grove is (and was) in a more humid region than the Cambria population, the influ-

ence of Xerothermic climate was not so great there, and hence cones of the Año Nuevo groves are not so large as those of the Cambria. However, they are larger than those produced by the Monterey population (Fig. 5), situated only 65 km south.

Immunochemical comparisons of seed proteins from the three California populations of *P. radiata* support the idea that they diverged recently, despite the great differences in mean cone size (Murphy 1981). The immunochemical differences measured between pairs of the California populations were approximately equal, but significantly less than differences measured between California populations and those on Guadalupe and Cedros Islands. If the *P. radiata* populations to the north and south were affected by the Xerothermic dry climate, how did the Monterey population escape? Is this population, which had a wider late Pleistocene distribution, an ancestral, relictual population that persisted under a favorable local climate, one that was less affected by warm, dry Xerothermic climate?

Persistence under local climate. The supposition that the origin and distribution of the *P. radiata* populations have been controlled by local climate is consistent with the influence of topography on climate along the central coast. Between Cape Mendocino and Point Conception there is only one major submarine canyon that heads in the near-shore area. This is the Monterey submarine canyon (Fig. 6), which is more than 2000 m deep and 22 km wide only 13 km from the shore at Cypress Point. It is as broad as, but deeper than, the Grand Canyon of Arizona in the area from Grand Canyon Lodge on the North Rim to Park Headquarters on the South Rim! By contrast, the continental shelf from Monterey to Cape Mendocino is fully 40 to 50 km wide out to the continental slope and it is not incised by major submarine canyons (for detail, see U.S. Coast and Geodetic Survey, Bathymetric Maps, 1308 N-12; 1307 N-18; 1307 N-11B; 1306 N-20; scale 1:250,000, 1974). A similar broad shelf extends south to Point Conception except for the locally narrower strip where it fronts the fault scarp at the north end of the Santa Lucia Range between Nepenthe and Lopez Pt. at Lat. 36°N (see Jennings 1975; this map also shows bathymetry).

The large, deep Monterey submarine canyon and its subsidiary branches to the north (Soquel Canyon) and south (Carmel Canyon) that reach close to shore are the sites of intense upwelling of deep, colder water that provides greater fog frequency in this area. Although temperature data are not available for comparison with the Año Nuevo and Cambria populations, maps of summer sea-surface tempera-

→
Fig. 6.   The coastal strip of central California is bordered by a broad, shallow continental shelf except for the Monterey area where the Monterey submarine canyon and its tributaries (Soquel and Carmel Canyons) come in close to the shore and locally on the Big Sur coast north of Lopez Pt.

ture (Calcofi Atlas 1963) and a map showing the distribution of mean annual heavy fog (days/year) along the coast (Peace 1969, fig. 1), indicate a foggier summer climate at Monterey. Furthermore, in discussion (Nov 1980) Dr. Larry Breaker (National Environmental Satellite Service, Redwood City) stated that his several years' study of satellite photos of the California coast shows that the present discontinuous groves of closed-cone pines are all at centers of high fog concentration. The fog is then dispersed by winds along the coast according to local terrain. He also stated that the Monterey area has the highest fog frequency in this sector of the central California coast. The Monterey submarine canyon probably would have ensured a greater fog frequency for the pine groves during the Xerothermic as compared with areas to the north or south where upwelling is not as pronounced, and where the influence of drought would be greater during the Xerothermic.

In this regard, the occurrence of fossil *P. radiata* (evidently the Monterey population in cone size) near the mouth of the Little Sur River is significant. The deposit, which is relatively young (about 10,000 years), is composed of species that represent a community much like that now at Monterey (Langenheim and Durham 1963), including *Pinus muricata* (?), *Cupressus goveniana* (?), *Pseudotsuga menziesii, Quercus agrifolia,* and a number of their usual shrubby associates, notably species of *Ceanothus, Garrya, Myrica, Ribes,* and *Rubus.* This forest probably disappeared from Little Sur, only 20 km south of Monterey, during the Xerothermic. This is consistent with the present occurrence of a few characteristically interior and southern taxa that are near their northern limit of distribution along the coast in this general area, notably *Salvia mellifera* and *Eriodictyon tomentosum.* They probably entered this coastal sector after the Little Sur forest disappeared and as coastal sage assumed dominance in this steep, well-drained terrain where fog is less frequent and persistent than at Monterey-Carmel.

Pinus radiata at Monterey, with smaller cones than those at Año Nuevo and Cambria, thus appears to be an ancestral, relict population. Its position at the head of Monterey submarine canyon during the Xerothermic probably afforded a more favorable, local climate than that in groves to the north and south, which responded to greater drought stress by developing larger cones. Local climate at Monterey probably accounts also for the persistence of the relict stands of *Cupressus macrocarpa* and *C. goveniana* which have even narrower distributions than the pine (see Griffin and Critchfield 1972). Both cypresses have fossil records north and south of Monterey, as does the *Pinus radiata* population associated with them (Fig. 4). Their restriction to the Monterey area during the later Pleistocene probably resulted from the spread of colder climate at the north and warmer, drier climate at the south, though not simultaneously.

Upwelling and Relict Distributions

Local climate controlled by upwelling of colder, deeper water near shore may account for the discontinuous distribution and relict occurrence of other endemics in coastal California and adjacent Baja California.

Pinus torreyana. This relict pine occurs in two patches on the coastal strip on both sides of Soledad River Valley, at Del Mar to the north and Torrey Pines State Park to the south (see Griffin and Critchfield 1972). The groves are situated near the head of La Jolla submarine canyon and also lie farther west—into the ocean—than La Jolla or San Diego. According to local informants, this is the foggiest part of the coast. The relict occurrence of the pine groves may therefore reflect the highly favorable land climate in this area where precipitation totals about 250 mm annually. As noted above, their occurrence on Linda Vista Terrace and on Eocene Torrey Sandstone may also provide moisture that rises by capillarity from associated siltstones in these formations and from the underlying shales of the Del Mar Formation. That the pine is a relict is evident from its distinct morphology among pines of sect. *Sabinineae* and from its occurrence on Santa Rosa Island west of Santa Barbara.

Pinus muricata-P. remorata. These pines occur on the coast of Baja California Norte near the mouth of Rio San Isidro, which is about 560 km (350 mi) south of their nearest mainland occurrence in the vicinity of Lompoc, California. Annual precipitation in the San Isidro area totals approximately 200–250 mm and vegetation is Diegan sage (Axelrod 1978). The occurrence of pines may be explained by upwelling that results in a greater fog frequency there during the warm months than elsewhere along the coast. As a result of the deep submarine terrain directly offshore (H.O., Chart BC 1206N), upwelling gives the warm months (June–September) sea-surface temperatures 3°–4° lower (i.e., 15–16°C vs. 19–20°C) in the area directly south of the San Isidro River valley where the pines occur than north of the valley where they are absent (Scripps Inst. 1962, p. 40–41). Other shrubs with relict distributions that require mild summer climate occur in this area as well as more widely to the north—but always near the coast—include *Comarostaphylis diversifolia* and *Ribes viburnifolium*. It is recalled that upwelling is also a determinant in the distribution of recent and fossil cold-water molluscan taxa on open exposed coasts, as reviewed by Valentine (1955; 1961, p. 525–527), Hubbs et al. (1962, p. 218; 1965, p. 112) and others to whom they refer.

The pine groves are also near Lompoc (Tranquillon Hills, Purisima Hills) and San Luis Obispo (Pecho Hills) [see Griffin and Critchfield 1972]. These areas are characterized by foggy summer climate and also lie farther west than the adjacent coast—jutting out into the

ocean. The importance of local fog in the persistence of these relict groves was especially evident during the record hot spell of late August 1981. At that time the mid-day temperature differential 12 km from the coast was on the order of 14°C (13° as compared with 27°C). Heavy fog was also persistent near Pt. Sal midway between these areas, a site where the pines lived during the late Pleistocene (Axelrod 1980).

Other taxa. Comarostaphylis diversifolia var. *planifolia* and *Cercocarpus blancheae* occur locally on the seaward slopes of the Santa Monica Mountains. In this area, with the Mugu, Dume, and Santa Monica submarine canyons directly off-shore, upwelling gives the locale a high fog frequency in summer favorable for these taxa that are otherwise largely of insular occurrence. *Coreopsis gigantea* also occurs in this area close to the coast as well as on the islands, ranging northward to southern San Luis Obispo County in scattered, well drained, foggy coastal sites.

Mode of Evolution

Many of these endemics occur on sandy sites, including stabilized dunes, elevated terraces, and old floodplains. As noted above, these sites are mesic and may well account for the persistence of older taxa derived from alliances of more humid regions during earlier times. It is also evident that these occurrences follow the pattern of edaphic endemism discussed by Raven (1964). In it geographically marginal (especially annual) populations may invade unusual or different substrates during movement of a species into a region. Subsequently, they change sufficiently to be recognized as minor taxa (vars., subspp.) or full species depending on the mode of change. This may be by saltational speciation with catastrophic selection and consequent rapid chromosomal reorganization in marginal populations, by hybridization (see *Arctostaphylos,* in Appendix), by mutation, or by other means that have occurred in regions of diverse terrain and substrates subject to fluctuating climate during the Quaternary. These modes have been especially effective in annuals because gene flow in plant groups is very local, the effective population size is therefore very small, and the life cycle is brief. Finally, it must be reemphasized (see Raven 1976) that the nature of species is so variable that all these taxa— species, subspecies, varieties—are not of equal rank just because they have been so designated. They have had diverse modes of origin and are separated also by a time factor in which varied and unequal genetic changes have taken place in them.

Summary

Most of the five small endemic areas in the outer, central Coast Ranges have diverse relief, climate, and substrates as well as a relatively high incidence of warm season rainfall, and two of them have

serpentine areas that support endemics. The Monterey endemic area, the richest one in the outer Coast Ranges, does not conform to this pattern.

High endemism at Monterey owes in part to the edaphic factor, represented by the wide occurrence of endemics on dunes, terraces, and other sandy sites. These substrates apparently contain sufficient moisture to support endemics derived from forest and forest-border ancestors that were in the lowlands during moister Pleistocene phases. Other endemics are allied to taxa that evidently penetrated the Monterey area from the interior during the Xerothermic and some are members of species-groups distributed in coastal sites. Some evidently originated from marginal populations left behind on unusual substrates and then changed slightly by diverse modes. The relict occurrence of two *Cupressus* species owes to their location at the head of Monterey submarine canyon, with the resultant higher fog frequency on-shore evidently providing a haven for survival during the Xerothermic. The more persistent fog blanket may account also for the smaller-coned population of *Pinus radiata,* which appears to be relictual and ancestral to the larger-coned populations at Año Nuevo and Cambria that evidently reflect response to the Xerothermic climate.

Evidence suggests that other relict endemics in the coastal strip, including *Pinus muricata, P. remorata* and *P. torreyana,* are confined to areas where favorable submarine topography near shore results in cold-water upwelling and higher fog frequency during summer months.

The fossil record shows that a rich, floristically diverse closed-cone pine forest formed a continuous belt along the coast into the late Pleistocene. During colder, wetter pluvial stages mixed conifer forest taxa became associated with coastal pine forest and in the drier interglacial and postglacial times interior taxa contributed new species (subspp., vars.) to open, sunnier sites. Thus, there is no need to invoke insular isolation to explain the evolution of its taxa, their present discontinuous distribution, or the endemic nature of the now local floras.

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APPENDIX. ENDEMIC TAXA OF THE MONTEREY ENDEMIC AREA, THEIR
GENERAL OCCURRENCE AND THEIR PROBABLE RELATIONSHIPS.
(species authorities follow Munz 1973.)

Pinaceae: *Pinus radiata.* The Monterey population has fossil records that suggest it is older than the larger-coned populations at Año Nuevo and Cambria, which may have originated during the Xerothermic in response to warmer, drier climate (see text).

Cupressaceae: *Cupressus goveniana.* Fossil record shows that it had a wider distribution to the north and south in the later Quaternary, and probably earlier as well.
Cupressus macrocarpa. Recorded as fossil at Drakes Bay (1 m.y. old) and Rancho La Brea (30,000 years ago). No very close allies. Restricted to quartz diorite on the north and south shores of Carmel Bay.

Amaryllidaceae: *Triteleia × versicolor.* (=*Brodiaea versicolor*). Known only from type collection made at Pt. Lobos State Park. Lenz (1975) considers it a natural hybrid.

Asteraceae: *Corethrogyne filaginifolia* var. *viscidula.* A local endemic of the species, which is represented by 13 vars. distributed from central California into southern California, with most of them in the interior and to the south.
Haplopappus eastwoodiae. Restricted to dunes about Monterey and Carmel Bays. L. C. Anderson reports (pers. comm., Feb 1981) that it is probably derived from *H. ericoides,* which is distributed along the coast from Marin Co. southward to Los Angeles area, chiefly on sand dunes near the coast.
Malacothrix saxatilis var. *arachnoidea.* From lower Carmel Valley, in sandy

sites. It is one of several varieties of the species that ranges from Monterey Co. southward into southern California.

Brassicaceae: *Erysimum ammophilum.* Allied to *E. menziesii, E. concinnum,* and *E. franciscanum,* a closely related group of taxa (R. C. Rollins, letter of Feb 1981). He suggests they may represent a linearly distributed group of species adapted to coastal sands that broke up, over time, to form the present taxa.

Ericaceae: *Arctostaphylos edmundsii.* According to P. A. Wells (letter, Feb 1981), *A. edmundsii* is a stabilized hybrid of *A. uva-ursi* × *A. tomentosa rosei. A. tomentosa* is a widespread, variable species on the central California coast. *A. uva-ursi* is basically a forest species from Marin Co. north, but has relict stations southward into Monterey Co. to Pt. Sur.

Arctostaphylos hookeri. P. A. Wells (letter, Feb 1981) states *A. hookeri* is derived from the *A. pungens* series. *A. pungens* is distributed from the inner south Coast Ranges into the southwestern United States and Mexico. *A. hookeri* occurs in the closed-cone pine forest and on dunes about Monterey.

Arctostaphylos montereyensis. A unique non-sprouter, possibly derived from or related to *A. columbiana-A. virgata* according to P. A. Wells. *A. columbiana* ranges from Marin Co. northward; *A. virgata* occurs marginal to redwood forest in Marin Co. *A. montereyensis* also occurs inland from Monterey for a short distance. On dunes in Monterey area.

Arctostaphylos pumila. Wells (letter, Feb 1981) states this is a stabilized hybrid of *A. uva-ursi* × *A. tomentosa tomentosa. A. uva-ursi* is a forest species chiefly from Marin Co. north, but has local relict occurrences south to Pt. Sur. *A. tomentosa* is a widely distributed, very variable species of the central California coast. The var. *tomentosa* is endemic to Monterey.

Arctostaphylos pajaroensis. This is a stabilized hybrid of *A. andersonii* × *A. tomentosa tomentosa* according to Wells, who also states *A. andersonii* is endemic to the Santa Cruz Mountains.

Arctostaphylos tomentosa. The forms *trichoclada* and *hebeclada* of *A. tomentosa* var. *tomentosa* are morphs that occur with var. *tomentosa* only about Monterey, according to Wells (letter, Feb 1981).

Fabaceae: *Lupinus tidestromii.* A dune to strand plant allied to and probably derived from *L. littoralis* of coastal strand and coastal sage from Mendocino Co. northward to British Columbia.

Trifolium polydon. Considered a variety of *T. tridentatum* by Jepson (1925), a view generally concurred in by Gillett (letter, Feb 1981) though he suggests it may only be a variety of *T. variegatum. T. tridentatum* is a widespread species in grassy places in cismontane California generally below 1520 m, ranging north to British Columbia. *T. variegatum* is found in moist grassy places in cismontane California, generally below 2440 m.

Trifolium trichocalyx. Gillett (letter, Feb 1981) suggested that it may be a sporadic hybrid between *T. microcephalum* and *T. variegatum,* widespread species in cismontane California below 2590 m. Since only one or two plants are known, it seems best to remove it from the list of Monterey endemics.

Liliaceae: *Allium hickmanii.* From around Monterey peninsula, but also near Jolon, in the interior. Related to a species complex of open places in forests of Coast Ranges; possibly more closely related to *A. unifolium* from Monterey Co. north to Del Norte Co.

Polemoniaceae: *Eriastrum virgatum.* Sandy sites about Monterey. Apparently allied to species now in drier places, chiefly to the south and interior.

Gilia tenuiflora subsp. *arenaria.* A segregate of the species that inhabits open places, river beds and sandy sites; distributed chiefly in the interior and southward to San Luis Obispo Co.

Polygonaceae: *Chorizanthe pungens.* On dunes around Monterey; the poorly defined var. *hartwegii* occurs in sandy places from Santa Cruz Mts. north to San Fran-

cisco. Allied to *C. cuspidata* of dunes and sandy places from Santa Cruz Co. north to Sonoma Co.

Eriogonum parvifolium subsp. *lucidum*. Pt. Lobos. A poorly defined segregate of this shrubby species that is common along coastal bluffs and dunes from Monterey south to San Diego Co.

Polygonum montereyense. Known only from the type material, collected "on hard dry clay, Monterey." Dr. J. C. Hickman reexamined the type material and reports (Mar 1981) it is a diseased or parasitized specimen of *P. ramosissimum*, a widespread species. It is therefore removed as a Monterey endemic.

Ranunculacae: *Delphinum hutchinsoniae*. Sandy places about Monterey. Allied to *D. variegatum*, widespread in the inland valleys.

Rhamnaceae: *Ceanothus griseus* var. *horizontalis*. Occurs at Yankee Pt., Monterey. A spreading, prostrate form of the species that ranges along the coast from Mendocino Co. to Santa Barbara Co.

Ceanothus rigidus. Inhabits sandy hills and flats, Monterey peninsula. Allied to *C. gloriosus* distributed in closed-cone pine forest from Marin Co. north to Mendocino Co. (see Nobs 1963, fig. 39).

Saxifragaceae: *Ribes menziesii* var. *hystrix*. From Monterey peninsula and border areas into the redwood forest on coastal slopes of Santa Lucia Mountains. Allied to subspecies *leptosmum* and *senile* in redwood forests northward into Sonoma Co.

Scrophulariaceae: *Cordylanthus littoralis*. Occupies dunes back of the strand and in closed-cone pine forest at Monterey. Dr. L. Heckard, who has monographed the genus, considers *C. littoralis* a subspecies of *C. rigidus*, with which it intergrades in Upper Carmel Valley (pers. comm., Feb 1981). The species *rigidus* is found chiefly in the inner south Coast Ranges.

Mimulus guttatus var. *arenicola*. Coastal strand and dunes, Monterey area. The species is widespread in coastal plant communities in California, represented by several varieties. The var. *arenicola* is allied to the subsp. *littoralis*, which ranges along the coast from Santa Barbara Co. north to Washington.

MOUNTAIN MEADOWS: STABILITY AND CHANGE

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Abstract

It is often assumed that mountain meadow ecosystems are fragile and temporary phenomena. An alternative hypothesis is that meadows are as stable over time as the surrounding vegetation. Evidence from palynological, stratigraphic, and successional studies on Sierran meadows supports the latter hypothesis. Three new working hypotheses on the causes of change in meadow ecosystems are proposed.

Discussions of mountain meadows often assume that meadows are "fragile," and that they are temporary phenomena. These two assumptions are directly related to our understanding of meadows as seral stages in the classic hydrosere of lakes developing into forests, and imply that meadows are unstable. This paper examines these assumptions by reviewing the evidence for two hypotheses: 1) meadows are as stable over time as the surrounding vegetation; and 2) meadows are temporary phenomena. This will be done using data and observations from the literature including my own research over the past several years. Most of the examples come from the Sierra Nevada, California. Before reviewing the evidence, it is necessary to discuss briefly the concepts of stability and succession in relation to mountain meadows.

Types of Meadow Stability

There are many ways of classifying the different types of meadow stability. For the purpose of this discussion, stability can be divided into biologic and geologic stability (Benedict and Major 1981). Biologic stability refers to the persistence and recovery of the biologic component of an ecosystem. For example, if the species composition of a meadow does not change over time it is considered stable. Geologic stability refers to the persistence of the geologic conditions which create an environment favorable for meadow formation. In the Sierra Nevada, geologic stability is directly related to the different physiographic meadow types (Benedict and Major 1981). For example, a meadow that forms in a bedrock basin as a result of water accumulation is considered stable as long as the basin is intact and continues to collect water. This meadow type is geologically more stable than a meadow in a basin formed by a morainal dam, which is more readily eroded than a bedrock dam (Benedict and Major 1981). When the

TABLE 1.   BIOLOGIC AND GEOLOGIC CONDITION IN RELATION TO VEGETATION CHANGE. Autogenic/allogenic changes, sensu Tansley 1929. Allogenic changes brought about by geologic instability may have a relatively greater effect on the vegetation than autogenic changes.

Geologic condition	Biologic condition	Vegetation change
Stable	stable	no change (climax stage)
Stable	unstable	autogenic succession
Unstable	stable	nonsensical
Unstable	unstable	allogenic succession (autogenic succession)

concepts of biologic and geologic stability are combined, they provide us with a structure to examine the successional status of meadows, and to decide if meadows are indeed temporary phenomena (Table 1).

Because ecosystems are continuously changing, the division between stable and unstable conditions is partly artificial. Human recognition of change is dependent on the rate of change and the effect change has on an ecosystem. For example, in a basin meadow formed by a glacial moraine, the morainal dam is probably continuously eroding. The erosion rate may vary with season, strata in the moraine, or general longterm climatic changes. If the ecosystem can compensate for the changes in erosion rate and the height of the dam, the changes will go unnoticed and the system will be considered stable. The effect change has on an ecosystem is dependent on threshold values for both the rate and magnitude of change. For example, the decrease in height of a morainal dam may not affect the meadow until some critical height is reached. Once this height is passed, the ecosystem may undergo drastic change and be considered unstable. The recognition of change and the role of threshold values in relation to vegetation change is a complex problem and deserves further consideration. In this paper change will be recognized using plants as biometers.

We can now state our hypotheses in more readily testable form: 1) meadows are both biologically and geologically as stable as the surrounding vegetation; and 2) meadows are temporary phenomena because they are a) geologically stable but biologically unstable, and/or b) both biologically and geologically unstable. It should be noted that these hypotheses are not necessarily exclusive of each other.

EVIDENCE FOR BIOLOGIC AND GEOLOGIC STABILITY

There are two sources of evidence supporting the hypothesis that meadows are both biologically and geologically as stable as the surrounding vegetation. The first is palynological evidence. Adam (1967) presents pollen diagrams at four locations in the Sierra Nevada. The

pollen record at Osgood Swamp (near South Lake Tahoe), and Soda Springs (near Tuolumne Meadows, Yosemite National Park) are pertinent to this discussion. At the time the pollen core was taken, Osgood Swamp consisted of a small, seasonal lake surrounded by a wet meadow and bog complex. The Osgood Swamp pollen record begins about 10,000 BP, the approximate beginning of the Holocene. The temporal relationships are substantiated by two radiocarbon dates (Adam 1967). Soda Springs is a spring mound near Tuolumne Meadows. No radiocarbon dates are given but the record is estimated at between 7000 and 9000 BP by comparison with the Osgood Swamp pollen record (Adam 1967).

From these two pollen records the following inferences can be made: 1) The geologic conditions that favored a hydric meadow environment and pollen preservation have existed at Osgood Swamp since approximately 10,000 BP, and at Soda Springs since approximately 7000–9000 BP. 2) Vegetation indicative of mesic and hydric meadow environments has been present for the entire period represented by these pollen records (see Cyperaceae, *Alnus, Isoetes,* etc.). 3) Species indicative of non-meadow vegetation have varied greatly in importance over the time period represented by these pollen cores (see *Abies, Acer, Artemisia, Quercus,* and TCT—Taxodiaceae, Cupressaceae, Taxaceae. 4) Although the hydric and mesic species composition may have changed during the time represented by these pollen cores, the surrounding non-meadow vegetation also changed during this same time period.

The second source of evidence comes from stratigraphic studies of montane meadows. Wood (1975) examined the stratigraphy of seven montane meadows in the southern Sierra Nevada. From his findings several conclusions can be drawn: 1) Five of the seven meadows have been in existence since 1200–3000 BP, and two of the meadows since 7700–9800 BP. Thus, the geologic and climatic conditions favorable for meadow formation have been present over those time periods. 2) Although no direct study of biologic change was made, the meadows have not changed to forest vegetation since 1200–3000 BP in five locations, and since 7700–9800 BP in two locations. 3) No lake sediments were found in any of the seven meadows. 4) The forest vegetation on these same sites has changed to meadow vegetation over the last 10,000 radiocarbon years (Wood 1975).

The above examples imply that these eight meadows and one bog have been biologically and geologically stable for various lengths of time ranging from 1200 BP to approximately 10,000 BP. They also imply that vegetation change has occurred in both meadow and the surrounding non-meadow ecosystems over the past 10,000 radiocarbon years. In addition, the stratigraphic record suggests that meadows develop into forests only when the geologic environment passes some threshold point.

Evidence for Geologic Stability and Biologic Instability

Two examples of secondary, autogenic succession (Tansley 1929) in meadows support this hypothesis. An unusual lightning-ignited fire in Ellis Meadow, Kings Canyon National Park, in 1977 severely burned parts of the meadow, leaving ash 1–20 cm deep and removing 100 percent of the plant cover in some areas (DeBenedetti and Parsons 1979a, DeBenedetti 1980). One year after the fire, plant cover was 36 percent for herbaceous plants and 31 percent for moss and liverworts, with no evidence of catastrophic change in the character of the meadow (DeBenedetti 1980). Yearly sampling has suggested that typical meadow vegetation will eventually be reestablished (DeBenedetti, pers. comm.). This implies that the geologic conditions are stable even though the biologic component of the Ellis Meadow ecosystem is presently unstable and will take an unknown number of years to stabilize.

The second example is the re-establishment of meadow vegetation after removal of grazing in the Sierra Nevada. The destruction of the biologic component of meadow ecosystems in the Sierra by grazing has been well documented (DeBenedetti and Parsons 1979b). In many of these meadows, typical meadow vegetation has reestablished itself (DeBenedetti and Parsons 1979b) although the lack of baseline data makes it difficult to judge the degree of similarity between current and pristine vegetation. The degree and rate of recovery from past overgrazing may vary depending on meadow type, with xeric meadows being slowest to recover fully (Ratliff 1974). This again implies that the geologic conditions favoring meadow formation have been stable even though the biologic component has been (and may still be) recovering from past disturbances and is thus unstable. In a few meadow ecosystems the disturbance from grazing may have been severe enough to destabilize the geologic conditions and make meadow establishment highly unlikely without manipulation of the ecosystem by man (DeBenedetti, pers. comm.).

Evidence for Biologic and Geologic Instability

In the montane meadow stratigraphy of the Sierra Nevada (Wood 1975) discussed earlier, if the entire record at each meadow is examined, it is clear that over the last 10,000 radiocarbon years these meadows have undergone dramatic changes. As summarized by Wood (1975), the generalized stratigraphic sequence is: 1) basal layer of alluvium deposited by pre-Holocene streams; 2) paleosol extending into basal layer dated at between 8705 and 10,185 BP, and developed under a mesic montane forest; 3) stratified sandy deposits dated at between 8700 BP and 1200–2500 BP, and developed under a fir, yellow pine, and lodgepole pine forest; and 4) stratified deposits of sedge peat, humus-rich sandy loams, and sorted grus deposited since 2300–2500

BP in a meadow environment. (As previously noted, two meadows described by Wood do not fit this generalized sequence because they have been in existence since 7700–9800 BP.) This suggests that the geologic conditions causing meadow formation and the biologic component of meadow ecosystems have been unstable over the past 10,000 radiocarbon years. It should be noted that, in a similar manner, the geologic conditions favoring forest vegetation, and the biologic component of forest ecosystems at the same locations, have also been unstable over this same time period (Wood 1975).

A second source of evidence is a man-induced "experiment" at Osgood Swamp. Osgood Swamp is dammed by a Wisconsin glacial moraine on the downstream side (Adam 1967). This created a wet basin favorable for formation of a meadow that had persisted for approximately 10,000 years. In 1963, this morainal dam was artificially breached (Adam 1967). Subsequently the water table lowered and a large number of *Pinus contorta* subsp. *murrayana* seedlings became established. This "artificial geologic instability" demonstrates the effects of passing a threshold of geologic change on the biologic stability of a meadow. It suggests also that naturally occurring geologic instability as a result of erosion can reach threshold values that will result in instability in the biologic component of meadows, and the subsequent establishment of forest trees.

A third source of support is the evidence that throughout the western United States various forest trees have invaded mountain meadows since approximately 1900 (Dunwiddie 1977, Franklin et al. 1971, DeBenedetti and Parsons 1979b, Vale 1981a,b). This suggests that the conditions favorable for meadow formation and maintenance have changed and are thus unstable, and that this results in biologic instability as indicated by tree establishment. An alternative explanation is that biologic instability has resulted in tree establishment even though the geologic conditions are favorable for meadow ecosystems. The latter would support hypothesis 2a.

The above evidence suggests that geologic and biologic instability is present in meadow ecosystems, and that forest vegetation in areas that have been occupied by meadows is also unstable.

Conclusion

Based on the above evidence, meadow ecosystems are as stable as the surrounding vegetation, and, like any vegetation type, can be viewed as temporary phenomena on a geologic time scale. Both forest and meadow ecosystems have experienced dramatic changes since the beginning of the Holocene. Some ecosystems may have changed less than others, i.e., high elevation *Pinus balforiana* forests, or subalpine and alpine meadows in the southern Sierra Nevada. In addition, meadow ecosystems may be more sensitive than forest ecosystems to

geologic change as a result of lower thresholds of tolerance to geologic change. The evidence suggests three new working hypotheses that should continue to be examined and debated: 1) Geologic meadow instability usually results in biologic instability that may lead to the establishment of forest vegetation. 2) Biologic instability combined with geologic stability can result in changes in species composition that may lead to a meadow climax, and that do not necessarily lead to a forest climax. 3) Biologic instability and autogenic changes are not great enough to overcome ultimately the stabilizing influence of the geologic conditions that maintain meadow ecosystems.

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PHENOLOGY, GERMINATION, AND SURVIVAL OF DESERT EPHEMERALS IN DEEP CANYON, RIVERSIDE COUNTY, CALIFORNIA

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Abstract

Phenology, germination, and survival in a desert ephemeral community was followed from January 1976 through January 1978. Cool season species germinated following rain in fall and/or winter. Germination of warm season C_4 ephemerals was restricted to May. Significant variations occurred in the phenology of plants germinating in response to the same rain storm. The shape of survivorship curves among cool season species dramatically varied depending on seasonality of precipitation.

The relationships between the germination of desert ephemerals and temperature and rainfall were established in a general sense by the work of Went (1948, 1949), Trevis (1958a,b), and Juhren et al. (1956). Germination requirements usually restrict ephemeral activity to a specific season coincident with adequate rainfall (Beatley 1974). Summer annuals usually have the C_4 photosynthetic pathway, assumed to be an advantage in hot, dry conditions, whereas winter annuals are typically C_3 and seem to have few specializations other than germination requirements that adapt them to desert environments (Mulroy and Rundel 1977). However, winter ephemerals have been shown to have differential ability to survive increasing water and temperature stress (Clark and Burk 1980). This indicates that a range of physiological adaptations to stress may be present in these "mesophytic" ephemerals. This study was designed to identify species with unique germination, phenological, and survival characteristics that could be used in future research on xerophytic adaptations in desert ephemerals.

Methods

The study was conducted at the Philip L. Boyd Deep Canyon Desert Research Center located on the north slope of the Santa Rosa Mountains about 300 m above the desert floor. The 17-year average rainfall is 109 mm, maximum temperature 47°C and minimum temperature 0°C. Rainfall is highly erratic with minima of about 40 mm in 1961 and 1971 and a maximum of 300 mm during 1976 (the first year for which data are presented here). Rainfall is typically concentrated in the winter months of November through March and in the late summer months of August and September. Each month has been without

measurable rain at least twice during the 17-year weather records for Boyd Center (Zabriske 1979). Precipitation values used in this study were recorded at Boyd Center less than 0.5 km from the study site.

The study area was located at the mouth of Coyote Canyon in a heterogeneous area consisting of sandy arroyo beds and habitats with an accumulation of boulders and/or desert pavement at the soil surface. Perennial vegetation consists of a wash woodland community along the arroyo margins and creosote bush scrub in the intervening areas (Burk 1977).

The 1.0 ha study area was gridded into 100, 100 m² plots from which 20 sample plots were selected at random. A 1.0 m² quadrat was systematically placed in the center of each of the 20 sample sites. Each 1.0 m² plot was further divided into 100, 1.0 dm² sub-samples from which 20 were selected for counting. Permanent stakes marked each sample site and allowed precise repositioning of the quadrat at each sampling. Dividers in the 1.0 m² quadrats were of 3 mm diameter stainless steel rod. Twelve sample sites were monitored from January 1976 until January 1977 and 8 additional sites were monitored through January 1978. Visits were made at 2–4 week intervals following rain storms in February 1976, September 1976, and January 1977 until all the ephemerals died. Repeat visits were not made in August 1977 and January 1978, but data were recorded after germination was presumed complete.

Individuals were counted in the 1 dm² sub-plots for density determination, and estimates of cover for each species estimated to occupy more than 1 percent of the sub-plot were made by visual inspection. At each sample site each species was recorded as being in one or more of the following conditions: vegetative, flower buds, flowers, or seeds. Phenology of ephemeral plants not in sample frames was also recorded. Density and cover data were used to estimate population values on m² basis by combining the results of all sample sites.

Seedlings of unknown species were marked with color coded plastic toothpicks until identification was possible (nomenclature follows Munz 1974). There were a limited number of instances when seedlings did not survive and could not be identified. These are not included in any of the calculations. Because of difficulties in distinguishing the various species of *Cryptantha* prior to flowering, individuals of *C. maritima, C. angustifolia* and *C. barbigera* are combined for purposes of analysis. This grouping may also contain an occasional individual of the genus *Pectocarya*. Even though no *Pectocarya* individuals reached anthesis in the counted plots, isolated individuals were observed in the vicinity.

<center>RESULTS</center>

Seedling establishment. Three occurrences of record monthly rainfall along with two other periods of more normal levels produced five
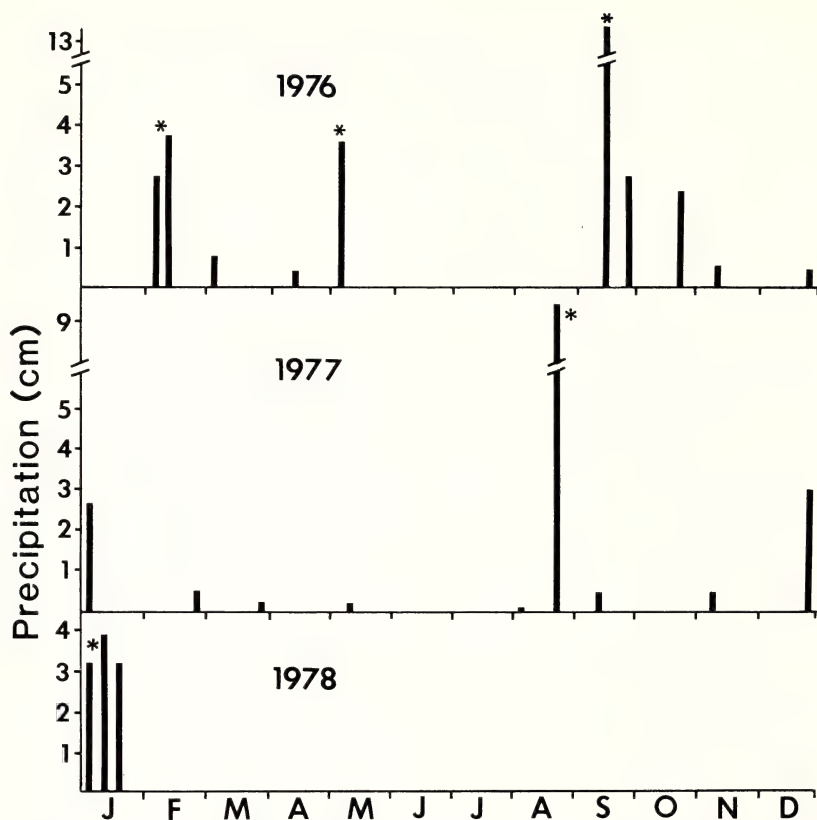
Fig. 1.   Total weekly precipitation records at Boyd Deep Canyon Desert Research Center for the period Jan 1976–Jan 1978. * indicates rainfall stimulating germination.

distinct periods of germination. Figure 1 shows the precipitation pattern for the period of the study. September has the highest average monthly rainfall during the year, registering a record 16.0 cm in 1976. The 17-year record for August was established in 1977 with 9.5 cm of rain; only September and December exceed August precipitation on the average. January 1978 had 11.0 cm, exceeding the long term average of 10.2, and setting a record for that month. Germination also occurred in response to precipitation in January 1977 and February 1976. The only other rainfall that stimulated germination occurred in early May 1976. Table 1 shows periods of germination for each species in relationship to season. Winter refers to germination responses to December, January, and February rain; late summer, to the August 1977 rainfall; and fall to establishment following September and October rainfall. The decision to distinguish August and September as

TABLE 1.   PERIODICITY OF GERMINATION OF DESERT EPHEMERALS JANUARY 1976–JANUARY 1978 AT BOYD DEEP CANYON DESERT RESEARCH CENTER.

	Dec–Feb	May	Aug	Sep–Oct
Filago californica	*			
Langloisia schottii	*			
Chorizanthe rigida	*			
Eschscholzia minutiflora	*			
Rafinesquia neomexicana	*			
Amaranthus fimbriatus		*		
Palafoxia arida			*	*
Chorizanthe brevicornu	*			*
Phacelia distans	*			*
Phacelia crenulata	*			*
Perityle emoryi	*			*
Chaenactis carphoclinia	*			*
Chaenactis fremontii	*			*
Camissonia claviformis	*			*
Schismus barbatus	*			*
Plantago insularis	*			*
Cryptantha spp.	*		*	*
Euphorbia spp.	*	*	*	*

different seasons was based on the (1) very different group of ephemerals that became established and (2) the average temperature in August, which is much more like that in July than in September.

