

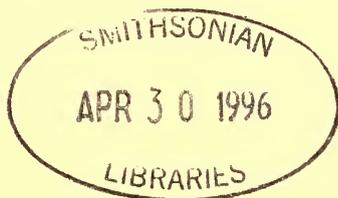
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MADROÑO

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GENETIC VARIATION IN THE ENDEMIC
CALIFORNIA SEDGE
CAREX HIRTISSIMA (CYPERACEAE)

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ABSTRACT

Carex hirtissima is a perennial sedge endemic to montane forests in the foothills of the Sierra Nevada and the Coast Ranges in central California. In a study of four natural populations and all known herbarium specimens from 63 herbaria, I investigated patterns of variation in allozymes, structural features and chromosome numbers. Seventeen putative enzyme-coding loci were assayed and five were found to be polymorphic. Deviations from Hardy-Weinberg equilibrium and high positive fixation indices suggested that inbreeding is the dominant mating system. Cluster analysis of genetic distances calculated among populations showed that populations of *C. hirtissima* are quite similar and that this species is probably more closely related to *C. gynodynamis* than to *C. mendocinensis*, two other species endemic to the California Floristic Province. Chromosome numbers were determined for *C. hirtissima* for the first time in this study and found to be $n = 35$ in one population and $n = 36$ in another. A new glabrous morph of *C. hirtissima* was found in one population, but both glabrous and pubescent morphs had the same chromosome number and similar allozyme frequencies.

Carex hirtissima Boott is a perennial sedge endemic to montane forests on the western slopes of the Sierra Nevada and in the Coast Ranges of central California. The species was described in 1880 by W. Boott based on a collection by A. Kellogg from Summit Camp, Bear Valley, in the Sierra Nevada. It has since been found in the foothills from Butte County south to Tuolumne County as well as on the western side of the Central Valley in the Coast Ranges (Fig. 1). *Carex hirtissima* is described as rare in Munz (1959).

The taxonomic placement of *C. hirtissima* within the genus has been problematic. Kükenthal (1909), in his world monograph of *Carex*, placed *C. hirtissima* in section *Hirtae*, while Mackenzie (in Abrams 1923) included it in section *Triquetrae* along with several other sedges having prominent pubescence on leaves, culms, and perigynia. Mackenzie (1935) later moved *C. hirtissima* to section *Sylvaticae* along with two other species endemic to the California Floristic Province, *C. gynodynamis* and *C. mendocinensis*, and Munz (1959) followed this treatment.

In conjunction with a monographic study of *Carex* section *Hymenochlaenae*, I assayed allozyme variation, determined chromo-

TABLE 1. SAMPLING SITES FOR *CAREX HIRTISSIMA*. All collection numbers are those of the author. Sample size for allozyme analysis is given in parentheses after each location.

Challenge (3564): Yuba Co., Challenge Cut-Off Road, 2 mi S of jct. with Forbestown Rd. 39°29'N, 121°16'W. (24)
Forbestown (3068/3069/3566): Butte Co., Plumas National Forest, 2 mi W of Forbestown along Ponderosa Way. 39°31'N, 121°19'W. (29)
Georgetown (3075/3567): Eldorado Co., 1 mi S of Georgetown on the W side of Hwy. 193. 38°54'N, 120°50'W. (11)
Round Burn (3580): Lake Co., ca. 2 mi S of the Elk Mountain Ranger Station, Mendocino National Forest. 39°16'N, 122°56'W. (20)

some numbers, and measured structural characters of *C. hirtissima* to determine patterns of variation within and among populations and to evaluate its relationship with *C. mendocinensis* and *C. gynodynama*. In this paper, I present the results of these studies and compare levels of genetic variation in *C. hirtissima* to those in other endemic *Carex* species.

METHODS

Field sampling. Four natural populations (Table 1) were studied in the field during the flowering season in March 1986. At each site, soil pH was determined colorimetrically using a soil pH test kit obtained from the Cornell Agronomy Department. Leaf samples for allozyme analysis were collected from randomly selected individuals at each site with sample sizes ranging from 11 to 29, depending on the size of each natural population. Voucher specimens, including flowering shoots where possible, were pressed from each sampled plant and are deposited at MTMG.

Chromosomes. At the Challenge and Forbestown sites, young staminate spikes just emerging from their sheaths were also collected from some of the same individuals to determine chromosome numbers. Sample size was limited by the number of plants at the correct developmental stage—all available were collected. Young staminate spikes were fixed in modified Carnoy's solution (6:3:1, ethanol:chloroform:propionic acid), stained using alcoholic hydrochloric acid-carmin (Snow 1963), and squashed in Hoyer's mounting medium (Radford et al. 1974). At least six cells were counted per individual. Voucher specimens are deposited at MTMG.

Allozyme analysis. Field-collected young shoots were stored in plastic bags at 4°C for up to one month prior to electrophoresis. No differences in staining activity were noted between fresh and refrigerated material except for alcohol dehydrogenase which stained more intensely when refrigerated material was used. Standard tech-

niques of horizontal starch gel electrophoresis of soluble enzymes were used to separate the electromorphs (Shields et al. 1983; Wendel and Weeden 1989) as previously described (Waterway 1990, 1994). Ten soluble enzymes were assayed: alcohol dehydrogenase (ADH, E.C. 1.1.1.1), glucosephosphate isomerase (GPI, E.C. 5.3.1.9), aspartate aminotransferase (AAT, E.C. 2.6.1.1), acid phosphatase (ACP, E.C. 3.1.3.2), and triosephosphate isomerase (TPI, E.C. 5.3.1.1) using a lithium-borate/tris-citrate discontinuous buffer system at pH 8.3, and phosphoglucomutase (PGM, E.C. 5.4.2.2), malic dehydrogenase (MDH, E.C. 1.1.1.37), 6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), menadiene reductase (MDR, E.C. 1.6.99.3), and NADH diaphorase (DIA, E.C. 1.8.1.4) using a histidine buffer system at pH 6.5.

The genetic basis for the observed banding patterns was inferred from comparison of pollen extracts and leaf tissue extracts (cf. Weeden and Gottlieb 1979) and known subunit composition and numbers of isozymes usually found in diploid angiosperms (Weeden and Wendel 1989). Putative loci and alleles were numbered and lettered, respectively, starting with those migrating the fastest. Naming of loci and alleles was identical to that in Waterway (1990), allowing direct comparison with related species in California.

Allele frequencies and average heterozygosities were calculated for each population and for the species overall. BIOSYS-1 (Swofford and Selander 1981) was used to calculate the mean expected heterozygosity under Hardy-Weinberg equilibrium, to test for deviations from Hardy-Weinberg equilibrium, and to calculate Wright's (1965) fixation index. Nei's gene diversity statistics H_T , H_S , and G_{ST} , unbiased for sample size (Nei and Chesser 1983) were calculated using GENESTAT (Whitkus 1985). Nei's (1972) genetic distance coefficients as modified by Sattler and Hilburn (1985) and U statistics (Mueller and Ayala 1982) to test for significant differences among populations and between *C. hirtissima* and two related species, *C. gynodynamis* and *C. mendocinensis*, were calculated using the program SIDGEND (Sattler and Hilburn 1985). Relationships among populations and species based on the allozyme data were determined by clustering the genetic distance coefficients using an unweighted pair group means analysis (UPGMA, Sneath and Sokal 1973).

Morphology. Observations on the field-collected specimens described above and from those collected at three of the sites in April, 1984 were supplemented by examination of herbarium specimens borrowed from BH, CAS, CHSC, DAV, DS, GH, MIN, MICH, NY, NYS, ROPA, UC, and US (abbreviations following Holmgren et al. 1990). Loans were initially requested from 63 North American herbaria, but only the 13 listed here had any specimens of *C. hirtissima*.

To assess variability within and among populations, the characters listed in Waterway (1990) were measured on 50 specimens of *C. hirtissima* representing 13 different populations. Principal components analysis (SAS Institute, Inc. 1985, procedure PRINCOMP) based on the 23 quantitative characters for which data were available for most specimens (Table 6, all characters except number 4) was used to visualize the pattern of structural variation within *C. hirtissima*. For comparison with the related species, *C. gynodynamis* and *C. mendocinensis*, a canonical discriminant analysis (SAS Institute, Inc. 1985, procedure CANDISC) in which the three species were considered statistical populations was calculated based on the same 23 characters measured from herbarium specimens. Each specimen was classified into one of the three species based on qualitative characters such as color and pubescence and these characters were not included in the canonical analysis. Log transformations were used in both analyses.

RESULTS

Habitat and geographic distribution. *Carex hirtissima* grows in openings in *Pinus ponderosa* forests at lower elevations on the western slopes of the Sierra Nevada from Tuolumne Co. north to Butte Co. It also occurs in similar habitats, but more rarely, in the Coast Ranges of Lake and Mendocino counties (Fig. 1). Twenty-four different collections representing 15 sites were found in a survey of specimens from 63 herbaria. The four populations sampled in this study were growing in soils with pH ranging from 7.4 to 7.6 and all were in seepage areas or along streams. Three of the four sites I sampled were in areas that had been clearcut within the last few years. The fourth site was a small wet meadow in a residential area.

Variation in chromosome number. The two populations of *C. hirtissima* from which chromosome counts could be obtained were each characterized by a different haploid number. Three individuals from the Challenge population all had haploid numbers of 35 while three plants from the Forbestown population each had $n = 36$ (Fig. 2). Normal meiotic pairing was evident in all cells examined.

Allozyme variation. Seventeen putative loci were scored from the ten enzyme systems assayed. All isozymes were interpreted as dimeric enzymes except for PGM and DIA which were monomeric and MDR which was tetrameric. Although the plants had relatively high chromosome numbers suggesting possible polyploidy, the numbers of isozymes observed were those normally found in diploid plants. The four populations were monomorphic for all loci except the five listed in Table 2 (*Aat-3*, *Pgm-1*, *Pgm-2*, *6-Pgd*, and *Mdh-4*). The smallest population (Georgetown) was monomorphic for the

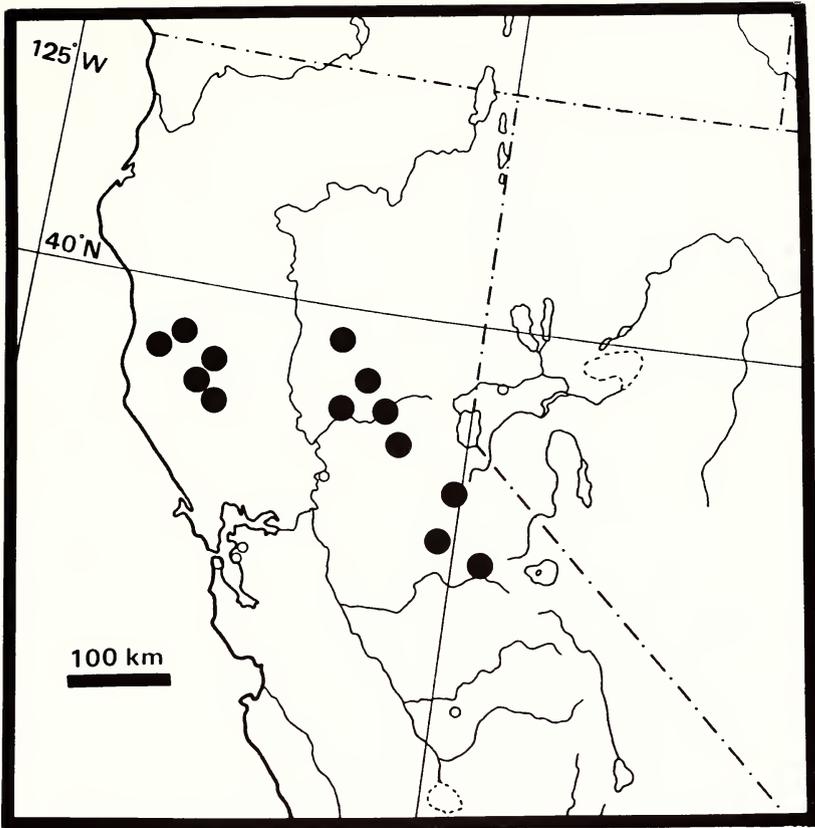


FIG. 1. Geographic distribution of *Carex hirtissima* in California.

most common allele at all loci sampled. *Carex hirtissima* shared many alleles with the closely related species *C. gynodynamis* and *C. mendocinensis* (Waterway 1990). It was monomorphic for the most common allele found in both *C. gynodynamis* and *C. mendocinensis* at *Gpi-1*, *Gpi-2*, *Dia-2*, *Tpi-1*, *Tpi-2*, *Acp-1*, *Mdh-2*, *Mdh-3*, and *Adh-1*. At *Mdr-1* and *Mdh-1*, *C. hirtissima* was monomorphic for the most common allele found in *C. gynodynamis* and at *Aat-2*, monomorphic for the most common allele found in *C. mendocinensis*.

Measures of polymorphism and heterozygosity were low for *C. hirtissima* (Table 3). Mean number of alleles per locus ranged from 1.0 to 1.2 per population and no locus had more than 2 alleles. Five of the 17 loci assayed were polymorphic within the species (29.5%) and the percentage of polymorphic loci per population ranged from 0 to 23.5 percent. Expected heterozygosity was very low, with pop-

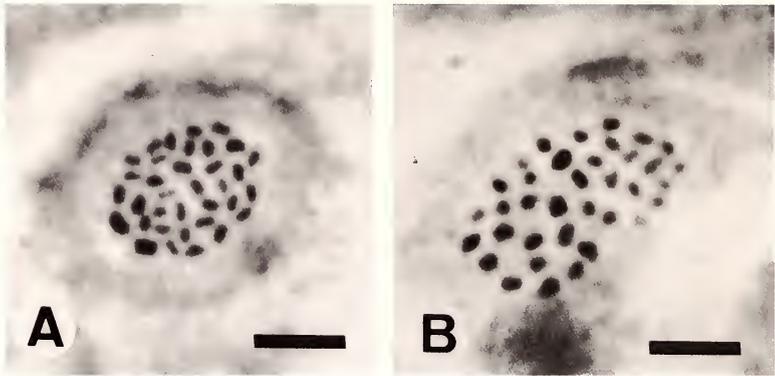


FIG. 2. *Carex hirtissima* chromosomes at metaphase I of meiosis. A) Georgetown population ($n = 35$); B) Forbestown population ($n = 36$).

ulations ranging from 0.03 to 0.07, while observed heterozygosity was even lower with values from 0 to 0.015. Allele frequencies differed significantly from those expected under Hardy-Weinberg equilibrium for all polymorphic loci within the populations. In each case, fixation indices were positive, indicating a deficiency of heterozygotes (Table 4). Nei's gene diversity statistics calculated from all 17 loci sampled were also very low for *C. hirtissima*. Values of H_s were less than 0.2 for each locus indicating low levels of variability within each local population. In contrast, values of G_{ST} , which measures the relative amount of diversity that can be apportioned among populations, were greater than 0.5 for the two most variable isozymes and averaged 0.361 over the polymorphic loci.

Genetic identities based on pairwise comparisons between populations averaged 0.954 ± 0.040 within *C. hirtissima*, higher than

TABLE 2. ALLOZYME FREQUENCIES AT POLYMORPHIC LOCI IN *CAREX HIRTISSIMA*.

Locus allele	Population			
	Challenge	Forbestown	Georgetown	Round Burn
<i>Aat-3</i> a	0	0	0	0.05
b	1	1	1	0.95
<i>Pgm-1</i> a	0.78	0.93	1	0.78
b	0.22	0.07	0	0.22
<i>Pgm-2</i> a	0.73	0.86	0	1
b	0.27	0.14	1	0
<i>Mdh-4</i> b	0.04	0	0	0
d	0.96	1	1	1
<i>6-Pgd</i> a	0.16	0.07	0	0.80
c	0.84	0.93	1	0.20

TABLE 3. GENETIC VARIABILITY MEASURES FOR THE FOUR SAMPLED POPULATIONS OF *CAREX HIRTISSIMA*. P = percentage of loci polymorphic; A = mean number of alleles per locus; H_{OBS} = observed heterozygosity; H_{EXP} = expected heterozygosity under Hardy-Weinberg equilibrium.

Population	P	A	H _{OBS}	H _{EXP}
Challenge	23.5	1.2	0.009	0.066
Forbestown	17.6	1.2	0.003	0.030
Georgetown	0	1.0	0.000	0.000
Round Burn	17.6	1.2	0.015	0.046
Overall	29.5	1.3	0.007	0.064

those comparing *C. hirtissima* with either *C. gynodynamis* or *C. mendocinensis* (Table 5). A cluster analysis of these genetic distances showed the two populations from *Pinus ponderosa* forests in the Forbestown area to be the most similar, with the population from a *Pinus ponderosa*/*Pinus lambertiana* forest in the Coast Range somewhat differentiated, and the population from a wet meadow in the Sierra foothills to be the most differentiated (Fig. 3). The cluster analysis also suggested that *C. hirtissima* is more similar to *C. gynodynamis* than to *C. mendocinensis*. The U statistics indicated significant differences between *C. hirtissima* and *C. gynodynamis* at the 0.1 level, and significant differences between *C. hirtissima* and *C. mendocinensis* at the 0.05 level (Table 5).

Variation in morphology. *Carex hirtissima* is similar to *C. gynodynamis* in having pilose leaves, culms, and perigynia, but differs from it by having longer and narrower leaves and perigynia and scales that are green to golden rather than dark purple as in *C. gynodynamis*. Populations of *C. hirtissima* in the foothills of the Sierra Nevada tend to have more densely pilose leaves and culms than those in the Coast Ranges. The pubescence on the perigynia is more consistent from population to population than that on the leaves and culms. I discovered a previously undescribed form at the Forbestown site in Butte Co., CA (3566). The leaves, culms and perigynia of these plants were completely glabrous. Approximately one-fifth

TABLE 4. FIXATION INDICES FOR POLYMORPHIC LOCI IN POLYMORPHIC POPULATIONS OF *CAREX HIRTISSIMA*.

Locus	Population		
	Challenge	Forbestown	Round Burn
<i>Aat-3</i>	—	—	1.000
<i>Pgm-1</i>	0.679	0.641	0.570
<i>Pgm-2</i>	0.895	1.000	—
<i>Mdh-4</i>	1.000	—	—
<i>Pgd-1</i>	1.000	1.000	0.688

TABLE 5. MEAN GENETIC DISTANCES AND U STATISTICS BETWEEN SPECIES. Mean genetic distances calculated according to Sattler and Hilburn (1985) based on all pairwise comparisons among populations are given in the lower left triangle. U statistics (see text) are given in the upper right triangle. † denotes significant differences between taxa at the 0.1 level, * at the 0.05 level.

Species	n	<i>C. hirtissima</i>	<i>C. gynodynamis</i>	<i>C. mendocinensis</i>
<i>C. hirtissima</i>	4	0.046 ± 0.040	0.135 ± 0.092†	0.266 ± 0.135*
<i>C. gynodynamis</i>	5	0.152 ± 0.093	0.000 ± 0.000	0.197 ± 0.112†
<i>C. mendocinensis</i>	3	0.323 ± 0.149	0.216 ± 0.118	0.081 ± 0.040

of the population at this site belonged to this glabrous morph. This character did not correlate with any other structural difference. In addition, both glabrous and pubescent morphs had the same chromosome number and similar allozyme frequencies. Glabrous individuals tended to occur in clusters within the population, but these clusters were found throughout the population. These observations suggest that the pubescence is probably under simple genetic control, possibly regulated by a single gene or gene complex. None of the herbarium specimens I examined included any glabrous individuals. It is possible that this form occurs in other populations but has

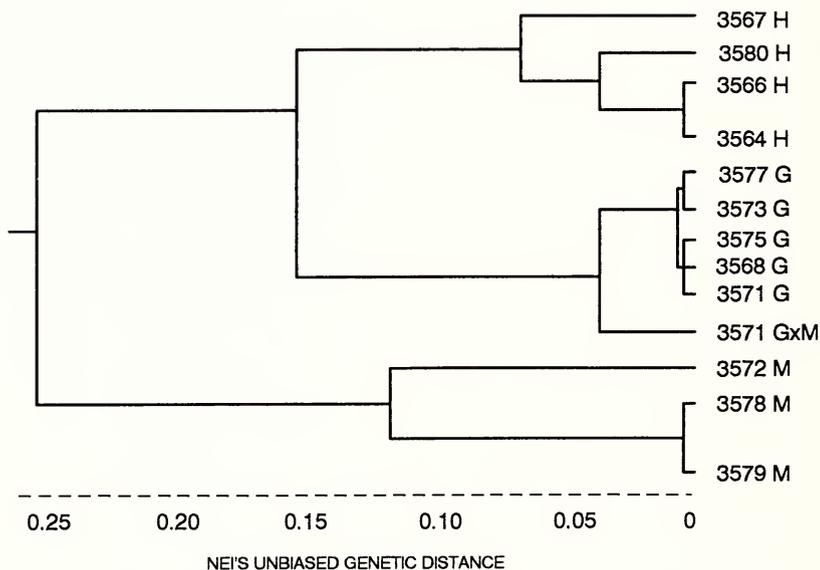


FIG. 3. Cluster analysis (UPGMA) of Nei's genetic distance coefficients as modified by Sattler and Hilburn (1985) based on allozyme frequency data from populations of *Carex hirtissima* (H), *C. gynodynamis* (G), and *C. mendocinensis* (M). Population numbers correspond to Table 1 for *C. hirtissima* and to Waterway (1990) for the other species.

TABLE 6. MEANS, STANDARD DEVIATIONS, AND RANGES OF THE 24 MORPHOLOGICAL CHARACTERS MEASURED ON 50 HERBARIUM SPECIMENS OF *CAREX HIRTISSIMA*. All measurements are in mm except number 15 which is a ratio.

Character	Mean	SD	Range
1. Staminate spike length	18.2	3.8	10–27
2. Staminate spike width	3.6	0.9	2.2–6.0
3. Staminate peduncle length	5.6	5.6	0.1–25
4. Bract length, staminate spike	4.3	1.3	2–7
5. Upper pistillate spike length	11.7	3.9	5–22
6. Upper pistillate spike width	4.4	1.1	2–7
7. Bract length, upper pistillate spike	7.9	5.9	1.3–25
8. Lowest pistillate spike length	20.2	4.2	12–30
9. Lowest pistillate spike width	4.6	0.9	2–6
10. Lowest pistillate peduncle length	9.6	15.0	0.1–98
11. Bract blade length, lowest pistillate spike	55.3	31.5	4–137
12. Bract sheath length, lowest pistillate spike	15.6	15.6	0.5–87
13. Perigynium length	3.6	0.5	2.5–4.2
14. Perigynium width	1.5	0.2	1.0–1.8
15. Perigynium shape (distance from base to widest point/length)	0.5	0.1	0.3–0.9
16. Perigynium beak length	0.7	0.3	0.2–1.9
17. Pistillate scale length	2.9	0.5	2.0–4.1
18. Pistillate scale awn length	0.5	0.3	0.1–1.3
19. Achene length	2.5	0.3	2.0–3.1
20. Achene width	1.3	0.2	1.0–1.7
21. Length of stipe at base of achene	0.2	0.1	0.1–0.6
22. Widest basal leaf, width	6.0	2.1	2.7–12.0
23. Widest basal leaf, length	240.1	76.4	110–430
24. Length of lowest bladeless sheath	15.9	6.9	4–40

not been collected; it is also possible that glabrous individuals have been identified and filed as other usually glabrous species and were therefore not included in the loaned material examined in this study. Additional field observations are needed to determine the distribution of this glabrous form.

Scatter plots of various combinations of the quantitative characters did not reveal any geographic trends in morphology. Nor were geographic patterns apparent from the principal components analysis (not shown) based on the quantitative characters. Individuals collected from both sides of the Central Valley and from different elevations in the Sierra Nevada were intermixed on the graph of the first three principal components describing the structural variation.

In addition to the color differences noted above, *Carex hirtissima* can be distinguished from the related species *C. gynodynamis* and *C. mendocinensis* based on the sizes of the pistillate and staminate spikes and peduncles, the perigynia, and the basal leaves (cf. Table 6 and Waterway 1990, table 3). Staminate spikes are comparable in size for *C. hirtissima* and *C. gynodynamis* but longer and narrower in *C. mendocinensis*. However, the staminate spikes are usually lon-

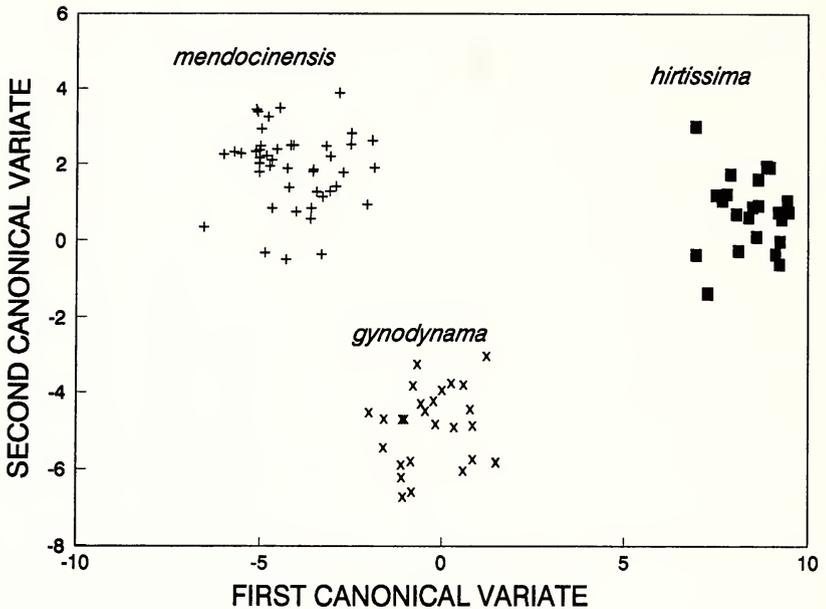


FIG. 4. Canonical discriminant analysis of structural data measured on herbarium specimens. Individuals of *C. gynodynamia* (×), *C. mendocinensis* (+), and *C. hirtissima* (squares) are positioned according to their first and second canonical scores.

ger peduncled in *C. hirtissima* than in *C. gynodynamia*, although the peduncles vary from about 1 mm to nearly 25 mm. Pistillate spikes of *C. hirtissima* vary from 0.5 to 3 cm in length and are shorter and narrower than those of *C. gynodynamia* or *C. mendocinensis*. Basal leaves are generally much longer in *C. hirtissima* than in *C. gynodynamia* or *C. mendocinensis*. Leaf widths vary from 2.7 to 12 mm, with a mean of 6.0 mm in *C. hirtissima*, narrower than the mean leaf width of 8.2 mm found in *C. gynodynamia* and wider than the mean leaf width of 3.7 mm found in *C. mendocinensis*. The mean perigynium length in *C. hirtissima* was 3.6 mm in comparison to a mean length of 4.3 mm for *C. gynodynamia* and 3.8 for *C. mendocinensis*.

The graph of the canonical discriminant scores (Fig. 4) illustrates the clear separation among the three species. Characters most heavily weighted on the first axis, which separates *C. hirtissima* from *C. mendocinensis* were the length of the basal leaves, the length and width of the staminate spikes, the length of the lowest staminate spike, and the length of the achene. On the second axis, which separates *C. hirtissima* from *C. gynodynamia*, the most heavily weighted characters were the length and width of the basal leaves,

the length of the staminate peduncle, the lengths of the pistillate spikes, and the length of the perigynium.

DISCUSSION

The amount of genetic variation within plant populations and within species may be influenced by many factors. Not surprisingly, the mating system has been shown to be one of the most important influences, with inbreeders having significantly lower levels of polymorphism and heterozygosity within populations and greater differentiation among populations than outcrossers (Hamrick and Godt 1989; Hamrick 1991). The allozyme data suggest that inbreeding is prevalent in *C. hirtissima*. Levels of heterozygosity were very low and values for all polymorphic loci showed significant deviations from Hardy-Weinberg equilibrium with positive fixation indices indicating a deficiency of heterozygotes. The rare alleles were found as homozygotes rather than as heterozygotes, suggesting that outcrossing is not very common. The inflorescence morphology with staminate spikes above, but close to, the pistillate ones, and the synchronous flowering phenology suggest that a high rate of selfing is likely. Substructuring within populations may also be an indication that inbreeding is common. The fact that the glabrous individuals in the Forbestown population were found in clusters rather than randomly throughout the population suggests that seeds do not disperse very far and mating occurs among these closely related individuals.

Differentiation among populations is also apparent in *C. hirtissima*. G_{ST} values for the polymorphic loci indicated that about 36% of the allozyme variation was apportioned among populations. Furthermore, chromosome number also appears to differ among populations. Chromosome numbers obtained from three individuals in each of two populations were the same within populations but different between them. Different chromosome numbers in different populations have also been noted in other *Carex* species (Waterway 1990; Hoshino 1992; Hoshino and Waterway 1994), and crosses between different chromosome races within a species do not necessarily show any reduced fertility in *Carex* (Whitkus 1988). As noted above, several structural features also vary both within and among populations. Genetic distance was not correlated with geographic distance as the populations of *C. hirtissima* from the foothills of the Sierra Nevada were quite similar to the one from the Coast Ranges. One rare allele was found only at Round Burn and two others were found only in the Forbestown area. In the cluster analysis, the two populations from the Forbestown area clustered more closely to the population from Round Burn in Lake Co. than to the Georgetown population. This disjunct distribution between

the Coast Ranges and the Sierra Nevada is quite common (Howell 1946) suggesting that transport of propagules from one area to another may occur quite frequently or that the disjunction is relatively recent. The Georgetown population was most distinct from the others, both in habitat and in allozyme frequencies. This population was in a small, isolated wet meadow and was monomorphic for all allozyme loci assayed, suggesting the possibility of a founder effect or a genetic bottleneck.

Levels of genetic variation and the pattern of differentiation among populations in *C. hirtissima* are quite comparable to those found in another rare sedge, *C. misera*, which is endemic to the southern Appalachians (Schell and Waterway 1992). Another related California endemic, *C. gynodynamis*, has even lower levels of polymorphism and heterozygosity within populations than either *C. hirtissima* or *C. misera* (Waterway 1990). In all three cases, inbreeding is probably the primary mating system. While low levels of variation in these endemic species may be a cause for concern about their evolutionary potential and therefore their persistence, the amount of allozyme variation is comparable to that of some more widespread inbreeding *Carex* species (reviewed in Schell and Waterway 1992). An important consideration for the conservation of species such as *C. hirtissima* is the genetic differentiation among populations and the resulting need for conservation of many populations to conserve the genetic diversity. In this study, most of the populations sampled were found in openings in the forest, often associated with logging activities. Disturbance events such as this may be important in creating habitat suitable for the germination and/or growth of *C. hirtissima*. Since *C. hirtissima* has been collected from only 15 localities, its conservation status should be considered. Additional field sampling is required to determine if this small number of sites reflects its actual abundance and geographic distribution. Further search should also be made for the glabrous form, thus far found only in the Forbestown area.

The allozyme data gathered in this study also support the classification of *C. hirtissima* in the same section with *C. gynodynamis* and *C. mendocinensis*. The cluster analysis (Fig. 3) and the similarities in structural features (Table 6, Fig. 4) suggest a close relationship to *C. gynodynamis*. The chromosome numbers of *C. hirtissima* at $n = 35$ or 36 are higher than any other species classified by Mackenzie into section *Sylvaticae* (Waterway 1988) and closer to *C. mendocinensis* ($n = 28, 29,$ or 30) than to *C. gynodynamis* ($n = 25$ or 26). However, aneuploid sequences within sections and within species of *Carex* are common, in part due to the holocentric chromosomes (Wahl 1940; Hoshino and Waterway 1994).

ACKNOWLEDGMENTS

I am grateful to M. J. Lechowicz, Y. Prénoveau, and G. Paul-Hus for field assistance, to N. F. Weeden for advice on the allozyme study, and to the curators of the listed herbaria for their cooperation. Financial support from an NSF Doctoral Dissertation Improvement grant BSR 85-14434, Sigma Xi and the H. E. Moore Endowment Fund is gratefully acknowledged.

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NOTEWORTHY COLLECTIONS

BAJA CALIFORNIA SUR

ACALYPHA OSTRYIFOLIA Ridd. (Euphorbiaceae).—Baja California Sur, 15 km al E de La Paz, Presa "La Buena Mujer," 24°13'N, 110°15'W, 370 m, matorral sarcocaula, ladera, 13 Oct 1987, Domínguez 552 (RSA).

Previous knowledge. Eastern United States to Arizona through much of mainland México to Central America.

Significance. First record from the Baja California Peninsula. This species can be readily separated from the other Baja Californian *Acalypha* by the combination of an annual habit and deeply divided pistillate bracts.

—VICTOR W. STEINMANN, Rancho Santa Ana Botanic Garden, 1500 N College Ave, Claremont, CA 91711.

NATURAL HYBRIDIZATION BETWEEN SPECIES OF
AMBROSIA AND *HYMENOCLEA SALSOLA* (COMPOSITAE)

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ABSTRACT

Hybrids between two of the most common shrubs of the Mojave and Sonoran deserts, *Ambrosia dumosa* and *Hymenoclea salsola*, are morphologically distinctive and geographically widespread. At the molecular level, individuals of *A. dumosa* × *H. salsola* can be diagnosed by additivity for distinctive ribosomal DNA markers of the parent species. Individuals of *A. dumosa* × *H. salsola* from the vicinity of Twentynine Palms, California, showed normal meiosis, with 18 pairs of chromosomes at diakinesis and metaphase I, but highly depressed pollen stainability (less than 5%). These results mirror evidence from natural hybrid individuals of *A. ambrosioides* × *H. salsola* from southern Arizona. Crossability and chromosomal similarity between shrubby species of *Ambrosia* and *H. salsola* conforms with phylogenetic evidence from recent morphological and molecular studies that *Hymenoclea* and most species of *Franseria* (now included in *Ambrosia*) are more closely related than previously appreciated. Low pollen stainabilities in the hybrids indicate considerable sterility barriers between the parental taxa, at least via pollen. Nevertheless, putative backcrosses or later-generation hybrids between *A. dumosa* and *H. salsola* in the Twentynine Palms area are known; gene flow between these often-sympatric desert dominants may occur.

Ambrosia dumosa (A. Gray) W. W. Payne and *Hymenoclea salsola* A. Gray are widespread, ecologically important plant species

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in the Mojave and Sonoran deserts. *Ambrosia dumosa*, a small shrub commonly known as burrobrush or burroweed, shares dominance with *Larrea tridentata*, the creosote bush, across ca. 70% of the Mojave Desert (Shreve 1942) and much of the Sonoran Desert (Burk 1977) on well-drained soils at low elevations (up to 1500 m in the Mojave Desert; Vasek and Barbour 1977). *Hymenoclea salsola*, the cheesebush, is a large, dominant shrub in washes up to ca. 1800 m in the Mojave and Sonoran deserts. Across both deserts, *A. dumosa* and *H. salsola* occur in close proximity along washes and in other areas of disturbance.

Ambrosia dumosa and *Hymenoclea salsola* are members of the ragweed subtribe Ambrosiinae (Heliantheae, Compositae), which is diagnosed in part by characteristics that are unusual in the sunflower family: only unisexual flowers, free anthers, and smooth, wind-transported pollen (see Karis and Ryding 1994). *Ambrosia* (including *Franseria*) and *Hymenoclea* are further distinguished from other members of Compositae by a suite of features associated with the unisexual heads. In both genera the staminate heads possess a cup-like involucre of united, uniseriate phyllaries; the pistillate heads are bur-like, with the multiseriate phyllaries coalescent around one or more pistillate florets. Close relationship between *Ambrosia* and *Hymenoclea* was proposed by Peterson and Payne (1973), but both species of *Hymenoclea* have always been treated as generically distinct from other Ambrosiinae.

