CONTENTS

NOTES

NEW SPECIES

BOOK REVIEW

NOTEWORTHY COLLECTIONS

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POSTFIRE CHAPARRAL REGENERATION UNDER MEDITERRANEAN AND NON-MEDITERRANEAN CLIMATES

Jon E. Keeley[1,2], C. J. Fotheringham[1,2] and Philip W. Rundel[2]
[1]U.S. Geological Survey, Western Ecological Research Center, Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271
[2]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095
jon_keeley@usgs.gov

Abstract

This study compares postfire regeneration and diversity patterns in fire-prone chaparral shrublands from mediterranean (California) and non-mediterranean-type climates (Arizona). Vegetation sampling was conducted in tenth hectare plots with nested subplots for the first two years after fire. Floras in the two regions were compared with Jaccard's Index and importance of families and genera compared with dominance-diversity curves. Although there were 44 families in common between the two regions, the dominant families differed; Poaceae and Fabaceae in Arizona and Hydrophyllaceae and Rosaceae in California. Dominance diversity curves indicated in the first year a more equable distribution of families in Arizona than in California. Woody plants were much more dominant in the mediterranean climate and herbaceous plants more dominant in the bimodal rainfall climate. Species diversity was comparable in both regions at the lowest spatial scales but not at the tenth hectare scale. Due to the double growing season in the non-mediterranean region, the diversity for the first year comprised two different herbaceous floras in the fall and spring growing seasons. The Mediterranean climate in California, in contrast, had only a spring growing season and thus the total diversity for the first year was significantly greater in Arizona than in California for both annuals and herbaceous perennials. Chaparral in these two climate regimes share many dominant shrub species but the postfire communities are very different. Arizona chaparral has both a spring and fall growing season and these produce two very different postfire floras. When combined, the total annual diversity was substantially greater in Arizona chaparral.

Key Words: Climate, dominance, fire, species diversity, spring and fall annuals.

Chaparral is a fire-prone evergreen shrubland that is the dominant vegetation in the mediterranean-type climate (MTC) region of California (Keeley 2000). From a global perspective this vegetation is somewhat unique in that it not only tolerates frequent fires but many of the species have fire-dependent reproduction, similar to shrublands in other mediterranean-climate regions (Rundel 1981; Keeley and Bond 1997; Keeley et al. 2005).

Chaparral shrublands, however, are not restricted to MTCs as this vegetation type is widely distributed in southwestern USA and disjunct to northeastern Mexico (Keeley and Keeley 1988). Arizona mirrors the MTC in the winter rains that taper off to a late spring drought, but departs from the MTC by addition of a second rainy season in the summer. However, the importance of summer rains to the dominant shrubs is a matter of some debate, as it appears that these rains play a minor role in shrub growth and reproduction (Vankat 1989). Northeastern Mexico has a winter drought and summer rain climate, but the physiological responses of the shrub dominants to drought are remarkably similar to Californian shrubs (Bhaskar et al. 2007).

Arizona chaparral covers more than two million hectares (Schmutz and Whitham 1962; Bolander 1982) and occurs in widely disjunct patches from near Prescott in the northeast to the southeastern mountains around Tucson and east to the southwestern edge of New Mexico (Cable 1975; Pase and Brown 1982; Whittaker and Niering 1964, 1965). Arizona and California are broadly similar in the shrub dominants that are shared between these two regions (Knipe et al. 1979). Northeast Mexico chaparral is restricted to patches of severe substrate in the Sierra Oriental Mountains south of Monterey, and this vegetation shares some of the same shrub species and genera as the Arizona and California chaparral communities.

The Arizona and Mexican chaparral are of interest for what they can potentially tell us about the evolution of chaparral taxa. Paleoecological studies have suggested that many chaparral shrub species originated in interior portions of the southwest (Wolfe 1964, Axelrod 1989) and contemporary populations in Arizona and northeastern Mexico are interpreted as remnants of a Tertiary chaparral like vegetation that comprises taxa that largely originated under non-medterranean type climates (Ackerly 2009; Keeley et al. 2012).

Although postfire chaparral responses have been studied in great detail in the winter rain region of California, little is known about
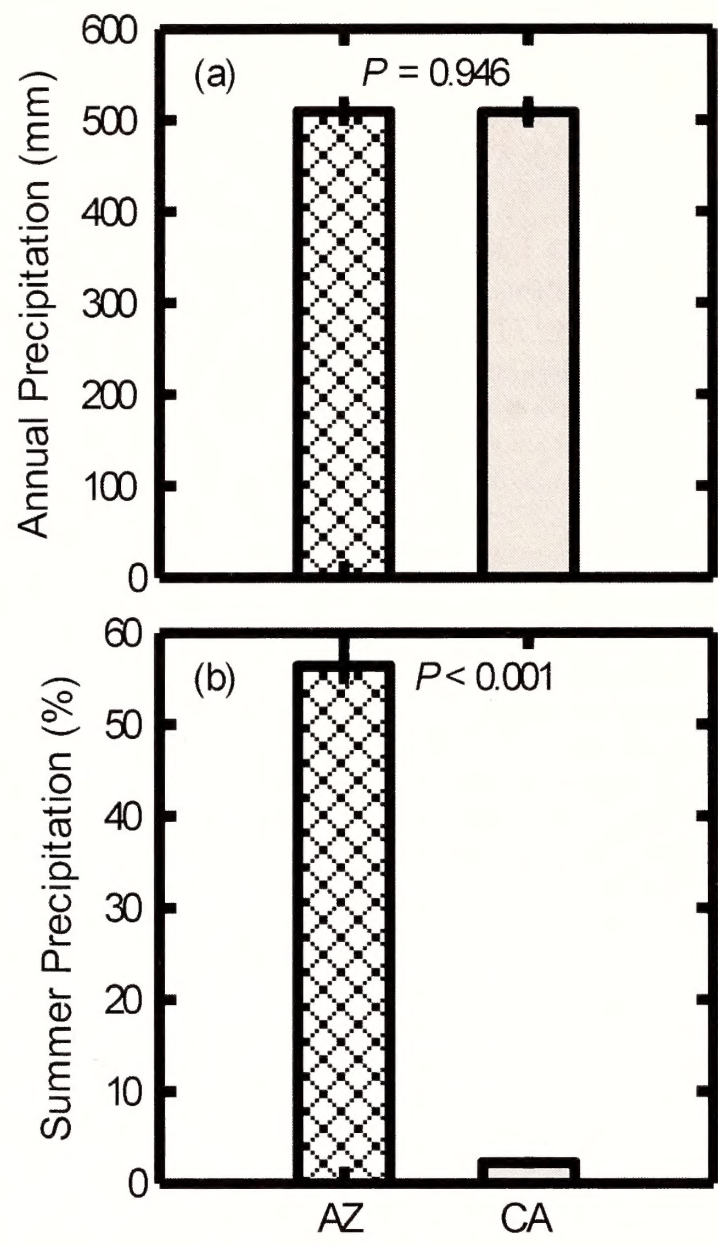
FIG. 1. Patterns of (a) long-term average annual precipitation and (b) proportion falling during the 'summer' rainy season (defined as July, August and September) for the nearest stations to the Arizona (AZ) and California (CA) study sites used in this project. Error bars are the standard error of the mean.

TABLE 1. FIFTEEN DOMINANT PLANT FAMILIES IN ARIZONA AND CALIFORNIA POSTFIRE CHAPARRAL SITES BASED ON AERIAL COVERAGE.

State/family	Normalized cover
Arizona	
Poaceae	1.00
Fabaceae	0.676
Asteraceae	0.327
Verbenaceae	0.138
Fagaceae	0.100
Molluginaceae	0.085
Convolvulaceae	0.074
Liliaceae	0.055
Malvaceae	0.054
Euphorbiaceae	0.043
Geraniaceae	0.032
Boraginaceae	0.025
Agavaceae	0.025
Rhamnaceae	0.018
Krameriaceae	0.016
California	
Hydrophyllaceae	1.00
Rosaceae	0.704
Cistaceae	0.345
Ericaceae	0.319
Fabaceae	0.254
Convolvulaceae	0.240
Rhamnaceae	0.237
Liliaceae	0.228
Asteraceae	0.174
Boraginaceae	0.168
Fagaceae	0.163
Poaceae	0.143
Papaveraceae	0.094
Scrophulariaceae	0.092
Fumariaceae	0.089

community responses in the bimodal rainfall region of Arizona. Postfire regeneration of Arizona chaparral has largely focused on shrub responses with relatively little attention to community responses and regeneration strategies of other life forms (Pase and Pond 1964; Pase 1965; Carmichael et al. 1978).

The purpose of this study was to contrast postfire recovery in the MTC California chaparral with postfire recovery in the non-MTC Arizona chaparral. We utilized data from studies of 2003 wildfires in California (same sites as in Keeley et al. 2008) and from studies of 2002 wildfires in Arizona (same sites as in Fotheringham 2009).

METHODS

Study Sites

The Arizona sites were burned in the late spring and summer of 2002 and were distributed across six fires in southeastern Arizona and southwestern

New Mexico (Fotheringham 2009). This study included 40 sites that were selected based on evidence of chaparral vegetation present prior to fire, fire size, range of fire severities, and accessibility, and were sampled in the first two postfire years. Sites were grouped by fire for analysis, except due to the small size and proximity of the Merritt and Ryan fires these were grouped together, and due to the large size of the Bullock Fire these were separated into two groups, the lower elevation Bullock and the higher elevation Upper Bullock. California sites were from five fires that burned in autumn 2003 and included 250 sites that were dominated by chaparral prior to the fires and sampled over the first two years; due to their proximity, the Grand Prix and Old fires were analyzed as a single fire. Both Arizona and California fires were distributed across a range of about 150–200 km but the former were distributed at about the same latitude in a west to east gradient and the latter along a north to south gradient (see Keeley et al. 2008 and Fotheringham 2009 for detailed maps). Chaparral sites studied in Arizona were at significantly higher elevation (AZ sites = 1620 m, CA sites 785 m).
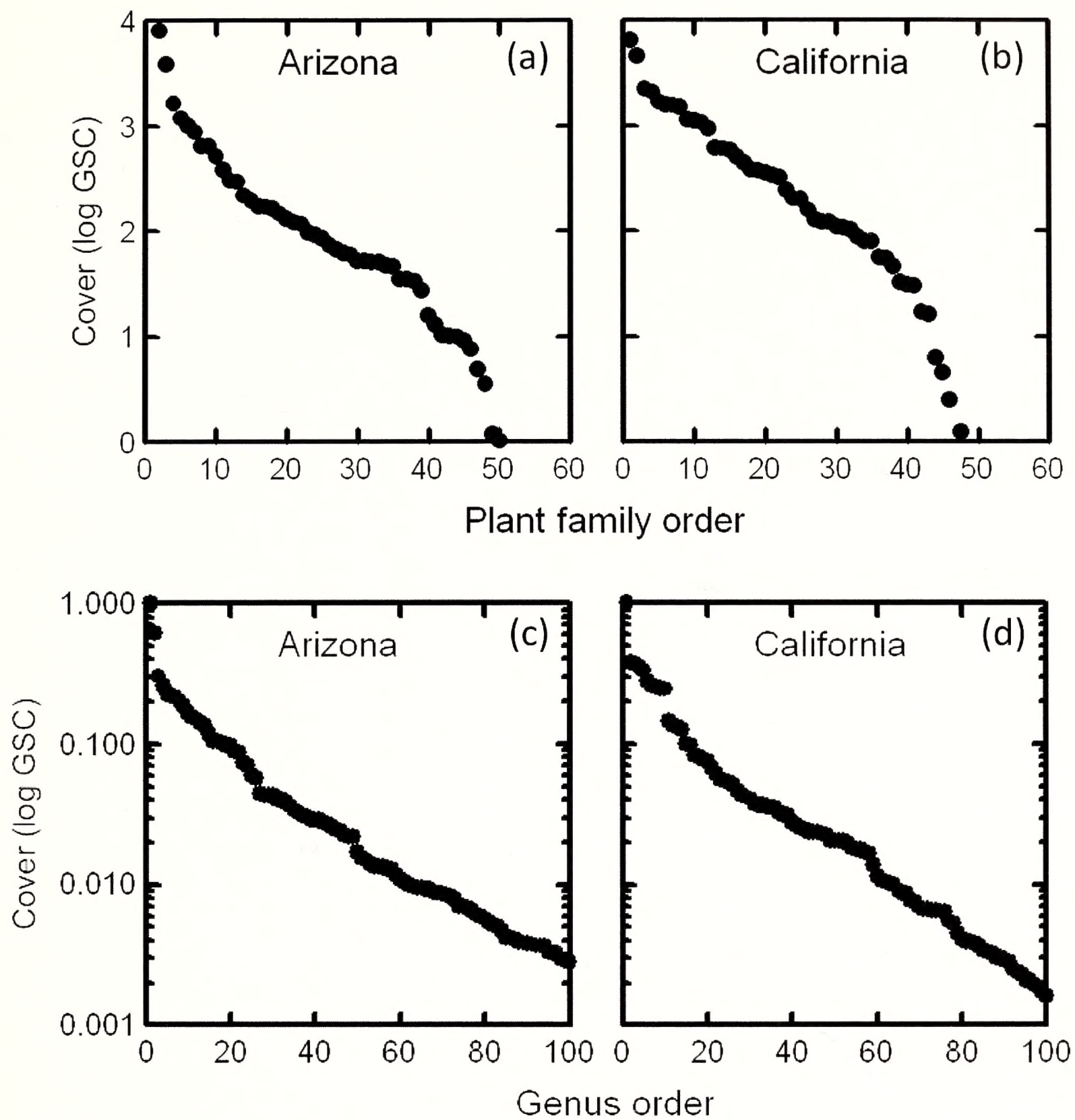
FIG. 2.   Rank order distribution of (a, b) plant families and (c, d) genera in Arizona and California. GSC is ground surface cover.

Field Methods

In Arizona, there were two growing seasons following both the summer rains and the winter rains so sampling was first done in fall 2002 and then again in spring 2003, and this sampling regime was repeated for a second year. In the winter-rainfall chaparral of California sampling was conducted only in spring of 2004 and 2005. Each site consisted of a 20 m × 50 m sample plot, positioned parallel to the slope contour, which is considered appropriate for capturing the greatest variation in community composition (Keeley and Fotheringham 2005). Each of these tenth hectare sites were subdivided into 10 nested 100 m²

square subplots, each with a single nested 1 m² square quadrat in an outside corner. Cover and density were recorded for each species within the quadrats, and a list of additional species was recorded from the surrounding subplot. Cover was visually estimated and a percentage of ground surface covered was recorded for each species. Density was recorded for each species with counts where density was less than approximately 25 individuals per quadrat, and with estimates at higher densities. Seedlings and resprouts of the same species were counted and recorded separately. Vouchers were collected for all specimens and have been deposited in the herbarium in J. Keeley 's laboratory. All plant

Table 2. Top 75 Native Genera in the Arizona and California Postfire Sites Based on Aerial Coverage.

Arizona	Normalized cover	Arizona	Normalized cover
Eragrostis	1.000	Amaranthus	0.029
Dalea	0.609	Portulaca	0.029
Glandularia	0.301	Bothriochloa	0.029
Bouteloua	0.258	Plagiobothryus	0.028
Bidens	0.227	Arctostaphylos	0.027
Quercus	0.218	Schinus	0.026
Muhlenbergia	0.217	Cryptantha	0.024
Lotus	0.200	Juniperus	0.024
Mollugo	0.187	Marina	0.022
Heterosperma	0.166	Gnaphalium	0.022
Mimosa	0.154	Boerhavia	0.022
Chamaecrista	0.150	Phaseolus	0.017
Melampodium	0.142	Chamaesyce	0.016
Urochloa	0.136	Yucca	0.015
Nolina	0.117	Cyperus	0.014
Aristida	0.105	Digitaria	0.013
Desmodium	0.104	Aeschynomene	0.013
Ipomoea	0.102	Anoda	0.013
Heliomeris	0.098	Opuntia	0.013
Panicum	0.097	Descurainia	0.013
Calliandra	0.089	Drymaria	0.012
Leptochloa	0.088	Eriogonum	0.011
Acalypha	0.073	Gymnosperma	0.010
Erodium	0.070	Commelina	0.010
Evolvulus	0.060	Dyssodia	0.010
Sida	0.056	Triticum	0.010
Sphaeralcea	0.044	Diodia	0.009
Lycurus	0.043	Gilia	0.009
Astragalus	0.043	Scleropogon	0.009
Schizachyrium	0.043	Garrya	0.009
Elionurus	0.040	Sanvitalia	0.009
Ceanothus	0.040	Linum	0.009
Crotalaria	0.038	Trachypogon	0.008
Krameria	0.036	Agave	0.008
Cathestecum	0.034	Hackelochloa	0.008
Prosopis	0.033	Erigeron	0.007
Dasylirion	0.031	Salvia	0.007
Chenopodium	0.030		

California	Normalized cover	California	Normalized cover
Adenostoma	1.000	Allophyllum	0.026
Phacelia	0.379	Solanum	0.025
Calystegia	0.364	Silene	0.025
Arctostaphylos	0.354	Cercocarpus	0.023
Lotus	0.331	Malacothamnus	0.023
Ceanothus	0.280	Styrax	0.023
Helianthemum	0.261	Navarretia	0.023
Cryptantha	0.256	Hypochoeris	0.022
Quercus	0.248	Garrya	0.020
Emmenanthe	0.245	Gastridium	0.020
Calochortus	0.145	Calyptridium	0.019
Eriodictyon	0.135	Minulus	0.018
Xylococcus	0.131	Erodium	0.018
Chlorogalum	0.100	Lepechinia	0.017
Antirrhinum	0.098	Helianthus	0.017
Marah	0.082	Nassella	0.012
Rhamnus	0.081	Penstemon	0.011
Chaenactis	0.077	Lupinus	0.010
Camissonia	0.075	Galium	0.010
Dicentra	0.068	Monardella	0.010
Dendromecon	0.061	Lomatium	0.009
Malosma	0.055	Erigeron	0.009
Salvia	0.055	Fremontodendron	0.009

TABLE 2. CONTINUED.

California	Normalized cover	California	Normalized cover
Dichelostemm	0.053	*Daucus*	0.008
Cneoridium	0.051	*Melica*	0.007
Chamaebatia	0.046	*Papaver*	0.007
Eriophyllum	0.042	*Cupressus*	0.007
Zigadenus	0.042	*Selaginella*	0.007
Pickeringia	0.041	*Elymus*	0.007
Nemocladus	0.037	*Muilla*	0.007
Gilia	0.037	*Apistrum*	0.007
Yucca	0.036	*Ribes*	0.006
Pterostegia	0.036	*Eriogonum*	0.006
Brassica	0.035	*Lonicera*	0.005
Hazardia	0.035	*Claytonia*	0.005
Filago	0.033	*Chorizanthe*	0.004
Rhus	0.031	*Pellaea*	0.004
Trichostema	0.031	*Leymus*	0.004
Mentzelia	0.028		

nomenclature follows Hickman (1993) for California and USDA (2009) for Arizona.

Precipitation data for Arizona were obtained from http://cdo.ncdc.noaa.gov/CDO/ data product (accessed May 2008) for climate stations nearest to the study sites. Precipitation data for California were obtained from the Western Regional Climate Center (http://www.wrcc.dri.edu/summary/Climsmsca.html; accessed April 2007). Average precipitation for the sites in Arizona and California were comparable (Fig. 1a). Both regions have significant winter rains followed by a late spring and early summer drought. In California drought continues until late fall whereas Arizona has summer rains that begin in July and extend through September. A substantial proportion of total rain occurs during the 'summer' (July, August and September) in Arizona in contrast to California (Fig. 1b).

Data Analysis

Statistical comparisons and regressions were calculated and displayed graphically with Systat 11.0 (Richmond, CA, USA). Comparisons between Arizona and California were made with a two-tailed t-test for all quantitative parameters.

Compositional differences between sites within a region and between regions were evaluated using Jaccard's similarity coefficient, which provides a measure of similarity between two sets of data. This coefficient was calculated using a modified form of Jaccard's index (see Table 10.2 in Mueller-Dombois and Ellenberg 1974), based on presence/absence as:

$$JI_{cov} = \frac{MC}{MA+MB} \times 100$$

where MC is the number of taxa present in both regions, MA is number of taxa present only in Arizona and MB is for taxa present only in

California, and the coefficient expressed as a percentage. The value ranges from 0%, where the two data sets share no taxa, to 100% with complete overlap in taxa. This index was calculated for all plant families and all genera shared between sites within a region and between regions, i.e., for all pairwise comparisons of sites within Arizona, and within California and then for all comparisons between Arizona sites and California sites. The non-parametric Wilcoxon signed ranks test was used to compare the Jaccard's indices calculated within Arizona to those calculated between Arizona and California sites to determine if Arizona sites were more similar to one another than they were to California.

RESULTS

Taxonomic Patterns

Between the Arizona and California sites there were 44 plant families in common and an additional 19 families recorded just at the Arizona sites and nine just at the California sites (Appendix 1). Based on total cover over the two years of study in both Arizona and California, the top 15 families were quite different (Table 1). Although about half of the top 15 families were shared between both regions, the most dominant families were different. In Arizona the top two families were the Poaceae and Fabaceae whereas in California it was the Hydrophyllaceae and Rosaceae. Families were generally more evenly distributed in California than in Arizona, as illustrated by the observation that the top 15 families were present in sites at all fires in California, whereas in Arizona only the top 10 families were represented at all fires.

A similar difference between regions is illustrated by the pattern of equitability in rank order distribution of families (Fig. 2a, b). In Arizona

TABLE 3. SPECIES FOUND IN BOTH THE ARIZONA AND CALIFORNIA STUDY SITES. This is not meant to suggest these are the only species found in chaparral of the two regions but just what was recorded from our 40 study sites in Arizona and 250 sites in California.

Annuals

Allophyllum gilioides (Benth). A. D. Grant & V. E. Grant	Polemoniaceae
Aristida adscensionis L.	Poaceae
Bowlesia incana Ruiz & Pav.	Apiaceae
Chenopodium berlandieri Moq.	Chenopodiaceae
Calandrinia ciliata (Ruiz & Pav.) DC.	Portulacaceae
Conyza canadensis (L.) Cronquist	Asteraceae
Cryptantha micrantha (Torr.) I. M. Johnst.	Boraginaceae
Cryptantha muricata (Hook & Arn.) A. Nelson & J. F. Macbr.	Boraginaceae
Daucus pusillus Michx.	Apiaceae
Eriastrum sapphirinum (Eastw.) H. Mason	Polemoniaceae
Galium aparine L.	Rubiaceae
Gilia leptantha Parish	Polemoniaceae
Lepidium virginicum L.	Brassicaceae
Lotus humistratus Greene	Fabaceae
Lupinus concinnus J. Agardh	Fabaceae
Lupinus sparsiflorus Benth.	Fabaceae
Malocothrix clevelandii A. Gray	Asteraceae
Pectocarya setosa A. Gray	Boraginaceae
Phacelia distans Benth.	Hydrophyllaceae
Phlox gracilis (Hook.) Greene	Polemoniaceae
Rafinesquia californica Nutt.	Asteraceae
Silene antirrhina L.	Caryophyllaceae
Stephanomeria exigua Nutt.	Asteraceae
Stellaria nitens Nutt.	Caryophyllaceae
Stylocline gnaphalioides Nutt.	Asteraceae
Thysanocarpus curvipes Hook.	Brassicaceae
Triodanis biflora (Ruiz & Pav.) Greene	Campanulaceae
Triodanis perfoliata (L.) Nieuwl.	Campanulaceae
Vulpia microstachys (Nutt.) Munro	Poaceae
Vulpia octoflora (Walter) Rydb.	Poaceae
Yabea microcarpa (Hook. & Arn.) Koso-Pol.	Apiaceae

Herbaceous perennials

Aristida purpurea Nutt.	Poaceae
Astragalus trichopodus (Nutt.) A. Gray	Fabaceae
Bothriochloa barbinodis (Lag.) Herter	Poaceae
Datura wrightii Regel	Solanaceae
Dichelostemma capitatum (Benth.) Alph. Wood	Amaryllidaceae
Gnaphalium bicolor Anderb.	Asteraceae
Gnaphalium canescens DC.	Asteraceae

Subshrubs or suffrutescents

Atriplex semibaccata R. Br.	Chenopodiaceae
Brickellia californica (Torr. & A. Gray) A. Gray	Asteraceae
Encelia farinosa A. Gray ex Torr.	Asteraceae
Eriogonum wrightii Torr. ex Benth.	Polygonaceae
Gutierrezia sarothrae (Pursh) Britton & Rusby	Asteraceae
Porophyllum gracile Benth.	Asteraceae
Rhus trilobata Nutt.	Anacardiaceae
Senecio flaccidus Less.	Asteraceae
Solanum douglasii Dunal	Solanaceae
Yucca schidigera Roezl ex Ortgies	Liliaceae

Shrubs

Arctostaphylos pungens Kunth	Ericaceae
Artemisia tridentata Nutt.	Asteraceae
Baccharis salicifolia (Ruiz & Pav.) Pers.	Asteraceae
Ceanothus greggii A. Gray	Rhamnaceae
Garrya wrightii Torr.	Garryaceae
Rhamnus crocea Nutt.	Rhamnaceae
Sambucus mexicana C. Presl. ex DC.	Caprifoliaceae

TABLE 3.   CONTINUED.

Annual species alien to Arizona and California	
Ambrosia artemisiifolia L.	Asteraceae
Brassica nigra (L.) W. D. J. Koch	Brassicaceae
Bromus madritensis L.	Poaceae
Bromus tectorum L.	Poaceae
Chenopodium album L.	Chenopodiaceae
Erodium cicutarium (L.) L'Hér. ex Aiton	Geraniaceae
Lactuca serriola L.	Asteraceae
Marrubium vulgare L.	Lamiaceae
Phalaris minor Retz.	Poaceae
Poa annua L.	Poaceae
Schismus barbatus (L.) Thell.	Poaceae
Sisymbrium altissimum L.	Brassicaceae
Sisymbrium irio L.	Brassicaceae
Salsola tragus L.	Chenopodiaceae
Sonchus tenerrimus L.	Asteraceae
Vulpia bromoides (L.) A. Gray	Poaceae

there was a much larger difference between the top few families and the remaining families, whereas in California cover was somewhat more equally distributed among families. For example two orders of magnitude cover below the top family in Arizona comprised only about 20 families, whereas in California it was almost double that number.

Unlike the family distribution, where the majority were in common between regions, many fewer genera were common between regions than were unique to one or the other region (Appendix 2). There were only 109 genera recorded from sites in both regions, but there were 148 genera recorded just in Arizona sites and 78 recorded just in California sites. Based on cover, of the top 75 genera in Arizona, only 16 were also in the top 75 in California and of the top 75 in California only 22 were in the top group in Arizona (Table 2). Genera important in both regions (defined as in the top 75) include the shrubs *Arctostaphylos, Ceanothus, Garrya,* and *Quercus,* subshrubs *Baccharis, Eriogonum, Salvia,* and *Yucca,* and suffrutescents *Erigeron* and *Lotus* (Table 2). The cover distribution for the top genera (Fig. 2c, d) followed similar curves in Arizona and California, indicating greater equitability in both regions than observed with families.

In Arizona there were substantially more species recorded from the 40 study sites (577) than for the 250 sites in California (439) despite covering a roughly similar-sized geographical area. However, in Arizona this covered an east-west gradient and in California a north-south gradient.

As a general rule none of the dominant herbaceous species in Arizona chaparral were present or well represented in California chaparral, and vice versa. One of the most conspicuous and widespread postfire species in Arizona was the fall germinating ephemeral herbaceous perennial *Verbena bipinnatifida* Nutt. (=*Glandularia b.*), a species not found in the California postfire chaparral. In California the most conspicuous postfire ephemerals were Hydrophyllaceae, most of which were absent or of very minor importance in Arizona chaparral.