Twenty species were observed in the sample plots with six species germinating only in response to winter precipitation. *Filago californica, Langloisia schottii* and *Eschscholzia minutiflora* germinated in response to both the moderate winter rainfall of 1976 and 1977, and the very wet January of 1978. *Chorizanthe rigida* and *Rafinesquia neomexicana* were observed in the plots only in January 1978.

Precipitation of 3.6 cm in May 1976 resulted in the establishment of the C_4 summer ephemeral *Amaranthus fimbriatus* and the C_4 annual/perennial *Euphorbia* spp. This was the only occurrence of *A. fimbriatus* in the plots. Storms during late spring of 1977 were rare and provided less than 4 mm of precipitation. No summer annuals were present during the summer of 1977. *Euphorbia* spp. included *E. setiloba,* an annual, and *E. polycarpa,* a perennial. Because of the difficulty in distinguishing the species in the pre-flowering stage, I am unsure which species germinated following the May 1976 storm since the seedlings did not survive. *Palafoxia arida* is a facultative perennial flowering in the first year and is often active during summer and winter. This species was common in the study area but germination was restricted to periods following late summer and fall rains.

Eight other species germinated in the fall and winter months (1977–1978). None of these germinated following the heavy rains of August 1977. One, *Chaenactis carphoclinia,* showed additional germination
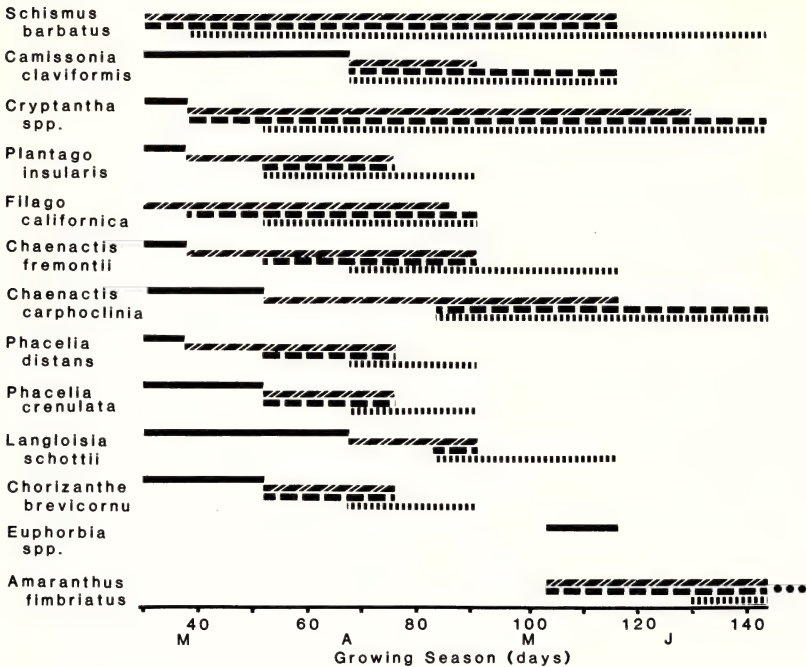
Fig. 2. Phenological events of ephemeral plants at Boyd Deep Canyon Desert Research Center, spring 1976. Solid lines represent pre-reproductive periods; diagonally hatched lines, flower buds; long bars, flowering; and short bars, the period of seed production. Growing season is measured as the number of days following the rainfall that stimulated germination.

in reponse to 41 mm of precipitation during April 1976. *Perityle emoryi* and *Chorizanthe brevicornu* did not appear in the study plots following all fall and winter rains.

The two genera that responded to rainfall during the greatest number of seasons were *Cryptantha* and *Euphorbia*. *Euphorbia* seedlings were found at all seasons during both years of the study and *Cryptantha* in all except May 1976.

Phenology. Interspecific variation in the timing of life cycle events is apparent in plants that were present during the winter and spring of 1976 (Fig. 2). Eleven species germinated in response to February rains and at the first sampling time (31 days) *Schismus barbatus* and *Filago californica* were already in the reproductive phase of the life cycle; *Schismus* was in flower and *Filago* in bud. The majority of species (82 percent) were in reproductive phase within 60 days. *Chaenactis carphoclinia* formed buds within 60 days but anthesis did not occur until at least 20 days later; it continued to flower well into
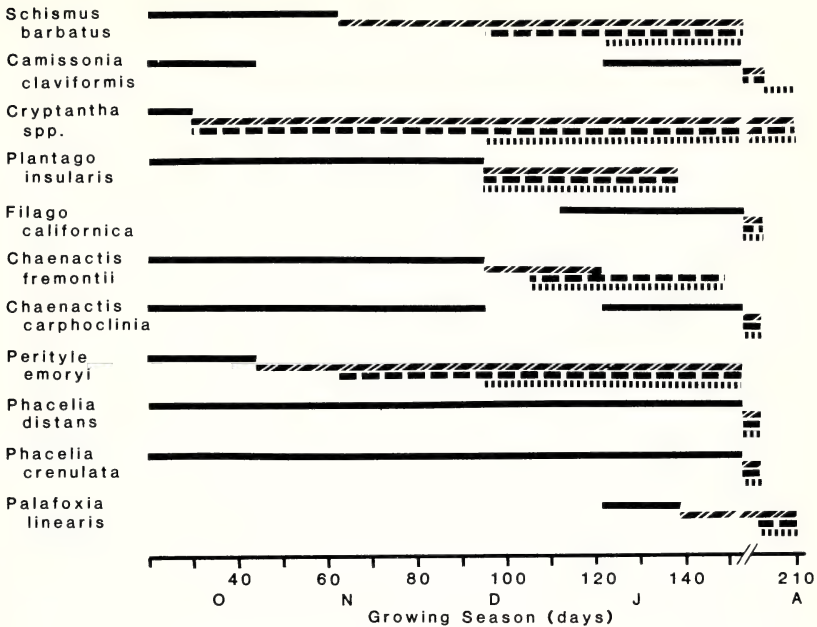
FIG. 3. Phenological events of ephemeral plants at Boyd Deep Canyon Desert Research Center following mid-September rainfall. See Fig. 2 for explanation of symbols. California *Palafoxia linearis* is now called *P. arida*.

summer, whereas most other species ceased flowering by late April or May. *Langloisia schottii* and *Camissonia claviformis* did not begin reproductive activity until after 60 days. *Camissonia claviformis* flowered into June but *Langloisia* reproduction was restricted to a period of less than two weeks. *Cryptantha* spp. had an extensive period of reproduction lasting from mid-March through June.

The next growing season was initiated by more than 13 cm of rain on 10–11 September 1976 (Fig. 3). The pre-reproductive period was longer in individuals that germinated in the fall than in those that germinated the previous spring, for all species except *Cryptantha*. *Cryptantha*, *Schismus barbatus* and *Perityle emoryi* entered the reproductive phase relatively early in the season; however, *Schismus* remained in the bud stage and did not flower until later. *Cryptantha* and *Perityle* began reproducing while ample soil moisture was available from 55 mm of precipitation in scattered storms during late September, October, and November. *Plantago insularis* and *Chaenactis fremontii* remained vegetative for a longer period, becoming reproductive prior to January rains. *Camissonia claviformis* and *Chaenactis carphoclinia* became established following fall rains but died without reproducing. (*Chaenactis* survived well into December.) *Phacelia distans* and *P. crenulata* remained vegetative throughout the winter sea-
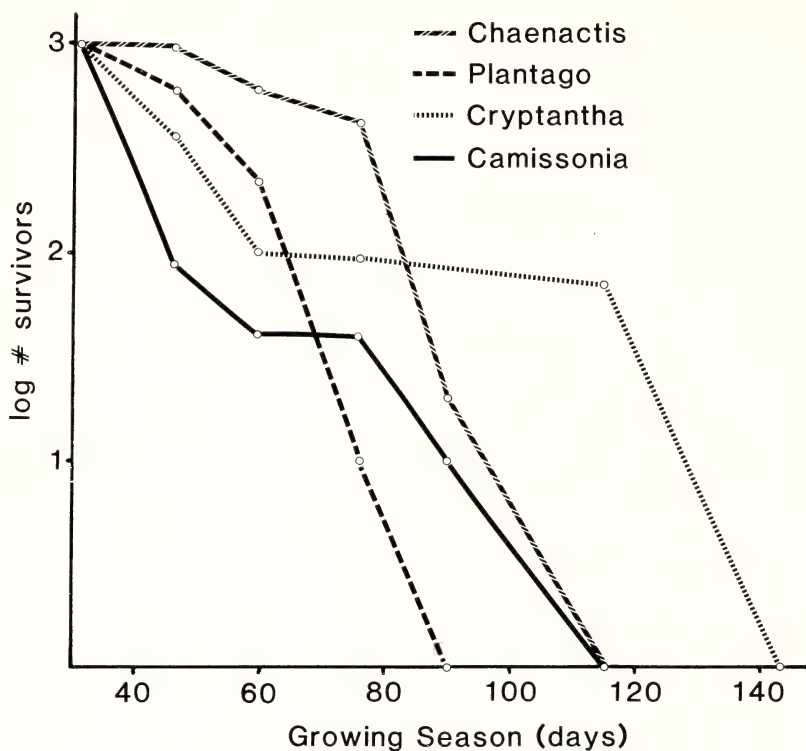
Fig. 4.   Survivorship curves for selected species of desert ephemerals, spring 1976.

son, initiating reproduction coincident with drying conditions during the spring. Recruitment following January precipitation was minimal for *Plantago* with none of the seedlings surviving to reproduce. All species set seed during February and March but only *Camissonia claviformis, Cryptantha* and *Palafoxia arida* remained alive until early April.

Survivorship. Examples of contrasting survivorship curves for the spring 1976 growing season are presented in Fig. 4. *Chaenactis fremontii* and *Plantago* had similar high survival of seedlings followed by rapid post-reproductive mortality, whereas *Cryptantha* spp. and *Camissonia claviformis* had greater mortality in the seedling stage. *Cryptantha* and *Camissonia* showed increased survival following a midseason rain, a phenomenon not noted in *Plantago* and *Chaenactis*.

Sampling methods made it impossible to construct survivorship curves for the 1976–1977 winter growing season because January recruits were indistinguishable from those germinating earlier. Early in the growing season, the survivorship curves of *Plantago* and *Camis-*

sonia did not have the concave form noted in Fig. 4. Instead, all species that germinated had very low mortality in the seedling stage and a more pronounced convex curve than during the previous spring.

DISCUSSION

Ephemerals are placed into three groups based on germination responses noted in this study. Most species germinate during the cool season, being either restricted to midwinter (January or February) or germinating in response to rain after August. Several species (e.g., *Camissonia claviformis* and *Chaenactis* spp.) germinated in September and again in midwinter without intervening seed production. This may imply that germination requirements are dimorphic in most members of the fall to winter germinating group. Further observations are necessary to assure that microhabitat differences and seed age did not cause differential reproduction. Only during the spring of 1976 was there establishment of seedlings after the February cohort. Only *Chaenactis carphoclinia* germinated in response to the midspring rain in 1976. The other species may have gone into secondary dormancy, or perhaps the seed pool was depleted by midwinter germination. The former hypothesis is the more plausible one for species subjected to increasing temperature and unpredictable rainfall in late spring.

The C_4 summer ephemerals were represented only by *Amaranthus fimbriatus* and *Euphorbia setiloba*. The number of C_4 annuals is very low compared to that in similar terrain farther to the east in the Chihuahuan Desert of New Mexico (Syvertsen et al. 1976). The lower amount of rainfall in Deep Canyon during the summer months is the probable reason. *Amaranthus* was associated with the organically richer and more shaded habitats provided by shrubs. It may be restricted to the moderated conditions provided by the shrubs.

The various species of *Cryptantha* form a complex of ephemerals that are potentially very long-lived and which can become established in any season from late summer through spring. The adaptations that allow plants that become established in August to remain alive and reproductive through December with less than 1 cm additional rain are the subject of further investigation in our laboratory.

Ephemerals that germinate in response to the same rainfall show remarkable variations in phenological patterns. Some, like *Plantago insularis, Phacelia distans,* and *Phacelia crenulata* are capable of completing the life cycle very quickly following February germination. However, these same species have an extended period of vegetative growth following September germination and do not initiate reproduction even when subjected to desiccation in October and November. It appears that the synergistic effects of soil water and temperature may be important in determining life cycle events in these species. *Camissonia claviformis* and *Chaenactis carphoclinia* may reproduce

only during the spring months because both died before flowering, presumably because of a lack of water following fall germination. In both species new January seedlings completed the life cycle during the spring, even though significantly less rainfall occurred.

Schismus barbatus is the only introduced ephemeral encountered in the sample plots. This species appears to be capable of: 1) initiating reproduction very early, whether germinating in fall or winter; 2) adjusting the life span effectively depending upon conditions; and 3) producing a large number of viable seeds. *Schismus* had a density about four times greater (288 vs. 70 m^{-2}) than the densest native species, *Filago californica*. High phenotypic plasticity and successful germination of large numbers of seedlings may be related to its success as an alien species.

Palafoxia arida was reported by Went and Westergaard (1949) (as *P. linearis*) to be unrestricted in germination. However, in that study, *Palafoxia* germinated only in the late summer and fall. It was observed flowering during all seasons in the vicinity of my plots.

Comparison of survivorship curves for species that germinate in different seasons or grow under different temperature and rainfall regimes shows that determination of a characteristic form for a species is not possible. For example, *Plantago insularis* had a typically convex survivorship curve when germinating in February, whereas September cohorts had a concave survivorship plot. Such variations in population dynamics in different cohorts may be associated with considerable flexibility in resource allocation patterns from season to season. Detailed comparisons of resource allocation patterns in individuals from fall and winter cohorts need to be made to clarify the relationship.

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THE VEGETATION OF THE RAE LAKES BASIN, SOUTHERN SIERRA NEVADA

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ABSTRACT

Stands of subalpine-alpine vegetation from the southern Sierra Nevada were sampled (n = 97) and compared using Braun-Blanquet methodology. The study was undertaken (1) to characterize, using floristic criteria, the prinicpal vegetation types occurring within the study area; (2) to consider the influence of environmental factors on vegetational patterns; and (3) to provide a basis for making floristic and vegetational comparisons within the study area and elsewhere. The vegetational relevés (stand surveys) were organized into tables and assigned rank in a hierarchical system solely on the basis of floristic affinities. Five alliances and twelve associations were recognized and described phytosociologically and ecologically. Four major environmental features were considered to order the vegetation in the landscape: moisture regime, snow cover, elevation, and substrate stability. *Festucion brachyphyllae* occurs in truly alpine sites within the study area. *Primulion suffrutescentis* is characteristic of both mid- and high-elevation sites, especially on north slopes where the snow lies late and the growing season is short. *Pino-Caricion exsertae* occurs on the gravelly slopes and terraces in the mid-elevation *Pinus albicaulis* subalpine forest. *Monardello-Holodiscion microphylli* is characteristic of the usually dry, stabilized talus of mid-elevations. *Dodecathion redolentis* represents the mid-elevation meadow of streamsides and topographic lows that remain moist to wet throughout the season. A total of 277 vascular plant taxa belonging to 38 families were found within the study area.

In the Sierra Nevada of California, areas of alpine habitat are extensive. The well-developed alpine flora is composed of a large endemic (locally derived) element and a relatively small cosmopolitan arctic-alpine group (Major and Bamberg 1967). The uniqueness of the alpine flora is not duplicated in any other temperate North American mountain system; yet very few qualitative or quantitative descriptions of the vegetation exist. The flora of the Sierra Nevada alpine zone has been described by Smiley (1915), Hall and Grinnell (1919), Sharsmith (1940), and Howell (1951). The earliest very generalized vegetation descriptions of the Sierra Nevada occur in the work of Klyver (1931) and Sharsmith (1940). Munz and Keck (1949, 1950) and Munz (1959) consider the alpine region to support one broad plant community in their scheme of vegetation classification. Klikoff's (1965) survey work in the Gaylor Lake Basin relating microenvironmental factors to vegetation pattern was followed by Pemble's (1970) more detailed phytosociological description of the Slate Creek, Dana Plateau, and Convict Creek alpine vegetation. Pemble, using 188 stand surveys with 175 species, characterized the vegetation of these areas, relating it to two

sequences of ecological factors: soil parent material (granitics, non-carbonate metamorphics, and marble) and topography, especially as it relates to water availability. Chabot and Billings (1972) discussed the phytogeography and physiological ecology of Sierra Nevada alpine plants near Bishop Pass. Taylor (1976) has characterized the timberline vegetation at Carson Pass, the northern limit for many alpine plants in the Sierra Nevada. The survey of the vegetation of the Rae Lakes Basin was made in a period of ten weeks during the summer of 1978. The aims of the survey were: 1) to characterize, using floristic criteria, the principal vegetational types occurring in the Rae Lakes Basin; 2) to provide a basis for considering the influence of environmental factors on spatial distribution and floristic composition of the vegetation; and 3) to allow floristic and vegetational comparisons to be made within the basin and with other areas in the Sierra Nevada and elsewhere.

METHODS

The field methods adopted followed standard Braun-Blanquet vegetation sampling procedures (Birks 1973, Mueller-Dombois and Ellenberg 1974). Uniform areas of vegetation (stands) were selected for description in the field. The selection of stands was subjective; an effort was made to record the variation of vegetation within the study area. One plot was sampled within each homogeneous stand area. The size and shape of the sample plots were not standardized, but were adjusted according to the character of the vegetation sampled. Estimates of percent cover of the plot area of rock, bare soil, and vegetation (by species and strata) were made. All taxa occurring within the plots, excluding bryophytes and lichens, were recorded and cover-abundance estimated visually according to the Braun-Blanquet combined scale: $r, +, 1, 2, 3, 4, 5$ (Mueller-Dombois and Ellenberg 1974, p. 60). Voucher specimens are deposited in DAV and in the Sequoia-Kings Canyon National Parks Herbarium. Nomenclature follows Munz (1959, 1968) unless otherwise noted. Environmental data for each stand, including slope, exposure, elevation, soil type, pH (Hellige pH kit), and moisture regime, were noted in the field. Estimates of moisture regime for surface and subsurface soils were assigned as follows: 1) dry throughout most of the growing season; 2) moist throughout the growing season; and 3) wet, soil at field capacity or surface water visible throughout the growing season.

Description of study area. The Rae Lakes Basin is located in Fresno County, California, about 30 km east of Cedar Grove and 20 km west of Independence. It lies in the southeastern Sierra Nevada, just west of the main crest (36°49′N, 118°24′W, USGS Mt. Pinchot quadrangle, 1953). The study area is an alpine lake basin that is approximately 1 km wide, tending north-south and bounded on the east, west, and

south by natural watershed divides. To the north, an arbitrary line above the limits of the red fir forest defines the study area. The topography of the Rae Lakes Basin is extremely rugged: repeated glaciation of the entire region during the Pleistocene has left a legacy of steep arêtes and ragged peaks, talus fields, and unstable scree slopes. This classically alpine topography, with its effects on local temperature and soil moisture, creates a myriad of microenvironments in a geographically small area. Elevation is from 3046–4040 m, encompassing a wide variety of subalpine and alpine habitats.

Climate may be regarded as consisting of moisture and heat regimes. Mean annual precipitation in the Rae Lakes Basin is calculated to be approximately 99 cm, based on extrapolation from Charlotte Ridge and Ellery Lake snow survey and precipitation records (Burke 1979). Although annual precipitation is high in the Sierra Nevada, it is concentrated in the form of snow in the non-growing season. In the summer, most cyclonic storms are diverted from the Sierra Nevada and, with the exception of occasional orographic thunderstorms, summer precipitation is generally low (Rae Lakes averaged 43–50 mm in summer precipitation for 1972–1976). Mean monthly temperatures are calculated to range from $-3°C$ (December) to $13°C$ (July). Using calculated mean monthly temperatures and precipitation figures, a Thornthwaite climatic diagram (Thornthwaite 1948, Thornthwaite and Mather 1957) was generated and evapotranspiration values determined (Burke 1979). Assuming 100 mm of available water stored in the soil, potential evapotranspiration (PotE) can exceed precipitation by 72, 91, 87, and 53 mm per month in June, July, August, and September, respectively. This results in use of soil-stored water and some drought (water deficit). In the Rae Lakes Basin, availability of and demand for water are out of phase.

Four separate granitic intrusive masses occur in the Rae Lakes Basin, underlying virtually all of the study area. Dark colored mafic igneous and hybrid rocks predominate in the southern end of the basin, however, and a single small outcropping of marble occurs towards the north end of the study area. No pedological studies have been carried out in the high country of the Sierra Nevada. Generally, most alpine soils are medium to coarse textured, excessively drained, have a low inherent fertility, contain large amounts of stone, cobble, and gravel, and are strongly acid. These soils are characterized by a high content of weakly decomposed organic matter in the surface horizons, weak granular structure, and silt loam textures with low (5–15 percent) clay content (Knapik et al. 1973). Due to the instability of the alpine landscape, alpine soils are generally immature with no or weakly developed horizons. Horizons that form are often mixed by frost disturbance or mass wasting, or destroyed by erosion. Acidic soils result wherever granitic rocks are weathering; where mafic or calcium rich rocks are weathering, more alkaline soils are formed.

Phytosociological classification. Although relevés were sampled in as wide a range of habitat conditions as possible, all vegetational relevés are organized solely on the basis of floristic affinities, irrespective of habitat. The matrix of stands and plant taxa in the association tables was initially sorted by the Ceska and Roemer computer program (1971) as modified by D. Randall and D. W. Taylor, and further rearrangements of the table were done by hand (Burke 1979). Figure 1 summarizes the final synthetic Rae Lakes Association Table (see Table 1 in Burke, 1979; 97 stands, 146 species; available at cost from author). The following list of the plants (Table 1) included in the species groups of the Rae Lakes Basin should be used in conjunction with the Rae Lakes Association Table Summary (Fig. 1). Based on a comparison of floristic relationships, relatively homogeneous relevés are grouped into associations, and each association assigned to an alliance. Syntaxa are named according to the published rules of the Code of Phytosociological Nomenclature (Barkman et al. 1976). Alliances are indicated by the "-ion" termination and associations by the "-etum" suffix.

DESCRIPTION OF THE RAE LAKES BASIN PLANT COMMUNITIES

Two levels of vegetational pattern are recognized, including five alliances and twelve associations. Detailed descriptions are provided only for the associations, the lowest ranking units in the classification. Careful use of the Association Table Summary (Fig. 1) together with the list of species groups will yield important floristic information about each association and should be considered an integral part of the following association descriptions. Ecological information about alliances may be obtained through generalization of the combined data for all associations included within a particular alliance. The letters within brackets are the abbreviations of association names used in Fig. 1. Number in parentheses is the number of stands sampled. Details on nomenclature type relevés is included in Table 1 in Burke (1979).

Associations of the Rae Lakes Basin

I. *Festucion brachyphyllae.*

A. The *Festuco-Penstemetum davidsonii* [Fe.-Pe.da.] (2) occurs at high elevation (3410–3512 m) and is best developed where local topography is favorable for snow accumulation. The sites are well drained and surface water is never present. Relief varies from flat ridges to very steep slopes, but best development is seen on stabilized gravelly or talus slopes, or in the rock crevices and shallow sandy terraces of granitic outcroppings. Type relevé: 027.

TABLE 1.　RAE LAKES BASIN SPECIES GROUPS.

SPECIES GROUP 1A: *Penstemon davidsonii, Carex helleri, Ivesia pygmaea, Silene sargentii, Festuca brachyphylla, Calamagrostis purpurascens.*

SPECIES GROUP 1B: *Erigeron compositus* var. *glabratus, Eriogonum ovalifolium* var. *nivale, Haplopappus macronema, Ribes cereum, Hulsea algida, Polemonium eximium, Ranunculus eschscholtzii* var. *Oxynotus, Oxyria digyna, Anelsonia eurycarpa* (Hitchcock et al. 1964), *Arabis lemmonii* vars., *Draba breweri, D. oligosperma, Poa rupicola, Androsace septentrionalis* subsp. *subumbellata.*

SPECIES GROUP 2A: *Sedum rosea* subsp. *integrifolium, Salix orestera, Erigeron petiolaris, Juncus drummondii, Potentilla breweri, Antennaria umbrinella.*

SPECIES GROUP 2B: *Carex exserta, Lewisia sierrae, Saxifraga aprica, Penstemon heterodoxus, Calyptridium umbellatum, Rumex paucifolius, Trisetum spicatum, Lewisia nevadensis.*

SPECIES GROUP 3A: *Pinus albicaulis, Juncus parryi, Selaginella watsoni, Poa nervosa, Eriogonum incanum, Antennaria alpina* var. *media, Antennaria rosea, Arabis platysperma* var. *howellii, Cryptogramma acrostichoides.*

SPECIES GROUP 3B: *Penstemon newberryi, Carex rossii, Phacelia frigida, Holodiscus microphyllus, Achillea lanulosa* subsp. *alpicola, Eriogonum nudum* vars., *Sitanion hystrix, Monardella odoratissima* vars., *Stipa occidentalis, Castilleja applegatei* vars., *Erysimum perenne, Cirsium tioganum, Muhlenbergia richardsonis, Leptodactylon pungens* subsp. *pulchriflorum, Artemisia ludoviciana* subsp. *incompta, Cystopteris fragilis, Carex straminiformis, Stephanomeria tenuifolia, Ribes montigenum, Melica stricta.*

SPECIES GROUP 3C: *Carex congdonii, Primula suffrutescens.*

SPECIES GROUP 3D: *Senecio fremontii, Hieracium horridum, Arenaria nuttallii* subsp. *gracilis, Pellaea breweri.*

SPECIES GROUP 4A: *Cryptantha glomeriflora, Polygonum kelloggii, Gayophytum ramosissimum, G. racemosum, Mimulus suksdorfii, Mimulus breweri, Collinsia parviflora, Potentilla diversifolia.*

SPECIES GROUP 5A: *Epilobium angustifolium, Phyllodoce breweri, Veratrum californicum, Habenaria dilatata, Senecio triangularis, Senecio pauciflora, Lilium kellyanum, Veronica wormskjoldii* (Hulten 1968).

SPECIES GROUP 5B: *Delphinium polycladon, Carex spectabilis, Agropyron trachycaulum, Helenium bigelovii, Aconitum columbianum, Salix lemmonii, Potentilla fruticosa, Castilleja miniata, Thalictrum fendleri, Aquilegia formosa, Deschampsia caespitosa.*

SPECIES GROUP 5C: *Muhlenbergia filiformis, Dodecatheon redolens, Senecio scorzonella, Allium validum, Trifolium monanthum* vars., *Phleum alpinum, Sibbaldia procumbens, Perideridia parishii, Epilobium halleanum, Carex microptera, Carex heteroneura.*

SPECIES GROUP 5D: *Calamagrostis breweri, Mimulus primuloides* var. *pilosellus, Aster alpigenus* subsp. *andersonii, Carex fissuricola, Swertia perennis, Ledum glandulosum, Vaccinium nivictum, Danthonia intermedia, Pedicularis attollens, Eleocharis pauciflora, Gentiana newberryi, Kalmia polifolia* var. *microphylla, Potentilla drummondii, Luzula orestera, Vaccinium occidentale.*

SPECIES GROUP 5E: *Epilobium oregonense, Calamagrostis canadensis, Gentiana holopetala, Carex rostrata.*

SPECIES GROUP 5F: *Scirpus criniger, Pedicularis groenlandica, Viola macloskeyi, Erigeron peregrinus* subsp. *callianthemus, Geum macrophyllum, Luzula comosa.*

ASSOCIATED TAXA: *Arabis lyallii* var., *Carex festivella, Carex multicostata, Carex phaeocephala, Carex raynoldsii, Epilobium hornemanii, Heuchera rubescens, Koeleria cristata, Pinus balfouriana, Pinus contorta* subsp. *murrayana, Poa incurva, Potentilla glandulosa, Senecio integerrimus* var. *major, Solidago multiradiata.*
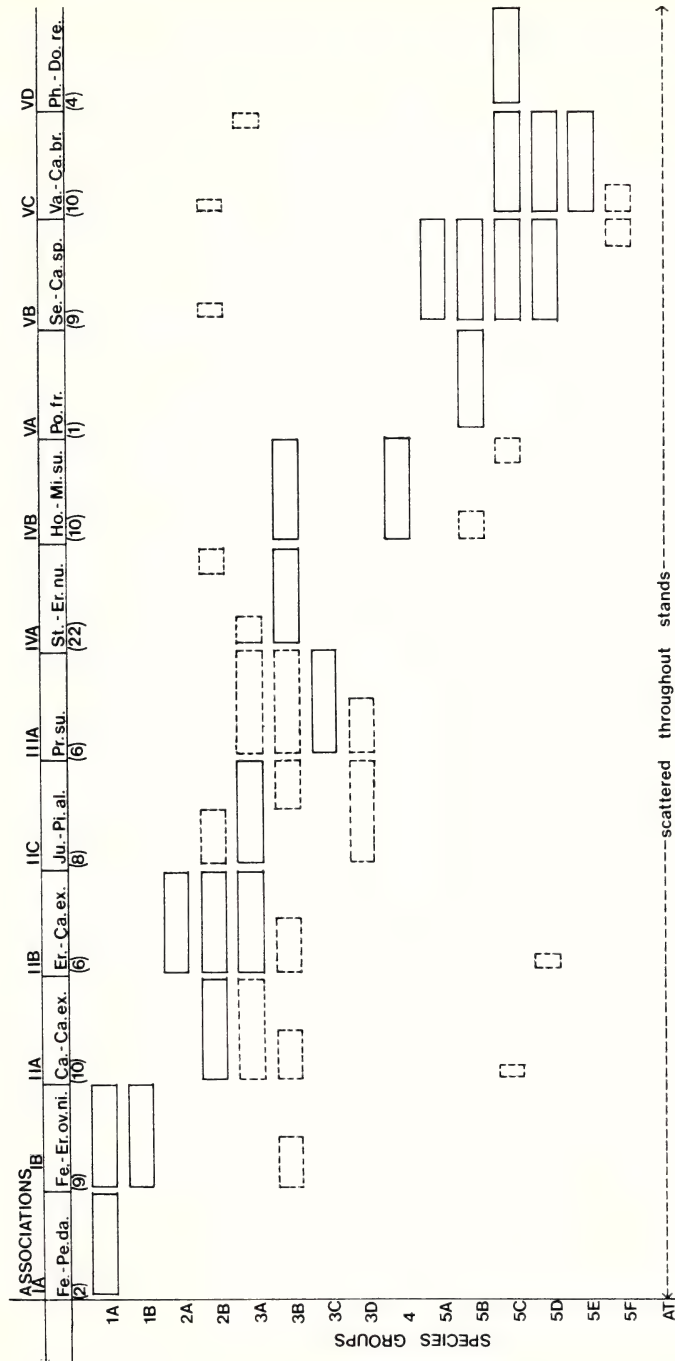
FIG. 1. Rae Lakes Association table summary. Names of associations are abbreviated across the top and are identified by a roman numeral and letter, following the numbering system used in the test description. Numbers of relevés per association follows in parentheses. A complete list of all taxa in species groups (1A to 5F) and associated taxa (AT) is included in Table 1. Complete data available in Table 1, Burke 1979.
Legend: ☐ Cluster of species group X present in all or almost all relevés of association. ⬚ Cluster of species group X present in some relevés of association. Dashed box drawn at less than full size represents the presence of a small percentage of relevés with a cluster of species group X.

B. The *Festuco-Eriogonetum ovalifolii* var. *nivalis* [Fe.-Er.ov.ni.] (9) occurs in very high elevation, truly alpine sites (3386–3712 m, av. 3535 m). It is common in steep, loose talus slopes where soil moisture is extremely low and wind exposure is very high. The topographic location—high windy ridgetops—of some of the stands suggests that it may be able to tolerate sites that are blown free of snow in the winter. Type relevé: 043.

II. *Pino-Caricion exsertae.*

A. The *Calyptridio-Caricetum exsertae* [Ca.-Ca.ex.] (10) is a *Carex exserta* meadow type, well-developed at mid-elevations (3162–3301 m, av. 3232 m). This association is well represented throughout the Rae Lakes Basin, covering large areas of moderately dry, gently sloping terraces. Although this association is found at rather high elevations, in the Rae Lakes Basin it is better considered a dry meadow type on open gravel within the *Pinus albicaulis* subalpine forest. *Carex exserta* consistently accounts for 25–75 percent of the cover in stands sampled for this association. Type relevé: 078.

B. The *Erigeronto-Caricetum exsertae* [Er.-Ca.ex.] (6) represents a *Carex exserta* meadow type occurring in relatively moist sites in the *Pinus albicaulis* subalpine forest. Although *Pinus albicaulis* is usually present, it has relatively low cover compared to the *Junco-Pinetum albicaulis*. Best developed at moderate to high elevations, this association was sampled at sites from 3159–3557 m (av. 3336 m). The sites have good drainage and although the surface is often dry, subsurface moisture is usually present. These sites often receive meltwater from late-lying snowbanks. The sites are often rocky, but with more vegetative cover than the higher elevation associations found on talus slopes. Type relevé: 052.

C. A high elevation forest type, the *Junco-Pinetum albicaulis* [Ju.-Pi.al.] (8) was sampled at elevations from 3192–3411 m (av. 3287 m). The soil is generally dry and bare rocky spots predominate under the open canopy of this forest. Surface moisture is rare where this association is well developed. It is characterized in part by a high *Pinus albicaulis* cover and the absence of a shrubby understory. *Pinus contorta* subsp. *murrayana* and *P. balfouriana* are also present at Rae Lakes and are common trees throughout this subalpine forest. Slopes range from relatively flat areas on the basin floor to 30°. Type relevé: 031.

III. *Primulion suffrutescentis.*

A. The *Primuletum suffrutescentis* [Pr.su.] (6) occurs on talus slopes at the upper limits of the *Pinus albicaulis* subalpine forest. Elevations are from 3295–3472 m (av. 3418 m). Soils are extremely dry and relatively acidic. The talus is generally large and stable on slopes from 12°–35° (av. 27°). This association is characterized in part by abundant

Primula suffrutescens, often associated with *Carex congdonii* and *Eriogonum incanum.* Type relevé: 046.

IV. *Monardello-Holodiscion microphylli.*

A. The *Stipo-Eriogonetum nudi* [St.-Er.nu.] (22) is extremely common throughout the study area at elevations from 3131–3460 m (av. 3295 m). This association is typical of very dry, rocky outcroppings or stable talus in the *Pinus albicaulis* subalpine forest. Sites are usually free of snow early in the season and the gravelly soils are moist only after a summer rain or snowfall. Slopes sampled are from 2°–52° (av. 26°). The association is best developed on slopes with western and southwestern exposures. Shrubby species, specifically *Holodiscus microphyllus* and *Ribes montigenum,* are a conspicuous part of this association in many relevés. Type relevé: 034.

B. The *Holodisco-Mimuletum suksdorfii* [Ho.-Mi.su.] (10) includes the only predominantly annual species group in the Rae Lakes vegetation (Species Group 4A) and occurs in small pockets of damp soil trapped on otherwise dry, sunny rock outcroppings. The soil often shows evidence of frost heaving, and needle ice was observed on a number of occasions. Locally, these small annuals can be exceedingly abundant and yet, because of their minute stature, they account for very little cover. This association was sampled in stands from elevations of 3192–3277 m, with an average of 3240 m. Slopes are generally steep, from 18°–48°, with an average 31°. Type relevé: 006.

V. *Dodecathion redolentis.*

A. The *Potentilletum fruticosae* [Po.fr.] (1) was sampled by a single relevé (relevé 104) on a marble outcropping northeast of Dollar Lake. This association occurs on wet seeps on mineralized soils at mid-elevations and is uncommon in the study area. Comparison of this relevé with association tables for Pemble's (1970) study of alpine vegetation in the central Sierra Nevada and Taylor's (1976) study of Carson Pass suggests that the *Potentilletum fruticosae* may be related to Pemble's *Salix anglorum antiplasta* alliance and Taylor's *Dasiphora fruticosa-Potentilla breweri* association. Further sampling is needed to characterize this vegetation unit more fully. Type relevé: 104.

B. The *Seneciono-Caricetum spectabilis* [Se.-Ca.sp.] (9) is a tall herb community at mid-elevations (3046–3228 m; av. 3125 m). It occurs on gentle to steep streambanks and in wet seeps. Slopes vary from 3°–45°, with an average of 18°. The soil is fairly well-drained, but retains a considerable amount of moisture throughout the field season. Where sites border seeps or slowly moving snowmelt streams, soils are generally at field capacity and are not well oxygenated. Standing water is rarely present. Shrub cover values exceed those of the herbaceous layer at some sites, with *Salix lemmonii* forming dense thickets. Because of their density and stature, the herbaceous plants

too may form tall thickets. The complexity of this meadow community suggests that it may be more than one association, but this is impossible to determine without further sampling. Type relevé: 088.

C. The *Vaccinio-Calamagrostietum breweri* [Va.-Ca.br.] (10) forms very dense meadows with few rocks or bare spots. This association was sampled at elevations between 3052 m and 3283 m, with an average elevation of 3194 m. Soils of these meadows often have a thick sod layer of matted roots, are commonly poorly drained, and are at field capacity. Standing water, sometimes stagnant, may be present in shallow hollows. These meadows are frequent in topographic lows along lakeshores and in areas where the runoff of melting snowfield is channelled by macrorelief. Microrelief is generally undulating or gently sloping. Type relevé: 085.