Ambrosia and *Hymenoclea* differ most noticeably by details of the involucre of pistillate heads. In *Ambrosia* the free tips of pistillate phyllaries are modified into narrow prickles or spines that promote animal dispersal of fruits. In contrast, the phyllary tips of pistillate heads of *Hymenoclea* are membranous, wing-like (non-spiny) structures that presumably promote wind or water dispersal of fruits. *Ambrosia dumosa*, like other species of *Ambrosia* once included in *Franseria*, bears pistillate heads with a distinctly multiseriate involucre of large, spine-tipped phyllaries (Fig. 1). Vegetatively, *A. dumosa* and *H. salsola* are easily distinguished by leaf shape, lobing, and size (Fig. 1). Leaves of *A. dumosa* are ovate to lanceolate, once to thrice pinnatifid or pinnately-lobed, and up to ca. 5 cm long; leaves of *H. salsola* are filiform, generally entire, and ca. 2 to 7 cm long. Leaves and young stems of *A. dumosa* are densely ashy-strigose, giving the plants a greyish blue-green appearance. In contrast, leaves and young stems of *H. salsola* are nearly glabrous, yellow-green, and shiny-glandular.

Herein, we provide evidence of natural hybridization between *A. dumosa* and *H. salsola* in the Mojave Desert, in California, and between *A. ambrosioides* (Cav.) W. W. Payne and *H. salsola* in the Sonoran Desert, in Arizona. The significance of hybridization between shrubby species of *Ambrosia* and *H. salsola* is discussed in

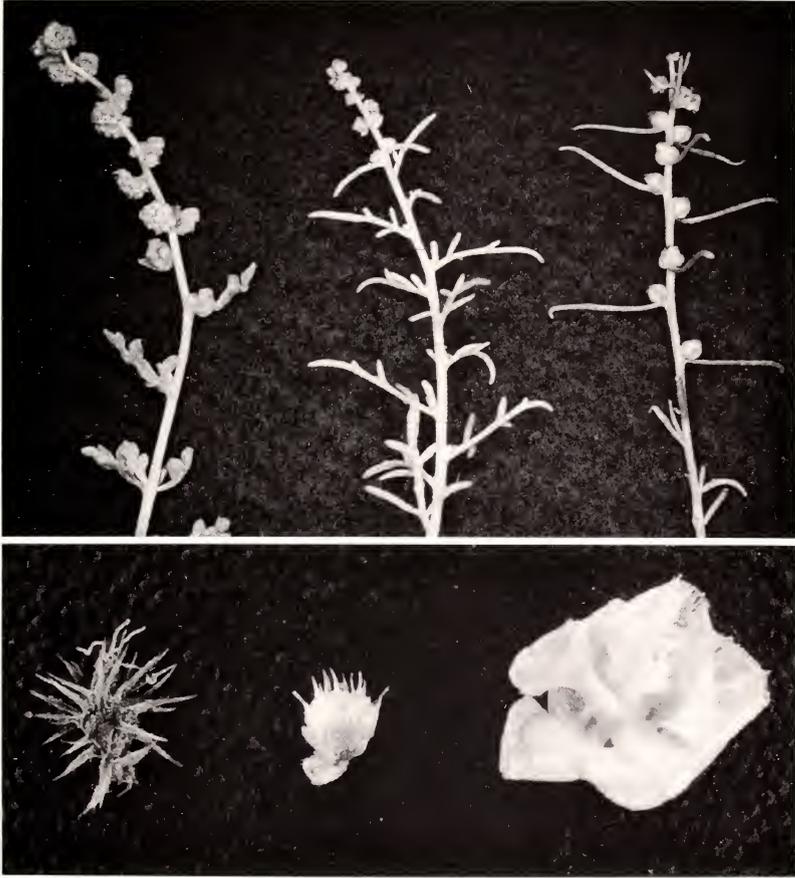


FIG. 1. Flowering branches (top) and pistillate heads (bottom) of *Ambrosia dumosa* (left), *Hymenoclea salsola* (right), and *A. dumosa* × *H. salsola* (center) from near the Kelso Mountains, California.

light of recent investigations of phylogenetic relationships in Ambrosiinae and the possibility of introgression between members of the two genera. We know of no previous documentation in the literature of natural or artificial intergeneric hybridization between members of *Ambrosia* and *Hymenoclea*, apart from unverified reports (e.g., Cronquist, 1994, p. 62).

MATERIALS AND METHODS

Putative hybrids between *Ambrosia dumosa* and *Hymenoclea salsola* were collected near Twentynine Palms, California, in a broad, braided wash (0.16 km north of junction of Sahara Avenue and

TABLE 1. SPECIMENS REFERABLE TO NATURAL HYBRIDS BETWEEN SPECIES OF *AMBROSIA* AND *HYMENOCLEA SALSOLA*.

Ambrosia dumosa × *Hymenoclea salsola*. CALIFORNIA. SAN BERNARDINO COUNTY. Twentynine Palms vicinity: *Baldwin, Kyhos, Martens & Vasek JT780-1, JT780-3, JT780-5, JT780-6, JT780-7* (JEPS). Music Valley, southeast of Twentynine Palms: *Vasek s.n.* (RIV); *Baldwin, Kyhos, Martens, & Vasek JT779-1, JT779-2, JT779-3* (JEPS). Near northwest road entrance to Joshua Tree National Monument, southeast of town of Joshua Tree: *Baldwin, Kyhos, & Martens JT780-11a, JT780-11b* (JEPS). Old Dad Mountain/Kelso Mountains region: *Baldwin, Martens, & M. LaCass 262* (UCSB); *Baldwin OD792-1, OD792-2* (JEPS). Castle Mountains: *D. Charlton 2153 with A. Romsport* (RIV). RIVERSIDE COUNTY. Coachella Valley, east of Fan Hill: *A. Sanders 16,744 with K. Rose* (RIV). NEVADA. NYE COUNTY. Nevada Test Site, Mercury Valley drainage: *R. Hunter s.n. & P. Medica* (ARIZ). MEXICO. BAJA CALIFORNIA. 101.6 km north of San Felipe on Highway 5: *F. Seaman & R. Hartman FS-82(3)* (UC).

Ambrosia ambrosioides × *Hymenoclea salsola*. ARIZONA. PIMA COUNTY. foothills of the Santa Catalina Mountains, Sabino Canyon vicinity: *Baldwin, S. Bainbridge, & R. VanDevender SC788-3, SC788-4* (JEPS); same plants as *T. VanDevender & R. VanDevender 90-47* (ARIZ, ASU), *91-524* (ARIZ), *91-525* (ARIZ). MARICOPA COUNTY. South Mountains: *M. Butterwick and T. Daniel 8874* (CAS).

Morning Drive; *Baldwin, Kyhos, Martens & Vasek JT780-1, JT780-3, JT780-5, JT780-6, JT780-7* (JEPS)). Five plants were uprooted and greenhouse-propagated for morphological, cytological, pollen, and molecular studies at the University of Arizona, Tucson, and (later) at Duke University. Material of two putative hybrids between *A. ambrosioides* and *H. salsola* was collected at 0.6 km and 1.0 km above the Sabino Canyon Recreation Area Visitor's Center along the road to Sabino Canyon in the foothills of the Santa Catalina Mountains, north of Tucson, Arizona [*Baldwin, S. Bainbridge, & R. VanDevender SC788-3, SC788-4* (JEPS); the same plants as *T. VanDevender & R. VanDevender 90-47* (ARIZ, ASU), *91-524* (ARIZ), *91-525* (ARIZ)]. Other putative hybrids between *A. dumosa* and *H. salsola* and between *A. ambrosioides* and *H. salsola* examined morphologically are listed in Table 1.

Morphological characters that showed marked variation among the putative hybrids and suspected parental species were measured or described from pressed, dried, field specimens. Individuals grown in cultivation under uniform conditions were examined for any variation in phenotypic characteristics.

Buds of staminate heads from the putative hybrids and parental species were fixed in modified Carnoy's solution (6 parts chloroform:3 parts absolute ethanol:1 part glacial acetic acid) for five days at room temperature and stored at -20°C prior to chromosomal analysis. Chromosomes were examined at diakinesis and meiotic metaphase I in squashed microsporocytes stained with acetocarmine mixed with Hoyer's solution. Pollen of putative hybrids and parents

was treated with cotton blue in lactophenol and examined for stainability.

Total DNAs were extracted from two grams of fresh leaf material from one individual each of *A. dumosa* [Baldwin, Kyhos, Martens, & Vasek JT779-4 (JEPS)], *H. salsola* [Baldwin SC788-1 (JEPS)], and the five greenhouse-propagated, putative hybrids between the two species using a modified CTAB method (Doyle and Doyle 1987), with one isopropanol precipitation, two ethanol precipitations, and purification of DNAs on cesium chloride gradients. Single-stranded DNAs of the internal transcribed spacer (ITS) region of 18-26S nuclear ribosomal DNA in *A. dumosa* and *H. salsola* were amplified by asymmetric polymerase chain reactions (PCR) using a 20:1 ratio of primers "ITS4" and "ITS5", following the procedures of Baldwin (1992). DNA sequences of ITS 1 of both species were obtained by Sanger sequencing of the purified single-stranded PCR products, using the "ITS5" primer as the sequencing primer (see Baldwin 1992). Restriction maps of the two DNA sequences were constructed using DNA Strider (Marck and CEA 1989) and examined for diagnostic differences. Double-stranded DNAs of the ITS region of *A. dumosa*, *H. salsola*, and the five putative hybrids were amplified using symmetric PCRs using an equimolar ratio of primers "ITS4" and "ITS5" (see Baldwin 1992). Purified PCR products were digested to completion with *Bsm*I and *Spe*I, using the recommended reaction conditions (New England Biolabs). Digested PCR products were electrophoresed on 4% agarose gels (3% NuSieve, 1% LE; FMC) with a 123 base-pair (bp) ladder (Gibco BRL) of molecular weight markers, stained with ethidium bromide, and examined on an ultraviolet light transilluminator.

RESULTS

Putative hybrids between species of *Ambrosia* and *Hymenoclea salsola* show intermediacy or combinations of character-states of the suspected parental species in characters associated with foliage coloration, leaf shape, and numbers and shapes of phyllaries in pistillate heads. Morphological characteristics of putative hybrids between *A. dumosa* and *H. salsola* were retained under greenhouse conditions, as was strong morphological uniformity among the five individuals. Foliage of suspected hybrids between *A. dumosa* and *H. salsola* is distinctly greyish olive-green, rather than yellow-green or greyish blue-green, which allows the plants to be identified at a distance. Leaves of putative hybrids of the combination *A. dumosa* × *H. salsola* are ovate in outline, as in *A. dumosa*, with filiform or narrowly linear leaf segments, like *H. salsola* (Fig. 1). Phyllaries of pistillate heads combine characteristics of both suspected parental species (Fig. 1): scarious margins (like *H. salsola*), length ca. twice

the width (intermediate), and presence of a rigid midrib and apical spine (like *A. dumosa*). In all of the above characteristics, the putative hybrids between *A. dumosa* and *H. salsola* conform to those in the description, illustration, and isotype [*F. Seaman & R. Hartman FS-82 (UC!)*] of *H. platyspina* Seaman from northern Baja California (Seaman 1975). Putative hybrids between *A. ambrosioides* and *H. salsola* show parallel patterns of similarity with the suspected parental species, with intermediacy in foliage characteristics and numbers and dimensions of phyllaries in pistillate heads (Figs. 2, 3). As in the suspected parent *A. ambrosioides*, the putative hybrids have leaves that are narrowly deltate in outline and phyllaries of pistillate heads with strong midribs, apical spines, and (sparse) glandular pubescence. As in *H. salsola*, the putative hybrids have leaves with narrow segments and phyllaries of pistillate heads with scarious margins.

Analysis of chromosomes in putative hybrids of both combinations revealed no evidence of reduced pairing or genomic structural heterozygosity. Eighteen pairs of chromosomes were seen in all of 111 diagnostic microsporocytes (38 in one plant, 73 in the other) examined in two putative hybrids of the combination *Ambrosia dumosa* × *Hymenoclea salsola* (Twentynine Palms vicinity) and in all of 20 diagnostic microsporocytes examined from one putative hybrid of the combination *A. ambrosioides* × *H. salsola* (Sabino Canyon vicinity). Chromosomal analysis of *A. dumosa* from near Twentynine Palms [*Baldwin, Kyhos, Martens, & Vasek JT780-9 (JEPS)*] revealed that the plants in proximity to the putative hybrids were diploids, with $n = 18$, rather than tetraploids or hexaploids, which are also known to occur widely in the Mojave Desert (Raven et al. 1968).

Pollen stainability, a direct indicator of pollen viability, in each of two plants of the putative hybrid combination *Ambrosia dumosa* × *Hymenoclea salsola* from near Twentynine Palms and in both putative hybrids of *A. ambrosioides* × *H. salsola* from near Sabino Canyon was less than 5%. Pollen samples from herbarium specimens of putative hybrids of the combination *A. dumosa* × *H. salsola* from nw of the Kelso Mountains, south of Baker, California [*Baldwin, Martens, & M. LaCass 262 (JEPS)*], and of the putative hybrid combination *A. ambrosioides* × *H. salsola* from the South Mountains near Phoenix, Arizona [*M. Butterwick and T. Daniel 8874 (CAS)*], were also less than 5% stainable. In contrast, pollen stainabilities of individuals of all suspected parental species from the vicinity of putative hybrids were greater than 65%.

Restriction digests of PCR products of the ITS region from individuals of *Ambrosia dumosa*, *Hymenoclea salsola*, and five putative hybrids from near Twentynine Palms yielded diagnostic markers for *A. dumosa* and *H. salsola*, all of which were present in the



FIG. 2. *Hymenoclea salsola* (top), *Ambrosia ambrosioides* (bottom), and *A. ambrosioides* × *H. salsola* (center) from near Sabino Canyon, Santa Catalina Mountains, Arizona.



FIG. 3. Pistillate heads of *Ambrosia ambrosioides* (left), *Hymenoclea salsola* (right), and *A. ambrosioides* \times *H. salsola* (center).

five putative *A. dumosa* \times *H. salsola* plants. With *Spe* I, the ITS products of *A. dumosa* were digested into two fragments of ca. 150 bp and ca. 600 bp; the ITS products of *H. salsola* were undigested and ca. 750 bp (Fig. 4). ITS products of the five putative hybrids digested with *Spe* I showed additivity for the two bands observed in the digest of ITS products of *A. dumosa* and the intact product of *H. salsola* (Fig. 4). With *BsmA* I, the digested ITS products of *A. dumosa* included two fragments of ca. 200 bp and ca. 350 bp; the digests of ITS products of *H. salsola* lacked similar fragments and included, instead, a fragment of ca. 550 bp, absent from *A. dumosa*. Digests of the ITS products of the five putative hybrids from Twentynine Palms with *BsmA* I showed additivity of the ca. 200 bp and ca. 350 bp fragments seen in the *A. dumosa* lane and the ca. 550 bp fragment observed in the *H. salsola* lane.

DISCUSSION

Comparisons of morphology, pollen stainability, and ITS sequences among putative hybrid individuals of the combination *Ambrosia dumosa* \times *Hymenoclea salsola* and the suspected parent species confirm natural hybridization between the two species in the vicinity of Twentynine Palms. Uniformity of morphological characteristics among the five hybrid individuals grown under similar greenhouse conditions strongly suggests that the plants are of the F_1 generation. Similarities in morphology and pollen stainability between the hybrids near Twentynine Palms and collections from the Kelso Mountains vicinity identify the Kelso Mountains plants as additional examples of natural hybrids between *A. dumosa* and *H. salsola*. Other plants referable to the combination *A. dumosa* \times *H. salsola* include *H. platyspina* Seaman from the Sonoran Desert of Baja California (Seaman 1975), and collections from California and

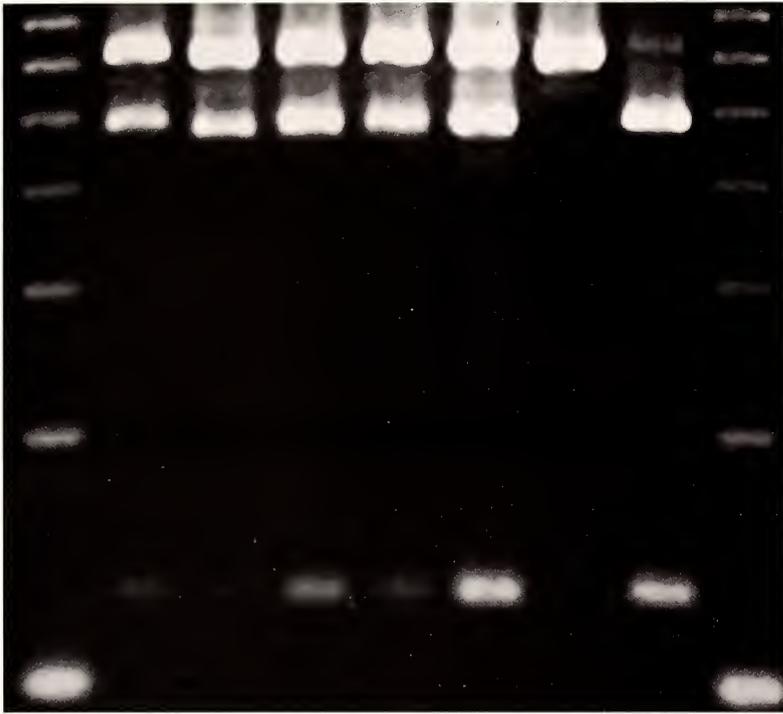


FIG. 4. Electrophoresed *Spe* I restriction fragments of the internal transcribed spacer region of nuclear ribosomal DNA from *Ambrosia dumosa*, *Hymenoclea salsola*, and five interspecific hybrids collected near Twentynine Palms, California. From left to right, a 123 bp ladder of molecular weight markers (lanes 1, 9), *A. dumosa* × *H. salsola* plants (lanes 2 thru 6), *H. salsola* (lane 7), and *A. dumosa* (lane 8). Note additivity for the markers of both parental species in the hybrids.

Nevada listed in Table 1. The parentage of *A. sandersonii* S. L. Welsh [*H. sandersonii* (S. L. Welsh) N. H. Holmgren], from Utah, is still uncertain and may have involved *A. eriocentra* (A. Gray) W. W. Payne and *H. salsola*, as contemplated by Welsh (1993). Vegetative and reproductive morphology of *A. sandersonii* and low pollen stainability (2.6%) in the isotype at CAS (*S. Sanderson 93-02*) indicate hybridity between a shrubby franseria and *H. salsola*.

Morphological characteristics and low pollen stainabilities of the two putative hybrids between *Ambrosia ambrosioides* and *Hymenoclea salsola* from Sabino Canyon verify natural hybridization between the two species. Similar morphology and pollen stainability of a plant collected from the South Mountains near Phoenix, Arizona (Table 1), indicate that that individual is referable to the same hybrid combination.

Lack of previous documentation of hybridization between members of *Ambrosia* and *Hymenoclea salsola* is surprising; the taxa co-occur widely in areas with varying levels of natural and human-caused disturbance. Natural hybridization between *A. dumosa* and *H. salsola*, in particular, appears to be a widespread phenomenon. Herbarium specimens (Table 1), personal communications (e.g., with B. Turner, D. Keil, B. Prigge, V. Yoder), and unverified reports (Cronquist 1994, p. 62) demonstrate that other botanists have suspected hybridization between *A. dumosa* and *H. salsola*. In recognition of the recurrent formation of natural hybrids between the two species across a broad geographic range, we here adopt the name *H. ×platyspina* Seaman based on *H. platyspina* Seaman pro sp. (Seaman, F. 1995. Madroño 23:111) for plants of the combination *A. dumosa* × *H. salsola*.

Systematic implications of hybrids. Close genetic similarity of *Ambrosia dumosa* and *A. ambrosioides* to *Hymenoclea salsola* is evident from normal pairing of chromosomes in interspecific hybrids. Low pollen fertilities of the intergeneric hybrids indicate that genetic differences between the parental species are nevertheless sufficient to impact fertility. Similarly, low pollen fertilities have been observed in other hybrid combinations with normal chromosomal pairing at meiosis, as in *Wedelia biflora* (L.) DC. × species of *Lipochaeta* sect. *Aphanopappus* (Rabakonandrianina and Carr 1981), and have been attributed to cryptic structural differences between the parental genomes (Stebbins 1950, 1971) or finer-scale genetic problems. Irrespective of levels of hybrid fertility, natural hybridization and normal pairing of chromosomes between members of different plant genera have rarely been reported, as might be expected if placement of species in different genera implies more ancient divergence from a common ancestor than the time of divergence of congeneric taxa (an assumption that is certainly not universally true). Hybridization between species of *Ambrosia* and *Hymenoclea* may reflect inadequacy of the long-standing generic classification of Ambrosiinae to express evolutionary relationships within the subtribe.

Results from recent phylogenetic investigations of Ambrosiinae based on morphological and chloroplast DNA (cpDNA) restriction site variation demonstrate that relationships between species of *Ambrosia* and *Hymenoclea* have been misunderstood. Wagner parsimony analysis of cpDNA restriction site data from members of *Ambrosia* sensu lato (including *Franseria*) and *Hymenoclea* by Miao et al. (1995) resolved a strongly supported (95% bootstrap) lineage comprised of *Hymenoclea salsola* and five species of *franseria* (including all shrubby taxa sampled), to the exclusion of *H. monogyra*, two species of *franseria*, and all species sampled of *Ambrosia* sensu

stricto. *Hymenoclea monogyra* was resolved as sister to the *H. salsola*/*Franseria* lineage, exclusive of *Ambrosia* sensu stricto and two species of franseria. Based on their cpDNA results, Miao et al. (1995) proposed that *Hymenoclea* be submerged taxonomically within *Ambrosia*. Results from a phylogenetic analysis of Ambrosiinae based on morphological data (Karis 1995) corroborate non-monophyly of *Ambrosia* sensu Payne (1964), with *Hymenoclea* resolved as sister to a lineage of two shrubby species of franseria, *A. eriocentra* and *A. ilicifolia*, to the exclusion of herbaceous species of *Ambrosia* sensu stricto (and *Xanthium*). The surprisingly close relationship of shrubby franseria species and *H. salsola* revealed by both phylogenetic investigations accords well with normal pairing of chromosomes in the natural hybrids reported here.

Karis's (1995) phylogenetic study of Ambrosiinae is also pertinent to the issue of hybridization between species of *Ambrosia* and *Hymenoclea salsola* because of inclusion of *H. ×platyspina*, i.e., the hybrid between *A. dumosa* and *H. salsola*, as a terminal taxon in his analysis. In the cladogram presented by Karis, *H. ×platyspina* is sister to a lineage consisting of *H. monogyra* and *H. salsola*. In turn, the three species of *Hymenoclea* are sister to shrubby species of franseria in Karis's tree. Absence of any derived morphological characteristics on the *H. ×platyspina* phylogeny branch and the placement of *H. ×platyspina* as sister to the rest of *Hymenoclea* in the cladogram support Karis's conclusion that the "species" is "... provided with characters that are 'transitional' between the two genera" (*Ambrosia* and *Hymenoclea*). The data presented here indicate that the "transitional" morphology of *H. ×platyspina* is not attributable to retention of characteristics of the most recent common ancestor of *Hymenoclea* species, but to origin of the plants via hybridization between *A. dumosa* and *H. salsola*.

Ecological implications of hybridization. The possibility of gene flow between species of *Ambrosia* and *Hymenoclea* is intriguing from an ecological perspective, especially with respect to the widespread species *A. dumosa* and *H. salsola*. Co-occurrence of *A. dumosa* and *H. salsola* in complex mosaics of natural disturbance over much of the Mojave and Sonoran deserts may offer diverse ecological opportunities for hybrids and backcrosses involving the two species. The tremendous success of *A. dumosa* and *H. salsola* across broad areas and environmental gradients may prove to be attributable in part to occasional gene flow between the species.

Low pollen stainability in the *Ambrosia*/*Hymenoclea* hybrids indicates limited potential for backcrossing or later-generation hybridization between species of the two genera. Ovulate fertility has not been assessed in the hybrids and could be considerably higher than pollen fertility, as seen in many hybrid combinations in plants (cf.

Rieseberg, 1995). If microhabitats wherein hybrids are better fit than parents exist in proximity to the parental species, then backcrossing and introgression might proceed even in the face of high levels of hybrid sterility in pollen and ovules, especially if the plants involved are long-lived perennials with recurrent opportunities for reproduction, as in the study species.

At the Twentynine Palms site, putative backcross plants were observed with morphological characteristics that appeared overall more like those of *A. dumosa* than those of the *A. dumosa/H. salsola* hybrid individuals. Follow-up studies that examine hybrid fruit set, hybrid seed viability, and characteristics of any viable progeny of the hybrids described in this investigation might prove enlightening about the natural potential for introgression between the species. Detailed research on the genetic constitution of individuals in areas of hybridization, such as the Twentynine Palms site, would be especially valuable to test rigorously the occurrence of gene flow between these desert plants.

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INVASION OF NORTHERN OAK WOODLANDS BY
PSEUDOTSUGA MENZIESII (MIRB.) FRANCO IN THE
SONOMA MOUNTAINS OF CALIFORNIA

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ABSTRACT

Invasion of Northern Oak Woodland by *Pseudotsuga menziesii* [Mirb.] Franco has been observed throughout the outer North Coast Range, including the Sonoma Mountains of southern Sonoma County, California. Studies at Annadel State park, reported here, include the correlation of physical and vegetational factors with *P. menziesii* dominance. Significant negative correlations were found between *P. menziesii* seedling and sapling densities, and (1) the distance to a seed source, (2) the cover of annual grasses, and (3) total living ground cover. A significant positive correlation was found between *P. menziesii* seedling and sapling densities and the percentage of the ground surface covered by leaf litter. A significant positive correlation was also found between *P. menziesii* sapling density and the basal area of trees of any species occurring on the sample plots. Stand age analysis revealed that *Quercus* spp. found on the sample plots were consistently much older than the oldest *P. menziesii* observed. This observation also applied to sites dominated by *P. menziesii*. Surges of *P. menziesii* establishment appear to be related to changes in management of the region, including fire suppression, increased oak canopy density, and the establishment of the state park. These results suggest that events which have changed the character and dynamics of the Northern Oak Woodland within this century have in turn produced conditions favorable to the establishment of *P. menziesii*. This pattern of *P. menziesii* invasion will result in a reduction of biological diversity in this region of Northern California.

Our observations of vegetation patterns in the southern portion of the range of Northern Oak Woodland reveal an increased presence of *Pseudotsuga menziesii* seedlings and saplings beneath the oak canopy. At some locations, *P. menziesii* has grown up through the canopy and appears to be shading out the oaks. This phenomenon is in evidence at Annadel State Park in Sonoma County, California. Park management is concerned with the potential replacement of the Northern Oak Woodland by *P. menziesii* forest, particularly because

such vegetation changes may be the direct result of the disruption of natural processes through past management.

Vegetation changes following the altering of management objectives (e.g., elimination of grazing, fire suppression, termination of wood cutting) have been documented for a number of vegetation types in coastal California (McBride and Heady 1968; McBride 1974; Elliot and Wehausen 1974; McBride and Stone 1976; Hektner and Foin 1977; Barbour et al. 1993). Comparatively little work has been done on changes in oak woodland/mixed evergreen forest in the California coast range. Wells (1962) concluded that chance is the major factor controlling the distribution of oak and other vegetation types in the San Luis Obispo area following fire. Waring and Major (1964) demonstrated a close correlation between certain environmental variables and the distribution of various vegetation types in the redwood region of Humboldt County. Griffin (1977) and Plumb and McDonald (1981) reviewed the general ecology of several oak woodland types in California. Their review did not, however, develop a comprehensive analysis of vegetation dynamics in these types. Sawyer et al. (1977) described the grassland-woodland-forest mosaic of the north coastal region as poorly understood and in need of investigation.

Several recent studies have focused on the oak woodland and hardwood forests in Sonoma County with particular reference to Annadel State Park. Anderson and Pasquinelli (1984) described the northern oak woodland at several sites along a moisture gradient within the county, including two sites in Annadel. They concluded that high oak canopy densities and lack of oak regeneration may result in the future dominance of mixed evergreen forest species at the more mesic end of the gradient. Tunison (1973) investigated the distribution of oak woodland and mixed evergreen forests on Bennett Mountain in the park. Noting the dominance of young *P. menziesii* and *Umbellularia californica* in the understory of many oak-dominated stands, he tentatively concluded that all of these oak types are seral to mixed evergreen forest. Tunison further suggested that this recent invasion of *P. menziesii* and *U. californica* is the result of the development of a closed oak canopy due to previous management. Barnhart (1978) has suggested a similar vegetation change, although he points out that the complex nature of the coast range vegetation makes it difficult to document successional trends. Wainwright and Barbour (1984) demonstrated the diverse nature of the mixed evergreen forest in Annadel, including the invasion of oak woodlands by *P. menziesii*. They did not develop any conclusions relative to successional relationships.

The encroachment of *P. menziesii* into the northern oak woodland has been demonstrated throughout the North Coast Ranges (Reed and Sugihara 1987; Sugihara and Reed 1987; Keter 1987). These

and other investigators (e.g., Wills 1991) have concluded that the principle reason for this encroachment is the drastic reduction in fire frequency since 1900. Frequent fires in presettlement times presumably maintained a more open woodland and eliminated *P. menziesii* seedlings before they became large enough to be fire resistant. Recently Finney and Martin (1992) have documented mean fire intervals in the oak woodlands of Annadel State Park from 6.2 to 23.0 years with over two-thirds of the records showing intervals of less than 10 years. These short fire intervals, dating back at least four centuries before settlement, are attributed primarily to the use of fire by Native Americans.

This paper reports the evidence regarding the variables influencing the establishment of *P. menziesii* within the oak woodlands in Annadel State Park. The objective of this study was two-fold: (1) to determine the correlation between selected site variables, both physical and vegetational, and *P. menziesii* regeneration, and (2) to demonstrate the sequence of *P. menziesii* and oak establishment through stand-age analysis of mixed stands of the principle taxa.

STUDY AREA

Annadel State Park is located immediately east of Santa Rosa, Sonoma County, California, in the Sonoma Mountains. This north-south trending range, primarily composed of Pliocene Sonoma Volcanics above older sediments (Jenkins 1951), is in the eastern portion of the county ca. 30 km from the Pacific coast. Climate patterns are typically Mediterranean, with mild winter temperatures (January mean daily minimum 2–3°C) and hot summer temperatures (July mean daily maximum 28–29°C) which are often moderated by morning fog. Total annual precipitation is ca. 750 mm/year with dry summers and wet winters (January mean 150 mm) (U.S. Weather Bureau 1964).

The vegetation of the park, typical of that found throughout the southern North Coast Range, is a complex mosaic of communities including coastal prairie, chaparral, northern oak woodland, and mixed evergreen forest (Munz and Keck 1950). Mixed evergreen forest occurs on northerly slopes and in moist drainages throughout the park, integrating with northern oak woodland, particularly in the center of the park. Northern oak woodland is predominant in the southwestern two-thirds of the park, although tree densities and composition vary with aspect. *Quercus garryana* occurs in relatively high densities on north-facing slopes, while south-facing slopes support more open savannas of oak hybrids (*Q. xexplingii*) as well as *Q. douglasii*, *Q. kelloggii* and *Q. agrifolia*. Chaparral occupies relatively small areas, usually on southern or western exposures and rock outcroppings. The prairie and grassland communities form

small to fairly extensive meadows throughout the park. It is important to note that these vegetation types form a mosaic; areas occupied by a given type are often small and boundaries between types often abrupt.

Historically, the area in which Annadel is located was extensively utilized by European settlers and their descendants (Futini 1976). Major types of activities included cattle ranching which began in the 1830s and was the dominant activity from 1930 to 1970. Cobblestone quarrying around the turn-of-the-century and extensive cutting of hardwood for cordwood and charcoal in the 1920s also occurred. These activities ceased when the park was established in 1972.

METHODS

1. Factors Influencing *P. menziesii* Regeneration

Thirteen large *P. menziesii* trees (>80 cm DBH) occurring in oak woodlands were selected from a population of over 100 similar trees observable on aerial photographs. Trees selected were at least 300 m away from any other tree chosen and a similar distance from any stand of *P. menziesii*. Each isolated tree was located on the ground and was used as a center around which sampling points were located. Four directional zones based on compass readings (NE = 0 to 90°; SE = 90 to 180°; SW = 180 to 270°; NW = 270 to 360°) were established around each tree. Each of these directional zones was divided into five concentric arcs 30 m wide. An initial sampling point was located in each of the four direction zones by choosing a random azimuth and a random distance (from 0.5 to 30 m) from the large *P. menziesii*. Subsequent sampling points within that directional zone were established at 30 m intervals along the same random azimuth. This procedure, which was repeated for each of the thirteen large *P. menziesii* trees, was adopted to insure that plots would be located at varying distances up to 150 m and in varying directions away from a *P. menziesii* tree of seed producing age. Using this procedure, 20 sampling points were located around each large seed tree selected for a total of 260 sampling points.

At each sampling point the percentage of ground cover was estimated from a 10 m² plot. Ground cover categories estimated were annual grass, perennial grass, broad-leaved herbaceous plants, ferns, leaf litter, base of tree, limbs and logs, rocks, and bare ground. Tree seedlings (plants <1 cm in diameter at ground level) were counted on 10 m² plots and saplings (plants >1 cm in diameter at ground level and <1.4 m tall) were recorded from 100 m² plots centered at the sampling point. Percent intercept of shrubs was determined using the line intercept method along two diagonal lines connecting opposite corners of each 100 m² plot.

The point-centered quarter method (Cottam and Curtis 1956) was used to determine tree density and basal area around each plot center. The distance from each plot center to the nearest *P. menziesii* tree in each of three diameter ranges (10–19.9 cm; 20–39.9 cm; and greater than 40 cm DBH) was also measured. Topographic conditions (aspect, percentage slope) were recorded at each sampling point.

The field data were used to establish correlations between each variable measured and (1) seedling density and (2) sapling density of *P. menziesii*. Pair-wise scatterplots were run between every possible combination of dependent variable (*P. menziesii* seedling and sapling density) and independent variable (percent ground cover in each category, total living ground cover, percent shrub cover, topographic condition, and distance to each diameter category of seed tree) in order to gain a preliminary understanding of the relationships among the variables. Subsequently, correlation analysis was used to determine the degree of association between these variables. Log (base 10), square root, and arcsine transformations were applied to the data in order to improve the linearity of the relationship (Sokal and Rohlf 1981). All correlations were tested at the 0.05, 0.01 and 0.001 significance levels.

Linear correlations were also determined between seedling and sapling densities and (1) the density (number/ha) of each tree species and (2) the basal area (m²/ha) of each species. Log (base 10) transformation was applied to the data in order to improve the linearity of the relationships. The “closest” individual method (Cottam et al. 1953) was used to calculate tree density and basal area. This method uses the distance (D) from the plot center to the nearest tree as a basis for calculating density and basal area. We modified this method by measuring the distance to the nearest tree of each species. A correction factor ($2 \times D$) proposed by Cottam and Curtis (1956) was applied to the distance measurement.