However, there were more than 30 minor species in common between both regions (Table 3); e.g., *Allophyllum gilioides* A.D. Grant & V.E. Grant, *Calandrinia ciliate* (Ruiz & Pav.) DC., *Lupinus sparsiflorus* Benth., *Malacothrix clevelandii* A. Gray, and *Rafinesquia californica* Nutt., all of which are spring annuals. Of the herbaceous perennials the one that stands out as being very common in both regions was *Dichelostemma capitatum* (Benth.) Alph. Most of the subshrubs listed were widespread but never locally common. Several shrubs were widespread in both regions, in particular *Arctostaphylos pungens* Kunth, *Ceanothus greggii* A. Gray and *Rhamnus crocea* Nutt. More than 15 alien species were common between both regions, and all were annuals (Table 3).

The main shrub species in Arizona were seedlings of the obligate seeders *Arctostaphylos pungens, Ceanothus greggii* and *C. fendleri* A. Gray and resprouts of *Quercus turbinella* Greene, *Rhus trilobata* Nutt., and *Baccharis salicifolia* (Ruiz & Pav.) Pers. Postfire sites in California were dominated by resprouts and seedlings of *Adenostoma fasciculatum* Hook. & Arn, *Arctostaphylos* spp., and *Ceanothus* spp. as well as resprouts of *Quercus berberidifolia* Liebm. Subshrubs and other less woody and shorter-lived suffrutescents were very different between these regions. In Arizona the genus *Dalea* was very important as well as *Krameria erecta* Willd. ex Schult. and species of *Senecio* and *Solanum,* but this niche was filled largely by *Lotus scoparius* (Nutt.) Ottley, *Helianthemum scoparium* Nutt.
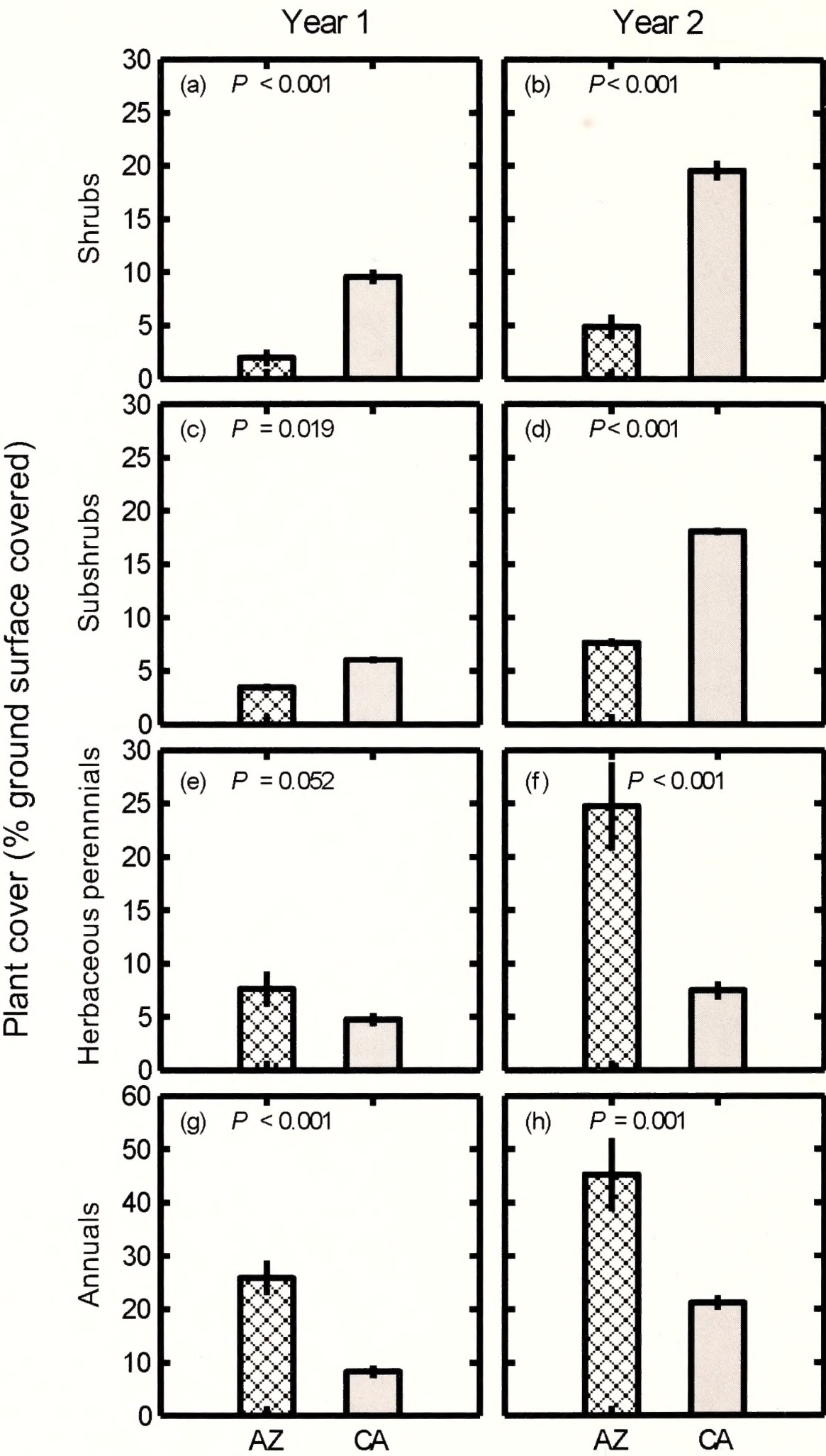
Fig. 3. Plant cover in spring of year 1 and year 2 presented by life form (AZ = Arizona, CA = California, subshrub category includes the weakly woody suffrutescents). Error bars are the standard error of the mean. Note the scale for annuals is double that for other life forms.

and *Calystegia macrostegia* (Greene) Brummitt in California. Herbaceous floras were very different between the two regions with Poaceae dominating in Arizona and Hydrophyllaceae in California.

Postfire Changes in Cover and Diversity

Total cover was around 20% in the first postfire year and not significantly different
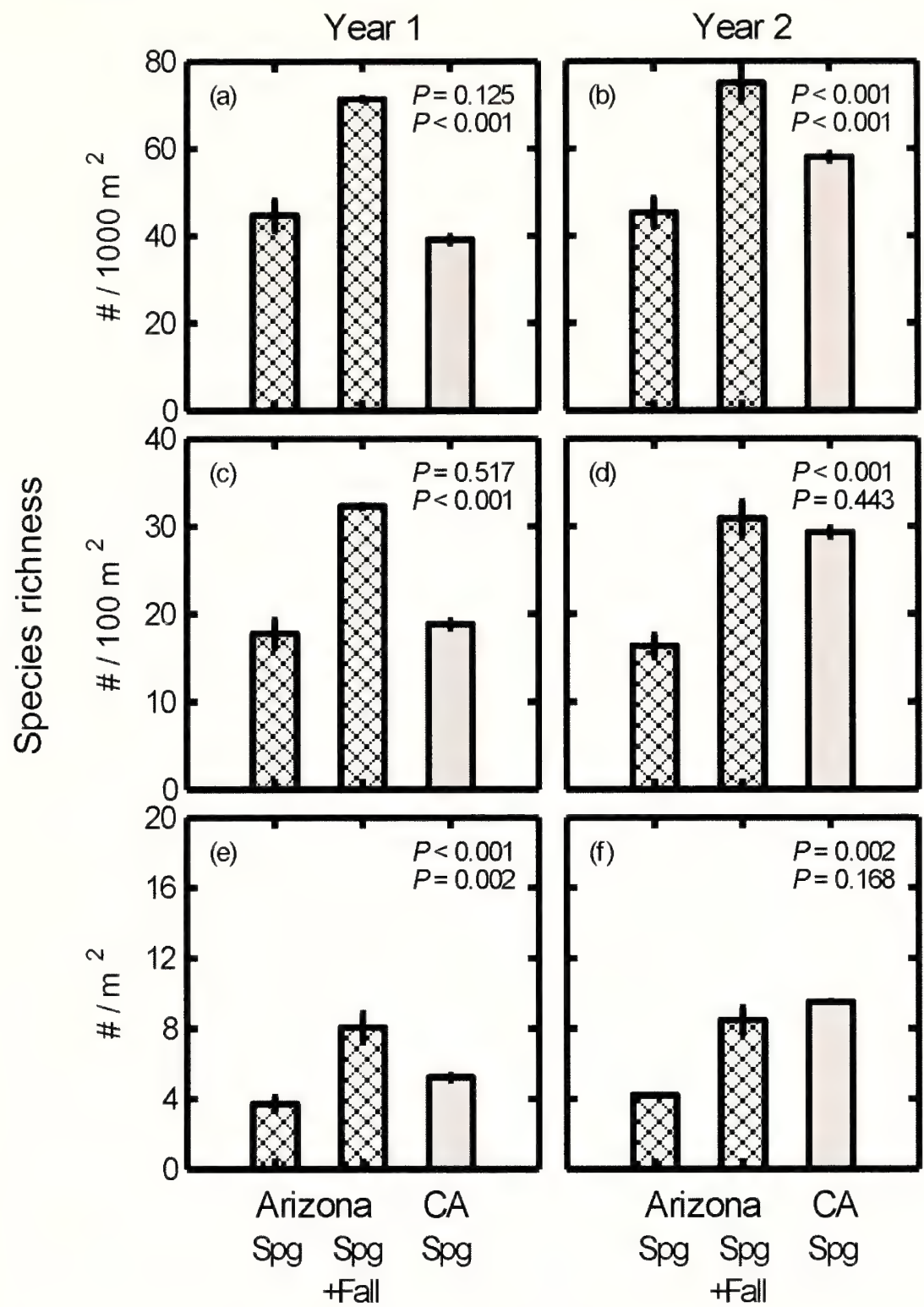
FIG. 4. Species diversity (including native and non-native species) for the spring flora and total flora in Arizona and spring flora in California at three scales in both years (Arizona, CA = California, Spg = spring). Two-tailed t-test for (top P-value) Arizona spring vs. California spring and (bottom P-value) Arizona total vs. California spring. Error bars are the standard error of the mean.

between Arizona and California, but in the second year cover more than doubled in California and was significantly greater than in Arizona (P < 0.001). These two regions differed markedly in the importance of different growth forms. Shrub cover was about five times greater in California than in Arizona in the first two postfire years (Fig. 3a, b), and subshrubs also had significantly greater cover in California (Fig. 3c, d). In contrast, herbaceous species, both perennials (Fig. 3e, f) and annuals (Fig. 3g, h) had significantly more cover in Arizona than in California. By the second postfire year herbaceous perennials, mostly grasses, had about four times more cover in Arizona and annuals had about twice as much as California. In short,

postfire cover in California was more or less equally distributed among different growth forms than in Arizona.

Species richness in the first spring after fire was slightly higher in California at the 1 m² scale (Fig. 4e), but not significantly different at larger scales (Fig. 4c, a). However, this does not capture the full annual diversity in Arizona due to the double growing seasons resulting from a bimodal rainfall pattern. As a consequence Arizona produced two different herbaceous floras, one in fall and one in spring. The total first year diversity (fall 2002 plus spring 2003 in Arizona vs. just the spring 2003 flora in California) was significantly higher in Arizona at all scales (Fig. 4a, c, e).
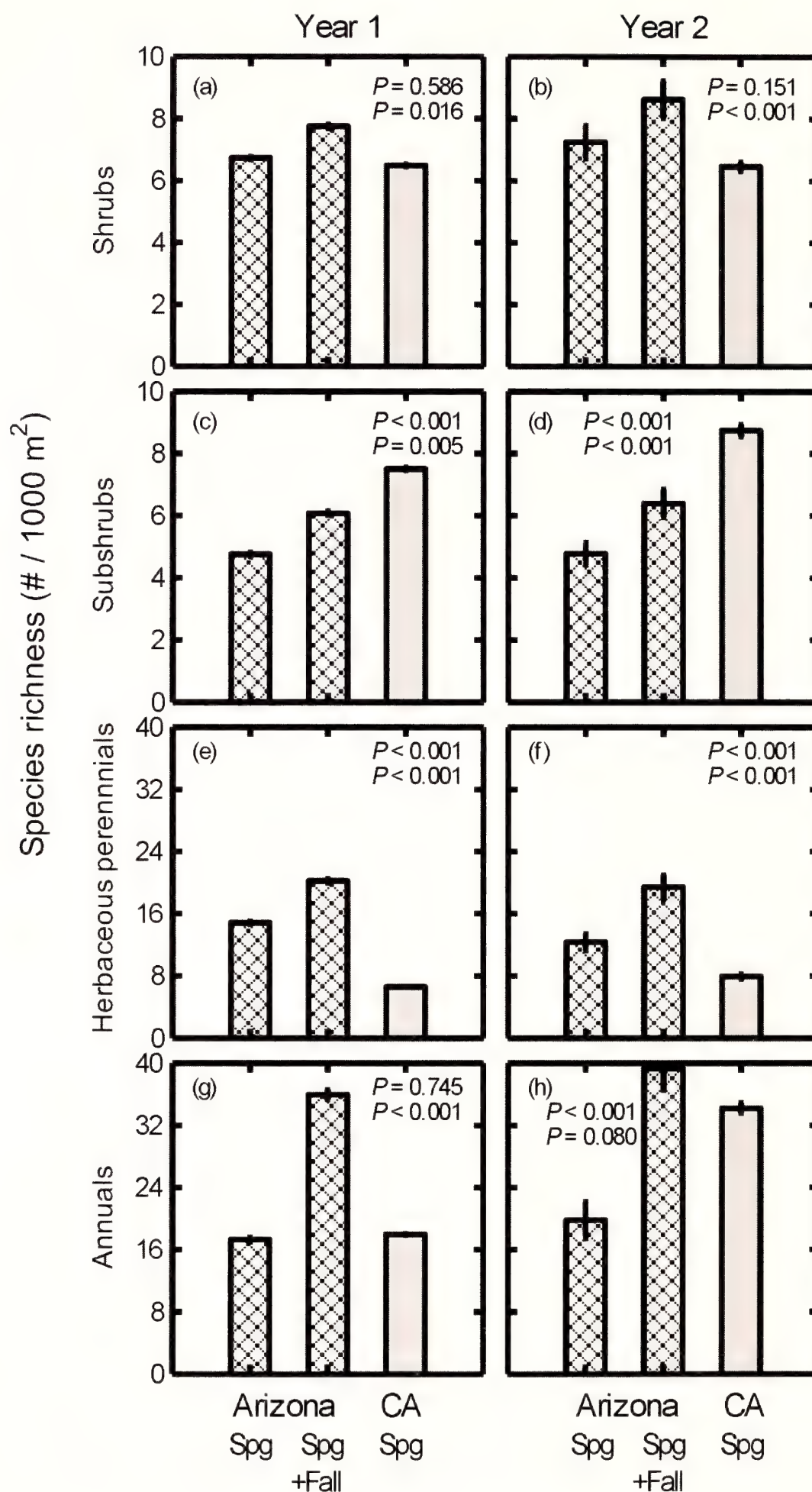
FIG. 5. Species diversity at the site level (tenth ha) for the spring flora and total flora in Arizona and spring flora in California in both years presented by life form (Arizona, CA = California, Spg = spring). Two-tailed t-test for (top P-value) Arizona spring vs. California spring and (bottom P-value) Arizona total vs. California spring. Error bars are the standard error of the mean.

In the second postfire spring, diversity rose at all scales in California but not in Arizona so spring floras were significantly more diverse in California at all scales (Fig. 4b, d, f). Total second year diversity was significantly greater in Arizona at the largest spatial scale (Fig. 4b).

The contribution of different growth forms to diversity at the site level (tenth ha) differed between regions. In the first spring following fire, woody plant diversity was similar between both regions (Fig. 5a), but when the fall flora in Arizona was added in the total for the year was
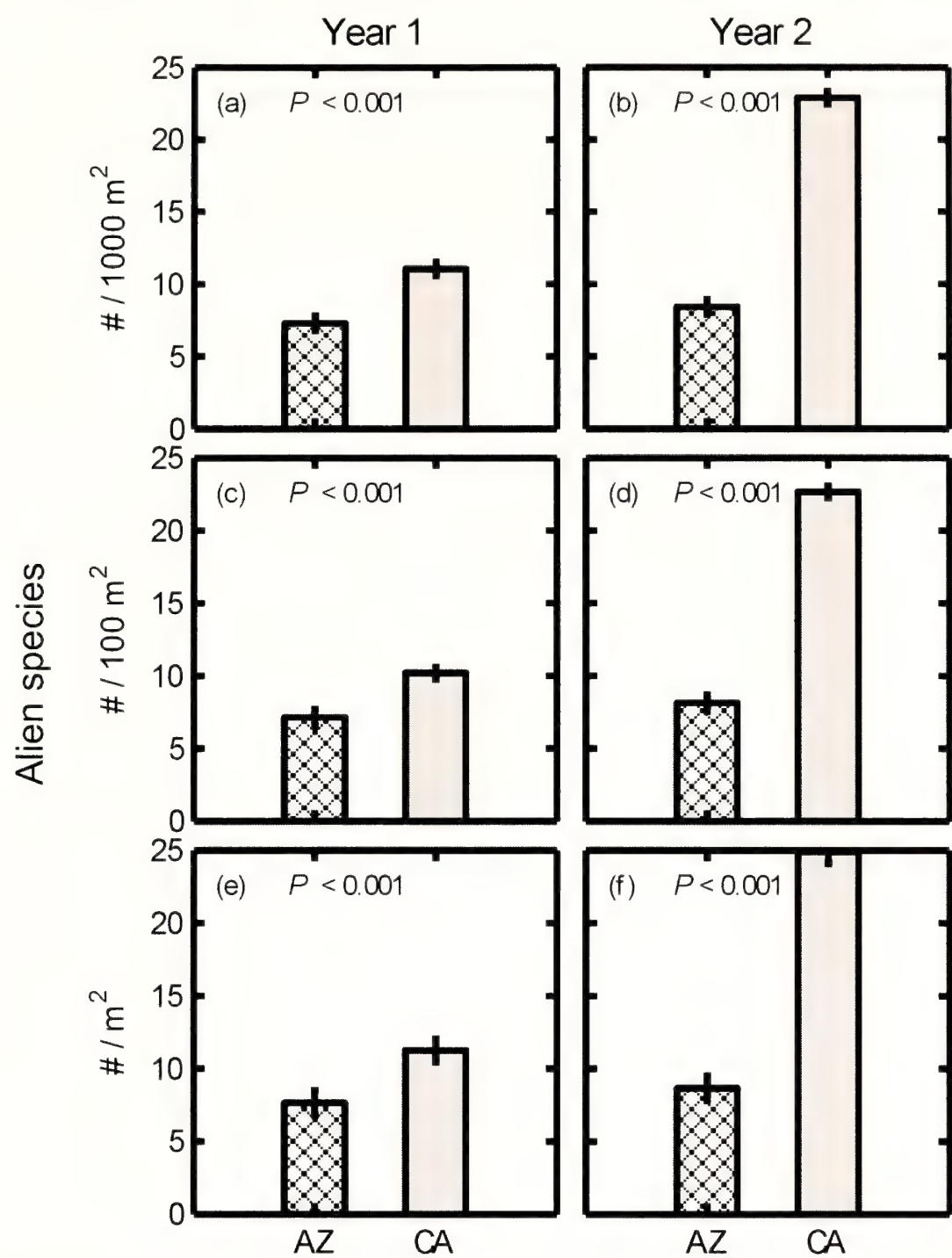
FIG. 6.   Alien species diversity at three scales for the annual total (combined fall and spring for Arizona and spring for California in year 1 and year 2 (Az = Arizona, CA = California). Error bars are the standard error of the mean. Note scale remains the same in all panels.

slightly greater in Arizona (Fig. 5a). Subshrub (including suffrutescents) diversity was greater in California than either the spring or spring plus fall total in Arizona (Fig. 5c). However, herbaceous perennial diversity was greater in Arizona in the spring and even greater when fall diversity was added in (Fig. 5e). Spring annual diversity was similar in both regions (Fig. 5g) but when the fall flora in Arizona was added in (Fig. 5g) diversity of annuals was substantially greater in Arizona. These patterns remained the same in the second year (Fig. 5b, d, f, h).

Alien plant cover comprised only a few percent of the total cover in the first year (measured in spring) and was not significantly different between Arizona and California (P = 0.486). However, by spring of the second year, total cover of aliens in California had increased about 5-fold and was significantly greater than in Arizona (P = 0.002). Species diversity of aliens

was significantly higher at all spatial scales in California in both years (Fig. 6). In the second year alien species comprised 8% of the Arizona flora and 22% of the California flora.

Community Similarity

Jaccard's index was used to compare the compositional similarity within regions and between regions. Since few species were important in both Arizona and California the focus was on plant families and genera. Sites were grouped by the six fires in Arizona and the four fires in California and comparisons were made on first year floras. Comparisons of Arizona sites vs. other Arizona sites, and Arizona sites vs. California sites were made for fall and spring. In California, there was only one growing season in the spring, so comparisons of fall families or fall genera in Arizona were made against spring floras in California.

TABLE 4. PERCENTAGE SIMILARITY BETWEEN BURNS USING PRESENCE/ABSENCE JACCARD'S INDEX. Arizona sites are presented from west to east and California sites from north to south. *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	AZ - Bullock	AZ - Upper Bullock	AZ - Merrit/Ryan	AZ - Darnel	AZ - Walnut	CA – Grand Prix/Old	CA - Paradise	CA - Cedar	CA - Otay
Families									
*Fall Az - Spring CA**									
AZ - Oracle	73	44	53	55	56	48	40	46	45
AZ - Bullock		45	55	60	61	43	39	44	40
AZ - Upper Bullock			47	44	42	33	33	34	36
AZ - Merritt/Ryan				68	60	37	32	35	37
AZ- Darnel					67	40	38	43	38
AZ - Walnut						39	42	44	41
Spring in AZ & CA									
AZ - Oracle	78	42	46	56	62	55	50	58	58
AZ - Bullock		48	48	58	67	57	49	59	60
AZ - Upper Bullock			49	44	35	36	36	37	42
AZ - Merritt/Ryan				57	44	29	31	35	33
AZ- Darnel					60	40	38	43	37
AZ - Walnut						40	38	43	37
CA - Grand Prix/Old							70	67	76
CA - Paradise								80	79
CA - Cedar									82
Genera									
*Fall Az - Spring CA**									
AZ - Oracle	54	28	31	37	37	14	9	13	10
AZ - Bullock		31	41	31	46	11	10	10	9
AZ - Upper Bullock			26	31	30	9	6	6	6
AZ - Merritt/Ryan				43	45	9	6	7	7
AZ- Darnel					49	8	7	7	5
AZ - Walnut						10	9	10	8
Spring in AZ & CA									
AZ - Oracle	54	33	31	28	42	17	14	17	15
AZ - Bullock		33	33	30	45	18	12	15	13
AZ - Upper Bullock			30	23	26	14	13	13	13
AZ - Merritt/Ryan				30	36	8	8	8	7
AZ- Darnel					42	8	6	7	5
AZ - Walnut						16	14	15	14
CA - Grand Prix/Old							49	49	54
CA - Paradise								63	54
CA - Cedar									61

Based on presence/absence the Jaccard's index for families and genera in fall and spring (Table 4) generally showed that intraregional comparisons of fires (AZ fires vs. AZ fires or CA fires vs. CA fires) were more similar than comparisons between regions (AZ vs. AZCA or CA vs AZCA).

In Arizona the two western most sites (Oracle and Bullock) were markedly similar in families and genera but that changed with elevation (Upper Bullock) and in comparison with the eastern most sites (Table 4). In California, sites were much more similar to each other than

observed within Arizona sites, despite being distributed across a similar-sized area.

For both families and genera the spring flora in Arizona was much more similar to California's spring flora than was the fall flora in Arizona. In addition, the western most sites in Arizona (Oracle and Bullock) were more similar to California than the eastern most sites (Darnel and Walnut).

To summarize these patterns the average Jaccard's index is presented for all Arizona site comparisons, for all California site comparisons and for all comparisons of Arizona and California sites

TABLE 5. COMPOSITIONAL SIMILARITY BETWEEN BURNED AREAS USING JACCARD'S INDEX BASED ON PRESENCE/ABSENCE FOR PLANT FAMILIES AND GENERA IN THE FALL AND SPRING, BASED ON DATA IN TABLE 4. AZ = average of all pairwise comparisons of Arizona sites grouped by fire, CA = average of all pairwise comparisons of California sites grouped by fire, AZCA = all pairwise comparisons of Arizona vs. California sites grouped by fire). *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	Average Jaccard's percentage similarity			P-value for Wilcoxon signed ranks test		
	AZ	AZCA	CA	AZ vs. CA	AZ vs. AZCA	CA vs. AZCA
Families						
Fall*	55	39	–	0.046	<0.001	–
Spring	53	46	75	0.046	0.069	0.028
Genera						
Fall*	39	9	–	0.046	<0.001	–
Spring	34	12	55	0.046	<0.001	0.028

(Table 5). Based on these averages it is apparent, at both the family and genus level, California sites were significantly more similar to one another than were Arizona sites. The average for regional comparisons between Arizona and California was much lower for families and markedly lower for genera than that index calculated within each region.

Aliens were not well represented in many Arizona sites and this likely contributed to the fact that at the level of both families and genera, similarity between sites was much less (Table 6) than for the flora as a whole (Table 5). This stands in contrast to the California sites where alien families and genera were quite similar between sites (Table 6). The average similarity within Arizona sites was not significantly different than the similarity index between Arizona and California sites, whereas California sites had a significantly higher index than that calculated between California and Arizona.

DISCUSSION

California chaparral occurs under a winter rain – summer drought climate in contrast to the bimodal rainfall pattern characteristic of Arizona chaparral. Although both have winter rains, California sites typically have higher winter rainfall than Arizona sites (40–60% of the annual total in California vs 20–30% in Arizona). These rainfall patterns contribute to differences in fire seasons; Arizona commonly has late spring – early summer fires and the California fire season is largely in the late summer and fall (Keeley 2000), although earlier in years with dry winters (Dennison et al. 2008).

In addition to occurring under a different climatic regime, Arizona chaparral tends to be distributed at higher elevations than in California sites, apparently because precipitation regimes conducive to chaparral occur at higher elevations in Arizona than in California (Mooney and Miller 1985). This likely accounts for why the ubiquitous Californian chaparral shrub *Adenostoma fasciculatum* is missing from Arizona; in California it drops out of interior sites with cold winters (Keeley and Davis 2007).

Arizona and California chaparral communities share many of the same dominant woody species, including species of *Arctostaphylos, Baccharis, Ceanothus, Cercocarpus, Eriogonum, Garrya,*

TABLE 6. ALIEN PLANT SIMILARITY BETWEEN BURNED AREAS USING JACCARD'S INDEX BASED ON PRESENCE/ABSENCE FOR PLANT FAMILIES AND GENERA IN THE FALL AND SPRING, BASED ON SIMILAR COMPARISONS AS SHOWN IN TABLE 4. AZ = average of all pairwise comparisons of Arizona sites grouped by fire, CA = average of all pairwise comparisons of California sites grouped by fire, AZCA = all pairwise comparisons of Arizona vs. California sites grouped by fire. *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	Average Jaccard's percentage similarity			P-value for Wilcoxon signed ranks test		
	AZ	AZCA	CA	AZ vs. CA	AZ vs. AZCA	CA vs. AZCA
Families						
Fall*	27	33	–	0.028	0.331	–
Spring	26	26	75	0.028	0.950	0.028
Genera						
Fall*	20	6	–	0.046	<0.001	–
Spring	19	12	59	0.028	0.022	0.028

Quercus, Rhamnus, Rhus, and *Salvia.* In both regions these dominants exhibit similar patterns of postfire recovery including resprouting and seedling recruitment from soil-stored seed banks. Following summer wildfires Arizona chaparral recovers very rapidly in concert with the summer rains that begin usually in July. All resprouting woody species initiate resprouts during this rainy season. In California, resprouting species may begin regrowth soon after fires but this appears to be dependent on soil moisture as it is commonly observed that resprouting in dry years it is delayed until the winter rainy season (Keeley 2000).