D. The *Phleo-Dodecathetum redolentis* [Ph.-Do.re.] (4) is another common streamside or wet lakeside community of mid-elevations. Stands sampled were from 3161–3228 m (av. 3201 m). This association occurs on moderate slopes ranging from 2°–22°, with an average 12°. The microrelief is usually convex and the sites are well-drained and generally a little drier relative to the moisture regime of the *Seneciono-Caricetum spectabilis*. The association is found along moderately flowing streams and where soils maintain a favorable moisture balance throughout the growing season. Type relevé: 040.

Environmental Analysis

Prominent discontinuous patterns characterize the vegetation of the Rae Lakes Basin. These distribution patterns can be related to gradients of the environmental complex.

Elevation. Elevation obviously exerts a controlling influence on the large scale vertical zonation of the study area; however, even at high elevation, topographic position and substrate stability are more accurate predators of vegetational patterns. Certain associations, specifically the *Festuco-Penstemetum davidsonii* and the *Festuco-Eriogonetum ovalifolii* var. *nivalis,* are characteristic of truly high elevation habitats.

Site moisture. Several of the Rae Lakes associations may be clearly separated by variation in the moisture regime of habitats (Fig. 2). At the wettest end of the spectrum, only one community, the *Vaccinio-Calamagrostietum breweri,* is found to be well-developed. Streambanks and well-drained seeps also show a favorable water balance

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Fig. 2. A. Moisture-pH summary. Each diagram summarizes both pH and site moisture data for moist-wet (data from 3 associations summarized), moderately dry (4) and dry associations (5) of the Rae Lakes Basin. Each box within each moisture-pH

A. MOISTURE-pH SUMMARY

moisture regime

moist to wet associations (3)

moderately dry to moist associations (4)

dry associations (5)

B. SLOPE / EXPOSURE

Stipo-Eriogonetum nudi

Calyptridio-Caricetum exsertae

Junco-Pinetum albicaulis
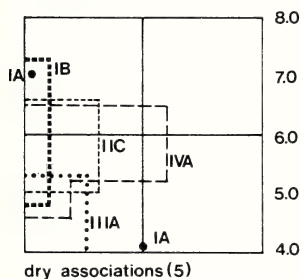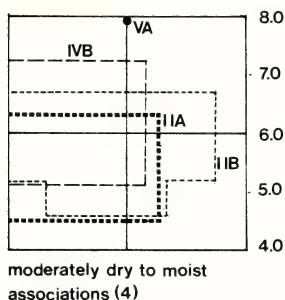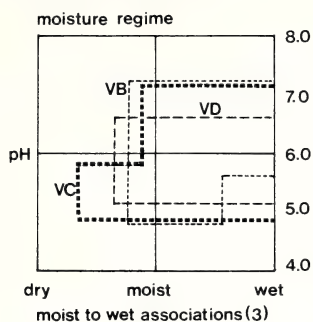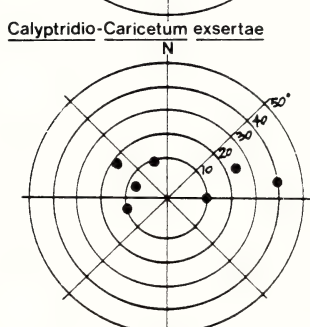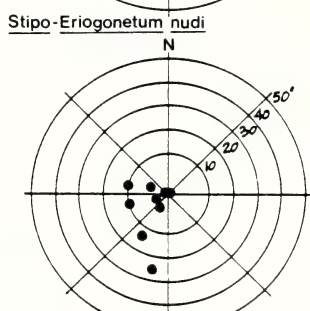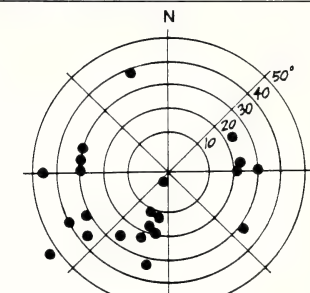
diagram summarizes the range of data points of all relevés within a single association. Dots represent single data points for associations with only 1 or 2 stands sampled. Each association is identified by a roman numeral and letter, following the numbering system used in the association description in the text. A general tendency from acidic to neutral soils is noted as one progresses along a moisture gradient from very dry sites to very wet sites. Detailed data for each association is available in Burke (1979).

B. Slope/exposure. In each slope-exposure diagram, the concentric rings represent degree of slope in 10° increments from 0° to 50° and the lines represent the azimuth directions in 45° increments (i.e., the direction of slope). *Stipo-Eriogonetum nudi* is characteristic of fairly steep slopes and is unusual on north-facing slopes; *Calyptridio-Caricetum exsertae* shows best development on slopes with a southwesterly aspect and stands of *Junco-Pinetum albicaulis* are rare on any southerly exposure.

throughout the growing season and support tall herb (*Seneciono-Caricetum spectabilis*) and characteristic fast-flowing streamside (*Phleo-Dodecathetum redolentis*) associations. Moderately dry to moist habitats at mid-elevations are utilized primarily by the relatively drier meadow types of the subalpine forest. The *Erigeronto-Caricetum exsertae* and *Potentilletum fruticosae* associations are best developed where the soil moisture regime is moderately moist throughout the growing season. Although surface moisture may be absent, subsurface moisture is usually available, often as meltwater seepage from late-lying snowbanks above the site. The *Holodisco-Mimuletum suksdorfii* represents clusters of annuals in pockets of damp gravel where melt-water or runoff is trapped in an otherwise dry, rocky habitat. These sites are subject to frost heaving early in the growing season and may be completely dry by mid-August. In a few of these sites, a continuous source of water is available throughout the dry summer season. The *Calyptridio-Caricetum exsertae* is the driest of the meadow types and is well-developed on moderately dry, sloping terraces. Habitats with the driest moisture regime are characterized by the *Festucion brachyphyllae* and *Primulion suffrutescentis* alliances above tree limit, with best development seen on dry talus slopes at high elevation. At mid-elevations, dry stabilized talus supports the *Stipo-Eriogonetum nudi* and dry, gravelly slopes and terraces support the sparse *Junco-Pinetum albicaulis*.

Snow cover. In North American alpine areas, depth and duration of snow have repeatedly been found to be crucial determinants of vegetational patterns (Pemble 1970, Taylor 1976, Komarkova 1978). A complex relationship of regional climate, wind, and topography controls the distribution of snow and soil moisture, and therefore, the vegetation above treelimit. The *Festuco-Eriogonetum ovalifolii* var. *nivalis* is found on high elevation slopes that experience some degree of snow deflation during the winter. The *Primuletum suffrutescentis* and *Festuco-Penstemetum davidsonii* occur above the treelimit in sites that experience snow accumulation and a shorter growing season. In the gravelly habitats of these two associations, good drainage accounts for the lack of soil moisture during the growing season in spite of the heavy winter snowpack. At mid-elevations, the *Stipo-Eriogonetum nudi* is snow-free early and very dry throughout most of the growing season. The wettest meadow association, the *Vaccinio-Calamagrostietum breweri,* is often seen in habitats where snow cover persists late into the growing season. In this association, occurring on sites where microrelief is flat or gently sloping and soil drainage is usually slow, winter snowpack correlates well with the availability of water throughout the growing season.

Slope and exposure. No associations are characteristic of habitats with a specific degree of slope. Both a dry meadow type (*Calyptridio-*

Caricetum exsertae) and a wet meadow type (*Vaccinio-Calamagros-tietum breweri*) may be characteristic of flats and terraces with a slight degree of slope. Most plant associations in the Rae Lakes Basin are represented by stands distributed over a variety of exposures. The *Calyptridio-Caricetum exsertae,* however, shows best development on slopes with a southwesterly aspect. Fifty-five percent of the stands of the *Stipo-Eriogonetum nudi* also occur on southwestern exposures. Both of these associations reflect dry habitats with relatively long growing seasons in the subalpine forest. In contrast, the forested stands of the *Junco-Pinetum albicaulis* are rare on any southerly exposures (Fig. 2).

Substrate characteristics. Because granitics underlie virtually all of the study area, few meaningful comparisons can be made between associations on the basis of parent material. However, it is noteworthy that the single relevé sampled on calcareous substrate (relevé 104) has a distinct enough assemblage of taxa to be considered a separate association, the *Potentilletum fruticosa*. It is, however, possible to characterize at least the high elevation associations on the basis of substrate stability. The *Festuco-Penstemetum davidsonii* and *Festuco-Eriogonetum ovalifolii* var. *nivalis* associations are both well represented at high elevation on dry soil. The *Festuco-Eriogonetum ovalifolii* var. *nivalis* is well-developed on scree and in the loose, gravelly soils of boulder fields. In contrast, the *Festuco-Penstemetum davidsonii* is best developed on stable substrates, from rock crevices and plateaus to trapped pockets of soil on stabilized talus slopes. The distribution of community types on the basis of soil pH is represented by Fig. 2. No obvious vegetation patterning is correlated with soil pH. A general tendency from acidic to neutral soils is noted as one progresses along a moisture gradient from very dry sites to very wet sites. Presumably, the snow meltwater may leach cations from the dry and wet sites equally in the early season. In wet sites and topographic lows, soil cations may be replaced by the cation-rich runoff from dry sites. Needles of *Pinus albicaulis* may also contribute to the acidity of some subalpine forest types.

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PINE SEEDLINGS, NATIVE GROUND COVER, AND LOLIUM MULTIFLORUM ON THE MARBLE-CONE BURN, SANTA LUCIA RANGE, CALIFORNIA

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ABSTRACT

Vegetation on 19 plots in crownfire-killed pine stands was studied. After three seasons pine seedling density ranged from 7/ha to 1685/ha in four *Pinus coulteri* stands. Pine seedling density was 188/ha in a *P. ponderosa* stand. In a stand dominated by *P. lambertiana* before the fire, pine seedlings numbered 3178/ha; but *P. coulteri* outnumbered *P. lambertiana* 7:1. Shrub layers of *Ceanothus* spp. seedlings and hardwood tree sprouts ranged from 16 percent to 68 percent cover in these stands. Species richness was low in the *P. lambertiana* stand, averaging 20 species/0.1 ha plot with only one important herb species. Species richness was higher in the *P. coulteri* stands with one stand averaging 74 species/0.1 ha plot. By the second season *Lolium multiflorum* dominated the herb layer in all *P. coulteri* stands, and the native herbs had low density and biomass. Low *Pinus* and *Ceanothus* seedling survival in two *P. coulteri* stands may have been related to *Lolium* competition.

The Marble-Cone fire of August 1977 covered 72,000 ha of the Santa Lucia Range in Monterey County, mainly in the Ventana Wilderness, Los Padres National Forest (Hammond 1977, Griffin 1978, Talley and Griffin 1980). Many mature pine forests on the higher ridges were heavily burned. This report summarizes observations on pine stands destroyed by crownfire on three of these ridges. Because of the burn's wilderness status, vegetation recovery was allowed to proceed under "natural" conditions. However, an introduced annual grass, *Lolium multiflorum,* was sown for erosion control on much of the burn (Hammond 1977). This study describes the effects of this planted grass on species richness, shrub regeneration, and tree seedling survival during three postfire seasons.

Mixed hardwood forests cover much of the Santa Lucia Range (Talley 1974, Sawyer et al. 1977). Three pine species are scattered in these hardwood communities, and stands dominated by each pine were studied. Within the Marble-Cone burn, *Pinus lambertiana* grows only on Junipero Serra Peak (JSP); *P. ponderosa* is more widely distributed with conspicuous mature stands on Pine Ridge (PR). *Pinus coulteri* is a minor component of most mixed hardwood forests and adjacent chaparral, and it has dominant stands concentrated in the Chews Ridge (CR) region.

Hammond (1977) summarized the large and expensive rehabilitation project that included the seeding of *Lolium multiflorum*. Large areas

TABLE 1.   LOCATION AND HABITAT DETAILS OF PINE REGENERATION STUDY
AREAS IN CROWNFIRE-KILLED FORESTS, MARBLE-CONE BURN.

Name and location	No. of plots	Elev., aspect, slope, soil series	Dominant pine, most important hardwood
Junipero Serra Pk. (JSP), within 0.5 km of lookout	4	1665–1760 m, 311–006°, 25–45%, Junipero loamy sand	*Pinus lambertiana* *Quercus chrysolepis*
Pine Ringe (PR), 0.5–0.8 km e. of summit	4	1360–1430 m, 171–231°, 20–30%, Junipero sandy loam	*P. ponderosa* *Lithocarpus densiflorus*
Chews Ridge region			
Finch Canyon (CR-1), 3 km e. of lookout	3	1130–1170 m, 045–070°, 20–23%, Sheridan coarse sandy loam	*P. coulteri* *Q. agrifolia*
China Camp (CR-2), 1.6 km s. of lookout	3	1360–1450 m, 170–257°, 55–70%, Sur-Junipero complex	*P. coulteri* *Q. chrysolepis*
Miller Ridge (CR-3), 3.1 km sw. of lookout	3	1405–1450 m, 134–186°, 15–45%, Sheridan coarse sandy loam	*P. coulteri* *Q. chrysolepis*
Summit (CR-4), 0.2 km ne. of lookout	2	1490–1500 m, 075–095°, 25–28%, Sur-Junipero complex	*P. coulteri* *Q. wislizenii*

of montane forest as well as chaparral were seeded. In October 1977,
460 t of seeds were aerially sown on 63,000 ha (7.8 kg/ha). Ground
sampling by the seeding project suggested that seed distribution was
reasonably uniform, but the final grass crop was patchy. Two regions
having concentrations of "sensitive" plants, including study areas JSP
and PR (Table 1), were excluded from the aerial seeding. In addition
fuelbreak scars were hand seeded with a mixture of domestic grasses.
This seeding included bulldozer trails near study areas CR-2,3,4 (Ta-
ble 1).

Although sediment loss and slope stability were studied in parts of
the burn by several projects, no general report on soil erosion was
compiled. No erosion data were gathered on my study areas or on
comparable habitats elsewhere in the burn. The following observa-
tions provide some background on how erosion affected my plots. On
slopes over 60 percent at CR-2, soil loss started soon after the fire
through dry creep. As Wakimoto (1979) emphasized, *Lolium* seeding
can not control this type of gravitational flow. In late December 1977,
hurricane force winds over the ridges blew ashes, soil, and some *Lol-
ium* seeds off of the most exposed places. Then heavy rains in early
1978 removed surface soil from all plots. Rock "pedestals," exposed
rocks, and bare roots suggested that 3–8 cm of surface soil had washed

off most of the plots with slopes over 20 percent. On the steepest places rills up to 30 cm deep eroded down into the new soil surface. This wind and water erosion occurred before the *Lolium* formed any effective ground cover. Conrad (1979) noted that slow development of *Lolium* cover was common in rehabilitation projects on chaparral burns.

STUDY METHODS

Species lists for several regions of the Marble-Cone burn were fortuitously included in previous work (Griffin 1975a). At PR and JSP (Griffin 1975b) I had specifically searched for plants on the sites that became study plots after the fire. Talley (1974, 1976) had prefire herb cover data relevant to the PR and JSP study areas, but his plots did not coincide with my plots.

During the first postfire season I established 19 permanent plots (20 × 50 m) in pine stands killed by crownfire (Table 1). I measured diameters of all trees (>1 cm dbh). These diameters were slightly undersized due to bark loss by charring. The burned trees could be easily identified to species by bark and cone characters.

In early summer of each season, during the period of maximum herb cover, I photographed every plot from permanent reference points. At the same time I counted all conifer seedlings per plot. *Pinus coulteri* seedlings could not be readily separated from *P. lambertiana* seedlings the first season but were easily separated in following seasons. Starting in 1978 I sampled a 20 × 50 cm quadrat every 2 m along each of four transects per plot for a total of 80 quadrats. Each season I counted all shrub seedlings, recorded the presence of all rooted species, and visually estimated the percentage of bare soil in each quadrat. In 1979 visual estimates of current year *Lolium* cover were added to quadrat data, and in 1980 I estimated the cover of *Lolium* mulch. Shrub cover was sampled at a point every 2 m along four transects through each plot for a total of 100 points. All plots were visited at least one additional time per season to search for additional species, to observe pine seedling growth, and to take additional photographs.

The two CR-4 plots were established too late in 1978 to complete quadrat sampling, but in following years they were sampled by the same methods as the other plots.

RESULTS

Species richness. The vascular flora of the general region around the three study areas approached 400 species (Griffin 1975a). I found 162 species on the 19 plots over three seasons. Numbers of species on individual plots ranged from 19 at JSP to 80 at CR-2; species on individual quadrats ranged from zero on several areas to 10 at CR-2.

TABLE 2. VASCULAR PLANT SPECIES RICHNESS ON THE STUDY AREAS. Species numbers represent trees (T), shrubs (S), and herbs (H) seen on 0.1 ha plots during three seasons and the average number of species per 20 × 50 cm quadrat each season.

Study area	No. species all plots 1978–1980				Average no. species per quadrat		
	T	S	H	Total	1978	1979	1980
JSP	3	5	27	35	0.5	1.7	2.0
PR	5	7	45	57	0.6	2.2	2.7
CR-1	6	9	53	68	2.3	2.7	2.6
CR-2	5	9	86	100	2.4	4.5	4.6
CR-3	6	7	24	37	1.5	2.0	2.0
CR-4	6	10	40	56	—	2.3	2.4

The JSP area had unusually few species in the understory before the fire (Griffin 1975b, Talley 1976) and few species after the fire (Table 2). In 1978 only nine herb species grew on the 320 quadrats sampled at JSP. Only one of these, *Lupinus cervinus,* had grown on the prefire plots (Talley 1976). The only common herb was *Gayophytum heterozygum.* No grassland species were present.

The richest *P. coulteri* area had almost three times as many species as JSP (Table 2). The CR-2 area had more species per plot than many oak woodland plots of the same size at lower elevations near Chews Ridge (Naveh and Whittaker 1979). During the first season at CR-2, 53 herb species were found on 240 quadrats. This forest borders a small grassland, and many species on the pine forest plots were typical grassland species.

Native herb dominance. Only four perennial herbs were common during the first three seasons (Table 3). I had seen these species on the study areas before the fire, and individuals of these species seen after the fire were mostly sprouts not seedlings. Some *Pteridium* sprouts at PR were 20 cm tall 30 days after the fire, and *Pteridium* at PR was the most dominant perennial on any study area by 1980 (Table 3). Several perennials that were absent from the study areas before the fire germinated from dormant seeds after the fire. *Lupinus abramsii* at JSP was a good example (Talley and Griffin 1980), but none of these perennials became common on the study areas.

The most common annuals (Table 3) were grassland species or plants that thrive in disturbed conditions. Several annuals reached a peak in coverage the second season and declined the third season— *Claytonia perfoliata* and *Allophyllum divaricatum* were good examples. *Allophyllum* was rare in roadcuts near CR-2 before the fire. By the second postfire year it was conspicuous on and around the CR-2 plots, but it was absent from the frequency quadrats and rare elsewhere on the plots the third year. The best example of continued

TABLE 3. AVERAGE FREQUENCY (%) OF COMMON HERBS ON STUDY AREAS DURING THREE POSTFIRE SEASONS. Included species had frequencies of at least 20% on a study area during at least one season; "+" indicates species on plot but not on frequency quadrats.

Species	Study areas																
	JSP			PR			CR-1			CR-2			CR-3			CR-4	
	78	79	80	78	79	80	78	79	80	78	79	80	78	79	80	79	80
Annuals																	
Lolium multiflorum	+	+	0	22	75	94	99	100	100	48	99	100	82	100	99	100	100
Gayophytum heterozygum	<1	19	94	0	1	1				+	<1	+				4	13
Claytonia perfoliata	+	+	5	+	2	<1	9	36	8	7	48	2	+	+	+	23	2
Phacelia grisea	+	+		+	0	0	<1	0	0	+	<1	0	13	36	26		
Lupinus nanus																18	24
Trifolium albopurpureum							3	<1	2	7	23	28	+	+	<1		
Allophyllum divaricatum										9	22	0					
Bromus mollis										1	4	5	9	23	11		
Lotus humistratus										5	16	20					
Chorizanthe membranacea										3	20	20					
Perennials																	
Galium californicum				7	10	13	13	12	18	16	18	20	+	+	+	+	+
Pteridium aquilinum				13	45	50				1	4	4					
Lathyrus vestitus							30	45	39	20	23	24		<1	<1		
Madia madioides										2	16	24					

expansion was by *Gayophytum heterozygum,* which I had not seen on JSP before the fire. In 1978 it was uncommon, but by 1980 it was ubiquitous over the summit.

Many species were locally important after the fire in adjacent portions of the burn but were rare on the study areas, e.g., *Argemone munita, Calystegia occidentalis, Cordylanthus rigidus, Dicentra chrysantha, Helianthemum scoparium,* and *Hulsea heterochroma. Phacelia brachyloba* and *P. grisea* are annuals that commonly respond to fire. Both were abundant in adjacent chaparral. *Phacelia brachyloba* was rare on the forest plots; *P. grisea* became common at CR-4 (Table 3).

Although Howitt and Howell (1964) reported *Eriogonum spergulinum* subsp. *reddingianum* on JSP, I could not find this montane disjunct on the peak prior to the fire. In 1978, however, a population less than 50 m in diameter grew on the summit near the plots. The following season this population declined to a few plants in the midst of dense *Gayophytum heterozygum.*

Ryegrass dominance. The JSP plots were not aerially seeded, and few seeds drifted in from adjacent seeding. In 1980 I saw no *Lolium* on the plots and few plants near the study area. The PR plots were not officially seeded either, but accidental seeding produced a sparse crop in 1978. This built up to 30 percent *Lolium* cover in 1980. Some nearby pine stands on PR had nearly 100 percent *Lolium* cover by 1979.

All of Chews Ridge was sown with about 400 *Lolium* seeds/m^2. This seeding produced a crop that Conrad (1979) described as generally "outstanding." Maximum height of this crop in 1978 was 120 cm, and in places I had difficulty walking through the grass.

The CR-1 plots were representative of the denser grass stands. The first season 24 percent of this area remained bare, but the bare spots were mainly deep ash beds. The vegetated ground had dense *Lolium* about a meter tall; 237 out of 240 quadrats contained *Lolium.* By the second season bare ground dropped to 4 percent, and *Lolium* had 87 percent cover. On 34 percent of the quadrats in 1979 I could find no species except *Lolium. Lolium* maintained significant live cover the third season, but the plants were shorter and more spindly. By this time large piles of *Lolium* mulch had accumulated (Fig. 1).

The CR-3,4 areas had *Lolium* density and cover approaching CR-1 levels (Fig. 1). Of the areas sampled, the most vigorous growth of *Lolium* was at CR-4.

At CR-2 *Lolium* density was low and cover was sparse the first year. Seventy-four percent of the soil remained bare; only half the quadrats contained any *Lolium. Lolium* cover at CR-2 never reached the levels of the other plots on Chews Ridge (Fig. 1).

Shrub regeneration. Pine forests on the study areas have periodically
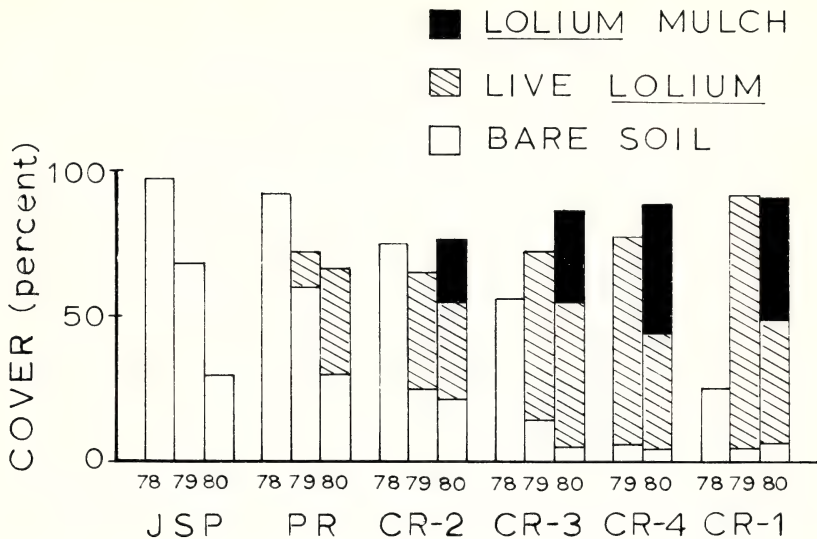
Fig. 1. Ground cover estimates of bare soil for three postfire seasons, *Lolium multiflorum* live cover (plus minor amounts of mulch) for second and third seasons, and accumulated *Lolium* mulch for third season.

supported shrub layers of non-sprouting species that start after fires. The most recent fires that could have regenerated these shrub layers on the study areas were: JSP, 1901; PR, 1916; CR-1,2,4, 1928; CR-3, unknown. Shrubs resulting from those fires had nearly disappeared from the forests by 1977. The new shrub layers have hardwood tree sprouts, scattered sprouts of arborescent shrubs such as *Rhamnus californica*, and abundant seedlings of three *Ceanothus* species. Only a small number of *Arctostaphylos glandulosa* sprouts and seedlings are present.

The most widespread postfire shrub is *C. integerrimus* (Table 4). At JSP *C. integerrimus* reached 40 percent cover despite the loss of half the initial seedlings (Table 4). The first season these seedlings had essentially no herb competition. Seedling mortality was most evident where the seedlings were clumped together.

At CR-3 not all the initial *C. integerrimus* seedlings could be counted because of the dense grass cover, and total seedling mortality was probably higher than shown in Table 4. By 1980 only a sparse cover of slow growing seedlings remained.

The most vigorous *C. integerrimus* shrubs were at CR-4. During the winter of 1980–1981 rodents killed about 10 percent of these healthy shrubs. *Thomomys bottae* (pocket gophers) ate roots, and *Microtus californicus* (California voles) girdled stems.

Ceanothus integerrimus was rare at PR, but *C. papillosus,* which

TABLE 4. TOTAL SHRUB COVER, *Ceanothus* SEEDLING COVER, AND *Ceanothus* SEEDLING DENSITY. Total shrub cover includes shrub seedlings, shrub sprouts, and hardwood tree sprouts in shrub layer; density given in parentheses; "+" indicates seedlings on plot but not on quadrats.

Study area	Total cover % 1980	*Ceanothus* cover % 1980 (*Ceanothus* density, no./m² 1978, 1980)		
		C. integerrimus	*C. sorediatus*	*C. papillosus*
JSP	43	40 (13.1, 6.7)		0 (+, 0)
PR	48	<1 (0.3, 0.3)	2 (0.1, 0.1)	32 (3.1, 1.2)
CR-1	16		5 (5.3, 0.5)	
CR-2	31	24 (2.3, 1.2)		
CR-3	27	13 (1.6, 0.6)		
CR-4	68	38 (?, 2.7)		

typically grows in chaparral, was the dominant shrub (Table 4). *Arctostaphylos* sprouts averaged 5 percent cover, the highest on any study area. At CR-1 *C. integerrimus* was also rare; at this lowest elevation study area *C. sorediatus* was important (Table 4). By 1980 this area had the lowest shrub cover and the lowest seedling density (Table 4).

Pine regeneration. The pines on JSP burned on 8 August 1977. This was a relatively early date to expect high seed viability in *P. lambertiana* cones (Krugman 1966). If the seeds did not come from scorched cones on plot trees, the seeds must have dispersed up to 100 m from live trees to reach some plots. The heavier *P. coulteri* seeds would disperse far less, and some *P. coulteri* seeds probably came from pre-1977 cones on burned trees on the plots. This species can store seeds in partially closed cones for several years (Minnich 1980). The viability of *P. coulteri* seeds in early August and any possible "ripening" effect in burned cones is not known.

Regardless of where the seeds came from at JSP, in 1980 *P. lambertiana* had only 415 seedlings/ha to replace 651 burned trees/ha; *P. coulteri* had 2760 seedlings/ha to replace 98 trees/ha (Table 5). The *P. coulteri* seedlings were also two to three times taller than the *P. lambertiana* seedlings. In neither pine did a significant number of seeds germinate after 1978.

The PR *P. ponderosa* trees burned a week before the JSP pines, and seeds falling from the dead pines at PR in early September had shriveled gametophytes that did not appear viable. Only 120 pine

TABLE 5. COMPARISON OF PREFIRE *Pinus* AND *Calocedrus* TREE DENSITIES IN CROWNFIRE-KILLED STANDS WITH SEEDLING DENSITIES THREE SEASONS AFTER THE FIRE. Density given in parentheses; an * indicates a few trees were present in the general area but were not on the plots.

Study area	Tree (seedling) density, no./ha	Percent tree (seedling) density			
		P. co.	*P. la.*	*P. po.*	*C. de.*
JSP	749	13	87		0
	(3178)	(87)	(13)		(<1)
PR	413	*		92	8
	(200)	(0)		(94)	(6)
CR-1	857	100			
	(7)	(100)			
CR-2	523	100			
	(310)	(100)			
CR-3	243	100		*	
	(90)	(100)		(0)	
CR-4	270	100			
	(1685)	(100)			

seedlings/ha could be found in 1978. A larger number started in 1979, but only 40 percent survived. The seeds that produced these seedlings must have come from live trees 20–100 m away from the plots. By 1980 PR had only 188 *P. ponderosa* seedlings/ha to replace 379 trees/ha (Table 5). *Calocedrus decurrens* seedlings were rare.

The *P. coulteri* study areas showed great variability in pine regeneration. On CR-1 plots 857 trees/ha were killed, and only 7 pine seedlings/ha survived in 1980 (Table 5). *Lolium* was too dense for all the initial pine seedlings to be counted, but the scarcity of surviving seedlings was clear. Since no *P. coulteri* trees survived within 500 m of this study area, additional seeds can not disperse into the area to supplement the rare 1978 seedlings. The CR-4 plots illustrate the other regeneration extreme. For each *P. coulteri* tree killed, six vigorous seedlings were growing after three years (Table 5). In 1980 some pine seedlings were 105 cm tall and already overtopping the *Ceanothus* shrub layer. Several dozen pine trees survived near the plots, and additional seeds might disperse onto the plots. However, almost no pine seedlings did start in 1979 or 1980.

DISCUSSION

Keeley et al. (1981) discussed southern California chaparral studies that show seeded *Lolium* growing at the expense of native herbs. In their own San Diego County survey, Keeley et al. found seeded burns with up to 28 percent *Lolium* cover. The dominance of *Lolium* on the Chews Ridge pine stands, however, greatly exceeded such chaparral

results. *Lolium* cover, up to 87 percent at CR-1, greatly reduced the space and resources available for native herbs. Unfortunately, without any unseeded control areas available on Chews Ridge this *Lolium* influence could not be quantified.

Lolium competition may not have prevented any native herbs from growing on the Chews Ridge plots, at least in low densities. But some species might not appear after the next fire because of unusually low dormant seed reserves returned to the soil by the few unhealthy herbs in the *Lolium* cover. If *Lolium* competition comparable to the CR-1,3,4 areas had occurred at JSP, the tiny *Eriogonum spergulinum* population would have been threatened.

The Chews Ridge area with the richest flora (CR-2) had the steepest slopes, the greatest erosion, and the least *Lolium* cover. Steep slopes increased the erosion, and the resulting soil loss reduced the supply of *Lolium* seeds. This soil loss also reduced the supply of native herb seeds. Yet, a variety of native species did start the first season. Proximity to a grassland seed source probably contributed to the higher species richness on these plots.

Conrad (1979) emphasized that high shrub seedling mortality, particularly in *Ceanothus,* was associated with *Lolium* cover. Data from two Chews Ridge areas support this generality. At CR-1 the 10-fold reduction in *C. sorediatus* seedling density must have been partly caused by *Lolium* competition in a relatively dry forest habitat. Low shrub seedling density and slow growth were also associated with high *Lolium* cover at CR-3. If *Ceanothus* understories are a desirable feature in the development of pine stands after fire in this landscape, *Lolium* seeding had a negative influence on the CR-1,3 plots.

In contrast, the results at CR-4 showed that *Ceanothus* can regenerate successfully in *Lolium* under some conditions. By 1980 these plots averaged 2.7 shrubs/m^2, and the shrubs were taller and more vigorous than at any other area—despite growing in dense grass. This area had a few seepage spots, and favorable soil moisture conditions may have contributed to high survival and rapid growth of *Ceanothus* seedlings. The only obvious threat to this developing shrub layer was heavy rodent browsing. *Lolium* provided a temporary grassland cover within the forest habitat. This unnatural grass cover permitted pocket gophers and voles to reach population highs. These browsers may locally thin the shrub layers until the rodents decline to more normal levels.

Successful pine regeneration was generally associated with successful *Ceanothus* regeneration. An abundance of pine seedlings started at JSP in the *C. integerrimus* layer. But there was a significant shift from *P. lambertiana* dominance in the prefire forest to *P. coulteri* dominance in the postfire seedling crop. In terms of seedling growth *P. coulteri* is clearly superior. The silvicultural literature suggests that with time *P. lambertiana* should surpass *P. coulteri* in height. For

several decades, however, *P. lambertiana* will be scattered within *P. coulteri* thickets.

At CR-4 there were more than enough healthy *P. coulteri* seedlings to replace the burned stand. At CR-2,3 not enough pine seedlings survived, and the new stands will be more open than their predecessors. This trend in declining *P. coulteri* regeneration ended with CR-1 where the stand may not be replaced. Until the seedlings now on the area reach cone bearing age, this stand is endangered. Another burn within the next decade would eliminate the stand.

By 1980 the PR plots did not have sufficient seedlings to replace the burned *P. ponderosa* trees. If no additional seedlings start, the new pine stand will have less than half the density of the old stand. The PR plots do have many live seed trees nearby, and there may be further seedling recruitment.

Seeded *Lolium* seldom produces enough fuel on chaparral burns to support an early reburn. However, the growth of *Lolium* on the Marble-Cone burn was so successful that fire became a real hazard. By July 1978 the dry grass provided continuous flash fuels that could have carried fire over significant portions of the burn. This flash fuel accumulation was greater the following two summers. A summer fire on the CR-1,3 areas would have killed pine and shrub seedlings with no new seed supplies yet available. A fire in the other areas would not have been as uniformly damaging. Native herb layers at JSP and PR would not have carried a destructive surface fire during this period.

Results of this pine forest study support those of many chaparral studies; significant soil eroded before *Lolium* cover developed; *Lolium* retarded growth of native herbs and increased shrub seedling mortality. In this case *Lolium* also increased pine seedling mortality and created a high hazard for an early reburn.

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FLORISTIC AFFINITIES OF THE HIGH
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ABSTRACT

The flora of the high montane, subalpine and alpine region of the Sierra Nevada of California is believed to include four derivation categories: Old Cordilleran, Circumboreal, Lowland Californian, and Great Basin Desert. Although these elements have mingled to the extent that species belonging to all four of them can be associated in the same community, nevertheless, they differ from each other with respect to the proportion of Sierran endemics that they have contributed, as well as with respect to growth habits and ecological preferences. The present review is regarded as a preliminary effort to provide a new tool for analyzing the phytogeographic, floristic, and ecological characteristics of the flora.

With great pleasure, I dedicate this paper to Jack Major. I have obtained the familiarity with the Sierran flora that has enabled me to prepare it in large part during excursions with him and his students, accompanied by lively and absorbing discussions of the problems involved. His scholarly paper on a very similar topic (Major and Taylor 1977) has been a valuable source for the present survey.

When an evolutionary botanist reviews the flora of a particular region, among the first questions that come to mind are: How did all the plant species get there? Did they come in from elsewhere, and if so, from how many directions? To what extent has the flora been enriched by the evolution of species in situ? What factors in the past history of the area have contributed to the present situation? Such questions can most easily be answered with respect to a region that is relatively homogenous and clearly defined. California's Sierra Nevada is such a region.

Four investigations of the Sierran flora have emphasized floristic affinities: those of Smiley (1921), Sharsmith (1940), Chabot and Billings (1972), and Major and Taylor (1977). The last three have confined their attention to the alpine and subalpine zones, leaving out the high montane coniferous forests. The difficulty with this approach, as Major and Taylor recognize, is that many species highly characteristic of the subalpine and even the alpine zone descend commonly to open communities of the montane zone, so that in many parts of the Sierra the distinction between high montane, subalpine, and alpine zones is hard to make. The irregularity of timberline in these mountains, as compared with its much more regular and even occurrence in many

other mountain ranges, is discussed carefully by Major and Taylor. For these reasons, I have selected as my floristic region the parts of the Sierra designated as upper montane and subalpine by Rundel et al. (1977) plus those regarded as alpine by Major and Taylor (1977). The region included, therefore, is almost the same as that included by Smiley (1921), except that I have set its northern boundary just south of Donner Summit, north of which large interruptions exist in the subalpine flora of the Sierran crest.

METHOD OF APPROACH

I have made a tentative arrangement as to probable origin of all of the species of vascular plants found in the three regions: upper montane, subalpine, and alpine. In the delimitation and nomenclature of species I have followed Munz (1959, 1968). The decision as to which species to include in the entire area was made for many species on the basis of personal observations. For many others, the statements of elevation in Munz (1959) were used as a guide. My experience indicates that in the northern Sierra, near Lake Tahoe, the boundary between the Lower Montane and Upper Montane Forests is about 2050 m. At the southern end of the Sierra, near Mineral King, it is about 2450 m (Smiley 1921). Consequently, I include only those species that in Munz (1959) are listed as occurring above this limit or that I have seen in the northern Sierra above 2050 m. Species that are found in the northern Sierra above 2600 m and that in the southern Sierra are listed as occurring above 2900 m are listed as occurring in the subalpine zone, whereas those occurring in the northern Sierra above 3150 m and in the southern Sierra above 3300 m were regarded as truly alpine.