2. Stand-Age Analysis

The ages of trees on sites exhibiting different *P. menziesii* height classes were determined. The region of Annadel State Park currently experiencing various stages of *P. menziesii* encroachment into oak woodlands was surveyed and specific sites were identified which exhibit the range of *P. menziesii* dominance from understory to overstory. Twenty-five plots were established which included five plots in each of five *P. menziesii* height classes:

- “A” plots *P. menziesii* saplings beneath healthy oak canopy
- “B” plots *P. menziesii* extending into, but not above, healthy oak canopy

- “C” plots *P. menziesii* forming a more or less open canopy above healthy oaks
“D” plots *P. menziesii* forming a well-developed canopy above declining oaks
“E” plots *P. menziesii* well above dead or dying oaks

The plots ranged in area from 100 to 1000 m² depending on tree density to assure the sampling of an adequate number of trees. About 30 trees per plot was considered an adequate number for the study. The position of each tree within each of the twenty-five plots was indicated on a coordinate plot map and assigned a number. All stumps, downed and dead trees were also marked on the plot map. The diameter at breast height was measured for all trees over 1.4 m in height. Ground level diameters and heights were recorded for trees less than 1.4 m tall. Tree age was determined from ring counts on increment cores taken at breast height and adjusted for the number of years for seedlings to reach that height based on the growth rates of seedlings and saplings in the plots. Sapling sized trees were aged from cross-sections cut at 3 cm above the ground.

RESULTS AND DISCUSSION

1. Factors Influencing Regeneration

The first series of correlation analyses identified several statistically significant correlations between the independent variables and the density of *P. menziesii* seedlings or saplings. These correlations shown in Table 1 are for simple linear correlations. Scatter diagrams for each relationship often suggest a curvilinear rather than a linear relationship between the independent and dependent variables (Fig. 1A, B). The low correlation values (r and r^2) are due, in part, to the difficulty of fitting a straight-line to a curvilinear distribution. Low values are also frequently encountered in studies involving multiple-factor analysis due to the stochastic nature of natural processes. “Square root”, “arcsine” and “log 10” transformations of the data were applied in an attempt to improve the correlations. Slightly higher values were obtained and additional relationships were shown to be significant or significant at higher levels with these transformations. However, both r and r^2 values remained relatively small ($r < 0.35$; $r^2 < 0.13$). These small values are nonetheless useful indicators of vegetation and site factors which control the invasion of oak woodlands by *P. menziesii* at Annadel State Park.

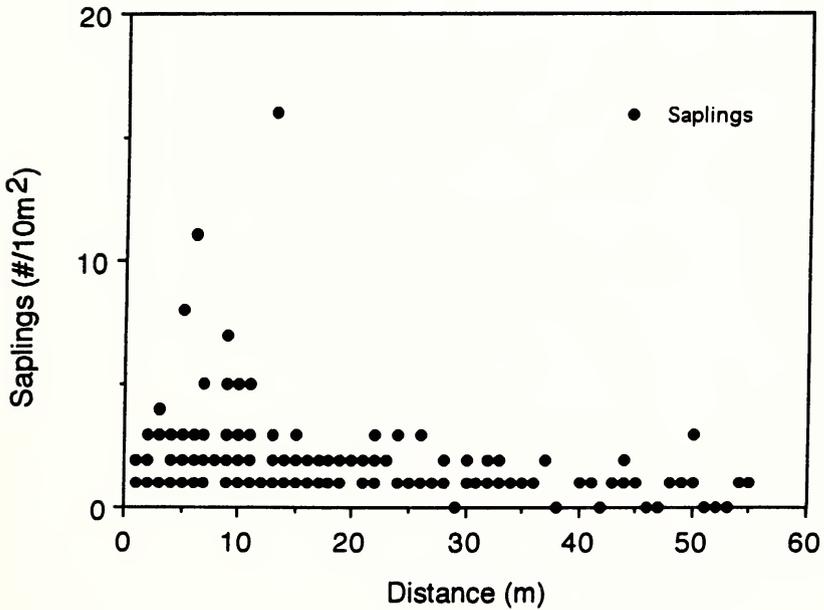
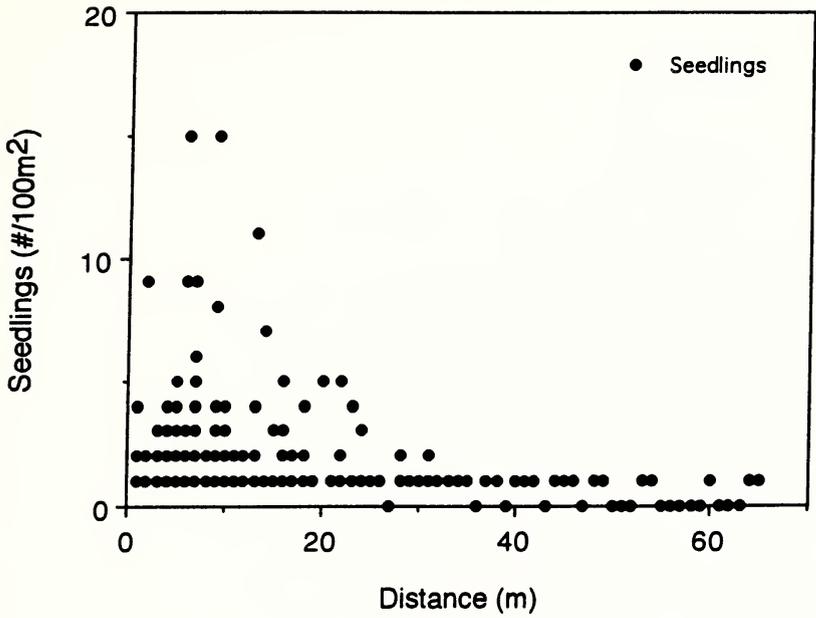
The negative correlation found between the distance to large (>40 cm DBH) *P. menziesii* trees and the density of *P. menziesii* seedlings and saplings suggests the importance of seed source in the invasion of oak woodlands by *P. menziesii*. The scatter diagrams (Fig. 1A, B) depict a curvilinear relationship which is typical of dispersal

TABLE 1. CORRELATION ANALYSIS OF INDEPENDENT AND DEPENDENT VARIABLES (*PSEUDOTSUGA MENZIESII* SEEDLING AND SAPLING DENSITY) RELATING TO *PSEUDOTSUGA MENZIESII* ESTABLISHMENT IN OAK WOODLANDS AT ANNADEL STATE PARK. (P values with the same superscript are significant at the following levels: a \leq 0.05, b \leq 0.01, c \leq 0.001)

Independent variables	Dependent variables					
	Seedlings			Saplings		
	r	r ²	P value	r	r ²	P value
Seedlings and saplings of other species:						
Total no. seedlings	0.157	0.025	0.011 ^a	-0.092	0.008	0.140
Total no. saplings	0.009	0.001	0.881	-0.037	0.001	0.557
Total no. seedlings and saplings	0.107	0.011	0.086	-0.088	0.008	0.154
Distance to nearest <i>Pseudotsuga menziesii</i> of three sizes:						
10-19 cm, DBH	-0.079	0.006	0.267	-0.055	0.003	0.489
20-39 cm, DBH	-0.126	0.016	0.058	-0.046	0.002	0.489
\geq 40 cm, DBH	-0.230	0.053	0.000 ^c	-0.183	0.034	0.005 ^c
Ground cover (%):						
Annual grass	-0.148	0.022	0.017 ^a	-0.156	0.024	0.012 ^a
Perennial grass	-0.105	0.011	0.090	-0.116	0.014	0.062
Forbs	-0.014	0.001	0.824	-0.011	0.001	0.864
Ferns	-0.048	0.002	0.437	-0.053	0.003	0.393
Bare soil	-0.010	0.001	0.872	-0.048	0.002	0.437
Base of tree	0.043	0.002	0.494	0.170	0.029	0.006 ^b
Leaf litter	0.201	0.040	0.001 ^b	0.205	0.042	0.001 ^b
Rock	0.019	0.001	0.763	0.040	0.002	0.521
Log	-0.056	0.003	0.369	-0.072	0.005	0.245
All living	-0.216	0.046	0.000 ^c	-0.224	0.050	0.000 ^c
Shrub cover	-0.045	0.002	0.470	-0.037	0.011	0.553
Aspect	0.080	0.006	0.198	0.012	0.000	0.852
Slope	-0.108	0.012	0.081	-0.027	0.001	0.668

patterns for wind-disseminated propagules (Wolfenbarger 1959; Roe 1967; Harper 1977). The failure to demonstrate statistically significant correlations between seedling or sapling density and smaller *P. menziesii* trees (<40 cm DBH) may be due to the lower seed producing capacities of smaller and younger trees. Open grown *P. menziesii* trees begin producing appreciable amounts of seeds between their 20th and 30th years, but maximum seed production occurs between the ages of 200 and 300 years (Isaac 1943). As will be shown later, most of the *P. menziesii* on our sample sites are less than 50 years old.

FIG. 1. Relationship between the number of Douglas-fir seedlings (A) and saplings (B) on 10 m² quadrats and the distance to the nearest Douglas-fir tree >40 cm DBH.



The correlation between the density of *P. menziesii* seedlings and the total number of seedlings of other tree species (Table 1) suggests that conditions favorable for the establishment of *P. menziesii* seedlings are also favorable for the establishment of other tree species. This contrasts with the findings of Isaac (1938, 1940) that high densities of *P. menziesii* seedlings are not associated with high densities of other species in the Pacific Northwest. However, *P. menziesii* establishment in the oak woodlands of Mediterranean climatic regions may be restricted to sites where other species can also regenerate. Favorable sites for all species may require understory and overstory conditions which reduce soil moisture depletion and evaporative stress during the late spring and early summer.

The various statistically significant correlations between the percentage of different ground cover types and the densities of *P. menziesii* seedlings and saplings are interpreted as indicators of the importance of soil moisture and its rate of depletion for the establishment of *P. menziesii* within the oak woodland. The negative correlations between (1) annual grass and (2) all living ground cover and *P. menziesii* seedling and sapling densities are interpreted as indicators of the importance of competition for soil moisture in the establishment of *P. menziesii*.

The positive correlation between leaf litter and the densities of *P. menziesii* seedlings and saplings can also be interpreted in terms of moisture availability and reduced evaporative stress since the larger the area covered by leaf litter on the sample plots, the smaller the cover by living plants. This would suggest reduced competition for soil moisture. Higher percent cover by leaf litter is also associated with greater crown cover. Increasing tree crown cover, which we believe was stimulated by the coppicing of the oak woodland in the period from 1900 to 1920, suggests a reduction in evaporative stress over the seedbed. A sensitivity to drought and higher levels of evaporative stress by *P. menziesii* seedlings has been suggested by several authors (Munger 1927; Isaac 1938, 1949; Isaac and Dimock 1958; Fowells 1965).

Finally, a positive correlation exists between the base of tree parameter (i.e., at least a portion of a tree base of any species within the sampling area) and *P. menziesii* sapling density, but no significant correlation is found relative to seedling density (Table 1). This suggests that seedlings can become established under proper moisture and understory conditions, but that survival into the sapling stage requires further environmental amelioration afforded by the presence of trees which provide shade. Foresters have used the term "nurse trees" for those trees which create suitable microclimates for the growth of young trees (McBride 1978).

The second series of correlations was intended to measure the relationship between each tree species in the overstory and the pres-

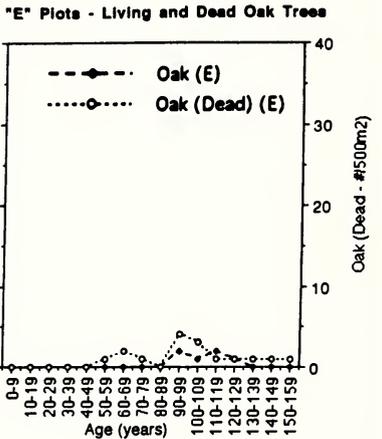
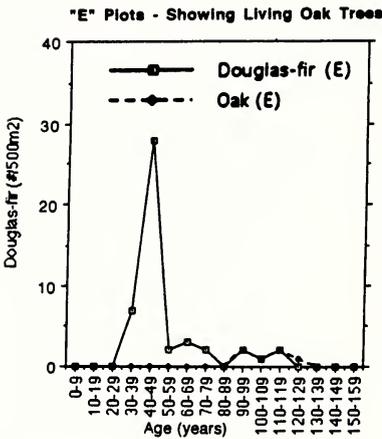
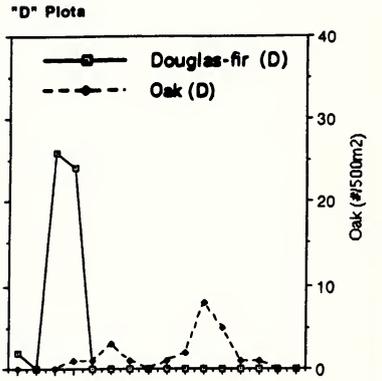
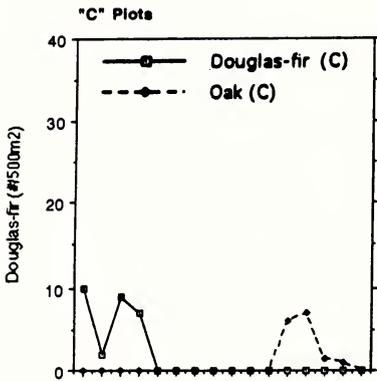
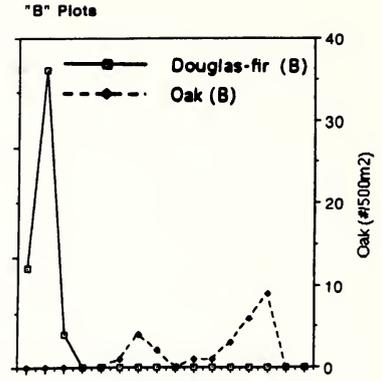
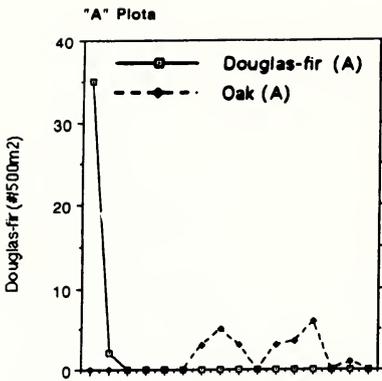
ence of *P. menziesii* seedlings and saplings. No significant correlation was established between either the density or the basal area of any individual tree species and *P. menziesii* regeneration. Correlation coefficients were extremely low for non-transformed data. A slight improvement in the correlations was achieved by transformation of the data to log (base 10). This suggests, as was the case with the previous series of correlations, that the relationships between the dependent and independent variables are not linear relationships.

The highest r^2 value obtained for combined seedlings and saplings could account for only about 1 percent of the variation in the *P. menziesii* regeneration. It is concluded, therefore, that no single species serves as a more important "nurse tree" for *P. menziesii* regeneration than any other. Correlations were run between the basal area and density of deciduous and evergreen hardwood species and the total density of seedlings and saplings of *P. menziesii*. The r^2 values for the correlation for evergreen trees where the independent variables were basal area and tree density were 0.00003 and 0.00005, respectively. Similar values for deciduous trees were 0.0006 (Basal Area) and 0.0042 (Density).

2. Stand-Age Analysis

The numbers of *P. menziesii* and oak trees in each 10 year age class (0–9, 10–19, 20–29, etc.) for the five plot types are shown in Figure 2A–E. Oak individuals are consistently older than *P. menziesii* individuals in all plots. Only in the "E" plots (largest *P. menziesii* and dead or dying oaks) do *P. menziesii* individuals exceed fifty years, and there are very few of these older trees. In contrast, few oaks are younger than sixty years of age, with many over one hundred years old.

The composite age distribution for *P. menziesii* from all plots and the annual precipitation for Santa Rosa from 1890 to 1985 are shown in Figure 3. This figure illustrates that *P. menziesii* regeneration has been more or less continuous since 1910. No significant correlation was found between annual precipitation and regeneration for the period from 1910 to 1985. However, significant positive correlations were found when shorter, more recent time periods were examined. For the period 1973 (the year after cattle were removed from the park) to 1985 significant positive correlations were found between regeneration and precipitation from April to June ($r = 0.26$), March to September ($r = 0.29$), and the hydrologic year ($r = 0.27$) in which establishment took place. Correlations between these precipitation parameters and the number of trees established for the periods 1940 to 1985 and 1946 to 1985 were not significant. Many factors could have contributed to tree mortality over those longer periods. One



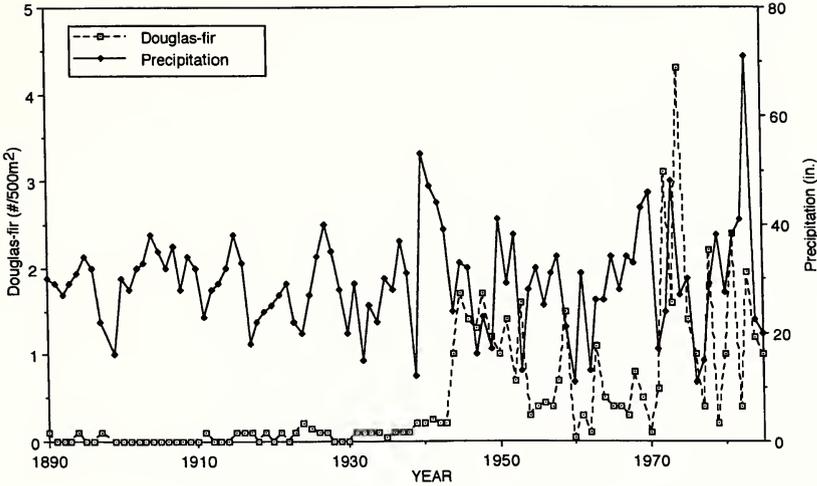


FIG. 3. Annual precipitation and establishment of Douglas-fir in oak woodlands at Annadel State Park.

would not expect to be able to demonstrate correlations between the precipitation parameters and tree establishment over such long periods. The correlations found for the more recent period support the conclusion of the study of factors (i.e., annual grass, all living plant cover, and litter cover) influencing *P. menziesii* regeneration. That is, moisture availability is an important factor in *P. menziesii* seedling establishment.

The *P. menziesii* age distribution data exhibit surges of establishment which may be related to factors other than precipitation. The abrupt increases in *P. menziesii* establishment in the early 1940s and the early 1970s are of particular interest. The surge in establishment in the early 1940s may have been a response to improved fire detection and suppression on the West Coast during World War II with the organization by the Office of Civilian Defense of the Forest Fire Fighters Service, the use of prison inmate labor, and the introduction of improved technology for fighting wildfires (Pyne 1982). The 1940's cohort of *P. menziesii* may also reflect the improved condition of seedling establishment as the oak canopy closed some 20

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FIG. 2. Age distribution of Douglas-fir and oak on plots at Annadel State Park. A = "A" plots (Douglas-fir saplings beneath healthy oak canopy), B = "B" plots (Douglas-fir extending into, but not above, healthy oak canopy), C = "C" plots (Douglas-fir forming a more or less open canopy above healthy oaks), D = "D" plots (Douglas-fir forming a well-developed canopy above declining oaks), and E = "E" plots (Douglas-fir well above dead or dying oaks).

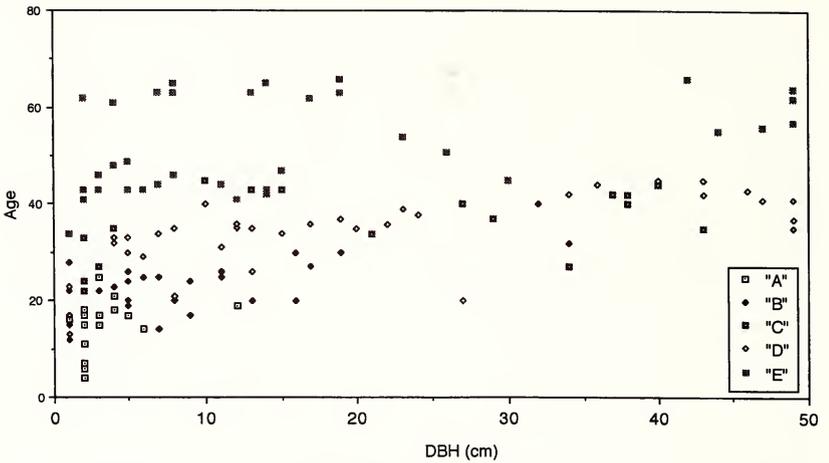


FIG. 4. Diameter range of Douglas-fir by age and plot type in oak woodlands at Annadel State Park.

years after the firewood harvesting in the 1920s. Crown closure of the oak woodland would contribute to those factors which were found to correlate positively with *P. menziesii* seedling and sapling density. This relationship is clearly illustrated by the data in Figure 2D. A lag time of about 20 to 30 years occurred between the peak of oak establishment (presumably from sprouts following extensive firewood harvesting in the 1920s) and the surge of *P. menziesii* regeneration. Similar surges in *P. menziesii* regeneration did not follow the peak of oak establishment in the 1880s (Figure 2D). Failure of *P. menziesii* regeneration following crown closure in the first decade of the 20th century was probably due to land management practices which included intensive grazing and some burning.

The second surge of establishment followed the establishment of the Park in 1972 and may be the result of the elimination of livestock combined with above average precipitation in 1972 and 1973 and an increased seed supply. *P. menziesii* trees established in the early 1940s would have been old enough to contribute to the seed supply during the surge of regeneration in the early 1970s.

The diameter (DBH) range of *P. menziesii* relative to age and type of plot sampled is shown in Figure 4. Two phenomena are clear from this analysis. First, the *P. menziesii* in a given plot type (A through E) are generally clustered into fairly distinct age groups (i.e. youngest in A plots and oldest in E plots). Of greater interest is the great disparity in diameters of trees of approximately the same age. Particularly in those plots exhibiting greater *P. menziesii* dominance (C, D and E) tree sizes are poorly correlated with age. This suggests

that many older trees remained suppressed in the understory for several decades while a few trees of the same age class assumed dominance and overtopped the hardwoods. The data suggests that these suppressed trees will die unless they break through the overstory within 40–50 years.

CONCLUSIONS

Pseudotsuga menziesii has become established in oak woodlands at Annadel State Park over the past 100 years as evidenced by the stand age analysis study. No statistical correlation could be established between annual seedling establishment and precipitation for the entire period from 1890 to 1985. However, a significant positive correlation was found between the number of trees established and the precipitation for the hydrologic years from 1973 to 1985. Within this span of years significant positive correlations were also found between the number of trees established and precipitation from April to June and from March to September. Two major periods of establishment occurred in the early 1940s and the early 1970s. These two surges of seedling establishment began in years of above average rainfall. The initial surge of seedling establishment (1943 to 1953) may have resulted, in part, from improved fire detection and control initiated in World War II. The second surge of seedling establishment (1972 to 1975) corresponds to the establishment of the Park and elimination of intensive livestock grazing. Fire control and an increased seed supply from the cohort of *P. menziesii* established in the 1940s would also have been factors of importance to the second surge of establishment. *Pseudotsuga menziesii* regeneration was highly correlated with the distance to larger *P. menziesii* trees. Obviously seed source is important in regeneration. Large *P. menziesii* trees release great quantities of seeds which drop to the ground in decreasing numbers with distance from the tree. Many sites were observed where a single old *P. menziesii* had given rise to a group of smaller trees which were currently adding to the local seed supply. The resulting pattern is suggestive of islands of *P. menziesii* trees emerging through the oak woodland canopy around an older "founding" veteran. Although *P. menziesii* trees can distribute seeds up to distances of 1200 to 1400 feet (Isaac 1938), effective dispersal is probably more on the order of two times the height of the tree.

Several interesting correlations were demonstrated between the density of *P. menziesii* seedlings and saplings and site characteristics. In general, those characteristics which one would associate with more mesic site conditions and less competition for soil moisture were positively correlated with *P. menziesii* regeneration. These site conditions all suggest that increased *P. menziesii* establishment within the oak woodlands has coincided with increased density and can-

opy closure of the woodlands. This change in the structure of the woodlands coincides in turn with dramatic changes in the fire-regime of the park area around the turn of the century and oak-wood harvesting.

The fire history of Annadel State Park (Finney and Martin 1992) indicates that fires were both widespread and frequent before 1900. Kniffen (1939), Stewart (1951) and Barrett (1952) concluded that Pomo Indians, whose territory included the Park, burned grasslands annually. According to Kniffen, fires set annually by the Pomo maintained the oaks in open "park-like" stands. Not all annual fires set in the grasslands and savannas would be expected to burn over all of the adjacent woodlands. Thus "islands" of periodic oak establishment were maintained which would remain non-favorable to the more shade-tolerant and less fire-tolerant *P. menziesii*.

This study provides evidence that *P. menziesii* is exhibiting a rapid invasion of oak woodlands at Annadel State Park. Some areas studied show clear evidence of the growth of *P. menziesii* through the crown canopy of the oak woodland followed by the suppression and death of the oaks. Succession to *P. menziesii* forest in all oak woodland stands currently exhibiting *P. menziesii* seedlings and saplings in the understory has been questioned by a few foresters in Northern California (Pete Passoff, U.C. Cooperative Extension; Jack Marshall, California Department of Forestry and Fire Protection). They contend that similarly established *P. menziesii* regeneration usually succumbs to attacks of bark beetles and branch cankers during drought years. They have pointed to recent mortality (during the 1987–1992 drought) and mortality following the drought of 1976–1977 near Covelo, California as evidence that *P. menziesii* established on marginal sites in oak woodlands will not persist to succeed the oak woodlands. These marginal sites are characterized by clay layers in the subsoil which result in perched water tables and restrict deeper penetration of *P. menziesii* roots. During drought years these perched water tables dry up leaving the *P. menziesii* regeneration stranded in a layer of very dry soil.

Field observations at Annadel State Park and over an extensive area to the east in Sonoma and Napa counties have not identified areas of *P. menziesii* mortality beneath or within the canopies of oak woodlands during the period of drought beginning in 1987. These observations combined with the differences in soils between Annadel State Park and the Covelo area indicate that the invading *P. menziesii* seedlings and saplings will not disappear. Similar conclusions have been derived from studies in the "bald hills" of Redwood National Park, Humboldt County (Reed and Sugihara 1987) and in southwestern Trinity County (Keter 1987).

Taken collectively, these data suggest that a number of environmental factors, including fire, have been instrumental historically in

keeping the woodlands open, thus encouraging the establishment of oak rather than *P. menziesii*. The lack of fire in these sites during the past fifty years plus other factors which have specifically encouraged the development of denser oak woodlands have collectively provided for the establishment of *P. menziesii* in areas of Annadel State Park where this species has not historically occurred. These trees have grown large enough in forty to fifty years to crown-out and kill the adjacent oaks, yet most of the *P. menziesii* of similar age remain small, suppressed and will eventually die as well. This pattern of *P. menziesii* establishment in oak woodlands will continue in this region as long as fire is excluded and woodlands remain unusually dense. Eventually *P. menziesii* will come to dominate many areas now supporting stands of Northern Oak Woodland. Loss of these woodlands in the mosaic of vegetation types will lead to an overall reduction in biological diversity in Annadel State Park and elsewhere.

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ANNOUNCEMENT

12TH ANNUAL SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM
THE LINNEAN HIERARCHY: PAST, PRESENT, AND FUTURE
MAY 24 & 25, 1996

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Early registration (prior to 30 April) for the symposium is \$40.00 per participant (\$25.00 for students). After 30 April registration is \$55.00 (\$40.00 for students). This fee includes the Friday evening social, boxed lunch on Saturday. The Saturday Evening Banquet costs \$35.00. For more information contact:

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DEFOLIATION RESPONSE AND GROWTH OF
NASSELLA PULCHRA (A. HITCHC.) BARKWORTH FROM
SERPENTINE AND NON-SERPENTINE POPULATIONS

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ABSTRACT

Restoration of stands of the native bunchgrass *Nassella pulchra* (A. Hitchc.) Barkworth in the California grassland requires suitable germplasm and conditions favoring survival, reproduction, and recruitment. In a common garden experiment, growth patterns of two populations of *Nassella pulchra* were compared. Because defoliation by herbivory and burning are ubiquitous influences on the California grassland, and have been suggested as having potential for manipulating the balance of native and non-native species, the response of each population to clipping in winter, winter and early spring, and late spring was also compared. The two populations exhibited genotypic variation in morphology, growth, and response to clipping. Clipping in winter had no significant effect on tiller number, number of inflorescences, or leaf length. Clipping in winter and early spring significantly reduced number of tillers and inflorescences in plants from one population, grown from seed collected on a serpentine site, but not from the non-serpentine population. Clipping in late spring severely reduced tiller numbers, number of inflorescences, and leaf length in plants from both sites. The need for use of local seed sources for restoration is well-recognized, but the characteristics of seed source site, as related to genetic characteristics, may also affect the success or failure of restoration efforts and management practices. In the populations studied, a perennial grassland restoration system using winter burning and/or grazing to influence annual grasses would not damage *N. pulchra* plants, but response to early spring treatments and frequency or duration of treatment varies by population.

The displacement of California's once extensive native prairie by introduced annual grass species began in the late 18th century following introduction of livestock and exotic plants (Heady et al. 1991), possibly augmented by changes in fire frequency brought about by Euro-American settlement. Native grasses now are uncommon, found mostly as relict stands within a few km of the Pacific

Ocean and farther inland on serpentine soils (Murphy and Ehrlich 1989). Recent increased interest in grassland conservation and restoration (Hatch et al. 1991) follows a long history of poor success at propagating native grasses (Kay et al. 1981). The success of native grassland conservation and restoration projects will in large part depend on development of propagation and management techniques informed by knowledge of potential species distribution, genetic variability of populations, and response to management techniques for maintaining and encouraging native species.

Found on a variety of sites, the widely distributed perennial bunchgrass *Nassella pulchra* is considered to be the former dominant of the Valley Grassland portion of the native prairie (Heady 1977) and is the most common native perennial in the grassland today (Bartolome and Gemmill 1981). The species is widely considered a primary candidate for use in restoring native grassland. Native grassland restoration projects in California are primarily geared towards seeding, transplanting, or increasing native perennial stands. Herbivory and fire are major ecological influences on the California grassland. It is likely that restoration and maintenance of native grasses will include some grazing (Murphy and Ehrlich 1989) or burning, but information on their effects on restoration outcomes is limited and sometimes seemingly contradictory, perhaps due to variation in restoration site conditions or the genetic characteristics of *Nassella pulchra*.

Early research by range ecologists investigated the effects of defoliation on native perennials including *Nassella pulchra* (Sampson and McCarty 1930; Parker and Sampson 1931) and the potential for native perennial-based range improvement (Jones and Love 1945; Kay et al. 1981). *N. pulchra* was found to be intolerant of grazing during spring (Parker and Sampson 1931), and subsequent recommendations for range improvement emphasized available non-native perennials, not natives (Love 1951). More recent research has gone beyond this cursory knowledge of the dynamics of the species, showing that *Nassella pulchra* is favored by fire (Hatch et al. 1991), and does not necessarily recover (Heady et al. 1991) or may even disappear with grazing removal (Bartolome and Gemmill 1981). A number of exotic annuals aggressively increase under conditions of light or no grazing and have been observed to exclude natives including *Nassella pulchra* (Bartolome and Gemmill 1981). Effective maintenance of *N. pulchra* in restored grasslands will depend upon selectively suppressing the aggressively competitive annuals without damage to perennials (Dennis 1989).

One proposed scheme to encourage *N. pulchra* uses late fall burning to kill germinated annuals and winter grazing to further reduce annual grass competition (Hatch et al. 1991). If this is to work, it also must not significantly damage *N. pulchra* plants. Dennis (1989)

found that *Nassella pulchra* was more tolerant than other native grasses to defoliation during winter and early spring. However, burning and grazing can result in reduced tiller numbers, reduced reproductive output, and reduced plant vigor, as occurred in one experiment in which these treatments were applied in summer (Langstroth 1991). All of this research has been done *in situ* in the California prairie, where the influence of annual species may make it difficult to evaluate the influence of defoliation on *Nassella pulchra* independent of environmental modification by annual species (Dennis 1989). In addition, nothing is known about the population genetics of *Nassella pulchra*, and how genetic variability may affect response to management. This study addresses both of these concerns.

In order to explore genetic variation in the species, a common garden experiment was carried out to compare growth patterns and response to management of *Nassella pulchra* from seed gathered from two distinct Bay Area populations. Because defoliation by herbivory and burning are ubiquitous influences on the California grassland, and have been suggested as having potential for manipulating the balance of native and non-native species, the response of each population to clipping in winter, winter and early spring, and late spring was also compared in controlled conditions. Tiller number, number and status of culms, and leaf length were used as measures of plant vigor and reproductive output.

METHODS

Approximately 500 seeds from randomly selected individuals of *Nassella pulchra* were collected at two sites along the shore of San Francisco Bay. The Ring Mountain site in Marin County, California, is on a serpentine soil similar to the Montara series (P. Zinke personal communication), tentatively identified as Henneke Stony Clay Loam (USDA, SCS 1985). Ring Mountain had not been grazed by livestock for 20 years prior to the study, but has previously supported large numbers of cattle. The other site was 10 km away at Point Molate, in Contra Costa County, on a non-serpentine soil, Los Gatos Clay (Welch 1977). Point Molate has been ungrazed by livestock since approximately 1940 (Havlik 1984). The vegetation at both sites was dominated by *N. pulchra* in association with other typical Bay Area coastal prairie species (Heady et al. 1977). Seeds were germinated in fall (germination rate was 80 percent) and seedlings grown in a greenhouse in a flat.

Phenology, growth, and clipping studies were conducted in specially constructed planter boxes located in Strawberry Canyon on the University of California, Berkeley Campus. The boxes were 4 × 8 × 2 feet on a slightly sloping concrete slab and filled with a Dibble Clay Loam Soil (Welch 1977), a commonly available garden

soil. A randomly selected group of three-month-old seedlings, 20 from the Point Molate non-serpentine population, and 20 from the Ring Mountain serpentine population plants, were transplanted from the greenhouse to the planter boxes in Strawberry Canyon. Plants were randomly located in a grid with 20 cm spacing. Plants grew under conditions normal for the San Francisco Bay Area in winter and early spring, with adequate soil moisture from rainfall until early May. Plots were kept free of other species during the experiment.

Twenty year-old plants from each population were randomly assigned to be clipped to a 5 cm stubble height in three different treatments plus unclipped controls: 1) Clipped in early winter only (December 8, $n = 10$), 2) Clipped in early winter and early spring (December 8 and March 11, $n = 10$), 3) Clipped in mid-spring (May 10, $n = 10$, and 4) unclipped ($n = 10$). Plant response was measured as total number of tillers/plant, number of flowering culms per plant, and length of leaf (blade + sheath) recorded from the longest leaf on six permanently tagged tillers measured per plant. Plants were measured on January 13 (mid-winter), March 11 (early spring), April 21 (mid-spring), and June 9 (late spring).

Results were analyzed by two-way ANOVA for significant response by population (Ring Mountain or Point Molate) and clipping treatment on the last measuring date (June 9), followed by mean separation using least significant differences. The last sample date was chosen for comparison because plants in the California prairie senesce in early summer or late spring. This date therefore takes into account all of the potential rain-year growth or re-growth. Differences in growth pattern between populations for the control plants were analyzed using separate one-way ANOVAs for each sample date. We rejected the null hypotheses of no significant treatment or population effect at $\alpha = 0.10$. The significance level was selected to balance power of the test against the low "risk" associated with Type I error.

RESULTS

There were differences in the growth patterns and morphological characteristics of plants from the two populations that were obvious visually and borne out by measurement. Plants from Point Molate appeared coarser than the finer textured plants from Ring Mountain, and matured faster. *Nassella pulchra* plants from Ring Mountain averaged more tillers per plant than those from Point Molate (Fig. 1). On the other hand, Point Molate plants grew earlier or faster, producing more inflorescences on the early spring sample date than the plants from Ring Mountain (Fig. 2), and losing tillers by June as they began to senesce (Fig. 1). Point Molate plants also had longer leaves at each sample date (Fig. 3).

The two populations also varied in their response to treatment.