The phenology of seedling recruitment in *Ceanothus* and *Arctostaphylos* shrub species is remarkably similar in that it occurs towards the end of the winter rainy season in both regions. Thus, the winter rainfall is one climatic characteristic that links these regions in terms of some functional type responses. Another is the spring postfire annual-dominated flora in both regions.

However, the ephemeral postfire floras exhibit a number of differences between regions. Most noteworthy is the duel postfire floras in Arizona. Not only do fall and spring rains result in two growing seasons but different floras are produced in fall and spring. The spring flora in Arizona bears a strong systematic resemblance to California whereas the fall flora is quite distinct and has elements that have a more neotropical affinity (Fotheringham 2009). As a consequence, the total yearly diversity is substantially higher in Arizona than in California from small to large scales (Fig. 4). At the community level (1000 m^2) species richness in Arizona is comparable to some of the most species rich communities known from temperate latitudes (Keeley and Fotheringham 2003).

Another prominent difference between these climatically different regions is the greater importance of herbaceous perennials in the Arizona chaparral. This is likely tied to the differences in summer drought between the two regions. In California the drought, on average, lasts from late spring to early fall and places a severe stress on survival of perennials, particularly herbaceous perennials. In Arizona the drought is cut short by summer rains and this works to favor survival of herbaceous perennials. One of the most striking differences in the postfire floras between these two regions is the prominence of Poaceae in Arizona, in particular the very diverse and dominant C$_4$ bunchgrass flora. The importance of C$_4$ bunchgrasses is to be expected in this summer rain climate and their near total absence in California is consistent with what is known about the distribution of C$_4$ grasses (Sage et al. 1999).

CONCLUSIONS

The number of similarities between California and Arizona are matched by the differences between these two regions. The most obvious similarity is that these plant communities share most of the same dominant species as well as a number of genera. The most prominent dissimilarity is that Arizona chaparral has both a spring growing season and a fall growing season which results in two very different postfire floras. Other dissimilarities include the prominence of perennial grasses in Arizona, which is promoted by the summer rains and perhaps by more open shrublands. This life form is largely nonexistent in California postfire chaparral because spring annuals are far better at persisting in landscapes dominated by a long summer drought and the closed canopy chaparral in California excludes herbaceous species to a greater degree than in Arizona. Thus, the primary differences are seen in the herbaceous component of these plant communities and are largely driven by summer rains in one region and absence in another.

The results from this study have implications for paleoecological reconstructions. Palaeo-communities are commonly reconstructed from macrofossils and generally these are restricted to the woody component of the community because herbaceous species are seldom preserved. Based on the woody component of the contemporary California and Arizona communities one would conclude that these are similar plant communities. However, the detailed community characterization demonstrated in this paper shows that these are radically different communities. When confronted with the duel fall and spring herbaceous communities and the major contribution of C$_4$ perennial grasses to the Arizona postfire community one must conclude that these two regions are dominated by quite different plant communities. Thus, paleofloras reconstructed from just the woody components would be potentially misleading in comparisons of these types of communities.

This is relevant to reconstructing the past history of chaparral as it appears that it originated under summer rain conditions, apparently in the southwestern portion of North America (Ackerly 2009; Keeley et al. 2012). If the Arizona chaparral is a reflection of earlier chaparral stages it strongly suggests that the primary similarity is in the woody flora. The contemporary postfire herbaceous flora in California chaparral appears to be a flora, with similarities to winter rain floras from Arizona chaparral, but largely missing the fall floras of Arizona chaparral. Although lacking in diversity of functional types, the Mediterranean-type climate appears to have played a role in adding to the diversification of the winter rain postfire flora. Many of the genera common in the spring floras of both regions have much greater diversity in California than in Arizona.

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APPENDIX 1

Plant families recorded from just Arizona or just California postfire sites, and families recorded from sites in both regions.

Only in Arizona (19)
Acanthaceae
Aceraceae
Aizoaceae
Asclepiadaceae
Cactaceae
Commelinaceae
Fouquieriace
Juglandaceae
Krameriaceae
Linaceae
Lythraceae
Molluginaceae
Pedaliaceae
Pinaceae
Plantaginace
Polygalaceae
Verbenaceae
Violaceae
Zygophyllacea

Only in California (9)
Cistaceae
Crassulaceae
Fumariaceae
Grossulariaceae
Orchidaceae
Orobanchaceae
Rutaceae
Sterculiaceae
Styracaceae

In both Arizona & California (44)
Agavaceae
Amaranthaceae
Anacardiaceae
Apiaceae
Asteraceae
Boraginaceae
Brassicaceae
Campanulaceae
Caprifoliaceae
Caryophyllaceae
Chenopodiaceae
Convolvulaceae
Cupressaceae
Cuscutaceae
Cyperaceae
Ericaceae
Euphorbiaceae
Fabaceae

Fagaceae
Fumariaceae
Garryaceae
Gentianaceae
Geraniaceae
Hydrophyllaceae
Lamiaceae
Liliaceae
Loasaceae
Malvaceae
Nyctaginaceae
Onagraceae
Papaveraceae
Poaceae
Polemoniaceae
Polygonaceae
Portulacaceae
Primulaceae
Pteridaceae
Ranunculaceae
Rhamnaceae
Rosaceae
Rubiaceae
Scrophulariaceae
Selaginellaceae
Solanaceae

APPENDIX 2

Plant genera recorded from just Arizona or just California postfire sites, and genera recorded from sites in both regions.

Only in Arizona (148)
Abutilon
Acacia
Acalypha
Acer
Adiantum
Aeschynomene
Agave
Agropyron
Alternanthera
Androsace
Anemone
Anisacanthus
Anoda
Astrolepis
Bahia
Baileya
Bidens
Boerhavia
Bothriochloa
Bouchea
Bouteloua
Brickellia
Bulbostylis
Calliandra
Carmentia
Cathestecum
Chaetopappa
Chamaecrista
Cheilanthes
Chloris
Commelina
Condalia
Corydalis

Crotalaria
Crusea
Cuphea
Cylandropuntia
Cynanchum
Cynodon
Cyperus
Dalea
Dasylirion
Dasyochloa
Desmanthus
Desmodium
Dicliptera
Digitaria
Diodia
Ditaxis
Drymaria
Dyschoriste
Dyssodia
Echinocereus
Elionurus
Enneapogon
Ephedra
Epilobium
Eragrostis
Eriastrum
Ericameria
Euphorbia
Evolvulus
Fallugia
Ferocactus
Fouquieria
Funastrum
Geraea
Glandularia
Gomphrena
Guilleminea
Gymnosperma
Hackelochloa
Hedeoma
Heliomeris
Heliotropium
Heteropogon
Heterosperma
Houstonia
Hymenopappus
Hymenothrix
Hymenoxys
Ipomoea
Ipomopsis
Isocoma
Juniperus
Krameria
Laennecia
Lappula
Lasianthaea
Leptochloa
Lycurus
Machaeranthe
Macroptilium
Macrosiphon
Mammillaria
Marina
Melampodium
Melinis
Microsteris
Mimosa
Mitracarpus

Mollugo
Monolepis
Myosurus
Nolina
Notholaena
Oreochrysum
Panicum
Pectis
Pennellia
Phaseolus
Physalis
Pinus
Piptochaetium
Platyopuntia
Portulaca
Proboscidea
Prosopis
Pseudognaphia
Psilactis
Psoralidium
Sanvitalia
Schistophrag
Schoenocrambe
Sclerocactus
Scleropogon
Senna
Setaria
Sida
Sorghum
Spermolepis
Sphaeralcea
Sporobolus
Stevia
Swertia
Symphyotrichum
Tagetes
Tephrosia
Tidestromia
Trachypogon
Trachypogon
Trianthema
Triticum
Urochloa
Verbesina
Viguiera
Zephyranthes
Zornia

<u>Only in California (78)</u>
Achnantherum
Acourtia
Adenostoma
Anagallis
Antirrhinum
Apiastrum
Brachypodium
Calyptridium
Calystegia
Camissonia
Caulanthus
Centaurea
Centaurium
Chaenactis
Chamaebatia
Chlorogalum
Chorizanthe
Clarkia
Claytonia
Cneoridium

Cordylanthus
Crassula
Cupressus
Delphinium
Dendromecon
Dicentra
Dichondra
Dodecatheon
Emmenanthe
Eriodictyon
Eriophyllum
Eschscholzia
Eucrypta
Filago
Fremontodendron
Gastridium
Hazardia
Helianthemum
Hemizonia
Heteromeles
Hieracium
Hirschfeldia
Horkelia
Hypochoeris
Keckiella
Lepechinia
Leymus
Lonicera
Malacothamnus
Malosma
Marah
Melica
Monardella
Muilla
Nassella
Navarretia
Nemocladus
Orobanche
Osmadenia
Papaver
Pedicularis
Phacelia
Pickeringia
Piperia
Plagiobothryus
Polycarpon
Pterostegia
Ribes
Scrophularia
Scutellaria
Styrax
Tauchsia
Thalictrum
Toxicodendron
Trifolium
Uropappus
Xylococcus
Zigadenus

In both Arizona and California (109)

Agoseris
Agrostis
Allium
Allophyllum
Amaranthus
Ambrosia
Amsinckia
Arabis
Arctostaphylos

Argemone
Aristida
Artemisia
Asclepias
Astragalus
Atriplex
Avena
Baccharis
Bowlesia
Brassica
Bromus
Calandrinia
Calochortus
Capsella
Carex
Castilleja
Ceanothus
Cerastium
Cercocarpus
Chamaesyce
Chenopodium
Cirsium
Claytonia
Conium
Conyza
Cryptantha
Cuscuta
Datura
Daucus
Descurainia
Dichelostemma
Draba
Elymus
Encelia
Erigeron
Eriogonum
Erodium
Galium
Garrya
Gilia
Gutierrezia
Helianthus
Heterotheca
Hordeum
Iris
Juglans
Lactuca
Lathyrus
Layia
Lepidium
Linanthus
Lineria
Linum
Lomatium
Lotus
Lupinus
Malacothrix
Marrubium
Mentzelia
Mimulus
Mirabilis
Monardella
Muhlenbergia
Oenothera
Pectocarya
Pellaea
Penstemon
Phacelia

Plagiobothrys
Plantago
Poa
Polygala
Polygonum
Porophyllum
Quercus
Rafinesquia
Rhamnus
Rhus
Salsola
Salvia
Sambucus
Schismus
Selaginella
Senecio

Silene
Sisymbrium
Solanum
Solidago
Sonchus
Stellaria
Stephanomeria
Streptanthus
Stylocline
Thysanocarpus
Trichostema
Triodanis
Vicia
Vulpia
Yabea
Yucca

MORPHOLOGICAL AND ISOENZYME VARIATION IN *RHODODENDRON OCCIDENTALE* (WESTERN AZALEA) (SECTION *PENTANTHERA*; ERICACEAE)

G. F. HRUSA

UC Davis Center for Plant Diversity, Department of Plant Sciences, Mail Stop 7, One Shields Avenue, Davis, CA 95616

California Dept. of Food and Agriculture Plant Pest Diagnostics Center, 3294 Meadowview Rd., Sacramento, CA 95832-1448
fhrusa@cdfa.ca.gov

ABSTRACT

Morphological and isoenzyme variation among populations of western azalea, *Rhododendron occidentale* (Torr. & A. Gray) A. Gray, were examined. Three regional parapatric groups were revealed: 1) the northern California outer North Coast Ranges; 2) the northern California and southern Oregon Klamath Ranges; and 3) the central California Sierra Nevada and southern California Peninsular Ranges. A highly variable but generally intermediate fourth group is restricted to ultrabasic substrates (serpentine) in the middle and inner North Coast Ranges of California. It is comprised of populations with recombined morphologies and alleles that were otherwise restricted to one or more of the three groups above. A revised intraspecific treatment is proposed, with the three regional groups above recognized as varieties. These are: *R. occidentale* (Torr. & A. Gray) A. Gray var. *occidentale* (outer North Coast Ranges), *R. o.* var. *paludosum* Jeps. (Klamath Ranges), and **Rhododendron. occidentale** var. **californicum** (Torr. & A. Gray) Hrusa comb. et stat. nov. (Sierra Nevada and Peninsular Ranges). Lectotypifications of *Azalea occidentalis* Torr. & A. Gray isotypes at PH and GH, *Azalea californica* Torr. & A. Gray in Durand, and *Rhododendron sonomense* Greene (NDG) are also provided.

Key Words: Azalea, isozyme, lectotype, morphometric, population, *Rhododendron occidentale*.

In addition to its large and fragrant flowers *Rhododendron occidentale* (Torr. & A. Gray) A. Gray has long been recognized for its diversity of growth habits, floral pigmentations, and vegetative forms (Kellogg 1855; Wilson and Rehder 1921; Jepson 1939, Munz and Keck 1959; Mossman and Smith 1969; Kron 1993). The only more or less invariant characteristic is the presence of a yellow nectar guide on the upper corolla limb. It has been suggested that this variation indicates the existence of multiple species (Mossman and Smith 1969; Mossman 1977). Other observers have interpreted these polymorphisms as randomly distributed genotypes or as environmentally induced (Breakey 1960). The most recent systematic treatment of section *Pentanthera* (Kron 1993) did not examine the presence or patterns of intraspecific variation in *R. occidentale*, and the same can be said of the discussion in Wilson and Rehder (1921). Indeed, there has been no detailed accounting of its regional diversity.

In horticultural circles its visible morphological variation has made *R. occidentale* a favorite of azalea breeders. Middle nineteenth- to early twentieth-century selections were prominent in these breeding programs (Mossman 1974). The results can be found for sale as the Knapp Hill and Exbury hybrid series. More recently, enthusiasts have been seeking out novel wild forms. Especially popular are those with unusual corolla shapes and color variations (Mossman 1974,

1977), which are sold with names such as 'Humboldt Picotee', 'Tatum's Pink', or 'Double Dig Twelve' (Jones et al. 2007). Accompanying the reports of these variants' discoveries were poorly documented assertions regarding polyploidy; wild distributions; regional variation patterns; and edaphic, moisture, and temperature tolerances in wild populations (Breakey 1960; Mossman and Smith 1968; Mossman 1972, 1974, 1977). Ultimately, experimental evidence for any of these interpretations is lacking.

Geographic Distribution

Rhododendron occidentale is distributed within the Coast Ranges of California, the Klamath Ranges of northern California and southern Oregon, the Sierra Nevada, and the Peninsular Ranges of southern California. Its distribution is largely coincident to the California Floristic Province (CFP) (Raven & Axelrod 1978) with its northernmost populations only about 75 miles north of the CFP along the Umpqua River in Douglas Co., Oregon. It is found at elevations extending from sea level to near 2800 m. Throughout its range it is restricted to sites of permanent moisture, although these may be subsurface sources. It is frequently found growing on ultrabasic soils, predominantly serpentine, particularly in the Klamath ranges and inner North Coast Ranges. Except for a single location at the northern tip of the Gabilan Range in

Monterey Co., *R. occidentale* is absent from the California South Coast Ranges and Transverse Ranges. It is presumed that the warming and drying of the post-Pleistocene eliminated it from these relatively dry mountains. Claims that *R. occidentale* has native populations in the Puget Sound area, the Olympic Peninsula, and on Mount Rainier in Washington (Mossman 1974) require confirmation.

This paper will present quantitative and qualitative analyses that describe the patterns of morphological and isoenzyme variation among wild populations of *R. occidentale*. A taxonomic treatment that accounts for the species' natural variation patterns will also be proposed.

MATERIALS AND METHODS

Sampling

Populations representing the species' full geographic range were analyzed. Thirty-six populations were used for the morphological analysis, and 37 populations were used for the isoenzyme analysis (Fig. 1 and Appendix 1).

All but three population samples contained a minimum of 25 individuals. The three smaller samples came from critically situated populations that did not contain that many individuals. *Rhododendron occidentale* is not rhizomatous, nor does it sprout from the roots. It may, however, form clones when fallen trees or branches press plants to the ground and adventitious roots develop. There was adequate visible variation among individuals in both growing and dormant structures so that duplicate clone collections were readily avoided. Sampling was random throughout except in the case of the smaller populations where every individual was examined.

The morphological samples included both spring-collected flowering material and winter-collected dormant inflorescence buds. Thus the dormant and flowering collections used for morphological examination did not necessarily represent the same individuals. This did not affect the analyses because the characters were defined as population summaries. Specimens for isoenzyme analysis were either fresh, spring-collected corolla tissue or mature, dormant vegetative branch tips.

The sampled populations are mapped in Figure 1. Locality descriptions and sample sizes are listed in Appendix 1, and representative vouchers from those populations have been deposited at CDA and DAV. All statistical analyses were performed in JMP 5.1 (SAS Institute).

Morphometric Data

Traditional morphological classifications of *Rhododendron* have emphasized variation in floral pigmentations and vegetative trichome types and their positions, in addition to quantitative physical data (Sleumer 1949; Kron 1993). The first two proved particularly useful in this study.

Quantitative data were taken from specimens collected, pressed, and dried specifically for these analyses. Because of the variable bilateral form of *Rhododendron occidentale* corollas, special handling and pressing of individual flowers after their removal from the inflorescence was necessary for consistent measurement of corolla tube and limb relationships. For the quantitative characters, values were defined as the mean of four measurement repetitions per structure per individual. As much as possible each measured structure was standardized by plant position and developmental stage. Phenotypic plasticity within leaf size, shape, venation patterns, and trichome length were demonstrated in a preliminary unpublished study (Hrusa 1991). Seed and capsule features including seed wing shape and capsule sizes and shapes were highly variable within individuals and were not used.

The raw measurements were taken at various scales. These were ranged to between 0 and 1 using Gower's Transformation (Sneath and Sokal 1973). The population-based quantitative characters were defined as the proportion of the range for a given population that fell in two of three equal classes that represented the upper and lower one-third of the structure's among-population range. Statistically, the central of the three quantitative classes for each character is always correlated to one of the outside thirds, and was excluded.

The qualitative character states were defined as their frequency within each population sample. Corolla coloration data were acquired from fresh material. Trichome position and density data were taken from dried specimens. The quantitative and qualitative characters are listed in Table 1.

Isoenzyme Data

Soluble enzymes were extracted from fresh plant samples and electrophoresed on horizontal starch gels composed of 12% hydrolyzed potato starch and 3% sucrose. Gel and electrode buffers were composed of 0.0009 M L-histidine-0.0003 M citric acid and 0.065 M L-histidine-0.019 M citric acid, both at pH 5.7. Electrophoresis proceeded for 13 hours at 3.5 watts.

Allelic variants were classified and identified by their relative migration distance against a standard allele at each locus. This allele was one present in every population and was usually the most common. Homologies among the variant electromorphs were determined by comparing them on common gels.
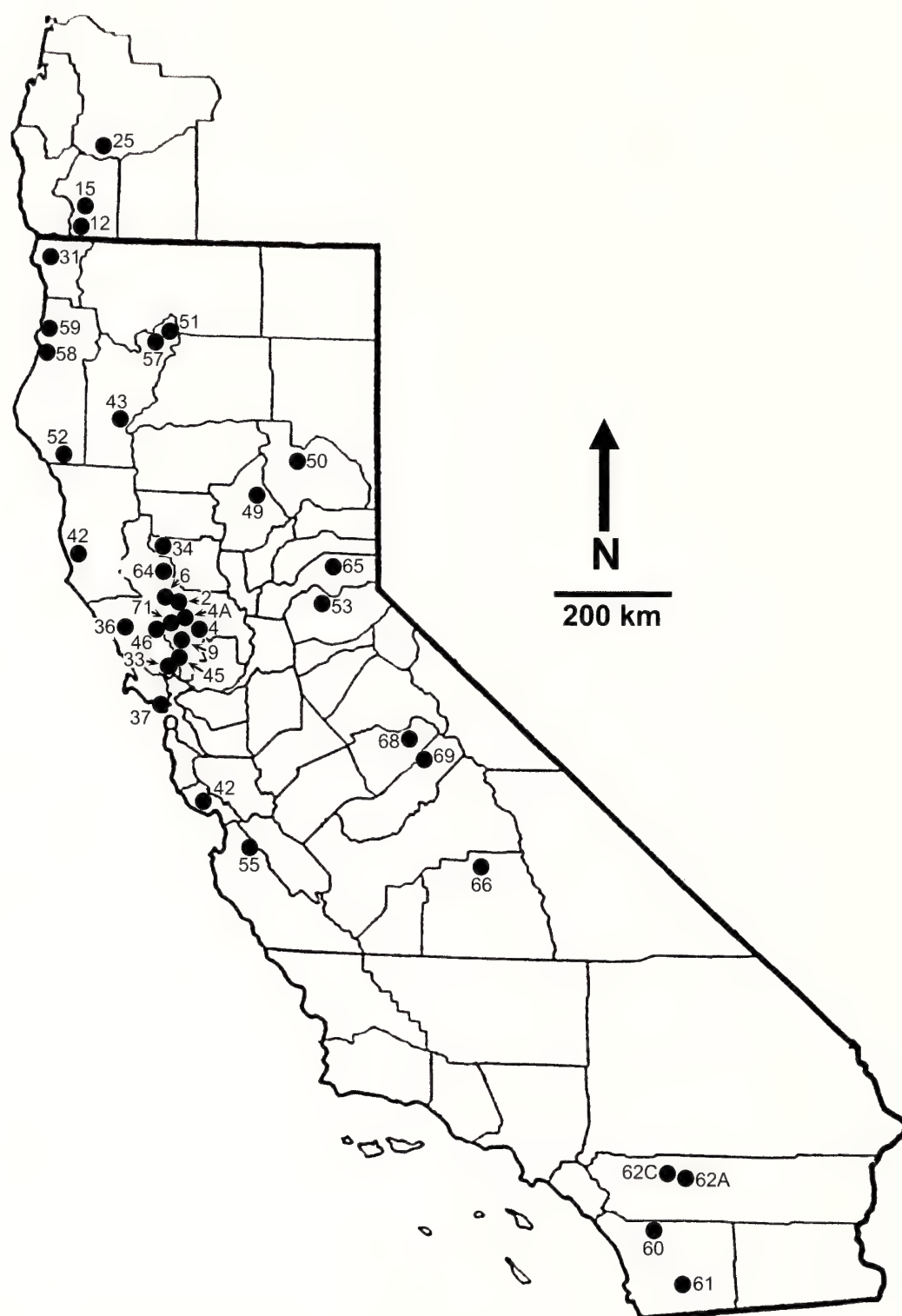
FIG. 1. Populations of *Rhododendron occidentale* used in the morphological and isoenzyme analyses. See Appendix 1 for geographic location and sampling details.

RESULTS

Morphological Variation

Thirty-eight outwardly visible features (21 quantitative and 17 qualitative) were described and measured or assessed (Table 1). The among-population comparisons were performed through principal components analysis of the among-population correlation matrices.

The first three principal components described 84.9% of the total variation, with four clusters of populations evident. These are plotted in Figure 2 and mapped in Figure 3. The Sierra Nevada and Peninsular Range populations (SNPR) grouped together. The populations of the Klamath Ranges (KR) and outer North Coast Ranges (ONCR) ordinated apart from

both each other and from the SNPR populations. With two exceptions, the inner North Coast Range Serpentine (INCRS) populations plotted between the ONCR, KR, and SNPR populations, much as they are situated geographically (Fig. 3). The exceptions, (P-64, Kilpepper Creek, Lake Co.; and P-34, Stony Creek, Colusa Co.) grouped among the SNPR populations. These two populations shared with those of the SNPR the characteristics of relatively long, generally white-colored corolla tubes, and a pubescent leaf abaxium.

Stepwise discriminant analysis was used to evaluate which characters were useful in distinguishing the four groups in Figure 2. The results indicated that individuals from the KR and ONCR populations shared combined glandular and eglandular multicellular trichomes on the leaf

TABLE 1. DEFINITIONS OF MORPHOLOGICAL FEATURES USED IN THE MULTIVARIATE ANALYSES. Asterisks (*) denote subset of nine systematically useful characters. Quantitative characters were defined as described in the text. Qualitative characters were defined as their frequency within the population sample.

Quantitative		Qualitative
1. Ovary length: classes 1, 3	11. Perianth tube: dark pink	*20. Leaf abaxium, secondary vein trichomes: absent
2. Anther length: classes 1, 3	12. Perianth veins: pink base to summit	21. Leaf margin trichomes: mixed glandular and strigose
3. Corolla length: classes 1, 3	13. Perianth veins: white except for vein tip	*22. Floral bud-scales, margin trichomes: glomerate
4. Corolla tube length: classes 1, 3	14. Perianth limb: pink	*23. Floral bud-scales, margin trichomes: ciliate
5. Corolla length/tube length ratio: classes 1, 3	15. Perianth limb: white	*24. Young twigs, vestiture: densely pubescent
6. Inflorescence bud length: classes 1, 3	*16. Leaf abaxium, midvein trichomes: mixed glandular and strigose	*25. Young twigs, vestiture: glabrous
7. Calyx lobe length, longest: class 1	17. Leaf abaxium, midvein trichomes: glandular	*26. Leaf abaxium, surface: single-celled pubescence
8. Calyx lobe length, shortest: class 1	18. Leaf abaxium, secondary vein trichomes: mixed glandular and strigose	27. Floral bud bract, surface vestiture: pubescent
9. Calyx lobes ratio, length of longest/shortest: class 1	*19. Leaf abaxium, secondary vein trichomes: strigose	28. Floral bud bract, surface vestiture: glabrous
*10. Leaf abaxium, multicellular trichomes per 25 mm^2: class 1 (<7) and 3 (>26)		

abaxial midvein and a lamina abaxium without unicellular hairs. There may occasionally be unicellular trichomes on and adjacent the midvein, but not on the abaxial surface. The ONCR populations alone were distinguished by: 1) a dense pubescence on the young twigs and dormant bud bracts; 2) winter bud bract-margin trichomes always of a glomerate-glandular type; 3) relatively large dormant flower buds; and 4) more than 25 multicellular trichomes per/25mm^2 of leaf abaxial surface. The distinguishing features are marked with an asterisk in Table 1 and with additional morphological features summarized among the groups in Table 3.

Klamath Ranges populations alone were distinguished by: 1) mostly glabrous young twigs and either glabrous or thinly ciliate bud bracts; 2) usually ciliate, occasionally glomerate winter bud bract-margins; 3) generally a pink- to red-pigmented corolla tube; 4) a short corolla tube length in relation to the throat plus limb; and 5) the lamina abaxial surface, excluding the midvein, was devoid or nearly so of trichomes. Populations from the immediate coast generally were transitional to the ONCR azaleas (glomerate bud bract-margin trichomes and less densely pubescent bud bracts and twigs). Overall the KR azaleas had the smallest corollas with the shortest floral tubes and the most pink to red pigmentations in the limb and tube. Among the KR populations, only the single northernmost and most interior was morphologically unusual (P-25, Cow Creek, Douglas Co. Oregon, Fig. 2). This population had: 1) infrequently, a unicellular

pubescence on the leaf abaxium (KR azaleas are generally glabrous abaxially) and 2) midvein trichomes of a single type only (these are usually mixed strigose and glandular in the KR). The presence of these two morphological states suggests plants of the SNPR populations. However, isoenzyme alleles characteristic of that group were absent.

The SNPR azaleas had: 1) one type of multicellular leaf midvein trichome, either glandular or eglandular, not those combined as in the KR and ONCR; 2) a unicellular pubescence throughout the lamina abaxial surface; 3) secondary vein multicellular trichomes of the same type as the midvein (glandular or eglandular); 4) absent or widely scattered multicellular trichomes on the tertiary veins (when present these were ≪ 25/25 mm^2); 5) a non-pigmented to rarely, slightly pigmented corolla tube; 6) corolla veins rarely with more than a hint of pigmentation at the distal tip. In general, SNPR corollas were either pure white or (infrequently) had a hint of pink in the tube or vein summit; and 7) the corolla tube was comparatively long in relation to the combined limb and throat. The SNPR plants were thus particularly distinctive morphologically. Only P-50 (Butterfly Valley, Plumas Co.) of the northern Sierra Nevada had glabrous leaf abaxia and often glabrous young twigs, both features unusual among the Sierran azaleas. Population 50 plotted between the SNPR and KR populations, the same as it is situated geographically (Fig. 3).