Separation of the species into four principal categories of geographic origin is more difficult but is the most logical and informative classification that can be made on the basis of current knowledge. It differs in several respects from those proposed by previous authors. The ten classes recognized by Smiley (1921) are very difficult to define upon the basis of modern knowledge of the western flora and cannot be related to those recognized in the present paper. I find almost equal difficulty with the nine recognized by Sharsmith (1940). His Pacific Cordilleran plus Rocky Mountain and Sierran Cordilleran correspond roughly to Old Western Cordilleran as recognized in this paper, except that some species of the latter category are placed here in the category of "Great Basin Affinities." His categories Boreal, Arctic-alpine and Beringian-Cordilleran correspond to Circumboreal as here recognized, whereas Widespread Mediterranean is like Lowland Californian. Great Basin is designated as such in both Sharsmith's and the present treatment. The three categories recognized by Chabot and Billings (1972) are much more similar to those presented here. Both of us recognize Western Cordilleran and Widespread Arctic-alpine (Circumboreal)

TABLE 1.   SPECIES WHOSE GEOGRAPHIC AFFINITY IS IN DOUBT.

Species	Present classification	Alternative
Leucothoe davisiae Torr.	Western Cordilleran	Boreal-Holarctic
Epilobium spp.	Western Cordilleran	Boreal-Holarctic
Paeonia brownii Dougl.	Western Cordilleran	Lowland Californian
Primula suffrutescens Gray	Western Cordilleran	Boreal-Holarctic
Sarcodes sanguinea Torr.	Western Cordilleran	Boreal-Holarctic
Horkelia tularensis (Howell) Munz	Western Cordilleran	Lowland Californian
Potentilla glandulosa Lindl. subsp. *nevadensis* (Wats.) Keck	Western Cordilleran	Lowland Californian
Castilleja miniata Dougl.	Western Cordilleran	Lowland Californian
Antennaria dimorpha (Nutt.) T. & G.	Great Basin	Western Cordilleran
Cirsium andersonii (Gray) Petrak	Great Basin	Western Cordilleran
Anelsonia eurycarpa (Gray) Macbr. & Payson	Great Basin	Western Cordilleran
Sisyrinchium idahoense Bickn.	Great Basin	Western Cordilleran

with similar limits; their third category, Endemic Western corresponds to Lowland Californian plus Great Basin as here recognized. Major and Taylor (1977) group a few dominant species with respect to their present distribution but make no attempt to speculate about their origins.

I arrived at the four categories presented below by placing a varying emphasis upon the distributional ranges of the species themselves, and those of species not found in the area under consideration that are believed to be the closest relatives of the species considered. When placing Sierran species that are endemic or have only a limited distribution outside the area, emphasis was placed upon the distribution of near relatives. On the other hand, with respect to species that occur chiefly in other regions, and particularly those that enter the upper montane region from below, the distribution of the species itself was given weight equal to or greater than that of related species.

The estimates of relationship are to a large extent subjective. Principal emphasis was placed upon morphological characters as outlined in taxonomic keys and descriptions. Chromosome numbers were considered when available, particularly if the Sierran species was a polyploid having obvious diploid ancestors in other regions. The principal sources of keys and descriptions were Munz (1959), Abrams and Ferris (1923–1960), Hitchcock and Cronquist (1973), and Harrington (1954). For *Carex,* the standard monographs of Kükenthal (1909) and Mackenzie (1940) were consulted, while for *Juncus,* Buchenau's (1906) monograph was essential. For information on the Circumboreal category, Hultén's (1941–1950) Flora of Alaska was consulted, as well as those of the USSR (Komarov 1934) and Central Europe (Hegi 1936).

TABLE 2. DISTRIBUTION OF SPECIES INTO CATEGORIES OF DERIVATION.

	Old Cordilleran	Circumboreal	Lowland California	Great Basin-Desert	Total
Entire flora	342 (39%)	227 (26%)	168 (19%)	139 (16%)	876
Alpine zone only	103 (50%)	58 (28%)	15 (7%)	31 (15%)	207

In spite of all efforts, some species proved difficult to assign to one of the four categories, and their position on the lists compiled is admittedly somewhat arbitrary. Some of the most puzzling are listed in Table 1.

The complete lists are too long to be included in this contribution, but will be supplied upon request.

RESULTS

The four sources. Table 2 lists the assignment made to each of the four categories of derivation for the 876 species recognized in the high montane flora as a whole, and the 207 species found in the alpine zone, above timberline. The reasons for recognizing these four categories are given below.

1. *Old Cordilleran* (OC). Compared with other mountain ranges in western North America, the Sierra Nevada is relatively young. Most of the uplift that elevated the range to its present height took place during the Pleistocene (Axelrod 1957, 1962; Bateman and Wahrhaftig 1966). Farther east, in the Rocky Mountain region, ranges high enough to support a subalpine and even an alpine biota have existed since the middle of the Tertiary (Axelrod 1968). Plant species adapted to these high mountains must have evolved as they were being elevated. Some species were preadapted to occupation of high montane, subalpine, and alpine zones as these zones became available following or during Sierran uplift. During the Pleistocene, when a glacial climate prevailed throughout the Sierra Nevada, the Cascade Mountains to the north must have contained much larger areas suitable to high montane, subalpine, and alpine species than they do at present. Migration southward along the Sierran Cascade axis is, therefore, the most probable immediate source of the Old Cordilleran species. Nevertheless, the Basin Ranges to the east most probably contributed some of these species. During the height of the Pleistocene pluvial epoch, when the valleys of the Great Basin region were filled with the waters of Lakes Bonneville, Lahontan, and others, the summit ridges of the mountain ranges that rose above the lake waters must have supported a much more mesic flora than they do now. The westernmost of these ranges, the White Mountains, is only 50 km from the Sierra, and the maximum distance between two neighboring ones of these parallel, north-south

oriented ranges is only 80 km. Consequently seed transport by birds or other vectors of species having easily dispersed seeds is highly probable. There is no way of saying which of these two avenues of entry was the principal one.

The 342 species assigned to the Old Cordilleran category either occur themselves in the Rocky Mountains or have close relatives there. The principal criterion determining their placement in this category rather than the Circumboreal group was the presence in North America of the majority of their relatives. Examples are *Hackelia, Agoseris, Antennaria, Arnica, Erigeron,* some sections of *Senecio, Arabis, Polemonium, Eriogonum* subgenus *Oligogonum, Lewisia,* some sections of *Penstemon,* and *Carex* sect. *Ovales.* As expected, this is the largest of the four categories, containing 39 percent of the total 876 species, and 50 percent of the 207 species found in the alpine region (Table 2).

2. *Circumboreal* (C). This category includes some species that occur at low elevations in the Pacific Northwest, and a few that occur or have relatives in the eastern United States. Some of them occur or have relatives in the Rocky Mountains, but they are peripheral to and do not have centers of diversity in that region. Examples are *Lonicera, Sambucus, Stellaria,* various *Ericaceae, Gentiana, Polygonum, Pyrola, Aconitum, Thalictrum, Amelanchier, Potentilla, Sorbus, Salix, Saxifraga, Veronica, Carex* except sect. *Ovales, Scirpus, Luzula,* and *Habenaria* (sens. lat.).

This is the second largest category, containing 227 species, 26 percent of the total, and 28 percent of the alpine species.

3. *Lowland Cismontane California* (LC). The 168 species that either originated in or are most closely related to species found in Lowland California constitute 19 percent of the total, but are much more poorly represented (7 percent) in the alpine zone than are any of the other categories. The great majority of them (81 percent) are found chiefly at middle or low altitudes, and enter the high montane zone, plus more rarely the subalpine zone, in warm, sunny, and dry places. They include such familiar species as *Silene verecunda, Madia elegans, M. gracilis, Arctostaphylos patula, Nemophila maculata, Lotus purshianus, Clarkia rhomboidea, Collomia grandiflora, Linanthus ciliatus, Eriogonum nudum, Claytonia (Montia) perfoliata, Ranunculus occidentalis, Ribes roezlii, Orthocarpus hispidus, Solanum xantii, Viola purpurea, Brodiaea (Triteleia) hyacinthina, Danthonia californica,* and *Habenaria elegans.*

4. *Great Basin.* The final category, species that have their closest affinities to the Great Basin and desert floras, contains the smallest number (139) of species, 16 percent of the total and 15 percent of those found in the alpine zone. The majority of the species occur also in the arid mid-montane zone on the east side of the Sierra, and many extend far into the pinyon-juniper belt of the Basin Ranges. Among the commonest representatives of this group are species of *Cryptantha, Arte-*

misia, Chrysothamnus, Machaeranthera, Descurainea, Astragalus, Phlox, Eriogonum, Ivesia, Galium, Lomatium, and annual species of *Mimulus.*

Endemism and speciation in the High Sierra Nevada. Compared with other parts of California, the High Sierra has not been an important center of speciation (Stebbins and Major 1965). Nevertheless, of the 876 species here recognized as occurring in the high montane to alpine zones, 119 or 13.5 percent are endemic to the High Sierra, while 65 percent extend beyond it only to the corresponding zones in the transverse ranges of southern California and/or the mountains of northwestern California, western Nevada and southern Oregon.

These endemics are a highly heterogeneous group, belonging to 87 genera and 31 families. The great majority of them are clearly related to more widespread species that occur outside the Sierra Nevada. This condition exists for all of the 15 endemic species of *Lupinus* and for 9 of the 11 endemic species of *Carex.*

The genus *Carex* illustrates in a striking fashion the degree to which the present flora of the High Sierra is a result of immigration rather than speciation in situ. Of the 72 species of *Carex* found in the High Sierra, at least 66, or 92 percent, entered the area without recognizable change, or underwent only a single event of speciation. More extensive speciation in this genus has been confined to the single large and complex section *Ovales.*

The genus *Lupinus* ranks first in number of endemics. The status of described species in this genus is obscure, and several of the 15 "species" endemic to the High Sierra and neighboring ranges may deserve recognition as no higher than subspecies or varieties. Until the Sierran species of *Lupinus* have been studied carefully in various ways, the question remains open as to whether or not the High Sierra has been a center of speciation for this large genus.

For four genera, the High Sierra appears to have been at least a minor center of speciation. Four of the six endemic species of *Castilleja* appear to be as closely related to each other as to species from the surrounding areas. The same could be true of the five species of *Draba,* although this genus needs to be studied much more carefully before the origin of its species can be deduced.

With respect to two genera, *Ivesia* and *Hackelia,* the High Sierra has definitely been a center of speciation. Of the 23 species in the genus *Ivesia,* nine occur in the High Sierra, seven of which are endemic. Of the remaining eight Californian species, two occur in the mountains of southern California, two in the Mohave Desert-Great Basin region to the east and south of the High Sierra, and the other four occur northward and northwest of the main Sierran axis. The High Sierra, therefore, is the center of distribution for this genus.

Of considerable interest is the distribution of endemics within the

TABLE 3.   RELATIVE FREQUENCY OF GROWTH HABITS AMONG CATEGORIES OF DERIVATION.

	Old Cordilleran	Circum- boreal	Lowland California	Great Basin- Desert	Total
Woody	21	46	11	14	92
Herbaceous perennial	312	174	104	103	693
Annual	9	7	53	22	91
	342	227	168	139	876

Sierran area. The range as a whole can be divided conveniently into two parts; north and south of Yosemite National Park. The northern half has relatively few summits that are truly alpine, but its high montane and subalpine areas are more mesic, as is evident from the greater abundance of two species of conifers, *Pinus monticola* and especially *Tsuga mertensiana*. Of the 119 endemic species, 45 occur throughout the range, 20 are endemic to the northern half, and 54 are endemic to the southern half. Among those that are endemic to the Sierra plus neighboring ranges, 55 occur throughout the Sierra, 8 are confined to the northern half and 2 to the southern half.

The larger number of Sierran endemics that occur only from Yosemite southward is due partly to the greater relief and consequently greater ecological diversity of the southern area. An additional factor is, most probably, the relatively light glaciation, and in many areas complete absence of glaciation, in the high ridges and plateaus of the southern area. This permitted the survival throughout the Pleistocene of a much larger number of subalpine and alpine species than was possible in the northern area.

Growth habit and derivation. With respect to growth habit, I have divided the species into three categories; woody (trees and shrubs); perennial herbs (including perennial grasses, sedges and ferns), and annuals (Table 3). Perennial herbs formed the majority (79 percent) of the total flora, whereas the percent of woody species (11 percent) is about equal to that of annuals (10 percent).

Among the categories with respect to derivation, the Old Cordilleran contains the highest percentage of perennial herbs (92 percent) and the lowest of woody species and annuals. The Circumboreal category, with 20 percent, has the highest proportion of woody species, due chiefly to numerous species of *Salix*. The proportions of woody species among the Lowland California and Great Basin elements are similar to those in the flora as a whole.

As might be expected, the species of Old Cordilleran and Circumboreal include very few annuals (2–3 percent), whereas the Great Ba-

TABLE 4. MOISTURE REQUIREMENTS AMONG CATEGORIES OF DERIVATION.

Mesic grade	Old Cordilleran	Circumbo- real	Lowland California	Great Basin- Desert	Total
Continuously moist	63	114	21	1	199
Occasionally dry	75	71	38	9	193
Mostly dry	82	28	46	10	166
Continuously dry	122	14	63	119	318
Total	342	227	168	139	876

sin-Desert element, with 15 percent annuals and particularly the lowland California element with 32 percent annuals, have an excess. These differences are entirely to be expected. Although statistics have not been compiled, it is likely that the floras of the Lowland California and Great Basin Desert regions contain percentages of annuals that are not very different from those in the samples of these floras that have reached the High Sierra.

Distribution of derivation categories with respect to moisture requirement. Among the diverse habitats found in the High Sierra, four degrees of moisture availability were recognized: (1) Moisture continuously available, as in wet meadows and lake and stream margins; (2) Generally moist, but with dry periods, as in the drier meadows, moist forests, and intermittent streams; (3) Generally dry, but the drought ameliorated by shade or abundant moisture during the period of snow melt; e.g., in dry forests, deep rock crevices, or rock basins; (4) Essentially xeric, such as dry rocky areas, sandy or gravelly flats, and ridge crests. The distribution into these four moisture grades of the four derivation categories is shown in Table 4. That of the species assigned to the Old Cordilleran category does not differ significantly from that of the flora as a whole. The Circumboreal species are predominant in the moister habitats; those with Lowland California affinities are more frequently adapted to the drier habitats, whereas the

TABLE 5. DISTRIBUTION OF SPECIES ACCORDING TO DERIVATION IN FOUR TYPES OF COMMUNITIES IN THE VICINITY OF WRIGHT'S LAKE.

	OC	CB	LC
Moist riparian forest	18	23	4
Dry forest	27	10	9
Open moraines	23	9	18
Dry rock crevices	29	8	17
Total	97	50	48

great majority of species having Great Basin affinities (86 percent) occur in the most xeric habitats. This distribution would be expected on the assumption that the great majority of the species that have entered the Sierra in relatively recent times either have not changed at all since they became part of the flora, or have undergone minimal evolution.

A preliminary study of individual communities in particular habitats of the region near Wright's Lake (2150 m) in the High Montane Zone of Eldorado County (summarized in Table 5) supports the summation presented in Table 4. Four kinds of habitats were selected: moist forests of the lake margin; dry forests; moraines in open areas having sandy or gravelly soil; and dry rock crevices. Because the number of species (6) in the Wright's Lake area having Great Basin affinities is too small to be considered, only the other three categories of derivation were included.

Table 5 presents a brief summary of the data, which will be presented in full in another publication. It reinforces the data summarized in Table 4, showing that the plants of circumboreal origin are the most mesic, and those of Lowland California and Great Basin origin are the most xeric. In the two drier habitats, species assigned to all four of the categories of derivation, including one or two having Great Basin affinities, existed side by side in the same plant community. At least in the High Sierra, modern plant communities contain elements that are derived from several different sources.

General Discussion and Conclusions

This contribution must be regarded as a preliminary rather than a final analysis. Nevertheless, I doubt that further studies will affect the general conclusions reached here. These are as follows:

(1) The largest number of species has evolved in association with mountain building and other effects (e.g., increasing climatic drought, particularly in summer) that have occurred in the western Cordillera during the Tertiary and Quaternary Periods.

(2) During the Pleistocene and recent epochs, the Sierra has been invaded by plants from three very different sources: (a) Montane and moist forested regions to the northward; (b) Foothills and lower montane regions to the west of the range; (c) Arid steppes and desert mountains to the east and southeast of the range. Some of these species of disparate origin have become closely associated with each other in the same plant community.

(3) Nevertheless, most of these relatively recent immigrants have adjusted themselves to Sierran habitats with relatively little evolutionary change. Exceptions to this rule, in the form of endemic species that are related to elements other than the Old Cordilleran, exist only in a few genera, such as *Ivesia* and *Astragalus*.

Using the four derivation categories as a phytogeographic, floristic, and ecological foundation, and following more careful investigations of the species concerned, a number of problems of general interest might be attacked. Among them are:

(1) In the colonization of a recent, relatively isolated mountain range, what are the relative roles of long distance dispersal and more continuous migration under the influence of different past climates?

(2) Are recent immigrants, such as LC and GB, likely to be more abundant, less abundant or about equally as abundant as older inhabitants? Are such differences correlated with growth habit or any other characteristics of the plants themselves?

(3) Are the more recent immigrants more or less randomly distributed according to habitat, or do they tend to occupy habitats that on the basis of geological evidence seem to have been formed recently?

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A GRADIENT PERSPECTIVE ON THE VEGETATION OF SEQUOIA NATIONAL PARK, CALIFORNIA

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ABSTRACT

The results of detrended correspondence analysis indicate that elevation is well correlated with vegetation differences and that topographic-moisture conditions are also important. Gradients of these two environmental factors are used as axes for plotting the distribution of 15 general vegetation types. Superimposed on the resulting vegetation chart are isolines of tree density, basal area, tree cover, woody plant richness, and woody plant diversity ($1/C$). It is concluded that the vegetation of the park is better considered as a series of continua rather than as discrete units. This perspective produces suggestions for future research and supports expanded use of gradient analysis techniques in studies of the vegetation of the Sierra Nevada.

Surprisingly little has been published on Sierra Nevada vegetation despite its economic and ecologic importance. Nearly all vegetation studies, as well as other ecological works, have treated the vegetation as divisible into discrete units and therefore classifiable into general categories such as those proposed by Munz (1959) for all of California. Because classification systems inherently emphasize discontinuities in vegetation, even detailed systems do not accurately represent field conditions where vegetation continua occur. Gradient analysis techniques can be used to illustrate vegetation continua (and discontinua). Thus, examination of vegetation data by gradient analysis can complement the classification approach (Mueller-Dombois and Ellenberg 1974, Whittaker 1975).

Because gradient analysis methodology seldom has been applied to data on Sierran vegetation, the purpose of this study is to develop a gradient perspective on the vegetation of Sequoia National Park in the southern Sierra Nevada.

METHODS

I utilized two kinds of data on woody species: (1) presence-absence data compiled from surveys of 108 stands of variable size and (2) cover, density, and basal area data (with an importance percentage calculated by summing relative values and dividing by 3) obtained from 92 belt transects (each 2 × 50 m). These data were collected in 1969 as part of a study on vegetation changes within the park (Vankat 1970). The stand surveys and belt transects were located in units of

relatively homogeneous vegetation and were scattered throughout much of the park in order to represent the variation within general vegetation types. Elevation, slope aspect and inclination, and recent land-use history data are available for the sites sampled. Vankat and Major (1978) presented other details about the field sampling methodology. No samples of young seral stages were used in the present study.

I analyzed separately the data from the stand surveys and belt transects, using the detrended correspondence analysis (DCA) program DECORANA (Hill 1979). Because this type of indirect gradient analysis is not subject to some of the intersample-distance distortions that occur with other ordination methods, it is considered the best such method of ordinating vegetation data (Hill and Gauch 1980). The results of these analyses led me to arrange the stand survey and belt transect samples on graphs that had elevation and topographic-moisture gradients as axes. Elevation within the park is from 390 to 4419 m. I defined a 10-unit topographic-moisture gradient from moist to dry. I considered sites near streams to be at the moist extreme; sites with slopes of northeast, north, northwest, east, west, southeast, south, and southwest exposures to be at intermediate and progressively drier positions; and sites on ridgetops to be at the dry extreme. I equated arbitrarily one unit with 10° of slope. Therefore, a sample collected on an 18°, southeast-facing slope would be placed at the ninth unit of the topographic-moisture gradient.

To increase the data base for my examination of the distribution of vegetation along the two gradients, I collected data from an unpublished vegetation map (circa 1939; available at the park headquarters). In addition to illustrating the locations of stands of various vegetation units, the map also shows contour lines and a grid of land-survey lines. I used the 12 major land-survey lines as though they were line transects and recorded line-intercept data. Specifically, for each stand of vegetation crossed by these lines, I noted the vegetation type, slope aspect and inclination, and maximum and minimum elevations along the line. This procedure provided 379 vegetation samples that I plotted on the same type of two-dimensional graph described above. The resultant graph, along with others produced with stand survey and belt transect data, provided the basis for a vegetation chart illustrating the distribution of the 15 general vegetation types listed in Table 1. Each division of the chart included the majority but not all of the samples of that vegetation type.

I used belt transect data to calculate tree density (individuals >1 year of age/100 m^2), basal area (m^2/ha), tree cover (percent), woody plant richness (number of species/100 m^2), and diversity ($1/C$ = the number of equally important species required to give the same Simpson's Index observed; after Peet 1974; $C = \Sigma\, p_i{}^2$, where p_i = importance percentage of the ith species). Isolines for these parameters were

TABLE 1. WOODY SPECIES CHARACTERISTIC OF THE 15 VEGETATION TYPES SHOWN ON THE VEGETATION CHART (FIG. 1). BLUE = Blue Oak Woodland, CHAM = Chamise Chaparral, MIXE = Mixed Chaparral, LOWL = Lowland Live Oak Woodland, UPLA = Upland Live Oak Woodland, BLAC = Black Oak Woodland, POND = Ponderosa Pine Forest, WHIT = White Fir Forest, JEFF = Jeffrey Pine Forest, JUNI = Juniper Woodland, REDF = Red Fir Forest, LODG = Lodgepole Pine Forest, SUBA = Subalpine Forest, MEAD = Meadow, and ALPI = Alpine.

Vegetation type

Species	BLUE	CHAM	MIXE	LOWL	UPLA	BLAC	POND	WHIT	JEFF	JUNI	REDF	LODG	SUBA	MEAD	ALPI
Quercus douglasii	X			X		X									
Rhamnus crocea	X			X		X									
Aesculus californica	X		X	X		X									
Quercus wislizenii	X		X	X	X	X									
Arctostaphylos viscida	X	X		X		X	X								
Adenostoma fasciculatum		X													
Ceanothus cuneatus		X													
Dendromecon rigida		X													
Eriodictyon californicum		X	X												
Ceanothus velutinus		X	X												
Fraxinus dipetela		X	X												
Fremontia californica		X	X												
Lonicera interrupta		X	X												
Rhus trilobata var. malacophylla		X	X												
Cercis occidentalis		X	X			X									
Cercocarpus betuloides		X	X			X									
Rhus diversiloba		X	X			X									
Quercus chrysolepis			X		X	X									
Umbellularia californica			X	X	X										
Quercus kelloggii						X	X	X							
Chamaebatia foliolosa							X								
Pinus ponderosa							X								
Pinus lambertiana							X	X							
Abies concolor							X	X	X						
Calocedrus decurrens							X	X	X						
Rosa spithamea							X								
Sequoiadendron giganteum							X								
Arctostaphylos patula									X						
Pinus jeffreyi									X	X					
Artemisia tridentata										X					
Cercocarpus ledifolius										X					
Juniperus occidentalis										X					
Pinus monophylla										X					
Abies magnifica											X				
Pinus contorta											X	X			
Ribes montigenum												X			
Pinus albicaulis													X		
Pinus balfouriana													X		
Pinus monticola													X		
Number of															
stand surveys	7	9	6	7	0	3	11	30	7	0	10	9	9	0	0
belt transects	14	0	0	2	0	3	11	30	5	0	10	9	8	0	0
map interceptions	13	30	9	—45—		—22—		40	12	4	39	52	27	24	25

superimposed on the vegetation chart. Because some of the vegetation types were represented poorly by belt transects, I used estimates based on stand surveys and personal field experience and, in a few cases, data of other researchers (Parsons 1976, Baker et al. 1981) to orient isolines.

Homologous vegetation charts with isolines of vegetation parameters have been produced for other mountainous regions by Whittaker (1956, 1960), Whittaker and Niering (1965), and Peet (1978).

Results and Discussion

Detrended correspondence analysis and the vegetation chart. DCA applied separately to stand survey and belt transect data produced ordination values along first axes that correlated strongly with elevation. For example, for the ordination based on importance percentage data from the belt transects (excluding Subalpine Forest transects because they are unique floristically), the correlation coefficient relating ordination value and elevation was -0.96822 (p $= 0.0001$). DCA produced little separation of samples along other axes, but where samples of different vegetation types had similar first axis ordination values they usually were from different topographic positions. Therefore, I plotted samples according to elevation and topographic-moisture conditions in order to produce the graphs upon which the vegetation chart is based.

Figure 1 is the vegetation chart. Most of the 15 categories of vegetation shown on the chart are widespread and nearly all are readily recognizable in the field. Table 1 lists characteristic species; greater detail has been provided by Vankat (1970), Vankat and Major (1978), Rundel et al. (1977), or other chapters of Barbour and Major (1977). Construction of the chart required simplification of the graphs of samples, because different vegetation types did not occupy discrete areas on the graphs but overlapped greatly. Consequently, the chart must be considered diagrammatic.

Vegetation gradients. I interpret the following as indicating that the vegetation of the park is better considered as a series of continua rather than as discrete units: first, samples of different vegetation types overlap in the DCA ordinations as discussed above; second, many species are characteristic of more than one vegetation type as shown in Table 1 and by Vankat and Major (1978); and third, samples of the same vegetation type vary considerably as shown in field data presented by Vankat (1970). The spacing of dashes in Fig. 1 illustrates diagrammatically the breadth of continua between adjacent vegetation types. In addition, some aspects of the continua are illustrated by plots of parameter isolines on the vegetation chart (Figs. 2, 3). The chart itself and the isoline plots provide good context for discussion of the vegetation of the park from a gradient perspective.
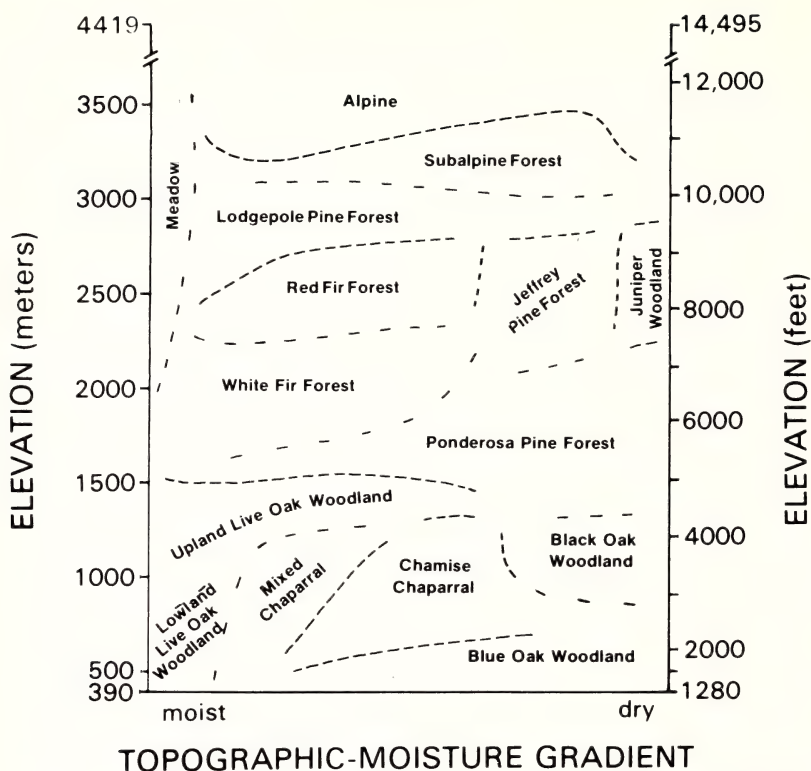
TOPOGRAPHIC-MOISTURE GRADIENT

FIG. 1. Diagrammatic chart illustrating the distribution of general vegetation types according to elevation and topographic-moisture gradients for Sequoia National Park, California. The spacing of dashes reflects the breadth of continua between adjacent vegetation types.

The lowest elevational band in the park is occupied by Lowland Live Oak Woodland in riparian habitats and Blue Oak Woodland elsewhere. Increasing moisture availability is accompanied by substantial and, in some cases, relatively abrupt increases in basal area, tree cover, richness, and diversity. These changes are paralleled by increasing relative importance of both *Aesculus californica* and *Quercus wislizenii* and decreasing importance of *Q. douglasii*. Some of these same shifts in composition and structure have also occurred during succession in Blue Oak Woodland stands on mesic sites not subject to periodic burning (Vankat and Major 1978). In general throughout the park, vegetation changes initiated by twentieth-century fire control and nineteenth-century livestock grazing add another dimension to interpreting vegetation gradients. However, as in this example, these changes frequently result in increasingly mesic condi-
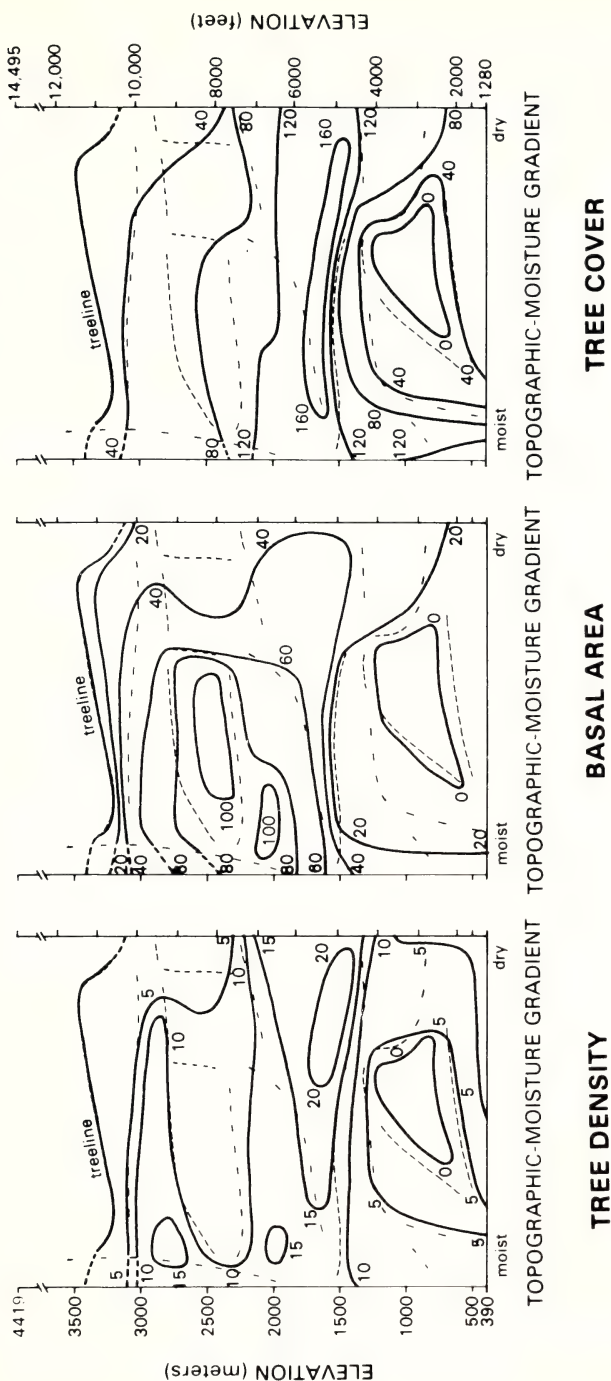
FIG. 2.   Isolines of vegetation structure parameters superimposed on the vegetation chart. Units are tree density—individuals >1 year of age per 100 m²; basal area—m² per hectare; and tree cover—percent.
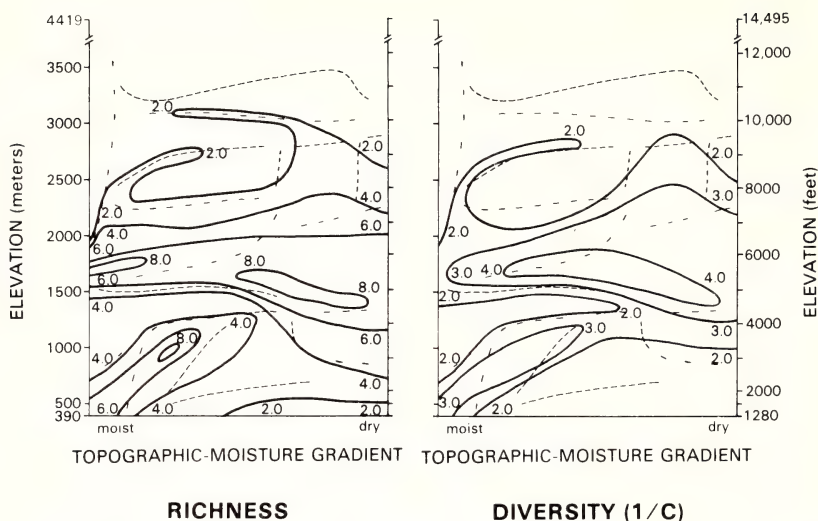
FIG. 3. Isolines of vegetation composition parameters superimposed on the vegetation chart. Units are richness—number of woody species per 100 m² and diversity (1/C)—number of equally important species required to give the same Simpson's Index observed or estimated (after Peet 1974).

tions and may parallel a shift in that direction along the topographic-moisture gradient. Vankat and Major (1978) described successional changes for most of the vegetation types considered here.

With increases in elevation at the moist end of the topographic-moisture gradient (i.e., in riparian habitats), there is a gradual transition in the vegetation from Lowland to Upland Live Oak Woodland. The most obvious vegetation changes include decreases in richness and diversity as *Quercus wislizenii* and *Aesculus californica* are replaced by *Q. chrysolepis* and as the shrub layer decreases in importance. At 1200 to 1500 m, Upland Live Oak Woodland extends across the topographic-moisture gradient toward drier conditions. Basal area and tree cover decrease along this gradient, especially in sites where the steepness of canyon walls retards soil development. The transition with the Ponderosa Pine Forest appears abrupt in many areas, but no quantitative data are available.

With increasing elevation in the midrange of the topographic-moisture gradient, Blue Oak Woodland is replaced relatively abruptly by chaparral vegetation. Although Chamise Chaparral is thought to occur under drier conditions and Mixed Chaparral under the presumably more mesic conditions of north-facing slopes, graphs of samples of these two vegetation types overlapped greatly. This may in part have resulted from inaccurate prediction of soil moisture conditions on the basis of topographic position, because chaparral vegetation has been

reported (for east of San Diego, CA) as having greater soil moisture on south-facing than on north-facing slopes (Ng 1974, see also Krause and Kummerow 1977). Regardless, gradients in vegetation structure between the two chaparral types are steep because of the lack of trees in the former and the relatively high importance of shrubby trees in the latter. Even steeper gradients exist in terms of composition. The Mixed Chaparral is characterized by some of the higher richness and diversity values of any vegetation type in the park, and Chamise Chaparral has relatively low values. Once more, a successional gradient is important in this portion of the vegetation chart. Parsons (1976) documented a decrease in species diversity and increases in total woody cover and dominance of *Adenostoma fasciculatum* in Chamise Chaparral with increased time since burning.

The distribution of Montane Chaparral is not shown on the vegetation chart, because stands are often successional in a coniferous forest sere (Hanes 1977) and because stands are interspersed throughout the chart area of all low- and mid-elevation coniferous forest types. The stands are, however, concentrated in the drier portion of the range of the Ponderosa Pine Forest.

The line that separates Mixed Chaparral and Lowland Live Oak Woodland on the vegetation chart was positioned largely arbitrarily because the two vegetation types intergrade. Baker et al. (1981) combined the two types, along with Upland Live Oak Woodland, as a "mixed-evergreen woodland." Although such terminology usefully unites continuously intergrading vegetation, it does not acknowledge the dominance of shrubs and shrubby trees in Mixed Chaparral as contrasted with the greater size and cover of trees in the Live Oak Woodlands, nor does it acknowledge floristic differences between the Live Oak Woodlands. Griffin (1977) recognized close floristic ties between mesic chaparral and a *Quercus wislizenii*-dominated live oak woodland in the Sierran foothills, but also acknowledged the arborescent growth form of the oaks in the latter. Sawyer et al. (1977) reviewed the mixed hardwood forests of California and described dry ridges with pure stands of *Quercus chrysolepis,* apparently similar to the Upland Live Oak Woodland described by Vankat and Major (1978). Therefore, I have continued to use the terms Mixed Chaparral, Lowland Live Oak Woodland, and Upland Live Oak Woodland for general vegetation types that are recognizable portions of vegetation continua. Perhaps an equivalent name for the Mixed Chaparral is Hane's (1977) "woodland chaparral" (following Horton 1960, for the San Bernardino Mountains of southern California).

At the drier end of the topographic-moisture gradient, increased elevation is accompanied by greater importance of the tree layer and by restriction of Blue Oak Woodland vegetation to the dry (ridgetop) end of the gradient. *Quercus douglasii* decreases in relative importance as *Aesculus californica* and especially *Q. kelloggii* increase. There are

increases in richness and diversity as such species appear and, in the case of *Q. kelloggii,* become increasingly important. Correlated with this elevation gradient is a disturbance gradient; stands sampled at lower elevations were either burned more recently than higher stands or were grazed in the winter by National Park Service pack animals. This may reflect proximity to the park highway rather than biological or environmental differences.

Higher elevation woodland stands are dominated by *Quercus kelloggii.* These Black Oak Woodland stands are restricted largely to ridges; however, some ridges in this elevational range have Chamise Chaparral vegetation. The Black Oak Woodland intergrades with the Blue Oak Woodland at lower elevations and with the *Quercus kelloggii* dominated stands of Ponderosa Pine Forest at higher elevations, but differs from the former in the dominant species and the latter in physiognomy. Griffin (1977) did not recognize a Black Oak Woodland, but Baker et al. (1981) considered it a phase of foothill woodland vegetation.