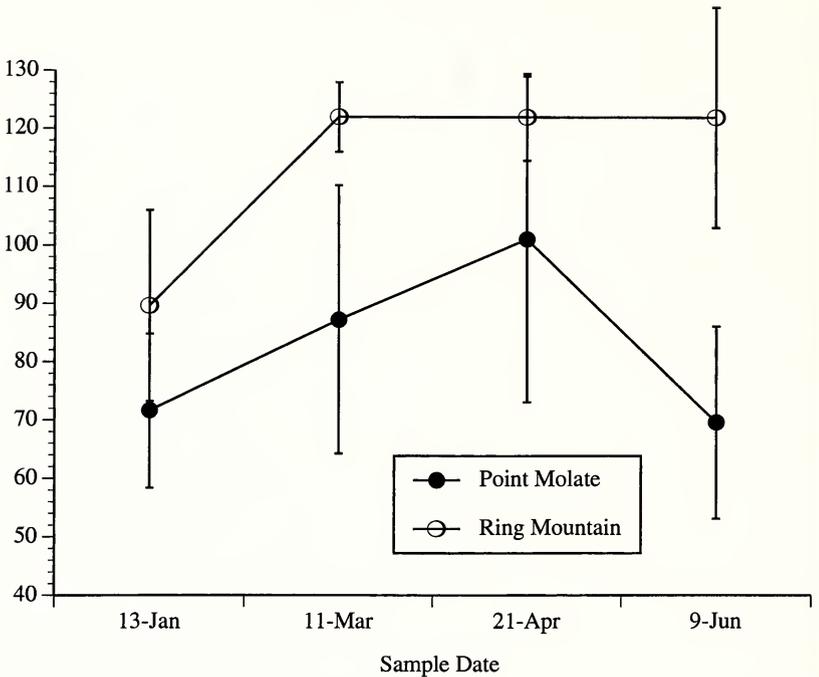


FIG. 1. Number of tillers per unclipped plant by sample date for plants from two populations, Ring Mountain serpentine and Point Molate non-serpentine. $n = 5$ for each data point. Only the difference between populations on June 9 is significant ($P < 0.1$).

Number of tillers per plant on June 9 differed significantly between populations and among clipping treatments (Fig. 4). Plants from Ring Mountain averaged $98 (\pm 11)$ tillers and plants from non-serpentine populations at Point Molate averaged $47 (\pm 6.5)$ tillers, a difference significant at $P < 0.001$. Plants clipped to a 5 cm stubble height on December 10 did not differ significantly from controls in number of tillers, but Point Molate plants clipped twice, in December and March, and plants from both populations clipped once in spring, on May 10, had significantly fewer tillers than controls ($P < 0.01$).

Number of inflorescences was significantly affected by clipping date ($P < 0.01$), with no effect from the single December clipping, significantly fewer inflorescences from the December plus March clipping in Ring Mountain plants, and markedly fewer inflorescences on both populations with the May clipping (Fig. 5).

Length of the longest leaf was significantly affected by clipping treatment ($P < 0.01$). December clipping did not show a significant

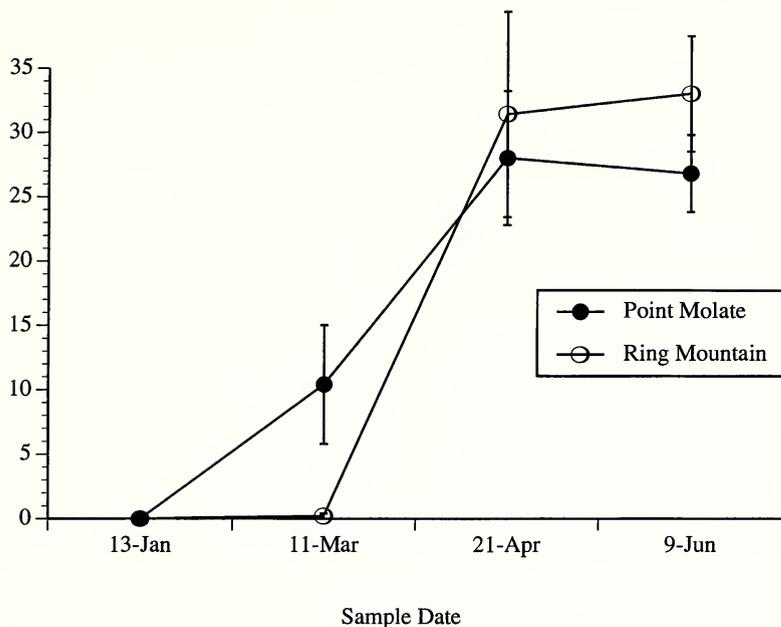


FIG. 2. Number of inflorescences per unclipped plant from two populations, Ring Mountain serpentine and Point Molate non-serpentine. $n = 5$ for each data point. Only the difference between populations on March 11 is significant ($P < 0.1$).

effect, but both populations produced shorter leaves after the December plus March and May treatments (Fig. 6).

DISCUSSION

The two populations differed significantly in their patterns of growth and in response to clipping when grown in common on the same soil. Plants from Ring Mountain produced more tillers per plant. Plants from Pt. Molate flowered earlier, produced longer leaves, and senesced earlier than plants from Ring Mountain.

When compared to controls, *Nassella pulchra* plants from both sites were little affected by December clipping, with no significant changes in number of tillers, number of inflorescences, and leaf length. When a second clipping was added to the December clipping, the plants from the two populations responded differently. Ring Mountain plants had a significant reduction in number of inflorescences and tillers, while Point Molate plants were no different from controls. This result is surprising because it contradicts the hypothesis of Parker and Sampson (1931), that the time of culm elevation is when grasses are most susceptible to losses in productivity due to defoliation. The Point Molate plants had more elevated culms at the March clipping date

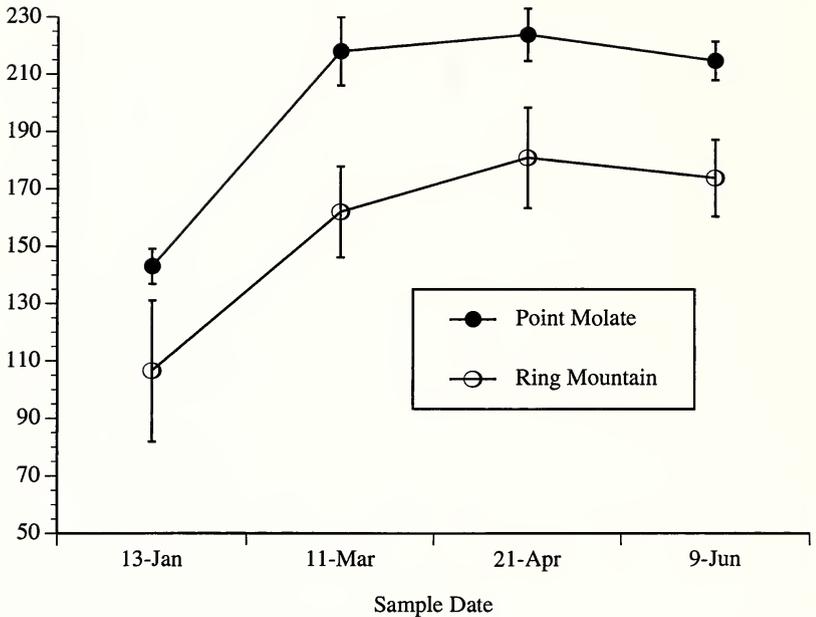


FIG. 3. Length of longest leaf for unclipped plants from two populations, Ring Mountain serpentine and Point Molate non-serpentine. The length is length of blade plus sheath for the longest leaf on six marked tillers on each plant. All differences between populations are significant except June 9 ($P < 0.05$).

than the Ring Mountain plants. Both populations had a shorter leaf length as a result of the double clipping, perhaps because regrowth of leaves was limited in late spring, while investment in tillers and inflorescences continued in the Point Molate plants. All plants, as predicted by previous work, were severely affected by May clipping, probably because they had only 4 weeks to recover before the June measurement and senescence.

The Ring Mountain plants were gathered from a serpentine site, while the Point Molate plants were from a non-serpentine associated population. In California today, most noticeable stands of *Nassella pulchra* and other native perennials are associated with serpentine soils, where competition from native annuals is reduced. It can be hypothesized that the growth patterns of the plants from the non-serpentine site reflect adaptation to a denser grassland, crowded with introduced plants. Earlier or more rapid growth and flowering, and larger leaves, may be important in competing with fast growing annuals. As with all greenhouse or lab experiments, it is also possible that response to treatment and growth characteristics may be influenced by environmental characteristics when the plants are in

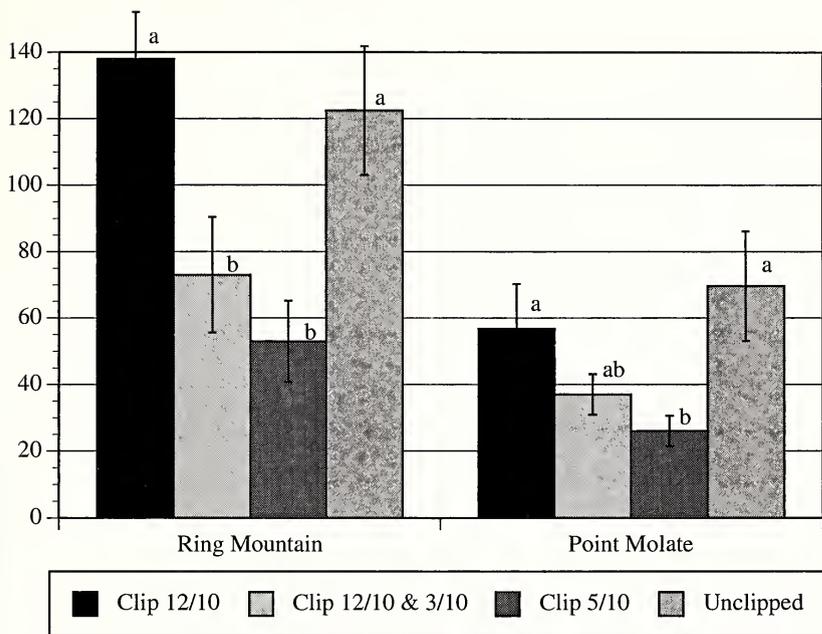


FIG. 4. Effect of clipping on number of tillers per plant on June 9 for two populations. Means for bars within populations sharing letters are not significantly different (LSD, $P < 0.05$).

the field. This study has controlled environmental factors in order to examine genetically-determined differences in population behaviors. Genetic variation in *Nassella pulchra* may help explain the varying results of restoration efforts and research.

As relic areas for native species are often found on serpentine sites, seed for restoration of both serpentine and non-serpentine sites is often collected from them. This study shows that matching the site characteristics of seed source and planting site, or at least using a mix of seed sources, may be just as important a consideration as simply looking for a "local" seed source. Re-vegetating non-serpentine sites with seed from serpentine-adapted populations may put the new plants at a disadvantage when the major constraints to growth are competitive rather than soil characteristics. Conversely, plants from non-serpentine sites might not flourish when soil nutrient regimes fail to support their genetically programmed growth pattern. Obviously, these hypotheses, while suggested by this research, require testing with broad replication using germplasm from a variety of serpentine and non-serpentine sites.

These results of treatment of these populations, corroborated by the research of Dennis (1989), indicate that winter grazing, mowing,

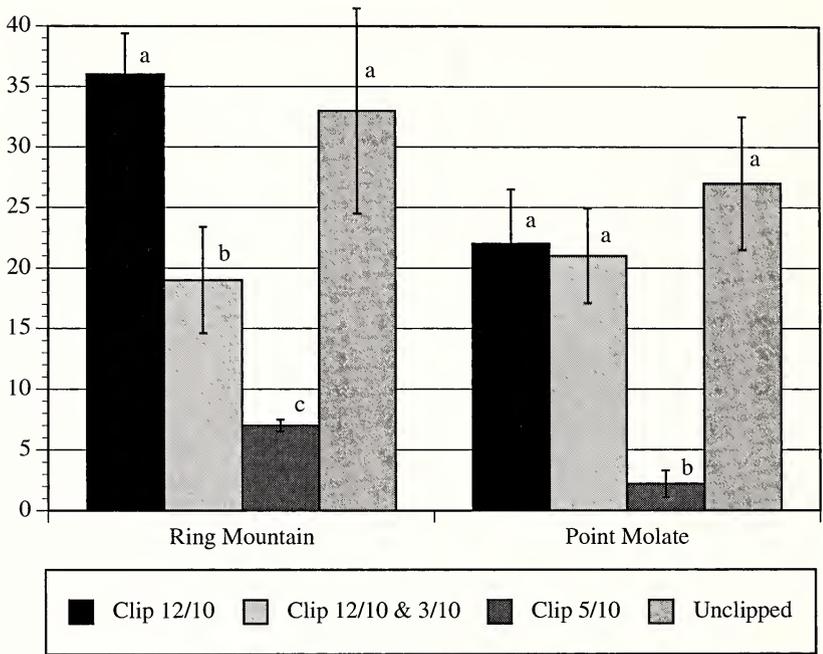


FIG. 5. Effect of clipping on number of inflorescences per plant on June 9 for two populations. Means for bars within populations sharing letters are not significantly different (LSD, $P < 0.05$).

or low-intensity burning of *Nassella pulchra* is unlikely to affect plant vigor or reproductive output. Management regimes designed to reduce competing annuals by concentrating defoliation in fall and winter show promise for the restoration and maintenance of *N. pulchra* stands. It also appears that timing of the removal of grazing or further defoliation in spring will be important and may differ for different *N. pulchra* populations. For Ring Mountain serpentine plants, the additional defoliation on March 10 significantly reduced the number of tillers and inflorescences at the end of the season compared to controls, while the number of inflorescences and tillers produced by Point Molate non-serpentine plants was not significantly affected.

Management systems using fall or winter burning and/or grazing to reduce competition from annual grasses are based on the premise that reduction of annual plant biomass and/or density allows perennials opportunity for better seedling survival and seed output. This should allow for increase of *Nassella* plant density and offer potential for grassland rehabilitation. However it is important to note that *N. pulchra* populations may respond differently to defoliation, and

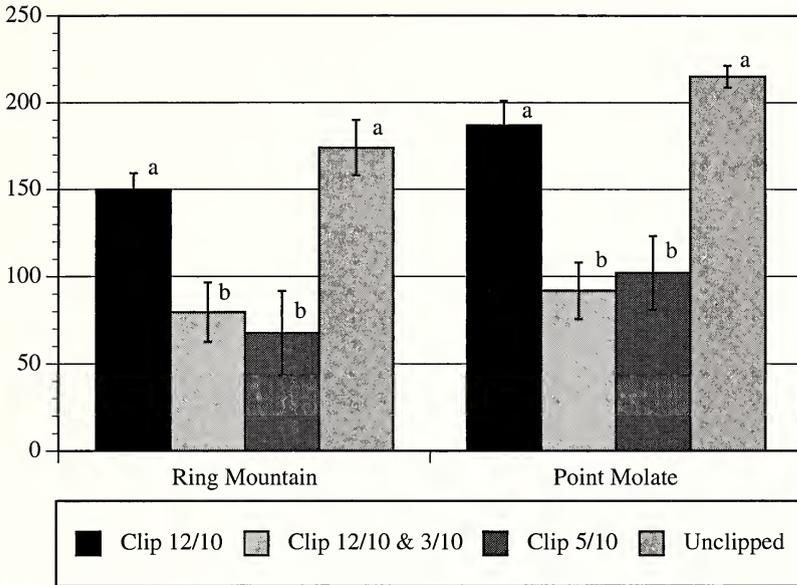


FIG. 6. Effect of clipping on length of longest leaf on June 9 for two populations. The length is length of blade plus sheath for the longest leaf on six marked tillers on each plant. Means for bars within populations sharing letters are not significantly different (LSD, $P < 0.05$).

that other native perennial grasses are affected very differently by defoliation and competition with exotic annuals (Dennis 1989).

Most of the evidence that *Nassella pulchra* or any other perennial bunchgrass once dominated the now annual Valley Grassland is inferred from supposed relict stands of native perennials and poorly tested successional models that suggest trends toward perennial grass dominance (Heady et al. 1992). One study using opal phytoliths produced the only direct evidence for former perennial grass dominance on a now annual site in the Valley Grassland (Bartolome et al. 1986). Heavy year-long grazing by livestock is usually considered to have weakened and killed the native grasses, allowing for the rapid colonization of annuals from the Mediterranean (Burcham 1957; Baker 1989). Yet direct evidence that livestock grazing eliminated the perennial grasses is lacking, suggesting that the simple introduction of Mediterranean annuals may have been enough to quickly eliminate native plants (Bartolome 1989) on sites where site factors such as serpentine soils do not inhibit the growth of the exotics. For these reasons, consideration of site specific population-level adaptations to serpentine vs. non-serpentine growing conditions, and to management regimes designed to maintain stands by reducing competition from exotics, should be an important consid-

eration in seed-source collection for restoration projects. Most restoration efforts today are necessarily on non-serpentine sites—perhaps the seed collected for these efforts should also come from non-serpentine sites, or from a variety of sites or populations, a challenge given the fact that the most extensive stands remaining are generally on serpentine areas.

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NOTEWORTHY COLLECTIONS

COLORADO

POLEMONIUM CONFERTUM A. Gray (POLEMONIACEAE).—Gunnison Co., Gunnison National Forest, 45.0 km N and 14.5 km E of Gunnison, in tundra and fellfield on summit of North Italian Mountain, T13S R84W S2, 38°55'N, 106°45'W, 4027 m, 19 July 1994, *R. Seagrist 569* (RMBL); Park Co., Buffalo Peaks Wilderness Area, Pike National Forest, 17.7 km N of Buena Vista, common along boulder-lined snow-melt streams on tundra-covered plateau 3.2 km NE of East Buffalo Peak summit, T12S R78W S22, 39°0'30"N, 106°5'W, 3780 m, 22 July 1995, *R. Seagrist 1008* and *K. Taylor 140* (RMBL, MO); Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 22.5 km N and 4.0 km W of Crested Butte, intermittent in tundra and fellfield along dividing ridge between Hasley Basin and Fravert Basin, T11S R86W S30, 39°3'30"N, 107°2'W, 3856 m, 3 August 1995, *R. Seagrist 1133* (RMBL); Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 20.9 km N and 2.4 km W of Crested Butte, intermittent in tundra and fellfield at Frigid Air Pass, T11S R86W S32, 39°3'N, 107°1'30"W, 3780 m, 13 August 1995, personal observation by R. Seagrist and K. Taylor; Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 22.5 km N of Crested Butte, in tundra and fellfield on Maroon Peak, T11S R86W S27, 39°4'3"N, 106°59'W, 3659 to 4316 m, 13 August 1995, personal observation by K. Taylor.

Previous knowledge. This species was first collected by Hall and Harbour (450) in 1862 from Jefferson Pass in Colorado's Mosquito Range and first described by Gray in 1864 (A. Gray, *Proceedings of the Academy of Natural Sciences, Philadelphia* 1863:73). Although some authorities regard *Polemonium confertum* as a variety of *P. viscosum* Nuttall, it is sufficiently distinct in several characters that it is considered to be a separate species by Brand (*Das Pflanzenreich* 250:44, 1907), Rydberg (*Flora of the Rocky Mountains and Adjacent Plains* 2nd ed., New York Botanical Garden, 1922), Wherry (*American Midland Naturalist* 27:741–760, 1942), Grant (*Botanical Gazette* 150(2):158–169, 1989), and Weber (*Colorado Flora: Eastern Slope*, Colorado Assoc. University Press, Boulder, 1990). Our field and herbarium observations agree with the above authorities that *P. confertum* is quite distinct. Our specimens have characteristics which meet the description of *P. confertum* provided by Grant (1989), including widely-spaced whorled leaflets, orange anthers, light blue corollas broadly funnelliform in shape with throats wider than 10 mm, and inflorescences 40–50 mm wide.

Significance. Our collections are the first from the Maroon Bells-Snowmass and Buffalo Peaks regions and extend the known range of this species considerably. Previously thought to be fairly rare, it appears that *P. confertum* is actually fairly common but grows in high elevation, hard-to-access habitats.

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ANTHER GLANDULARITY IN THE AMERICAN MYRTINAE (MYRTACEAE)

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ABSTRACT

A survey of anther glandularity in the American Myrtinae (Myrtaceae) (83 spp.) and related Myrtaceae (42 spp.) was conducted to discover any taxonomic tendencies that might exist. Of the larger genera, *Calycolpus* typically has 9–19 glands per anther in most species; *Campomanesia*, 0–1; *Mosiera*, 1–2; and *Psidium*, 1–4. Certain species differ greatly from the standard values for their genera. Thus, anther glandularity can be taxonomically valuable at both the generic and specific levels.

RESUMEN

Se hizo un estudio de glandularidad de anteras en Myrtinae (Myrtaceae) Americanas (83 spp.) y otras mirtáceas parientes (42 spp.) a fin de descubrir tendencias taxonómicas que podrían existir. En los géneros más grandes el número típico de glándulas por antera en la mayoría de las especies es: *Calycolpus* (9–19); *Campomanesia* (0–1); *Mosiera* (1–2); and *Psidium* (1–4). Algunas especies difieren bastante de los valores típicos de sus géneros. Así es que la glandularidad de anteras puede ser de valor taxonómico a nivel genérico o específico.

The American species of the subtribe Myrtinae (Myrtaceae) comprise a group of ca. 165 species in 15 genera. An approximately equal number of genera and species of Myrtinae are found in Australasia and a single species, *Myrtus communis*, is found in the Mediterranean region. The purpose of this study was to conduct a survey of anther glandularity in American Myrtinae. Preliminary observations had indicated that anther glandularity might be of taxonomic value in this group at either the generic or specific level. Landrum (1989) used it as an aid in placing the anomalous species *Myrtus alternifolia* in *Calycolpus*, and had also found it a useful character in distinguishing *Campomanesia speciosa* from other species of that genus (Landrum 1986).

METHODS

Anthers were extracted from 299 herbarium specimens of 125 species of Myrtaceae. Most (83 spp.) belonged to American Myr-

tinae but representative species of other subtribes and Old World Myrtinae were also sampled. Anthers were soaked in bleach (5.25% sodium hypochlorite) for about 15 minutes until relatively white. They were rinsed in water or mounted directly on glass slides with water and covered with a cover slip. Sometimes a little pressure was applied to the cover slip. Slides were observed immediately at 100 \times . The glands do not change color in the short time the anthers soak in bleach, but rather remain a light yellow-brown to reddish-brown color, their contents not readily mixing with water. They stand out clearly in contrast to the whitened tissue of the rest of the anther and can usually be easily counted (Fig. 1). The tissue of the anther softens in the bleach, so care has to be taken not to leave the anthers in the bleach too long. Anthers that become too soft can easily fall apart. Five anthers were observed for each specimen and a sketch was made of a representative. Counts for the five anthers were averaged.

RESULTS

Results of this study are summarized in Table 1 and are provided in a more complete form in Appendix A. The mean number of glands per anther varies essentially continuously from zero in several species (e.g., *Pimenta racemosa*) to over 60 in *Calycolpus warscewiczianus*. In Table 1 the continuum was broken arbitrarily into five categories of mean number of glands per anther: A, 0–0.9; B, 1.0–1.9; C, 2.0–3.9; D, 4.0–9.9; E, 10.0 or more. For any particular species one to several specimens were sampled. A letter in Table 1 may represent one to a several specimens. By simple observation one can see, for instance, that species of *Calycolpus* tend to be in the D to E range, species of *Campomanesia* and *Mosiera* tend to lie in the A to B range, and species of *Psidium* are mainly in the B to D range. Certain contrasts are evident. Within *Calycolpus*, one species, *C. legrandii* stands out by having anthers with one or no glands and in *Campomanesia*, a single species is conspicuous by having several glands. The closely related genera *Acca* and *Myrrhinium* (Landrum 1986) differ widely in gland number.

In *Psidium*, most species have a moderate number of glands, but there seem to be three complexes of species that sometimes have numerous glands: *P. guineense*; *P. acutangulum* and *P. friedrichsthalianum*, closely related species of South and Central America respectively; and the Caribbean complex of *P. amplexicaule*, *P. cy-mosum*, and *P. dictyophyllum*.

The four species of Old World Myrtinae sampled fell within the B and D ranges. Of the 18 American Eugeniinae sampled, 16 fell in the A to B range, and only three specimens had any anthers with more than one gland. Of the 16 American Myrciinae sampled, all

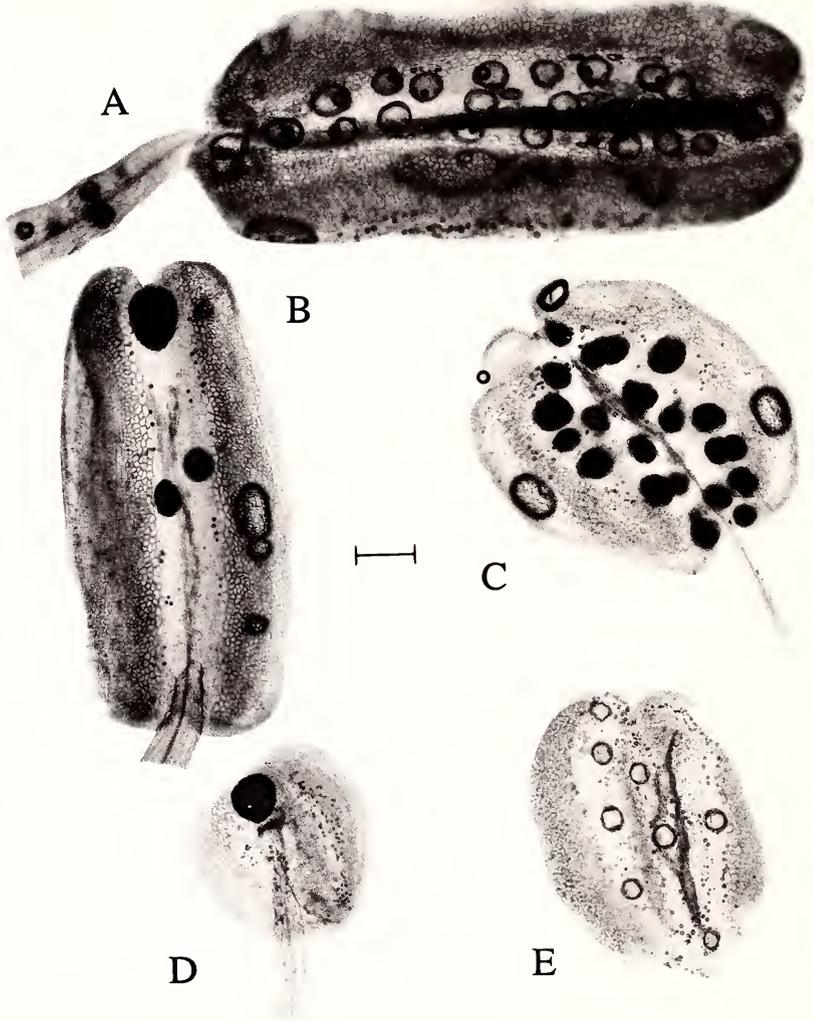


FIG. 1. Anthers of American Myrtinae. A. *Calycolpus moritzianus* (Grifo & Hahn 338A, MO). B. *Psidium guineense* (Landrum 5678, ASU). C. *Campomanesia speciosa* (Morawetz & Wallnofer 11-30985, ASU). D. *Campomanesia guaviroba* (Kummrow 2833, ASU). E. *Myrrhinium atropurpureum* (Silva 200, ASU). Bar = 0.1 mm in B, C and E and = 0.2 mm in A and D. Colorless bubbles are present in B on the right side and in C near the apex and on both sides. They are easily distinguished from glands when color is evident.

TABLE 1. SUMMARY OF ANTHER GLANDULARITY IN AMERICAN MYRTINAE. Species are classified as to the mean number of glands in the anther connectives. A, 0–0.9. B, 1.0–1.9. C, 2.0–3.9. D, 4.0–9.9. E, 10.0 or more. Each letter in the table represents at least one specimen. See appendix for more complete data.

	A	B	C	D	E
<i>Acca macrostema</i>	A				
<i>Acca sellowiana</i>	A	B			
<i>Amomyrtella guili</i>	A				
<i>Amomyrtus luma</i>	A				
<i>Amomyrtus meli</i>	A				
<i>Blepharocalyx cruckshanskii</i>		B			
<i>Blepharocalyx salicifolius</i>		B			
<i>Calycolpus alternifolius</i>			C	D	E
<i>Calycolpus bolivarensis</i>				D	
<i>Calycolpus calophyllus</i>					E
<i>Calycolpus goetheanus</i>					E
<i>Calycolpus legrandii</i>	A				
<i>Calycolpus moritzianus</i>					E
<i>Calycolpus revolutus</i>				D	E
<i>Calycolpus surinamensis</i>					E
<i>Calycolpus warszewiczianus</i>					E
<i>Campomanesia adamantium</i>	A				
<i>Campomanesia aurea</i>		B			
<i>Campomanesia espiritosantensis</i>		B			
<i>Campomanesia eugenioides</i>		B			
<i>Campomanesia grandiflora</i>		B			
<i>Campomanesia guaviroba</i>		B			
<i>Campomanesia guazumaefolia</i>		B			
<i>Campomanesia laurifolia</i>	A				
<i>Campomanesia neriiflora</i>		B			
<i>Campomanesia pubescens</i>	A				
<i>Campomanesia sessiliflora</i>		B			
<i>Campomanesia speciosa</i>					E
<i>Campomanesia velutina</i>	A				
<i>Campomanesia viatoris</i>	A				
<i>Campomanesia xanthocarpa</i>	A	B			
<i>Chamguava gentlei</i>		B	C	D	
<i>Chamguava schippii</i>	A				
<i>Legrandia concinna</i>	A				
<i>Mosiera bullata</i>		B			
<i>Mosiera contrerasii</i>		B			
<i>Mosiera ehrenbergii</i>	A		C		
<i>Mosiera longipes</i>		B			
<i>Mosiera moaensis</i>		B			
<i>Moseira ophiticola</i>		B			
" <i>Psidium</i> " <i>saxicola</i>		B			
" <i>Eugenia</i> " <i>xerophytica</i>		B			
<i>Myrrhinium atropurpureum</i>					E
<i>Myrteola acerosa</i>		B			
<i>Myrteola nummularia</i>		B			
<i>Myrteola phyllicoides</i>		B			
<i>Pimenta dioica</i>		B			
<i>Pimenta pseudocaryophyllus</i>		B			
<i>Pimenta racemosa</i>	A				

TABLE 1. CONTINUED

	A	B	C	D	E
<i>Psidium acutangulum</i>	A	B	C		E
<i>Psidium amplexicaule</i>			C	D	E
<i>Psidium appendiculatum</i>	A				
<i>Psidium arayan</i>		B			
<i>Psidium australe</i>		B			
<i>Psidium cattleianum</i>		B			
<i>Psidium cinereum</i>		B	C		
<i>Psidium cuneatum</i>		B			
<i>Psidium cymosum</i>					E
<i>Psidium densicomum</i>		B	C		
<i>Psidium dictyophyllum</i>				D	
<i>Psidium firmum</i>		B			
<i>Psidium friedrichsthalianum</i>		B		D	E
<i>Psidium guajava</i>		B	C	D	
<i>Psidium guineense</i>		B	C	D	E
<i>Psidium kennedyanum</i>		B			
<i>Psidium laruotteanum</i>		B	C		
<i>Psidium longipetiolatum</i>		B	C		
<i>Psidium luridum</i>	A	B			
<i>Psidium maribense</i>		B	C		
<i>Psidium missionum</i>			C	D	
<i>Psidium montanum</i>			C	D	
<i>Psidium multiflorum</i>			C		
<i>Psidium myrsinthes</i>			C	D	
<i>Psidium persoonii</i>		B	C	D	
<i>Psidium riparium</i>		B	C		
<i>Psidium rufum</i>		B		D	
<i>Psidium salutare</i>		B	C		
<i>Psidium sartorianum</i>		B	C		
<i>Psidium spatulatum</i>		B			
<i>Psidium striatulum</i>		B	C		
<i>Ugni candollei</i>		B	C	D	
<i>Ugni molinae</i>	A				
<i>Ugni myricoides</i>	A	B	C		

fell in the A to B range and none had more than one gland per anther. Larger samples of these enormous subtribes of hundreds of species will have to be made before any conclusions can be drawn, but the small sample in this study seems to indicate that highly glandular anthers may be a rarity in American Eugeniinae and Myrciinae.

Just as a mean number of glands per specimen was calculated, a mean for each species in the four principal genera of American Myrtinae was also calculated. The generic ranges of these species means are as follows: *Campomanesia*, 0–1.1, excluding *C. speciosa* with 20.9; *Mosiera*, 1–1.8; *Calycolpus*, 9.3–18.9, excluding *Calycolpus legrandii* with 0.2 and *Calycolpus warscewiczianus* with 65.4; and *Psidium*, with 1–4 in most species, but with 0 in *Psidium*

appendiculatum, and a few species with means exceeding 4, viz., *P. montanum* (5.5), *P. amplexicaule* (5.7), *P. dyctophyllum* (7.2), *P. cymosum* (11.2), *P. friedrichsthalianum* (11.6), and *P. guineense* (13.2).

DISCUSSION

To our knowledge, anther glandularity has never been used taxonomically in the Myrtaceae before except for the studies by Landrum cited above. With this survey we have found that it can be an important character at the generic and specific level. Additional surveys in the family should prove interesting.

Studies of anther glandularity have the advantage of being inexpensive to conduct and cause little damage to herbarium specimens, which normally have numerous anthers in flowering specimens. A survey could easily be included as a part of monographic studies.

What is the purpose of glands in anthers? Three potential answers occur to us. 1) the glands may provide a floral aroma; 2) they may be a protection against insects that eat anthers; or 3) their contents may be a food source for insect visitors as has been hypothesized for *Thryptomene calycina* (Lindl.) Stapf (Myrtaceae) by Beardsell et al. (1989) and for *Prosopis juliflora* (Sw.) DC. (Leguminosae) by Chaudhry and Vijayaraghavan (1992). Studies of insects visiting flowers of *Campomanesia* and *Calycolpus* might provide answers, because these genera differ markedly in anther glandularity. *Psidium guineense*, a widespread and variable species might also be of interest, because it varies more in anther glandularity than any other in the genus.

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APPENDIX A

Each specimen is identified by collector, collection number, and herbarium. The highest and lowest of five counts are given first (if these are the same, only a single number is given), followed by the average of five counts. Thus, "1, 1.0" means all anthers had a single gland; "0-1, 0.8" means that anthers had zero to 1 gland and that the mean number for the specimen was 0.8.

AMERICAN MYRTINAE

Acca macrostema (Ruiz & Pavón ex G. Don) McVaugh: *Smith & Buddensiek 10860* (ASU), 1, 1.0; *Valencia 1627* (ASU), 1, 1.0.

Acca sellowiana (Berg) Burret: *Lehto 5942b* (ASU), 1, 1.0; *Viana et al. 8218* (ASU), 1, 1.0; *Wasum et al. 4757* (ASU), 0-1, 0.8.

Amomyrtella guili (Sprengel) Kausel: *Legname & Cuezso 9640* (US), 0-1, 0.2; *Solomon 11018* (CAS), 0-1, 0.6.

Amomyrtus luna (Molina) Legrand & Kausel: *Landrum 7606* (ASU), 0-1, 0.2; *Landrum 8099* (ASU), 0-1, 0.2; *Landrum 8157* (ASU), 0, 0.0.

Amomyrtus meli (Philippi) Legrand & Kausel: *Landrum 8098* (ASU), 0, 0.0.

Blepharocalyx cruckshanksii (Hook. & Arn.) Niedenzu: *Gardner & Page 4982* (ASU), 1, 1.0; *Landrum 5861* (ASU), 1, 1.0; *Landrum 5873* (ASU), 1, 1.0.