In general, the southern California Peninsular Range azaleas had the largest and least pigmented
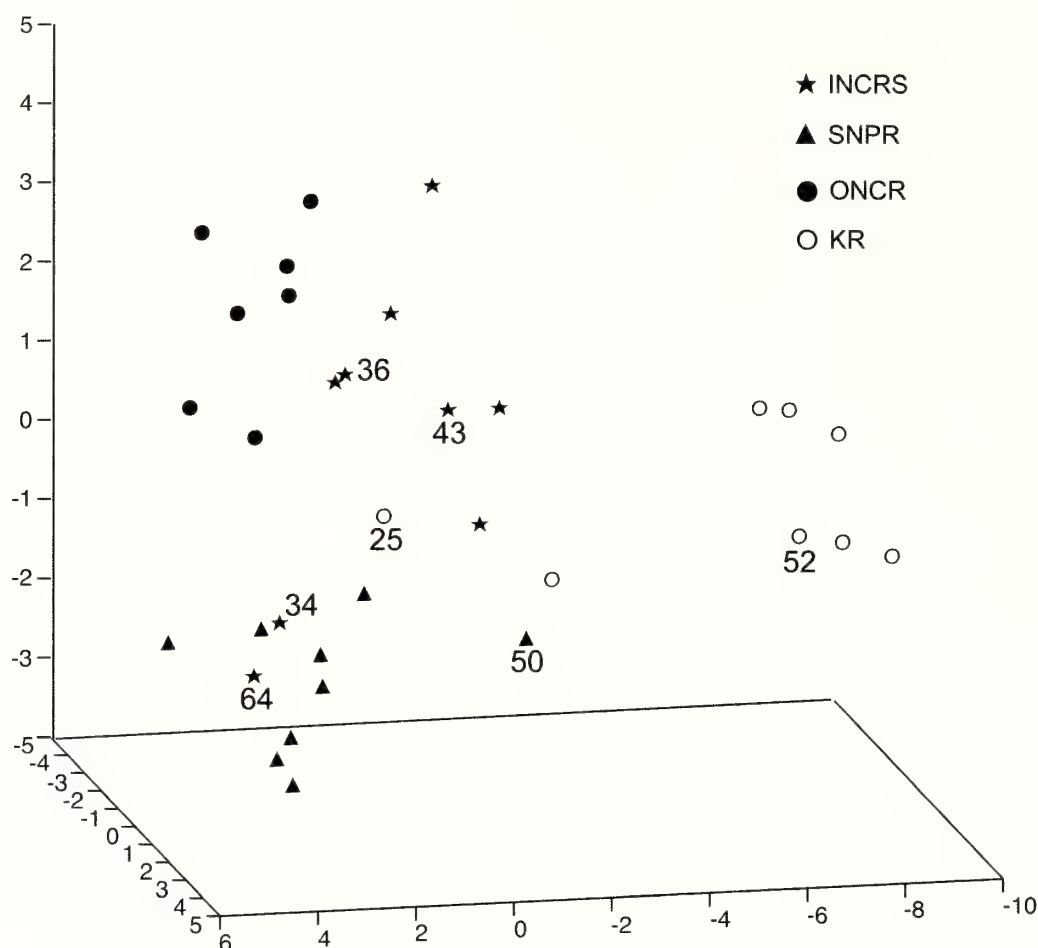
FIG. 2.   Scatter plot of the first three principal component scores for the morphological dataset. Populations 64 and 34 occur in the inner North Coast Ranges on serpentine, plotted here with Sierra Nevada populations. Labeled populations are discussed in the text.

flowers with the longest floral tubes. Overall, excluding the INCRS azaleas, a cline exists from north to south in which corolla coloration diminishes and the corollas become larger overall and have relatively longer tubes.

Even excluding P-34 (Stony Creek, Colusa Co.) and P-64 (Kilpepper Creek, Lake Co.) that ordinated among the SNPR, the INCRS populations were weakly differentiated. They were distinguishable morphologically only by a shortest calyx lobe that was generally less than 1 mm in length, and sometimes nearly obsolete. Their multivariate scattering across the space between the KR, ONCR, and SNPR groups (Fig. 2) was the result of both quantitative intermediacy and mosaic patterns among the qualitative features. This variation was spread among the first three principal components and is suggestive of segregation and recombination among the analyzed features.

Definitions of three readily visible and at least partially regionally distinctive features proved problematic and were not included as population-level characters in the multivariate analyses. Darkly anthocyanous new growth was a distinctive feature of both sun- and shade-grown INCRS azaleas. Elsewhere, azaleas growing on ultrabasic-derived soils often had at least some anthocyanin pigmentation in the young twigs, particularly in plants growing in full sun. This pigmentation (and lack of same from non-pigmented populations) was maintained in greenhouse-grown

seedlings, indicating it is under genetic control, at least in the INCRS (Hrusa 1991). Although the non-INCRS anthocyanin pigments were not as dark as that among individuals within the INCRS populations, this distinction could not be consistently delimited into a set of qualitative categories. Such coloration is a feature of many ultrabasic-adapted taxa (Kruckeberg 1984).

Strongly bifacial leaves that were lighter on the abaxial surface characterized many populations, mostly those of the SNPR. Several INCRS populations were similarly bifacial. Some of the latter were dimorphic for that characteristic, and in those populations the intensity of the bifacial condition was particularly variable, often varying in intensity even within individuals.

The timing of flower bud opening relative to leaf break is generally species specific within *Rhododendron* section *Pentanthera* (Kron 1993). Inflorescences may open concurrently to or after foliage maturation. In *R. occidentale* both conditions occur. Plants of the KR and most of the INCRS open flowers and leaf buds concurrently. Exceptions may occur in densely shaded plants where bud (and often leaf) break may be delayed. However, most followed the pattern of inflorescence break in concert with foliar emergence. One population from the INCRS (P-64, Kilpepper Creek, Lake Co.) broke flower buds only after new growth had fully matured; yet plants in the closely related and nearby P-34 (Little Stony
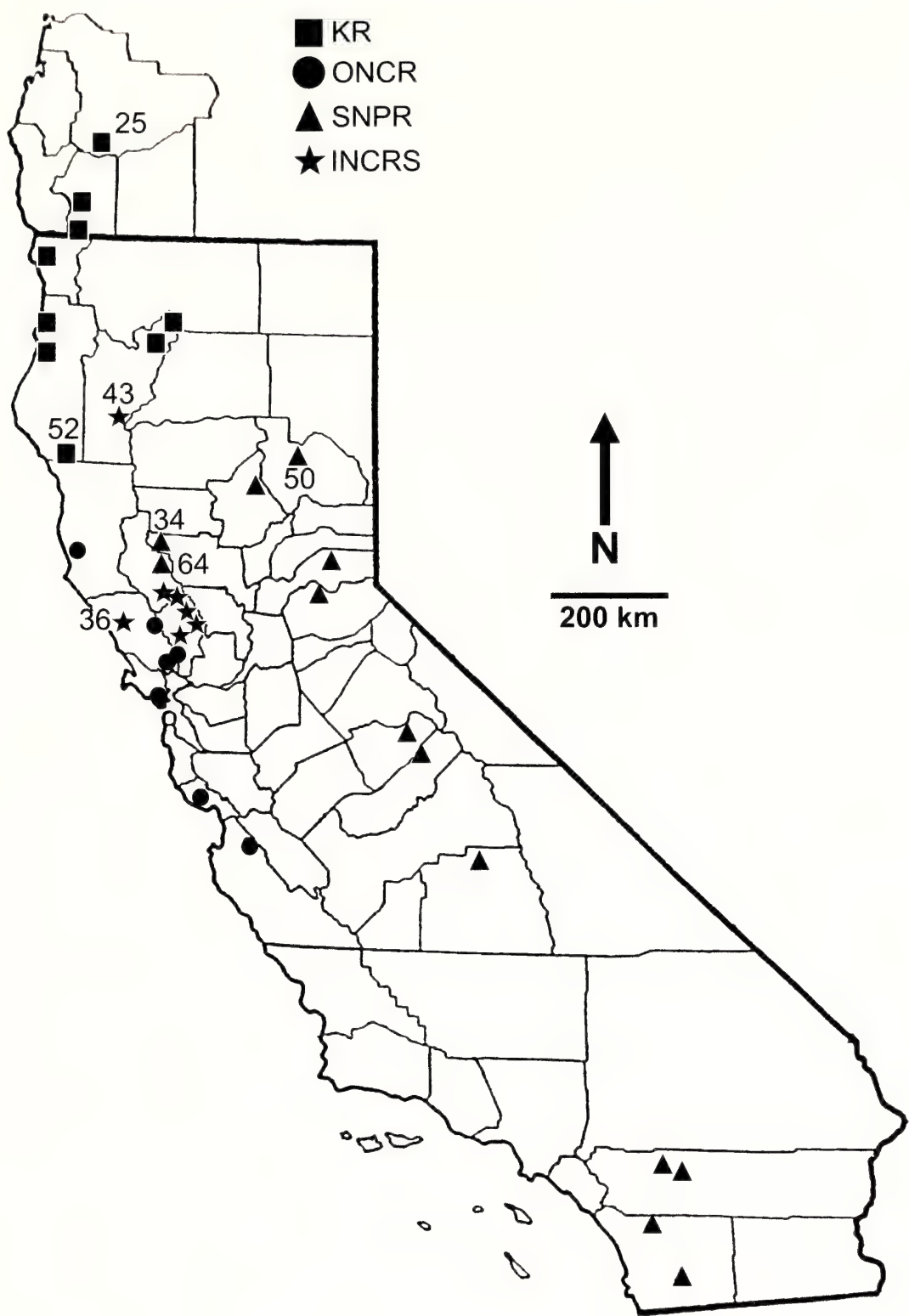
FIG. 3. Map of the population clusters based on morphological variation as identified in Fig. 2. Labeled populations are discussed in the text.

Creek, Colusa Co.) opened concurrent to bud break. With one exception each, plants of the ONCR and SNPR opened their inflorescences after the foliage had fully expanded and matured. Only the ONCR P-45 (Hogback Mountain, Sonoma Co.), growing on a highly insolated and relatively dry hillside, pushed its flower buds late-concurrent to leaf break. Again with one exception, Sierra Nevada populations flowered after leaf maturity. Population 49 (Pulga Rd., Butte Co.), from an open, south-facing serpentine slope, opened its flowers with new growth expansion. Thus, while bud and leaf break patterns are mostly consistent regionally, the exceptions suggest that local environmental conditions or selection in open habitats influence timing of flower bud break.

Isoenzyme Variation

Forty-two alleles were resolved at seven loci from four enzyme systems. The resolved variants were in malate dehydrogenase (MDH-1, MDH-2, MDH-3, 11 total alleles), phosphoglucomutase (PGM-1, PGM-2, 6 total alleles), 6-phosphoglu-conate dehydrogenase (6-PDH, 1 locus, 5 total alleles), and glucose-6-phosphate-isomerase (GPI-2, 20 total alleles).

At each locus there was a most-frequent (primary) allele with the remaining allele(s) at lower frequencies. The presence or absence and frequency of the alternate alleles varied widely among populations. Only in P-64 (Kilpepper Creek, Lake Co.) and P-61 (Cuyamaca Peak, San Diego Co.) did the alternate alleles at PGM
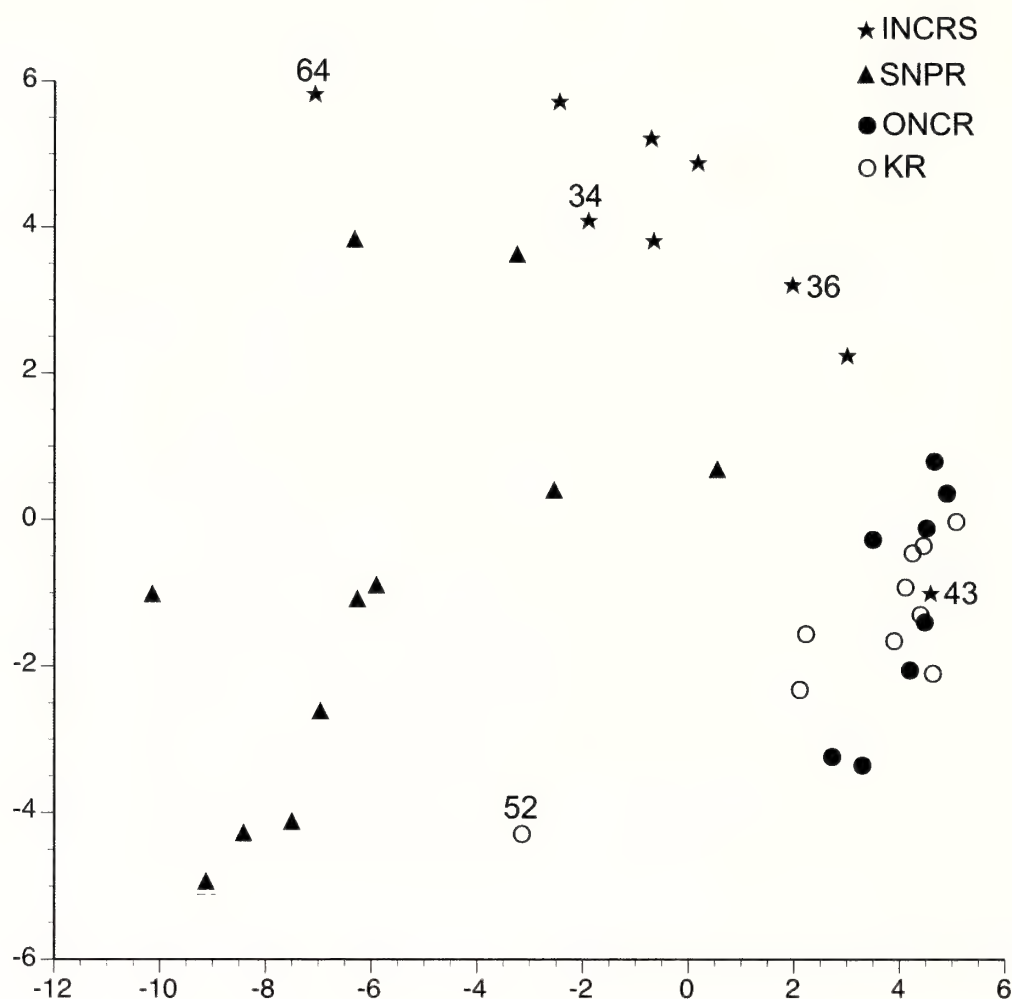
Fig. 4. Scatter plot of the first two principal component scores for the isoenzyme dataset. Labeled populations are discussed in the text.

exceed slightly the frequency of the primary allele. In no case did an alternate allele replace the primary one.

The first three principal components recovered 95.0% of the variation. Three population groups were evident, as opposed to four for the morphological data. The groups are plotted in Figure 4 and mapped in Figure 5.

The multivariate patterns were similar to those using morphology, except for the superposition of the KR and ONCR populations. With five endemic alleles the KR group might have been expected to occupy its own isoenzyme multivariate space as it did its own morphological space. That it does not is due to the presence of the non-private endemic alleles in only a few populations, and at relatively low frequencies.

The SNPR and INCRS populations plotted over a broader multivariate space than did the adjacent KR + ONCR cluster, due to their greater allelic diversity and higher alternate allele frequencies. Moreover, those frequencies varied considerably among the populations. In terms of allele presence or absence the SNPR and INCRS were similar. However, the shared alleles were not at similar frequencies, and this is responsible for their plotting in a slightly different, but adjacent, multivariate space. A characteristic INCRS allele was MDH-3B; although this allele was also found widely scattered at generally low frequencies among the KR, SNPR, and ONCR populations, it was in every INCRS population and at higher

frequencies than all but one population outside that group.

Two populations of the North Coast Ranges also classified differently between the morphological and isoenzyme datasets. Population 43 (Wildwood, Trinity Co.), the northernmost morphologically like the INCRS group (Figs. 2, 3), contained allelic complements characteristic of the KR, not those of the INCRS.

Population 52 (Red Mountain, southern Humboldt Co.) grouped morphologically among the KR populations. However, its isoenzyme complement placed it between the SNPR and KR + ONCR populations, but on the opposite side of the multivariate space occupied by the likewise intermediate INCRS group (Fig. 4). Although P-52 contains the same SNPR and KR alleles that characterized most of the populations included here in the INCRS, it was distinguished from them by a high frequency of allele MDH-2E and a low frequency of MDH-3B, the reverse of the frequencies found in the INCRS populations. Overall P-52 has mostly KR alleles. Its SNPR connection is via relatively high frequencies of alleles PGM-2B and PGM-2A as found throughout the SNPR and INCRS populations.

In relation to the four geographic regions evident in the morphological analyses, four allele distribution patterns were discernible: 1) widespread, not ubiquitous, but occurring across geographic regions; 2) alleles common in one region, but uncommon and localized in another,
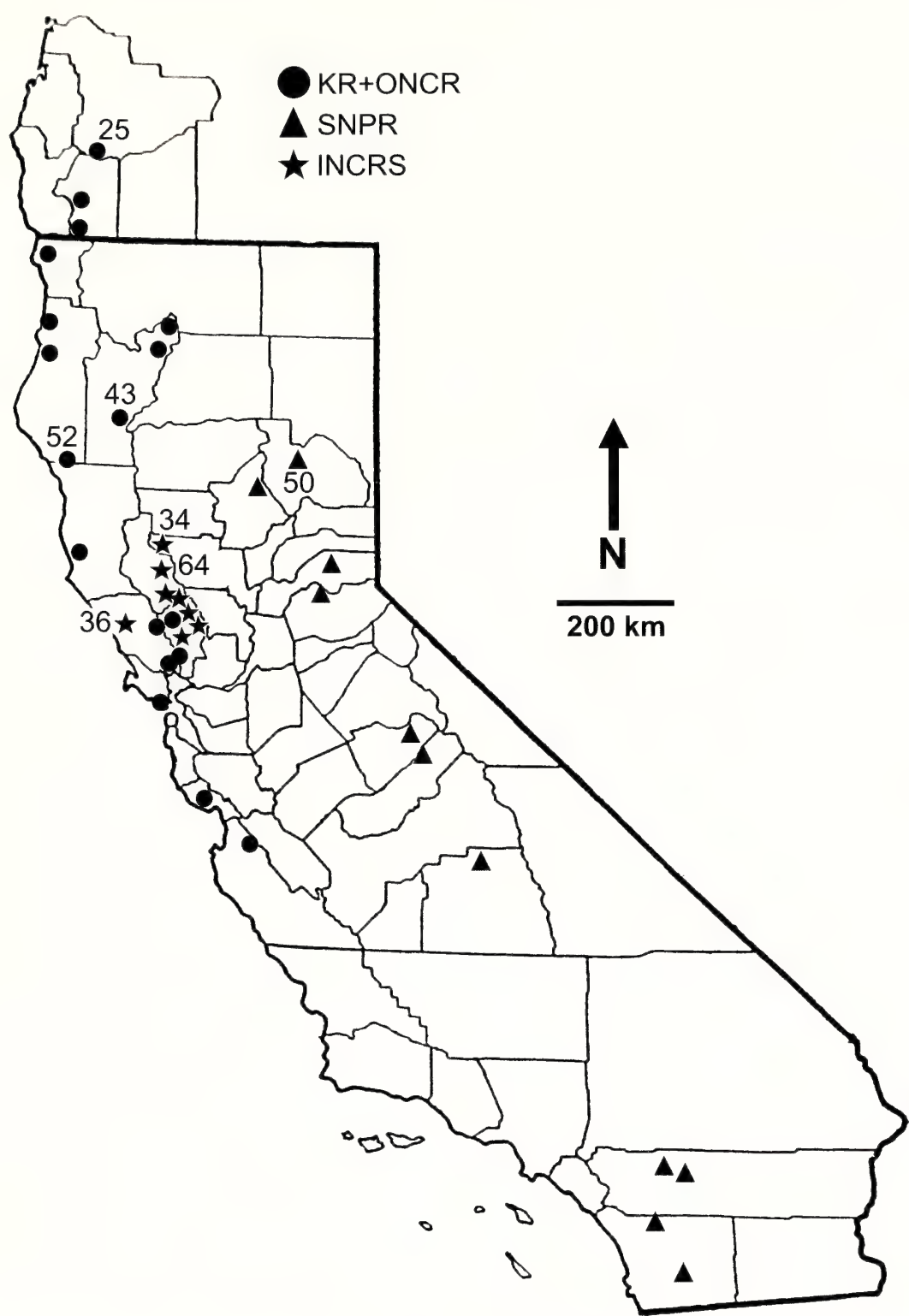
FIG. 5. Map of population clusters based on isoenzyme allele variation as identified in Fig. 4. Labeled populations are discussed or mentioned in the text.

sometimes disjunct region; 3) endemics, restricted to multiple populations within a single region, but absent elsewhere; and 4) private alleles known only from a single population.

Systematically, PGM-2 was the most distinctive. The SNPR and INCRS populations had three PGM-2 alleles (PGM-2A, PGM-2B, and PGM-2C) all at more or less equal frequencies. In contrast, the ONCR and KR populations contained exclusively or were dominated by PGM-2C, the most frequent allele at PGM-2. This PGM-2 dichotomy between the KR + ONCR and SNPR + INCRS was consistent throughout the species' range. The pattern was maintained even when the populations were in geographic proximity, a situation suggestive of restricted gene flow. Whatever is ultimately responsible for the consistently different allele frequency patterns

at PGM-2 in the SNPR + INCRS versus those of the KR + ONCR, the distinction of these two combination groups is supported by allele patterns at other loci, and by morphology.

Among the 42 total alleles identified, seven were restricted to the KR region, of which two were private and five were shared among at least two populations (endemic alleles). Nine total alleles were restricted to the SNPR region; four endemics and five private. While there were also three private alleles (all P-61, Cuyamaca State Park, San Diego Co.) and one endemic allele not found in the Sierra Nevada that occurred among the Peninsular Ranges populations, there were also several alleles shared between those two regions that did not extend beyond them.

Two private alleles were in population 36 (Gilliam Creek, Sonoma Co.) of the INCRS,

TABLE 2. VARIANT ALLELES OCCURRING IN THE INCRS POPULATIONS AND THEIR DISTRIBUTION OUTSIDE THAT GROUP. 'X' = alleles found in at least one population within the group at a frequency above 0.100 (10%); '+' = alleles not found in that group at a frequency above 10%.

	Geographic regions			
Allele	INCRS	SNPR	KR	ONCR
PGI-2^{a,5}	X	+		
PGI-2^{b}	X	X		
PGI-2^{f}	X	X		
PGI-2^{g}	X		X	X
PGI-2^{k}	X	X		
PGI-2^{m}	X	+		X
PGM-2^{a}	X	X	+	X
PGM-2^{b}	X	X	+	
MDH-1^{a}	X		+	
MDH-1^{d}	+		X	
MDH-2^{b}	X	+	+	
MDH-3^{b}	X	+	+	X
6-PDH^{b}	X	X		
6-PDH^{d}	+	X	+	
Total shared + (%)	14	11 (78.6)	8 (57.1)	4 (28.6)
Shared at >10% + (%)	12	7 (63.6)	2 (25.0)	4 (100)
Shared, both >10% (%)	—	6 (50)	1 (8.4)	4 (33.4)

but no endemic alleles occurred among the INCRS populations. Likewise, neither private nor endemic alleles occurred within the ONCR.

DISCUSSION

From the data, four main points may be made. First, it is clear that the azaleas of the Peninsular Ranges are allied to those of the Sierra Nevada. This is not surprising given the floristic, geologic, and climatic similarities of the forested parts of the two regions (Munz 1974; Axelrod 1976; Raven and Axelrod 1978). Azalea populations of the Sierra Nevada and Peninsular Ranges shared a distinctive allele frequency pattern at PGM where the two region's populations all had relatively equal frequencies of three different alleles. In contrast only one of the two alternates was even a rare occurrence in either the KR or ONCR populations. Despite the presence of endemic GPI alleles in some Peninsular Range azaleas that suggests a long post-disjunction history, their morphological similarity to the azaleas of the Sierra Nevada, particularly the high southern Sierra Nevada, was marked. It would appear that these two regions were formerly part of a continuous interbreeding azalea population. Fossil azaleas of Pliocene age (pre-Sierra Nevada time) were found in the Chalk Hills flora of western Nevada (Axelrod 1962). These azaleas were associated with *Sequoiadendron* and other montane taxa that the western azalea is associated with in the Sierra today. However, Coast Range elements, including the Monterey Co. endemic *Abies bracteata* were also present. The leaf and capsule impressions were examined by this author, but are not assignable below section *Pentanthera*.

Second, while the KR and ONCR azaleas had similarly low frequencies of alternate alleles, the allele complements were different. Morphologically, the azaleas of these two regions were quite distinct. It may be instructive here that Kron et. al. (1993) found no allelic differences (or variants) at enzyme systems GPI and PGM between *Rhododendron canescens* (Michx.) Sweet and *R. flammeum* (Michx.) Sarg., two morphologically quite distinct species. In *R. occidentale*, some morphological intermediacy occurred along the immediate coastline north of Fort Bragg, Mendocino Co. There the pubescent new growth and outer dormant flower bud bracts of the adjacent, more southern ONCR azalea appeared as a thin pubescence in populations that otherwise were like the more frequently glabrous KR azalea. These northern coastal azaleas did not have the multicellular leaf tertiary vein trichomes that were generally characteristic of the ONCR, and their isoenzyme complements were those of the KR. As is true for the Sierra Nevada azaleas, the ONCR and KR populations are each associated with certain distinctive forest taxa such as *Sequoia sempervirens* (D. Don) Endl.and *Cupressus* (*Chamaecyparis*) *lawsoniana* A. Murray bis, respectively. Based on the fossil record (Axelrod 1962, 1976; Raven and Axelrod 1978), these taxa and their associates occupied widespread geographic regions long before being restricted to their current distribution in west coast cismontane habitats.

Third, shared endemic alleles, similar within-population allele frequencies (as at PGM-2), and certain distinctive morphological features such as the superimposition of glandular and non-glandular trichomes in KR + ONCR in contrast to restriction of those trichome types to different

TABLE 3. MORPHOLOGICAL VARIATION WITHIN *RHODODENDRON OCCIDENTALE* AMONG GEOGRAPHIC REGIONS. Parenthetical = standard deviation. *Higher number = shorter tube relative to the total corolla length.

Character	KR	ONCR	INCRS	SNPR
Corolla color, tube	white to dark pink	white to pink	gen. white, occ. pink	white/greenish
Corolla color, limb	white to dark pink	mostly white, occ. pink	white, rarely with some pink	white
*Ratio, overall corolla length/corolla tube	1.45 (0.10)	1.41 (0.06)	1.37 (0.06)	1.34 (0.05)
Multicellular trichomes, midvein	mixed glandular and eglandular, or of one type	mixed glandular and eglandular, rarely of one type	mixed glandular and eglandular, glandular, or of one type	glandular or eglandular
Multicellular trichomes, tertiary veins	absent	absent or glandular, rarely eglandular	absent or glandular	absent or glandular
Multicellular trichomes, abaxial density	zero or << 5/25 mm²	few to freq. >25/25 mm²	zero, or <<5/25 mm²	zero, or <<5/25 mm²
Leaf abaxial surface, unicellular trichomes	glabrous	glabrous	pubescent or glabrous	pubescent
Inflorescence bud length (s.d.)	12.9 mm (1.81)	14.9 mm (1.84)	12.2 mm (1.59)	13.0 mm (2.56)
Inflorescence bud, vestiture	mostly glabrous	densely pubescent	variable, densely pubescent to glabrous	thinly pubescent, variable
Inflorescence bud, bract margin trichomes	ciliate	glomerate	diliate or glomerate	ciliate or glomerate
Young twig unicellular pubescence	glabrous to thinly pubescent	pubescent	glabrous to pubescent	glabrous to pubescent
Inflorescence bud break vs. veg. bud break or maturity	concurrent	post vegetative maturity	concurrent, rarely post leaf break, not post veg. maturity	post vegetative maturity, rarely semi-concurrent.

individuals in the SNPR, distinguished the azaleas of these two regions. This morphological and genetic break coincides with the floristic and paleobotanical line dividing the Klamath Ranges and the Sierra Nevada/Cascade axis (Axelrod 1962, 1976; Raven and Axelrod 1978). Again, this is evidence supporting the hypothesis that there has been a long genetic separation between the SNPR azaleas and those of the northern California coast.