The transition between Black Oak Woodland and Ponderosa Pine Forest involves some of the more abrupt shifts in structure and composition shown by the isoline plots. The change in physiognomy from woodland to forest is reflected in increases in tree density and cover. The parameters reach very high values in the Ponderosa Pine Forest where fire protection during much of this century has resulted in a very dense understory of small trees (Vankat and Major 1978). However, large trees are scattered and the increase in basal area from the Black Oak Woodland to the Ponderosa Pine Forest is less dramatic. The sparseness of large trees also may be related to the high values of richness and diversity. Whittaker (1975) indicated that environmental heterogeneity produced by open canopies tended to result in high plant diversities, especially in mid- to dry portions of moisture gradients.

Despite relatively abrupt changes between Black Oak Woodland and Ponderosa Pine Forest, floristic gradients can be recognized. Baker et al. (1981) denoted a black oak forest community on north-facing slopes above 1200 m. Vankat and Major (1978) described a variety of plant communities along a xeric to mesic gradient involving both elevation and topographic position: under xeric conditions communities were dominated by mature *Quercus kelloggii* with scattered mature *Pinus ponderosa*; more mesic sites had mature individuals of both species combined with scattered mature *Calocedrus decurrens* and an understory of *C. decurrens* and *P. ponderosa*; and still more mesic sites had all three species as codominants with an understory of *Abies concolor* and *C. decurrens.* Both of these understory species had increased in density where stands were no longer burned periodically.

With increasing elevation and moisture availability, tree density,

tree cover, richness, and diversity peak in the Ponderosa Pine Forest and decline along a gradient into the White Fir Forest. Basal area increases along this gradient as average tree size becomes larger. Accompanying floristic changes include decreases in relative importance of *Quercus kelloggii, Pinus ponderosa,* and *Chamaebatia foliolosa,* as well as shrub cover in general. Increases in importance are shown by *Abies concolor, Calocedrus decurrens,* and *Pinus lambertiana.* Sellers (1970) reported similar findings along a moisture gradient near the Kings River in Kings Canyon National Park (which is adjacent to the northern boundary of Sequoia National Park). The intergradation of the Ponderosa Pine and White Fir Forests makes it difficult to differentiate between them in the mid-range of the elevation and topographic-moisture gradients. In fact, some authorities have combined the two as "yellow pine forest" (e.g., Munz 1959); however, at least for the park region it is better to consider them as two general forest types separated by a broad vegetation continuum. The elimination of periodic burning has contributed to this continuum as *Abies concolor* has increased in density in high-elevation Ponderosa Pine Forest stands (Vankat and Major 1978).

Toward the dry end of the topographic-moisture gradient, the Ponderosa Pine Forest is replaced at higher elevations by Juniper Woodland that is dominated by *Juniperus occidentalis* with some *Pinus monophylla* and *P. jeffreyi.* Although quantitative data are lacking, I hypothesize that this elevation gradient is paralleled by decreases in the vegetation parameters illustrated.

Under somewhat less xeric conditions the Ponderosa Pine Forest is replaced at higher elevations by Jeffrey Pine Forest. DCA produced an array of belt transects from the Jeffrey Pine Forest that correlated well with the topographic-moisture gradient. At approximately 2200 m, this gradient involves gradual replacement of *Pinus jeffreyi* by *Abies concolor, Calocedrus decurrens,* and, near riparian areas, *Populus trichocarpa.* There are accompanying increases in basal area and tree cover.

The White Fir Forest occurs in the mesic half of the topographic-moisture gradient at mid-elevations. I define the forest as including the geographically scattered groves of *Sequoiadendron giganteum*; on the vegetation chart these are concentrated in the mid- to upper mid-elevations of the more mesic half of the area indicated as White Fir Forest. Sites of *S. giganteum* groves may be even more mesic than indicated by position on the topographic-moisture gradient. Rundel (1972) hypothesized that precipitation at elevations above the largest grove in the park (Giant Forest) resulted in subsurface flow of water into the grove where favorable soil moisture levels were maintained throughout dry summers. Tree density and basal area parameters reach maximum or at least high values in the stands of White Fir

Forest with *S. giganteum*. In contrast, tree cover and diversity reach maximum values in stands that intergrade with the Ponderosa Pine Forest.

The elevation gradient within the White Fir Forest is paralleled by an increase in basal area and decreases in density, tree cover, richness, and diversity. Floristic changes along this gradient include an increase in the relative importance of *Abies concolor* (except in high elevation stands where *A. magnifica* becomes important), a decrease in *Pinus lambertiana,* and the sequential losses of *Quercus chrysolepis, Corylus cornuta, Cornus nuttallii, Quercus kelloggii, Calocedrus decurrens,* and *Sequoiadendron giganteum.* Most of these trends also are apparent when stands with *S. giganteum* are analyzed separately.

The transition from the White Fir Forest to the Red Fir Forest is marked by decreases in richness and diversity and a switch in the relative importances of *Abies concolor* and *A. magnifica.* The Red Fir Forest is relatively homogeneous. Except for a peak in basal area and a decrease in tree cover, there are no significant vegetation gradients correlated with increasing elevation until *Pinus contorta* becomes important at the upper elevational limit of the forest. The presence of *P. contorta* results in higher richness and diversity values along a relatively narrow ecotone between the Red Fir and Lodgepole Pine Forests.

Tree density is high in Lodgepole Pine Forest stands on moist sites including edges of meadows where encroachment by *Pinus contorta* has been occurring since early in this century (Vankat and Major 1978). This and other structure parameters show decreases as elevation increases through the Lodgepole Pine Forest to the Subalpine Forest to treeline. Richness and diversity values also decrease to treeline, except for an increase in richness values along the Lodgepole Forest-Subalpine Forest ecotone. Floristic changes with increasing elevation include the loss of *Abies magnifica,* followed by a shift in dominance from *P. contorta* to subalpine species, especially *P. balfouriana* and, in some sites, *P. albicaulis* and *P. monticola.*

Alpine vegetation occurs above timberline. Its stands are dominated by herbs, as are stands of Meadow vegetation. The latter are found in wet habitats above 2000 m; however, many wet sites are forested and this is indicated by dashed isolines across the Meadow region of the vegetation chart.

Comparison with previously published figures. Baker et al. (1981) plotted the distribution of foothill vegetation types of the park on a polar diagram of slope aspect with elevation. Their diagram may be compared to Fig. 1, although my topographic-moisture gradient is not based solely on slope aspect. The "mixed-evergreen woodland" of Baker et al. (1981) combines the Mixed Chaparral and both Live Oak Woodlands of Vankat and Major (1978). Its distribution corresponds closely with that of the Mixed Chaparral and Lowland Live Oak

Woodland shown in Fig. 1; however, Baker et al. (1981) indicated a "black oak forest" at the position of Upland Live Oak Woodland in Fig. 1. Another difference is that they portrayed foothill woodland vegetation as extending farthest upslope on southeast and east aspects, i.e., the mid- to mid-dry range of my topographic-moisture gradient. My data indicate maximum elevations for Blue Oak Woodland at the dry portion of the gradient, i.e., on south and southwest exposures and ridges (they acknowledged the ridge sites in their text).

Rundel et al. (1977) presented a schematic vegetation chart based on their collective field experience. The chart had elevation and moisture gradients for axes and illustrated Sierran coniferous forests around 37°N latitude, which is approximately 50 km north of the park boundary. Their depiction of the distribution of lower elevation coniferous forests, i.e., the Ponderosa Pine and White Fir Forests, is similar to that shown in Fig. 1, but the two vegetation charts differ greatly and increasingly in portraying the distribution of vegetation at higher elevations.

Both charts show the Red Fir Forest limited to the more mesic portion of the moisture gradient, but Rundel et al. (1977) extended its upper elevational limit to 3000 m near the middle of their moisture gradient. They also depicted the Lodgepole Pine Forest at a higher elevation than shown in Fig. 1 and as covering substantial elevational ranges toward both the mesic and xeric ends of their moisture gradient. They based this moisture gradient relationship on data collected in the Rocky Mountains, but data examined in my study do not support that extrapolation. Stands of Lodgepole Pine Forest in the park are most common in relatively mesic sites such as on plateau-like areas where they are near meadows or on gentle slopes somewhat above meadows and/or streams.

Rundel et al. (1977) also indicated a band of foxtail pine (subalpine) forest decreasing regularly in elevation from an approximately 3650–3850 m band on the mesic extreme of the moisture gradient to approximately 3200–3500 m on the xeric extreme. This band falls well within the zone indicated for Alpine vegetation in all but the drier portion of the topographic-moisture gradient on my vegetation chart. Also, they indicated that the upper elevational limit of their foxtail pine forest decreased steadily with decreasing moisture conditions; however, my data indicate that it is better to represent treeline as increasing in elevation along a topographic-moisture gradient, as for example from a north-facing slope to west- and south-facing slopes. Treeline, however, does decrease in elevation in very low moisture situations such as along ridgetops.

Conclusions

This study is the first to apply a gradient analysis perspective to the range of vegetation found over a large area of the Sierra Nevada. The

results indicate that elevation is the primary environmental factor associated with vegetation differences and that topographic-moisture conditions are also important. Some relatively steep vegetation gradients occur in the park, but the vegetation is better considered as a series of continua, rather than as discrete units.

Vegetation charts of the type produced in this study have been useful tools for portraying the environmental relations of general vegetation types (Whittaker 1975). The schematic chart for Sierran coniferous forests published by Rundel et al. (1977) is similar to that presented in this study in regard to lower elevation forests, but differs sharply for higher elevation forests. Comparison of my vegetation chart with the foothill vegetation-elevation-slope exposure diagram published by Baker et al. (1981) also shows similarities and differences. Unfortunately, the nature of their diagram precludes combining it with the chart of Rundel et al. (1977) so that vegetation transitions between foothill and montane zones could be compared to the transitions shown in Fig. 1.

Vegetation charts are also useful for illustrating gradients in vegetation parameters. The data presented and discussed in the previous section show that tree density is greatest in low elevation stands of the Ponderosa Pine Forest, basal area is greatest in the Red Fir Forest and White Fir Forest stands with *Sequoiadendron giganteum,* and tree cover is greatest in low elevation stands of both the Ponderosa Pine and White Fir Forests. Woody plant richness peaks in the Mixed Chaparral and low elevation stands of both Ponderosa Pine Forest and White Fir Forest stands with *S. giganteum,* and diversity reaches maximum values in low elevation stands of both the Ponderosa Pine and White Fir Forests.

Of the vegetation types listed in the previous paragraph, only the White Fir Forest stands with *S. giganteum* have been studied extensively in the park or nearby areas (see references in Vankat and Major 1978, Parsons and King 1980). My findings indicate that other subjects of potentially profitable research include the Lowland Live Oak Woodland, Mixed Chaparral, Red Fir Forest, low elevation stands of both the Ponderosa Pine and White Fir Forests, and transitions between these two forests and between mid-elevation forests and low-elevation woodlands and shrublands. In addition, greater application of gradient analysis techniques in investigations of Sierran vegetation is merited. The use of a gradient based on direct measurement of soil-plant moisture conditions is needed, because relationships between topographic position and moisture conditions cannot always be predicted. Also, studies using a larger number of vegetation samples and covering broader geographic ranges are desirable, and attempts to complement environmental gradients with succession gradients may be rewarding.

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REVIEWS

Flora of Chiapas. Part 1. *Introduction to the Flora of Chiapas.* By DENNIS E. BREED-LOVE. 35 p. California Academy of Sciences, San Francisco 94118. 1981. $2.50. Not an exchange item.

Producing a flora for a tropical region is a staggering task. At present hardly any tropical countries have up-to-date floras, though several have earlier versions and many have works in progress, e.g., Costa Rica, Ecuador, Ceylon, Malesia, etc. It is gratifying to see so many tropical areas receive the attention they deserve, especially in view of the irony that some of the earliest floras attempted were of tropical areas, e.g., Flora Zeylanica (1747) and Aublet's Histoire de Plantes de la Guiane Francoise (1775). The flora of Chiapas, covering an area that is technically subtropical, is a critically important project that will include plants in a transitional region, one lying on the border of the Neotropics and one that we know very little about. The area has been very active tectonically and the geology is complicated, so one might imagine that a documented flora will contribute greatly to our understanding of historical plant geography in Central and South America.

Breedlove began collecting 16 years ago for this flora of an area exceeding 74,000 km². Based on the number of collections made since then (42,000). Chiapas contains 8248 species, perhaps 1000 to 2000 species short of the estimated grand total to be expected. This may be compared to the figures for Guatemala: 109,000 km²/7749 species; and the California Floristic Province: 324,000 km²/4452 species (CFP data from Raven and Axelrod, Univ. Calif. Publ. Bot., Vol 72. 1978). The state appears to be richer floristically and more diverse geographically than Guatemala and is certainly richer and more diverse than any other Mexican state.

This volume is an excellent introduction to the flora. The discussion of phytogeographic regions, geological history (a bit brief), and vegetational history will provide a context for understanding the floristic data in future volumes (Part 2, Pteridophytes is reviewed in this issue). Bald catalogues of tropical species are overwhelming, so an interpretation of the results is as important as the catalogue itself.

The vegetational formations described are based on Beard's (1944) durable classification, and sometimes they seem based on little more than the number of tree layers. Tenuous as this sounds, it seems to work in a practical sense. We all know the difficulties of classifying vegetation. The problem is much greater in the tropics than it is in temperate regions. Breedlove has thus provided a listing of Chiapas forest types referred to by other authors, and where possible, he has included the Holdridge Life Zone terminology; most vegetation types are illustrated by excellent photographs.

Vegetation nomenclature in some works is frequently subjective to the point that little information is conveyed by designation of "Cloud Forest" or "Lower Montane Rain-forest," for instance; therefore, the use of synonyms overcomes individual subjectivity to some extent and allows comparison with one's own experience in other areas. I was at first skeptical of the alleged presence of buttressed trees in "Evergreen Cloud Forest," because buttresses are not typically found in the cloud forest of most authors. The term here applies to formations between 2000 and 2900 m, with a canopy up to 40 m. It matters less what you call it as long as you describe it.

Little progress can be made toward sensible economic development of tropical regions without reliable data. The basic information in this flora, when it has been completed, will, we hope, be helpful to present and future generations of Mexicans as they wrestle with the problem of how to use land without destroying it. Because it is possible that clearing of tropical forests, as is happening in Chiapas, affects areas well outside tropical latitudes, we can all hope so.—C. DAVIDSON, Idaho Botanical Garden, P.O. Box 2140, Boise, ID 83701.

Flora of Chiapas (D. E. Breedlove, ed.), Part 2, *Pteridophytes.* By ALAN R. SMITH. 370 p. California Academy of Sciences, San Francisco 94118. 1981. Price $30.00.

This pteridophyte flora of Chiapas, the most southerly state of Mexico, treats 104 genera and 609 species, and notes additional species of adjacent regions that may occur in Chiapas. The work is based on about 5000 collections, most of them by Breedlove and collaborators, which provide an unusually extensive coverage for a tropical American fern flora.

The keys, nomenclature, descriptions, ecology, distribution and comments have all been carefully prepared. The fine line drawings of 90 genera and 106 species, including details as well as general habit, provide a useful aid for recognition of genera as well as illustrations of critical species. This is a scholarly treatment with obvious attention paid to detail and to accuracy. The work includes nearly all of the species of the wet tropics of Mexico and thus will have application well beyond Chiapas. The treatment of the large genus *Thelypteris,* with 53 species in seven subgenera, will be useful for identification and assessment of the genus over a broad area of the American tropics, and the account of *Asplenium* with 52 species will be equally useful.

The species taxonomy has been studied in a monographic manner. There are frequent comments concerning uncertainties in the classification due to inadequate knowledge, which serve to point out areas for further work. The genera of ferns are arranged in an alphabetical sequence that avoids the difficulties of presenting a family classification, still an unsettled area of systematic pteridology. Although this is a fern flora of a relatively small part of the American tropics, its basic information provides a firm foundation for further studies of one of the major groups of tropical plants.—ROLLA TRYON, Gray Herbarium, Harvard University, Cambridge, MA 02138.

ANNOUNCEMENT

FLORA OF THE EASTERN MOJAVE DESERT

The flora of the eastern Mojave Desert, which appeared in Aliso 10(1):71–186, has been reissued as a separate by Southern California Botanists. Covering the high ranges (Kingston, Providence, New York, Clark, Ivanpah, and Mesquite Mts.) and the Kelso Dunes, the flora is the result of over 10 years of field work by the authors, R. F. Thorne, B. A. Prigge, and J. Henrickson. The plant list itself is carefully set in the context of the geography, climate, and geology of the region, and the plant communities, grouped according to Thorne's community classification system, are each discussed in detail. Microhabitat, plant association, frequency, elevation, and Mojave distribution are given for each species. The flora is based on ca. 10,000–12,000 collections made over the years by many botanists in addition to the authors (notably C. B. Wolf) and represents a total of 783 species. The phytogeographical relationships of the flora and a statistical summary are presented at the end. This work may be ordered from SCB Booksales, % Gardner, 777 Silver Spur Rd., Rolling Hills, CA 90274. Price $7.00 incl. tax.

NOTEWORTHY COLLECTION

Galápagos Islands

Cenchrus incertus M. A. Curtis (Cyperaceae).—Ecuador, Galápagos Ids., Wolf (Wenman) I., "Spiny-seeded Grass," 23 Feb 1979, *Nancy Jo s.n.* (CAS).

Previous knowledge. (See DeLisle, Iowa St. J. Sci. 37:314–316. 1963.)

Significance. First record for the archipelago, the nearest known populations being in Costa Rica and Panama. It joins the closely related endemic *C. platyacanthus* Anderss. and the introduced *C. echinatus* L. as an addition to the known grass flora. *Cenchrus incertus* is common on the uninhabited and little-visited Isla Wolf (R. I. Bowman, pers. comm.), whence it probably was introduced by migrating birds.—Duncan M. Porter and Mary Linda Smyth, Dept. Biol., Virginia Polytechn. Inst. & State Univ., Blacksburg 24061.

NOTEWORTHY COLLECTION

New Mexico—Texas

Salvia summa A. Nelson (Lamiaceae).—New Mexico, Doña Ana Co., Organ Mts., Rattlesnake Ridge (32°14′10″N–106°31′W), 1800 m, 31 May 1980, n. slope and base of limestone outcrop, *R. D. Worthington 6050* (UTEP, COLO, NMC); San Andres Mts., n. side of San Andres Pk., growing on limestone cliff, 19 Oct 1975, *T. K. Todsen 510198* (NMC); TX, El Paso Co., Franklin Mts., 0.5 km wnw. from top of South Franklin Mountain (31°51′54″N–106°29′44″W), 1940 m, 10 Jul 1977 and 30 May 1981, n. slope and base of tall limestone cliff, *R. D. Worthington s.n.* and *7136* (UTEP, TEX).

Significance. These are the first records of the species from outside the Guadalupe Mts. where reported to be endemic (Correll and Johnston, Man. Vasc. Pl. TX, 1970) and extend the known range 160 km w.—Richard D. Worthington, Dept. Biol. Sci., Univ. Texas, El Paso, 79968.

NOTEWORTHY COLLECTION

California

Abies lasiocarpa (Hook.) Nutt. (Pinaceae).—USA, CA, Siskiyou Co.: Marble Mountain Wilderness Area, west of Wilson's Cabin, Upper Shelley Meadows (T42N R10W S. 23) 1880 m: 18 Jul 1978, *Sawyer & Cope 3240* (HSC): at junction of Sky High Lake and Shackleford trails (T33N R12W S. 26) 1910 m: 14 Jul 1971, *Sawyer 2423* (HSC); slopes nw. of Deep Lake (T43N R11W S. 15) 2150 m: 16 Jul 1971, *Sawyer 2431* (HSC). (The Russian Peak population (Sawyer et al. 1970. Madroño 20:413–415) was the first verified in California.)

Significance. The California population can no longer be considered 80 km disjunct from those in Oregon. The new sites are n. of Russian Peak area, which still supports the largest population. The Shelley Meadows and most Russian Peak populations are associated with wet habitats. The other two are dry slope sites. This suggests that more populations are probable in California.—John Sawyer and Edward Cope, Dept. Biol. Sci., Humboldt State Univ., Arcata, CA 95521.

NOTES AND NEWS

Notes on the Distribution of *Malacothrix* on the California Islands.—The purpose of this note is to update my recent paper on the distribution of *Malacothrix* (Asteraceae; Lactuceae) on the California Islands (p. 227–234 in *The California Islands,* ed. D. Power. 1980).

A collection of *M. similis* Davis & Raven from Santa Cruz Island (*Brandegee,* April, 1888, UC 92228) which was inadvertently omitted from my paper has been re-examined and confirmed as that species. In addition, a collection of *M. similis* from San Miguel Island has been discovered (*Greene s.n.,* September 1886, CAS 734).

To the list of species on the islands should be added *M. glabrata* Gray on Los Islas Coronados (*R. Surnurr s.n.,* 1920. LL). Also from Los Islas Coronados are specimens that appear to be *M. saxatilis* var. *tenuifolia* (Nutt.) Gray (*Blakley 6488* & *6737,* SBBG) but they are sterile and cannot be confirmed as that species with certainty.

In connection with a study of *M. saxatilis* and related taxa I have examined specimens from Santa Catalina Island and find forms that are referrable to both *M. saxatilis* var. *saxatilis* and *M. saxatilis* var. *tenuifolia.*

Representatives of a population of *M. indecora* Greene from Santa Cruz Island (*Junak SC-312,* SBBG) and of a population of *M. squalida* Greene from middle Anacapa Island (*Philbrick & Hochberg B78-288,* SBBG) have been grown in cultivation and the chromosome number of the former is $2n = 14$ and of the latter is $2n = 28$.

Lastly, a recent collection of *M. insularis* Greene from Los Islas Coronados, south island, has come to my attention (*Moran 23158,* SBBG)—W. S. Davis, Dept. of Biology, University of Louisville, Louisville, KY 40292.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

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DEDICATION OF VOLUME 29

There are those scientists who are known for their own research and those known for having produced a number of fine students. And there are a few who have managed to have the best of both worlds. Ecologists are familiar with Jack Major's contributions to the ecological literature, and now David Parson's tribute to him in this issue points out his very large contribution in motivating many fine ecology students. The July Madroño (29:3) contained papers presented at a symposium held in Davis, California, honoring Jack Major on the occasion of his retirement, and all the presentations were made by Jack's former students. We doubt that Jack has really retired from anything: teaching and field work are too much a part of what he is, and we take great pleasure in dedicating this volume of Madroño to him.

THE ROLE OF PLANT ECOLOGICAL RESEARCH IN SIERRAN PARK MANAGEMENT: A TRIBUTE TO JACK MAJOR

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Abstract

The contributions of Jack Major and his students to plant ecological research in the Sierra Nevada of California is reviewed.

Introduction

Management policies of the National Park Service call for the preservation of naturally functioning ecosystems. In practice, Park managers often find these policies difficult to implement. This difficulty stems both from ambiguities in the interpretation of pertinent legislation (Bonnickson and Stone 1982) and the requirement that visitor use be allowed, and even encouraged. In addition to direct impacts of visitor use, such external influences as air pollution and the introduction of exotic species, make the preservation of natural ecosystem processes difficult, if not impossible (White and Bratton 1980).

It has only been relatively recently that the National Park Service has recognized the importance of baseline ecological research upon which to base resource management programs (Leopold et al. 1963). Much of this research is now carried out by Park Service scientists stationed in the larger Parks, or through Cooperative Park Studies Units (CPSUs) that have been established on University campuses in most of the larger Western States (the most recent CPSU to be established is at the University of California, Davis). The other major source of scientific expertise and research data is that provided by university scientists. It is in this regard that Jack Major has provided significant contributions to the research input needed to manage the National Parks of the Sierra Nevada. His interest, as well as that of his students and associates, in the plant ecology of the Sierra Nevada has contributed to a basic understanding of the vegetation, which in turn provides a basis for effective resources management throughout the Sierra.

Jack Major first developed his interest in the mountains as a child growing up in Utah. Born and raised in the Salt Lake City area, he frequently explored the Uinta Mountains, both in the summer and winter, with his brother Ted. Jack received his first real training in botany as a high school student of A. O. Garrett. He attended the

University of Utah and Utah State Agricultural College in Logan as an undergraduate, receiving a bachelors degree in Range Management from the latter in 1942. During the next eight years he worked for the U.S. Forest Service Intermountain Forest and Range Experiment Station in Ogden as well as serving in the 10th Mountain Division during World War II (he was a ski instructor among other things).

In 1953 Jack received his doctorate in Soils Science from the University of California, Berkeley. He taught plant ecology and related courses in the botany department at the University of California, Davis from that time until his retirement in 1981. During that period he spent as much of his time as possible in the field, preferably in the subalpine and alpine reaches of the Sierra Nevada. Anyone privileged enough to accompany Jack on one of his many field trips can appreciate his eager enthusiasm and genuine concern both for nature and his fellow man. In addition to directing the field research of fourteen Ph.D. and five masters students, Jack found time to publish over 170 scientific articles and book reviews. Special awards and honors include a Fulbright Fellowship to study in Innsbruck, Austria and receipt in 1977 of the Distinguished Service Award from the Ecological Society of America. Throughout all of this special credit must be given to Jack's wife Mary. She has been a partner in much of his work and the driving force behind much of his success. Together, they have made an eager and able field team under even the most trying of circumstances.

Throughout his professional career Jack Major has shown a special interest in the ecology of the Sierra Nevada. Spending as much time as possible in such spots as Convict Creek, Rock Creek, and Sequoia National Park. Jack never tired of the mountains. The fact that the products of much of his research were to be of value in managing the very mountains he was so fond of made things even better. In the remainder of this paper I review selected examples of the research contributions made by Jack Major, and his students, to the basic knowledge of Sierran ecosystems and how they relate to many of the management problems faced by the National Park Service.

IMPACTS OF FIRE SUPPRESSION AND GRAZING

Of all the management activities that have occurred in the Sierran National Parks, fire suppression and grazing have had the greatest impact on altering natural ecosystems (Leopold et al. 1963). Both of these practices have occurred for many years and have long lasting impacts. Under the guidance of Jack Major, John Vankat became interested in the effects of these activities. His doctoral dissertation (Vankat 1970) provided a detailed historical review of both fire suppression and grazing in Sequoia National Park. This carefully documented work used historical photographs, personal accounts, and

vegetation transects to document presettlement conditions as well as provide the first quantitative analysis of such associated impacts as an increased threat of wildfire, shifts in successional patterns and the destruction of montane and subalpine meadows. It provided a valuable baseline upon which fire and grazing management programs have been developed.

The chaparral and coniferous forests of the Sierra Nevada evolved with periodic lightning and Indian-caused fires (Kilgore and Taylor 1979, Parsons 1981). However, during the early days of National Park management, fire, like other external influences, was considered to be bad and was to be avoided at all costs. Effective fire suppression resulted in fuel accumulations and subsequent threats of unnaturally hot and destructive wildfires. As a result of altered burning patterns shifts in species succession have occurred (Vankat 1977, Vankat and Major 1978, Parsons and DeBenedetti 1979). The documentation of the undesirable impacts of fire suppression has led to the recent establishment of integrated fire management programs that include the use of naturally ignited and prescribed burns to reintroduce fire to what is thought to have been its natural role in park ecosystems (Parsons 1980). The work of Vankat (1970, 1977) and Vankat and Major (1978) played a significant role in the successful establishment of these programs.

The grazing of domestic livestock (sheep, cattle, horses, and mules) in Sierran woodlands and meadows was started long before the establishment of the Sierran parks (Vankat 1970, DeBenedetti and Parsons 1979). Vankat (1970) and Vankat and Major (1978) have documented the history as well as the destructive impacts of such grazing on the plant communities of Sequoia National Park. They conclude that grazing has had the greatest impacts in the low elevation oak woodlands and high elevation subalpine meadows. This type of data, together with ongoing Park Service studies, provides a basis for establishing limits on grazing in backcountry meadows.

Interest in the history and effects of livestock grazing led to a recognition of a lack of understanding of basic ecological and geological history of Sierran meadows. Under Jack Major's direction, Nathan Benedict became interested in these questions and pursued his dissertation research on the vegetation and origins of Sierran meadows in the Kern River drainage of Sequoia National Park (Benedict 1981). The first published product of this research, a physiographic classification of subalpine meadows (Benedict and Major 1982), identifies two basic meadow types and discusses their formation and maintenance in light of meadow stability and management.

Other students of Jack Major who have completed studies of low or middle elevation vegetation in the Sierra include Roman Gankin (1957; ecology of *Arctostaphylos myrtifolia*), Rod Myatt (1968; ecology

of *Eriogonum apricum*) and Gary Sanford (1972; plant ecology of Sierran streams). The basic information provided by these studies is essential for effective vegetation management.

Subalpine and Alpine Vegetation Studies

One of the most serious threats facing Sierran parks is the increasing number of backcountry users (van Wagtendonk 1981) and their associated impacts on high elevation plant communities. In order to evaluate the impacts of backcountry use, park managers need detailed background information on the subalpine and alpine vegetation of the Sierra Nevada. The acquisition of such baseline descriptive data has long been of special interest to Jack Major and his students. For example, Jack's chapter with Dean Taylor (Major and Taylor 1977) on the alpine zone of the Sierra reviews and compiles all available vegetation information on that zone. In addition, several of Jack's students have carried out detailed ecologic, descriptive, or taxonomic studies of many high elevation Sierran plant communities.

Dean Taylor's (1976a) doctoral study of the ecology of timberline vegetation around Carson Pass provides a thorough description of the vegetation and factors affecting its distribution and survival in the central Sierra Nevada. Although Carson Pass is not located within a National Park the plant communities and habitat requirements are similar to those found in the parks and thus Taylor's findings are of considerable relevance to park scientists and managers. Taylor has continued to show a wide-ranging interest in Sierran plant ecology. He has provided valuable assistance and support to other investigators as well as compared Sierran floristic relationships with other areas (Taylor 1976b, 1977).

Merry Lepper's dissertation study on environmental relationships of limber pine (*Pinus flexilis*) in the Sierra Nevada and Rocky Mountains provides interesting insights into the factors influencing the distribution, and survival and germination requirements of that high elevation species (Lepper 1974). The distributional requirements of another subalpine tree species, mountain hemlock (*Tsuga mertensiana*), was the subject of an undergraduate, NSF-sponsored study under Jack Major's direction by this author (Parsons 1972). That experience helped solidify my interests in Sierran vegetation and provided a strong impetus for future graduate studies in plant ecology.

The contribution of nitrogen fixation by mountain alder (*Alnus tenuifolia*) to the nutrient budget of a small watershed in the Lake Tahoe basin was investigated by Michael Fleschner as his dissertation study (Fleschner 1975). His findings showed alder to be a significant source of nitrogen input. Jim Neilson (1971) also analyzed the vegetation of the Tahoe Basin region and provided a basis for understanding im-

pacts of existing and proposed developments. Neilson (1961) also studied plant associations on glaciated granite at Sterling Lake in Nevada County.

Other regional vegetation studies in the Sierra were conducted under Jack's guidance by Rich Pemble and Mary Burke. Pemble's dissertation (Pemble 1970) described the alpine vegetation of several Sierran locations as related to topography and soil parent material. The vegetation classification he developed was based on associations of species that can be arranged to reflect a mosaic of habitat conditions. Burke (1979) also used floristic criteria to characterize subalpine and alpine vegetation types in her phytosociological study of the flora and vegetation of the Rae Lakes Basin in Kings Canyon National Park. Burke's study provided an understanding of vegetational patterns in terms of environmental factors and also provided a basis for making floristic and vegetational comparisons with other areas. She found that the four major environmental factors ordering the vegetation in the landscape are moisture regime, snow cover, altitude, and substrate stability (Burke 1979).

Jack Major has always been particularly interested in the influence of substrate on vegetation composition and diversity. One three-year study he directed compared the flora of granitic and calcareous sites in the southern Sierra Nevada. Barbara Rice carried out much of this work, which culminated in a comprehensive checklist of plant species for the Mineral King area of what was then Sequoia National Forest and is now part of Sequoia National Park (Rice 1969). This checklist has provided a valuable basis for identifying potential threatened or endangered plants of the Mineral King area.

Finally, Jack has recently co-directed Sue Conard's study of interactions, succession, and environment in the montane chaparral–white fir (*Abies concolor*) vegetation of the northern Sierra Nevada (Conard 1980). He has also collaborated with Bob Curry (U.C. Santa Cruz) in researching and writing a recently completed survey of sites in the Sierra Nevada to be included in the Natural Landmark Program for the U.S. Department of Interior.

Conclusions

In addition to the valuable works produced by his students it is important that we recognize the interest and ability Jack Major himself has shown in field studies in the Sierra. He has provided valuable consultation and inspiration to countless undergraduate as well as graduate students of his colleagues both at U.C. Davis and elsewhere. His broad interest in Sierran plant ecology is further reflected in a wide variety of publications (Major 1963, Major and Bamberg 1963, 1967; Major and Taylor 1977, Stebbins and Major 1965).

Jack Major has always been, regardless of the time of year or the

weather conditions, eager and willing to embark on rigorous field expeditions. He can always be counted on to spend as much time as needed or possible in the field with his students and classes, or to provide consultation or advice to whoever might ask. Whether it is a downhill ski traverse of Meyers grade, a cross country ski expedition into Rock Creek to observe snow accumulation patterns on subalpine meadows, a day hike on Dana Plateau, a rigorous backpack trip through Kings Canyon to review ongoing wilderness impact and big-horn sheep research, or one of his undergraduate plant ecology classes on a trans-Sierran field trip, Jack has always been eager and willing to share his experiences and knowledge. His Munz flora in hand, and the latest European or Russian text to be reviewed in his pack, Jack Major in the field is a familiar sight to plant ecologists throughout the west. His interest in Sierran plant ecology, while seldom aimed specifically at management problems, provides an excellent example of the value and need of basic research both in furthering our understanding and improving our management of the types of ecosystems preserved in our Sierran National Parks.

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PLANT SPECIES DIVERSITY IN ARIZONA

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ABSTRACT

The influence of elevational range, area, and collecting time on the absolute gamma diversity of 20 local floras in Arizona is determined by multiple regression. Elevational range and collecting time together account for 77% of the variance in species number among the floras. Residuals from the prediction equation are used to derive a measure of the relative gamma diversity of each flora. The remaining variance is associated with vegetation community-types, presence of permanent water, and occurrence of major canyon environments. Vegetation community types that are rich in species are Madrean evergreen woodland and desert grassland. Sonoran desert scrub and interior chaparral are relatively poor in species.

The state of Arizona, covering over 29 million hectares and ranging in elevation from near sea level to over 3800 m, supports about 3400 species of vascular plants. Although it is readily apparent that these species are not evenly distributed across the state, little work has been done to analyze objectively patterns in species diversity among various vegetation types and geographical areas in the state.

The terms "diversity" and "richness" have several meanings and connotations. Whittaker (1972) distinguishes three components of diversity. Alpha diversity is the number of species in standard size sample plots, whereas beta diversity describes the change in species composition between such plots. Gamma diversity, the number of species in a regional or local flora, can be formally defined as the product of the alpha diversity of the component communities and the degree of beta differentiation between them (Whittaker 1972). Diversity and richness usually refer to the absolute number of species in a flora. However, when used as adjectives, they imply that a flora not only possesses many species, but that it presumably has more species than most other floras. We make a distinction between absolute diversity, the number of species in a flora, and relative diversity or richness, the comparative richness or poorness in species from place to place. This paper is concerned with relative gamma diversity among regional or local Arizona floras.

A few studies have examined relative alpha and beta diversity within a single geographical region of Arizona (Whittaker and Niering 1965, 1968; Brady 1973, Wentworth 1979). For the most part, gamma diversity of local Arizona floras has been discussed only in subjective terms (Toolin et al. 1980, Smith 1974, Lehto 1970) or by quantitative

comparison with another flora (Bowers 1980, Burgess 1965). Although numerous local and regional floras have been compiled within Arizona, direct comparison of absolute gamma diversity is not meaningful because these floras vary considerably in the amount of area covered, habitat diversity, and collection history. Our purpose is to provide an objective basis for comparing relative gamma diversity among local Arizona floras, identify regions and vegetation types of high and low relative diversity, and suggest other factors that appear to contribute to variation in diversity among local floras.

METHODS

Bowers (1981) reviewed floristic work in Arizona. From her bibliography we selected 20 floras for which the following data were available: number of species, elevational range, areal extent, and collecting time (Table 1). We tended to avoid floras compiled for relatively small areas (<100 ha), or for discontinuous areas (e.g., Montezuma Castle National Monument, Navajo National Monument). We added to the flora of Santa Cruz County the number of Pteridophyta and Cyperaceae reported in Kearney and Peebles (1969) and the number of Gramineae reported in Gould (1973) for that area. When not stated in the original flora, elevational ranges and areas were obtained from USGS topographic maps. Collecting time was defined as the number of years (to the nearest 0.5 year) invested in collecting for and compiling each flora. Where two or more floras for the same area are cited in Bowers (1981), we used the number of years between the earliest and the most recent lists as our estimate of collecting time.

We examined relative diversity by comparing for each flora the observed number of species (S) with a computed estimate of the expected number of species (Ŝ). Floras encompassing large areas or elevational ranges or compiled over many years would be expected to have more species than floras covering smaller areas, less elevational range, or compiled over shorter periods. The extent to which S is related to these factors—area, elevational range, and collecting time—can be determined by multiple regression (e.g., Conner and Simberloff 1978). We used both S and the natural log of S (ln S) as dependent variables; independent variables were elevational range (E), ln E, area (A), ln A, collecting time (T), and ln T; i.e., all linear, semilog, and log-log relationships were tested. The residuals, i.e., the differences between the observed and expected numbers of species (S − Ŝ), were then used to derive an expression for relative richness.