Blepharocalyx salicifolius (Kunth) Berg: *Hatschbach 28095* (ASU), 1, 1.0; *Hatschbach 53600* (ASU), 1, 1.0; *Zardini 7806* (ASU), 1, 1.0.

Calycolpus alternifolius (Gleason) Landrum: *Do Amaral 1516* (ASU), 6-9, 7.4; *Holst 3748* (ASU), 7-11, 9.0; *Huber et al. 10206* (ASU), 6-9, 8.4; *Maguire & Politi 27521* (MICH), 0-4, 2.0; *Steyermark & Wurdack 1200* (F), 14-22, 18.4; *Steyermark & Wurdack 1200* (MICH), 21-26, 23.2.

Calycolpus bolivarensis Landrum: *Fernández 3068* (ASU), 8-11, 9.8.

Calycolpus calophyllus (Kunth) Berg: *Maguire & Wurdack 35587* (MICH), 17-20, 18.2; *Maguire et al. 36475* (NY), 11-20, 15.6; *Prance et al. 30058* (ASU), 15-26, 20.0.

Calycolpus goetheanus (DC.) Berg: *Holst 3029* (ASU), 16-19, 17.0; *Huber 9312* (NY), 14-20, 17.0; *Philcox et al. 7429* (NY), 10-13, 11.4.

Calycolpus legrandii Mattos: *Amorim et al. 1513* (ASU), 0-1, 0.2; *Plowman 12777* (NY), 0-1, 0.2.

Calycolpus moritzianus (Berg) Burret: *Aymard 1027* (MO), 17-26, 19.8; *Grifo & Hahn 338A* (MO), 10-29, 18.2; *Zaruchi & Betancur 6422* (ASU), 12-20, 18.6.

Calycolpus revolutus (Schauer) Berg: *B. W. 4197* (US), 4-7, 5.8; *Cowan 38859* (MICH), 11-15, 12.8; *Maas & Westra 3519* (MICH), 6-14, 9.4.

Calycolpus surinamensis McVaugh: *Irwin et al. 55186* (US), 12-19, 13.8; *Rosa 231* (MICH), 20-27, 23.6.

Calycolpus warszewiczianus Berg: *de Nevers et al. 7710* (ASU), 34-50, 40.6; *Dwyer et al. 4705* (MICH), 62-84, 75.2; *Croat 7682* (F), 62-72, 68.4; *Croat 7682* (NY), 63-85, 77.2.

Campomanesia adamantium (Cambess.) Berg: *Gottsberger & Gottsberger 22-25990* (ASU), 0, 0.0; *Gottsberger & Gottsberger 22-25990* (ASU), 0, 0.0.

Campomanesia aurea Berg: *Wasum et al. 4946* (ASU), 1, 1.0.

Campomanesia espiritosantensis Landrum: *Folli 301* (ASU), 1, 1.0.

Campomanesia eugenioides (Cambess.) Legrand: *Hatschbach & Hatschbach 54629* (ASU), 1, 1.0.

Campomanesia grandiflora (Aublet) Sagot: *Acevedo 3489* (ASU), 1, 1.0; *Silva 1450* (ASU), 1, 1.0.

Campomanesia guaviroba (DC.) Kiaerskov: *Kummrow 2833* (ASU), 1, 1.0; *Poli-guesi 28* (ASU), 1-2, 1.4; *Silva 380* (ASU), 1, 1.0.

Campomanesia guazumifolia (Cambess.) Berg: *Gentry et al. 59409A* (ASU), 1, 1.0; *Vanni & Cáceres 675* (ASU), 1, 1.0; *Zardini & Velázquez 15158* (ASU), 1, 1.0.

Campomanesia laurifolia Gardner: *Hatschbach 48785* (ASU), 0, 0.0.

- Campomanesia neriiflora* (Berg) Niedenzu: *Hatschbach 49843* (ASU), 1, 1.0.
Campomanesia pubescens (DC.) Berg: *Gentry et al. 59272* (ASU), 0, 0.0; *Gottsberger & Gottsberger 15-141090* (ASU), 0, 0.0; *Gottsberger & Gottsberger 32-41090* (ASU), 0, 0.0.
Campomanesia sessiliflora (Berg) Mattos: *Hatschbach 48473* (ASU), 1, 1.0; *Hatschbach & Hatschbach 52621* (ASU), 1-2, 1.4; *Pott 5698* (ASU), 1, 1.0.
Campomanesia speciosa (Diels) McVaugh: *Foster 11330* (ASU), 16-24, 20.2; *Morawetz & Wallnofer 11-30985* (ASU), 20-23, 21.6.
Campomanesia velutina (Cambess.) Berg: *Gottsberger & Gottsberger 11-24990* (ASU), 0, 0.0; *Gottsberger & Gottsberger 12-25990* (ASU), 0, 0.0; *Gottsberger & Gottsberger 14-24990* (ASU), 0, 0.0.
Campomanesia viatoris Landrum: *Amorim et al. 1500* (ASU), 0, 0.0.
Campomanesia xanthocarpa Berg: *Hatschbach 52388* (ASU), 1, 1.0; *Jaster 232* (ASU), 0, 0.0; *Kummrow 3084* (ASU), 1, 1.0.
Chamguava gentlei (Lundell) Landrum: *Contreras 10882* (ASU), 3-5, 3.6; *Gentle 8552* (ASU), 1-2, 1.6; *Landrum 6538* (ASU), 7-11, 8.4.
Chamguava schippii (Standley) Landrum: *Gentle 8354* (ASU), 0, 0.0.
Legrandia concinna (Philippi) Kausel: *Landrum 7628* (ASU), 0, 0.0.
Mosiera bullata (Britton & Wilson) Bisse: *Britton & Cowell 13328* (F), 1, 1.0; *Britton et al. 13246* (F), 1, 1.0.
Mosiera contrerasii (Lundell) Landrum: *Durán 990* (MO), 1, 1.0.
Mosiera ehrenbergii (Berg) Landrum: *Johnston et al. 11161* (NY), 0-1, 0.8; *Purpus 5211* (UC), 2-3, 2.8.
Mosiera longipes (Berg) Small: *Curtis No. E* (GH), 1, 1.0; *Killip 43241* (US), 1, 1.0; *Proctor 9018* (GH), 1, 1.0.
Mosiera moensis (Britton & Wilson) Bisse: *Webster 3795* (MICH), 1, 1.0.
Mosiera ophiticola (Britton & Wilson) Bisse: *Acuña 12609* (NY), 1, 1.0; *Howard 6003* (NY), 1, 1.0; *León et al. 20240* (NY), 1, 1.0.

The following two species apparently belong to *Mosiera* but have not yet been transferred.

- Psidium saxicola* Britton & Wilson: *Clemente 5340* (NY), 1, 1.0.
Eugenia xerophytica Britton: *Miller et al. 6493* (ASU), 1, 1.0.
Myrrhinium atropurpureum Schott: *Kummrow 2792* (ASU), 8-15, 11.4; *Silva 200* (ASU), 18-23, 20.6; *Wasum & Brinker 6265* (ASU), 20-26, 23.2.
Myrteola acerosa (Berg) Burret: *Ferreira & Acleto 15299* (ASU), 1, 1.0.
Myrteola nummularia (Poirot) Berg: *Clemants et al. 2245* (ASU), 1, 1.0.
Myrteola phyllicoides (Benth.) Landrum: *Dillon et al. 6442* (ASU), 1, 1.0; *Mostacero et al. 1147* (ASU), 1, 1.0; *Stein 2497* (ASU), 1, 1.0; *van der Werff & Palacios 9455* (ASU), 1, 1.0.
Pimenta dioica (L.) Merr.: *Balick 3135* (ASU), 1, 1.0; *Ihrig & Staples 609* (ASU), 1, 1.0; *Martínez 11774* (ASU), 1, 1.0.
Pimenta pseudocaryophyllus (Gomes) Landrum: *Poliguesi 18* (ASU), 1, 1.0.
Pimenta racemosa (Mill.) J. Moore: *Ihrig & Staples 608* (ASU), 0, 0.0; *Lau 2416* (ASU), 0, 0.0.
Psidium acutangulum DC.: *Froes 1927* (MICH), 1, 1.0; *Irwin et al. 55388* (MICH), 1, 1.0; *Krukoff 1089* (NY), 1-3, 2.0; *Prance & Silva 58834* (MICH), 3-4, 3.8; *Prance et al. 5917* (MICH), 0-1, 0.2; *Prance et al. 14133* (MICH), 2-4, 3.6; *Prance et al. 14133* (NY), 2-5, 3.6; *Revilla & Carrillo 1503* (MICH), 10-14, 12.0; *Vázquez & Jaramillo 9283* (ASU), 1, 1.0.
Psidium amplexicaule Pers.: *Ekman 18861* (NY), 3-5, 4.0; *Fishlock 94* (NY), 7-15, 10.0; *Smith 10574* (MICH), 4-6, 5.0; *Smith 10574* (NY), 3-5, 3.6.
Psidium appendiculatum Kiaerskov: *Facultad de Ciencias Forestales s.n.* (NY), 0, 0.0.
Psidium arayan (Kunth) Burret: *Luteyn & Callejas 11782* (ASU), 1, 1.0.

- Psidium australe* Cambess.: *Hatschbach 50322* (ASU), 1, 1.0; *Hatschbach & Hatschbach 55798* (ASU), 1, 1.0; *Silva 739* (ASU), 1, 1.0.
- Psidium cattleianum* Sabine: *Krapovickas & Cristóbal 43513* (ASU), 1, 1.0; *Rosato & Alii 4861* (ASU), 1, 1.0.
- Psidium cinereum* Martius: *Harley 26964* (ASU), 2-3, 2.8; *Hatschbach 27710* (ASU), 2-3, 2.2; *Hatschbach & Hatschbach 55874* (ASU), 1-2, 1.8; *Ribas 199* (ASU), 2-3, 2.2.
- Psidium cuneatum* Cambess.: *Carnevali 4947* (ASU), 1-3, 2.0; *Krapovickas & Cristóbal 44444* (ASU), 1, 1.0; *Landrum 5717* (ASU), 1-3, 1.6.
- Psidium cymosum* Urban: *Alain 1194* (NY), 10-13, 11.2.
- Psidium densicomum* DC.: *Ayala 310* (ASU), 1-2, 1.2; *Cid 4144* (ASU), 0-5, 2.0; *Gentry & Perry 78002* (ASU), 2-4, 3.0.
- Psidium dictyophyllum* Urban & Ekman: *Zanoni et al. 33501* (ASU), 6-9, 7.2.
- Psidium firmum* Berg: *Irwin & Soderstrom 5129* (CAS), 1, 1.0.
- Psidium friedrichsthalianum* (Berg) Niedenzu: *Grijalva & Grijalva 1777* (MO), 11-20, 15.6; *Guzmán 1804* (MO), 15-18, 17.0; *Heyde & Lux 2984* (MO), 8-13, 10.2; *Landrum 6555* (ASU), 12-22, 15.6; *Marshall & Neill 7093* (MO), 8-11, 9.8; *Matuda 18733* (CAS), 12-15, 13.6; *Schmid 1972-8* (MICH), 13-18, 15.2; *Skutch 3989* (MO), 4-8, 5.8; *Woronow & Juzepczuk 4865* (MO), 1-2, 1.8.
- Psidium guajava* L.: *Arvigo 239* (ASU), 7-10, 8.4; *Boege 475* (CAS), 1-2, 1.2; *Delgado 150* (CAS), 2-4, 2.4; *Etienea s.n.* (CAS), 2-3, 2.2; *Hatschbach & Hatschbach 52449* (ASU), 4-5, 4.4; *Hinton 5637* (ASU), 2-4, 2.8; *Howell 8457* (CAS), 1-2, 1.2; *Landrum 5677* (ASU), 3-4, 3.4; *Landrum 5681* (ASU), 1-3, 2.0; *Landrum 5683* (ASU), 3-4, 3.2; *Landrum 5684* (ASU), 2-5, 3.5; *Landrum 5689* (ASU), 1-7, 3.6; *Landrum 5690* (ASU), 3-4, 3.4; *Landrum 5742* (ASU), 2-3, 2.6; *López 1164* (CAS), 2-4, 2.8; *Nelson & Nelson 5180* (DS), 1, 1.0; *Pipoli 9058* (ASU), 5-7, 5.8; *Pipoli 9096* (ASU), 3-6, 4.6; *Robertson 12* (DS), 4-7, 6.0; *Skog 1518* (CAS), 4-6, 4.8; *Torres 201* (CAS), 3-4, 3.4.
- Psidium guineense* Sw.: *Allen 1007* (MICH), 6-11, 9.0; *Bang 287* (CAS), 5-10, 7.0; *Bang 2831* (NY), 3-7, 4.8; *Brother Paul 465* (MICH), 24-43, 34.4; *Harley 26590* (ASU), 2-3, 2.2; *Hatschbach 30415* (ASU), 3-6, 4.0; *Hatschbach 54720* (ASU), 34-52, 46.0; *Irwin et al. 21204* (MICH), 40-55, 46.6; *Jansen-Jacobs 89* (ASU), 15-25, 18.6; *King 593* (MICH), 6-12, 9.4; *Landrum 5678* (ASU), 4-7, 5.8; *Landrum 5679* (ASU), 4-7, 6.0; *Landrum 5680* (ASU), 5-9, 7.0; *Landrum 5708* (ASU), 5-6, 5.8; *Landrum 7865* (ASU), 8-9, 8.4; *Longhi et al. SPF34954 CFCR 5894* (ASU), 1-2, 1.0; *Maas & Maas 500* (MICH), 5-12, 9.0; *Maguire & Maguire 40214* (MICH), 10-14, 12.2; *Montes 14792* (CAS), 0-5, 2.2; *Ribeiro 1489* (CAS), 3-5, 4.0; *Tressens et al. 3470* (ASU), 2-4, 3.4; *Witsberger 847* (MICH), 12-23, 18.0.
- Psidium guajava* × *guineense*: *Landrum 5682* (ASU), 3-4, 3.4; *Landrum 5686* (ASU), 3-9, 6.4; *Landrum 5695* (ASU), 4-9, 7.0.
- Psidium kennedyanum* Morong: *Hatschbach & Hatschbach 52495* (ASU), 1, 1.0; *Zardini & Velázquez 19804* (ASU), 1-2, 1.2.
- Psidium laruoetanum* Cambess.: *Gottsberger & Gottsberger 11-141090* (ASU), 3-4, 3.4; *Harley 26608* (ASU), 1, 1.0; *Hatschbach & Hatschbach 53638* (ASU), 1, 1.0.
- Psidium longipetiolatum* Legrand: *Hatschbach 15250* (NY), 2-4, 3.0. *Hatschbach 15289* (NY), 1, 1.0; *Kuniyoshi 4722* (ASU), 1, 1.0.
- Psidium luridum* (Sprengel) Burret: *Ekman 2048* (MICH), 0-1, 0.6; *Ekman 2048* (NY), 0-1, 0.4; *Hatschbach 54810* (ASU), 0-1, 0.2; *Rosengurt b-4183* (NY), 1, 1.0. *Zardini 7247* (ASU), 1-3, 1.8.
- Psidium maribense* DC.: *Davidse & González 13083* (MO), 1-5, 3.2; *Davidse & González 14065* (MO), 1, 1.0; *Davidse & González 14709* (MO), 1-4, 3.2.
- Psidium missionum* Legrand: *Krapovickas & Cristóbal 44607* (ASU), 3-4, 3.4; *Landrum 5735* (ASU), 3-5, 4.0.
- Psidium montanum* Sw.: *Harris 3183* (NY), 3-4, 3.6; *Proctor 26438* (MICH), 6-10, 7.8; *Proctor 32738* (NY), 3-7, 5.0.

Psidium multiflorum Cambess.: *Gottsberger & Gottsberger 11-27990* (ASU), 2-3, 2.4; *Hatschbach 43388* (ASU), 2-3, 2.6.

Psidium myrsinthes DC.: *Irwin et al. 9132* (MICH), 2-3, 2.6; *Irwin et al. 9132* (NY), 4-6, 5.2; *Irwin et al. 10203* (MICH), 2-4, 2.6; *Maguire et al. 57100* (MICH), 3, 3.0.

Psidium persoonii McVaugh: *Cid et al. 746* (CAS), 1-2, 1.6; *De Granville et al. 9635* (ASU), 3-6, 4.2; *van Donselaar 3731* (MICH), 1-4, 3.0.

Psidium riparium Martius ex DC.: *Macedo 4059* (MO), 2-5, 3.2; *Silva 2715* (MO), 1, 1.0; *Silva 2715* (NY), 1, 1.0.

Psidium rufum DC.: *Harley 26373* (ASU), 1-2, 1.4; *Harley et al. 25891* (ASU), 1, 1.0; *Hatschbach 15252* (MICH), 1, 1.0; *Williams 8061* (MO), 4-6, 5.2.

Psidium salutare (Kunth) Berg: *Jansen-Jacobs 87* (ASU), 1-3, 2.2; *Landrum 6521* (ASU), 1-3, 1.6; *Liesner & González 11064* (ASU), 1-3, 1.6; *Zarucchi & Barbosa 3749* (ASU), 1-3, 2.2.

Psidium sartorianum (Berg) Niedenzu: *Landrum 6524* (ASU), 3, 3.0; *Silva 279* (ASU), 3-5, 3.8; *Torres 9811* (ASU), 1-2, 1.2.

Psidium spatulatum Mattos: *Hatschbach 17675* (MICH), 1, 1.0; *Hatschbach 17675* (NY), 1, 1.0.

Psidium striatulum DC.: *Dubs 981* (ASU), 1-2, 1.0; *Ferreira 9638* (ASU), 2-3, 2.4.

Ugni candollei (Barnéoud) Berg: *Gentry et al. 53489* (ASU), 1-3, 1.6; *Landrum 5907* (ASU), 3-5, 4.0; *Landrum 5909* (ASU), 1-3, 2.0.

Ugni molinae Turcz.: *Landrum 5881* (ASU), 0-1, 0.8; *Taylor et al. 10367* (ASU), 0-1, 0.6; *Taylor et al. 10377* (ASU), 0-1, 0.2.

Ugni myricoides (Kunth) Berg: *Davidse et al. 25949* (ASU), 0-2, 1.0; *Landrum 6559* (ASU), 1-3, 1.8; *Liesner 23311* (ASU), 0-1, 0.6; *Méndez 8385* (ASU), 1-4, 2.0; *Tenorio 7498* (ASU), 0-2, 0.4.

OLD WORLD MYRTINAE

Decaspermum alpinum P. Royen: *Conn LAE 69313* (ASU), 1, 1.0.

Decaspermum gracilentum (Hance) Merr. & Pers.: *Kao 7330* (ASU), 1, 1.0.

Myrtus communis L.: *Lehto 16884* (ASU), 3, 3.0; *Lehto 18231* (ASU), 3-7, 5.4; *Poelt s.n.* (ASU), 3-6, 4.8.

Rhodomyrtus tomentosa (Ait.) Hassk.: *Faircloth 1797* (ASU), 5-8, 6.2.

AMERICAN EUGENIINAE

Calycorectes grandifolius Berg: *Prévost 1692* (ASU), 16-21, 18.6.

Calycorectes yatauae McVaugh: *Liesner 16997* (ASU), 1, 1.0.

Eugenia axillaris (Sw.) Willd.: *Glassman 5018* (ASU), 1-2, 1.6.

Eugenia capuli (Schlidl. & Cham.) Berg: *Ventura 30* (ASU), 1, 1.0.

Eugenia farameoides A. Rich.: *Hernández 1316* (ASU), 3-4, 3.4.

Eugenia octopleura Krug & Urban ex Urban: *Haber 758* (ASU), 1, 1.0.

Eugenia oerstedeaana Berg: *Ventura 8106* (ASU), 0-1, 0.4.

Eugenia pseudopsidium Jacq.: *Prévost 1691* (ASU), 0, 0.0.

Eugenia puniceifolia (Kunth) DC.: *Caballero s.n.* (ASU), 1, 1.0.

Eugenia stipitata McVaugh: *Peters 146* (ASU), 1, 1.0.

Eugenia uniflora L.: *Ortiz 753* (ASU), 0, 0.0.

Myrcianthes mato (Griseb.) McVaugh: *Landrum 5772* (ASU), 1, 1.0.

Myrcianthes pungens (Berg) Legrand: *Hatschbach & Hatschbach 55787* (ASU), 1, 1.0.

Myrcianthes rhopaloides (Kunth) McVaugh: *Solomon 8653* (ASU), 1, 1.0.

Myrciaria cordifolia Legrand: *Cordeiro 344* (ASU), 0, 0.0.

Myrciaria delicatula (DC.) Berg: *Krapovickas & Schinini 38202* (ASU), 0-1, 0.8.

Myrciaria floribunda (West ex Willd.) Berg: *Hatschbach 54928* (ASU), 1, 1.0.

Neomitranthes glomerata (Legrand) Legrand: *Hatschbach 19578* (ASU), 0, 0.0.

AMERICAN MYRCIINAE including the anomalous genus *Luma* that may or may not belong to this subtribe

- Calyptranthes amshoffae* McVaugh: *Larpin* 846 (ASU), 0, 0.0.
Calyptranthes concinna DC.: *Cordeiro* 688 (ASU), 1, 1.0.
Calyptranthes longifolia Berg: *Wallnofer* 11-13788 (ASU), 0, 0.0.
Luma apiculata (DC.) Burret: *Landrum* 5872 (ASU), 0, 0.0.
Luma chequem (Molina) A. Gray: *Gardner et al.* 4427 (ASU), 0, 0.0.
Myrceugenia campestris (DC.) Legrand & Kausel: *Hatschbach* 52288 (ASU), 0, 0.0.
Myrceugenia chrysocarpa (Berg) Kausel: *Gardner* 3503 (ASU), 1, 1.0.
Myrceugenia miersiana (Gardner) Legrand & Kausel: *Kummrow* 2904 (ASU), 1, 1.0.
Myrceugenia myrcioides (Cambess.) Berg: *Silva* 313 (ASU), 1, 1.0.
Myrceugenia obtusa (DC.) Berg: *Landrum* 8214 (ASU), 1, 1.0.
Myrcia calyptranthoides (Berg) Mattos: *Hatschbach* 53588 (ASU), 1, 1.0.
Myrcia citrifolia (Aublet) Urban: *Pirani* 1221 (ASU), 1, 1.0.
Myrcia cuprea (Berg) Kiaerskov: *Mori et al.* 17512 (ASU), 0-1, 0.6.
Myrcia fallax (A. Rich.) DC.: *Sobel et al.* 4580 (ASU), 1, 1.0.
Myrcia guianensis (Aublet) DC.: *Lewis et al.* SPF 36940, CFCR 7140 (ASU), 1, 1.0.
Myrcia saxatilis (Amshoff) McVaugh: *Larpin* 740 (ASU), 1, 1.0.

OLD WORLD LEPTOSPERMAE

- Chamaelaucium uncinatum* Schauer: *Earle* 23 (ASU), 1, 1.0.
Choricarpia leptopetala (F. Muell.) Domin: *Coveny* 15872 (ASU), 1, 1.0.
Metrosideros fulgens Gaertn.: *Weston* 1192 (ASU), 0, 0.0.
Metrosideros polymorpha Gaud.: *Clements* 17 (ASU), 5-8, 6.0.

ENVIRONMENTAL DETERMINANTS OF FLOWERING DATE
IN THE COLUMNAR CACTUS *CARNEGIEA GIGANTEA* IN
THE NORTHERN SONORAN DESERT

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ABSTRACT

Spring flowering of some woody plants in the Sonoran Desert is triggered by the first substantial rain of the cool season. The columnar cactus *Carnegiea gigantea*, as a massive succulent, might be expected to use internal moisture reserves for flower production, thus blooming independently of rainfall. To investigate the environmental signals for flowering in this species, phenological data were collected for 7 to 10 plants from 1967–1988 at Tumamoc Hill, Tucson, Arizona. Climatic and flowering data from 1978–1988 were used to model developmental requirements for the annual peak bloom in May. The models suggested that flowering of *Carnegiea* is controlled by cool-season rain, increasing daylength, and a combination of increasing solar radiation and warming temperatures. A cool-season (November–March) rain of at least 5–9 mm is probably the initial trigger; a post-solstice photoperiod of about 10.5 hr is the second. After days reach 10.5 hours in length, solar thermal units (daily mean temperature \times total daily solar radiation) above a base temperature of 10°C must accumulate to about 489,500 for half the population to flower. Precisely timed seed release is vital to reproductive success in this species. In effect, the rainfall trigger coordinates flowering with soil-moisture availability, and the daylength trigger ensures seed release at the most favorable season for germination.

For most plant species, the timing of flowering and fruiting is an important aspect of reproductive success. In deserts, where germination, emergence, and recruitment are highly episodic (Shreve 1917; Barbour 1968; Sheps 1973; Ackerman 1979; Sherbrooke 1989), the timing of reproduction can be critical. For example, *Fouquieria splendens* Engelm., a drought-deciduous shrub with many wandlike stems, flowers in spring and disperses seeds that germinate during the summer rainy season (Shreve 1917). Unless the summer rains are early and heavy (≥ 25 mm), animals consume the seeds before they can germinate (Bowers 1994). A shift in flowering phenology to a somewhat later bloom might solve this problem, but, as Waser (1979) has demonstrated, the flowering season is tightly constrained by the major pollinators, migratory hummingbirds present only for three to four weeks in March and April. The flowering phenology of *F. splendens* thus reflects a web of climatic and biotic interactions with profound effects on seedling recruitment and eventually on the demography of adult populations. The climatic variable that coordinates these interactions from year to year is the flowering

trigger, in this case the first cool-season storm ≥ 10 mm (Bowers and Dimmitt 1994).

Phenological triggers can be regarded as switches that break bud dormancy and start developmental processes such as leafing and flowering. Once set in motion, these processes advance as a function of temperature, daylength, or some combination of the two (Loomis and Connor 1992). Only three environmental triggers for flowering have been identified: photoperiod, temperature, and moisture (Rathcke and Lacey 1985; Loomis and Connor 1992). Other conditions, such as a particular ratio of soil nutrients, may be prerequisites for normal flower development (Kinet 1993); however, these are not triggers as defined here.

Because rainfall in deserts is temporally and spatially variable, phenological triggers are of particular importance in coordinating flowering, fruiting, and seed dispersal with favorable moisture conditions. The woody Sonoran Desert plants *Larrea tridentata* (DC.) Cov., *Fouquieria splendens*, *Ambrosia deltoidea* (A. Gray) Payne, *Encelia farinosa* A. Gray, and *Acacia constricta* Benth. all flower in response to significant rain, for example (Bowers and Dimmitt 1994). Neither temperature triggers nor photoperiod triggers can accurately coordinate their periods of bloom with periods of greatest soil moisture. Bowers and Dimmitt (1994) suggested that photoperiod is most likely to trigger flowering where the environment is predictable. For example, *Cercidium microphyllum* (Torr.) Rose & Johnston, a small Sonoran Desert tree with photosynthetic bark, blooms once a year during the late spring dry season, one of the few predictable climatic features of the northern Sonoran Desert. Its flowering trigger is apparently a daylength of about 11 hours (Bowers and Dimmitt 1994).

Phenological requirements of most Sonoran Desert plants have not been determined, making it difficult to assess potential feedback mechanisms between flowering phenology and recruitment success. One deterrent has been the lack of a suitable method for the combined analysis of flowering dates and climatic phenomena. Regression or correlation analysis, methods commonly used in arid regions (for example, Sharifi et al. 1983; Nilsen et al. 1987; Turner and Randall 1987; Friedl 1993), may demonstrate which climatic factors are most strongly correlated with flowering, but neither method can identify specific triggers or determine the required developmental heat sums. In this paper, I use a recently developed method (Bowers and Dimmitt 1994) to determine the climatic requirements for flowering in *Carnegiea gigantea* (Engelm.) Britt. & Rose, the giant cactus or saguaro, and to assess the implications of its rather narrow period of bloom. Because *Carnegiea*, like *C. microphyllum*, flowers once a year during the late spring dry season, I expected that its flowering would be cued by daylength also. Moreover, as a columnar

cactus, *Carnegiea* presumably could use internal moisture reserves to produce dry-season flowers, and flowering might therefore be independent of rainfall.

Carnegiea gigantea is conspicuous throughout the Arizona Upland of the Sonoran Desert (Shreve 1951). Mature plants grow to 12 m or more and first bloom at about 2.2 m (approximately 30–35 years of age) (Steenbergh and Lowe 1977). Near Tucson, Arizona, the earliest flowers appear during the last two weeks of April; peak flower occurs during the last week of May through the first week of June (Steenbergh and Lowe 1977). It has long been assumed that daylength and warming temperatures control *Carnegiea* flowering (Johnson 1924; Steenbergh and Lowe 1977); however, the exact phenological requirements have not been studied, and the flowering triggers are unknown. In this study, 10 years of climatic and flowering data from Tumamoc Hill, Tucson, Arizona, were used to derive several models of phenological requirements for *Carnegiea* bloom, including the type of trigger and the heat sum required for flower development. The models that explained the greatest amount of variance in flowering date formed a basis for describing the actual flowering requirements of *Carnegiea*.

METHODS

Study area. Tumamoc Hill, located at 32°13'N, 111°05'W, is a rocky outlier of the Tucson Mountains near Tucson, Arizona. Elevations range from 703 to 948 m above sea level. The rocky, basaltic-andesitic slopes are dominated by *Cercidium microphyllum*, *Encelia farinosa*, *Fouquieria splendens*, *Larrea tridentata*, *Carnegiea gigantea*, *Ambrosia deltoidea*, *Opuntia engelmannii* Salm-Dyck, and other woody perennials characteristic of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951; Goldberg and Turner 1986). The *Carnegiea* plot is located on a rocky basaltic-andesitic island slightly west of Tumamoc Hill at an elevation of about 703 m.

Daily maximum and minimum temperatures have been recorded at a weather station located about halfway up the hill at the Desert Laboratory (814 m, hereafter referred to as the hill shelter) from 1907 to 1939, 1943 to 1956, and 1976 to the present. From 1932 to 1939, maximum and minimum temperatures were also recorded at the north base of the hill (703 m, hereafter referred to as the base shelter). Between 1978 and 1988, average maximum and minimum January temperatures at the hill shelter were 19.9°C and 7.9°C. In June they were 39.8°C and 24.5°C. The precipitation record extends from 1907 to the present. Rainfall averages 250 mm/year. Almost half falls during July, August, and September; most of the remainder

comes between November and March. Late spring (April to June) and early autumn (October) are typically without rain.

Carnegiea data collection. From 1959 to 1988, a group of *Carnegiea* plants on a 10 m × 10 m plot near the west base of Tumamoc Hill was regularly monitored by staff members of the University of Arizona and the U.S. Geological Survey. The plants were observed weekly from April to October during the period of flowering, fruiting, and active growth. At other seasons, they were generally observed monthly. At each observation, the height of the main stem and of any branches was measured so that growth rates could be determined (Hastings 1961). From 1967 to 1988 (except in 1974 and 1975), the presence of flower buds and flowers on main stems and branches was noted. From 1975 to 1988, the presence of fruits was also recorded. In 1967, the group consisted of 11 plants, 7 of them reproductively mature. In 1984, one of the original 11 died. By 1986, 9 of the 10 remaining plants were old enough to flower, and, in 1988, all 10 flowered.

For 17 of the 22 years from 1967–1988, there was enough information to determine average first and last date of flower, average duration of bloom (the number of days between first and last flower), and the first date when at least half the reproductive plants were in bloom (average flower date). For all but one of the years between 1975 and 1988, it was possible to determine the average first and last dates of fruit, average duration of fruit (the number of days between first and last fruit), and average length of reproductive season (the number of days from first flower to last fruit).

Climate data. No temperatures were available for the *Carnegiea* plot, but, based on elevation, it was assumed that *Carnegiea* plot temperatures would be close to those at the base shelter, which was in operation from 1932–1939. A regression of base versus hill temperatures was used to generate a record of estimated maximum and minimum temperatures for the *Carnegiea* plot for 1978 to 1988. The months used in the regression analysis were January–May 1934. The regression equation for minimum temperature was $y = 0.909x - 2.918$, where y = base shelter temperature and x = hill shelter temperature ($R^2 = 0.845$, $P < 0.001$). For maximum temperature, the equation was $y = 0.927x + 2.809$ ($R^2 = 0.986$, $P < 0.001$).

Determining the heat sum. Phenological analysis is necessarily empirical (Loomis and Connor 1992) and involves comparing the date of flower in a series of years with climatic conditions in each year. Although for most species the date of flower will vary from one year to the next, the accumulated heat, or heat sum, required for flowering should be about the same in every year.

One measure of accumulated heat, often expressed in degree days,

can be defined as the sum of mean daily temperatures above an appropriate base temperature. The summation starts with the date of trigger and ends with the date of flower. The heat sum can be calculated as

$$T_s = \sum (T_d - T_b) \quad \text{if } (T_d - T_b) > 0,$$

where T_s is degree days, T_d is the mean daily temperature, and T_b is the mean daily temperature above a base temperature (a minimum temperature required for growth).

A second measure of accumulated heat, solar thermal units, is a product of daily total solar radiation in langleys and daily mean temperature above a given base (Caprio 1973). Because CO_2 uptake in many cacti increases with daily total solar radiation (Gibson and Nobel 1986; Nobel 1988), it seemed possible that solar thermal units might be a more appropriate measure of heat requirements for saguaro bloom than degree days. Solar thermal units, which can be expressed as langley-degree days, can be calculated as

$$L_s = \sum [(L_d)(T_d - T_b)] \quad \text{if } (T_d - T_b) > 0,$$

where L_s is langley-degree days and L_d is daily total hemispheric solar radiation on a horizontal surface in langleys (Caprio 1973). The University of Arizona, 6 km east of Tumamoc Hill, was the closest station for daily total solar radiation.

When neither the heat requirements nor the date of trigger are known, as was the case for *Carnegiea*, it is necessary to select a range of appropriate trigger dates, then calculate the heat sum between each potential trigger date and the flower date for all years of record (Bowers and Dimmitt 1994). Valid triggers should produce heat sums that converge toward the same value year after year, whereas spurious triggers should produce values that vary greatly from one year to the next. My process of trigger selection is discussed in detail below.

Determining the base temperature. When the base temperature for growth is not known, the heat-sum calculations are made for each trigger date using several potential base temperatures (Arnold 1959). The temperatures used in this study (0, 5, 10, and 15°C) span the range of temperatures at which plants of warm-temperate or subtropical affinities are likely to grow (Hutchinson et al. 1992). The heat sums above a given base were averaged for the years of interest. The base temperature giving the smallest coefficient of variation is considered to be the most likely threshold (Arnold 1959), and the average heat sum above that base represents the amount of heat required for flower development. For this study, heat sums were calculated in both degree-days and langley degree-days.

Determining the dates of flower. In any year, the duration of flower within a population can be several days or weeks. For phenological analysis, it is necessary to select from this time span a single flower date. One common criterion is the first date in each year when half the population is in bloom (Loomis and Connor 1992), referred to here as the average flower date. A preliminary analysis of the *Carnegiea* plot data suggested that the number of plants in the sample was too small to provide a reliable average flower date. Because the apices of the several branches and main stem are typically at different heights above the ground, they experience somewhat different temperature regimes and do not necessarily flower simultaneously. Therefore, instead of the total number of plants (10–11 from 1978–1988), the total number of stems (17–18 from 1978–1988) was used in this analysis. The average flower date then became the first observation date in each year when 50% of the stems were in flower. This changed the flower date in three years: from May 26 to May 19 in 1978, from May 19 to May 27 in 1980, and from May 15 to May 21 in 1987. The average flower date for the ten-year period was the same in either case. The data from 1986 were dropped from the analysis because fewer than half the plants were in bloom on any observation date. Many blackened flower buds were observed, which suggests that a plant pathogen might have been involved.