Thus, although the details may be unknown, it is clear that the western azalea at present is a relict species that had a formerly more widespread and continuous distribution. Further, the possibility cannot be discounted that the morphological and isoenzyme allele groups recognizable in this study were already distinct at the time their primary associates occupied a much wider region of western North America than they do today (Axelrod 1962, 1976).

Fourth, the isoenzyme variants present among the KR and ONCR populations combine with the alleles of the SNPR azalea to form the diverse allele complements among the INCRS populations (Table 2). Moreover, a complex morphological variation more or less paralleled the isoenzyme variation. These populations are discussed in more detail below.

The "INCRS" Azalea

The INCRS azalea populations are those growing on serpentine substrata in the hot, dry, interior parts of the North Coast Ranges of Lake, Napa, and Colusa Counties. They were represented in this study by populations 2, 4, 4A, 6, 9, 34, 36, and 64 (Figs. 1, 3, 5). Population 43 shares partial morphologies with these populations but not isoenzyme alleles and is excluded from this discussion.

These azalea populations occur in permanently wet habitats on high pH ultrabasic soils within open, sunny, foothill pine–leather oak–live-oak chaparral and woodland. Such an unusual habitat for azaleas has caused them to receive some research attention (Leiser 1957; Drake 1987), and the unusual ecological situation was also a factor motivating the initiation of this study. These azalea populations on the serpentine outcrops in Napa Co. east of Mount St. Helena were misinterpreted by Jepson (1925, 1939) to be *Rhododendron occidentale* var. *sonomense* Rehder. Indeed, after his proposal of *R. sonomense*, Greene himself used that name for his own azalea collections from the same area. Although of a similar dwarfed size, he apparently did not recognize the distinctive morphological differences between the serpentine plants east of the mountain and the more coastal "Petaluma" specimen on which he had based his description. As determined in this study, the azalea populations east of Mount St. Helena contained mosaic mixtures of isoenzyme alleles otherwise found in disparate areas (Table 2). The mosaic isoenzyme allele pattern extended to the morphological variation with the complement of features in some populations like those in nearby populations; in others, the complement of features resembled the plants of distant regions. Moreover, there were distinctive mosaics of morphological characteristics and alleles within as well as among the INCRS populations. For example, by morphology, INCRS P-34 (Stony Creek, Colusa Co.) and P-64 (Kilpepper Creek, Lake Co.) plotted among the SNPR populations (Figs. 2, 3), however, by isoenzymes they plotted among the other INCRS populations (Fig. 4).

This intermediacy and among-population variability would best be explained via interbreeding among the KR, ONCR, and SNPR genotypes followed by recombination within and among the INCRS populations. The result is also a higher average number of alleles per locus: 2.11 for the INCRS populations; with 2.03 (SNPR), 1.97 (KR), and 1.48 (ONCR) for the other geographic groups. The INCRS populations intermediate geographic position parallels this genetic mixing, and lends support to the interpretation that these are the populational remnants of an ancient ecotone. The survival of azaleas in this region is apparently due to the fractured serpentine substratum that resulted in the presence of permanent springs and streams in an otherwise xeric region. The history of climatic and floristic change in this region combined with the juxtaposition of sharply delimited habitats has made it a favored area for the study of plant adaptation and evolution (Major 1967; Stebbins and Hrusa 1995).

The most distinctive population of the INCRS was P-36 (Gilliam Creek, Sonoma Co.). Morphologically this population had strongly bifacial leaves, darkly anthocyanous new growth, and corollas frequently with some pink pigmentation in the tube and limb, this latter an infrequent condition among the INCRS populations. Its isoenzyme complements included single private alleles at both PGM-2 and GPI-2, the almost equal distribution of PGM-2 alternate alleles seen in both the INCRS and SNPR populations, and GPI-2 alternate alleles characteristic of both the northern SNPR populations and of the ONCR. This latter can be explained by its proximity to ONCR populations along the coast. However, its private alleles were the only ones in the INCRS group. The private GPI-2 allele was the highest frequency GPI variant in the population, and among all the populations the PGM-2 private allele was only the fourth allele seen at that locus. Overall, this population has the aspect of a coastal form of the generally interior INCRS azalea. The distinctive morphology and isoenzyme variation of P-36 suggests some uniqueness

for the azaleas on the endemic-rich serpentine habitats of the "The Cedars" in the East Austin Creek region.

Azalea genetics and morphologies characteristic of the Sierra Nevada in the inner North Coast Ranges are not anomalous if one accepts that glycolytic isoenzyme variation parallels or contributes to physiological adaptation (Gillespie 1991). Except for the azalea populations in or near The Cedars of western Sonoma Co. discussed above, most of the INCRS azaleas are in the rain shadow of several ridges and peaks including Mount Atlas, the Palisades, Goat Mountain, and Snow Mountain. These highlands block coastal air and moisture giving their shadows a hotter and drier summer and colder winter climate than that of the outer North Coast Ranges only a few miles westward. Such isoenzyme and morphological correlation to distinctive habitats implies that the three geographic regions—KR, ONCR, and SNPR—support differently adapted genotypes. The discontinuous and mosaic patterns among INCRS alleles and morphologies are likely the end result of local population fragmentations, contractions, and re-expansions during the post-Pleistocene. Anacker et al. (2010) analyzed phylogenetic signals among plant taxa that occur in either serpentine or non-serpentine habitats. Their conclusion was that most serpentine-restricted taxa are younger than non-serpentine taxa in the same genus. The data presented here support that interpretation.

Thus, the evidence suggests a relatively recent origin for the INCRS azaleas. However, an accounting for the presence of distant Sierran alleles and two private alleles in the far western isolated serpentine Cedars region suggests that those azaleas may have a unique history within *R. occidentale*.

The described local recombinant patterns are in contrast to the variation within the more widespread ONCR, KR, and SNPR forms. These three groups are coherent in their regions, share morphologies and some alleles within (but less so among them) and would appear to have occupied the same ecologically distinct, if not allopatric regions for a long time.

TAXONOMIC TREATMENT

The three regional azalea groups determined in this study (KR, ONCR, and SNPR) were morphologically and genetically distinctive, yet vary toward each other where approaching contact, as along the northern California coast and in the northern Sierra Nevada. A treatment at varietal rank seems most appropriate as it recognizes both their distinctiveness and close relationship. As to the INCRS azaleas, further study may reveal a historical coherence worth of taxonomic recognition, but these populations are not afforded such at this time.

Rhododendron occidentale (Torr. & A. Gray) A. Gray in W. H. Brewer & S. Watson, Botany of California 1:458. 1876. *Azalea occidentalis* Torr. & A. Gray in Torr., Botany of the Expedition, Pac. Railr. Rep. 4:116. 1857.—Type: USA, California, Sonoma Co., Laguna de Santa Rosa, 1854, *J. M. Bigelow s.n.* (lectotype NY!, designated by K. A. Kron 1993; isolectotypes: GH!, PH! here designated).

The lectotype of *Azalea occidentalis* Torr. & A. Gray (Torrey 1857) designated by Kron (1993) (NY!) is clearly part of the ONCR group, as are duplicates at GH! and PH!.

Rhododendron occidentale (Torr. & A. Gray) A. Gray in W. H. Brewer & S. Watson var. *occidentale.* Synonyms - *Rhododendron sonomense* Greene, Pittonia 2:172. Sept. 1891. *Rhododendron occidentale* var. *sonomense* Rehder, Monograph of Azaleas; 127, 1921 (var. *novus* based on *Rhododendron sonomense* Greene). —Type: USA, California, Sonoma Co., "near Petaluma," May 24, 1891, *Miss Carlton s.n.*, (lectotype: here designated, left specimen, NDG 037326!, [pre-1966 Herbarium Greeneanum 10866]).

There are two individuals mounted on NDG 037326, both apparently sourced "from Petaluma, Miss Carlton, May 24, 1891" (on ticket in pocket). The left specimen is the more complete and is here designated as lectotype. This is the only known azalea specimen seen by Greene whose gathering predates the protologue and was also purportedly collected within the species' described distribution. Both left (lectotype) and right (non-type) specimens are considered here to be a local form of the typical variety.

Rehder consistently used the term "comb. nov." when shifting epithets or changing ranks. Although he clearly based his new variety on *R. sonomense* Greene, with a citation of the basionym and a partially accurate paraphrasing of Greene's description, after the intraspecific epithet Rehder added "var. nov." It is therefore interpreted here as a newly proposed variety with same type and epithet as *Rhododendron sonomense* Greene.

Two names have been misapplied to *R. occidentale* var. *occidentale.* The first is *Rhododendron calendulaceum* (Michx.) sensu Hook. & Arnott, Bot. Beechey Voy. 362. 1839, not sensu Torr., Fl. N. Middle United States 1:425. 1824. The other is *Azalea calendulacea* Michx., sensu G. Bentham, Plantae Hartwegianae 321, 1848, not sensu Michaux, Fl. Bor. Amer. 1:151. 1803. Both of these misapplications were based on specimens (!) collected near the coast by David Douglas (probably San Francisco Bay region) and T. Hartweg ("*in uliginosus prope* Santa Cruz"), respectively.

The typical variety, *Rhododendron occidentale* var. *occidentale*, occurs in the Outer North Coast Ranges, from northern Mendocino County south to northern Monterey and San Benito counties, California.

Rhododendron occidentale (Torr. & A. Gray) A. Gray var. **californicum** (Torr. & A. Gray in Durand) Hrusa, comb. et stat. nov. Basionym: *Azalea californica* Torr. & A. Gray in Durand, Plantae Prattennianae Californicae, J. Acad. Nat. Sci. Philadelphia ns 3(2):94, June 1855, not *Azalea californica* (Hook.) Kuntze, Rev. Gen. 2:387. 1891. —Type: USA. "Nevada, California, *Henry Pratten*" s.n., s.d. (lectotype: PH!, here designated).

An *Azalea* specimen at PH! with an annotation by Durand attributing the epithet "californica" to Gray and labeled as "*Azalea californica* T. & G.," is here designated as lectotype for *Azalea californica* Torr. & A. Gray in Durand (Durand 1856). The protologue indicates the specimen was collected in "shady hills along Deer Creek" without mention of collection date or further locality information. While the lectotype label has written on it only "Nevada, California" without the locality "Deer Creek," in the introduction to "Plantae Pratennianae" Durand equated these locations by describing Pratten's collecting localities as "in the vicinity of Nevada, a place situated along Deer Creek ..." According to Durand (1856), Pratten's Deer Creek collections were taken in 1851. This proposed lectotype of *Azalea californica* Torr. & A. Gray ex Durand (PH!) is matched by the SNPR azalea.

The variety occurs in the Interior North Coast Ranges, the Peninsular Ranges, and the Sierra Nevada of California.

Rhododendron occidentale (Torr. & A. Gray) A. Gray var. *paludosum* Jeps., Man. Fl. Pl. Calif., 741. 1925. —Type: USA, California, Humboldt Co., "Fortuna to Eureka, filling sedgy bogs in the meadows near Loleta", 1902, *Jepson #1916* (holotype: JEPS!).

The holotype of *Rhododendron occidentale* var. *paludosum* Jeps (JEPS!) is unequivocally representative of the KR azalea.

This variety occurs in the Klamath Ranges of Mendocino Co., California, to Douglas Co., Oregon.

Incertae sedis: *Azalea nudiflora* var. *ciliata* Kellogg, Proc. Calif. Acad. ser. 1, 1:60. 1855 (published 1873). (n.v., probably destroyed 1906). Reported by Kellogg as "from the interior", the specimen is not currently extant.

KEY TO VARIETIES

1. Leaf abaxium generally with unicellular pubescence, not obscuring surface; multicellular trichome type on mid-vein or secondary veins of one kind, glandular or eglandular; corolla buds and open corolla white, often with a blush of pink at the lobe summits, rarely with a light pink blush in the tube, the tube otherwise white to greenish-white. Sierra Nevada, Peninsular Ranges, (inner North Coast Ranges as introgressants), California. . . . . var. *californicum*
1' Leaf abaxium generally glabrous, rarely with a few unicellular hairs; multicellular trichomes on the midvein mixed eglandular and glandular types; corolla buds and open corolla tube and veins usually colored dark to light pink, or less often pure white, often with a pale to dark pink pigmentation in the limb
  2. Abaxial secondary veins with multicellular trichomes, these often mixed eglandular and glandular types; tertiary veins often with associated multicellular trichomes; dormant bud bracts densely pubescent, the margin trichomes glomerate; twigs of the current season densely unicellular pubescent. Outer North Coast Ranges, California . . . . var. *occidentale*
  2' Abaxial secondary veins generally lacking multicellular trichomes, or of a single type; absent on the tertiary veins; dormant bud bracts glabrous or thinly pubescent, the margins most often ciliate, occasionally glomerate; twigs of the current season glabrous to subglabrous. Klamath Ranges of California and Oregon, from Humboldt Co., California north to Winchester Bay, Oregon . . . . .var. *paludosum*

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APPENDIX 1

GEOREFERENCED LIST OF *Rhododendron occidentale* POPULATIONS

Population numbers correspond to those in Figure 1. Elevations are given in meters. All counties are in California except where specified. Representative vouchers are housed at CDA and DAV.

Pop.	County	Latitude/longitude	Elevation	Description
2	Napa	38°38'49"N, 122°21'42"W	175	Pope Creek, 3.5 km E of Pope Valley Rd–Chiles Valley Rd junction
4	Napa	38°32'45"N, 122°21'30"W	240	Chiles Valley Rd, 2 km N of junction of Hwy 128
4A	Napa	38°33'00"N, 122°22'00"W	245	Chiles Valley Rd, 2.5 km N of junction of Hwy 128
6	Napa/Lake	38°41'30"N, 122°26'47"W	200	Butts Cañon, between Pope Valley and Middletown
9	Napa	38°29'10"N, 122°23'18"W	80	Hwy 128 at Conn Dam (Lake Hennessey)
12	Josephine, OR	42°03'15"N, 123°44'45"W	510	Lone Mountain (Wimer) Rd, 3.5 km SW of O'Brien
15	Josephine, OR	42°14'00"N, 123°40'15"W	390	Eight Dollar Mountain Rd, ~7 km W of U.S. 199
25	Douglas, OR	42°55'10"N, 123°30'30"W	400	Cow Creek, ~1/2 km upstream of bridge on Hwy 321, 10 mi E of Riddle, OR
31	Del Norte	41°49'30"N, 123°59'30"W	500	French Hill Rd, ~4 km NE of U.S. 101
33	Sonoma	38°20'00"N, 122°26'00"W	280	Middle Nathanson Creek, 1.5 km above Gehricke Rd terminus
34	Colusa	39°17'30"N, 122°33'30"W	475	Cedar Mountain Rd, confluence Little Stony Creek and Frenzel Creek, Mendocino National Forest
36	Sonoma	38°34'21"N, 123°01'12"W	165	Gilliam Creek, canyon below Redwood Lake, Austin Creek State Recreation Area immediately N of Armstrong Redwood State Reserve
37	Marin	37°54'45"N, 122°36'13"W	380	Mount Tamalpais, Bootjack Creek approx. 1 km E of Bootjack Camp parking
42	Mendocino	39°10'15"N, 123°40'00"W	35	Navarro River, 7 km upstream Hwy 1
43	Trinity	40°24'00"N, 123°07'00"W	1100	State Hwy 36, ~9 km W of Wildwood, W fork Salt Creek, Telephone Ridge
45	Sonoma	38°20'30"N, 122°26'00"W	350	Hogback Mountain , headwaters of Agua Caliente Creek
46	Sonoma	38°35'00"N, 122°37'45"W	275	Franz Valley School Rd, immediately W Napa/Sonoma Co. line
49	Plumas	39°47'30"N, 121°27'15"W	500	Hwy 70, 1/8 mi W of Pulga Rd
50	Plumas	40°00'38"N, 120°59'33"W	1165	Plumas National Forest, Butterfly Valley Botanical Area, Darlingtonia bog
51	Trinity	41°07'15"N, 122°39'00"W	1530	Unnamed tributary, headwaters East Fork Trinity River, N side Bonanza King Ridge, ~9 km N of Bonanza King Lookout
52	Humboldt	39°54'50"N, 123°39'00"W	1000	Red Mountain, headwaters of School Section Creek
53	Eldorado	38°54'30"N, 120°38'40"W	1250	UC Blodgett Experimental Forest, Mutton Creek
55	San Benito	36°42'40"N, 121°25'25"W	430	Gabilan Range, Pescadero Creek, Grass Valley, ~10 km S of Hollister
56	Santa Cruz	37°10'00"N, 122°13'00"W	340	Big Basin State Park, Blooms Creek.
57	Trinity	41°06'16"N, 122°42'11"W	950	Scorpion Creek, approx. 3 km SE of Hwy 3 E of Trinity Campground
58	Humboldt	40°55'00"N, 124°04'15"W	75	McKinleyville, Azalea State Reserve
59	Humboldt	41°13'00"N, 124°06'00"W	155	Stagecoach Hill, Kane Rd approx 1 km E of U.S. 101
60	San Diego	33°20'00"N, 116°53'00"W	1500	Upper Doane Valley, Palomar Mountain State Park
61	San Diego	32°58'15"N, 116°36'00"W	1650	Azalea Glen, Cuyamaca Rancho State Park
62A	Riverside	33°47'45"N, 116°43'40"W	1800	San Jacinto Mountain., Azalea Trails Girl Scout Camp, head of Dark Canyon.
62C	Riverside	33°47'45"N, 116°45'00"W	1600	San Jacinto Mountains , Fuller Mill Creek, along Hwy 243
64	Lake	39°10'00"N, 122°30'15"W	525	Intersection of Kilpepper Creek and Bartlett Springs Rd
65	Placer	39°03'30"N, 120°33'30"W	1600	Placer Redwood Grove
66	Tulare	36°45'00"N, 118°58'15"W	2000	Sequoia National Park, Grant Grove
68	Mariposa	37°44'00"N, 119°33'30"W	1300	Yosemite National Park, Happy Isles
69	Mariposa	37°30'45"N, 119°36'20"W	1400	Yosemite National Park, Mariposa Grove
71	Napa	38°33'40"N, 122°24'30"W	500	Las Posadas State Forest, upper Moores Creek

MEASUREMENT OF SPATIAL AUTOCORRELATION OF VEGETATION IN MOUNTAIN MEADOWS OF THE SIERRA NEVADA, CALIFORNIA AND WESTERN NEVADA

Dave A. Weixelman
USDA Forest Service, Range Ecologist, 631 Coyote Street, Nevada City, CA 95959
dweixelman@fs.fed.us

Gregg M. Riegel
USDA Forest Service, Pacific Northwest Region, Area Ecology Program, 63095 Deschutes
Market Road, Bend, OR 97701

Abstract

The presence of autocorrelation invalidates all standard statistical tests unless special corrections are made. Because of this, it is important to know the degree of spatial autocorrelation in order to know how to sample. Mountain meadows were sampled to determine spatial autocorrelation of vegetation at the plant community level. A total of 40 meadows were sampled in the eastern Sierra Nevada, California. At each meadow a dominant plant community was selected for sampling. Sampling consisted of placing 10×10 cm quadrats at 1-m intervals on a 20-m transect and recording the presence for all vascular plant species rooted in the quadrats. Sites varied in plant species composition and number of species present. For each plot, ordination analysis in the form of reciprocal averaging was used to derive positions for each quadrat on axis 1. The scores from axis 1 were analyzed by semivariance to obtain the spatial dependence of the quadrats. Overall, three semivariance patterns were seen; A) plant communities that were autocorrelated at distances of less than one meter; B) communities that were autocorrelated between 1 m and 15 m; C) communities that were autocorrelated at distances greater than 20 m. Results indicate that for semivariogram type B, on average, sites were autocorrelated to a distance of 3.6 m, meaning that quadrats separated by greater than 3.6 m were independent. Beta diversity was significantly ($P < 0.05$) lower for semivariance type C than for either semivariance types A or B. These results are useful for determining spacing of sample points in mountain meadows to ensure spatial and statistical independence for presence/absence data.

Key Words: Beta diversity, meadow, sampling, spatial autocorrelation, vegetation.

One of the general patterns in ecology is that, on average, sites that are closer will be more similar (Fortin 1999). This is known as positive spatial autocorrelation (Mistral et al. 2000). The presence of autocorrelation invalidates all standard statistical tests unless special corrections are made (e.g., Dale et al. 1991). Because of this, it is important to know the degree of spatial autocorrelation in order to know how to sample. In this study, mountain meadows in the eastern Sierra Nevada, California were sampled to estimate the amount of autocorrelation within plant community types.

Methods for analyzing spatial autocorrelation in ecology have commonly been for univariate data (Fortin 1999). Such methods have been used, with single-variate indices such as Moran's I or Geary's c, on individual variates such as fruit production (Koenig and Knops 1998), plant height and diameter (Kuuluvainen et al. 1998), flower and vegetative characters (Chung and Noguchi 1998) and gene frequencies (Sokal et al. 1998). However, communities comprise many species, and are hence multi-variate. To examine the spatial pattern of gradients, workers such as Palmer (1988), Jonsson and Moen (1998), Ohlson

and Økland (1998), Meisel and Turner (1998), and Wagner (2003) summarized the whole community into ordination scores, and analyzed them by semivariance. This approach examines spatial variation in the major gradients, using only that fraction of the variation in species composition that is captured in the ordination.

Our aim is to document the spatial pattern for Sierra Nevada mountain meadow communities. We sampled with a fixed quadrat size (10×10 cm) using quadrats at 1-m intervals along a transect of 20 m length. The size of the quadrat from which species associations are calculated, as well as the length of transects may influence the detected association pattern (e.g., Ver Hoef et al. 1989). With very long transects, covering multiple habitat types and communities, environmental gradients will be captured (Rydgren et al. 2003). Such gradients are likely to occur as a result of environmental variation rather than as a cause of species interactions within specific plant communities. At the opposite end, with very short transects, stochastic effects, due to few individuals, may restrict the ability to detect significant spatial patterns among species (Jonsson and Moen 1998) within communities. The focus of
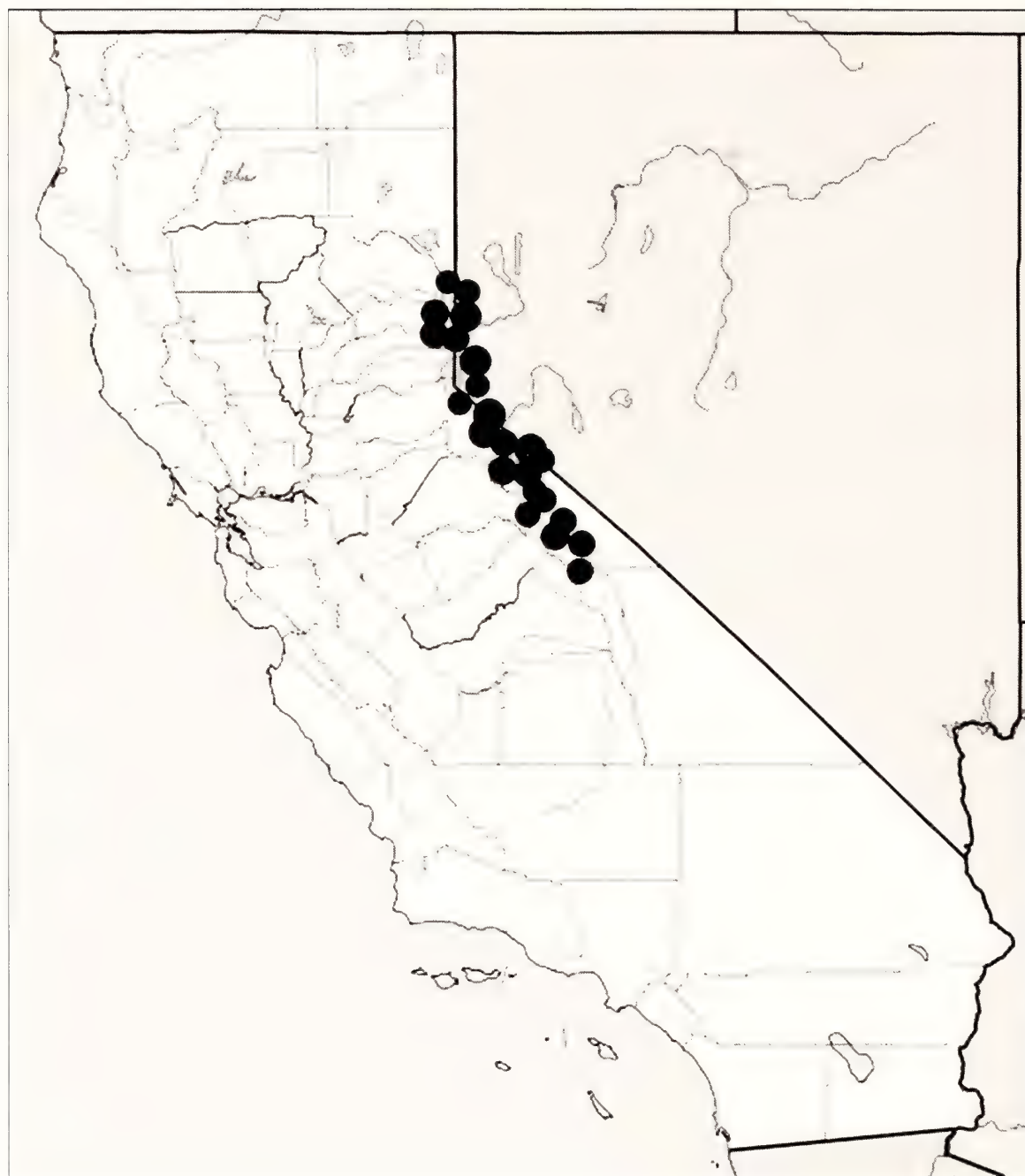
FIG. 1.   Location of study sites in Sierra Nevada mountain range, California and eastern Nevada.

this paper is at intermediate scales, e.g., at the plant community level, where patterns in species associations and beta-diversity relate to the intrinsic patch sizes present within the plant community being sampled.