RESULTS AND DISCUSSION

The best equation for predicting S was the linear regression with elevational range and collecting time:

$$\hat{S}_{E,T} = 47 + 0.349E + 8.20T \tag{1}$$

with total significant ($p < 0.05$) $R^2 = 0.77$. In our sample, area was not as good a predictor of S as was elevational range. Elevational range is probably the better measure of habitat diversity in Arizona, where climate, soils, and vegetation change dramatically with changes in altitude (Shreve 1922, Whittaker and Niering 1965).

The absolute diversity of a flora should increase with collecting effort. Furthermore we expect that the number of species encountered in an area should be a decreasing function of collecting time. Therefore, it is surprising that T provided a better fit than ln T, after correcting for the variance accounted for by E. Possible explanations for the better linear fit might be: 1) over long periods of time significant changes in habitat occur that favor immigration of new species; 2) in arid regions, longer periods of time are more likely to include favorable seasons when additional species, particularly annuals, can be collected; and 3) our method of quantifying collecting time might not be linearly correlated with actual effort, particularly over longer periods involving the publication of updated check-lists.

It is our thesis that the remaining 23% of the variance of S, i.e., that not accounted for by E and T, is relevant to the concept of relative diversity. An examination of the residuals of equation (1) can provide insight into additional factors that influence gamma species diversity. By expressing the residuals from equation (1) as percentages, we define relative richness (R) as

$$R = \frac{100(S - \hat{S}_{E,T})}{\hat{S}_{E,T}}.$$

The R values for each flora are given in Table 2, which ranks the floras from high to low relative richness. The interpretation of these R values is straightforward. For example, the R value for Grand Canyon National Park is 26, meaning there are 26% more species in the flora than would be expected on the basis of the elevational range and collecting time for that flora; the R value of -31 for Cabeza Prieta Game Range means there are 31% fewer species than expected. The floras in Table 2 are ranked from high to low R.

Three factors that appear to be associated with relative richness are vegetation, aquatic habitats, and canyon environments. We have identified four vegetation community-types that are related to relative richness. Floras of areas dominated by Madrean evergreen woodland or desert grassland tend to have high R values, while floras from Sonoran desert communities or interior chaparral have low R values (Table 2). Montane conifer forests are somewhat equally distributed among floras with high and low R, while the small number of other

TABLE 1. LOCAL ARIZONA FLORAS USED IN ANALYSIS OF RELATIVE GAMMA DIVERSITY. References can be found in Bowers (1981).

Flora	No. species	Elevational range (m)	Area (ha)	Collecting time (yr)
Aquarius Planning Unit	500	1520	135,000	2.0
Cabeza Prieta Game Range	304	825	380,000	13.0
Canyon de Chelly National Monument	518	630	34,000	3.0
Chiricahua National Monument	687	630	4300	36.0
Grand Canyon National Park	1574	2450	493,000	42.0
Hualapai Planning Unit	697	2280	247,000	2.0
Lake Pleasant Regional Park	364	265	5830	5.5
McDowell Mountain Regional Park	286	754	8475	2.0
Organ Pipe Cactus National Monument	522	1160	134,000	12.0
Phelps Cabin Natural Research Area	195	110	126	24.0
Rosemont Area, Santa Rita Mtns.	416	590	6500	1.5
Santa Cruz County	1148	1880	323,000	32.0
Sierra Ancha Experimental Forest	735	1270	5200	35.0
Sierra Estrella Regional Park	330	1070	7530	1.5
Sycamore Canyon Natural Area	624	427	932	45.0
Three Bar Wildlife Area	521	1750	15,750	14.0
Tonto National Monument	270	460	454	4.0
Tumamoc Hill	438	226	1036	68.0
Walnut Canyon National Monument	248	128	761	29.0
White Tank Mtns. Regional Park	332	830	11,560	1.0

vegetation types in our sample preclude drawing conclusions about their contribution to relative richness.

Madrean evergreen woodlands are dominant in four of the eight floras with positive R values. Desert grassland communities occur in these four floras as well. Areas in which Madrean evergreen woodland and desert grassland contribute to high R are largely confined to southeastern Arizona, where mild temperatures, high summer rainfall, and spring rainfall provide a favorable environment. Although richness in both community types is due largely to numerous annual and perennial herbs that proliferate during and immediately after summer rains, precipitation and temperature are also adequate to support a spring flora in these communities. Brady (1973) and Wentworth (1979) suggest that the scattered canopies of oaks at the upper margin of the desert grassland and the lower margin of the Madrean evergreen woodland create a heterogenous environment in which many species of herbs can flourish. Such a situation occurs at the Rosemont Area, where oak woodland and desert grassland interdigitate in shallow canyons and rolling hills. Species with Madrean floristic affinities contribute significantly to the diversity of Sycamore Canyon, Chiricahua National Monument, and Rosemont, where they comprise 15, 14, and 11%, respectively, of the floras.

TABLE 2. RELATIVE RICHNESS, LANDSCAPE FEATURES, AND VEGETATION COMMUNITY-TYPES ASSOCIATED WITH 20 LOCAL FLORAS. R = relative richness; AQ = aquatic habitats (permanent streams, lakes, ponds); CA = canyon(s) dominating landscape; SF = subalpine conifer forest; SG = subalpine grassland; MF = montane conifer forest; GW = Great Basin conifer woodland; PG = plains and Great Basin grassland; IC = interior chaparral; GD = Great Basin desert; MD = Mohave desert scrub; MW = Madrean evergreen woodland; DG = semidesert grassland; SD = Sonoran desert scrub. Major community-types within the boundaries of the flora denoted by X, minor community-types by (X). Distribution of community-types follows Brown and Lowe (1977).

Flora	R	AQ	CA	SF	SG	MF	GW	PG	IC	GD	MD	MW	DG	SD
						Vegetation community-type								
Lake Pleasant Regional Park	97	✓												X
Canyon de Chelly National Monument	78	✓	✓			(X)	X			(X)				
Rosemont Area, Santa Rita Mtns.	57	✓										X	X	
Grand Canyon National Park	26	✓	✓	(X)		X	X	(X)	(X)	X	X	X	X	
Chiricahua National Monument	22	✓				(X)						X	X	
Santa Cruz County	19					(X)						X	X	
Tonto National Monument	12	✓	✓											X
Sycamore Canyon Natural Area	10	✓	✓				(X)					X	(X)	
White Tank Mtns. Regional Park	−4	✓												X
Organ Pipe Cactus National Monument	−5	✓												X
Sierra Ancha Experimental Forest	−6	✓	✓			X	(X)		X					X
McDowell Mountain Regional Park	−13											(X)		X
Aquarius Planning Unit	−16	✓					(X)		(X)				(X)	X
Hualapai Planning Unit	−19					(X)	(X)		X		X		(X)	X
Sierra Estrella Regional Park	−24													X
Walnut Canyon National Monument	−25		✓			X	(X)							
Cabeza Prieta Game Range	−31													X
Phelps Cabin Natural Research Area	−31			X	(X)									
Tumamoc Hill	−36													X
Three Bar Wildlife Area	−36					(X)			X			(X)		X
Number of floras with R >0		5	5	1	1	4	2	1	1	2	1	4	4	2
Number of floras with R <0		3	1	1	1	4	4	0	4	0	1	2	4	10

Although Whittaker and Niering (1965) found that the north-slope shrub-phase Sonoran desert community in the Santa Catalina Mountains is among the richest in the United States, most desert regions in our sample are relatively poor in species. Ten of the 12 floras that include Sonoran desert communities had negative R values. The north-slope shrub-phase community studied by Whittaker and Niering may have a high alpha diversity compared to other Sonoran desert communities because it is ecotonal between the desert and desert grassland and because it is located in canyons. Relative gamma diversity for most desert areas in our sample is low because low beta diversity across large expanses of desert masks the input from occasional communities with high alpha diversity. Richerson and Lum (1980) found that the desert areas of California were also relatively poor in species compared to other parts of the state.

Lake Pleasant Regional Park is a Sonoran desert area notable in having the highest R value of all 20 floras included in the sample. This area is on the northern boundary of the Sonoran Desert, and its flora contains a high proportion of introduced and aquatic species. Still, these factors do not seem entirely to explain its high diversity.

Areas dominated by interior chaparral also demonstrate low relative richness. Not only are interior chaparral communities composed of relatively few dominant species, but the closed canopy precludes development of a species-rich herbaceous understory (Cable 1975). Interior chaparral is best developed in western and central Arizona, a region receiving less summer rainfall than the Madrean woodland and desert grassland areas of southeastern Arizona.

Presence of aquatic habitats in otherwise arid or semi-arid regions contributes to high relative richness in a number of floras. Of the eight floras with R ≥ 10, five occur in areas with permanent streams, lakes, or ponds. Of the nine floras with R ≤ -10, only one is for an area with permanent aquatic habitats. Aquatic habitats are particularly important at Lake Pleasant Regional Park, a Sonoran desert region with a high R value, where aquatic and wetland species comprise 8% of the flora. The flora of Organ Pipe Cactus National Monument has a higher R value than most of the other desert areas in our sample partly because of the many aquatic and semi-aquatic species found in and around sources of permanent water at the Monument.

When a canyon comprises a substantial proportion of an area, the flora is often relatively rich. Six of the floras are for areas centered about major canyon features and five have positive R values. Canyon environments promote high relative richness by providing a variety of microhabitats congenial to species that would not otherwise occur in close proximity (Toolin et al. 1980). Canyon environments contribute to the high relative richness of Sycamore Canyon Natural Area, Grand Canyon National Park, Canyon de Chelly National Monument, Chiricahua National Monument, and Tonto National Monument.

As more local floras become available, particularly for areas containing vegetation community-types poorly represented in our sample, this analysis can be revised and expanded. Floras of natural areas, rather than political or administrative units, would be particularly valuable. Our analysis of relative diversity does show that local floras constitute a previously underutilized data base for studying regional patterns in species distribution.

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A NEW SPECIES OF ERICAMERIA (ASTERACEAE-ASTEREAE) FROM NORTH-CENTRAL MEXICO

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ABSTRACT

A new species, **Ericameria riskindii**, is described from north-central Mexico, near Saltillo. It is remarkable for its remote relationship to other species in this area, its closest relative seemingly being *E. juarezensis* of Baja California.

Recent explorations in northern Mexico by Dr. James Henrickson and colleagues has revealed a remarkable *Ericameria,* which we describe below. Urbatsch (1978) treated the genus for north-central Mexico (i.e., the Chihuahuan desert species) but, not having seen material of the present collection, was unable to include the taxon. Because of its decidedly spatulate leaves, the plant will not key in his treatment.

Ericameria riskindii Turner & Langford, sp. nov.

Fruticuli humiles rotundati ad 25 cm alti. Folia spatulata glandulario-punctata conferta. Capitula solitaria terminalia sessilia vel fere sessilia. Involucrum glutinosum late turbinatum 3–4-seriatum. Rami stylorum appendicibus longis linearibus puberulis (Fig. 1).

Rounded shrublets 10–25 cm high. Stems minutely hispid; internodes 1–5 mm long. Leaves spatulate, 8–10 mm long, 4–5 mm wide, sparsely rough-hispid, glandular-punctuate, the very bases of the petioles persisting as a series of rough scales on the old stems. Heads terminal, sessile or nearly so. Involucre broadly turbinate to nearly hemispheric, 6–7 mm high, 7–8 mm across, 3–4-seriate, the bracts glutinous, acute to narrowly obtuse. Receptacle convex, scaly-alveolate. Ray florets ca. 13; tube ca. 2.5 mm long; ligule 4–5 mm long, 1.5–2.0 mm wide. Disk florets 30–50; corolla 5–6 mm long; tube ca. 2 mm long, gradually ampliate into a cylindrical throat 3–4 mm long, the lobes narrowly acute, ca. 1 mm long. Anther appendages narrowly acute. Style branches with linear, minutely puberulent appendages, ca. 2 mm long. Achenes 2.0–2.8 mm long, moderately pubescent throughout with stiffly appressed hairs; pappus of numerous white, persistent, bristles, 3–5 mm long.

TYPE: Mexico, Coahuila, ca. 24 km e. of Saltillo, s. side of the Sierra de Viga, ca. 6.5 km e. of Jamé along wood cutters road. Grow-
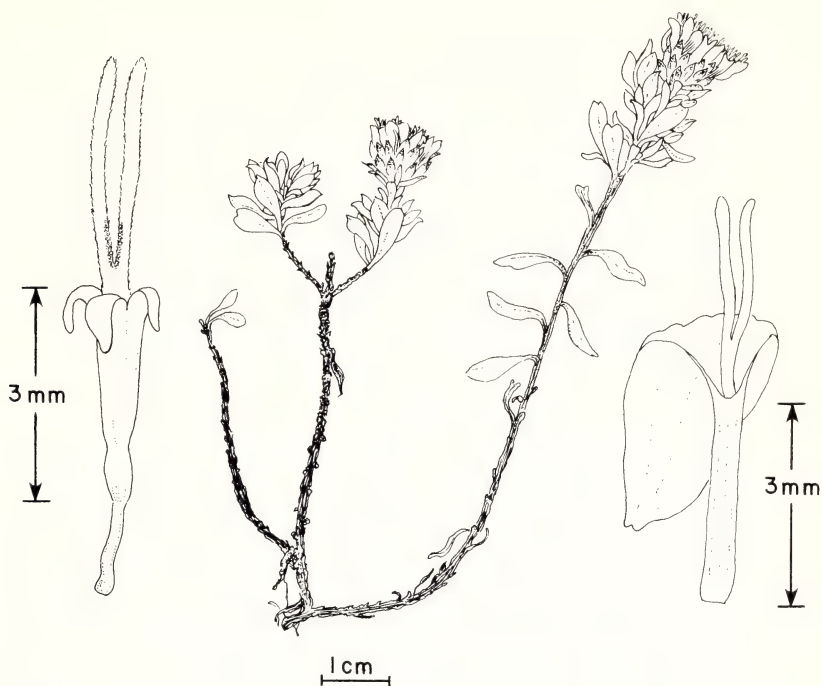
FIG. 1.   Sketch from holotype of *Ericameria riskindii*. Center, habit sketch; left, disc corolla (anthers not shown); right, ray corolla.

ing in woodland with *Pinus arizonica, Quercus greggii, Pseudotsuga, Arbutus,* etc., "10,000 ft.," 15 May 1977, *James Henrickson et al. 16156b* (Holotype: TEX; isotypes: MEXU, RSA).

PARATYPE: Nuevo Leon, Galeana Distr., Santa Rita, 2100 m, 25 Apr 1981, *G. B. Hinton 18192* (TEX).

Ericameria riskindii is an exceptionally distinct species. Superficially it resembles *Isocoma veneta* (H.B.K.) Greene, but in all of its floral characters it relates to *Ericameria*. Within the latter genus, it most resembles *E. juarezensis* (Moran) Urbatsch, having the general habit and leaf shape of that species. Their floral features are also similar, both possessing very elongate stylar appendages; but those of *E. riskindii* are merely puberulent, whereas those of *E. juarezensis* are decidedly hispid-pubescent.

The collectors of the holotype described the plants as "Low-rounded shrublets, aromatic, flowers yellow, in exposed limestone areas." It is a pleasure to name the species for one of its discoverers, Mr. David Riskind, Naturalist with the Texas State Parks System and avid student of the Texas-Mexico border flora.

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ANNOUNCEMENT

FIRST INTERNATIONAL CONFERENCE ON THE BUFFALO GOURD

Speakers will cover a broad range of topics centered on the development of *Cucurbita foetidissima* as an agricultural crop plant. This will be the first opportunity for botanists and agronomists to meet and exchange research ideas on cultivation and development of this plant, which shows promise of producing a number of agricultural commodities under dry-land and minimal irrigation regimes. The conference will be held in Sydney, Australia from 16–19 Jan 1983. Further information can be obtained from Dr. Allen Gathman, Dept. of Plant Sci., Univ. of Arizona, Tucson 85721, USA.

MORPHOLOGICAL DIVERSITY AND TAXONOMY OF CALIFORNIA MESQUITES (PROSOPIS, LEGUMINOSAE)

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Abstract

Mesquites in California extend in distribution over 480 km from the Mexican border to about 16 km north of Death Valley, and from Parker Dam east to Bakersfield. *Prosopis* populations are found at −60 m to 1090 m in areas where the mean maximum July temperature is 38°C and the annual rainfall is less than 20 cm. Twenty-six populations belonging to *P. velutina* and *P. glandulosa* var. *torreyana* were examined. *Prosopis velutina* is very rare in California and has been reported from a few locations in Imperial, Riverside, and Kern Counties. Its present distribution is in proximity to the Butterfield stage route that once connected San Francisco and St. Louis. The presence of *P. velutina* in California is probably due to human introduction. *Prosopis glandulosa* var. *torreyana* is the most common species of *Prosopis* in California. It possesses a considerable degree of morphological variability. Principal component and cluster analyses showed that most of the variation falls in general trends that are habitat-related and sometimes form a continuum along suspected routes of dispersal. Cluster analysis revealed possible morphological intergradation among populations of *P. velutina* and sympatric populations of *P. glandulosa* var. *torreyana*. This is probably due to hybridization. The two taxa overlap in several morphological characteristics but could be separated on the basis of a few characters, particularly leaf pubescence. Correlation between morphological characters was examined in terms of their importance in the systematics of the genus.

The taxonomically difficult genus *Prosopis* L. (Mimosoideae) comprises some 44 shrubby and tree species, 40 of which are native to the New World (Burkart 1976a). The species are distributed in the arid and semiarid regions of Southwest Asia, Africa, and America. Five to seven species are found in the Southwestern United States (Isley 1972, Burkart 1976a); among these, *P. velutina* Wooton, *P. glandulosa* var. *torreyana* (L. Benson) M. C. Johnst., and *P. pubescens* Benth. extend in distribution to California. The North American species have been studied by Standley (1922, 1926), Britton and Rose (1928), Benson (1941), Graham (1960), Johnston (1962), Isley (1972), and Simpson (in Solbrig et al. 1977). A considerable amount of morphological diversity, ecotypic differentiation, and interspecific hybridiza-
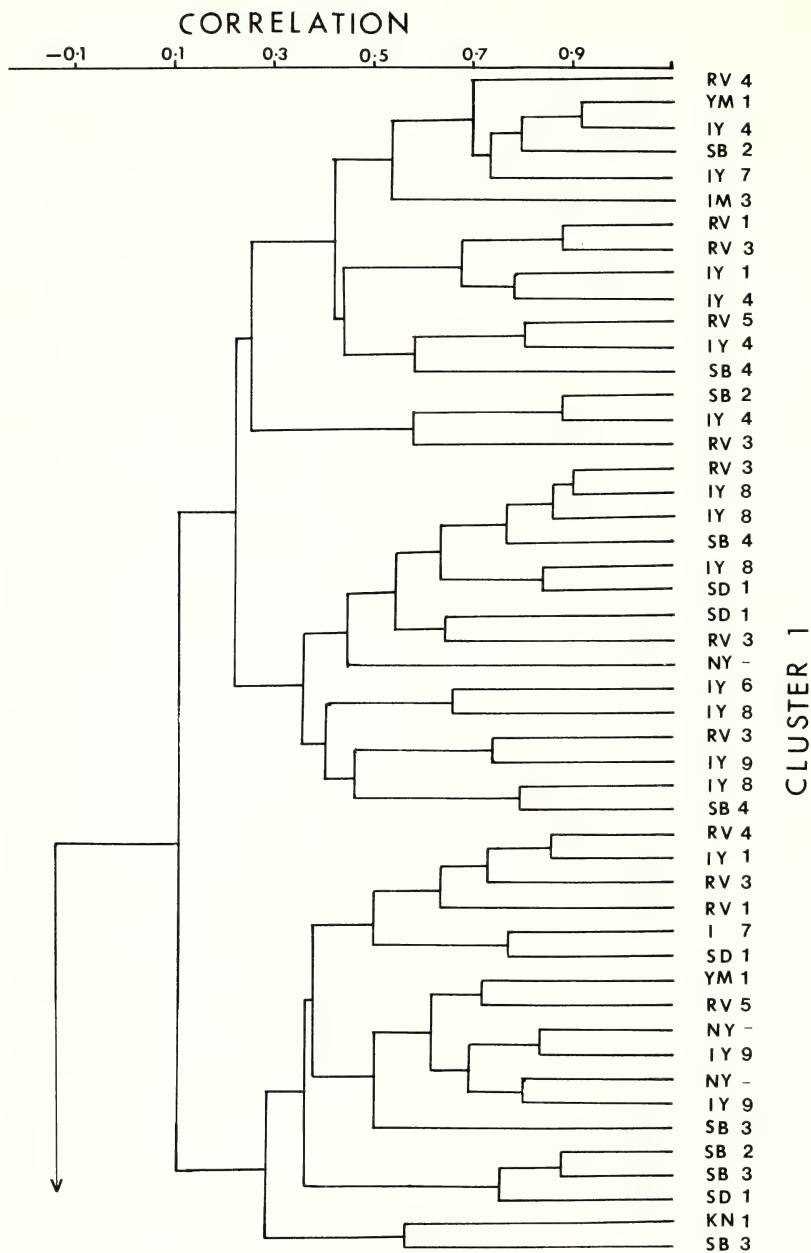
CORRELATION

FIG. 1. Cluster 1 of a phenogram representing the clustering of 107 collections belonging to *P. velutina* and *P. glandulosa* var. *torreyana* from California and adjacent places in Arizona and Nevada. Clusters 2 and 3 are continued in Fig. 2. Symbols at

tion particularly between *P. velutina* and *P. glandulosa* has been reported (Peacock and McMillan 1965, Hunziker et al. 1975). These aspects, coupled with suspected conspecific affinities to some South American species, have made the North American taxa a taxonomically difficult group. The California populations of *P. velutina* and *P. glandulosa* have not yet been examined. These populations are important because California represents the northwestern extreme of *Prosopis* distribution and also the western part of the disjunct distribution of *P. glandulosa* var. *torreyana*. In this study, the morphological patterns of variation and ecological diversity of *P. glandulosa* var. *torreyana* (western honey mesquite) and the allied *P. velutina* (velvet mesquite) will be analyzed using numerical techniques.

Methods

One hundred and seven collections belonging to four populations of *P. velutina* and 22 populations of *P. glandulosa* var. *torreyana* were examined (Figs. 1, 2). Field observations and plant collections were conducted over several field trips undertaken primarily during the pod ripening seasons at various elevations. An Air Guide altimeter was used to measure elevations and was continually calibrated by checking with roadside elevation markers. For long-term field observations, trees were labeled with aluminum tags, marked with spray paint and photographed with their identification numbers. Herbarium specimens were made for all the trees examined and are filed with TAIC.

The 107 collections were examined for 13 leaf and 2 pod characters. Two measurements per specimen were taken for each character and the average was used in this study. These characters are: length of largest leaf (LFL), petiole length (PTL), maximum number of pinnae per leaf (PNN), length of largest pinna (PNL), width of largest pinna (PNW), maximum number of leaflets per pinna (LTN), length of largest leaflet (LTL), width of largest leaflet (LTW), average distance between fifth and sixth leaflets (LTD), leaflet apex (LTX), petiole pubescense (PBP), leaf pubescense (PBL), number of nodes with more than one leaf/total number of nodes (NDR), fruit length (FRL) and fruit width (FRW). Leaf apex was scored as a bistate character, leaf and petiole pubescense as multistate characters and the rest as continuous characters.

Mean, range and standard deviation were calculated for the characters (Table 1). Cluster analysis, principal component, and discrim-

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←

each OTU identify populations from the following counties: RV = Riverside, YM = Yuma (Arizona), IY = Inyo, SB = San Bernardino, IM = Imperial, SD = San Diego, NY = Nye (Nevada), KN = Kern, CK = Clark (Nevada). CK- and NY-collections belong to populations SB3 and IY1, respectively.

inant function techniques were performed on the data. Cluster analysis and principal component were computed using the NT-SYS package of computer programs (Rohlf et al. 1976). Matrices for both Q-correlation and distance were generated from the standardized data, and clustering was then performed using the unweighted pair-grouped method with simple arithmetic averages (UPGMA). Principal component analysis was based on product-moment correlation coefficient that was computed for all characters using standardized scores. The first five eigenvectors were extracted and the first three were used as axes in producing two-dimensional scatter diagrams. The Statistical Package for the Social Sciences, SPSS (Nie et al. 1970), was employed for computing the discriminant function. Stepwise-Wilks method was used in which variables were selected for entry into the analysis on the basis of their importance in maximizing the overall multivariate F ratio for the test of differences among the group centroids. Minimum F to enter and Maximum F to remove a character were 1.00. The SPSS program also predicts group membership, i.e., the probability of membership of each operational taxonomic unit (OTU) to the groups. The OTUs were then reclassified with the group to which they had the highest affinity. Six OTUs of *P. glandulosa* var. *torreyana* were excluded from the discriminant function analysis because of lack of data on the fruit.

Taxonomy

The taxonomic treatment of *Prosopis* has been revised repeatedly (see Isley 1972 and Burkart 1976a,b for details). Difficulties in the classification of the genus are due primarily to the considerable amount of variation in vegetative and pod characteristics and to the occurrence of intermediate forms. The species in the United States are commonly referred to sections *Algarobia* and *Strombocarpa* of *Prosopis* (Burkart 1940, 1976a; Benson 1941, Johnston 1976, Isley 1972). However, earlier authors (Gray 1852, Britton and Rose 1928, Hutchinson 1964) supported the split of *Prosopis,* placing the United States' species under the genera *Neltuma* Raf. [*=Algarobia* (DC.) Benth.] and *Spirolobium* D'Orbigny (*Strombocarpa* Englm. & A. Gray). Burkart (1976a) indicated that the spines and spiny stipules, which are the main characters used for segregating the genus, are useful only at the subgeneric level; and that the uniformity of leaf, floral and fruit characters do not support splitting *Prosopis.* We concur with Burkart's taxonomic view. Accordingly, the California taxa *P. glandulosa* var. *torreyana* and *P. velutina* belong to sect. *Algarobia,* whereas *P. pubescens* (screwbean) belongs to sect. *Strombocarpa.*

The taxonomic status of the two taxa in sect. *Algarobia* has been disputed. Bentham (1875), Sargent (1902), Standley (1922), and Benson (1941) considered them as varieties of *P. juliflora* (Sw.) DC., while Standley (1926) referred them to *P. chilensis* (Molina) Stuntz. Burkart

(1940, 1976b), Burkart and Simpson (1977) and Isley (1972) treated them as separate species. Graham (1960) preferred to remain uncommitted regarding their taxonomic rank.

According to Johnston (1962), *P. juliflora* sensu stricto is a tropical coastal plant that does not occur in the United States. The relationship between the North American species of sect. *Algarobia* and the South American *P. chilensis* was suspected by Burkart (1940). In his last monograph of the genus, Burkart (1976a,b), reaffirmed the similarity between these two but acknowledged the differences in flavonoid chemistry. Benson (1941) rejected the relationships between *P. chilensis* and the North American taxa, and Johnston (1962) indicated that they are morphologically distinct. We support the latter point of view, especially in the light of the pronounced differences in phenolic compounds (Carman 1973).

The other part of the controversy is whether *P. velutina* and *P. glandulosa* belong to the same or different species. The two are shrubs or small trees with deciduous foliage and axillary spines. Leaves are bipinnate and pubescent in *P. velutina* and glabrous in pure *P. glandulosa*; pinnae in both species are usually in 1–2 pairs, each with several leaflets. Pods are straight. They are generally distinguished on the basis of leaf pubescence, number of leaves per node, and size and distance between leaflets (Table 1). Sargent (1902) recognized a form of *P. glandulosa* with shorter and more crowded leaflets in the western part of the distribution. Benson (1941) formally recognized this form as var. *torreyana*. The latter seems to bridge some morphological gaps between *P. velutina* and *P. glandulosa*. Varieties *glandulosa* and *torreyana* show intergradation in all characters wherever their populations overlap in distribution in New Mexico and western Texas (Benson 1941). Intergradation between *P. glandulosa* var. *torreyana* and *P. velutina* has also been reported in several other localities (Benson 1941, Johnston 1962, Isley 1972). The three taxa are identical in flavonoid constituents (Carman 1973) and their taxonomic status is open to question.

In many scattered locations around homes in Barstow, Riverside, Indio and Desert Shores (north of Salton City), a South American species, *P. alba* Grisebach, is used as an ornamental tree. *Prosopis strombulifera* (Lam.) Benth. was reported (Munz 1973) to have escaped from the Experiment Station at Bard, Imperial County. The species is native to Argentina and its occurrence in the United States has been rejected by Isley (1972) because of lack of herbarium specimens.

DISTRIBUTION AND ECOLOGY

The range of mesquite in California extends slightly over 480 km from the Mexican border to Big Sands Springs, approximately 16 km north of Death Valley National Monument, and from Parker Dam to

TABLE 1.   MEAN, STANDARD DEVIATION, AND RANGE OF QUANTITATIVE CHAR-
ACTERS OF *P. glandulosa* VAR. *glandulosa* AND VAR. *torreyana* AND *P. velutina*. Data
on *P. glandulosa* var. *glandulosa* are compiled from literature cited in this paper. The
number of accessions used for each measurement is denoted by n.

Char-acter	var. *torreyana* (n = 90)			var. *glandulosa*	*P. velutina* (n = 17)		
	Mean (mm)	S	Range (mm)	Range (mm)	Mean (mm)	S	Range (mm)
LFL	106.0	26.2	58–178	—	97.2	18.7	81–129
PTL	30.0	15.3	2–84	6–60	26.8	18.1	4–45
PNN	1.1	0.28	1–2	1–2	1.4	0.55	1–2
PNL	77.0	17.7	43–117	60–170	65.6	10.3	50–76
PNW	33.0	9.3	16–65	30–46	20.4	3.7	16–26
LTN	12.6	2.4	8–22	6–17	17.2	4.1	12–22
LTL	20.7	4.4	10–33	24–63	11.8	0.8	11–13
LTW	3.7	1.2	2–11	15–45	3.4	0.6	3–4
LTD	6.1	1.6	3–11	7–18	3.6	0.6	3–4
FRL	145.0	37.0	55–275	80–120	147.0	38.3	108–199
FRW	8.7	1.4	5–12	7–13	9.8	2.6	7–14
NDR	67.0	32.0	0–100	—	52.0	47.0	5–100

Buena Vista near Bakersfield. The elevation ranges from −60 m in
Death Valley to 1090 m in a wash on the south end of Saline Valley
(Inyo County). Most of the mesquite (including the Bakersfield pop-
ulations) occurred in areas with an average maximum July tempera-
ture of 38°C and less than 20 cm annual rainfall in either low lying
sinks or along streams where there was abundant groundwater. Ex-
treme cases are those of Death Valley and Scissors Crossing (near
Julian) with ca. 5 cm and 43 cm annual rainfall, respectively. The
mesquites in California, therefore, grow under environmental condi-
tions that are more extreme than those of the rest of the Americas,
and comparable to those of Saudi Arabia (see U.S. Dept. Comm. Publ.
1977). *Atriplex* species are common associates of *Prosopis,* particularly
along the edges of dry lakes and in sink areas. An exception to this is
the presence of mesquite with chapparal vegetation including live oak,
chamise, manzanita, and Great Basin sage along Highway 79 between
Temecula and Warner Springs (ca. 80 km north of San Diego).

The dominant species throughout the region is by far *P. glandulosa*
var. *torreyana*. In areas where the groundwater is closer to the surface,
P. pubescens becomes very abundant, e.g., 1.6 km north of the Salton
Sea; along irrigation canals in El Centro; in swampy areas of Harper
Lake (northwest of Barstow); and Ash Meadows, Nevada, 10 km east
of Death Valley Junction. *Prosopis velutina,* which has its main dis-
tribution east and southeast of California, has been observed at a few
sites in California including Bakersfield, Temecula, 19 km east of
Julian (at 78-S2 intersection) and north of Westmoreland. We suggest

that the presence of *P. velutina* is most probably due to human intro-
duction.

PATTERNS OF MORPHOLOGICAL VARIATION

Prosopis velutina. Q-correlation and distance techniques of the clus-
ter analysis segregated *P. velutina* OTUs to different extents. Corre-
lation technique, which is based on a matrix of similarities, grouped
P. velutina populations in one subcluster that included samples from
two populations of *P. glandulosa* var. *torreyana* from Riverside and
San Diego Counties. The *P. velutina* subcluster, however, was a sub-
unit of a larger *torreyana*-cluster (Fig. 2). Distance technique, which
is computed on the basis of dissimilarities between OTUs, revealed a
better separation of *P. velutina* from *P. glandulosa* var. *torreyana*.
Two populations of *P. glandulosa* var. *torreyana* from Riverside and
Kern Counties again clustered with *P. velutina*.

Principal component analysis was very effective in separating *P.
velutina* from *P. glandulosa* var. *torreyana* (Fig. 3, group A) and in
further segregating the Bakersfield and the southern populations of *P.
velutina* (Fig. 3, groups A1 and A2, respectively). The first three prin-
cipal component factors that were used as axes for scatter diagrams,
accounted for 54% of the total variation and were, therefore, empha-
sized. Percent variation of the first three factors and loading of the
characters in each factor are displayed in Table 2. Factors 1 and 2
seem to be equally important in segregating out *P. velutina*. The most
important characters in this segregation were leaflet length, pinna
width, average distance between leaflets, and leaf length in Factor 1;
and number of leaflets, leaf length, pinna length and leaf pubescence
in Factor 2. When Factor 3 was used along with Factor 1 as axes for
a scatter diagram, the former completely separated the Kern County
populations from the southern ones.

Means, standard deviations, and ranges of the quantitative char-
acters of *P. velutina* and *P. glandulosa* var. *torreyana* were compared
(Table 1). Stepwise discriminant-function was used to evaluate the
degree of differences between the two. The characters that signifi-
cantly contributed to the discrimination between *P. velutina* and *P.
glandulosa* var. *torreyana* and their importance, as signified by the
character weight, were: blade pubescence (1.03), leaflet width (0.35),
number of pinnae (0.31), average distance between fifth and sixth leaflets
(0.29), and relative number of nodes with more than one leaf (0.24).
The difference between the two groups was highly significant ($F =
47.8$; 5, 41 degrees of freedom). The low Wilks lambda (0.28) and high
canonical correlation (0.85) are indicative of the high contribution of
these characters to the discrimination between the two taxa. It is ev-
ident from the discriminant function and Table 1 that leaf pubescence
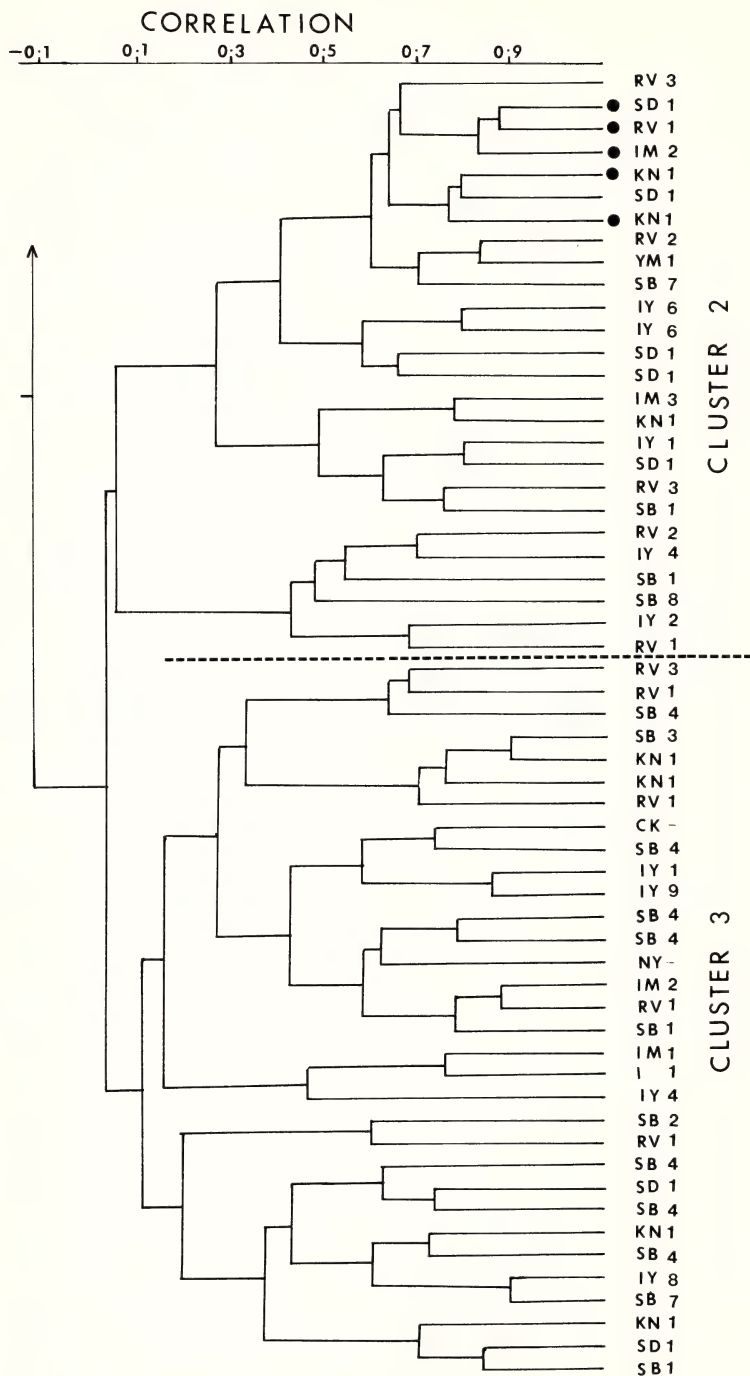was the most important character. The considerable degree of varia-

FIG. 2. Clusters 2 and 3 of a phenogram representing the clustering of *P. velutina* (marked by solid circles) and *P. glandulosa* var. *torreyana*. This phenogram is a continuation of Fig. 1. Symbols at each OTU identify populations from the following counties: RV = Riverside, YM = Yuma (Arizona), IY = Inyo, SB = San Bernardino, IM = Imperial, SD = San Diego, NY = Nye (Nevada), KN = Kern, CK = Clark (Nevada). CK- and NY-collections belong to populations SB3 and IY1, respectively.
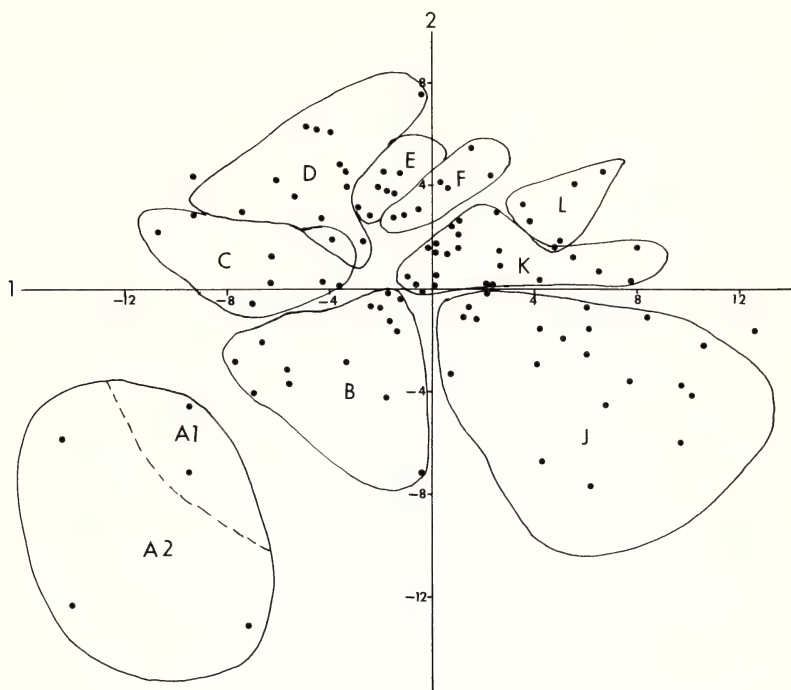
FIG. 3. Distribution of the various samples of the 26 populations of *P. velutina* and *P. glandulosa* var. *torreyana* along the first two factors of the principal component. Description of the groups A–L is in the text. Scores on the two axes were multiplied by 10.

tion in most of the other characters (Table 1) has minimized their importance in differentiating between *P. velutina* and *P. glandulosa* var. *torreyana*. Group membership predictability was 100% for both groups, a result indicative of the effectiveness of the discriminant functions.