Determining the phenological triggers. Because the trigger for *Carnegiea* bloom was not known, rainfall, photoperiod, and temperature were considered as potential triggers.

Rains probably act as a flower trigger by raising soil moisture to some threshold value, at which point, given suitable temperatures, flowering processes are initiated. Rainfall amounts are simply useful proxies for soil moisture measurements, which usually are not available. The smallest effective rainfall trigger known for Sonoran Desert shrubs is 9 mm (Bowers and Dimmitt 1994). In the northern Sonoran Desert, rain-triggered plants that flower in spring typically do so in response to the first substantial storm of the cool season (November–March) (Bowers and Dimmitt 1994). These early cool-season rains are an effective means of breaking dormancy, which in some species can be induced by the hot, rainless days of late September and October (for example, *Encelia farinosa* [Ehleringer 1982] and *Grayia spinosa* (Hook.) Moc. [Ackerman et al. 1980]). For this analysis, all cool-season rains ≥ 5 mm were treated as potential triggers for *Carnegiea* bloom. (Lack of October rainfall in 1979, 1981, and 1982 made it seem unlikely that autumn rains are triggers.) When rain fell on several consecutive days, the cumulative total was used as the trigger amount. When two or more different rain events seemed equally likely to have triggered a given flowering

event, heat sums were calculated above the four base temperatures for each one, then the rainfall trigger and base temperature that produced the smallest coefficient of variation were selected.

The following dates were used as potential daylength triggers: October 11 (11.5 hours of daylight), October 27 (11 hours), November 14 (10.5 hours), January 1 (10 hours), January 28 (10.5 hours), February 15 (11 hours), March 1 (11.5 hours), March 17 (12 hours), and March 31 (12.5 hours). This range of daylengths spans the decreasing photoperiods of late autumn and early winter and the increasing photoperiods of late winter and spring.

In cold-temperate climates, where spring warming brings many plants out of winter dormancy, temperature can be an effective means of cuing flower development to climatic trends (vernalization) (Caprio 1973). In the warm-temperate Sonoran Desert, where many winter days are warm enough for plant growth, no plants have been reported to require vernalization. Between November and March, minimum temperatures may range from 0 to 10°C over the course of a single week, and daily maxima as high as 25°C are not uncommon. Given this wide range of daily temperatures in winter and spring and the absence of a prolonged period of winter cold, it seemed unlikely that flowering in *Carnegiea* is triggered by a particular temperature threshold, therefore potential temperature triggers were not analyzed in this study.

Determining flowering requirements. Two types of models for formulating phenological requirements were derived, one type based on rainfall triggers, the other on photoperiod triggers. Climatic and flowering data from 1978–1988 were used to determine the base temperature and required heat sum (in degree days and langley-degree days) as described above. (These 10 years were those for which complete weather records existed.) As noted above, flowering was poor in 1986, and the data for that year were omitted from the analysis.

For each type of trigger and each type of heat sum considered, the best model solution was defined as the one that produced the lowest coefficient of variation. This produced four models, two using degree days, two using langley-degree days. The fit of these models was evaluated with linear regression, using the Julian flower date or the development period as the dependent variable. The development period was defined as the number of days from the date of trigger to the date of flower. The independent variables were: 1) degree days during the development period (rain trigger), 2) degree days per day during the development period (rain trigger), 3) degree days during the development period (photoperiod trigger), 4) degree days per day during the development period (photoperiod trigger), 5) Julian date of the degree-day rain trigger, 6) langley-degree days

during the development period (rain trigger), 7) langley-degree days per day during the development period (rain trigger), 8) langley-degree days during the development period (photoperiod trigger), 9) langley-degree days per day during the development period (photoperiod trigger), 10) langley degree-days from rain trigger to photoperiod trigger, and 11) Julian date of the langley-degree-day rain trigger.

RESULTS

Carnegiea flowering dates. From 1968–1988, the date of average flower, that is, the first date when at least 50% of reproductive plants were in bloom, occurred as early as April 25 and as late as June 1. The mean was May 19 (SE = 1.84). One plant produced flowers and fruits in May 1986, then twice initiated flower buds, which aborted, in August of the same year. First flower occurred as early as April 18, last flower as late as June 20. The average date of first flower was May 8 (SE = 1.70). June 12 was the average date of last flower (SE = 1.66). Duration of bloom averaged 36 days (SE = 2.33).

Carnegiea fruiting dates. The dates of first and last appearance of fruit were May 27 (SE = 2.15) and July 1 (SE = 1.74). Fruit duration averaged 41 days (SE = 1.85). The reproductive season from first flower to last fruit averaged 64 days (SE = 2.54).

Flowering requirements. Of the many model solutions considered, the best were: 1) first cool-season rain ≥ 5 mm, heat sum = 546,944 langley-degree days above 10°C (CV = 0.056); 2) daylength = 10.5 hr (January 28), heat sum = 489,460 langley-degree days above 10°C (CV = 0.062); 3) first cool-season rain ≥ 9 mm, heat sum = 1039 degree days above 10°C (CV = 0.057); and 4) daylength = 10.5 hr (January 28), heat sum = 1995 degree days above 0°C (CV = 0.050) (Fig. 1a, b).

In the linear-regression analysis, several independent variables explained a significant proportion of the variance in flower date: degree days/day from the rain trigger to the flower date ($R^2 = 0.869$, $P < 0.001$), langley-degree days/day from the rain trigger to the flower date ($R^2 = 0.900$, $P < 0.001$), langley-degree days from the photoperiod trigger to the flower date ($R^2 = 0.70$, $P < 0.006$), and degree days from the photoperiod trigger to the flower date ($R^2 = 0.50$, $P < 0.03$) (Table 1). No matter which dependent variable was used (flower date or length of the development period), langley-degree days explained a higher proportion of the variance than degree days, and therefore seems a more suitable unit for determining heat sums.

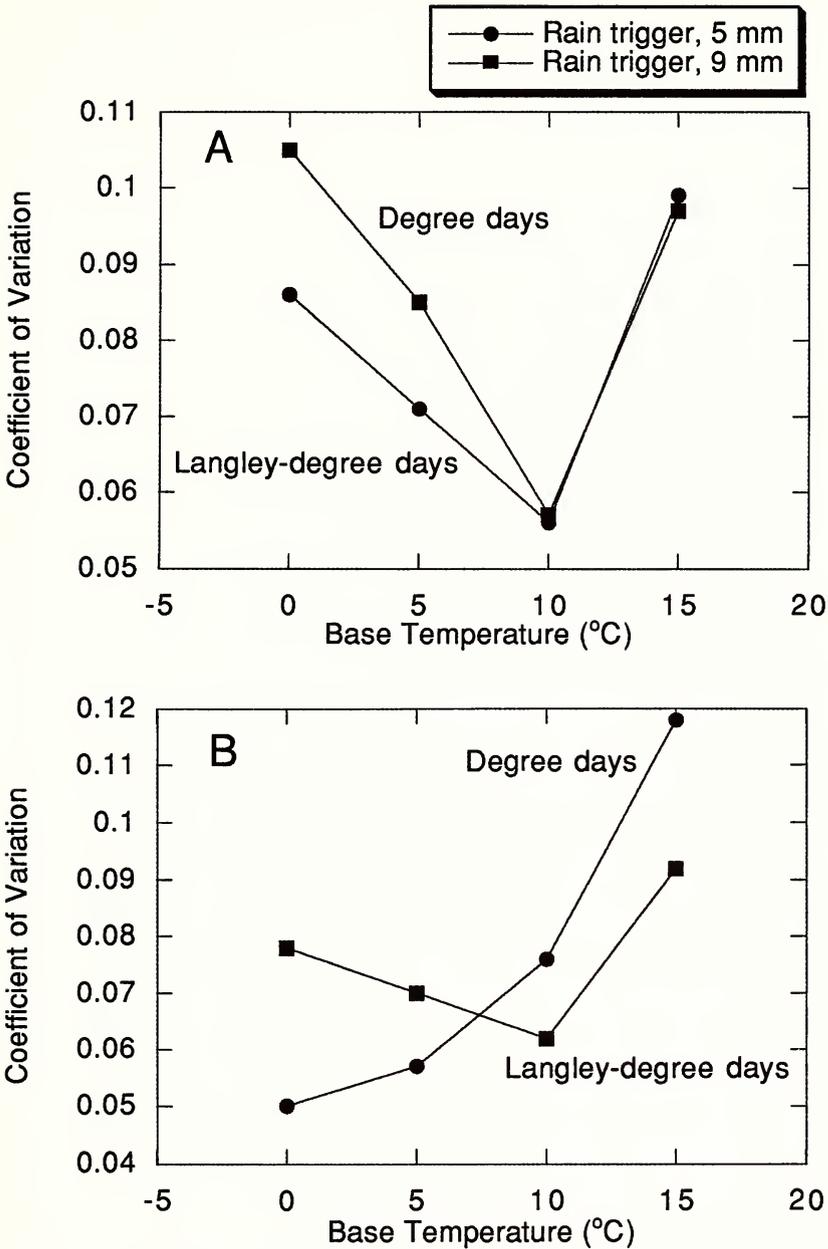


FIG. 1a. Relationship between base temperature and the coefficient of variation for average flower of *Carnegiea gigantea* from 1978–1988 using heat sums calculated from rainfall trigger to date of flower.

FIG. 1b. Relationship between base temperature and the coefficient of variation for average flower of *Carnegiea gigantea* from 1978–1988 using heat sums calculated from photoperiod trigger to date of flower.

TABLE 1. R² VALUES FROM THE LINEAR REGRESSIONS OF *CARNEGIEA* FLOWER DATE VERSUS 7 CLIMATIC VARIABLES. All dates were converted to ordinal numbers. DD = degree days (for base temperature, see text), DD/D = degree days/day, LDD = langley-degree days, LDD/D = langley-degree days/day, RTD = rain trigger date, PTD = photoperiod trigger date (10.5 hours after winter solstice), FD = flower date.

Independent variable	Dependent variable	R ²	P
Degree-day models			
DD from RTD to FD	Flower date	0.004	0.862
DD from PTD to FD	Flower date	0.504	0.022
RTD	Flower date	0.074	0.447
DD/D from RTD to FD	Days from RTD to FD	0.869	0.000
DD/D from PTD to FD	Days from PTD to FD	0.191	0.207
Langley-degree day models			
LDD from RTD to FD	Flower date	0.203	0.223
LDD from PTD to FD	Flower date	0.698	0.005
LDD from RTD to PTD	Flower date	0.113	0.377
RTD	Flower date	0.130	0.340
LDD/D from RTD to FD	Days from RTD to FD	0.900	0.000
LDD/D from PTD to FD	Days from PTD to FD	0.009	0.805

DISCUSSION

On the basis of the model solutions, it appears that flowering in this species is a complex phenomenon involving several different climatic signals. The model that uses a rain trigger and the average daily temperature sum (langley-degree days/day) explains 90% of the variance in length of the development period (Table 1). This model produces a strong inverse correlation between the length of the development period and the average daily heat sum (Fig. 2). This is not surprising; if the model works, a short development period would necessarily be correlated with higher daily temperature values, because there would be fewer days in which to achieve the required temperature sum. Put another way, warmer days speed cell development, thus producing shorter development periods. It appears virtually certain, therefore, that rainfall is involved in triggering *Carnegiea* bloom.

Other evidence supports this hypothesis, as well. The two best rain-trigger models produced strongly V-shaped curves and, at a base temperature of 10°C, low coefficients of variation (Fig. 1a). These traits are apparently typical of rain-triggered perennials in the Sonoran Desert, e.g., *Larrea tridentata* and *Encelia farinosa* (Bowers and Dimmitt 1994). The salient characteristic of a valid trigger is the strong convergence from year to year on a single heat sum (Bowers and Dimmitt 1994). Among the many potential rain triggers for *Carnegiea* bloom, all but two produced linear, rather than V-shaped, curves and comparatively large coefficients of variation; in short, they failed to converge on a single heat sum. It appears, there-

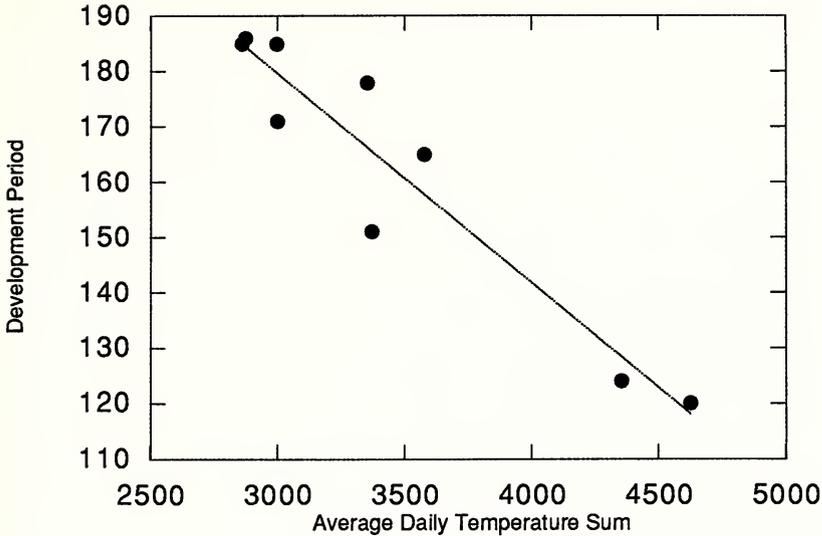


FIG. 2. Length of the development period in days as a function of the average daily temperature sum in langley-degree days above 10°C. The development period extends from rainfall trigger to date of flower.

fore, that most of the potential rain triggers examined in this study had no bearing on *Carnegiea* bloom. Two, however, the first cool-season rains ≥ 5 mm and ≥ 9 mm, stood out from the rest, making it seem very likely that cool-season rain plays a vital role in triggering *Carnegiea* bloom.

The photoperiod/langley-degree day model accounts for almost 70% of the variance in flower date, strongly suggesting that photoperiod is also involved in the timing of *Carnegiea* bloom. If this high correlation were due solely to the mechanical interaction between temperature and time, such that the highest temperature sums were accumulated during the longest periods of time, one would expect a strong positive correlation between langley-degree days/day and length of the development period. This does *not* occur, however (Fig. 3), indirectly supporting the idea that photoperiod does indeed play a role in *Carnegiea* flower development.

Carnegiea plants apparently integrate the two triggers and the required heat sum in a complex way. The rainfall trigger might make the plant apex "competent" (McDaniel 1994). In the case of *Carnegiea*, the initial trigger may be a rain of at least 5–9 mm. Competence, sometimes referred to as "floral induction" (McDaniel 1994), occurs when leaves undergo physiological changes that make them capable of responding to a trigger that stimulates floral initiation (Kinet 1993), also called "floral evocation" (McDaniel 1994).

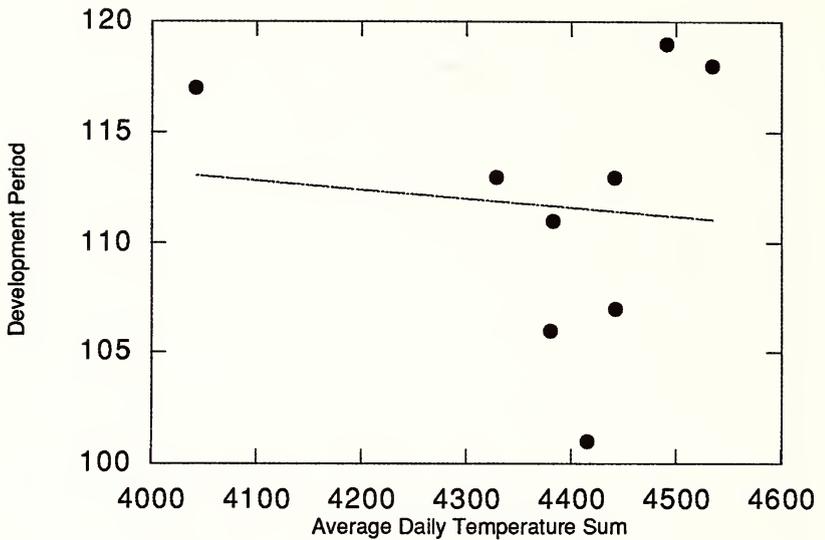


FIG. 3. Length of the development period in days as a function of the average daily temperature sum in langley-degree days above 10°C. The development period extends from photoperiod trigger to date of flower.

In *Carnegiea*, the trigger for floral evocation might be the 10.5-hour photoperiod. At the floral-evocation stage, meristematic cells at the plant apex are committed to flower production (Kinet 1993; McDaniel 1994). Further flower development then occurs as a function of warming days and increasing solar radiation. For *Carnegiea*, roughly 489,500 langley-degree days above 10°C are required for half the population to bloom.

Whether this verbal model accurately describes flower development in *Carnegiea* is not known. The physiological processes and anatomical stages involved are best studied in a laboratory setting. This model identifies environmental factors that could be the focus of experimental work.

Dual flowering triggers are known for other species. Opler et al. (1976) suggested that in the lowland tropical dry forest of Costa Rica, flower induction is triggered by short days and that further flower development is triggered by the first rain of 25 mm. Many crop species, including winter wheat and winter barley, have both vernalization and photoperiod requirements (Loomis and Conner 1992; Kinet 1993).

Daylength is known to trigger flowering in other cacti, including *Schlumbergera truncata* (Haw.) Moran, and also affects flower production and stem tip growth (Nobel 1989). In *Carnegiea*, the existence of a photoperiod requirement is indirectly confirmed by the

fact that the plants flower only once a year despite substantial late summer storms in most years. Rainfall is also known to trigger flowering in cacti; the small cactus *Mammillaria microcarpa* Engelm. can flower as many as three times a year, always after a substantial storm (Mark A. Dimmitt unpublished data). Certain indirect evidence also points to the importance of rainfall as a flowering trigger in *Carnegiea*. In a marginal population in southeastern California, only 8% of plants of reproductive age flowered after a very dry winter (Brum 1973). All the flowering plants grew in washes where they presumably harvested more water than nonflowering plants on adjacent flats (Brum 1973).

I had anticipated that *Carnegiea*, as a succulent plant with a large volume: surface area ratio, would flower independently of rainfall. This is apparently not the case. Stored water alone might not be sufficient to initiate flowering in this species. The flowering requirements emphasize the extent to which even a massive cactus like *Carnegiea* apparently depends on rainfall of the current growing season. As for other rain-triggered species in the northern Sonoran Desert, the requirement for substantial cool-season rain apparently coordinates floral induction with soil moisture and perhaps prevents flowering in extremely dry years.

One effect of the daylength trigger is to ensure that the plants do not flower at a time of year when their reproductive effort would almost certainly be wasted. A number of circumstances combine to make this seem a likely hypothesis. *Carnegiea* disperses its seeds in late spring and early summer, germinates only during the summer rainy season, and has limited seed viability (Steenbergh and Lowe 1977). The fallen seeds are rapidly consumed by a variety of granivores (Steenbergh and Lowe 1977). *Carnegiea* circumvents these hazards to some extent by dispersing seeds immediately before or with the onset of summer rains. Virtually all germination that occurs in the wild happens within the first few weeks after seed dispersal (Steenbergh and Lowe 1977). Based on 67 years of record, Greene (1963) stated that a reasonable approximation for average onset of summer rains at Tucson is July 2; the *Carnegiea* flowering record on Tumamoc Hill shows that the average date of last fruit is July 1. The date of last fruit varies little from year to year (a standard deviation of only 6 days). Clearly, one effect of the daylength trigger is to restrict flowering, and therefore seed dispersal, to the season when reproductive success is most likely.

As the flowering record at Tumamoc Hill shows, the date when half the *Carnegiea* population is in bloom can vary considerably from year to year, despite the invariability of the photoperiod trigger. This is because flowering is earlier in a warm year, when the required heat sum is achieved fairly quickly, and later in a cool year, when solar thermal units accumulate more slowly. Variation in flow-

ering time also occurs across the range of the species. In a given year, the plants flower earlier at lower latitudes (Steenbergh and Lowe 1977), largely because the lower elevations result in milder winters, and solar thermal units therefore accumulate more rapidly. As noted above, within-year variation may occur at a given locality, as well. In the Tucson area, rare individuals have been observed in bloom in August (Elizabeth A. Pierson personal communication), September, October, December, and January (Steenbergh and Lowe 1977). Triggers for these aberrant individuals are not known. Some apparently never flower in spring (Raymond M. Turner personal communication), and these may possess genetic variation in their daylength triggers. Individuals that flower outside the normal blooming period rarely if ever produce offspring (Steenbergh and Lowe 1977).

The relatively brief duration of *Carnegiea* bloom (an average of 36 days) contrasts with the long flowering periods of some other columnar cacti in the northern Sonoran Desert, particularly *Stenocereus thurberi* (Engelm.) Buxb., which flowers from April to July, and *Lophocereus schottii* (Engelm.) Britt. and Rose, which flowers from April to August (Wiggins 1964). Kochmer and Handel (1986) pointed out that selective pressure exerted by pollinators generally does not push flowering times beyond the boundaries imposed by phylogenetic constraints. Because the flowering of *Carnegiea* in April and May occupies only a small portion of the lengthy flowering season available to columnar cacti as a group, it seems possible that some factor other than (or in addition to) phylogeny has determined its flowering time. Likely selective factors include competition for pollinators, pollinator availability, and seed germination needs (Rathcke and Lacey 1985). At present, insufficient data are available to decide which if any of these factors have exerted selective pressure on flowering time of *Carnegiea*.

The annual flowering of *Carnegiea* reflects a network of climatic and biotic interactions. Clearly, properly timed seed release is vital to reproductive success in this species. Because *Carnegiea* seeds are short-lived and avidly consumed, few if any survive past the summer rainy season. Early and heavy rains are therefore crucial for seedling emergence, and, just as important, seeds must not be released too early or too late. The timing of the first substantial winter storms varies greatly from year to year. Such a variable phenomenon could produce a broad range of potential flower dates and thus lengthen the period of seed dispersal. Because it does not vary from year to year, a photoperiod trigger might restrict the period of bloom to a much narrower window. In effect, the photoperiod trigger ensures that the seeds will be dispersed in time for germination during the summer rains.

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FLOWER ABUNDANCE IN A POPULATION OF SKY
LUPINE (*LUPINUS NANUS*) OVER THREE YEARS IN
CENTRAL COASTAL CALIFORNIA

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ABSTRACT

Three consecutive years of monitoring *Lupinus nanus* bloom in central California demonstrates over an 11 fold difference in peak inflorescence numbers among years. Bloom duration was longest during those years that had the highest peak blooms. The level of peak annual bloom did not necessarily correlate with the total annual rainfall amount, but instead with the amount of rainfall during the period of January through March when seed induction and germination occur. High annual variation in the numbers of available flowers (during times when few other flower species are available) may have profound implications for early season bee fauna that utilize pollen of this species to complete their life cycle. These pollinator fluctuations might affect the pollination success of *L. nanus* and may ultimately produce the facultatively autogamous mating system observed in this species. In addition, the observed variation in flower abundance of this nitrogen-fixing species may have implications for nutrient availability within the ecosystem, thereby influencing the abundance and productivity of other plant species.

Lupinus nanus Benth. is an abundant annual herb, up to 50 cm tall, which forms dense patches in open or disturbed areas within old-fields, grasslands and oak savannas in California (Dunn 1956; Hickman 1993). A number of studies have documented large genetic variability within *L. nanus* for reproductive traits, such as flowering time, flower size, flower color and pollen production (Harding and Horovitz 1967; Horovitz and Harding 1972; Harding et al. 1974). The plant is also facultatively autogamous (Karoly 1992) and there are genetic differences between populations in outcrossing rates (Horovitz and Thorp 1970; Horovitz and Harding 1972). There are also differences between populations in their required rates of pollinator visitation and, in some cases, pollinator availability can limit reproductive success (Karoly 1992).

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Plant population sizes can vary substantially from year to year and in California this variability is often related to both the amount and the timing of rainfall (Harding 1970; Pitt and Heady 1978; Allison 1992). Indeed, Dunn (1956) reported that populations of *Lupinus nanus* "vary in size from year to year and may even disappear at intervals depending upon the weather during the period of germination." Here we report three consecutive years of flower abundance levels for *L. nanus* and discuss the implications of bloom variability for insect and other plant populations that depend upon pollen and nitrogen produced by lupine populations.

METHODS

Study site. Our study population of *Lupinus nanus* was located at the Hastings Natural History Reservation in Monterey Co., 42 km SE of Carmel in coastal-central California (36°23'N, 121°33'W). The climate of this region is characteristic of a Mediterranean area, with hot, dry summers and moderate wet winters (Major 1977). The mean annual precipitation is 538 mm, but precipitation varies from 261 mm to 1112 mm. More than 90% of the rain falls between November and April (Fig. 1). Records of rainfall during the three year lupine monitoring period were recorded at the Hastings weather station, located about 500 m northeast of the study population. Daily values were used to calculate monthly mean maximum, average and minimum values of temperature and total monthly rainfall during our study period.

Lupine phenology. Bloom abundance in our study population was monitored with three parallel transects approximately 30 m apart. Sampling plots were set at 5 m intervals along each transect and were one m² in area. All of these transects were bisected by a creek (Big Creek) so that eight sampling plots extended perpendicularly from either side of the creek, producing a total of 48 plots. As an estimate of total bloom, plots were censused on a weekly basis for numbers of inflorescences with at least one open flower. The same plots were used each year of the study and were reused by relocating metal spikes set in the ground at each sampling plot. Sampling days were Mondays in 1990 and Sundays in 1991 and 1992. Transects were monitored as long as flowering occurred in the sampling plots.

Bee diversity and phenology. Collections of bees were made at various times during the bloom period of *L. nanus* from 1989–1992 with a hand-held insect net. In addition, we tested for seasonal synchrony between *L. nanus* and one of its common bee visitors, the cavity nesting solitary bee *Osmia lignaria* (Megachilidae) by arraying sampling units in the vicinity of our lupine study plots during 1990; this bee ordinarily nests in small cavities found naturally in

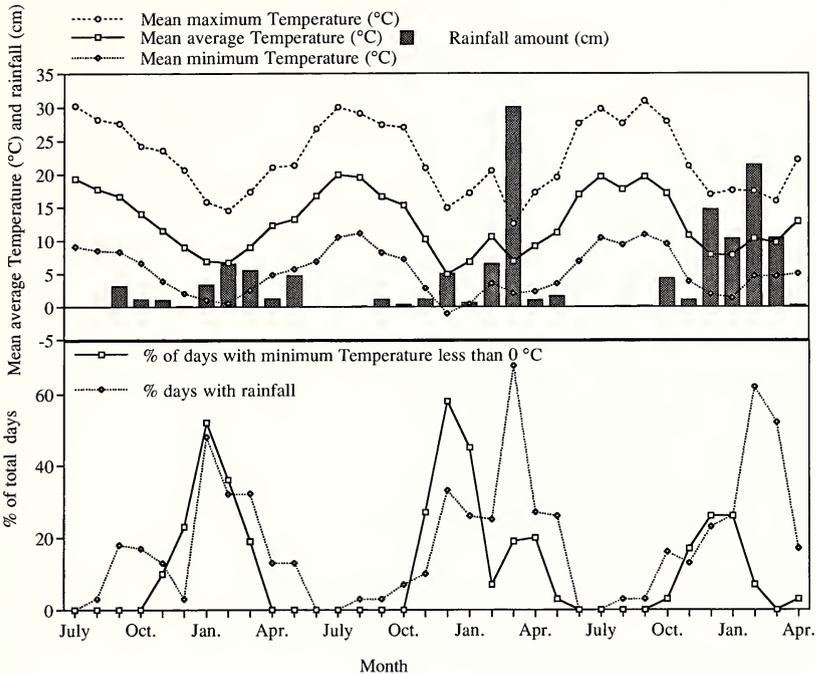


FIG. 1. Graphs of (a) precipitation as well as mean maximum, mean average, mean minimum temperatures and (b) the % of days per month with rainfall and the percentage of days per month with a minimum temperature less than 0°C at Hastings.

and around oak forests, and will readily nest in artificial sampling units made from wooden subunits called "trap-nests" (Krombein 1967). Each trap-nest had dimensions of 12.0 × 2.5 × 2.0 cm, with a single hole drilled to a 10 cm depth down its length. Four trap-nests for each of three hole diameters (0.50, 0.65 and 0.80 cm) were systematically arranged within a 5.0 × 12.0 × 12.0 cm sampling unit and hung with wire from nails at 1.5 m heights on living oak trees near Big Creek. Fifteen sampling units were spread approximately equidistantly along each of three belt transects within the creek basin ($n = 45$). Field replacements were made on the same day of each week (Sundays), one day before lupine censusing.

RESULTS AND DISCUSSION

We found striking, statistically significant, differences in flower abundance among years, with the peak in the average number of open inflorescences per m² ranging from 5.5 in 1990 to 61.0 in 1991 (One-way Anova, F ratio = 19.4, 2 degrees of freedom, $P < 0.000$). An average of 46.2 inflorescences per m² was recorded as the peak

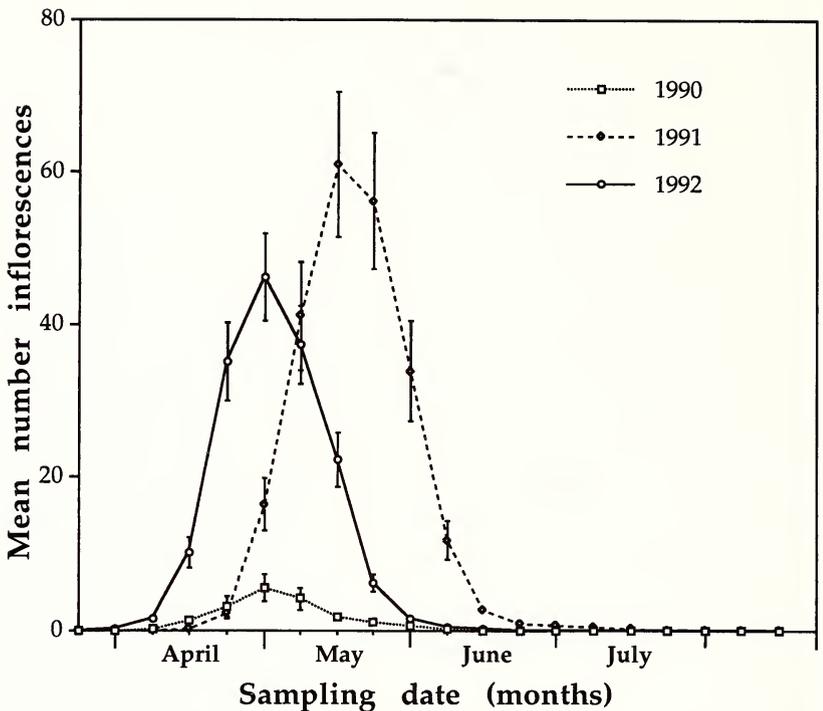


FIG. 2. Mean number of inflorescences per plot of *Lupinus nanus* in three years. Given are the means \pm 1 SE. Sampling was at weekly intervals beginning on March 26 of 1990, March 24 of 1991 and March 22 of 1992.

in 1992 (Fig. 2). The total rainfall during 1990 was 26.5 cm, 47.1 cm during 1991 and 61.5 cm during 1992. The fact that the year with the highest peak number of flowers (1991) did not occur during the year of greatest total rainfall (1992) suggests that not only annual rainfall, but also the timing of heavy rainfall periods within years influences germination levels and subsequent flower abundances.

Seeds of *Lupinus nanus* do not necessarily germinate each year and do not have an inner dormancy (Harding 1970). Minimum temperature is therefore not likely to influence germination. Rather, they depend on a hard seed coat which requires decomposition or abrasion for the control of germination (Dunn 1956). In general, decomposition in Mediterranean ecosystems is strongly influenced by the availability of water (Hart et al. 1992), thus the amount of water during the time of germination is likely to not only directly influence seed germination, but also to influence microbial populations that decompose organic matter. The number of days from seed imbibition to flowering in *L. nanus* has been reported to range from 46 to 70

TABLE 1. COMPARISON OF ONSET, PEAK AND END BLOOM DATES FOR *LUPINUS NANUS* 1990–1992.

Year	Onset date	Peak date	End date	Duration
1990	9 April	30 April	11 June	9 weeks
1991	14 April	12 May	28 July	14 weeks
1992	29 March	26 April	21 June	11 weeks

days (depending on genotype), with an average of 54 and a median of 52 days in a greenhouse study (Horovitz and Harding 1972), which is consistent with field data collected by Dunn (1956). This implies that seed induction and germination occur during the period of January to March in our study population. We see no striking difference in rainfall during this period between the 1990 and 1991 flower seasons and the difference between peak flower abundance levels of these two years was the least of all three years, supporting the view that this early period of the year is important for germination. In addition, the period of December to January of 1992 was much wetter than in the previous two years and the onset and peak flowering dates were also earlier that year (Fig. 1, Table 1). Flower abundance during 1991 was probably most influenced by continuous rain storms during the month of March (Fig. 1). These probably wetted the top soil levels (where the seeds are present) for a longer period and may have resulted in a build-up of microbial populations in the soil (increasing seed coat decomposition) as well as increased moisture levels for germinating seeds. An alternative explanation of the observed differences in flower abundance is that the germination rates remained constant and that the seedling to adult survival rate varied strongly between the years. However, *L. nanus* does have a substantial seedbank (Harding 1970) and depends on a hard seed coat, and not an inner dormancy for the control of germinating (Dunn 1956). In addition, drought is likely to be the main factor influencing the survivorship of the seedlings and we found no striking drought period in 1990, which could have caused a large mortality in that year. These factors support the hypothesis that differences in germination are the cause of the observed differences in flower abundance between the years.

Lupinus nanus is reported to be autogamous to a large extent (Dunn 1956; Karoly 1992). However, the mating system of this species is strongly influenced by the availability of pollinators as documented in outcrossing studies (Horovitz and Harding 1972; Karoly 1992). We have thus far recorded 20 different bee species visiting *L. nanus* at Hastings (Table 2). One of these, *O. lignaria*, is a common cavity nesting solitary bee species that forages from early April until late May (Barthell 1992; Thorp et al. 1992). Females of this species are known to shift sex ratios of their progeny from female-

TABLE 2. BEE SPECIES OBSERVED VISITING *LUPINUS NANUS*.

Family	Species
Halictidae	<i>Halictus farinosus</i> Smith
Andrenidae	<i>Andrena atypica</i> (Cockerell) <i>Andrena</i> sp.
Megachilidae	<i>Osmia lignaria propinqua</i> Cresson <i>Osmia regulina</i> Cockerell <i>Osmia tristella</i> Cockerell <i>Osmia atrocyanea</i> Cockerell <i>Osmia nemoris</i> Sandhouse <i>Osmia zephyros</i> Sandhouse <i>Osmia</i> sp. <i>Panurginus</i> sp.
Anthophoridae	<i>Habropoda depressa</i> Fowler <i>Habropoda</i> sp. <i>Synhalonia</i> sp. 1 <i>Synhalonia</i> sp. 2
Apidae	<i>Apis mellifera</i> Linnaeus <i>Bombus caliginosus</i> Cresson <i>Bombus edwardsii</i> (Frison) <i>Bombus vosnesenskii</i> Radoszkowski

to male-biased proportions as floral resource quality decreases over the nesting season, suggesting that pollen availability is an important determinant in the bee's life history strategy (Torchio and Tepedino 1980).