METHODS

Study Sites

Forty meadow sites were sampled in the eastern Sierra Nevada of California and Nevada at latitudes between 38° and 40° (see Fig. 1). All sites were located on National Forest lands. Livestock grazing had occurred on all sites since the 1860's and the sites are generally representative of the history of livestock grazing use in the Sierra Nevada. Sampling occurred between June of 1994 and August of 1996. Elevation of sites ranged from 7100 to 9600 feet. Depth to water table varied from 0 (at the surface) to 50 cm in mid-summer. All sites were classified as wet or moist meadow types using the USDA Forest

Service classification for Sierra meadows (Weixel-man et al. 1996) and the dominant soil taxon was Typic Cryaquoll (Soil Survey Staff 1998). Species composition generally consisted of sedges, rushes, and forbs. Dominant species included Nebraska sedge (*Carex nebrascensis* Dewey), blister sedge (*Carex vesicaria* L.), western aster (*Aster occidentalis* Nutt.), Kentucky bluegrass (*Poa pratensis* L.), and yarrow (*Achillea millefolium* L.). At each site, a transect line 20 m in length was randomly located within a homogenous plant community and 10 × 10 cm quadrats were placed at 1 m intervals along the transect for a total of 20 quadrats on each transect. Previous studies using presence absence methods in mountain meadows have used a 10 × 10 cm quadrat size for sampling (Mistral et al. 2000; Moseley et al. 1986, 1989; Weixelman et al. 1996; USDA Forest Service 2008). The vegetation data consisted of presence/absence for each vascular plant species rooted in the 10 × 10 cm quadrat. Plant nomenclature used in this paper conforms to Hickman (1993).
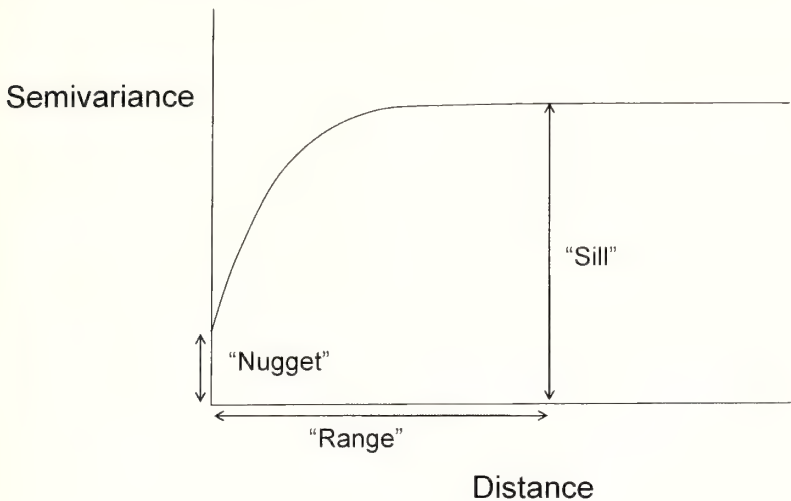
Fig. 2.   Theoretical interpretation of a semivariogram with an asymptotical model showing the proportion of variance found at increasing distances of paired samples. The 'sill' is the variance around the average value of the variable. The 'range' is the maximum distance at which samples show spatial dependence, the 'nugget' is the variance found at a scale finer than the smallest sampling scale.

Statistical Analysis

Species presence/absence data for each quadrat on a transect line was analyzed using reciprocal averaging (RA), an ordination program. RA is an indirect ordination technique which extracts gradients present in the species composition data assuming a unimodal relationship between the species abundance and the gradients (Hill 1973). To obtain a regionalized variable reflecting species composition, we used the ordination scores from reciprocal averaging (RA). RA then calculated scores on axis 1 for each quadrat. If the species composition in neighboring quadrats is similar, the ordination should place these quadrats close to each other in ordination space. However, if the species composition is unrelated to the spatial location of the quadrats, samples close to each other in ordination space may be considered randomly located in geographical space. Each site was analyzed for spatial independence using the data from the 20 quadrats. The ordination analyses were performed with the package PC-ORD version 3.0 (McCune and Mefford 1997).

Scores for each quadrat on axis 1 of RA were then analyzed by semivariogram (Robertson 1987) to examine the distance at which quadrats were autocorrelated within transects. Semivariograms are plots of the spatial dissimilarity (measured by semivariance) between points separated by known distances, plotted against those distances. Normally, points in close proximity are more similar than points farther apart, so that semivariance among points increases with distance until a maximum semivariance, called the sill, is reached (see Fig. 2). The distance at which the semivariance stops increasing is called the range, and the point where the semivariance begins (distance equals zero) is called the nugget.

Samples separated by distances closer than the range are statistically dependent, while those separated by distances greater than the range, are not, because at distances greater than the range the semivariance equals the sample variance, implying zero spatial correlation (Trangmar et al. 1985).

Using the geostastistical package GS+, we calculated semivariograms of the quadrats using the axis 1 scores from ordination. Semivariances were calculated up to within 10 pairs of the maximum distance between all points (i.e., 20 m). For transects that exhibited spatial autocorrelation, semivariogram models for range, nugget, and sill were fit using a non-linear least squares technique (Robertson 1987). These models included linear with a sill, spherical, exponential, and Gaussian curves. We chose the best fitting of these four curves based on the best fit of the residuals about the curve, particularly at the sill and nugget ends of the curve. If a transect exhibited zero autocorrelation, the sample variance was used for sill and nugget variances and zero was used for the range. If a transect exhibited spatial autocorrelation with no sill it was considered to have a nonstationary mean (Trangmar et al. 1985). In this case, the samples were dependent out to the maximum distance of the transects, in this case 20 m. Because mountain meadows are made up of a patchwork of a number of plant communities, the size of each community is sometimes less than 20 m and sometimes greater than 20 m. Based on the author's experience, at distances much greater than 20 to 30 m, changes in environment, including changes in hydrology, become significant and changes in plant composition are more likely due to environmental gradients.

Beta Diversity

Robert H. Whittaker (1960) defined beta diversity as the variation in species composition among sites in a geographic area. In our case, this is the variation in species composition among quadrats along the transect line. Whittaker (1960) established a straightforward measure of beta diversity, which will here be called β_w:

$$\beta_w = (s/a) - 1$$

where β_w = beta diversity, s = total number of species occurring on the transect, and a = average number of species occurring in the quadrats. The measure β_w is easy to calculate and explicitly relates the components of diversity a and β, to overall diversity, s.

Statistical Tests

All statistical tests were performed using SPSS version 9.0 (SPSS 1998). Tests of significance
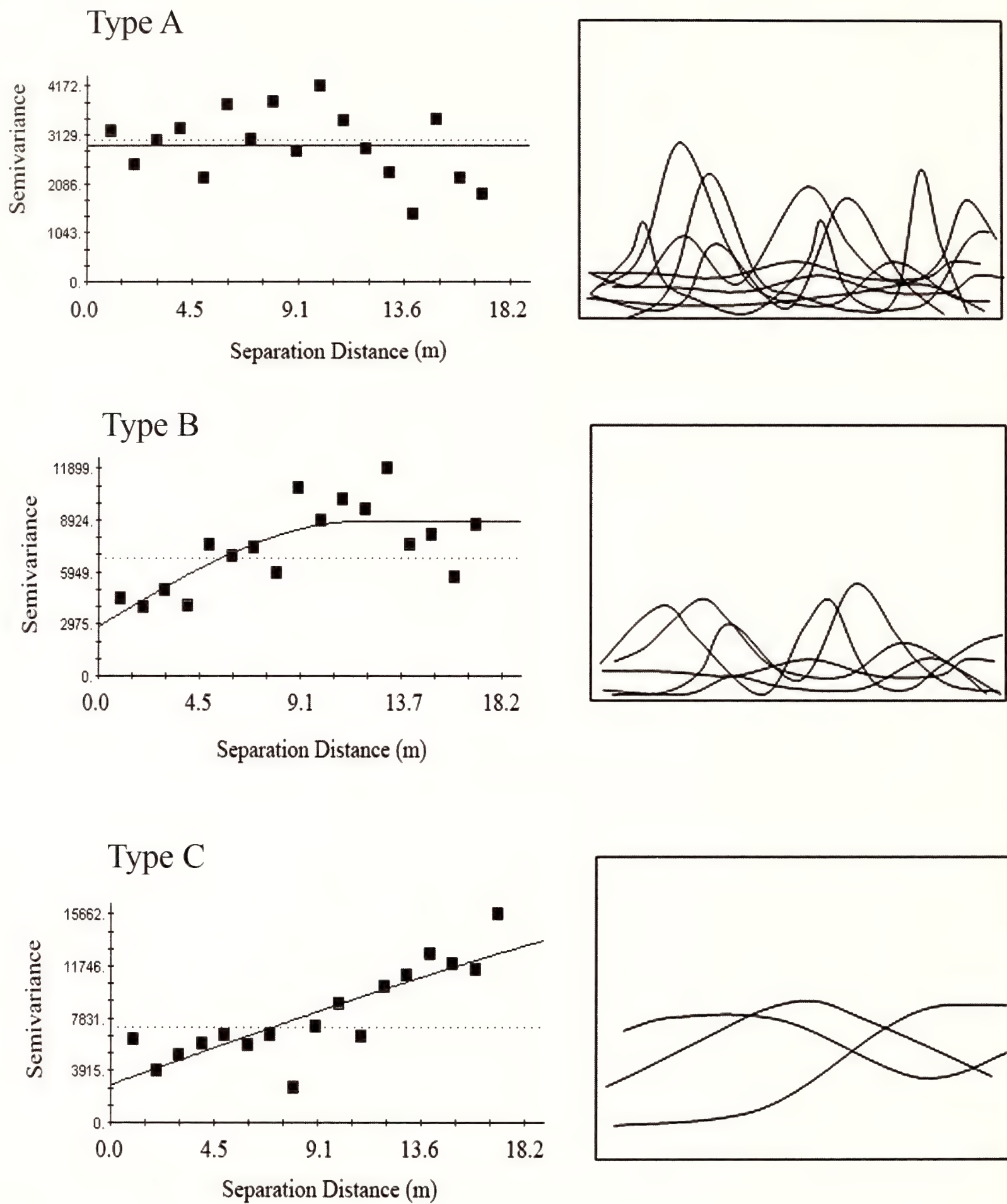
FIG. 3. Semivariograms of data taken from three individual sites to illustrate three types of spatial pattern. The dashed lines denote the semivariance around the average value. Type A: communities that showed no clear spatial pattern, i.e., autocorrelation of less than 1 m; type B: meadow communities with a clear range and sill; and type C: meadow communities with an increasing semivariance beyond 20 m separation, i.e., autocorrelation to distances beyond 20 m. Also shown are stylized diagrams illustrating species turnover (curved lines on the right) along a transect.

TABLE 1.   MEAN AND STANDARD DEVIATION OF BETA DIVERSITY AND AVERAGE NUMBER OF SPECIES BY TYPE OF SEMIVARIOGRAM. Superscripts that are different within the same column represent a statistically significant difference (P < 0.05).

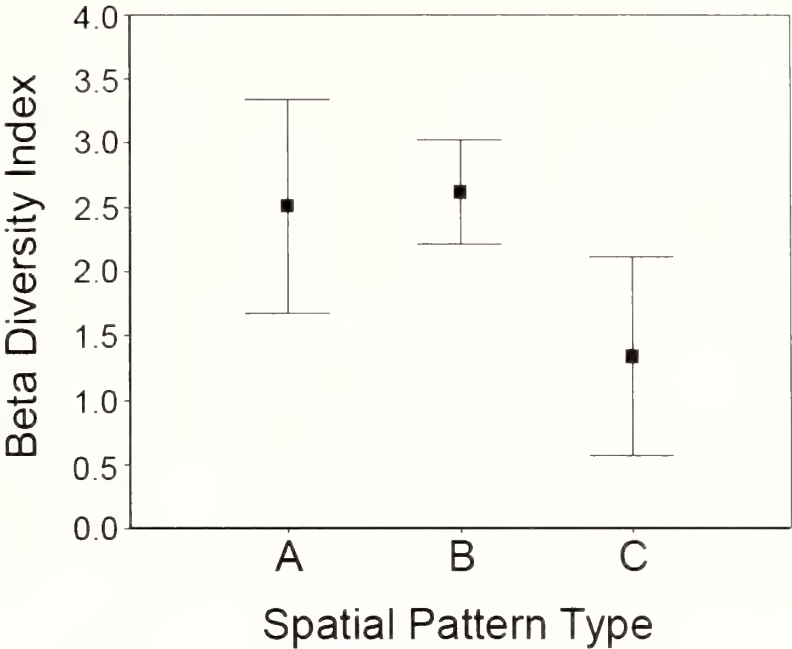| Type of semivariogram	Beta diversity	Average number of species	Average elevation (m)
A (n = 20)			
Mean	2.56[a]	11[a]	2679[a]
SD	1.28	6	328
B (n = 13)			
Mean	2.59[a]	12[a]	2686[a]
SD	0.88	5	208
C (n = 7)			
Mean	1.33[b]	7[b]	2668[a]
SD	0.92	2	360

FIG. 4.   Comparison of beta diversity among the three types of spatial pattern seen (A, B, and C), see text for explanation of types of spatial pattern. Error bars represent 95% confidence interval.

were used to determine if differences existed in beta diversity and number of species on a site for classes of differing spatial pattern.

RESULTS

Results of ordinating quadrat data followed by semivariance analysis showed three general spatial patterns of vegetation (see Fig. 3): Type A, B, and C. The semivariogram for type A communities was generally flat, with no range evident. Therefore, plant species in this type were autocorrelated at distances of less than 1 m, which was the smallest scale measured in this study. These sites were higher in beta diversity and contained many species. The semivariogram for type B communities exhibited a distinct range and sill between 1 m and 20 m. Sites in type B were positively autocorrelated to a distance of 3.6 m on average. The semivariogram for type C communities showed a continual rise with no sill or range visible. Quadrats in this type were positively autocorrelated at distances greater than 20 m.

In type A communities, species turnover as indicated by the β-diversity index was high (see Table 1) as was the average number of vascular plant species on the sites. In type B communities, β-diversity was also high. Sites in this type typically had high numbers of species with rapid turnover in composition along transects as indicated by the high β-diversity index for these sites. The semivariogram for type B showed a range at distances ranging from 3 m to 15 m (Fig. 3, type B). The average distance at which quadrats were autocorrelated in type B communities was 3.6 m. The β-diversity index averaged nearly the same as for type A (Table 1). The number of species for type B was also similar to type A. Type C plots had the lowest β-diversity of the three semivariance types (Table 1). In addi-

tion, type C had the lowest average number of species on each site. Significant differences (P < 0.05) in β-diversity were found between type A and B as compared to type C communities.

DISCUSSION

Spatial patterns of herbaceous species in meadows vary with environment, species ecological characteristics, species interactions, grazing, and ground disturbing activities. In this study, sites were located within a plant community in order to limit variation based on environmental factors. Therefore, results of this study are most applicable in situations where one is interested in spatial variation within meadow plant communities that typically occur in the Sierra Nevada.

The three types of plant community spatial patterns were different in their pattern of spatial autocorrelation (Fig. 3). In this study, plant community spatial patterns were positively autocorrelated according to the following rank distances: type A < type B < type C. Type C communities were typically homogeneous stands dominated by clonal graminoid species including sedges and/or rushes. These stands had fewer species than either type A or B. In contrast, type A and B communities were composed of many small forbs including species indicating disturbance as well as clonal graminoid species. Most species present were either obligate wetland (OBL), facultative wetland plant species (FACW) or facultative wetland species (FAC) using the U.S. Fish and Wildlife wetland rating system for plants (U.S. Fish and Wildlife Service 1988).

Robert H. Whittaker (1960) defined beta diversity as the variation in species composition among sites in a geographic area. In our case, this is the variation in species composition among

quadrats along the transect line. Using Whitaker's equation provides an index of the variation in number of species present in each quadrat along the transect line, in this case 20 m. For homogenous plant communities, such as clonal patches of sedges, the beta diversity was low. The 95% C.I. for beta diversity in type C ranged from 0.55 to 2.2. Plant communities in this group were typically clonal, rhizomatous sedge species and included Nebraska sedge (*Carex nebrascensis*), Blister sedge (*Carex vesicaria*), and analogue sedge (*Carex simulate* Mack.). Beta diversity in type A and B were higher due to more species and higher density of individual plants and ranged from 1.9 to 3.4 in type B and 2.2 to 3.1 in type A (95% C.I). Type A and B communities were not different in beta diversity even though semivariance diagrams were different between the two groups. Type A communities did show a higher beta diversity for some plots but generally overlapped type B when the 95% C.I. was plotted (see Fig. 4). Type A communities were autocorrelated at distances of less than one meter, while type B communities were autocorrelated at an average distance of 3.6 m. Type and A and B communities were composed of early successional forbs and a mix of graminoid species. Typical plant species present in type A and B communities included Kentucky bluegrass (*Poa pratensis*), western yarrow (*Achillea millefolium*), and western aster (*Aster occidentalis*). These types were representative of disturbance communities and meadow types with larger seasonal fluctuations in water table.

Significant differences ($P < 0.05$) in β-diversity were found between type A and B as compared to type C communities. Thus, knowing the β-diversity of a plant community using the methods described here could potentially be used to determine which type of spatial pattern exists in a meadow community. Spatial pattern will depend both on the size of the quadrat being used and the distance separating the quadrats. Spatial pattern may also vary depending on soil moisture types, drier meadows would be expected to be different than wet meadows based on wider spacing of plants in drier meadows.

For practical considerations and sampling in the field, beta diversity can be used as a rough indicator of spatial autocorrelation in plant communities. When determining rooted frequency using the 10×10 cm frame as in this study and 1 meter spacing along transect lines, a beta diversity value using the Whitaker index of less than about 2.2 would indicate, with high probability, a spatial autocorrelation distance greater than 20 m. While a beta diversity index of greater than 2.2 would indicate a spatial autocorrelation distance closer to that expected for semivariance types A and B. It is reasonable to expect the spatial relationships of the plant community to vary in different environments, and some care must be taken when trying to extrapolate the results of this work.

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REAPPEARANCE OF THE VANISHING WILD BUCKWHEAT: A STATUS REVIEW OF *ERIOGONUM EVANIDUM* (POLYGONACEAE)

Naomi S. Fraga, Elizabeth Kempton, LeRoy Gross and Duncan Bell
Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, CA 91711
nfraga@rsabg.org

Abstract

Eriogonum evanidum Reveal is an annual herb in the buckwheat family that is endemic to southern California, USA and northern Baja California, Mexico. It was described by James Reveal in 2004 and was determined to be extinct due to the lack of recent observations and accessioned specimen collections. During field surveys conducted in 2007 and 2008 this species was rediscovered across its known range in southern California. Three of 10 historic occurrences that were presumed extirpated were located. One new occurrence was documented in the vicinity of Holcomb Valley, San Bernardino Mountains, CA. Location and habitat information are provided and the current conservation status of this species is discussed.

Key Words: California, conservation, *Eriogonum*, endemic, extinct, Polygonaceae, rare, rediscovery.

Eriogonum evanidum Reveal (vanishing wild buckwheat) is an annual herb in the buckwheat family (Polygonaceae) that was recently described (Reveal 2004; Fig. 1). This species was given the common name 'vanishing wild buckwheat' because it was presumed extinct due to the lack of recent observations and herbarium specimen records (Reveal 2005; CNPS 2011). Focused surveys were conducted by botanists at Rancho Santa Ana Botanic Garden (RSABG) in late summer and fall of 2007 and 2008 to locate *E. evanidum* across its known range in southern California, USA. *Eriogonum evanidum* was found to be extant across its historic range within the United States, although the status of this species in Baja California, Mexico is unknown. Although several occurrences were located, it is likely that some occurrences have been extirpated (Fig. 2). Details of the 2007 and 2008 field surveys are discussed here, including additional information on distribution, habitat, and conservation status.

Taxonomic and Collection History

Eriogonum evanidum was discovered during herbarium studies by Reveal (2004). The new species was described from specimens that were previously identified as *Eriogonum foliosum* S. Watson. In his description, Reveal (2004) stated that "this distinctive species has been hidden quietly under *Eriogonum foliosum* S. Watson awaiting rediscovery of an extant population so that it might be more precisely characterized than possible from dried material." Reveal designated a holotype that was collected in 1902 (*Abrams 2894*) and paratypes collected from as early as 1893 (*Alderson 399*) to 1967 (*Ziegler s.n.*). Based on accessioned herbarium specimen records examined by Reveal (2004), it appeared that

most of the documentation for *E. evanidum* took place between 1920 and 1940, primarily from the vicinity of Big Bear Valley in the San Bernardino Mountains of southern California (Reveal 2004; Table 1); an area that has experienced substantial development over the last century. *Eriogonum evanidum* was "presumed extinct" in the Flora of North America (Reveal 2005) and considered "possibly extirpated" in the second edition of the Jepson Manual (Baldwin et al. 2012), although Reveal has reported seeing specimens of the *E. evanidum* that were collected in the late 1990's (Costea and Reveal 2011). Two specimens that were not cited in the original description, and therefore not likely viewed prior to its description, are housed at RSA and were collected in 1976 (*Davidson 4471*) and 1994 (*Hirshberg s.n.*).

Field Survey Methods

Surveys for *E. evanidum* were conducted by botanists at RSABG using a focused, or intuitive-controlled, field survey method (USDA FS 2005), which targets habitats with the highest potential for locating target species at the appropriate time for proper identification. Herbarium specimen records (RSA, UCR), databases (CalFlora, Consortium of California Herbaria, and California Natural Diversity Database), and literature reports were used to identify historic populations of *E. evanidum* and these were targeted for field surveys. Surveys by botanists at RSABG were conducted during August 2007, and August and September of 2008. U.S. Department of Agriculture (USDA) Forest Service Element Occurrence forms were used to document all populations of *E. evanidum* that were encountered (e.g., exact location, population status, existing or potential threats or disturbances, habitat, associated

FIG. 1. *Eriogonum evanidum* in flower with a fisher space pen (9.6 cm × 0.8 cm) for scale.

species). Herbarium specimens were collected and deposited at the RSA herbarium and photographs of plants were contributed to the CalPhotos database (calphotos.berkeley.edu). USDA Forest Service Element Occurrence forms, along with U.S. Geologic Survey (USGS) maps of surveyed populations, were submitted to the California Department of Fish and Game (CDFG), and USDA Forest Service. Plant identifications were made using taxonomic keys and descriptions in *The Jepson manual: higher plants of California* (Hickman 1993), *A flora of southern California* (Munz 1974), and *Flora of North America* (Reveal 2005). Identifications were verified through comparison with annotated specimens in the RSA herbarium.

DISTRIBUTION

In the United States, *E. evanidum* is restricted to southern California and has been documented in the San Bernardino Mountains in San Bernardino County, San Jacinto Mountains in Riverside County, and the Laguna Mountains in San Diego County (Fig. 2). *Eriogonum evanidum* has also been reported from northern Baja California, Mexico (Costea and Reveal 2011).

Occurrences previously documented in the vicinity of Big Bear Lake and Baldwin Lake in the San Bernardino Mountains were not found in 2007 or 2008. It is possible that these occurrences have been extirpated due to development in the region (Table 1).

There are three occurrences in southern California that are doubtful and not supported by herbarium specimens (Table 1). These include reports from Valencia in Los Angeles County, Warner Springs in Riverside County, and Viejas Mountain in San Diego County (CNPS 2011; CNDDB 2011). The only source for the reported occurrence at Valencia in Los Angeles County is a report prepared by Dudeck and Associates (unpublished) to the CDFG and Newhall Land and Farming Company (CalFlora 2011; CDFG 2011). The population at Warner Springs was referenced by Reveal (1989) in his treatment of *E. foliosum*. The source for the occurrences at Viejas Mountain is from Craig Reiser's 1994 account in Rare Plants of San Diego County (CNDDB 2011). None of these occurrences has been verified in the field, and none are documented by herbarium specimens. In addition, all three are reported at lower elevations than vouchered occurrences and therefore they may lack suitable habitat (Table 1). Future surveys should be conducted to verify if *E. evanidum* occurs at these locations.

HABITAT

In previous floristic treatments, habitat for *E. evanidum* was described as sandy to gravelly flats and slopes, in sagebrush communities, oak woodland and montane conifer woodlands at 1150–2300 meters in elevation (Reveal 2005; CNPS 2011; Costea and Reveal 2011; Fig. 3). The described habitat requirements were substantiated while conducting surveys, except that plants were not found in oak woodland. Oak woodland vegetation was presumably included in the habitat description because of the previous reference of this species at Warner Springs in Riverside County. Occupied habitat for *E. evanidum* included sandy soils derived from decomposed granite, in primarily full sun with little to no leaf litter, on a flat aspect in sagebrush scrub dominated by *Artemisia tridentata* Nutt. The sagebrush community was often surrounded by coniferous forest dominated by *Pinus jeffreyi* Balf. or *P. ponderosa* P. Lawson & C. Lawson. *Eriogonum evanidum* was also observed to occur in dry meadows dominated by *Artemisia tridentata* in Holcomb Valley, San Bernardino Mountains, CA.

The following is a list of species associated within *E. evanidum* compiled from several locations throughout its range (* denotes not native species): *Artemisia tridentata*, *Astragalus douglasii*
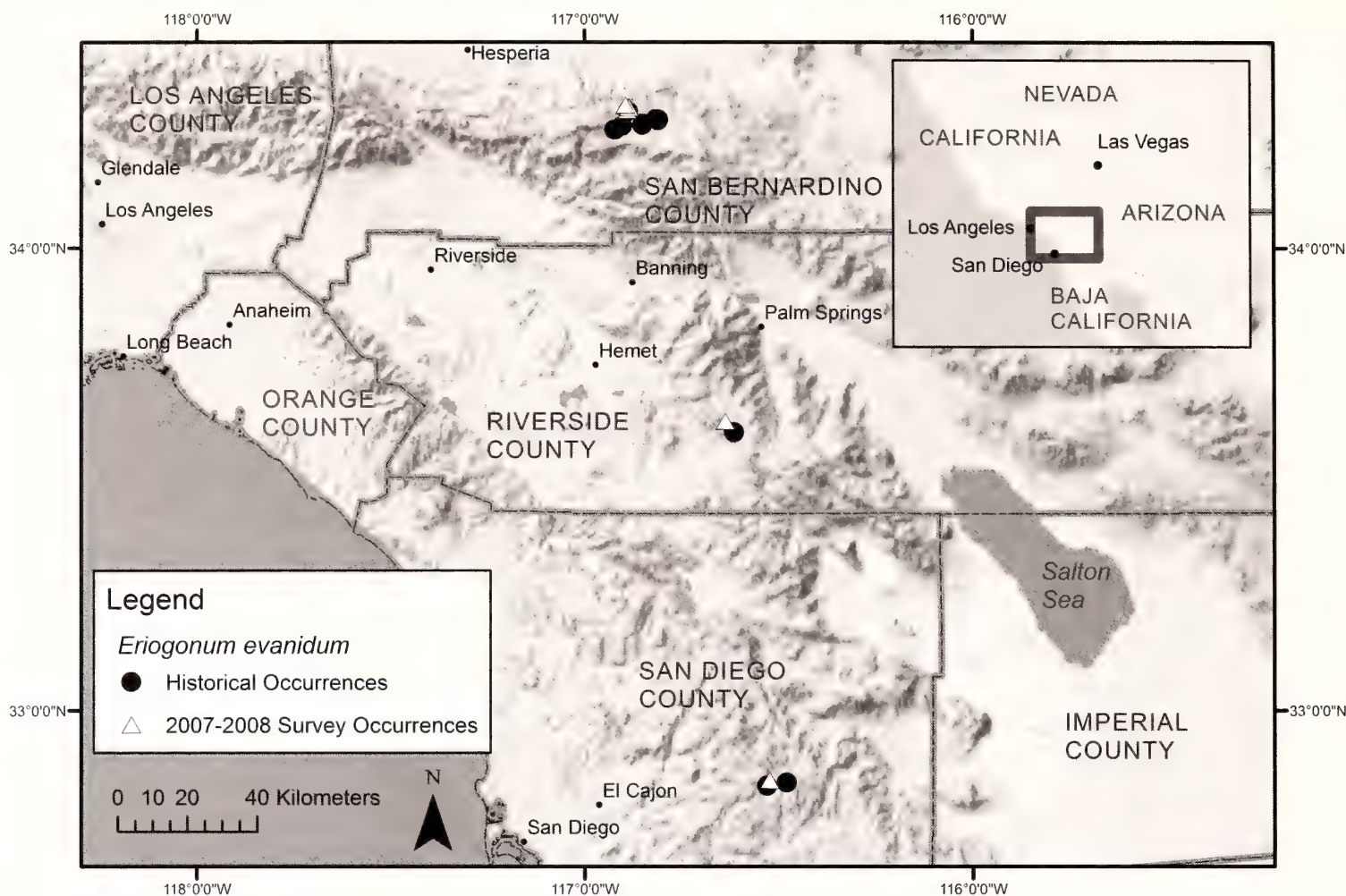
Fig. 2. Distribution of *Eriogonum evanidum* based on vouchered occurrences. Historic occurrences are represented by a black circle and occurrences located in 2007 and 2008 are represented by a white triangle. See Table 1 for detailed information (source herbaria, collection date, locality, etc.) for each occurrence.