Prosopis glandulosa var. *torreyana*. The mixed clustering of populations from different geographic areas (Figs. 1, 2) is indicative of considerable intrapopulational variation and interpopulational affinity within var. *torreyana*. Members of the various populations, however, were divided into three major clusters that are recognizable at a phenon line of 0.00 correlation. Discriminant function analysis was performed on these three clusters in order to assess the significance of their separation and to point out the characters that contributed most to their grouping. The differences between clusters were highly significant (p < 0.000). Plotting the OTUs and centroids of clusters (groups) on the basis of the two discriminant functions revealed good separation, particularly between clusters 1 and 2 (Fig. 4). Cluster 3
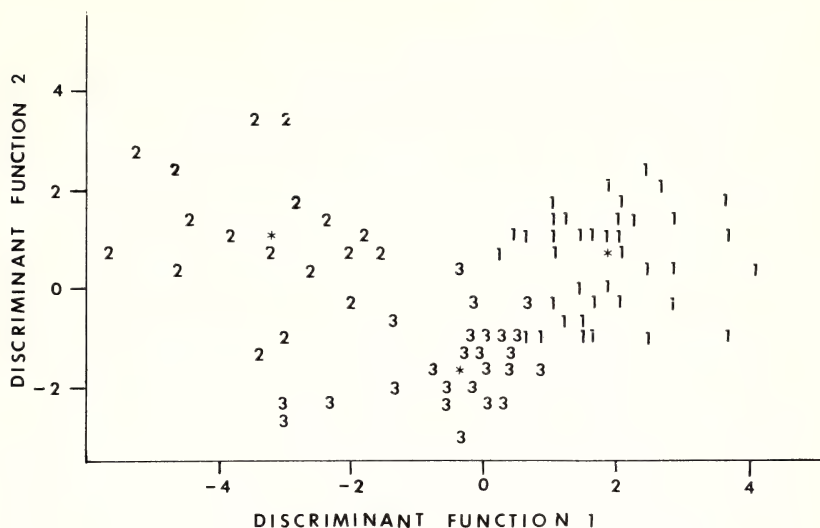
TABLE 2. LOADINGS (ABSOLUTE VALUES) OF 15 CHARACTERS ON THE FIRST THREE FACTORS IN A PRINCIPAL COMPONENT ANALYSIS OF *P. glandulosa* VAR. *torreyana* AND *P. velutina*. Characters are listed in descending order according to the loading on the first factor. Factors 1, 2, and 3 accounted for 30%, 14%, and 10% of the variation, respectively.

Fac-tors	Characters														
	LTL	PNW	LTD	LFL	PNL	PTL	PBL	PBP	LTW	NDR	LTN	LTX	FRL	PNN	FRW
1	0.86	0.82	0.80	0.77	0.70	0.56	0.55	0.54	0.53	0.35	0.33	0.15	0.09	0.08	0.04
2	0.16	0.01	0.08	0.55	0.54	0.31	0.51	0.37	0.02	0.09	0.70	0.24	0.19	0.48	0.35
3	0.01	0.14	0.07	0.02	0.26	0.22	0.24	0.47	0.11	0.65	0.42	0.46	0.23	0.33	0.40

FIG. 4. Centroids (symbolized by asterisks) and dispersions of clusters 1–3 of *P. glandulosa* var. *torreyana* plotted on the basis of the two discriminant functions.

exhibited some overlapping with the other two. The first function was effective in separating the three clusters, whereas the second function contributed mostly to the discrimination between cluster 3 and the other two. Pinna number was by far the most important discriminating character in the first function. Other characters such as petiole and pinna length and leaflet number were fairly important (Table 3). Function 1 accounted for over 77% of the variance and consequently is heavily weighted. Leaflet apex was most important in the second function, followed by relative number of leaves per node, leaflet number and pinna width. Predictability of group membership was very high with a few OTUs of clusters 1 and 2 reclassified with cluster 3 (Table 4). This confirms the distinctness of the three groups.

Principal component analysis was most useful in segregating the morphological variations in *P. glandulosa* var. *torreyana*. The first three factors accounted for over half of the variance and, therefore, will be emphasized in the analysis. The percent of variance accounted for by the first three factors and the loadings of the various characters are summarized in Table 2. When factors 1 and 2 were used as axes for a scatter diagram, populations of *P. glandulosa* var. *torreyana* appeared in nine mostly overlapped groups (Fig. 3). These groups are: B—southern populations from San Diego, Riverside and Yuma (Arizona); C—Kern County populations; D—predominantly San Bernardino populations; E—populations from the Salton Sea area; F—Death

TABLE 3. TEN MOST IMPORTANT CHARACTERS USED IN DISCRIMINATING BETWEEN THE THREE GROUPS OF *P. glandulosa* VAR. *torreyana* ARRANGED IN A DESCENDING ORDER OF THEIR CONTRIBUTION (ABSOLUTE VALUES) IN THE FIRST FUNCTION. Percents of variance in functions 1 and 2 were 73 and 27, respectively.

Func-	Characters											
tions	PNN	LFL	PNL	PNW	PBP	LTL	NDR	LTN	FRL	PBL	FRW	LTX
1	0.76	0.74	0.35	0.34	0.33	0.29	0.27	0.21	0.20	0.09	0.04	0.01
2	0.22	0.47	0.29	0.34	0.58	0.23	0.56	0.39	0.05	0.48	0.30	0.68

Valley and Saline Valley; J—populations that extend along the Colorado River from Palo Verde to Needles then north along the Nevada border through Death Valley to Saline Valley; K—San Bernardino and Inyo County populations; and L—Riverside County populations. Although the Kern County populations appeared as a fairly distinct group (C), the first factor revealed a trend of variation from this group to San Bernardino and Inyo populations (group K). The three most important characters for this axis are leaflet length, pinna width, and the average distance between the fifth and sixth leaflets. This trend seems to be associated with decreasing xeric conditions. The second factor of the principal component revealed a trend of variation from the southern populations (group B) to Kern County (group C) and east to San Bernardino populations (group D). This factor has also shown a south–north trend along the eastern side of the state (groups J, K, L, F) where the San Bernardino mountains do not present a physical barrier. The important characters for this axis are leaflet number per pinna, leaf length, and pinna length.

Because the principal component uses a character-character correlation matrix, a phenogram representing character correlations was generated (Fig. 5). The computed 0.87 cophenetic value shows that this phenogram well represents the matrix and has but a minimum

TABLE 4. PREDICTABILITY OF GROUP MEMBERSHIP OF 97 *P. glandulosa* VAR. *torreyana* COLLECTIONS. The three groups represent the clusters obtained from cluster analysis (Q-correlation).

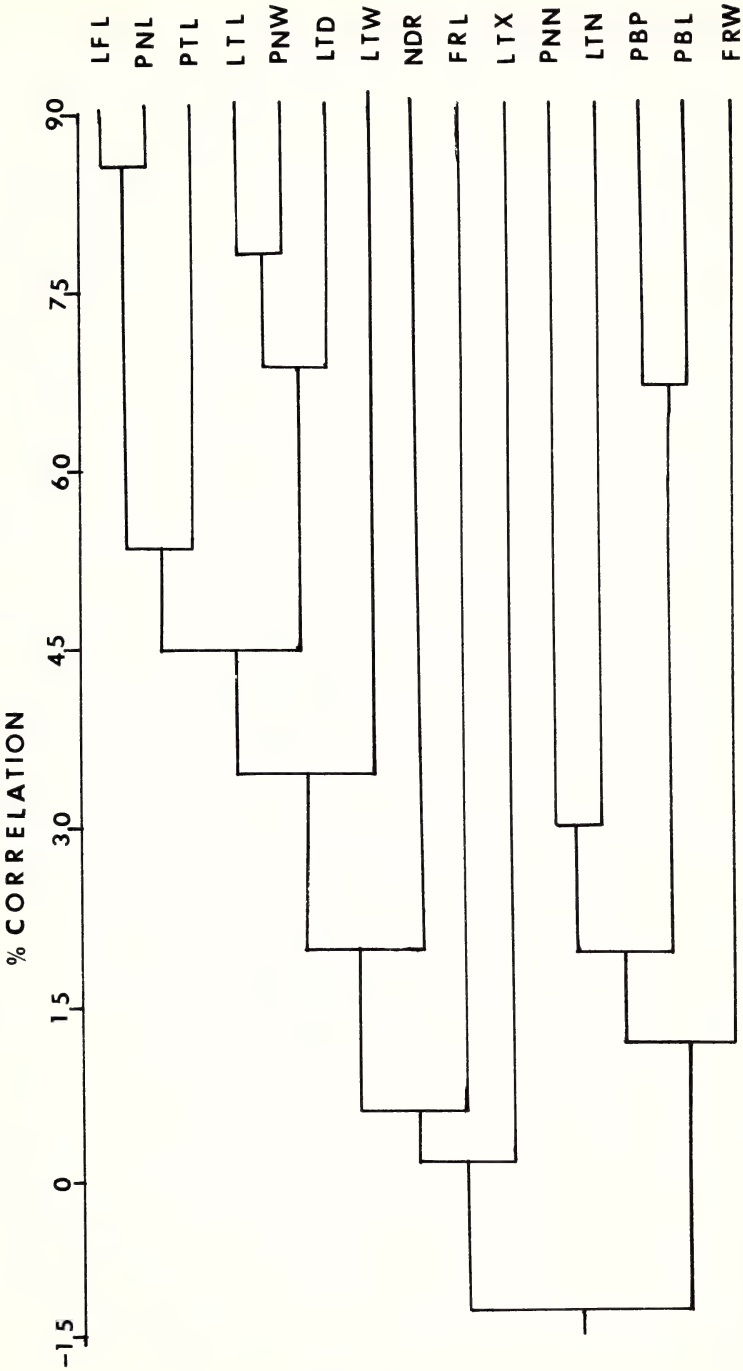| Actual groups	No. of cases	Predicted group membership		
		1	2	3
1	43	39 91%	0 0%	4 9%
2	25	0 0%	23 92%	2 8%
3	29	2 7%	0 0%	27 93%

Fig. 5.   Clustering of the 15 characters used in this study. Key to character symbols is in the Methods section.

amount of distortion. Leaf length is strongly correlated with pinna length and should be merged. However, in cases where there is more than one pair of pinnae, the distance between each along the rachis should be considered as a separate character. Leaf and pinna length seem to show some correlation with petiole length. Leaflet length and pinna width are highly correlated and ought to be combined because the former is indicative of the latter. These two traits appear to be correlated with the distance between leaflets. Leaflet width is independent of leaflet length. Leaflet and petiole pubescence were clustered at 0.67 correlation which indicates good correlation. Some relation (although very weak) seems to exist between number of pinnae and leaflets. Width and length of the fruit were negatively but weakly correlated and consequently the two could be used simultaneously. Graham (1960) observed negative correlation between number of pinnae and size of leaflets, which is depicted in the phenogram at a very low correlation level (0.11). Simpson (in Solbrig et al. 1977) indicated that the longest leaflets were the widest and that leaves with greatest number of pinnae also had the largest number of leaflets. Both correlations are evident in the phenogram, though not especially high.

Discussion

Prosopis velutina has its main distribution in southern Arizona and Mexico. Shreve (1951) indicated that this taxon is an important species in the Arizona Upland and the Plains of Sonora, and is the dominant or codominant tree on the flood plains and well watered level areas in the foothills of Sonora. The species has been observed in California at a few sites including Bakersfield, Temecula, 19 km east of Julian, and north of Westmoreland. This stretch of distribution is in proximity to the Butterfield Stage route that once connected San Francisco and St. Louis. Therefore, we believe that the presence of *P. velutina* in California is most probably due to human introduction through this route. Mesquite and screwbean are useful plants and have been an important food source for southern California Indians (Castetter and Bell 1951, Barrow 1967, Felger 1977) because of their very high yield of nutritious pods (Felker 1979). The expansion of *P. velutina* into California is apparently beyond its northern geographic range as implied by its rare occurrence in the state.

Although our sample size of *P. velutina* is small, the morphological data do not deviate greatly from the descriptions of the species elsewhere (Benson 1941, Johnston 1962, Burkart 1976b). Cluster analysis and principal component techniques have shown good, but not clearcut separation of *P. velutina* from *P. glandulosa* var. *torreyana*. Based on Q-correlation, *P. velutina* appeared at a level that could not justify a specific rank (Fig. 1). However, when the analysis was based on differences (distance method), a better separation was achieved, but

not without some OTUs from *P. glandulosa* var. *torreyana*. Distance technique is known to be more effective in displaying differences between close neighbors (Sneath and Sokal 1973). The discriminant function analysis showed significant differences between the two taxa but discrimination was based mainly on leaf pubescence. A considerable overlap between *P. velutina* and *P. glandulosa* var. *torreyana* in various morphological characteristics is evident (Table 1). The first two factors of the principal component segregated *P. velutina* from *P. glandulosa* var. *torreyana*. Factors 1 and 3 divided the northern and southern populations of *P. velutina* and placed them closest to those of *P. glandulosa* var. *torreyana*. The question whether *P. velutina* and *P. glandulosa* var. *torreyana* belong to the same or different species could not be answered satisfactorily here because of our small sample of the former. Nevertheless, the study revealed high affinities between the two. The discriminant function analysis showed that discrimination between *P. velutina* and *P. glandulosa* var. *torreyana* is based primarily on leaf pubescence, a quantitative and rather variable character. *Prosopis glandulosa* var. *torreyana* seems to bridge the morphological gaps between *P. glandulosa* and *P. velutina* (Table 1). These findings are supported by the reported hybridization between the two species (Peacock and McMillan 1965, Hunziker et al. 1975) and the absence of differences in flavonoid compounds (Carman 1973). Isley (1972) stated "I have difficulty regarding *P. velutina* as more than a desert form of *P. glandulosa*."

Prosopis glandulosa is abundant in valleys and dry uplands from Mexico to southern Kansas and from Louisiana to California (Isley 1972). The range of its distribution in the United States is interrupted in Arizona and Texas (Nueces Co.) by *P. velutina* and *P. laevigata* (Humb. & Bonpl. ex Willd.) M. C. Johnst. (Johnston 1962, Isley 1972). The Pecos River divides the eastern var. *glandulosa* from the western var. *torreyana*. Occasional occurrence of the varieties across the line and intergradation in morphology have been reported (Benson 1941, Isley 1972). Morphological differences between the two varieties are summarized in Table 1. Although our study showed a wider range of variation in some of the morphological traits of *P. glandulosa* var. *torreyana*, the two varieties are recognizable despite some overlap (Table 1).

The various accessions of *P. glandulosa* var. *torreyana* clustered in three groups. Cluster 1 included populations primarily from the Salton Sea, Whitewater Canyon, Saline Valley, and Death Valley. The northern and southern populations are connected by a strip along the Colorado River and the eastern borders of California where the mountains do not present a physical barrier to introduction. This cluster corresponds with groups J and F of the principal component (Fig. 3). The Saline-Death Valley and Salton Sea areas have some environmental similarities. Their annual rainfall and maximum July temperatures

are comparable. Both areas are drainage sinks of their surrounding mountains, their water tables are near or above the soil surface, and fast evaporation in the two locations results in accumulation of salts. The eastern range along the Colorado River seems to represent a route of introduction from the southern to the northern areas. The characters that contributed most to the variation in this trend are leaflet number and leaf and pinna length.

Cluster 2 encompassed the populations of *P. velutina* and those of *P. glandulosa* var. *torreyana* that are sympatric in distribution with them. Discrimination between this cluster and cluster 1 was contributed by function 1 of the discriminant function while both functions contributed equally in discriminating between clusters 2 and 3 (Fig. 4). The discrimination in functions 1 and 2 was based primarily on pinna number, leaf length, leaf apex, and petiole pubescence (Table 3). These characters also are important in separating *P. velutina* from *P. glandulosa*. The affinities between *P. glandulosa* var. *torreyana* and *P. velutina* as depicted by the cluster analysis and principal component techniques could imply some gene flow between the two. Populations of these taxa are sympatric. Benson (1941) and Johnston (1962) have also observed morphological intergradation between *P. velutina* and *P. glandulosa* in the southwestern United States. They attributed this to possible hybridization.

Cluster 3 included populations from San Bernardino and Kern Counties along with a few accessions from the other two clusters. The clustering of plants from San Bernardino and Kern Counties signifies an introduction of *P. glandulosa* var. *torreyana* from the eastern section of California along a route north of the Transverse Ranges to Kern County. This trend is also observed in the principal component in which Kern County plants (group C) intergrade into the San Bernardino plants (group D). Factor 2 of the principal component seems to be more effective than Factor 1 in showing this trend.

The present study has clearly reflected the enormous amount of variation in *P. glandulosa* var. *torreyana* (Figs. 1–3). Both cluster and principal component analyses revealed the high magnitude of variation within populations and the tendency for interpopulation grouping. Numerical analysis showed that the variation exhibits some general trends that can be correlated with habitats and suspected routes of dispersal. Variability in long-lived perennial plants, particularly those occupying harsh and unpredictable environments, has a strong selective advantage. Perennials maintain their variability by outcrossing, low development of sterility barriers, and high chromosome numbers (Grant 1958). This variability buffers the population from environmental shocks and helps avoid decimation. This is especially true of the arid-adapted, nitrogen-fixing trees of *Prosopis* (Peacock and McMillan 1965, Felker and Clark 1980). These plants colonize infertile

soils and often form nearly monotypic stands in parts of their ranges (ca. 30 million hectares) in the United States (Parker and Martin 1952). *Prosopis* achieves high genetic variability in populations by means of self-incompatability (Simpson 1977) and high chromosome numbers, $2n = 28$ in diploids (Hunziker et al. 1975). The outcrossing mechanism has facilitated hybridization at the intraspecific and interspecific levels (Hunziker et al. 1975, Burkart 1976a, Felker, Boyd, and Hilu unpubl. data) and contributed to the high degree of morphological variation. Numerical techniques proved to be particularly useful in understanding the trends of this variation.

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SYMPLOCOS SOUSAE, A NEW SPECIES OF SYMPLOCACEAE FROM MEXICO

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Abstract

Symplocos sousae, distinguished by solitary, axillary, 5-merous flowers, persistent floral bracts, and glabrous drupaceous fruits, is described from the Sierra Manantlán in Jalisco and the region of San Andres Chicahuaxtla in Oaxaca, Mexico. Its closest affinities are with *S. coccinea* Humb. & Bonpl. and *S. prionophylla* Hemsl., both of which are also endemic to Mexico.

Ongoing exploration of montane forest vegetation in areas of western and southern Mexico continues to yield collections of new woody taxa exhibiting restricted or patchy distributions. *Symplocos,* with approximately 15 species in Mexico, is sometimes locally abundant in these upland forests, yet many of the species remain poorly understood. A persistent problem in clarifying the taxonomy of *Symplocos,* even on a regional basis, lies in the difficulty of correlating specimens collected in either flowering or fruiting condition. Although material of the new species described herein has slowly accumulated in herbaria since 1949, an understanding of its diagnostic features and probable relationships emerged only after studying the flowering and fruiting specimens recently collected by Sousa in Oaxaca. In recognition of his contribution to this study I take pleasure in naming the species for Mario Sousa Sanchez who has generously assisted many botanical colleagues in their investigations of the Mexican flora.

Symplocos sousae Almeda, sp. nov.

Frutex vel arbor parva (1–)3–7 m. Folia coriacea, integra vel serrulata, petiolata, elliptica, elliptico-ovata vel elliptico-obovata, ad basem rotundata vel obtusa vel acuta, ad apicem acuta vel acuminata. Lamina 5–11 cm longa et 2.3–5.8 cm lata supra glabra, subtus strigosa vel strigillosa. Flores 5-meri sessiles vel subsessiles in foliorum superiorum axillis solitarii; calyx 3.5–5 mm longus, lobis ovatis, ciliatis; corolla rosea (fide collectore), campanulata, 1.2–1.6 cm longa, glabra, lobis oblongis vel obovatis, 6–10 mm latis. Stamina multiseriata. Stylus glaber, 7–11 mm longus. Fructus glaber, obovoideus vel ellipsoideus, 16–24 mm longus, 12–19 mm latus, 4-locularis (Fig. 1).

Shrubs reportedly 1–3 m tall or trees mostly 5–7 m. Juvenile branchlets and vegetative buds mostly sericeous to strigose but varying to
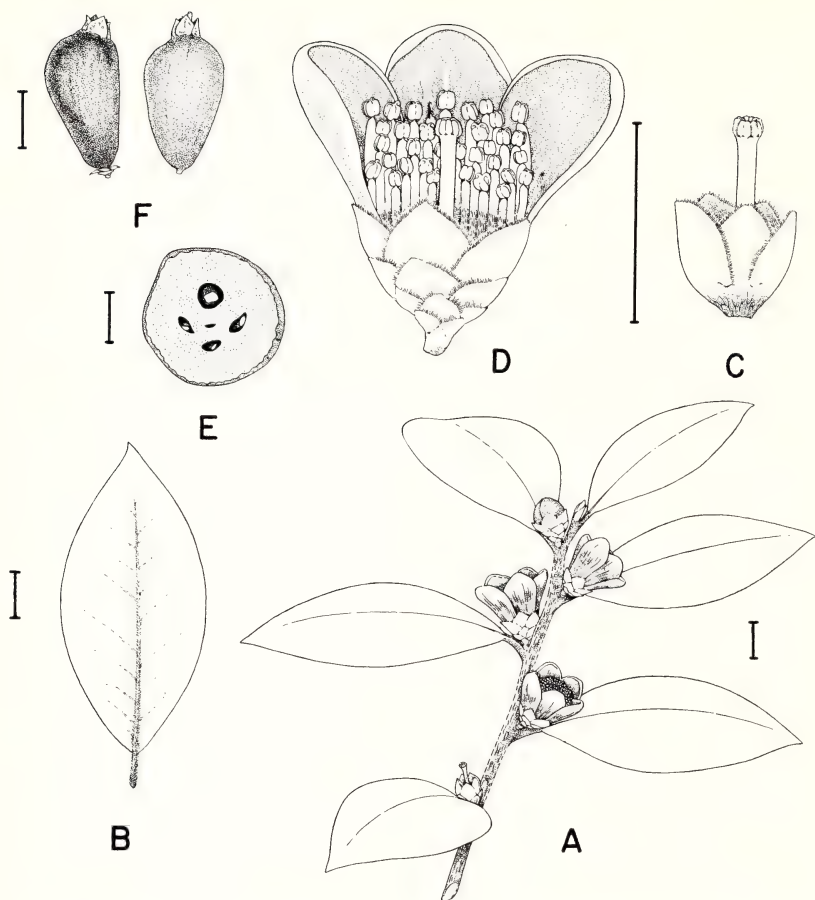
Fig. 1. *Symplocos sousae* Almeda. A, habit; B, representative leaf (abaxial surface); C, calyx lobes, style, and stigma; D, floral dissection (with two corolla lobes removed) showing floral bracts, calyx lobes, multiseriate staminal arrangement, and corolla lobes; E, cross section of mature drupe; F, mature drupaceous fruits with persistent calyx lobes. (A–D from *Boutin & Brandt 2562*, CAS; E from *McVaugh et al. 23156*, MICH; F from *Sousa et al. 5163*, CAS.) All scale lines equal 1 cm.

glabrate. Petioles canaliculate above, 3–8 mm long and 1.5–2.0 mm broad. Principal leaves coriaceous, entire but varying to distally serrulate, elliptic to elliptic-ovate or elliptic-obovate, 5–11 cm long and 2.3–5.8 cm broad, apically acute to acuminate, basally rounded but sometimes varying to obtuse or acute, glabrous and ± vernicose above, densely to sparsely strigose or strigillose below with only the median nerve prominently elevated. Flowers sessile or subsessile, solitary, erect, borne in the leaf axils of distal branchlets and closely subtended by

6–7 sessile, imbricate, persistent, glabrous bracts; lowermost bracts suborbicular to reniform, apically rounded, 1.5–2.5 mm long and 1.5–3 mm broad, margins mostly ciliate but sometimes entire and ± hyaline, the uppermost bracts broadly deltoid, apically obtuse, 3–4.5 mm long and 3.5–5 mm broad, the margins prevailingly ciliate. Calyx 5-lobed, the lobes ± imbricate, ovate, 3.5–5 mm long and 3–4.5 mm wide at the base, glabrous, margins entire, ciliate, and auriculate basally between sinuses. Corolla sympetalous, glabrous, ± campanulate, 1.2–1.6 cm long, 5-lobed, reportedly pink but drying red; lobes connate basally for 2–3 mm and adnate to the filament tube for 4–6 mm basally, oblong to obovate, apically rounded, 6–10 mm wide, the margins erose-ciliolate and markedly involute. Stamens multiseriate; filaments connate basally for 5–7 mm, free portions of the filaments ligulate, 3–6 mm long and 0.5–1.0 mm wide, often separating into clusters opposing the corolla lobes. Anthers bilocular, ± globose to quadrate, mostly 1 mm long and wide, white to pale yellow. Ovary inferior, glabrous, the summit strigillose to nearly glabrous. Styles straight, glabrous, 7–11 mm long; stigma subcapitate, deeply 5-lobed. Fruits drupaceous, glabrous, obovoid to ellipsoid, 16–24 mm long, 12–19 mm broad, quadrilocular in cross section with a massive marginally repand woody endocarp.

TYPE: México, Jalisco, se. of El Chante and Aserradero along road near El Guisar, an abandoned lumber mill, 2743 m, 24 Nov 1968, *Boutin & Brandt 2562* (Holotype: CAS!; isotypes: HNT! MEXU!).

PARATYPES: México, Jalisco: Sierra de Manantlán, 29 Jan 1970, *Boutin & Kimnach 2979* (HNT—2 sheets); Sierra de Manantlán, w. of El Guisar, 30 Jan 1970, *Boutin & Kimnach 2998* (HNT); Sierra de Manantlán (25–30 km se. of Autlan), along lumber roads e. of the road crossing called La Cumbre between El Chante and Cuzalapa, 20–21 Mar 1965, *McVaugh et al. 23156* (MICH); hardwood-pine-fir forest in mountains of Manantlán, ca. 15 miles sse. of Autlan by way of Chante, 28 Jul 1949, *R. L. & C. R. Wilbur 1936* (MICH). Oaxaca: San Andres Chicahuaxtla, Distr. de Putla, Dec 1966, *MacDougall s.n.* (CAS—2 sheets, MEXU); Cerro Zarzamora, San Andres Chicahuaxtla, 15 Apr 1962, *MacDougall s.n.* (CAS, MEXU, MICH); 1 km n. of Chicahuaxtla, municipio of Chicahuaxtla, 8 Feb 1976, *Sousa et al. 5163* (CAS, MEXU—2 sheets).

Distribution. The species is endemic to Mexico, where it reportedly occurs along streams and steep ravines on the Sierra de Manantlán of Jalisco at 2500–2750 m in forests with *Abies, Cupressus, Pinus,* and *Quercus.* It is also known from forested areas in the vicinity of San Andres Chicahuaxtla and Cerro Zarzamora in Oaxaca at 2490 m. These sites very likely represent collecting localities readily accessible from roads. Additional populations are to be expected in intervening montane regions of Michoacan and Guerrero.

The salient features of *S. sousae* include sessile, or subsessile, solitary, axillary flowers; persistent, glabrous floral bracts; basally auriculate, ovate calyx lobes; 5-parted, glabrous corollas with involute, apically rounded lobes; and obovoid to ellipsoid fruits that are glabrous at maturity. The two known populations of this species exhibit some consistent morphological differences worthy of note. Collections from Jalisco typically have elliptic to elliptic-ovate entire leaves that are acute to acuminate apically and the summit of the ovary surrounding the style is essentially glabrous. In contrast, the Oaxaca specimens have elliptic-obovate, distally serrulate leaves that are short-acuminate apically and the ovary summit is invariably strigillose. Additional collections would be desirable to determine the extent of variability in these characters. I am inclined to attach little importance to these differences in view of the distance separating known populations. A peculiar feature of some collections of this species from both Jalisco and Oaxaca is the tendency of the ovary summit to become enlarged and distended beyond the persistent calyx lobes on mature fruits. The significance of these structures is unclear for they do not appear to be characteristic of all mature fruits examined.

Among described congeners, *S. sousae* most closely resembles *S. coccinea* Humb. & Bonpl. and *S. prionophylla* Hemsl., both of which are also known only from Mexico (Brand 1901, Standley 1924). Foliar shape and the solitary, sessile flowers give *S. sousae* an aspect reminiscent of *S. coccinea* but the latter differs in having hirtellous or hirsute distal branchlets, sericeous bracts and calyx lobes, flowers with 10–15 apically cuspidate to acuminate corolla lobes, basally pilose styles, and oblong to ellipsoid fruits that are moderately to copiously hirsute. To a lesser degree *S. sousae* also resembles *S. prionophylla* by virtue of the 5-parted corolla and elliptic or oblong-obovate leaves. *Symplocos prionophylla* is otherwise sharply differentiated by its uniformly serrulate leaves, early deciduous floral bracts, densely canescent bracts and calyx lobes, paniculate or fascicled inflorescences of 3–5 flowers borne on short peduncles (mostly 5 mm or less), and narrowly cylindric, strigillose fruits.

According to label information on *Sousa et al. 5163* the new species is commonly known as "tunihia" or "tu-nihia" in Oaxaca, and the fruits are eaten upon turning black at maturity.

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A SURVEY OF THE CORTICOLOUS MYXOMYCETES OF CALIFORNIA

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Abstract

Thirty-eight species of corticolous myxomycetes are reported from California, most of which were collected from tree bark placed in moist chambers. Included in this number are several recently described species. The substrates and California counties where each taxon was obtained are listed, along with notes on distinguishing features of each species.

The corticolous myxomycetes are a diverse group inhabiting the bark surface of living woody plants. Most have minute fruiting bodies that are very difficult to detect in the field. The bark surface of living plants as a myxomycete habitat was rarely investigated until Gilbert and Martin (1933) used moist-chamber culture techniques with samples of tree bark. These methods allow close observation of bark under conditions favorable to the development of myxomycete fruiting bodies.

More recently, Keller and Brooks (1973, 1975, 1977) have made thorough collections of corticolous myxomycetes using a hand lens in the field. The myxomycetes they collected as natural fruitings following rainfall are identical to ones obtained in moist chambers, and the concept of a distinct corticolous myxomycete flora has become well recognized.

The myxomycete flora of California, including several corticolous species, has been extensively studied (Kowalski 1966, 1967, 1973; Kowalski and Curtis 1968, 1970). Most of the smaller corticolous species listed by Kowalski were obtained by collecting bark samples bearing more conspicuous corticolous myxomycetes and examining the substrate in the laboratory. The present study was undertaken to expand the corticolous myxomycete flora of California using moist-chamber culture techniques. Although bark samples were obtained throughout California, Butte and Lassen Counties were emphasized. A total of 38 myxomycete species were obtained in moist chambers, including seven new state records and six new species, which have been described elsewhere.

Kowalski (1973) gives the number of myxomycete species reported from California as 231, about half the species recognized by Martin and Alexopoulos (1969) in their world monograph. Thus, the 38 species

reported here on the bark surface of living plants constitute a significant portion of the state flora. Additionally, many areas of California have yet to be investigated; undoubtedly many other unreported or undescribed corticolous myxomycetes await discovery.

Materials and Methods

In preparing moist chambers, Petri dishes were lined with filter paper. A sample of bark was placed on the paper, then the dish was flooded with distilled water. After 2–3 hours the excess water was poured off, and the moist chambers were incubated at room temperature or 12–15° C. The lower temperature has been suggested as optimum for certain corticolous species (Whitney 1980). Observations of the bark samples with a stereoscopic microscope were started within 24 hours. Myxomycete fruiting bodies can be expected to develop on the bark over a period of 4–6 weeks. Permanent collections of the fruiting bodies of larger, sturdier species were dried on the bark and mounted in small paper boxes. Smaller, more delicate specimens were picked off the substrate with fine jeweler's forceps and mounted in lactophenol solution on a microscope slide. These slide mounts were made more or less permanent by sealing the coverslip with clear fingernail polish.

Collections of each taxon listed are deposited in the Herbarium of the University of California, Berkeley (UC). Nomenclature follows that of Martin and Alexopoulos (1969), except where noted.

Liceales

Liceaceae

Licea biforis Morgan

Substrates: *Arbutus menziesii* Pursh, *Populus fremontii* Wats., *Quercus* sp., *Q. suber* L., *Vitis californica* Benth.   Distribution: Butte Co., Marin Co. Probably cosmopolitan.

This species is common and often forms extensive fruitings on bark. It is easily overlooked, however, because the sporangia are dark at maturity and usually blend in well with the bark surface. The fruiting bodies of *L. biforis* are elongate, sessile, and open by an apical, longitudinal slit.

Licea castanea G. Lister

Substrates: *Juglans* sp., *Quercus* sp.   Distribution: Butte Co., Los Angeles Co. (Santa Catalina Island). Throughout Europe and North America.

Licea castanea has chestnut-brown sporangia and is common but inconspicuous. The peridium of this species is divided into platelets by preformed lines of dehiscence. At maturity, the platelets reflex to allow spore escape.

Licea kleistobolus Martin

Substrates: *Juniperus occidentalis* Hook., *Platanus racemosa* Nutt., *Vitis californica.*   Distribution: Butte Co., Lassen Co. North America, Europe.

This is an extremely common corticolous species with operculate sporangia. The operculum is copper-colored and has a convex center, whereas the rest of the fruiting body is dull brown to black. It can be readily obtained on grapevine bark, and often produces hundreds of sporangia per moist chamber.

Licea parasitica (Zukal) Martin

Substrates: *Castanea dentata* L., *Chamaecyparis lawsoniana* (A. Murr.) Parl., *Cupressus macnabiana* A. Murr., *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus lobata* Nee, *Q. suber, Umbellularia californica* (H. & A.) Nutt., *Vitis californica.*   Distribution: Butte, Marin, and Sonoma Cos. Throughout Europe and North America.

This is perhaps the most commonly encountered *Licea* in California. It is operculate, with the sporangium wall and lid dull black in color. Freshly matured sporangia in moist chambers show a distinct pale line circumscribing the lid, but after drying the sporangia shrivel and the operculum becomes less distinct.

Licea pedicellata (H. C. Gilbert) H. C. Gilbert

Substrates: *Casuarina* sp., *Quercus lobata.*   Distribution: Butte Co., Los Angeles Co. (Santa Catalina Island). Known from Europe and North America.

This species has stipitate sporangia with the peridium divided into several platelets. These divisions are best seen in fresh sporangia because the sporangia take on a wrinkled appearance when dry.

Licea perexigua Brooks & Keller, in Keller and Brooks, Mycologia 69: 674. 1977.

Substrates: *Quercus douglasii* H. & A., *Q. lobata, Quercus* sp., *Umbellularia californica.*   Distribution: Butte, Marin, and Sonoma Cos. Known from Arkansas, Kansas, Kentucky, and Missouri. Probably occurs throughout North America.

This species is very small, less than 100 μm in height, and is somewhat difficult to detect. The sporangia are subsessile to short stipitate, and are metallic gray in color. This minute myxomycete often fruits abundantly in moist-chamber culture.

Licea pusilla Schrad.

Substrate: *Juniperus occidentalis.*   Distribution: Lassen Co. Known from Europe and North America.

A single collection of this species was obtained on bark, but it is probably more common than this appears to indicate. Kowalski (1966) reported this species from Butte County on decayed wood, a common substrate for *L. pusilla.* This species is similar to *L. castanea* in that

both have peridia broken into platelets and have sessile sporangia of similar sizes. In *L. pusilla* the sporangia are purple-brown to black, and the spores are dark olive-brown. *Licea castanea* has pale brown sporangia with pale yellow-brown spores.