Osmia lignaria females appear to rely upon *L. nanus* for pollen (Barthell et al. 1996). In addition to the distinctive orange pollen found on foragers at flowers and in their nest cells (dissected from trap-nests), a striking coincidence in nest cell and flower abundance peaks were observed in 1990 (Fig. 3). A similar coincidence was noted the following year (1991) in an unrelated study conducted in the same area (Barthell 1992), suggesting that *O. lignaria* may track the bloom phenology of *L. nanus* during its nesting season at Hastings. The large depressions in annual, peak flower abundances that we observed in our study could therefore influence the reproductive success of potentially resource-sensitive pollinators such as *O. lignaria* and thereby lower the availability of pollinators in subsequent years. The facultative autogamous habit of this species may circumvent such potential pollinator limitation, while maintaining sufficient variability through outcrossing to prevent inbreeding.

Lupine species are often abundant in early successional stages of grasslands in California (Heady 1977) and can locally contribute a substantial amount of nitrogen to the ecosystem by fixing atmospheric nitrogen (Woodmansee and Duncan 1980; Fahey et al. 1985; Halvorson et al. 1992). Nitrogen is considered to be the most limiting nutrient in these grasslands (Woodmansee and Duncan 1980;

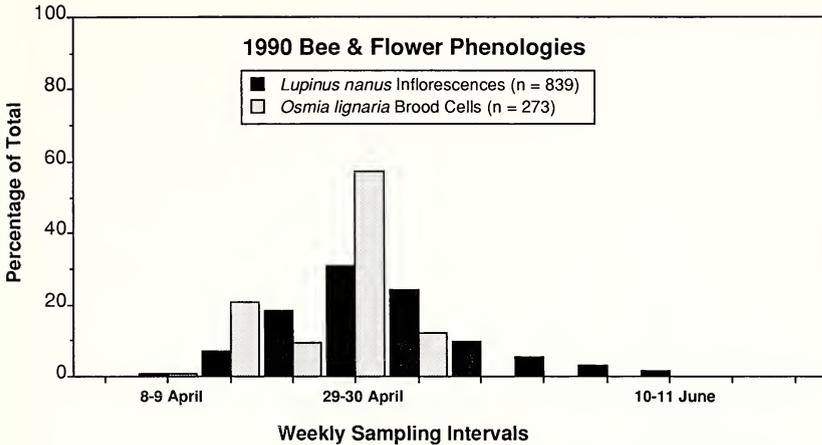


FIG. 3. Weekly proportions of the total number of *Lupinus nanus* inflorescences and nest cells of *Osmia lignaria* during 1990.

Menke 1989). Therefore, variation in lupine abundance not only influences the insect populations depending on them for pollen, but may also influence the availability of nitrogen, thereby influencing ecosystem productivity and composition.

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NOTE

FIRST-YEAR RESPONSE TO FIRE BY THE CALIFORNIA GRASSLAND PERENNIAL, *DODECATH-EON CLEVELANDII* SPP. *PATULUM* (PRIMULACEAE).—Robert Schlising, Department of Biological Sciences, Gregory Treber, Department of Agriculture, and Caroline Warren, Department of Biological Sciences, California State University, Chico, CA 95929.

Much of the literature on North American grasslands and fire deals with middle portions of the continent, centering on the Great Plains (Daubenmire, *Advances in Ecological Research* 5:209–266, 1968; Vogl *in* Kozlowski and Ahlgren, *Fire and Ecosystems*, Academic Press, 1974; Risser *in* Chabot and Mooney, *Physiological ecology of North American plant communities*, Chapman and Hall, 1985; Collins and Wallace, *Fire in North American tallgrass prairies*, University of Oklahoma Press, 1990; Coupland, *Natural grasslands*, Elsevier, 1992). Published information specifically on plants and fires for the annual grasslands of California is scarce (Huenneke and Mooney, *Grassland structure and function*. California annual grasslands, Kluwer Academic Publishers, 1989; Heady et al. *in* Coupland 1992), and work on this region mainly emphasizes vegetation responses to fires, such as changes in species composition, plant densities, and production. Although Keeley (*in* Mooney et al., USDA, Forest Service, GTR WO-26, 1981) has noted that California's mediterranean climate annual grasslands represent one of the most fire-resilient of all herbaceous plant communities, there is surprisingly little detailed information on responses to fire—especially on reproductive responses—by individual species in these grasslands.

For grasslands in general, individual species of both grasses and forbs are known that show increased reproductive growth, including increases in flowering and seed production after fires (Daubenmire 1968; Vogl 1974; Risser 1985), and Heady (*Proceedings of the Tall Timbers Fire Ecology Conference* 12:97–107, 1973) has suggested that aboriginal people may have set fires to stimulate flower, fruit, and seed production in grasslands. But such increased fruit and seed production after burns is very poorly documented for California species, and only a few studies lend strong support for increased reproduction after burns. In one early study specifically for Californian grasslands, Hervey (*Journal of Range Management* 2:116–121, 1949) reported both increases and reductions in height and in “yield” for several naturalized forbs and grasses measured in adjacent burned and unburned areas. While there is much research on the widespread native perennial bunchgrass *Nasella* (*Stipa*) *pulchra*, there is little published on increased reproductivity for this plant in burned areas (although increased seed weight was noted by George et al., *Journal of Range Management* 45:436–440, 1992). A study by Hunter (Madroño 33:305–307, 1986) has documented significantly higher fruit numbers per plant after a burn for the native annual forb, *Sidalcea calycosa* (Malvaceae), that grows in swales and shallow pools in annual grasslands. Mitchelson (M.S. thesis, California State University, Chico, 1993) has documented a highly significant increase in fruits per plant for the perennial geophyte *Zigadenus fremontii* (Liliaceae) growing in a burned grassland in the northern Sacramento Valley. Our study was initiated to investigate reproductive responses to fire by a non-geophytic perennial growing in these same grasslands.

Dodecathion clevelandii E. Greene ssp. *patulum* (E. Greene) H. J. Thompson, the lowland shooting star, is native and widespread in cismontane California—especially in and about the Central Valley (Hickman, *The Jepson Manual: Higher Plants of California*, University of California Press, 1993; Thompson, *Contributions of the Dudley Herbarium* 4:73–154, 1953). This hemicytophyte grows a new rosette of basal leaves from a shallowly-buried caudex, following the resumption of rains each fall. By February in the northern Sacramento Valley, the plants produce solitary

scapes with several nodding, whitish, black-tipped flowers. Flowering is usually completed by mid-March. The leaves wither soon after flowering, but the green scape and young capsules may continue to supply photosynthate to the developing seeds. While exceedingly common and obvious in the grasslands before most associated species have completed much aboveground growth, this perennial essentially disappears when most grasses and forbs mature and become reproductive in April. The fruits of the shooting star ripen in late April here, but the dried scapes and their fruits can be found all summer.

This study was carried out at the Vina Plains Preserve, a region of annual grassland and vernal pools owned by the California Nature Conservancy, in southernmost Tehama County about 19 km north of Chico. The area in which this study was conducted is in sections 28 and 33, T24N, R1W (Richardson Springs 7.5' USGS quadrangle map), where the elevation is about 65 m above sea level. The region has the characteristic mediterranean climate of central California, with cool, moist winters followed by very hot and dry summers. Broyles (M.A. thesis, California State University, Chico, 1983; Madroño 34:209–227, 1987) has listed 287 species of vascular plants in the flora of the preserve, of which 90 (33%) are introduced species and of which 50 (17%) are native and introduced grasses. Topography here consists of very gently rolling terrain, with only a few meters change in elevation. Soils of the study area are well-drained, and belong to the Tuscan Series (Soil Survey of Tehama County, California, USDA, 1967).

On 15 July 1993, a fire that started accidentally at Highway 99 to the west, spread eastward across the Preserve. The area chosen for the present study within this burn had not been submitted to fire-suppression equipment or chemicals. Precipitation and mean temperatures for the fall/winter months following this fire, and through the spring months of this study are based on weather data taken at Orland, about 18.5 km southwest of the Preserve and the nearest site maintaining complete weather records (Climatological Data: California, National Oceanic and Atmospheric Administration, 1993, 1994). These data show that the amount of rainfall varied considerably from the longterm monthly mean for most months during the first growing season following the fire. Most months, except February, had less than normal precipitation: November, -45 mm (below mean); December, -36 mm; January, -23 mm; February, +71 mm (above mean); March, -71 mm; and April, -12 mm. Monthly temperatures in degrees C were above longterm means for all months except February (November, +0.6; December, +0.3; January, +2.5; February, -0.9; March, +2.3; and April, +1.5).

The major hypothesis was that there would be no difference in first year growth (size) and reproduction of these established perennial plants growing in the burned and in the adjacent unburned areas. To test this, 10 parallel 30-m belt transects 1-m wide, were established on two adjacent well-drained areas. Half of each transect occurred within the area burned in 1993, and the other half extended into area not burned. For each transect, the middle 10 m (5 m in burned and 5 m in unburned) was kept as the "burn line buffer zone" and was not sampled; only the outer 10 m in each transect was used. Each of the resulting 10 m × 1 m transects, both in burned and in unburned areas, was divided into gridded 1-m-squares, where random numbers were used to sample 1 plant per square meter—for a total of 100 burned-area plants and 100 unburned-area plants.

Transects were set up on 28 February 1994, when all rosettes were at full size, but the plants were not yet in full flower. Plants were sampled only if the beginning of a flower scape was visible (that is, only plants flowering in 1994 were to be sampled). The basal rosettes of the 200 sampled plants were assessed in the field by measuring the rosette diameter; these plants were then marked with stringed tags. On 7 March, flowers were collected immediately adjacent to sample areas (1 flower from each of 3 plants per transect) in both burned and unburned areas, for laboratory determination of ovule number per ovary.

On 25 April, tagged scapes (with ripe fruits) were harvested by cutting the scape

TABLE 1. VEGETATIVE AND REPRODUCTIVE FEATURES SHOWN BY PLANTS OF *DODECATHEON CLEVELANDII* SSP. *PATULUM* THE SPRING AFTER A SUMMER FIRE, IN ADJACENT BURNED VS. UNBURNED AREAS OF ANNUAL GRASSLAND. Measurements are given as mean \pm SE (with sample size in parentheses). Student's t-tests indicate that means for both rosette area and scape height are highly significantly different ($P < 0.0001$). Means for other features are not significantly different at the 95% level. ¹ Lower sample numbers reflect scape destruction by rodents. ² Fruits per plant based on all plants with 0-6 fruits, including fruits with 0 seeds. ³ Seeds per plant and seeds per fruit based on fruits with 0-62 seeds. ⁴ Seed weights based only on plants that produced 1 or more seeds.

Feature	Burned area	Unburned area
Rosette area (sq cm)	25.8 \pm 1.2 (100)	37.5 \pm 1.8 (100)
Scape height (cm) ¹	4.8 \pm 0.2 (83)	5.8 \pm 0.2 (87)
Fruits per plant ²	1.2 \pm 0.1 (83)	1.3 \pm 0.1 (87)
Aborted flowers per plant	1.8 \pm 0.1 (83)	1.6 \pm 0.1 (87)
Plants with fruit	51	58
Seeds per plant ³	25.8 \pm 3.4 (51)	25.9 \pm 4.3 (58)
Seeds per fruit ³	13.4 \pm 1.3 (98)	13.2 \pm 1.4 (114)
Ovules per ovary	134.6 \pm 6.7 (30)	135.2 \pm 5.3 (29)
Ovule/seed ratio	10.8	9.9
Seed wt per plant (mg) ⁴	20.1 \pm 2.5 (38)	18.9 \pm 2.9 (45)
Seed weight (mg) ⁴	0.6 \pm 0.03 (38)	0.5 \pm 0.03 (45)

as close to the rosette as possible. These scapes were assessed in the laboratory for the following parameters: scape height (to the nearest 0.1 cm, measured to the point of the lowest fruiting pedicel); number of developed fruits; number of additional (aborted) flowers that did not develop into fruits; and number of seeds per fruit. On 8 July, after over 10 weeks of air-drying, the seeds for each fruit were weighed on a Sartorius analytical balance. Statistical analyses were performed by checking for equality of variances and then doing the appropriate t-tests to compare means.

Measurements and calculations assessing first-year growth of the plants sampled are shown in Table 1. Measurements of leaf rosette diameter were used to calculate rosette area, a clearly vegetative (non-reproductive) parameter of the plants' growth. Means for rosette area and scape height are both highly significantly different in the burned vs. unburned areas. Means for the remaining (reproductive) parameters are not significantly different.

In general, plants show enhanced growth and increased reproduction after fires (Risser, 1985; Heady, Rangeland Management, McGraw Hill, 1975; Chapman and Crow, Bulletin of the Torrey Botanical Club 108:472-478, 1981; Anderson *in* Collins and Wallace 1990). But according to generalizations in the literature (e.g., Daubenmire 1968; Heady et al. 1992), grassland fires may have little effect on plant habitat; our data indicate that this may be true for the habitat of the shooting stars we studied. For instance, summer fires in the California annual grasslands tend to move through an area rapidly due to the fine fuels and extreme dryness, and burn at relatively cool temperatures. For these reasons, although there is some loss of nitrogen and sulphur during a fire, and the potential for either wind displacement of ash or leaching of nutrients exists, the overall effect on the soil chemistry may be minimal. Therefore, higher soil fertility and resulting enhanced growth of plants is not necessarily to be expected after a burn.

Larson and Duncan (Journal of Range Management 35:701-703, 1982) found no increases in herbage in a burned area the first year in their study at the San Joaquin Experimental Range NE of Fresno, and in the burned areas of our study at the Vina Plains the leaf rosettes were actually significantly smaller than in the adjacent un-

burned areas (Table 1). This is difficult to explain, but these size differences may be due to a combination of abiotic factors relating to litter removal by the fire. The unburned areas of our study, like most annual grassland sites in California, were covered by a considerable layer of mulch, and the differences in rosettes may be the result of factors such as moisture retention in soil, compaction of bare ground by raindrops, and light availability. The litter may have acted as a canopy that lowered light intensity (Evans and Young *in* Huenneke and Mooney 1989; Huenneke and Mooney *in* Huenneke and Mooney 1989; Menke *in* Huenneke and Mooney 1989) to the rosettes of the shooting stars. The plants may have responded to shading within the deep layer of dead plant material by producing larger leaves. Similarly, significantly taller scapes (Table 1) in heavy mulch may represent an etiolation-like response by the study plants. This mulch was thick at the study site due to above-normal precipitation during the growing season before the fire (NOAA 1993).

In contrast to these two essentially vegetative parameters, the reproductive features measured in our study showed no significant differences for burned vs. unburned grassland habitat (Table 1). Although Risser (1985) notes a general increase in flowering and seeding for plants in recently burned areas, Wallace (*in* Collins and Wallace 1990) states in her epilogue in *Fire in North American Tallgrass Prairies* that fire influences on sexual reproduction are as varied as the plant species being studied. Several other studies have demonstrated variation in reproductive response. Another species of shooting star (*Dodecatheon meadia*) studied in the tallgrass prairie documented more flowers per plant in burned areas compared with unburned (Glenn-Lewin et al. *in* Collins and Wallace 1990). For the few species studied in California, observations on common geophytes, such as several species of *Calochortus* and *Dichelostemma pulchella* (Muller et al., Bulletin of the Torrey Botanical Club 95:225–231, 1968), and detailed research on *Zigadenus fremontii* (Mitchelson 1993), show marked increases in flowering and fruiting after fire. Fossum (M.S. thesis, University of California, Davis, 1990) studied flowering and seed weights of the hemicyptophytic grass *Nassella pulchra*, and found that the first-year fire response showed a 55% decrease in seed number, but a 12% increase in seed weight. Our data, indicating neither a positive or negative effect on reproduction in *D. clelandii* by fire, provide a valuable addition to the very sparse literature on individual grassland species in California.

These data on the lowland shooting star were collected in a year with all months except February receiving lower than normal rainfall and higher than normal temperatures. Year-to-year total precipitation in California's mediterranean grasslands is extremely variable, and whether these drier and warmer conditions affected the plants is not known. The period of greatest precipitation did coincide with early flowering (February received 71 mm above the long-term mean), and soil moisture conditions appeared to be near field capacity during flowering and fruiting. Reproductive success (Table 1) on *both* sites seemed low (with a mean of only about 13 seeds per fruit in both burned and unburned areas, and an ovule/seed ratio of only 10.8 and 9.9).

All of the parameters measured concerning flowering, fruiting, and seeding support the original hypothesis that there would be no difference in first-year growth and reproduction in *Dodecatheon clelandii* ssp. *patulum*. But both rosette area and scape height in this perennial forb were found to be larger in unburned grassland habitat here, strongly suggesting a non-beneficial influence from fire, at least concerning plant size.

We thank the California Nature Conservancy for permitting this study at the Vina Plains Preserve. We also thank the following individuals for help in collecting and analyzing data and for taking part in discussions from which, in part, this manuscript derived: Caragwen Bracken, Andy Delmas, Elizabeth Hubert, John Matel, Jim Murphy, Michelle Sculley, and Heidi West.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

SHEPHERDIA CANADENSIS (L.) Nutt. (Elaeagnaceae).—Siskiyou Co., Parks Creek Road, 5.1 miles above junction with Stewart Springs Road, T41N, R6W, SW¼ of NW¼ sec. 22, China Mtn. quad., elev. approx. 1731 m, along a small springfed stream through predominantly peridotite country rocks, although there are also blocks of gabbro in the stream. Selected associated species: *Calocedrus decurrens*, *Abies concolor*, *Pinus* spp., *Cornus sericea*, *Rhododendron occidentale*, *Quercus vaccinifolia*, *Lonicera conjugialis*, *Paxistima myrsinifolia*, *Darlingtonia californica*, *Rudbeckia californica* var. *intermedia*, *Streptopus amplexifolius*, *Campanula rotundifolia*, *Calochortus nudus*, *Sisyrinchium idahoense*; 30 July 1995, Janet and Stephen Edwards s.n. (UC).

Previous knowledge. This species ranges from Alaska to northeast Oregon, and east to Idaho, Montana, Utah, Colorado, New York, and eastern Canada.

Significance. First record for California. The closest previously recorded localities (UC; Abrams, Illustrated Flora of the Pacific States, Stanford Univ. Press, 1951) are in the Strawberry Mts. of Grant County, NE Oregon, and in the Ruby Mts. in Elko County, NE Nevada. The closer location, in the Strawberry Mts., is some 250 miles distant and separated by two geologic provinces (Great Basin, Cascades) from the Siskiyou County locality, in the Klamath Mts. just north of Mt. Eddy. A poor and problematic but interesting specimen from Santa Barbara County, California (UC 141102) was annotated *S. canadensis* by McMinn on 12-26-33. Its vestiture resembles this species in some respects, but McMinn did not subsequently include *S. canadensis* in his 1939 Manual of California Shrubs.

—JANET S. EDWARDS and STEPHEN W. EDWARDS, Regional Parks Botanic Garden, % Tilden Regional Park, Berkeley, CA 94708.

NEVADA

ASTRAGALUS KENTROPHYTA VAR. *JESSIAE* (M. E. Peck) Barneby (Fabaceae).—Humboldt Co., Bilk Creek Mts., 4.7 road miles N of Quinn River Crossing on highway 140, then 1 mile east of highway, T44N, R31E, S24, 4500 ft, on light-colored ash deposits, 21 May 1995, Arnold Tiehm 12089 (CAS, NY determined by R. C. Barneby, OSC, RENO).

Previous knowledge. Known from the Owyhee Desert section of SE Oregon and SW Idaho, disjunct to SW Wyoming and adjacent northern Utah (Barneby, Intermountain Flora 3B:82–84, 1989).

Significance. First record for Nevada and a range extension of over 100 miles SW from SE Oregon.

HYMENOPAPPUS FILIFOLUS Hook. var. *FILIFOLIUS* (Asteraceae).—Humboldt Co., Sheldon National Wildlife Refuge, Virgin Valley, W side of Virgin Valley Ranch antennae bluff west of the ranch, T45N, R25E, S24, 5050 ft, with *Atriplex*, *Tetradymia* on light-colored ash outcrops, 21 Jun 1995, Tiehm 12142 (CAS, NY, OSC, RENO).

Previous knowledge. Known from E Washington, E Oregon nearly as far south as Nevada, east into Owyhee County, Idaho (Cronquist, Intermountain Flora 5:131–132, 1994).

Significance. First record for Nevada and a range extension of 35 miles SW from Cottonwood Canyon in the Pueblo Mts. of Harney Co., Oregon (K. L. Chambers personal communication, 1995).

—ARNOLD TIEHM, P.O. Box 21387, Reno, NV 89515.

OREGON

CROCOSMIA × *CROCOSMIIFLORA* (Burb. & Dean) N.E.Br. (Iridaceae).—Lincoln Co., Seal Rock, along U.S. Hwy. 101 by junction with Park St., assoc. genera: *Juncus*, *Lotus*, *Equisetum*, *Rubus*, *Polystichum*, *Epilobium*, T12S, R12W, sect. 25, elev. 18 m, 28 August 1983, *R. Halse* 2741 (OSC); Lane Co., along U.S. Hwy. 101 by bridge over Tenmile Creek, about 9.5 km south of Yachats, assoc. genera: *Holcus*, *Lotus*, *Rubus*, *Alnus*, *Dactylis*, *Potentilla*, *Equisetum*, T15S, R12W, sect. 27, elev. 7 m, 30 July 1995, *R. Halse* 4958 (OSC, duplicates to be distributed).

Previous knowledge. In California this escaped and naturalized cultivar is known from disturbed coastal areas from the north coast to the south coast (The Jepson Manual, 1993). It has also become naturalized in Hawai'i (Manual of the Flowering Plants of Hawai'i, vol. 2, 1990).

Significance. New to Oregon. This taxon is common along the coastal highway in Lane and Lincoln Counties and is to be expected elsewhere.

HERNIARIA HIRSUTA L. (Caryophyllaceae).—Josephine Co., Rogue River Canyon, 8 km above Galice, sandbars along the river, a single plant, elev. 244 m, 4 July 1948, *H. D. Ripley* & *R. C. Barneby* 9620a (WILLU); Josephine Co., Rand Ranger Station on the Rogue River, Siskiyou National Forest, river sand bar, T34S, R8W, sect. 24 NE½, 6 September 1936, *O. L. Ireland* 856 (ORE), determined by *R. Halse*.

Previous knowledge. This Old World species is found in various areas throughout California (The Jepson Manual, 1993).

Significance. First report for Oregon. This plant has apparently not been recollected in Oregon since 1948; it was not found during a search of the area in 1995.

ORNITHOPUS COMPRESSUS L. (Fabaceae).—Lincoln Co., Newport, volunteer in newly planted landscaped area at the Oregon Coast Aquarium, 12 April 1992, *B. Llewellyn* s.n. (OSC); same locality, T11S, R11W, sect. 17, elev. 9 m, 1 June 1995, *R. Halse* 4904 (OSC, duplicates to be distributed).

Previous knowledge. Two other species in this European genus are known from the central coastal areas of California (The Jepson Manual, 1993).

Significance. New to Oregon. Since it was first collected in 1992 this species has persisted and spread so that now it is a common weed in the landscaped areas around the parking lots at the aquarium.

PETUNIA PARVIFLORA A. L. Juss. (Solanaceae).—Multnomah Co., Lower Albina, Portland, on ballast, 21 July 1902, *E. P. Sheldon* S9933 (ORE); same locality, 15 September 1902, *E. P. Sheldon* S11325 & S10309 (ORE), determined by *R. Halse*.

Previous knowledge. This plant is found from southern California east to the southeastern U.S. and south to South America (The Jepson Manual, 1993).

Significance. First report for Oregon. The specimens were originally identified as species of *Gilia*, *Nama* and *Bacopa*. The species has apparently not been recollected in Oregon since 1902.

—RICHARD R. HALSE, Department of Botany & Plant Pathology, Oregon State University, Corvallis, OR 97331.

REVIEWS

California Vegetation. By V. L. HOLLAND and D. J. KEIL. 1995. Kendall/Hunt Publishing Company, Dubuque, Iowa. xii + 516 pages. ISBN 0-7872-0733-0.

California Vegetation is a welcome addition to the limited market of textbooks available for courses emphasizing the plant communities of California. Holland and Keil provide a good grounding in floristics and community description as well as a summary of the major topographic, geographic, geologic, and socioeconomic influences on the vegetation of California. As the authors state in the introduction, information about each of the communities is intermediate in informational content between *California Plant Life* (Ornduff 1974) and *Terrestrial Vegetation of California* (Barbour and Major 1977). Both the Ornduff and the Barbour and Major texts are excellent but offer too little or too much detail, respectively, for a class in California plant communities. Holland and Keil's work is ideal for an upper-division undergraduate course. It is a major plus that the nomenclature is up-to-date, relying on *The Jepson Manual* (Hickman 1993) as a taxonomic reference. *California Vegetation* could also be a nice complement to a course in plant taxonomy.

Chapter one provides an informative compilation of "fun facts" about California's botanical diversity and the factors that shape this diversity both presently and historically. It is useful to have this information published in a textbook context. For example, statistics on land area, numbers of exotic, endemic, and rare species are provided with their changes in representation through time.

Chapters two and three discuss the abiotic factors that influence the distribution of California's plant communities. Although it is difficult to comprehensively cover any topic, I would have liked to have seen at least some mention of biogeochemistry and other ecosystem level considerations, perhaps as another subheading in chapter two.

Chapter four provides a succinct but thorough summary of the formation of the present floristic diversity in California.

By necessity, Holland and Keil have generalized plant communities for the genre in chapter five. Although they include a comparison of their system with the California Native Plant Society system by Sawyer and Keeler-Wolf (1995) in the appendix, I would have liked to have seen the Sawyer and Keeler-Wolf system integrated more throughout. The need for the standardization of plant community classification within California has been long standing. It is likely that *California Vegetation* will become a training manual for many years of California botanists to come and thus it is the ideal forum in which to encourage unification on the community classification front.

The core of the book (chapters 7 through 21) describes, in a general fashion, the major plant communities of California. The community descriptions are very readable and the level of detail is adequate. A list of dominant and subdominant species is provided in an organized manner for each major community. For example, chapter 15 addresses oak woodlands; a list of subdominants is provided and six specific communities (Coastal Live Oak, Valley Oak, Foothill, Northern Oak, Southern Oak and Island Oak) are discussed in more detail. Chapter 11 on grasslands presents an objective summary of the composition of valley grasslands in presettlement times. The human impact sections at the end of a number of the chapters is particularly useful in a modern survey course.

One of the real benefits to this volume is the last two chapters on the anthropogenic affects to native plant communities, a topic that can not be avoided when discussing California's natural environment. However, the weed list easily could have been more extensive, too many important species are missing. Serious widespread wildland pests

listed by the California Exotic Pest Plant Council are not included, such as *Arundo donax*, *Carpobrotus edulis*, *Cortaderia jubata*, *Eucalyptus globulus*, *Pennisetum setaceum*, *Tamarix* spp. and *Ulex eropaeus*.

Minor annoyances are the poor print quality, which is particularly noticeable in the photos and figures, and an overabundance of typographical errors.

I am currently using this text in a plant ecology course and, other than the complaint that the price is excessive for a paperback (\$47.00), the students have received *California Vegetation* quite favorably. This group of students has interests ranging from botany to cell biology to wildlife management and find the book informative and the writing style clear and concise. *California Vegetation* has value not only as a textbook but also as the most current desk and field reference on general plant community information. Academics, agency botanists, and consulting biologists should all find something of use in this valuable source.

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—KRISTINA A. SCHIERENBECK California State University, Fresno, Department of Biology, Fresno, CA 93740.

Hybrid Zones and the Evolutionary Process. Edited by R. G. HARRISON. 1993. Oxford University Press, New York. 364 pages. Hardcover \$72.00. ISBN 0-19-506917-X.

This book is a collection of papers that were presented as part of a symposium on hybrid zones given at the Fourth International Congress of Systematic and Evolutionary Biology (ICSEB) at College Park, Maryland, in 1990. Additionally, the editor solicited chapters from persons who were not part of the original symposium. The book is divided into two major parts; the first four chapters examine some of the major concepts identified with hybrid zones. The second part consists of eight chapters that are case studies of hybrid zones, but only one of the eight is an example from the plant kingdom. All of the chapters are well illustrated.

From the onset I must say that as a botanist I was disappointed that the book is heavily concentrated on zoological examples, although most evolutionary biologists would agree that natural hybridization in plants is much more common than in animals. In my view this is a serious flaw and it may limit the interest and benefit that the book will have for botanists; because aspects of hybrid zones, including their origin, structure, evolutionary consequences, and fate in plants undoubtedly will be different than for animals. One can not simply extrapolate the aspects of hybrid zones for plants based on animal examples.

In chapter 1, editor Richard Harrison, discusses the hybrid zones from a historical perspective. He explains the basic differences in hybrid zones between animal and plants; plant hybrid zones tend to be diffuse, characterized by local hybrid swarms, whereas animal hybrid zones tend to be well defined. He goes on to define "hybrid" and "hybrid zone" as used by evolutionary biologists of the past and present and explains the controversy that surrounds the definition of these terms. He also introduces the major issues (controversies) in hybrid zone research. Briefly the issues are; the taxonomic treatment of the hybrids and species concepts; origins of hybrid zones, dynamics of stable hybrid zones (Do they represent stable equilibria?); fates of hybrid zones; and causes and consequences of introgressive hybridization.

Chapter two, by N. H. Barton and K. S. Gale, addresses the genetic analysis of

hybrid zones and discusses the methods that can be used to analyze cline width, cline shape, and patterns of linkage disequilibria using a variety of data from morphology, cytology, and electrophoretic (isozymes). The chapter provides an excellent background for those researchers who wish to quantitatively analyze their hybrid zone data. Daniel Howard has authored the third chapter, which discusses the concept of reinforcement, which he defines as "the evolution of prezygotic isolating barriers in zones of overlap or hybridization (or both) as a response to selection against hybridization." He discusses the hypothesis of reinforcement in light of its origin, dynamics and fate. One of the expected outcomes of reinforcement is reproductive character displacement and the author discusses many examples of such. He also presents his recommendations for studying reproductive character displacement. In the end he concludes that although the concept of reinforcement has not often invoked because of numerous strong theoretical objections, it is still widely used by evolutionary biologists to explain the patterns they find in nature.

The fourth of the introductory chapters concerns introgression and its evolutionary consequences in plants and is authored by Loren Rieseberg and Jonathan Wendel. They define and discuss both localized and dispersed introgression in their chapter. A major portion of the chapter is dedicated to a discussion through examples of the evolutionary consequences of introgression including factors such as increase in genetic diversity, transfer of adaptations, origin of new adaptations, origin of new types (and eventually taxa), and reproductive barrier reinforcement to mention a few. Most of their examples rely heavily on electrophoretic (isozymic) and molecular data. They acknowledge that introgression undoubtedly plays a major role in plant evolution, although much remains to be understood. They also present a review of problems that have been encountered when studying introgression. They conclude by indicating future directions in introgression research in plants and point out that molecular markers will continue to provide the best means of studying introgression. We may anticipate that the relatively new techniques molecular will greatly enhance our ability to study introgression with respect to mechanisms and evolutionary consequences. All in all this is an excellent chapter.

The second part of the book that represents case studies of hybrid zones is disproportionately zoocentric. The editor attempts to dismiss the zoocentricity by indicating that few examples of a multidisciplinary approach to the study of introgression exist for plants; apparently the only example worthy of a chapter is one on the Louisiana Irises. Rieseberg and Wendel cite many examples in their chapter and several examples appear to have involved a multidisciplinary approach, these include examples from *Quercus*, *Aesculus*, *Salix*, *Carduus* and especially *Helianthus*.

The chapter on the Louisiana Irises was written by the acknowledged experts on the group, M. L. Arnold and B. D. Bennett. The authors use data from isozymes, rDNA, and RAPD's to strongly support their hypothesis for the origin of hybrid populations. Their chapter, like Rieseberg and Wendel's (chapter 4), also emphasizes the unquestionable utility of genetic data in studying plant taxa and their hybrids. They also point out that most plants offer the opportunity to study the fate of individuals in hybrid zones over time, which is information not so easily attained in most animal studies. This chapter is very well-written and is an excellent summary of the past 60 years research on the Irises of Louisiana.

The remaining seven chapters deal with various animal examples including grasshoppers (2 chapters), flickers, *Heliconius* butterflies, toads, pocket gophers, and eutherian mammals. I found the chapters on *Caledia* grasshoppers from Australia and *Bombina* toads from Europe to provide the most convincing evidence of hybrid zones because the multifaceted approaches that have been applied to the problem using a diversity of data from morphology, cytology, isozymes, nrDNA, and mtDNA. The chapter on *Heliconius* butterflies, while only using morphological data, is particularly fascinating because of the complex morphological patterns that exist in different races of these butterflies.

In summary, I find that the major drawback to this book for botanists is its con-

centration on zoological examples. I don't agree with the editor's contention that only one good plant example (Irises) could be found. The chapters by Arnold and Bennett on Irises and by Rieseberg and Wendel on introgression, as well as the other three chapters from Part I of the book, are very worthwhile reading, but I'm not sure whether this warrants the purchase of the book. For researchers interested in the general phenomenon of hybrid zones across both the plant and animal kingdoms, this book might be a very worthwhile purchase.

—RANDALL J. BAYER, University of Alberta, Department of Biological Sciences, Edmonton, AB T6E 2E9, Canada.

The Wild Orchids of California. By RONALD A. COLEMAN. Comstock Publishing Associates, Cornell University Press, 572 E. State St., Ithaca, NY 14850, USA, 1995, xvi, [i], 201 pp., 39 [i.e., 40] pp. pls. (col.), text ill. (B&W), ISBN 0-8014-3012-7 (HB), \$45.00.

Until now there never has been a book on the native orchids of California. Ronald A. Coleman's superb *The Wild Orchids of California* now rectifies this deficiency. He treats 11 genera, 33 species (all native but the alien *Epipactis helleborine*), and 3 hybrids (*Platanthera* × *estesii*, *P.* × *lassenii*, *P.* × *media*). The hybrids, a "Spiranthes undescribed" (p. 166), and the appropriately newly described *Piperia colemanii* Morgan & Glicenstein (*Lindleyana* 8:89, 1993) are not in *The Jepson Manual* (JM; 1993). Other differences from the JM's orchid part done by Dieter H. Wilken and William F. Jennings are Coleman's recognition of *Platanthera dilatata* var. *leucostachys* (in JM as *P. leucostachys*) and varieties for *Calypso bulbosa* (var. *occidentalis*) and *Corallorhiza trifida* (var. *verna*) (consistently, *Malaxis monophyllos* ssp. *brachypoda* in JM appears in Coleman as var. *brachypoda*).

Excellent color pictures (124 total) illustrate all 36 taxa Coleman accepts; all but the hybrids and undescribed *Spiranthes* have county distribution maps with a single dot for each county record. The floral vignettes prefacing the species accounts are more decorative than diagnostic. The only real orchid flower diagrammed is the generalized figure on page 5. The lack of meaningful drawings is a minor defect forcing overreliance on the color photos. The elaborate accounts are the heart of the book, indeed 135 pages for the 32 taxa treated (3 pages are on the hybrids and undescribed *Spiranthes*). Other than their etymology, extensive synonymy, and common names, the species accounts are in literary rather than telegraphic format, with detailed information for the morphological description, distribution, habitat, phenology, conservation, and (often) notes and comments. Bolding these subject headers would have made the information more accessible.

The introductory 27 pages discuss orchid structure, phenology and distribution of Californian orchids (with three tables, a two-page phenology table, and two maps), biogeography and climate of California, chief geographic areas of the state (with one map), and habitat protection. The introduction concludes with an unillustrated key to genera that is simpler and probably more useful than its counterpart in JM. Genera with more than one species also have keys. One appendix gives herbarium documentation for the Channel Islands and the 58 counties in California. Another appendix lists potential new county records as well as *Cypripedium parviflorum* var. *makasin* and *Spiranthes infernalis* as potential new species for California. A concise glossary, ten-page bibliography, and detailed index finish this fine work.