(Torr. & A. Gray) A. Gray var. *parishii* (A. Gray) M. E. Jones, *Bromus tectorum* L., *Castilleja cinerea* A. Gray, *Chenopodium leptophyllum* (Moq.) Nutt. ex S. Watson, *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Cryptantha micrantha* (Torr.) I. M. Johnst., *Gutierrezia sarothrae* (Pursh) Britton & Rusby, *Ericameria pinifolia* (A. Gray) H. M. Hall, *Eriogonum baileyi* S. Watson, *E. davidsonii* Greene, *E. wrightii* Torr. ex Benth. var. *subscaposum* S. Watson, *Eriastrum sapphirinum* (Eastw.) H. Mason, *Lessingia glandulifera* A. Gray, *Nicotiana attenuata* Steud., *Penstemon centranthifolius* (Benth.) Benth., *Pinus jeffreyi*, *P. ponderosa*, *Sisymbrium altisimum* L., *Stephanomeria exigua* Nutt., and *Trichostema micranthum* A. Gray.

IDENTIFICATION

Eriogonum evanidum co-occurs with other annual taxa in the genus *Eriogonum* that it may be confused with including: *E. baileyi*, *E. davidsonii*, and *E. gracile* Benth. *Eriogonum evanidum* can be distinguished from these species by its relatively small flowers (0.8–1.2 mm), outer perianth lobes that are more or less hastate in fruit, and stems that are tomentose. In contrast *E. baileyi* has flowers that are 1.5–3 mm, the outer perianth lobes oblong to oblong-obovate, generally constricted near middle, and stems are glabrous or tomentose. *Eriogonum davidsonii*

has flowers that are 1.5–2 mm, the lobes are oblong-obovate, and stems are glabrous. *Eriogonum gracile* has flowers that are 1.5–3 mm, the lobes are lanceolate to oblong, and stems are generally tomentose, or sometimes glabrous (Baldwin et al. 2012).

Although not co-occurring within the United States, there are two additional species (*E. foliosum* and *E. hastatum* Wiggins; both endemic to Mexico) that may be confused with *E. evanidum* in Baja California, Mexico. *Eriogonum evanidum* can be distinguished from both of these species on the basis of several morphological characters—both *E. foliosum* and *E. hastatum* have sprawling habits, foliaceous inflorescence bracts, and elliptic basal leaves while *E. evanidum* has an erect habit, scalelike inflorescence bracts, and broadly ovate to orbicular or reniform basal leaves.

CONSERVATION STATUS

Eriogonum evanidum is not listed by the State of California or Federal government as threatened, or endangered, but is considered by the California Native Plant Society as "seriously endangered in California" (California Rare Plant Rank 1B.1; CNPS 2011). *Eriogonum evanidum* is also on the Sensitive species list for the Cleveland and San Bernardino National Forests. Presumably several populations have been extirpated in

TABLE 1. REPORTED LOCATIONS FOR *ERIOGONUM EVANIDUM* IN THE UNITED STATES. Herbarium acronyms: SD = San Diego Natural History Museum, RSA = Rancho Santa Ana Botanic Garden, JEPS = Jepson, UC = University of California Berkeley, POM = Pomona College. CDFG = California Department of Fish and Game. County Abbreviations: SD = San Diego, RIV = Riverside, SBD = San Bernardino. Other abbreviations: SBM = San Bernardino Mountains, E = Possibly Extirpated.

Source	Date last collected	CO.	Elev. (m)	Location	Notes
SD22661, RSA741151, RSA393366, SD114052, RSA597761	25-Aug-08	SD	1160	Laguna Mountains N end of Pine Valley.	A portion of this occurrence was extirpated due to housing development (CCH 2011)
Reveal 2004	NONE	SD	975	Warner Hot Springs	Not verified
RSA190624, RSA735612	16-Sep-08	RIV	1365–1402	San Jacinto Mountains Garner Valley. W side of, and close to Highway 74.	
Rare Plants of San Diego (Reiser 1994)	NONE	SD	548	Alpine	Not verified
RSA392669, POM2334, POM155993	5-Aug-1902	SBD	2100	SB Mountains, Bear Valley.	E, Development
POM193462	5-Oct-1929	SBD	2134	SBM Along stream south of Peter Pan Woodland Club, Bear Valley.	E, Development
JEPS57523, UC501513	3-Aug-1931	SBD	2100	SBM, flat above Big Bear Lake (Lundy's Landing).	E, Development
RSA723043, RSA393122	14-Aug-07	SBD	2224	SBM Upper section of Van Dusen Canyon. Along Caribou Creek. About 3 mi from Highway 38.	
RSA735660, RSA735665, RSA735465, RSA735656	20-Aug-08	SBD	2225–2236	SBM Caribou Creek meadow. E of Holcomb Valley Campground.	
POM172771, POM193239, RSA65979	23-Aug-1929	SBD	2073	SBM, Baldwin Lake.	Not in CNDDB, not relocated in 2008, but possibly extant
UCR125005	7-Sep-1931	SBD	2058–2073	SBM between Big Bear Lake and Baldwin Lake	E, not in CNDDB
CDFG	1-Sep-2006	LA	356	Entrada site, Valencia	Not verified

Fig. 3. Typical habitat for *Eriogonum evanidum*. Photo from Pine Valley, San Diego County, CA.

the vicinity of Big Bear Lake and possibly Baldwin Lake due to development in the region. In addition, one population in Pine Valley has been extirpated due to development; Hirshberg revisited a population she previously documented in 1994 and states that "there is now a house there, and the population has apparently been extirpated" (CCH 2011). The primary threats to this species include development, dispersed recreation (vehicle use off designated roads, hiking, equestrian use, etc.), and non-native plant establishment (CNPS 2011).

SURVEY RESULTS

There are ten documented locations of *E. evanidum* (Fig. 2); four of these are known to be extant (Table 1). Several occurrences in the vicinity of Big Bear Lake and Baldwin Lake were not located and are possibly extirpated (Table 1). One historic occurrence in the San Jacinto Mountains in Garner Valley (Hemet Valley), one historic occurrence in the Laguna Mountains in Pine Valley, and one occurrence in the San Bernardino Mountains along Van Dusen Canyon Road were located. An occurrence in the vicinity Holcomb Valley in the San Bernardino Mountains was newly documented as a result of this study (Table 1). There are several reported locations for which there are no voucher

specimens (Valencia, Warner Springs, and Alpine, Table 1), therefore the existence of these occurrences is suspect until verified. In 2008 a survey was conducted at Warner Springs and no suitable habitat found.

DISCUSSION

There are several factors that may have influenced the lack of recent documentation for this species and previous conclusion that this species was extinct. First, *E. evanidum* has a highly limited distribution, only occurring in localized microsites within its distribution, and is generally not locally common. Second, this species commonly occurs in the general vicinity of similar looking species (e.g., *E. baileyi*, *E. davidsonii*). Third, *E. evanidum* has exceedingly small flowers and therefore diagnostic characteristics can be difficult to detect in the field. Lastly, *E. evanidum* flowers from August to September, a time of year when few botanists make collections. Other summer to fall-blooming plants, such as *Deinandra mohavensis* (D. D. Keck) B. G. Baldwin have been mistakenly considered extinct (Sanders et al. 1998). This brings to bear the importance of collecting plant specimens late in the growing season in the summer and fall months.

There are undoubtedly additional occurrences of *E. evanidum* that have not been documented

and we recommend additional surveys are conducted to further assess the status of this species. The status of CNPS list 1B.1 is appropriate given the current information. All extant occurrences are known from National Forest lands, and are therefore currently protected from development; however, this species may also be present in undocumented locations on private property. While *E. evanidum* is extant throughout its current range within the U.S., this species has been impacted by anthropogenic disturbances (e.g., dispersed recreation, OHV use, development). Specifically plants in Pine Valley in San Diego County have been impacted by development. This was noted by Hirshberg (CCH 2011) who was unable to locate an occurrence she previously documented because it has been extirpated by development (CCH 2011). The conservation status of *E. evanidum* was brought to light because it was presumed extinct in recent floristic treatments; if not for these recent publications, this species could have remained undetected and hidden in herbaria.

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PTYCHOSTOMUM PACIFICUM (BRYACEAE), A NEW FEN SPECIES FROM CALIFORNIA, OREGON, AND WESTERN NEVADA, USA

JOHN R. SPENCE
Glen Canyon National Recreation Area, P.O. Box 1507, Page, AZ 86040-1507

JAMES R. SHEVOCK
California Academy of Sciences, Department of Botany, 55 Music Concourse Dr.,
Golden Gate Park, San Francisco, CA 94118-4503
jshevock@calacademy.org

ABSTRACT

Ptychostomum pacificum J. R. Spence & Shevock, a new and highly distinctive species restricted to fen habitats within coniferous forests in California, Oregon, and extreme western Nevada is described and illustrated. This species appears to be related to *P. turbinatum* (Hedw.) J. R. Spence but is easily distinguished by a combination of features including large size, percurrent yellowish-brown costa with numerous incrassate cells at the leaf tip, strongly recurved leaf margins, and elongate cylindrical to narrowly pyriform capsules.

Key Words: *Bryum*, cascades, mosses, Sierra Nevada.

The genus *Bryum sensu lato* with nearly 450 currently recognized species (Crosby et al. 2000) remains a complex and taxonomically challenging group of mosses. However, this polyphyletic genus has recently been divided into several segregate genera (Spence 2005, 2007; Spence and Ramsay 2005; Holyoak and Pedersen 2007). The Bryaceae are a major component of the bryoflora along the Pacific slope of North America, and California, with 60 taxa, leads all other states and provinces of North America in the number of species in this family (Norris and Shevock 2004; Malcolm et al. 2009; Spence unpublished data). Historically, bryologists generally avoid collecting *Bryum* if sporophytes are lacking since most keys have relied heavily on sporophytic characters. This collecting approach has greatly hindered work on this group of mosses since many useful gametophytic characters are currently recognized to make identification of sterile collections possible. During the course of developing the treatment of the Bryaceae for the Flora of North America Project (FNA Vol. 28 in prep.), the first author determined that several additional taxa remain undescribed, and many of these new taxa reside in California. This paper is an effort to reduce this backlog of species awaiting formal publication.

This new species is described in the genus *Ptychostomum* Hornsch., which has been shown to be distinct from *Bryum sensu stricto* (*B. argenteum* Hedw. and its allies) by both molecular and morphological studies (Pedersen et al. 2003; Spence 2005; Holyoak and Pedersen 2007). Most of our familiar boreal-temperate species of *Bryum* actually belong in *Ptychostomum*, and have been transferred elsewhere for the Bryophyte Flora of North America (Spence 2005, 2007).

Based on the herbarium record examined to date (CAS, UC), "P. pacificum" was first collected by the second author in 1975. This collection was sent to Dan Norris (UC) who at the time at Humboldt State University was working toward a California moss flora. The specimen was returned as "*Bryum* sp. possibly undescribed." Many collections of this fen species were subsequently obtained by the second author but sporophytes remained unknown. In 1999, a population of "P. pacificum" was discovered by David Toren (CAS) in Lake County, California that contained a few sporophytes, and a couple years later the second author found sporophytes in a Sierra Nevada occurrence. Of the nearly 75 occurrences documented by herbarium vouchers, sporophytes have only been documented seven times. Interestingly, Andrews (1935) describes "sterile forms" of *Ptychostomum turbinatum* (Hedw.) J. R. Spence from the west (without specific localities) with stem lengths reaching 10 cm or more, which suggests that at least some prior collections of "P. pacificum" may exist in other herbaria and are likely to be labeled as *P. turbinatum*, a much smaller species.

TAXONOMIC TREATMENT

Ptychostomum pacificum J. R. Spence & Shevock, sp. nov. (Figs. 1, 2). —TYPE: USA, California, Fresno Co., Sierra National Forest, Highway 168 above Huntington Lake, 37°12′59.7″N, 119°11′30.4″W, 7375 ft., 2 Sep 2002, *Shevock & Ertter 22887* (holotype: CAS; isotypes H, KRAM, MO, NY).
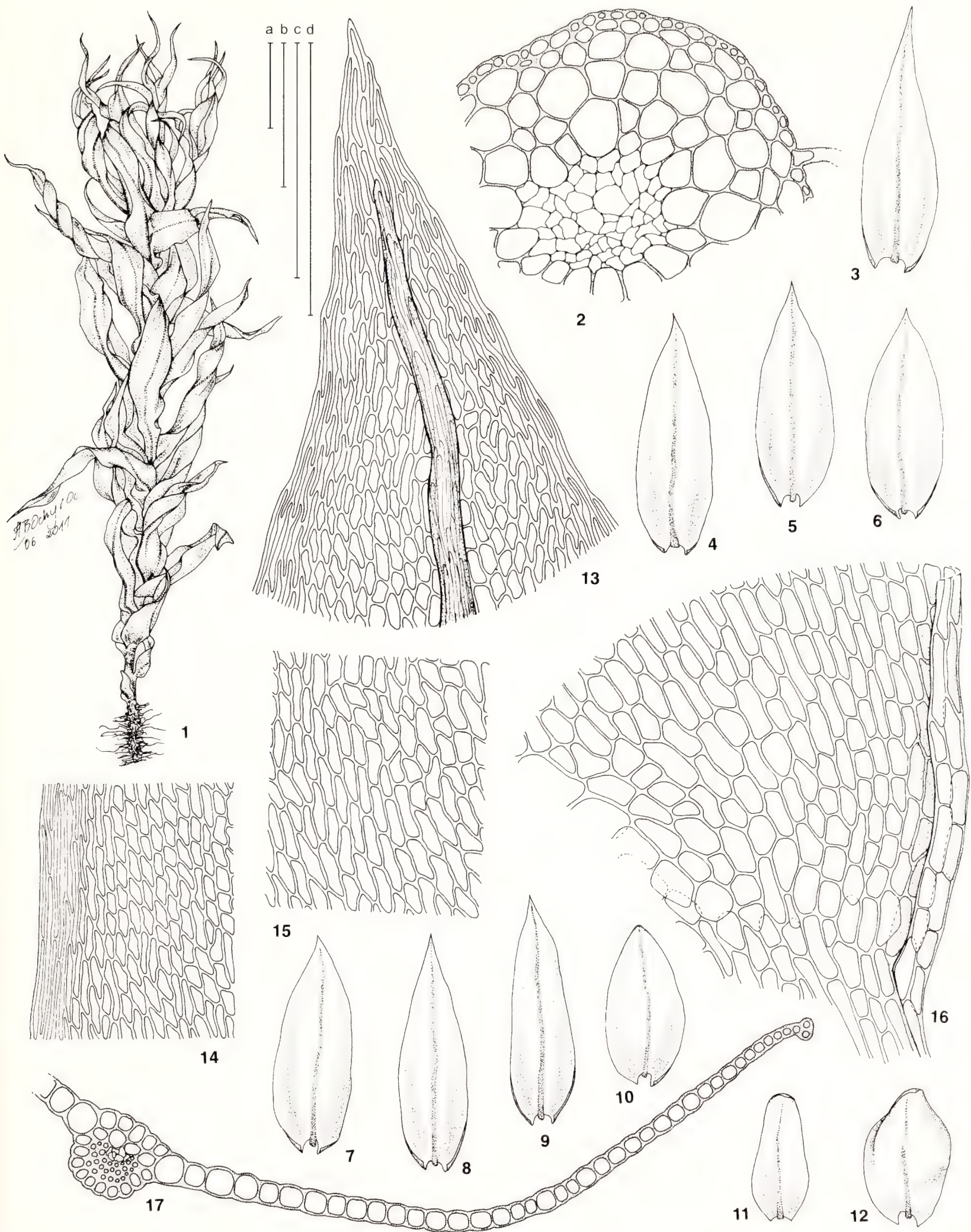
FIG. 1. *Ptychostomum pacificum* J. R. Spence & Shevock. 1. Sterile plant, dry. 2. Portion of stem transverse section. 3–9. Vegetative leaves from upper and median portion of stem. 10–12. Lower stem leaves. 13. Leaf apex. 14. Mid-leaf cells at margin. 15. Mid-leaf cells. 16. Basal cells. 17. Leaf transverse section. (All from *Toren 9586B*, KRAM). Scale bars: a – 100 μm (13–17); b – 100 μm (2); c – 0.5 cm (1); d – 0.5 cm (3–12).
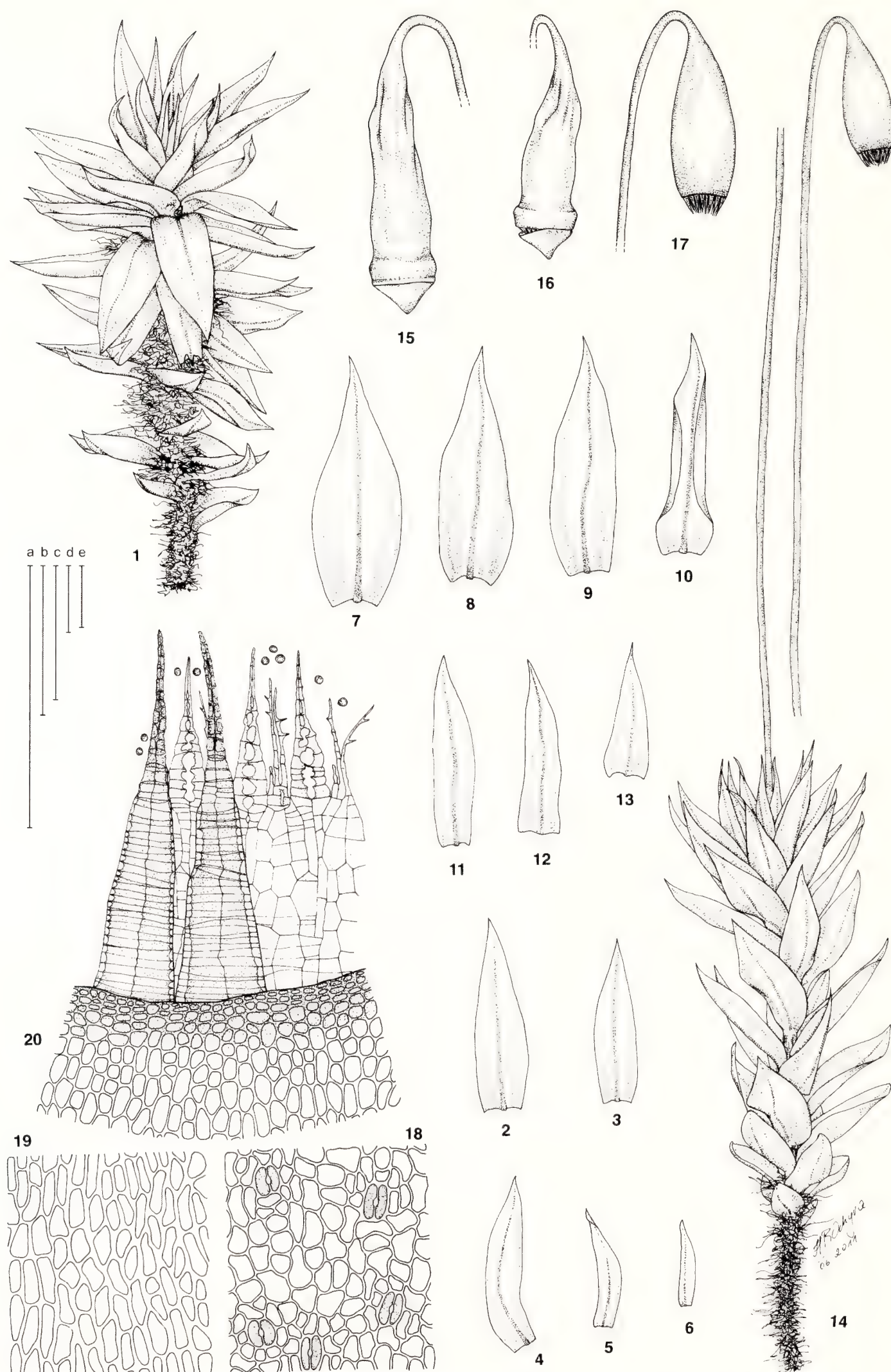
FIG. 2. *Ptychostomum pacificum* J. R. Spence & Shevock. 1. Male plant. 2–6. Perigonial bracts, sequentially from outermost to innermost. 7–13. Perichaetial leaves, sequentially from outermost to innermost. 14. Female plant with mature capsule, wet. 15–16. Operculate capsules, dry. 17. Deoperculate capsule, wet. 18. Exothecial cells at base of urn and stomata. 19. Mid-urn exothecial cells. 20. Exothecial cells at orifice, portion of peristome and spores. (1–6 from *Shevock 14233*; 7–20 from *Toren 9586B*; both in KRAM). Scale bars: a − 0.5 cm (2–13); b − 0.5 cm (14); c − 0.5 cm (1); d − 1 mm (15–17); e − 100 μm (18–20).

Plantae robustae, caulibus usque 12 cm; margines folii proximales recurvae, limbidio pervaldo, ex 2–4– stratis composito, partim bistratoso, ad apicem folii cellulis distalibus laminalibus incrassatis, saepe rubro-brunneis, costa apicem folii non attingenti vel percurrenti; capsula elongata, cylindrica vel clavata, 3–5 mm, brunnea, symmetrica.

Plants medium to robust, in dense or open turfs, green or yellow-green. Stems 2–12 cm, red-brown, lacking central strand, evenly foliate to somewhat crowded distally, often strongly radiculose. Leaves narrowly to broadly ovate-lanceolate to ovate, 3–5 mm, somewhat enlarged towards stem apex, weakly concave distally, leaves below becoming strongly concave and sometimes cucullate, weakly to moderately keeled, yellow-green to bright green, becoming blackish to red-brown when old, strongly contorted when dry, distally spirally twisted, erect-spreading to spreading wet, not or weakly decurrent; apex acute to acuminate, often colored golden-brown, margins revolute to mid-leaf, smooth to weakly serrulate distally, costa brown to red-brown, strong, not reaching apex to percurrent, rarely very short excurrent in stout serrulate awn, limbidium extremely strong, 2–4 rows, yellowish, partially bistratose below, distal and median laminal cells rhomboidal to hexagonal, 15–25 μm wide, 30–70 μm long, mostly 2–3:1, thin walled except colored distal cells which are strongly incrassate, proximal laminal cells gradually rectangular, about the same width or somewhat narrower than cells above, somewhat longer than cells above, 15–20 (25) μm wide, 40–90 μm long, often reddish, alar cells not differentiated. Specialized asexual reproduction absent. Sexuality dioecious; outer perichaetial leaves similar to vegetative leaves, inner leaves smaller, more triangular, with more acuminate apex; perigonium distinctly enlarged and conspicuous, outer leaves similar to vegetative leaves, inner leaves broadly ovate and abruptly acute. Seta 2–4 cm, straight, red-brown to yellow-brown, slender. Capsule elongate cylindric to clavate, 3–5 mm, brown, symmetric, mouth brown to red-brown, somewhat constricted when mature below mouth, exothecial cells irregularly elongate, 15–25 μm wide, 30–60 μm long, mostly 4:1, shorter in 2–3 rows at mouth; peristome well developed, exostome teeth yellow, lanceolate, 500–650 μm long, strongly trabeculate; endostome membrane high, ½ height of exostome, pale hyaline to yellowish, processes well developed, perforations oval, smooth, cilia somewhat variable, 2–3, sometimes short, mostly appendiculate; operculum low convex, apiculate. Spores pale yellow or pale brown, finely papillose, 12–16 μm.

Paratypes: USA. CALIFORNIA. **Alpine Co.**: Stanislaus National Forest, McCormick Creek drainage, S base of The Dardanelles, 7830 ft, 6 Aug 2007, *Willits 500* (CAS). **El Dorado Co.**:

1.5 mi N of Grass Valley near Tahoe Rim Trail, *Nichols 221* (USFS-LTBMU). **Fresno Co.**: Kings Canyon National Park, Pacific Crest Trail, Middle Fork Kings River, Le Conte Canyon between Ranger Station and Grouse Meadow, 8400 ft, 8 Sep 1999, *Shevock & Haultain 18634* (CAS, NY); Sierra National Forest, Kaiser Wilderness, tributary of Rancheria Creek, 9240 ft, 16 Jul 2001, *Shevock 20994* (CAS, H, KRAM); E of Idaho Lake, 8875 ft, 16 Jul 2001, *Shevock 21004* (CAS, UBC); forest road 10S66 above Bear Creek Rd., 8300 ft, 27 Jul 1996, *Shevock & Bourell 13994* (CAS, KRAM); West Snow Corral Meadow, 7100 ft., 27 Jul 1996, *Shevock & Bourell 14022* (CAS, DUKE, F, NY); between House and Ahart Meadows, 7200 ft, 28 Jul 1996, *Shevock & Bourell 14040* (CAS, KRAM, UC); John Muir Wilderness, Wet Meadows, between Rancheria and Crown Valley, 8550 ft, 16 Aug 1996, *Shevock & York 14117* (CAS, DUKE, MO, NY, OSC) & *14118* (CAS, H, KRAM, UBC, US); near Spanish Lake, 8600 ft, 17 Aug 1996, *Shevock 14165* (CAS, COLO, H, UC); Hoffman Meadow, 6800 ft, 30 Jul 2000, *Shevock & Norris 19856* (CAS, US). **Humboldt Co.:** Shasta-Trinity National Forest, Headwaters of Kerlin Creek about 5.4 air mi WSW of Hyampom, 5460 ft, 23 Jul 2009, *Lenz 4226* (CAS). **Glenn Co.**: Mendocino National Forest, Telephone Camp W of Plaskett Meadows, 6900 ft, 18 Jul 1998, *Toren 7224* (CAS, MO, NY). **Lake Co.:** Mendocino National Forest, Mt. Sanhedrin, headwaters of Mill Creek, 5450 ft, 17 Oct 1999, *Toren, Dearing & Heise 7633* (CAS); Cirque of N slope of Hull Mountain, 6300 ft, 6 Sep 1999, *Toren 7620* (CAS, NY); Snow Mountain Wilderness, Milk Ranch Meadow, 6300 ft, 25 Jun 2002, *Toren 9151* (CAS) and East Peak, 6400 ft, 26 Jun 2002, *Toren 9167* (CAS). **Lassen Co.:** N slope of Dyer Mtn., 3.4 air mi SSW of Westwood, 5900 ft, 22 Jun 2005, *Lenz 1835 & 1837* (CAS). **Madera Co.**: Devils Postpile National Monument, meadow N of Rainbow Falls, 7450 ft, 25 Sep 2001, *Shevock & Dulen 21310* (CAS); Sierra National Forest, 1.2 mi NW of Beasore Road at Cold Saddle, 7250 ft, 24 Sep 2001, *Shevock 21231* (CAS, H, KRAM); near Chipmunk Meadow, 6850 ft, 11 Jul 2003, *Shevock 24166* (BOL, CAS, KRAM, NY); W of Grey Mountain, 6800 ft, 19 Jun 2002, *Laeger 1466* (CAS); NE of Fresno Dome, 7450 ft, 6 Jul 2000, *Shevock & Kellman 19622* (CAS, DUKE); Central Camp Rd near Gaggs Camp, 5875 ft, 11 Jul 2003, *Shevock 24156* (CAS, DUKE, F); Poison Meadow, 6850 ft, 18 Jun 2002, *Shevock, Norris, & Clines 22420* (CAS, UC); China Meadow off of FS road 8S70, 6000 ft, *Shevock & Norris 20241* (CAS); Yosemite National Park, between Grouse and Crescent Lake, 8300 ft, 29 Jul 2009, *Shevock & Smith 33206* (CAS, MO, NY, UC). **Mariposa Co.:** Yosemite National