Licea scyphoides Brooks & Keller, in Keller and Brooks, Mycologia 69:679. 1977.

Substrates: *Quercus lobata, Q. suber, Quercus* sp., *Salix* sp., *Vitis californica.*   Distribution: Butte, Los Angeles (Santa Catalina Island), Marin, and Sacramento Cos. Known from several locations in the United States.

A common corticolous species in California, *L. scyphoides* has dull black, stipitate sporangia with a more or less equatorial line of dehiscence. After drying the sporangia often dehisce, leaving a cup-like portion of the peridium attached to the stipe. This is a new California record.

Cribrariaceae

Cribraria violacea Rex

Substrates: *Juglans* sp., *Platanus racemosa, Quercus lobata, Vitis californica.*   Distribution: Butte, Santa Barbara, and Tehama Cos. Cosmopolitan.

The long-stipitate, dark purple sporangia of this species are easily recognized and should be confused with no other corticolous myxomycete. It is fairly common although it did not fruit in great abundance during this study. Bark collected in riparian areas frequently yields this species when placed in moist chambers.

ECHINOSTELIALES

Echinosteliaceae

Echinostelium apitectum Whitney, Mycologia 72:954. 1980.

Substrates: *Juniperus occidentalis, Quercus* sp.   Distribution: Lassen Co. Reported from Australia (D. W. Mitchell, pers. comm.).

This species is common on juniper bark in Lassen County, but it has not been found elsewhere in California. It is distinguished by the presence of a minute columella borne beneath a sporelike covering at the stipe apex.

Echinostelium brooksii Whitney, Mycologia 72:957. 1980.

Substrates: *Cupressus macnabiana, Cercocarpus ledifolius* Nutt., *Juniperus occidentalis, Pinus* sp.   Distribution: Butte Co., Lassen Co. Known from North America and Europe.

The darkly pigmented, lenticular columella and large pink spores with a thin area in the wall distinguish this species. *Echinostelium brooksii* is especially common in Lassen County on juniper bark. Often

hundreds of sporangia occur on a single piece of bark in moist-chamber culture.

Echinostelium coelocephalum Brooks & Keller, in Keller and Brooks, Mycologia 68:1212. 1976.

Substrates: *Acer negundo* L., *Quercus lobata.*   Distribution: Butte Co. Known from several locations in the United States.

The white to cream-colored sporangia of this species are usually less than 70 μm in height and are quite difficult to detect in moist chambers. This species has a sporelike columella and spores with distinct spore-to-spore articular surfaces. It was collected from a single location in Butte County (Pine Creek Ranch, 23 km northwest of Chico), but it probably occurs on similar substrates elsewhere in the state.

Echinostelium colliculosum Whitney & Keller, Mycologia 72:641. 1980.

Substrates: *Juniperus occidentalis, Quercus lobata, Vitis californica.*   Distribution: Butte, Lassen, and Sacramento Cos. Known from Europe and North America. Reported from Australia (D. W. Mitchell, pers. comm.).

This species resembles *E. coelocephalum,* but *E. colliculosum* has larger sporangia and spores, and less prominent spore articular surfaces.

Echinostelium corynophorum Whitney, Mycologia 72:963. 1980.

Substrate: *Juniperus occidentalis.*   Distribution: Lassen Co. North Carolina. Reported from Australia (D. W. Mitchell, pers. comm.).

This species has been found on juniper bark in Lassen County and is only rarely encountered in California. It is distinguished by a hyaline to pale yellow-brown, hemispheric columella, and white spores bearing articular surfaces at points of spore-to-spore contact.

Echinostelium fragile Nann.-Brem.

Substrates: *Artemisia tridentata* Nutt., *Cupressus* sp., *Juniperus occidentalis, Quercus lobata.*   Distribution: Lassen, Los Angeles (Santa Catalina Island), and Sacramento Cos. Known from Europe and North America.

This is another common species on juniper bark in Lassen County, and it is occasionally found in other areas of the state. *Echinostelium fragile* has a fusiform, darkly pigmented columella and pink spores with a thin region in the spore wall.

Echinostelium lunatum Olive & Stoianovitch, Mycologia 63:1050. 1971.

Substrates: *Cupressus macnabiana, Vitis californica.*   Distribution: Butte Co., Sacramento Co. North Carolina. Puerto Rico.

This is one of the smallest known myxomycetes, with sporangia usually less than 50 μm in height. The sporangia are easily overlooked in moist chambers, and this probably accounts for the apparent rarity of

this species. It is recognized easily by its small size and the tan, crescent-shaped columella that supports the spores.

Echinostelium minutum de Bary

Substrates: *Juniperus occidentalis, Quercus lobata, Pseudotsuga menziesii.* Distribution: Throughout California. Cosmopolitan.

Echinostelium minutum is fairly common in California, especially on the bark of Douglas fir. This species is the tallest member of the genus, with sporangia up to 500 μm in height. The spore mass is white to pinkish, and a delicate branching capillitium arises from a short columella.

Echinostelium paucifilum Whitney, Mycologia 72:974. 1980.

Substrate: *Juniperus occidentalis.* Distribution: Known only from Lassen Co.

This species is characterized by large, pink spores, an elongate, dark brown columella, and a sparse capillitial system. It is one of the largest *Echinostelium* species, with sporangia up to 350 μm in height.

Clastodermataceae Alexopoulos & Brooks,
Mycologia 63:926. 1971.

Clastoderma pachypus Nann.-Brem., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., C Sect. 71:44. 1968.

Substrate: *Cupressus macnabiana.* Distribution: Butte Co. Known from Europe and North America.

This species occurs frequently on bark of Macnab cypress, a serpentine endemic. The chocolate brown sporangia and the capillitium forming a globose net distinguish this species. This is a new California record.

Trichiales

Dianemaceae

Calomyxa metallica (Berk.) Nieuwl.

Substrates: *Castanea dentata, Platanus racemosa, Populus fremontii.* Distribution: Butte Co., Sacramento Co. Cosmopolitan.

This species can be found on dead wood as well as bark. The fruitings on bark in moist chambers usually consist of widely scattered sporangia, in contrast to collections on dead wood, which normally occur as aggregates of sporangia. Sporangia of *C. metallica* are sessile and iridescent purple when freshly matured; the spores are bright yellow.

Trichiaceae

Perichaena chrysosperma (Currey) A. Lister

Substrate: *Quercus* sp. Distribution: Los Angeles Co. (Santa Catalina Island). Cosmopolitan.

Perichaena corticalis (Batsch) Rost.

Substrates: *Juglans* sp., *Quercus lobata, Vitis californica.*   Distribution: Butte Co., Tehama Co. Cosmopolitan.

These two species of *Perichaena* are very similar and somewhat difficult to separate. Both have reddish brown to black peridia and bright yellow spores. *Perichaena chrysosperma* tends to produce scattered plasmodiocarps, whereas *P. corticalis* usually forms clustered sporangia.

Hemitrichia abietina (Wigand) G. Lister

Substrates: *Cupressus macnabiana, Pseudotsuga menziesii.*   Distribution: Butte Co. Probably cosmopolitan.

This species normally occurs on dead wood, but it is not uncommon on bark. *Hemitrichia abietina* has a thin, iridescent peridium that falls away in the upper portion of the sporangia at maturity, exposing the yellow spore mass and leaving behind a distinct cup.

STEMONITALES

Stemonitaceae

Enerthenema papillatum (Pers.) Rost.

Substrate: *Juniperus occidentalis.*   Distribution: Lassen Co. Cosmopolitan.

This species occurs on bark and decayed wood but is more frequently encountered on the latter substrate. The black stipitate sporangia with a shining apical disc distinguish this species.

Macbrideola cornea (G. Lister) Alexop.

Substrates: Common on a wide variety of woody plants.   Distribution: Butte, Marin, Monterey, Sacramento, Santa Barbara, and Sonoma Cos. Probably cosmopolitan.

Macbrideola decapillata H. C. Gilbert

Substrate: *Juniperus occidentalis.*   Distribution: Lassen Co. Probably cosmopolitan.

Macbrideola is a common genus on bark in moist chambers, occurring as scattered, brown, stipitate sporangia. The two listed species are similar in appearance, and can be distinguished only by microscopic characteristics. *Macbrideola cornea* has a rigid capillitium, and the tips of the capillitial threads are distinctly blunt. *Macbrideola decapillata* has a sparse to absent capillitial system that, when present, has sharply pointed free ends.

Lamproderma arcyrionema Rost.

Substrates: *Cupressus macnabiana, Vitis californica.*   Distribution: Butte Co. Cosmopolitan.

This is the most common species of *Lamproderma* on bark in California. The sporangia have long, slender stalks and a persistent, iridescent peridium.

Comatricha acanthodes Alexop.

Substrates: *Castanea dentata, Catalpa speciosa, Quercus* sp. Distribution: Butte Co., Sonoma Co. Known from Virginia and Greece.

This species seems to be fairly rare in California. It can be distinguished from other *Comatricha* species by the rigid, sparse capillitium and the distinctly spiny spores. This is a new California record.

Comatricha fimbriata G. Lister & Cran

Substrates: Common on a wide variety of tree species. Distribution: Throughout California. Cosmopolitan.

Comatricha fimbriata is a commonly encountered corticolous myxomycete. The major distinguishing feature is the swollen tips of the capillitial threads.

Comatricha laxa Rost.

Substrates: *Populus fremontii, Yucca brevifolia* Engelm. Distribution: Butte Co., Riverside Co. Probably cosmopolitan.

Comatricha laxa is commonly found on dead wood, but it is seen occasionally on bark in moist chambers. This species has ovoid to cylindric, reddish brown sporangia and brown spores.

PHYSARALES

Physaraceae

Badhamiopsis ainoae (Yama.) Brooks & Keller, in Keller and Brooks, Mycologia 68:836. 1976.

Substrates: *Juglans* sp., *Quercus* sp., *Quercus lobata.* Distribution: Butte Co., Sonoma Co. Known from Japan and North America.

Badhamiopsis ainoae is characterized by effused plasmodiocarps and sporangia, granular lime deposits on the upper surface of the peridium, and calcareous spikes running between the upper and lower peridia. It is common in California and often forms large fruitings on bark in moist chambers.

Badhamia affinis Rost.

Substrate: *Quercus lobata.* Distribution: Butte Co., Marin Co. Cosmopolitan.

This is one of the few corticolous myxomycetes easily collected in the field. *Badhamia affinis* often forms extensive fruitings on living trees, the large, white, stipitate fruiting bodies often covering the trunk and extending well into the branches.

Badhamia bispora Whitney, Mycologia 70:672. 1978.

Substrate: *Juniperus occidentalis.* Distribution: Known only from Lassen Co.

Badhamia nitens Berk.

Substrates: *Cupressus macnabiana, Quercus lobata.*   Distribution: Butte Co. Probably cosmopolitan.

Badhamia bispora and *B. nitens* are similar in most charateristics and can be distinguished best using spore morphology. *Badhamia nitens* has spores in clusters of four to twenty. *Badhamia bispora* has spores that fuse together in pairs.

Physarum crateriforme Petch

Substrates: Common on a wide variety of tree species.   Distribution: Common throughout California. Probably cosmopolitan.

This species has stipitate sporangia with white, limy peridia. A large, central lime-filled columella is usually present and is distinctive. This species is fairly easy to obtain in the field due to its relatively large, stipitate sporangia.

Physarum decipiens Curtis

Substrate: *Quercus lobata.*   Distribution: Butte Co. Probably cosmopolitan.

This species is characterized by its yellowish to orange, calcareous peridium and its plasmodiocarpous habit. It is not common on bark in California.

Didymiaceae

Trabrooksia applanata Keller, Mycologia 72:396. 1980.

Substrates: *Juglans* sp., *Quercus lobata.*   Distribution: Butte Co., Marin Co. Known from Europe and North America.

The flattened plasmodiocarps of this species are limeless and somewhat iridescent. They blend in well with the bark surface and are easily overlooked. It is common in California.

Diderma chondrioderma (de Bary & Rost.) G. Lister

Substrates: *Diospyros* sp., *Juglans* sp., *Quercus suber.*   Distribution: Butte Co. Probably cosmopolitan.

Diderma chondrioderma is seen occasionally on bark in California. It can be recognized readily by the flattened white sporangia and the pinkish columella. The granular lime deposits on the peridium are often quite thick, giving the sporangia a distinctly chalky appearance.

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NOTES AND NEWS

GYNODIOECY IN *Saxifraga integrifolia* (SAXIFRAGACEAE).—*Saxifraga integrifolia* Hook. is a perennial herb found principally in vernally wet, mossy and grassy meadows at low elevations west of the Cascade Mountains in southern British Columbia, Washington, and Oregon. In a population on a small Puget Sound island at Deception Pass, Washington, some plants were found that had only small, green to brown anthers while other plants had larger, orange anthers. Inflorescences were collected from this population, segregated according to anther type, and preserved in Carnoy's solution. Anatomical studies of flowers using standard paraffin embedding, sectioning, and staining techniques showed that, in flowers with green anthers, microsporogenesis fails, leading to male-sterility, but that embryo sac development is normal. In flowers with orange anthers, microsporogenesis appears normal, abundant pollen is produced, and embryo sac development is normal. These flowers are hermaphroditic.

During three field seasons, 1100 inflorescences were examined to determine the ratio of hermaphrodites to male-steriles. The ratio remained constant at 2:1. In the first year, plants were marked according to anther type and re-examined each year. Male-steriles remained male-steriles and hermaphrodites remained hermaphrodites. Male sterility in plants at Deception Pass involves a complete abortion of microsporogenesis and is not influenced by environmental factors known to affect pollen development in other plants (Jones, Amer. J. Bot. 63:657–663. 1976). The population of *S. integrifolia* at Deception Pass is gynodioecious.

For comparative purposes, specimens were collected from Deception Pass and from populations of *S. integrifolia* that did not exhibit gynodioecy. From these specimens, ovule number per carpel, percent seed set, and pollen stainability were determined. In addition, hermaphroditic plants from Deception Pass were brought into a greenhouse and were selfed in an insect-free cage to determine if they were self-compatible.

The results in Table 1 show no significant differences between hermaphrodites and male-steriles at Deception Pass in ovule number per carpel or percent seed set. Plants

TABLE 1.   OVULE NUMBER PER CARPEL AND POLLEN STAINABILITY FOR *S. integrifolia* AND PERCENT SEED SET OF FIELD PLANTS COMPARED WITH THAT OF EXPERIMENTALLY SELFED PLANTS FROM DECEPTION PASS. $\bar{x}$ is the average ± standard deviation (S.D.). Numbers in parentheses refer to collections by Elvander, vouchers at WTU.

	No. flowers/ no. plants	$\bar{x}$ ± S.D.
Number of ovules/carpel		
San Juan Islands/Columbia River Gorge		
(*563, 575, 600, 607*)	44/12	106 ± 40.0
Deception Pass (*543, 819*)	27/13	154 ± 36.1
Male-steriles	14/7	154 ± 24.8
Hermaphrodites	13/6	154 ± 46.4
Percent pollen stainability		
Columbia River Gorge (*563, 566, 585, 813, 814*)	44/44	77 ± 17.1
Deception Pass (*543, 545, 588, 819*)	6/6	87 ± 9.4
Percent seed set/Deception Pass (*543, 819*)	27/13	78 ± 11.7
Male-steriles	14/7	78 ± 12.5
Hermaphrodites	13/6	78 ± 11.3
Selfed hermaphrodites	10/3	38 ± 22.4

at Deception Pass had a higher average number of ovules per carpel and percent pollen stainability than for other populations of *S. integrifolia*. The differences in ovule number and percent pollen stainability seem to indicate that the gynodioecious population has slightly higher potential fecundity than the other populations examined. The hermaphrodites from Deception Pass that were selfed had an average 38% seed set and thus, are at least partially self-compatible. Gynodioecy has been associated with self-compatibility as well as with effects of severe inbreeding and with maintenance of hybridity (Lewis and Crowe, Evolution 10:115–125. 1956; Jain, Genetics 46:1237–1240. 1961; Levin, Taxon 20:91–113, 1971).

Gynodioecy has not been noted previously for *Saxifraga* (Lewis, New Phytologist 50: 56–63. 1941; Biol Rev. Cambridge Philos. Soc. 17:46–67. 1942; Lewis and Crowe, Evolution 10:115–125. 1956) though two dioecious species have been described (Engler and Irmscher, Das Pflanzenreich. 1916; Chambers, Madroño 17:203–204. 1964). Male-sterile plants have been reported from the San Juan Islands, Washington (personal observation) and irregular meiosis has been reported in plants from southwestern British Columbia and Vancouver Island (Beamish, Canad. J. Bot. 39:567–580. 1961). These populations have not yet been studied. The full extent and significance of gynodioecy in *S. integrifolia* is not yet known. I thank Melinda Denton and the Department of Botany and Plant Pathology, Oregon State University, Corvallis. This study was part of a Doctoral Dissertation at the Department of Botany, University of Washington, Seattle. A portion of this study was supported by a National Science Foundation grant.— PATRICK E. ELVANDER, Biology Board, University of California, Santa Cruz 95065. (Received 14 Aug 1981; revision accepted 20 Dec 1981.)

EFFECTS ON *Lomatium triternatum* OF THE 1980 ASH FALLOUT FROM MT. ST. Helens.—Three populations of *Lomatium triternatum* (Pursh) Coult. & Rose (Umbelliferae) that were in the path of the ash fallout had been monitored for several consecutive years prior to the eruption of Mt. St. Helens on 18 May 1980. These populations are from Deary, Idaho; Pullman, Washington, on the corner of Stadium Way and the Moscow highway; and Magpie Hill, a kilometer north of Pullman. Annually-assembled data included population size, height, and sex ratios of tagged plants. In addition to these three populations, two others several hundred km to the south of the ash zone had been monitored. These are located 32 km west of Burns, Oregon, highway 20, and in the Challis National Forest of Idaho, 4 km from the junction of Wild Horse Creek and Fall Creek on the trail toward Moose Lake.

No significant differences were found in plant size, number of leaves, or sex ratio between plants in populations within and outside of the zone of ash fallout. It is particularly fortunate that both groups of populations continued to be monitored during the eruption year because of the striking difference in percent flowering individuals per population between 1980 and 1981. The same sorts of differences, however, occurred regardless of whether or not the populations were within the zone of ash fallout. The ash had no noticeable effect on plant height, number of leaves or sex ratios nor on the proportion of individuals of the populations that flowered. Flowering of this herbaceous perennial fluctuates greatly from year to year in the same population.

Data are interpreted as partly resulting from the time of ashfall relative to the life cycle of this species. *Lomatium triternatum* had already begun to set seed at the time of maximum fallout. Had it not passed its flowering peak it might have suffered some setback, but still without local extermination, much as Mack (Science 213:537–539) noted with *Veratrum* and *Balsamorhiza*. *Lomatium triternatum* is not a forest dweller

and receives no protection from other plants, but its linearly dissected leaves with lax leaflets facilitated the movement of the ash through the plant without damaging leaves or stem. In view of the frequency of Cascade Range volcanism during the past several hundred millenia and the prevailing westerlies, this species from eastern Washington and Idaho may have evolved the structure that permits it to endure during ash fallouts. Support is acknowledged from the NSF, DEB 80-20937, Notice #82.—AMY JEAN GILMARTIN, Department of Botany, Washington State University, Pullman 99164. (Received 16 Sep 1981; revision accepted 20 Dec 1981.)

NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

POLYSTICHUM KRUCKEBERGII Wagner (POLYPODIACEAE).—Canada, B.C., Cassiar District, 1 km s. of W. Kwanika Cr. (55°33'N, 125°21'W), 1050 m, 27 Jul 1981, *A. L. Kruckeberg 204* (UBC). Locally frequent on steep scree of serpentine barren.

Previous knowledge. Species known from the vicinity of Lillooet, B.C., s. to CA and NM. Herbaria consulted: UBC, ORE.

Significance. A range extension of ca. 580 km nnw.; also the first record of the species from the Sub-boreal Spruce zone of British Columbia.—ARTHUR LEO KRUCKEBERG, Dept. Botany, Univ. British Columbia, Vancouver, Canada V6T 1W5. (Received 28 Jan 1982).

CALIFORNIA

CYMOPTERUS RIPLEYI Barneby (APIACEAE).—Inyo Co., Coso Range, slopes of Owens Valley (T19-20S R37E); 27 Apr 1974, *DeDecker 3403* (RSA and private herbarium), a few plants on a slope n. of Haiwee Reservoir (T19S R37E S34nw¼); 11 May 1978, *DeDecker 4663* (UC and private herbarium), a well established population along the Cactus Flat Rd. e. of Haiwee Reservoir (T20S R37E S2nw¼); and 15 Apr 1978, Mary Ann Henry, verified by DeDecker, e. of Olancha (T19S R37E S25n½).

Previous knowledge. Known from Esmeralda, Lincoln and Nye Cos., NV.

Significance. First record for CA, and most w. location, a disjunction of 160 km. Considered rare in CA, common elsewhere, by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980).

CRYPTANTHA SCOPARIA A. Nels. (BORAGINACEAE).—Inyo Co., Inyo Mts.; 20 Jul 1971, *DeDecker 2776* (RSA and private herbarium), established in gully and along roadside on the e. slope of Mazourka Pk., w. of Badger Flat (T11S R35E S23sw¼); 6 Jul 1974, *DeDecker 3549* (Private herbarium), same location as above; 13 Jul 1974, *DeDecker 3552* (SB, CAS, RSA and private herbarium), same location as above; 20 Jun 1980, *DeDecker 5047* (Private herbarium), Hines Rd. s. of Waucoba Rd. (T10S R36E S6ne¼).

Previous knowledge. Known from WA, OR, ID, WY and NV.

Significance. First record for CA. Although infrequent, it is probable that it is more widespread than has been noted. Considered rare in CA, common elsewhere, by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980).

ASTRAGALUS ARGOPHYLLUS Nutt. ex Torr. & Gray var. ARGOPHYLLUS (FABACEAE).—Mono Co., Fish Slough (T5S R32E S30sw¼); 14 May 1974, *DeDecker 3481*

(RSA, CAS and private herbarium); 15 Jul 1976, *DeDecker 4106* (Private herbarium); 2 Jun 1978, *DeDecker 4716* (Private herbarium); 20 Jun 1978, *DeDecker 4730* (NY and private herbarium), verified by R. C. Barneby. All of the above were from the vicinity of BLM Spring, 1280 m, where the colony is limited to about 10 plants. Another population has been noted about 1 km nw. of that spring.

Previous knowledge. According to Barneby (R. C. Barneby, Atlas of North American Astragalus, Part II, 1964) the plant is known from central and nw. NV to ID, WY, MONT and central UT.

Significance. First record for CA, apparently the most southerly occurrence, a disjunct population, possibly having followed the waterways of the Pleistocene Epoch. Considered rare in CA, common elsewhere, by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980).

ERIOGONUM PUBERULUM S. Wats. (POLYGONACEAE).—Inyo Co., Panamint Range, Cottonwood Mts., Tin Mountain, Death Valley Natl. Mon.; 7 Jul 1978, *DeDecker 4754* (CAS and private herbarium), summit Tin Mountain, 2728 m (ca. 36°02′N, 117°27′W); 24 Jul 1978, *DeDecker 4760* (UC and private herbarium), summit Tin Mountain; 25 Jul 1978, observed by DeDecker and Pavlick on s. slope of Tin Mountain, 2440 m. Confirmed by John Thomas Howell and James R. Reveal.

Previous knowledge. Known from UT and NV.

Significance. First record for CA, as well as the most westerly occurrence, and possibly the highest in elevation, a disjunction of perhaps 250 km. Considered rare in CA, common elsewhere, by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980). Although this plant has been known as an *Eriogonum*, the fact that its "involucres" are actually nodal bracts raises a question as to its generic position.—MARY DEDECKER, P.O. Box 506, Independence, CA 93526. (Received 29 Oct 1981)

HIERACIUM ARGUTUM Nutt. var. PARISHII (Gray) Jepson.—San Diego Co., Corte Madera ranch, just s. of Pine Valley, 60 km e. of San Diego, 1300 m, 10 Aug 1980, *van der Werff 4123* (SD, CAS); 5 Jul 1981, *van der Werff 4334* (LA).

Previous knowledge. Southern face of the San Gabriel and San Bernardino Mts. to Ventura Co. Mainland stations for the typical variety are Santa Barbara and San Luis Obispo Cos. Herbaria consulted: SD, RSA, POM, LA.

Significance. First record for San Diego Co., a range extension of 200 km.

CYPSELEA HUMIFUSA Turpin.—San Diego Co., Corte Madera ranch, just s. of Pine Valley, 60 km e. of San Diego, 1300 m, 10 Aug 1980, *van der Werff 4128* (SD, CAS); 5 Jul 1981, *van der Werff 4332* (LA). Not rare, on drying lake shore.

Previous knowledge. A West Indian species. In California recorded only from the lower San Joaquin River, Santa Cruz, Marin, Sonoma, and Lake Cos. Herbaria consulted: SD, RSA, POM, LA.

Significance. First record for southern CA, a range extension of 700 km.

NELUMBO LUTEA (Willd.) Pers.—San Diego Co., Corte Madera ranch, just s. of Pine Valley, 60 km e. of San Diego, 1300 m, 30 Aug 1980, *van der Werff 4136* (SD, CAS, LA). Well-established in a small, man-made lake. Possibly introduced with cattle from Texas.

Previous knowledge. From e. Oklahoma, e. Texas to Florida, New England.

Significance. First record for CA.

LASTHENIA GLABERRIMA DC.—San Diego Co., Corte Madera ranch, just s. of Pine Valley, 60 km e. of San Diego, 1300 m, 3 Jul 1980, *van der Werff 4017* (SD, CAS, LA; additional duplicates distributed by SD).

Previous knowledge. From Washington to s. Monterey Co. Herbaria consulted: SD, RSA, POM, LA.

Significance. First record for southern CA, a range extension of about 500 km.—
HENK VAN DER WERFF, 4239 Arden Way, San Diego, CA 92103. (Received 29 Nov 1981)

ERIOPHYLLUM CONGDONII Brandg. (ASTERACEAE).—Mariposa Co., along n. side of South Fork of Merced River from Zip Cr. to Devil Gulch 6.5 km intermittently, 620–915 m, 23 Apr 1981, *Botti 92* (CAS); summit and nw. ridge of Iron Mtn., Sierra Natl. Forest, 1190–1890 m, 15 May 1981, *Botti 113* (CAS).
Previous knowledge. Known only from Merced River canyon on ridges adjacent to Rancheria Flat at El Portal.
Significance. This is the first record of *E. congdonii* in the South Fork of the Merced drainage and the first collection from outside the localized area surrounding Rancheria Flat. The vast number of plants observed more than doubles the known population. Also, the collection from Iron Mtn. (1890 m) is the highest known station for *E. congdonii*. This may be significant in determining the relationship between *E. congdonii* and its closest relative *E. nubigenum,* which grows at a similar elevation. Due to the meagerness of known collections, *E. nubigenum* was at one time thought to be a dwarf alpine representative of *E. congdonii,* and the two were thought to grow at greatly varying elevations (Constance, L. 1937, A systematic study of the genus *Eriophyllum* Lag. Univ. Calif. Publ. Bot. 18:69–135). *E. congdonii* is listed in the Federal Register (45FR8248082569) by the Endangered Species Office as a taxon for which enough information exists to support listing as an endangered or threatened species. It is considered "rare and endangered" by the California Native Plant Society (Smith et al., Inv. rare and endang. vasc. pls. Calif., CNPS Spec. Publ. 1, ed., 2, 1980).

LEWISIA CONGDONII (Rydb.) J. T. Howell (PORTULACACEAE).—Mariposa Co., Sierra Natl. Forest, summit of Iron Mtn. and along nw. ridge extending to South Fork of the Merced River, 915–1890 m, 15 May 1981, *Botti 117* (CAS). Approximately 7000 plants were located in areas of sparsely vegetated metamorphic rock, mostly facing north. Associated species include *Allium yosemitense* and *Eriophyllum congdonii,* both extremely rare and localized.
Previous knowledge. Known from El Portal and Chowchilla Mtn. in Mariposa Co., CA, and near Yucca Point along Hwy. 180, Fresno Co., CA.
Significance. This collection establishes only the fourth known site for *L. congdonii.* The large size of the newly discovered population is important in assessing the rarity of the taxon. In the December 15 1980 Federal Register (45FR8248082569) the Endangered Species Office listed *L. congdonii* within Category 1, which includes taxa for which enough information exists to support listing as an endangered or threatened species. Considered "rare and endangered" by the California Native Plant Society (Smith et al., Inv. rare and endang. vasc. pls. Calif., CNPS Spec. Publ. 1, ed. 2, 1980). The new population also establishes an intermediate link between the El Portal site 8 km to the ne. and the Chowchilla Mtn. site 5 km to the s.—STEPHEN BOTTI, Resources Management Specialist, Yosemite Natl. Park, CA 95389. (Received 10 Dec 1981)

OXYTHECA WATSONII Torrey & Gray (POLYGONACEAE).—Inyo Co., 1.3 km nne. of jct. State Hwy. 190 and Saline Valley Rd., Santa Rosa Wash vicinity, extreme s. end of Santa Rosa Flat (T18S R40E, S15 projected), 24 Sep 1980, *Stone, Castagnoli, and de Nevers 316* (CAS, MARY, RSA). Verified by B. Ertter, 1981. Population of over 100 plants over a broad, fully exposed area (1 ha or greater), 1480 m.
Previous knowledge. The collection *Parish & Parish 1241* from "N slope of San Bernardino Mts., near Cushenberry (sic) Springs, May 1882," originally but erroneously referred to *Oxytheca watsoni* (sic), is now the type for *Oxytheca parishii* Parry var. *goodmaniana* Ertter. *Oxytheca watsonii* is otherwise known only from four scattered localities in c. and wc. Nevada (Ertter, *Brittonia* 32:80, 1980).
Significance. Currently under review for listing as threatened or endangered (US Fish

& Wildlife Serv., Federal Register 45:82525, 15 Dec 1980). This record is the first *correct* one for *Oxytheca watsonii* from California and represents a 225 km range extension from the nearest Nevada locality.—R. DOUG STONE, Environmental Field Program, University of California, Santa Cruz 95064. (Received 19 Jan 1982)

COLORADO

ERIASTRUM DIFFUSUM (A. Gray) H. L. Mason (POLEMONIACEAE).—Mesa Co., nw.-facing slope of knoll, Rabbit Valley, se. from junction of Rabbit Valley Rd. and Interstate 70 (T10S R104W S16, 30°11′N, 109°0′W), 1400 m, 23 May 1980, *Kelley 80-33* (Mesa College Herb.), 16 Jun 1980, *Kelley 80-92* (Mesa College Herb., CS).
Previous knowledge. Widespread from s. CA, AZ, nw. MEX, sw. NM, w. TX n. to NV and UT. Herbaria consulted: BRY, COCO, COLO, CS, RM, USFS, Mesa College.
Significance. This is the first record of the species and the genus in CO, representing a 200 km disjunction from nearest known localities in Garfield and San Juan Cos., UT.

CRYPSIS ALOPECUROIDES (Pill. & Mitlerp.) Schrad. (POACEAE).—Jefferson Co., se. shore of Standley Lake near north Kipling St. (39°52′N, 105°7′25″W), 1520 m, 5 Sep 1980, *Walter and Lormond s.n.* (CS).
Previous knowledge. Widespread from n. CA to s. WA and known from 1 locality each in ID and WY (Hammel and Reeder, Syst. Bot. 4:267–280. 1979).
Significance. This is the first record of the species and the genus in CO, representing a 240 km disjunction from the nearest known locality in Goshen Co., WY. As noted by Hammel and Reeder (1979) this species is spreading rapidly throughout w. N. Amer. as an Old World introduction.—WALT KELLEY, Dept. of Biology, Mesa College, Grand Junction, CO 81501; GENEVIEVE BRYANT and DIETER WILKEN, Dept. of Botany and Plant Pathology, Colorado State University, Fort Collins 80523. (Received 29 Jan 1982)

Correction. For the chromosome count of *Tanacetum huronense* Nutt., Madroño 29:62, 1982, the county should have been given as Emmet County, MI, not Cheboygan County, and, although there are other plants from the same population in the herbarium at MICH, the voucher actually grown from the plants that were counted is deposited at MO.—Peter H. Raven, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166.

REVIEW

Bromelioideae (Bromeliaceae). By LYMAN B. SMITH and ROBERT J. DOWNS. Flora Neotropica Monograph No. 14, Part 3:1493–2142, New York Botanical Garden, Bronx, NY 10458. 1979. ISBN 0-89327-210-8. $65.00!

This volume is another in the growing list of welcome treatments in the Flora Neotropica Monograph series. Appearance of this particular title, however, gives the botanical community special reason for celebration because it marks completion of the largest family of angiosperms yet to be treated in the ongoing series. Treatments for subfamilies Pitcairnioideae and Tillandsioideae appeared as Monographs No. 14, Part 1 (1974) and No. 14, Part 2 (1977) respectively.

The Bromelioideae are technically distinguished from the other subfamilies by the inferior ovary, indehiscent baccate fruits, and naked seeds but the group is probably best known to both botanist and layperson through the pineapple (*Ananas*) and various greenhouse ornamentals such as *Aechmea, Billbergia,* and *Cryptanthus.* As interpreted by Smith and Downs this subfamily consists of 27 genera and 723 specific and infraspecific taxa with a geographic distribution extending from Mexico and the West Indies south to Chile and Argentina. By any estimate, however, the Bromelioideae are best represented in Brazil.

In content and general style this volume adheres to the effective format used in previous monographs of the series. For all species and infraspecific taxa the authors present a statement of synonymy; concise descriptions; collector(s), locality and physical location of the type specimen(s); a statement of habitat, elevational range, and geographical distribution supported by citation of specimens examined. Lists of hybrids and cultivars are appended to treatments for many of the genera and the volume concludes with a numerical list of taxa, list of exsiccatae, and a general exhaustive index. Unfortunately pages 2099–2102 are missing from the index to my review copy, so available stock of the press run should be checked for this defect. The text is enhanced by numerous distribution maps and over 200 line drawings that vary in clarity and detail. All maps depict collective ranges of species in a genus or subgenus instead of ranges for specific taxa—a prudent and justified practice because so many of the taxa are known from few collections. At a time when tropical vegetation throughout the world is facing rapid, irreversible destruction, it is distressing to learn that 195 of the taxa treated in this volume are known from type collections only. Dozens of others in the Bromelioideae are known only from the type locality or from specimens in cultivation.

After perusing this volume in some detail, I felt the desire to learn more about relationships of the species, something of their variation, and in some cases reasons for the particular taxonomic treatment chosen by the authors. Commentaries with this information are lacking in this volume and understandably reflect the fact that much remains to be learned about this curious, complex and little-collected subfamily of Bromeliaceae. Like all monographic and floristic publications dealing with tropical plants, this volume provides a useful progress report that can be reviewed and emended as new information comes to light. Smith has published voluminously on the Bromeliaceae for decades and completion of the Flora Neotropica treatment will certainly be viewed as a crowning achievement in this phase of his long and productive career. To be sure, Smith and Downs have produced a monumental treatise on the Bromeliaceae that will serve as the standard and indispensable reference for decades to come.—FRANK ALMEDA, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118.

REVIEWERS OF MANUSCRIPTS

Perhaps the most difficult task facing an editor is the selection of appropriate re-
viewers for manuscripts. He faces the dual responsibility of finding people who can
provide thoughtful, constructive criticism for the author and of not overworking
any given set of reviewers. Frequently those most capable of providing the kinds of
advice most severely needed are the busiest people in their fields. The people listed
below have generously contributed their time, over and above their own research
commitments, toward maintaining the quality of Madroño, and their assistance in
the preparation of Volume 29 has been greatly appreciated.

David P. Adam
Edward F. Anderson
G. D. Barbe
Spencer Barrett
Jerry Baskin
Meredith Blackwell
Mary T. Burke
Kenton L. Chambers
Curtis Clark
Susan G. Conard
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Richard J. Vogel
Robert Wright

EDITOR'S CONFESSIONS FOR VOLUME 29

Between 1 Jul 1981 and 30 Jun 1982, 77 manuscripts were received. This represents a 17% increase over the submission rate of 1980–1981. Of this year's manuscripts, 45 (58%) were articles, a 12.5% increase over last year; 22 were noteworthy collections, a 46% increase; and 10 (13%) were notes, a 1% decrease. Current statuses of manuscripts are as follows: in review, 17; in revision, 22 (includes a few holdovers from 1980–1981); accepted and awaiting publication, 23 (a 53% increase over 1980–1981); published in volume 29, 26 articles (52%), 16 noteworthy collections (32%), and 8 notes (16%). Corresponding figures for 1980–1981 were 27, 19, and 15. The 53% increase in backlog represents something of a problem because of the increase in publication costs. Pages published in Madroño have increased from 192 (vol. 27), to 279 (vol. 28), and ca. 280 (vol. 29). The Society faces these critical alternatives: increase dues, increase rejection rate of manuscripts, decrease the size of Madroño. A few papers were rejected this year, but Madroño's absolute rejection rate remains low.

Transition of the editorial office from Los Angeles to Idaho occurred smoothly, and I have been able to keep up with my duties. I have even been ahead of things a couple of times. Time from final acceptance to publication is now one year, an increase from 1981. I have received one compliment, one complaint, and no hate mail. Most authors appear to accept Madroño as a suitable outlet for their work and I am pleased with the continuing diversity of material received.

The editorial office will continue to welcome suggestions and criticisms from members.

C. D. 12 Jul 1982

Dates of publication of MADROÑO, volume 29

No. 1, pp.　　1–66: 15 January 1982
No. 2, pp.　67–125: 29 April 1982
No. 3, pp. 127–218:　9 July 1982
No. 4, pp. 219–281: 12 October 1982

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