Park, Turner Meadow, 7365 ft, 28 Jul 2009, *Shevock, Taylor, Smith, & Colwell 33181* (CAS, MO, UC); McGurk Meadow, 6900 ft, 24 Sep 2001, *Shevock 21232* (CAS, YM); Mono Meadows, 6940 ft, 24 Sep 2001, *Shevock 21239* (CAS, MO, YM) and 11 Jul 2009, *Shevock & Hutten 33174* (CAS). **Modoc Co.:** Modoc National Forest, Headwaters of Lassen Creek, 5.8 air mi SE of Sugar Hill, 6550 ft, 23 Oct 2007, *Lenz 4097* (CAS). **Nevada Co.:** Tahoe National Forest, Pat Yore Flat, 6165 ft, 22 Jul 2010, *Wishner 10291* (CAS, UC). **Placer Co.:** Tahoe National Forest, Duncan Fen, 6710 ft, 17 Oct 2008, *Wishner 9721* (CAS, UC); Gates Fen, 5435 ft, 17 Oct 2008, *Wishner 9731* (CAS, UC); Tadpole Creek Fen, 6260 ft, 17 Oct 2008, *Wishner 9711* (CAS, UC). **Plumas Co.:** Plumas National Forest, Daly Cow Camp Fen, head of Big Pine Ravine, 1 km NNE of Camel Peak, 1591 m, 8 Nov 2006, *Toren & Janeway 9505* (CAS, MO, UC) and *Janeway & Toren 8952* (CHSC); Vaca Fen near head of S Branch Middle Fork Feather River, 1743 m, 8 Nov 2006, *Toren & Janeway 9507* (CAS, NY, UBC, UC) and 10 Jun 2009 *Dillingham & Toren 2572* (CAS); above Black Rock Campground W of Little Grass Valley Reservoir, 5150 ft, 15 Jun 2007, *Toren 9586B* (CAS, KRAM, UC); S Branch of Ward Creek, 6670 ft, 7 July 2005, *Dillingham & Toren 2057* (CAS, UC); Bucks Summit, 5360 ft, 14 Nov 2003, *Dillingham et al. 1123* (CAS); 3 mi W of Bucks Lake, 5255 ft, 13 Nov 2003, *Dillingham 1048* (CAS, UC); China Gulch Fen, 5410 ft, 10 Oct 2003, *Dillingham & Toren 1036* (CAS, UC); SE of Red Mountain, 5200 ft, 13 Nov 2003, *Dillingham & Toren 1187* (CAS); E of Tamarack Flat, 5400 ft, 13 Sep 2001, *Dillingham & Norris 404* (CAS); 7.5 mi NE of Quincy, 6285 ft, 23 Aug 2004, *Dillingham 1654* (CAS, UC); tributary to Rabbit Creek, 5300 ft., 16 Jun 2005, *Dillingham 2042* (CAS). **San Bernardino Co.:** San Bernardino National Forest, Champion Lodgepole Meadow about 0.5 mi. from Siberia Creek trailhead, 7475 ft., 26 Sep 2011, *Eliason & Williams SE09F&G* (CAS). **Shasta Co.:** Shasta-Trinity National Forest, Clark Creek ca. 2 mi E of Red Mountain, *Norris, Lenz, & Hillyard 108204* (CAS, UC); Lassen Volcanic National Park, Dersch Meadows, 6590 ft, 22 Aug 2008, *Shevock & Showers 31901* (CAS, NY). **Sierra Co.:** Tahoe National Forest: Sierra Buttes Fen, 7250 ft, 17 Aug 2009, *Wishner 12013* (CAS, UC). **Tehama Co.:** Lassen Volcanic National Park, N base of Mt. Conard, 7175 ft, 22 Aug 2008, *Shevock & Showers 31925* (CAS, MO, NY, UC, US). **Trinity Co.:** Shasta-Trinity National Forest, Headwaters of West Branch Crow Creek, 0.5 air mi SSW of Mumbo Lake, 6260 ft, 21 Jul 2009, *Lenz 4201* (CAS). **Tulare Co.:** Sequoia National Forest, Headwaters of Freeman Creek, 7000 ft, 19 Jul 1975, *Shevock 4599* (CAS) and *10638* (CAS); Freeman Creek Trail,

7000 ft, 24 Aug 1996, *Shevock 14233* (CAS, KRAM, UC); Quaking Aspen Campground, 7000 ft, 15 Jun 2001, *Shevock 20954* (CAS); Cold Spring below Portuguese Pass, 7200 ft, 2 Sep 1996, *Shevock 14314* (CAS, KRAM); Clicks Creek, 7900 ft, 24 Aug 1996, *Shevock 14252* (CAS, MO, NY); Golden Trout Wilderness, Jacobsen Meadow, 8400 ft, 23 Oct 2000, *Laeger 394* (CAS), between Redwood Crossing and Long Meadow, 6800 ft, 27 Jul 1983, *Shevock 10604* (CAS, UC), and 9 Nov 1997, *Shevock 16713* (CAS, MO, NY, UC); Sirretta Meadows, Ernest C. Twisselmann Botanical Area, 8800 ft, 16 Aug 1998, *Shevock 17522* (CAS) and stringer of Sirretta Meadows, 9000 ft, 26 Aug 2006, *Laeger & Cone 3586* (CAS); Machine Creek E of Round Meadow, 9060 ft, 29 Sep 2001, *Shevock, et al. 21380* (CAS, MO, NY, UBC, US); Round Meadow, 9000 ft, 2 Sep 1996, *Shevock 14320* (CAS, UC); Mosquito Meadow, 8800 ft,10 Jul 1999, *Shevock 18416* (CAS, CONC, MO); Woodcock Meadow near Buena Vista, 7300 ft, 25 Oct 1997, *Shevock 16659* (CAS, H, MO, NY); Weston Meadow, 6800 ft, 28 Jun 1996, *Shevock & York 13650* (CAS, KRAM); Jennie Lakes Wilderness, between Marvin Pass and Mitchell Peak, 9300 ft, 11 Oct 1996, *Shevock 14553* (CAS, MO, NY) and Rowell Meadows, 8850 ft, 2 Aug 2002, *Laeger & Hayden 1611* (CAS); Sequoia National Park, Quinn Snow Survey Cabin NW of Soda Butte, 8200 ft, 24 Oct 2000, *Laeger 430* (CAS); Log Meadow, Giant Forest, 6800 ft, 25 Oct 1997, *Shevock 16679* (CAS); NE of Bald Dome, 8595 ft, 23 Jul 2008, *Jones 315D* (COLO, KRAM). **Tuolumne Co.:** Stanislaus National Forest, Sapps Meadow, 6725 ft, 4 Jun 2009, *Willits 501* (CAS); Yosemite National Park, ridge SE of Kibbie Lake, 7365 ft, 12 Sep 2008, *Colwell et al. 08-596a* (CAS, YM); E of Knapp, *Colwell et al. 09-494* (CAS, YM). NEVADA. **Washoe Co.:** Sierra Nevada, Humboldt-Toiyabe National Forest, Tahoe Meadows, 8740 ft, 13 Sep 2009, *Wishner 9512* (CAS, UC). OREGON. **Douglas Co.:** wetland in basin below jct. of forest road 250 and 251, 5475 ft, 6 Aug 2007, *Wagner m2308* (CAS). **Lane Co.:** Willamette National Forest, E side of Little Groundhog Mountain at jct. with forest road 452, 6.5 mi ESE of south end of Hills Creek Reservoir, 5240 ft, 23 Jul 2004, *Wagner m1390* (CAS, UC); Three Sisters Wilderness, Quaking Aspen Swamp, 8 mi E of McKenzie Bridge, 4465 ft, 8 Aug 1999 & 1 Oct 2009, *Wagner m0730a, m2556a & m2556b* (CAS).

Etymology: the species is named for its distribution along the Pacific Coast of the United States in California, Nevada, and Oregon.

Taxonomic Relationships

Ptychostomum pacificum has previously gone un-noticed due to its morphological similarity to

several related species in western North America. The new species appears to be closest to *P. schleicheri* (Schwägr.) J. R. Spence and *P. turbinatum* (Hedw.) J. R. Spence, but also mimics large specimens of *P. pseudotriquetrum* (Hedw.) J. R. Spence & Ramsay. All these species occur on wet sites on soil, organic muck, and sometimes wet rocks, and all can occur in various kinds of wetlands. Until sporophytes were discovered it was generally thought to be a robust form of *P. turbinatum*. However, that species has broadly turbinate capsules, a plane leaf margin (occasionally revolute proximally), usually short-excurrent costa, and is a much smaller plant with smaller leaves (to 4 mm) and shorter stems (to 3–4 cm). *Ptychostomum schleicheri* is also robust, but is characterized by its broad, uncontorted, yellowish leaves, very broad laminal cells, and turbinate capsules. *Ptychostomum pseudotriquetrum* differs from *P. pacificum* by its strongly decurrent leaves, distinctly short-excurrent costa, shorter proximal lamina cells, and unistratose limbidium.

The most distinctive features of *P. pacificum* include the large size, colored leaf tip with incrassate cells, mostly percurrent or shorter costa, proximally recurved leaf margins, very strong limbidium, large conspicuous perigonia, and elongate capsule.

HABITAT AND ECOLOGY

Ptychostomum pacificum is restricted to perennially wet fen habitats within coniferous forests primarily dominated by *Pinus contorta* Lounon, *Abies concolor* (Gordon & Glend.) Lind., *Abies magnifica* A. Murray, or a combination of these species. Few flowering plants occur among populations of *Ptychostomum pacificum*. Taxa listed on herbarium labels for multiple occurrences of *P. pacificum* include *Camassia quamash* (Pursh) Greene, *Dodecatheon jeffreyi* Van Houtte, *Drosera rotundifolia* L., *Eriophorum crinigerum* (A. Gray) Beetle, *Kalmia polifolia* Wangenh., *Ledum glandulosum* Nutt., *Pedicularis groenlandica* Retz., *Phalacroseris bolanderi* A. Gray, *Rhododendron occidentale* (Torr. & A. Gray) A. Gray, *Saxifraga oregana* Howell, *Salix* spp., *Vaccinium uliginosum* L. ssp. *occidentale* (A. Gray) Hultén, and *Veratrum californicum* Durand. Bryophytes generally associated with *Ptychostomum pacificum* include *Aulacomnium palustre* (Hedw.) Schwägr., *Drepanocladus aduncus* (Hedw.) Warnst., *Philonotis americana* (Dism.) Dism., *P. tomentosa* Mol. *in* Lor., *Ptychostomum weigelii* (Spreng.) J. R. Spence, *Sphagnum* spp., and occasionally, *Meesia triquetra* Ångstr. Fen habitats throughout the range of *Ptychostomum pacificum* are acidic in pH and all populations contain one or more members of the Ericaceae, usually *Vaccinium*, *Kalmia*, or *Ledum*. *Ptychostomum turbinatum* is reported to be mildly calciphilous, *P. schleicheri* is reported to

be acidophilous, and *P. pseudotriquetrum* appears to be tolerant of a relatively broad range of pH conditions.

At first glance, *P. pacificum* colonies (especially male plants) are reminiscent of *Rhizomnium pseudopunctatum* (Bruch & Schimp.) T. Kop. in stature and mat growth-form, although *P. pacificum* is considerably more yellow-green in color. However, with a hand-lens inspection it is clear that this plant is actually a member of the Bryaceae and not the Mniaceae.

DISTRIBUTION

Populations of *Ptychostomum pacificum* range from the Cascades of central Oregon in the Three Sisters Wilderness, Willamette National Forest, Lane Co. southward to the southern portion of the Sierra Nevada of California on the Sequoia National Forest, Tulare Co. with a disjunct occurrence recently discovered in the San Bernardino Mountains, San Bernardino National Forest. In northern California this species also extends west and south from the Klamath Mountains into the Northern Coast Ranges, Mendocino National Forest and just east of Lake Tahoe in Nevada, Humboldt-Toiyabe National Forest. Although *P. pacificum* occurs across a wide geographical area, the actual habitat of perennially wet fens within montane to subalpine coniferous forests is considerably restricted. Populations range in the north from 4465 feet to over 9300 feet in the southern portion of its range. Based on the herbarium record, this species is more frequently encountered in the Sierra Nevada of California, especially from Yosemite National Park southward. However, this may be an artifact of the more systematic bryophyte inventory work that has occurred in this portion of the species' range.

CONSERVATION IMPLICATIONS

Fens throughout the Pacific Slope are very fragile habitats and are ecologically diverse and species-rich environments. Within the coniferous zone these fens comprise less than two percent of the landscape. Some of these fens have been adversely impacted by intensive grazing activities, or have been drained, channelized, or the water flow through them altered by road construction or erosion by headcutting. However, these riparian systems today are viewed as important habitat types for biodiversity. Nearly all reported populations of *Ptychostomum pacificum* are on public lands either administered by the USDA, Forest Service or the USDI, National Park Service. Since fen habitats are increasingly likely to receive a wide variety of protective measures by these land-management agencies, the long-term conservation of this narrowly distributed species seems secure.

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A NEW COMBINATION IN *LINANTHUS* (POLEMONIACEAE) FROM IDAHO AND OREGON

JOANNA L. SCHULTZ
1060 Driscoll Ridge Road, Troy, ID 83871

ROBERT PATTERSON
Department of Biology, San Francisco State University, San Francisco, CA 94132
patters@sfsu.edu

ABSTRACT

In preparing the treatment for Polemoniaceae for the Flora North America North of Mexico it is necessary to propose a new combination in *Linanthus* (Polemoniaceae).

Key Words: Endemism, *Leptodactylon*, *Linanthus*, Polemoniaceae.

As many as 10 infraspecific taxa have been recognized for *Leptodactylon pungens* (Torr.) Nutt. (IPNI 2008), and while floristic treatments have differed in use of infraspecific taxa, we consider *Leptodactylon pungens* subsp. *hazeliae* (Peck) Meinke distinctive and warranting recognition. When Porter and Johnson (2000) revised the taxonomy of Polemoniaceae, conforming to the goal of recognizing only monophyletic genera, they transferred all seven species formerly recognized as *Leptodactylon* to *Linanthus*; however, they did not consider infraspecific taxa that had previously been recognized in *Leptodactylon pungens*. In preparation for the treatment of *Linanthus* for the Flora North America north of Mexico project, a new combination is required: **Linanthus pungens** subsp. **hazeliae**.

TAXONOMIC TREATMENT

Linanthus pungens (Torr.) J. M. Porter & L. A. Johnson subsp. **hazeliae** (Peck) J. L. Schultz & R.Patt., comb. nov. Basionym: *Leptodactylon hazelae* Peck, Proc. Biol. Soc. Wash. 49:111. 1936; *L. pungens* subsp. *hookeri* (Dougl. ex Hook.) Wherry f. *hazelae* (Peck) Wherry, Amer. Midl. Naturalist 34:383; *L. pungens* subsp. *hazeliae* (Peck) Meinke, Madroño 35(2):107. 1988. — Type: USA, Oregon, Wallowa Co., dry rocky slope, Snake River Canyon near mouth of Battle Creek, 13 April 1934, *Barton s.n.* (holotype: WILLU 18415).

Linanthus pungens subsp. *hazeliae* is a rare and very narrow endemic to the Snake River Canyon region that forms part of the Idaho-Oregon border. It occurs within the overall range of *Linanthus pungens* subsp. *pungens*, but the two subspecies are not sympatric. *Linanthus pungens* subsp. *hazeliae* has opposite, soft-filiform distal leaf lobes, while subsp. *pungens* has alternate, acicular, sharp-tipped distal leaf lobes. Meinke (1988) and Moseley (1989) provide careful and complete discussions of the distinctive features and habitat of the subspecies, including comment on its rarity.

Descriptions and discussions of infraspecific taxa of *Linanthus pungens* have been inconsistent and often lacking in detail; however, analytical approaches have improved since these taxa were described, and there are more botanists today who can contribute valuable field information. Therefore, it seems an appropriate time for a thorough systematic study of *Linanthus pungens* throughout its range.

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REVIEWS

Research & Recovery in Vernal Pool Landscapes. Edited by D. G. Alexander and R. A. Schlising. 2011. Studies From The Herbarium, No. 16. California State University. Chico, CA. 175 pp. ISBN 978-0-9761774-3-2. Price: $12.00, paperback.

Vernal pools are seasonally ephemeral wetland ecosystems, generally of regions with a Mediterranean climate. Vernal pool basins become inundated during the winter, support a colorful procession of highly specialized plants and animals through the spring, and then become completely dry by summer. These charismatic ecosystems have intrigued scientists from a variety of disciplines: evolutionary biology, ecology, genetics, taxonomy, geology, hydrology, and (increasingly) conservation biology. This broad spectrum of workers has produced a large and diverse body of literature pertaining to vernal pools, much of which has been first presented to the scientific community in a series of vernal pool symposia and subsequent proceedings (Jain 1976b; Jain and Moyle 1984; Ikeda and Schlising 1990; Witham et al. 1998; Schlising and Alexander 2007). In the introduction to the proceedings from the first vernal pool symposium at the University of California at Davis, editor Subodh Jain acknowledged that he and other symposium organizers wondered if "there is enough known about vernal pools to hold such a meeting" (Jain 1976a). Many dozens of academic papers, six vernal pool conferences (counting the first), and 35 years later, scientists who study vernal pool ecosystems have again contributed original papers toward a conference proceedings: *Research & Recovery in Vernal Pool Landscapes* (Alexander and Schlising 2011). As with previous vernal pool conference proceedings, this most recent volume presents timely research on this important and imperiled California Floristic Province ecosystem.

The 14 contributed papers in this volume are arranged into five sections: Plants, Animals, Geology and Soils, Management, and Preservation History and Recovery Plans.

The Plants section begins with a paper by keynote address speaker Ellen Bauder, a plant ecologist who has studied the vernal pools of southern California for over 20 years. Drawing upon this experience, Bauder provides guidance on the topic of appropriate experimental design in vernal pool ecosystems, which can be highly variable spatially and temporally. The three other papers in this section include a population genetics analysis of Butte County meadowfoam

(*Limnanthes floccosa* ssp. *californica*) by Sloop; a far-reaching study of the ecology and evolution of vernal pool *Lasthenia* species by Emery et al.; and an ecological study by Leong examining the relationship between a vernal pool endemic plant species (*Blennosperma bakeri*) and its pollinators in naturally occurring and created vernal pools.

The Animals section comprises three research articles: the first is a methodologically innovative study of the migration distance of terrestrial-phase California tiger salamanders (*Ambystoma californiense*) by Searcy and Shaffer; the second is a contribution by Bogiatto et al. quantifying the usage of inundated vernal pools by geese and swans; and the third is an editors' summary of the presentation given by Rogers on macroinvertebrate bioassessment.

The Vernal Pools Geography and Soils section is composed of two papers. The first is a continuation of the important work of Holland to document the distribution and areal extent of vernal pool landscapes in the Central Valley. In this Herculean study, Holland prepared maps of vernal pool landscapes by manually photointerpreting high-resolution (1-m) National Agricultural Imaging Program (NAIP) imagery in a Geographic Information System (GIS). Using the resulting GIS layer, Holland calculated vernal pool extent as of 2005, overall loss since baseline conditions were evaluated (1976–1995), loss by county, and loss to various land-use types. Three color figures nicely illustrate the method employed, and a fold-out, full-color plate showcases the resulting map of vernal pool landscapes of the Central Valley. Also in this section is a paper prepared by the editors that summarizes an oral presentation by Conlin on substrates encountered during the Butte Area Natural Resources Conservation Service Soil Survey. Although brief, this paper is nicely illustrated and informative.

The Management and Preservation History and Recovery Plans sections together comprise five papers. Bauder and Bohonak describe a promising new method for vernal pool functional assessment in southern California; Schohr highlights the growing coalition of individuals and groups that support managed grazing of California landscapes (including vernal pool landscapes); and the editors provide a summary of a talk by Witham on the planning process associated with the construction of UC Merced. These sections conclude with two papers on the topic of vernal pool conservation planning in California and adjacent Oregon: one by a long-time water rights activist and vernal pool conservationist, and the other by a biologist from the U.S. Fish

and Wildlife Service. These contributions provide an interesting insight into the process, and yes, politics, of conservation planning.

This volume would be a solid addition to the bookshelves of anyone interested in the natural history of western North America, as many of the contributed papers are of general biological interest. For those who study vernal pools, however, this book is the latest in a series of indispensable vernal pool conference proceedings that together constitute a substantial portion of the research on these fascinating ecosystems. The volume is not perfect; for example, some might question the editors' choice to include summaries of oral presentations where the original presenter elected to not contribute a paper. But considering the strength of the contributed papers, the very low price ($12.00 + tax, shipping), and the fact that any income from sales beyond the cost of printing benefits the non-profit organization Studies From the Herbarium, any minor critiques seem immaterial.

Additional information on this volume can be found at:

http://www.csuchico.edu/herbarium/index.shtml
http://www.csuchico.edu/herbarium/studies/detailed-book-list.shtml

–C. MATT GUILLIAMS, UC/JEPS Herbaria & Department of Integrative Biology, University of California, Berkeley CA 94720-2465; matt_g@berkeley.edu.

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NOTEWORTHY COLLECTION

Montana

Mimulus clivicola Greenm. (PHRYMACEAE). —Sanders Co., Lolo National Forest, Clear Creek drainage, ca. 9.6 km WNW of Thompson Falls, 47.6160N, −115.4785W (WGS84), in upland montane forest with *Pinus ponderosa, Pseudotsuga menziesii, Pseudoroegneria spicata, Collinsia parviflora, Hypericum perforatum, Centaurea stoebe* ssp. *micranthos, Carex geyeri,* and *Spiraea betulifolia,* in grassy 0.02-hectare opening among mature conifers, well-drained gravelly silt loam, SSE aspect, 55% slope, elev. 1168 m, approx. 900 plants primarily in bare soil patches, 22 July 2010, *C. Odegard 48* (MONTU).

The collection location is one of eight sites in the Clear Creek drainage where *M. clivicola* was found in July 2010 and June–July 2011. Collectively, these sites consist of a single "element occurrence" (NatureServe 2012a) that contains about 11,000 *M. clivicola* plants. All of the sites are on partially forested, southerly, 55–70% slopes; site elevations vary from 840 to 1250 m.

Previous knowledge. Mimulus clivicola (bank monkeyflower, hill monkeyflower, North Idaho monkeyflower) is endemic to the inland Pacific Northwest, from northern and west-central Idaho to northeastern Oregon. A historic (1889) collection from "Washington" has not been confirmed; no extant populations are known from the state (Washington DNR 2012). In northern Idaho *M. clivicola* is found in open conifer stands on southerly slopes at elevations below 1250 m, while in west-central Idaho and northeastern Oregon it often occurs in unforested habitats at elevations up to 1675 m (Lorain 1993). Throughout its range *M. clivicola* is typically found in open pockets of vernally moist, exposed mineral soil (Lorain 1993; Consortium of Pacific Northwest Herbaria 2012).

Mimulus clivicola is documented within 13 km of the Montana border in the Coeur d' Alene, St. Joe, and North Fork Clearwater river basins of northern Idaho (IFWIS 2011). At the headwaters of the North Fork St. Joe River south of Lookout Pass, it occurs less than 2 km from the state line (IFWIS 2011).

Significance. The collection is the first report of *M. clivicola* in Montana. The Clear Creek sites are ca. 24 km east of the nearest documented *M. clivicola* site in Idaho (IFWIS 2011). Considering the species' close proximity to the Montana border south of Lookout Pass, *M. clivicola* should also be searched for in western Mineral County, Montana.

In the early 1990's *M. clivicola* was a candidate for federal listing as a threatened or endangered species (USDI, FWS 1995), and it was managed as a Forest Service sensitive species on national forest lands throughout its range in the 1990's. It is now considered globally secure (G4), but vulnerable (S3) in both Idaho and Oregon (NatureServe 2012b). It is provisionally ranked S1S3 in Montana while its conservation status is reviewed (MTNHP 2012). Due to the species' rarity in Montana and potential impacts to the Clear Creek sites from proposed forest management activities, in 2011 the Forest Service Northern Region designated *M. clivicola* as a sensitive species in Montana.

—Craig Odegard, Botanist, Plains Ranger Station, Lolo National Forest, 408 Clayton St, Plains, MT 59859. codegard@fs.fed.us.

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NOTEWORTHY COLLECTION

California

TRIFOLIUM TRICHOCALYX A. A. Heller (FABACEAE). —Mendocino Co., The Conservation Fund, Big River Forest, 9 mi. E of Russian Gulch State Park, 1.6 mi. SW of McGuire Hill (742 ft.), East Branch Little North Fork Big River, 214 m (702 ft.), Mathison Peak 7.5′ quadrangle, *39°20.102′N, 123°38.176′W*, [NAD83], May 27, 2011, *Hulse-Stephens* 1952 (UC); same site different location along road, *39°20.093′N, 123°38.195′W*, [NAD83], June 2, 2011, *Heise* 2916 (UC).

Observed at two locations, within 0.25 miles of each other, one with approx. 5000 plants the other with 50 plants, on road 21020, north-facing slope within redwood/Douglas fir/tanoak forest. Plants were growing in shaded, moist soil of a seasonal logging road that was last graded 5 years prior. Associated species include: *Trifolium dubium, T. variegatum, Hypochaeris radicata, Acmispon parviflorus, Gamochaeta ustulata, Deschampsia elongata, Bromus carinatus* var. *carinatus, Juncus patens, Rubus ursinus, R. leucodermis, Iris douglasiana, Cirsium vulgare, Cyperus eragrostis, Equisetum telemateia* subsp. *braunii.*

Previous knowledge. Trifolium trichocalyx (Monterey clover) is an herbaceous annual endemic to California and is both state and federally endangered (CNDDB 2012). Previously the species was only known to occur in a 206-acre (83 ha) area in the central portion of the Monterey Peninsula within naturally occurring Monterey pine forest. This area is completely surrounded by residential and recreational development so there is little habitat available for the species to expand into. In its closed-cone forest habitat *T. trichocalyx* is very responsive to fire and other disturbances, and without it becomes scarce. Up to 1000 plants were observed following a 1987 fire, thereafter none in 1992 and only 22 in 1995 (USFWS 2009). We know of no recent reports.

Significance. This northern population extends the range of the species approximately 200 mi (322 km) north of the Monterey Peninsula. The habitat here is markedly different in terms of geology, soils, and forest composition thus adding significantly to our knowledge of the ecology and distribution of this species. In Mendocino County *T. trichocalyx* is a species of old logging roads situated on mesic north-facing slopes of redwood/Douglas fir forest and in lieu of fire appears to be dependent on grading, which reduces shade and competition.

At least at the pre-flowering stage (R. Morgan, CNPS fellow, personal communication) the two forms are identical in all respects, except that the Mendocino form differs in having a faint chevron on the leaflets. According to Morgan "the chevron difference could indicate that the Mendocino occurrence may represent a long-standing native population rather than a recent introduction". No apparent differences were seen between the Mendocino and Monterey forms after examining herbarium sheets of *T. trichocalyx* from the Pacific Grove Museum of Natural History (V. Yadon, Director Emeritus, Pacific Grove Museum of Natural History, personal communication).

Total DNA was prepared from a dried leaf sample of the Mendocino County *T. trichocalyx* using the DNeasy Plant Mini Kit (QIAGEN, Germany) and following the manufacturer's recommended protocol, except that the elution buffer was pre-heated to 65°C. The nuclear internal transcribed spacer region of 18S-26S rDNA and the chloroplast *trn*L intron region were amplified and sequenced as previously described (Ellison et al. 2006). DNA homology searches of the GenBank DNA sequence database were conducted using BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) to establish sequence identities. Both sequences were found to be identical to those reported previously for the Monterey population of this species (Ellison et al. 2006).

—Kerry Heise, 453 Mendocino Dr., Ukiah, CA 95482; Geri Hulse-Stephens, 915 East Hill Road, Willits, CA 95490; Nicholas Ellison, Grasslands Research Centre, Tennent Drive, Private Bag 11008, Palmerston North 4442, NZ. kheise@copper.net.

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