—RUDOLF SCHMID, University of California, Berkeley.

ANNOUNCEMENT

THE ALFRED BROUSSEAU PROJECT: NATIVE WILDFLOWERS OF CALIFORNIA

Brother Alfred Brousseau F.S.C. (1908–1988) made a collection of 35 mm color slides of native wildflowers of California, which consists of over 20,000 slides of over 2000 species. The object of this project is to make this material available to all. The project is not-for-profit and asks for a donation of \$35.00 to help defray production costs.

The first output of this project is in the form of CD-ROM's containing 2000 pictures of 665 species of flowers. These pictures were scanned using a Barneyscan and saved as 8-bit PICT files for use on the MAC and changed to 8-bit TIFF files for the DOS version. It is intended to continue this project in the attempt to make Brother Alfred's complete collection available.

There are two versions of the CD (one for the MAC, the other for DOS). The MAC version contains standalone Supercard files of the flowers arranged in alphabetical order by Latin name. Each card contains information about the flowers (including Latin name, family name, common name, as well as information as to date and place of picture taking) as well as a button to access the full-screen picture of the flower (PICT file format; 8 bit, 256 colors). Text files are available which present indices for the flowers (indexed by family name, Latin name, and common name).

The DOS version contains TIFF file format (8 bit, 256 colors) pictures of the same flowers as the MAC version, but now grouped according to botanical family. Text files contain information about the flowers, including the Latin name, family name, common name, as well as information as to the date and place of picture taking. There are also indices by family name, Latin name and common name.

For information, contact Brother Eric Vogel, F.S.C., Saint Mary's College of California, 1928 St. Mary's Road, Moraga, CA, 94575. (510) 631-4296.

Internet: evogel@stmarys-ca.edu
WWW: <http://altair.stmarys-ca.edu/~evogel/wildflowers.html>

ANNOUNCEMENT

SOCIETY OF ETHNOBIOLOGY 19TH ANNUAL CONFERENCE

27-30 MARCH 1996

SANTA BARBARA MUSEUM OF NATURAL HISTORY

PROGRAM SUMMARY

Special Exhibition: "First People: Animals in Native Californian Art" in the Museum Gallery

Wed. 27 March: Evening: Welcome reception and registration

Thu. 28 March: Oral and poster sessions, Botanic Garden tour, Reception

Fri. 29 March: Oral and poster sessions, Evening banquet
Keynote Address: Dr. Larry Agenbroad
"Latest news on old bones: Interactions between humans and mammoths in North America"

Sat. 30 March: Field trips

For further information, including rates for Native American participants and Latin American students, contact: Jan Timbrook, Anthropology Department, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. (805) 682-4711. FAX (805) 569-3170.



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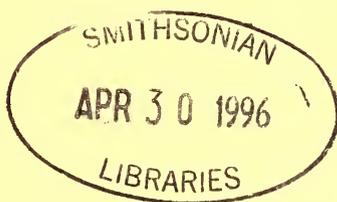
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WETLANDS OF CALIFORNIA, PART I: HISTORY OF WETLAND HABITAT CLASSIFICATION

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ABSTRACT

A review of the history of vegetation classification in California reveals a serious underestimation of the diversity, extent, and functions of the state's wetlands and consequently, a misrepresentation of the perceived paucity of wetlands in California and the arid West. We review the classification systems of California's wetlands, beginning with early efforts in vegetation typing by the U.S. Forest Service, and illustrate that a detailed comprehensive methodology for the classification and description of wetlands and deepwater habitats is required before they can be protected and managed adequately.

Wetlands can be classified within a system of categories distinguished by origin, structure, flooding frequency, water chemistry, dominant organisms, or some other combination of physical and/or biological attributes. A hierarchical classification of wetlands is a system of classification where wetlands are ranked in categories one above another. Cowardin et al. (1979) produced a hierarchical classification of wetlands for the U.S. Fish and Wildlife Service that incorporated a ranking of systems, subsystems, classes, and subclasses. We have adopted this classification (Ferren et al. 1995) as a starting point and have modified and expanded it formally to include water regimes, water chemistry, hydrogeomorphic units, and substrate and dominance-type categories (see Part II, Ferren et al. 1996a; and Part III, Ferren et al. 1996b). Although Cowardin et al. (1979) provided modifiers for the classification in the form of categories for water regimes, chemistry, and dominance types, these

were never formally incorporated into the classification, and in addition, no landform/habitat information was provided. Thus, it was not possible in their classification to distinguish a wetland based upon its ecosystem context, such as a structural basin estuary, montane alkali lake, or coastal plain stream.

California has a complex interface of environmental factors; therefore it is necessary to employ a classification of wetlands that portrays adequately the richness of wetland types resulting from this complexity. A classification methodology demonstrating differences among wetlands is essential if conservation efforts are to preserve at least some representation of the state's natural wetland heritage. Largely because of the rapid urbanization of California, it will be difficult to conserve wetland resources that are not identified as distinct or sufficiently described. Classifying and describing different wetland types will help establish a link, for example, between a specific wetland habitat and any existing or potentially significant or unique ecosystem function (e.g., endangered species habitat) or socioeconomic value (e.g., wetlands as nurseries for economically important fish such as halibut). To date, no previous attempts at classifying California wetlands have approached the level of detail that is required to articulate the richness of the state's wetlands. In this paper we provide a history of the classification of wetlands in California to demonstrate the various weaknesses in previous classification efforts. We then propose a classification methodology in Part II (Ferren et al. 1996a) and a key to and catalogue of example types in Part III (Ferren et al. 1996b) as contributions toward the wetland conservation effort and an improvement in documentation techniques.

ENVIRONMENTAL SETTING

California is climatically, topographically, and geologically diverse, which contributes to its great habitat richness (Barbour and Major 1988). Factors that influence the formation and differentiation of wetlands can include, elevation, exposure, landform, bedrock, soil, rates of erosion or sedimentation, temperature, rainfall, accumulation of salts, distance from the ocean, tidal regimes, energy of water flow, and artificial disturbances. Wetlands of the state extend topographically from marine wetlands exposed irregularly at extreme low tide, to glacial ponds and alpine habitats. The great richness of habitat types and environmental parameters, including potentially large seasonal variation in local weather patterns, has undoubtedly contributed to the evolution of equally rich and often unique biological resources. Biological endemism is a particular characteristic of wetlands with special hydrogeochemical features,

such as alkali meadows, serpentine and tar seeps, vernal pools, and salt marshes.

Wetlands in central and southern California occur in various ecosystem contexts and have origins related to several major physical processes. Wetlands that develop as a result of fluvial processes occur in riparian corridors along streams and rivers, such as the Santa Margarita and San Luis Rey rivers in San Diego County. Riverine and palustrine wetlands also may occur in proximity to estuarine and marine wetlands where a river reaches the coast and sea water mixes with fresh water of continental origin, such as at the mouths of the Santa Ynez, Ventura, and Santa Clara rivers. Elsewhere, structural basins with high or perched water tables may serve as sediment sinks and support the development of alkali flats, as in the Temescal Wash and Lake Elsinore area along the eastern margin of the Santa Ana Mountains in Riverside County. Other basinal hydrogeomorphic units and their associated wetlands can develop as a result of: (1) eolian processes that form dune swale wetlands, such as at the San Antonio Terrace Dunes on Vandenberg Air Force Base in Santa Barbara County; (2) earthquake faults along which can form "sag-ponds", such as Lost Lake in San Bernardino County; (3) historic glaciation that has produced ponds impounded by moraines, such as Dollar Lake in the San Gorgonio Wilderness; (4) volcanism that can create calderas, such as Zaca Lake in Santa Barbara County; or (5) artificial creation of basins including the impoundment of lacustrine reservoirs, such as Big Bear Lake in San Bernardino County, Cachuma Lake in Santa Barbara County, Lake Casitas in Ventura County, and Twitchell Reservoir in San Luis Obispo County.

In addition to the creation of wetlands and deepwater habitat wetlands associated with artificial structures such as reservoirs, various impacts to ecosystems also can result in the conversion of wetlands from one type to another, further compounding the process of classification. For example, at Ballona Wetlands (Playa Vista) in Los Angeles County, natural estuarine wetlands were converted to non-tidal, impounded, palustrine wetlands when berms and tide gates were installed. These artificial palustrine wetlands were used temporarily for agricultural purposes. The resulting degraded wetlands support a mixture of native hydrophytes and exotic weedy species in a soil topography typical of tilled areas. A large-scale restoration project has been approved for portions of the Ballona Wetlands (National Audubon Society 1986), which will return tidal circulation to previously estuarine habitats and also introduce the process of wetland restoration to the classification and description of the site's habitats.

Superimposed on the origin (e.g., fluvial, structural, eolian, glacial, volcanic), ecosystem context (e.g., estuaries, streambeds, lake

margins), and disturbance history (natural or artificial) of wetlands are the influential attributes of strongly seasonal, wet and dry periods, and a wide range of edaphic differences among sites. The combination of these environmental features results in the formation of a truly vast number of hydrogeomorphic units (i.e., wetland habitats such as bars, banks, channels, pools, and seeps) and their corresponding wetland types. This is the origin of the rich wetland heritage of California.

Scarcity and losses. Because of the generally dry climate of the ecoregions of southern California, dogma apparently has developed in many professional and lay circles that wetlands of the region are uncommon and by inference are limited in type, numbers, and importance. Generalizations abound. For example, "... marshes and swamps are scarce throughout the [Californian estuary] province" (Cowardin et al. 1979, p. 28). Recent evidence, such as that presented herein (Part II, Ferren et al. 1996a), demonstrates that wetlands of the California province are very diverse. Some wetlands such as those associated with riparian corridors are more common, whereas others are rare and even unique, such as natural lacustrine lakes (e.g., Baldwin Lake in San Bernardino County, Cuyamacha Lake in San Diego County, and Mystic Lake in Riverside County) of coastal southern California, each of which is represented by only one example. The incomplete and largely superficial approach to classification, description, and inventory of wetlands in California has led to many difficulties in the protection and management of these wetlands, as well as in the simplification and generalization of important ecosystem functions. In direct terms, the recognition of fewer wetland types and fewer examples of these types has translated to less protection for the unrecognized natural diversity and for the extent of this diversity.

As might be expected, we have found that many wetlands have been destroyed before they were identified, studied, and protected. In the United States during the past 200 years, the lower 48 states have lost an estimated 53% of the original 221 million acres of wetlands; 22 of these states have lost 50% or more of their original wetland acreage (Dennis and Marcus 1984; Dahl 1990). Dennis and Marcus (1984) estimated nearly a decade ago that approximately 9% (ca. 450,000 acres) of the wetland resources remain as compared to when California became a state in 1850 (ca. 5 million acres). This translates to a loss of 91% of the state's wetlands, and a reduction of total surface of the state in wetlands from approximately 5% of the land to less than one-half of one percent of the land (Dahl 1990).

The California Department of Parks and Recreation (CDPR 1988) reports that at the state-wide level, California has lost approximately 80% of the coastal salt marshes, 95% of the riparian wetlands, 90%

of freshwater marshes, and 90% of the vernal pools. Along the southern coast of California, CDPR (1988) estimates there has been a 75% reduction in wetlands, from approximately 53,000 acres to 13,000 acres. In southern California, notable examples of wetland categories for which losses have been extensive include: (1) estuarine wetlands (i.e., salt marshes) as an entire subsystem at 75–90% (Zedler 1982; California Department of Fish and Game 1983; California Coastal Commission 1989); (2) “the riparian community” at 90–95% (Faber et al. 1989) including loss of 40% of the riparian wetlands in San Diego County during the last decade alone (CDPR 1988); and (3) vernal pools at 90% (Zedler 1987). These losses have contributed directly to the endangerment of the biological resources of California, as evidenced by estimates that 55% of the animals and 25% of the plants designated as threatened or endangered by the State depend on wetland habitats for their survival.

It is with general interest in our California wetland heritage and with concern for the rate and extent of habitat loss that we have integrated a compilation of information into a hierarchical classification (see Part II, Ferren et al. 1996a) based on a modified version of Cowardin et al. (1979). The scope of this classification includes all wetlands from the five wetland systems identified for North America (i.e., marine, estuarine, riverine, lacustrine, palustrine), each of which occurs in California. Only through detailed analysis can we appreciate fully the richness of wetland habitats and biota in California, and can we hope to protect and manage those wetlands that remain.

CLASSIFICATION OF CALIFORNIA WETLANDS

Early efforts. From 1927 to 1941, the U.S. Forest Service conducted the Vegetation Type Map Survey of California, which was based largely on upland types of vegetation cover (e.g., chaparral). It included only a few broad categories of wetlands (e.g., coastal marshes) and several aquatic features (e.g., large bodies of water). The great majority of wetland types, however, were not identified and most of the vegetation maps were never published. In addition to this generalized federal effort, individual researchers published detailed floras and technical papers on particular sites or habitats such as vernal pools in San Diego County (Purer 1939) and marshlands at Newport Bay (Stevenson and Emery 1958). Munz (1959, 1968) typically has been cited as the reference for vegetation classification provided in the statewide floristic treatment, *A Flora of California*. However, he treated vegetated wetlands in only several broad categories (e.g., coastal salt marshes, freshwater marshes, and alkali sink). More typically, Munz referred to the habitat in which particular wetland species occurred (e.g., “along streams”, “rather

deep water”, “shallow ponds”, “vernal pools”, “muddy places”); or he provided an indication that the wetland community was within a larger context such as “Foothill Woodland”, “Chaparral”, or “many Plant Communities”. No clear explanation of palustrine scrub-shrub or forested wetlands occurred in this classification. The importance and impact of the publication of Munz (1959), however, cannot be minimized in the treatment of the state’s flora or its vegetation. His tendency to overlook the richness of wetland types has had a profound effect to the present (e.g., Holland 1986; Sawyer and Keeler-Wolf 1995).

Perhaps the most important publication on the flora of California wetlands was authored by Mason (1957) two years before the issue of Munz (1959). In *A Flora of the Marshes of California*, Mason compiled a compendium on the wetland flora and included much information on wetland habitats, although he proposed no formal classification of types of wetlands or wetland vegetation. He included many insightful comments for the time, including:

Generalizations regarding the floristic organization of the marsh and wetland habitats are difficult, because such organization centers around the intergrading environmental variables that not only account for different combinations of habitat conditions, but, through natural selection, permit a high degree of overlapping of species between habitats. Communities of plants therefore are rarely definitive in relation to what may appear to be distinctive habitat. The three most important sets of environmental variables are:

1. *The relative permanence of water, or the character of the intermittence of water in the habitat*
2. *The relative salinity and the hydrogen-ion concentration of the soil solution*
3. *The habitat variables related to seasonal temperature and length of the growing period*

Some aspects of each of these three sets of variables are evident in every marsh or wetland habitat. They combine in various ways to produce exceedingly complex habitat diversity . . . (Mason 1957, p. 7)

Many of the observations made by Mason for the state, especially his extensive research in central California wetlands (Mason n.d.) nearly forty years ago, are true today but have been overlooked during recent efforts to classify wetlands.

Improvements and additions. The first major effort to provide a statewide, hierarchical classification of habitats was provided by

Cheatham and Haller (1975) as an unpublished manuscript, which originally was intended for inclusion in Barbour and Major (1977). Cheatham and Haller (1975, p. 2) defined habitat type or one of its subdivisions as: "an assemblage of natural features of the landscape that lead us to the subjective conclusion that one area is sufficiently different from another to warrant separate description." They described their "Major Categories" as approximating "Vegetation Types" in Munz (1959), and their "Habitat Types" as approximating "Plant Communities" in Munz. They also added "Major" and "Minor Subdivisions" of the Habitat Types. In their work for the University of California's Natural Reserve System, Cheatham and Haller (1975, p. 2) found that "... it was obvious we were working with habitat types that fell between [Munz's] categories." They subsequently stated that their document "... goes into a more detailed level and attempts to pick up where [Munz] leaves off" (Cheatham and Haller 1975, p. 2). Several major subsequent works on the classification of California vegetation (e.g., Holland 1986; Sawyer and Keeler-Wolf 1995) elaborate upon the effort set forth by Cheatham and Haller. Relevant examples of the Cheatham and Haller categories with selected subcategories are presented in Table 1.

At about the same time that Cheatham and Haller (1975) was in preparation, the California Native Plant Society held a symposium entitled *Plant Communities of Southern California* (Latting 1976), during which Thorne (1976) provided another classification of vascular plant communities of California. This classification also was described as a replacement for Munz (1959):

The [Munz] classification of plant communities has served a most useful purpose in the past but it omits numerous recognizable plant communities or combines several under one overly broad heading. Most neglected are the aquatic communities with surfweed, marine meadow, vernal pool ephemeral, bog, and riparian communities largely ignored and freshwater marsh and stream, lake, pond, and reservoir aquatic communities combined under freshwater marsh (Thorne 1976, p. 5).

Table 2 includes the aquatic communities presented in numerical order by Thorne (1976).

Both classifications by Cheatham and Haller (1975) and Thorne (1976) made important contributions to classify the vegetated and nonvegetated wetland resources in California. However, neither provided a methodology that was sufficiently detailed for the identification, classification, and nomenclature of the great richness of wetland types that occur in California. In 1980, The Nature Conservancy and the California Natural Diversity Data Base (Holstein 1980) at the California Department of Fish and Game released a

TABLE 1. EXAMPLES CALIFORNIA HABITAT "CATEGORIES" WITH SELECTED "SUBCATEGORIES" THAT INCLUDE WETLANDS AS PORTRAYED BY CHEATHAM AND HALLER (1975).

1.0 COASTAL AND SHORELINE HABITATS	4.5 Meadows and Seeps
1.1 Open Water	4.51 Montane Meadow
1.11 Bays and Harbors	4.52 High Elevation Meadows
1.12 Coastal Esteros	4.54 Alkali Meadows
1.2 Coastal Wetlands	4.55 Alkali Seep
1.21 Tidal Flats	4.56 Freshwater Seep
1.22 Salt Marshes	5.0 BOGS AND MARSHES
1.3 Exposed Open Coast	5.1 Bogs and Fens
1.31 Exposed Sandy Beach	5.2 Marshes and Swamps
1.32 Exposed Cobble Beach	5.21 Coastal Salt Marshes
1.33 Exposed Mixed Beach	5.22 Coastal Brackish Marshes
1.34 Exposed Rocky Shore	5.23 Alkali Marshes
1.4 Protected Open Coast	6.0 RIPARIAN HABITATS
3.0 SCRUB AND CHAPARRAL	6.1 Bottomland Woodlands and Forests
3.6 Alkali Scrub	6.2 Streambank Woodlands and Forests
3.62 Alkali Sink Scrub	6.3 Alluvial Woodlands and Forests
3.621 Intermittently Moist Alkali Sink	6.3 Palm Oasis Woodland
3.622 Permanently Moist Alkali Sink	7.0 WOODLANDS
3.63 Alkali Seep	7.4 Alluvial Woodlands (see 6.3)
4.0 GRASSLANDS, VERNAL POOLS, AND MEADOWS	10.0 AQUATIC HABITATS
4.4 Vernal Pools	10.1 Springs
4.41 Great Valley Vernal Pools	10.2 Streams
4.411 Sacramento Valley Vernal Pools	10.21 Mountain Streams
4.412 San Joaquin Valley Vernal Pools	10.22 Foothill and Valley Streams
4.42 Coast Range Vernal Pools	10.23 Coastal Streams
4.43 Southern California Vernal Pools	10.3 Rivers
4.431 Interior Cismontane Vernal Pools	10.4 Lakes and Streams
4.432 San Diego Mesa Vernal Pools	10.5 Cave Aquatic Habitats

TABLE 2. A CLASSIFICATION HIERARCHY THAT INCLUDES THE "AQUATIC COMMUNITIES" OF CALIFORNIA PRESENTED BY THORNE (1976).

1. MARINE AQUATIC	7. RIPARIAN WOODLAND
a. Surfweed	10. PACIFIC CONIFEROUS FOREST
b. Marine Meadow	d. Redwood forest (in part)
3. COASTAL SALT MARSH	16. MOUNTAIN MEADOW
a. Tidal marsh	a. Montane Meadow
b. Salt-flat succulent	b. Subalpine Meadow
4. FRESHWATER AQUATIC	c. Alpine Meadow
a. Freshwater marsh	20. DESERT SCRUB AND WOOD-
b. Lake, pond, and quiet stream aquatic	LAND
c. Reservoir semiaquatic	h. Desert oasis woodland
5. VERNAL POOL EPHEMERAL	i. Desert riparian woodland
6. SPHAGNUM BOG	21. ALKALINE SCRUB
a. Floating bog	b. Alkali sink scrub
b. Darlingtonia bog	c. Alkali meadow and aquatic
c. High nutrient bog	

draft version of the *California Vegetation Cover Types*, which included a hierarchical list of types based on vegetation cover and arranged in systems, cover classes, cover types, and community types. The list provided no information on locations or habitats and did not separate wetland from upland types. As with many efforts, Holstein (1980) excluded habitats lacking vegetation cover, but he did include systems for bryophytes, lichens, and algae.

Agency efforts. State and federal agencies also have developed classifications of vegetation. The U.S. Fish and Wildlife Service developed a comprehensive classification methodology to inventory and map the nation's wetlands as part of the National Wetland Inventory (NWI) Program. This classification, entitled *Classification of Wetlands and Deepwater Habitats of the United States* (Cowardin et al. 1979), has provided the definition of wetlands accepted in our classification (see Part II and III, Ferren et al. 1996a&b), emphasizing the presence of wetland hydrology, hydrophytic vegetation, or hydric soils. Under a more recent interpretation of the U.S. Fish and Wildlife Service definition, however, a wetland must be periodically saturated or covered by shallow water during a portion of the growing season, regardless of the presence of hydrophytes or hydric soils (Tiner 1989). National Wetland Inventory (NWI) maps, based on high altitude aerial photography and plotted on 7.5" U.S.G.S. quadrangle maps, exist for most of California; however, they often are incomplete and general in the categorization of wetland types. As in our previous comments, this classification provided the primary structure for the higher levels of our hierarchical classification, but it is insufficient to portray accurately the richness of wetland types

because it lacks most elements of hydrogeomorphology that are essential in the differentiation of types.

In a series of publications (Payson et al. 1980, 1982; Hunter and Payson 1986), the U.S. Forest Service offered a hierarchical classification and guides for the state. One such publication, *A Vegetation Classification System Applied to Southern California* (Payson et al. 1980), included the following hierarchical elements based on plant structure (i.e., physiognomy) and cover: Formations (e.g., Herbaceous), Subformations (e.g., Aquatic), Series (e.g. Pondweed Series), Associations (i.e., a plant community or the basic unit of the classification), and Phases (i.e., local variants). The authors state that:

The Vegetation Classification System for Southern California is compatible at all levels with a national land classification system being proposed by the Forest Service and which incorporates the international system for classifying vegetation. . . . The system is based upon a hierarchical stratification of plant cover. . . . The nomenclature for Association reflects the dominant overstory species, and the most prevalent (or distinguishing) associated species. . . . The Associations have not yet been developed. They can be identified on the ground on a project basis of identified uniformity for the entire southern California area after adequate field samples are taken (Payson et al. 1980, p. 2).

This classification system is open ended in that the Associations and Phases are generally left undescribed. As with most other efforts, nonvegetated areas are not included, and only physiognomy and vegetation cover are used to classify the upland and wetland vegetation. In a related effort, the U.S. Forest Service has undertaken an ecosystem-type classification for its lands, including reconnaissance and intensive sampling and ecological type description (Allen 1987). The "Ecological Type" is the basic unit of the classification model and ". . . is defined as a classified category of land with a unique plant association and physical site characteristics, differing from other categories of land in its ability to produce vegetation and respond to management" (Allen 1987, p. 2). This classification apparently is meant largely for upland ecological types, and would include only vegetated wetlands on Forest Service lands.

In 1990, the U.S. Environmental Protection Agency (EPA), Region IX, prepared a draft, *List of Priority Wetland and Aquatic Habitats of California* (Leidy 1990). As stated in the document, "The . . . list represents the initial efforts to identify priority wetland and aquatic habitats within California. This list identifies particularly important and vulnerable wetland and aquatic habitats in order that

these areas can receive improved levels of protection by EPA under its various review and regulatory authorities” (Leidy 1990, p. 1). The extensive, annotated list includes by region, the name, location, habitat types, function, categorized socio-economic value, threat, and status of the wetlands and aquatic habitats. The following “habitat types” are used: (1) estuarine; (2) lagoon/bay, open ocean; (3) riverine [perennial stream, intermittent stream, pool/riffle sequence]; (4) lacustrine; (5) mud flat; (6) vegetated shallows; (7) emergent wetland [salt marsh, brackish marsh, freshwater marsh]; (8) riparian woodland/wetland; (9) farmed wetland; (10) vernal pool; and (11) other. In a recent effort, EPA IX funded a study of the assessment of ecosystem functions of the waters of the United States, including wetlands, in the Santa Margarita Watershed (L. C. Lee & Associates, Inc. 1994). Wetland nomenclature for the inventory of types followed an earlier draft version of our modified Cowardin et al. approach.

State agencies also have undertaken efforts to classify California’s vegetation, habitats, and ecosystems. The California Department of Parks and Recreation (CDPR) initiated a project in 1979 to conduct an inventory of “terrestrial and semiterrestrial vegetation” included on their lands (Jensen 1983). Most state efforts are agency specific, however, and do not consider lands outside the jurisdiction of a specific agency. The CDPR vegetation classification is part of a multi-hierarchical classification system of ecosystem, biotic communities, and habitats. The Natural Diversity Data Base of the California Department of Fish and Game has made several efforts at conducting inventories and assessments and at improving the classification of vegetation. Jensen (1983) conducted an inventory using Cheatham and Haller’s classification and produced a document on their occurrences for The Nature Conservancy entitled *The Status of California’s Natural Communities: Their Representation on Managed Areas*.

Perhaps the most important and widely-used addition to classification efforts has been contributed by the Department of Fish and Game, *Preliminary Descriptions of the Terrestrial Natural Communities of California* (Holland 1986). Holland’s treatment is based on a thorough reorganization of Cheatham and Haller, resulting in a hierarchical, numerical classification with element codes, names, descriptions, and characteristic species presented for each community. Approximately 68 wetland community types are identified in this statewide effort. Although this document and classification has been the most useful to date, many wetland types were omitted or grouped with other types. For example, no clear separation of wetland and upland riparian was established. Certain relevant portions of the Holland classification are found in Table 3.

Currently the California Department of Fish and Game, in con-

TABLE 3. PORTIONS OF THE HOLLAND (1986) "TERRESTRIAL COMMUNITY" CLASSIFICATION FOR CALIFORNIA, INCLUDING APPARENT WETLAND "ELEMENT CODES AND NAMES."

40000	GRASSLANDS, VERNAL POOLS, MEADOWS, OTHER HERB COMMUNITIES
44000	Vernal Pool
44100	Northern Vernal Pool
	44110 Northern Hardpan Vernal Pool
	44120 Northern Claypan Vernal Pool
	44130 Northern Volcanic Vernal Pool
44300	Southern Vernal Pool
	44310 Southern Interior Basalt Flow Vernal Pool
	44320 San Diego Mesa Vernal Pool
45000	Meadow and Seep
45100	Montane Meadow
	45110 Montane Wet Meadow
	45120 Montane Dry Meadow
	45200 Subalpine Meadow
	45300 Alkali Meadows and Seep
	45400 Freshwater Seep
46000	Alkali Playa Community
50000	BOG AND MARSH
51000	Bog and Fen
52000	Marsh and Swamp
	52100 Coastal Salt Marsh
	52200 Coastal Brackish Marsh
	52300 Alkali Marsh
	52400 Freshwater Marsh
	52500 Vernal Marsh
	52600 Freshwater Swamp
60000	RIPARIAN AND BOTTOMLAND HABITAT
61000	Riparian Forests
	61100 North Coast Riparian Forests
	61200 Central Coast Riparian Forest
	61300 Southern Riparian Forests
	61400 Great Valley Riparian Forests
	61500 Montane Riparian Forests
	61600 Modoc-Great Basin Riparian Forests
	61700 Mojave Riparian Forests
	61800 Colorado Riparian Forests
62000	Riparian Woodlands
63000	Riparian Scrubs
90000	ALPINE HABITATS
91000	Alpine Boulder and Rock Field
	91200 Alpine Talus and Scree Slope
	91210 Wet Alpine Talus and Scree Slope

junction with the California Native Plant Society Plant Communities Committee, has undertaken the task of producing a new classification to supersede Holland (1986). The final document (Sawyer and Keeler-Wolf 1995) is entitled *A Manual of California Vegetation*. We have worked with the Committee in an attempt to coordinate

our efforts so that the two classifications have some compatibility. Information provided in Ferren (1989), "A Preliminary and Partial Classification of Wetlands in Southern and Central California with Emphasis on the Santa Barbara Region," provided a vehicle to discuss some level of coordination. One result of the interest in wetlands was the organization of the information in Holland into a "Preliminary Key to California Wetland Vegetation" (Keeler-Wolf 1992). The coordination also has been useful in that Sawyer and Keeler-Wolf (1995) incorporated some aspects of the Cowardin et al. (1979) classification. However, inclusion or exclusion of a series as wetland or upland is based upon Reed (1988), *National List of Plant Species That Occur in Wetlands: California (Region 0)*. Unfortunately, many plants that characterize wetlands in California are not included, or are incorrectly categorized on this list, and therefore, wetlands dominated or characterized by them are not included as wetlands in Sawyer and Keeler-Wolf (1995). Table 4 includes the proposed list of series that contain wetland examples.

The Sawyer and Keeler-Wolf list represents the first time there has been an effort to provide a statewide listing of vegetated wetland dominance types or series. However, the scope of the classification (1) does not include wetlands not dominated by vascular plants; (2) does not include hydrogeomorphic units or classes; and (3) generally does not adequately separate wetland and upland types when they occur in the same series. Throughout the volume there is an uneven application of the water regimes. Nonetheless, Sawyer and Keeler-Wolf (1995) attempt to bridge the gap between the traditional superficial treatment of wetlands in California and the nationwide effort to classify wetlands differently than uplands, such as has been spearheaded by Cowardin et al. (1979).

Additional classification efforts. Other attempts that have contributed toward a better understanding and classification of wetlands in North America and particularly the American West include a variety of classifications. Most notable is a classification system recently developed by Moyle and Eliason (1991), which is a hierarchical system for inland waters of California, based largely on patterns of fish distribution, and including fishless habitats. Although this classification is useful for describing general patterns of fish distribution, it does not reflect adequately the great diversity of hydrogeomorphic units and riverine wetland types within the study region, especially those that are fishless or do not support other well known aquatic organisms.

Another system of vegetation classification in California currently under development by the National Biological Service, is the Gap Analysis Project of the actual vegetation of California (Davis et al. 1995). Its purpose is to assess the protection status of plant com-

TABLE 4. CALIFORNIA WETLAND VEGETATION "SERIES" PROPOSED IN SAWYER AND KEELER-WOLF (1995). Additional series were included in an earlier key to wetland series (Keller-Wolf 1992); however, all series characterized by plants not included on the *National List of Plant Species That Occur in Wetlands* (Reed 1988) were excluded from a wetland affiliation in the latter work whether or not wetland examples are found in California.

WETLAND SERIES DOMINATED BY HERBACEOUS PLANTS	WETLAND SERIES DOMINATED BY TREES
Alkali sacaton series Kentucky bluegrass series One-sided bluegrass series Cordgrass series Ashy ryegrass series Creeping ryegrass series Saltgrass series Sedge series Spikerush series Bulrush-cattail series Bulrush series Cattail series Darlingtonia series Pickleweed series Duckweed series Mosquito fern series Bur-reed series Pondweed with floating leaves series Pondweed with submerged leaves series Yellow pond-lily series Ditch-grass series Quillwort series Beaked sedge series California oatgrass series Common reed series Giant reed series Introduced perennial grassland series Nebraska sedge series Pacific reedgrass series Rocky Mountain sedge series Tufted hairgrass series	[One Dominant Conifer Species] Alaska yellow-cedar stands Engelmann spruce stands Sitka spruce stands Beach pine series Lodgepole pine series [One Dominant Non-conifer species] Aspen series Black cottonwood series Fremont cottonwood series California sycamore series Hinds walnut series Arroyo willow series Black willow series Hooker willow series Pacific willow series Red willow series Sitka willow series Mixed willow series California bay series Fan palm series Foothill pine series Mesquite series Mixed oak series Red alder series Subalpine fir series Water birch series White alder series [Forests Where More than One Species Important] Black cottonwood series Fremont cottonwood series Valley oak series California walnut series Blue palo verde-ironwood-smoke tree series Mixed willow series Enriched stands in the Klamath Mountains
WETLAND SERIES DOMINATED BY SHRUBS Mountain alder series Sitka alder series Arrow weed series Buttonbush series Mexican elderberry series Mountain heather-bilberry series Mule fat series Narrowleaf willow series Sandbar willow series Bush seepweed series Greasewood series Iodine bush series Spine scale series Tamarisk series Winter fat series	HABITAT SERIES Alpine habitat Mountain meadow habitat Montane wetland shrub habitat Fen habitat Subalpine meadow habitat Subalpine wetland scrub habitat

munities, animal species, and vertebrate species richness in the state. In the first of a series of publications by Davis and his colleagues (Davis et al. 1995), plant communities and plant species distributions are described at a rather large scale of resolution (e.g., one hectare). Davis et al. suggest that their methodology necessarily neglects small vegetational units, many of which are wetlands. One of their important conclusions, however, is that many of the threatened or endangered plant communities in southwestern California are wetlands (e.g., "San Diego Mesa Hardpan Vernal Pool", "Southern Willow Scrub", etc.).

Another recent classification developed by Rosgen (1994) is a hierarchical, semiquantitative stream classification that employs indices of channel morphology. The system was developed for application at the river reach scale and is a helpful tool for viewing riverine wetlands within a watershed context. However, our methodology has been developed to describe riverine wetlands below the level of the reach, at the level of hydrogeomorphic unit as defined in our classification. Other classifications relevant to our study include those of: (1) aquatic plant life forms (Schuyler 1984); (2) the "riparian system" (Johnson et al. 1987); (3) California vegetation (Barry 1982; Holland and Keil 1989); (4) marine and estuarine natural communities of Washington (Dethier 1992); (5) meandering glide and spring streams in Idaho (Rabe et al. 1994); (6) aquatic and semiaquatic wetland natural areas in Idaho and western Montana (Rabe and Chadde 1994); (7) the flora of California (Hickman 1993); (8) meadows of the Sierra Nevada (Ratcliffe 1985); (9) subalpine meadows of the Sierra Nevada (Benedict and Major 1982); (10) montane meadows of the southern Sierra Nevada (Halpern 1986); (11) alluvial scrub vegetation of the San Gabriel River floodplain (Smith 1980); (12) old growth coastal redwood vegetation (Lenihan 1990); (13) California bioregions (Welsh 1994); and (14) riparian forest and scrublands of Arizona and New Mexico (Szaro 1989).

CONCLUSIONS

Although we began our endeavor with a thorough but relatively simple classification in mind, and with what seemed at the time an extensive preliminary list of wetland types, in our journey through a large part of California and through the process of a three-year study, we have arrived at one indisputable conclusion: an accurate representation of the State's wetland resources cannot be prepared without a classification that includes sufficient detail to capture the range of ecological attributes necessary to differentiate the many wetland types. In spite of all past efforts at simplicity, California's great wetland diversity requires a classification methodology that

portrays this diversity. Thus, conservation of California's wetland heritage may depend on our ability to articulate the habitat and biotic richness, both past and present.

The many efforts to provide a framework within which to organize a classification of the State's wetlands have failed to include enough information to distinguish differences among the many types. The result has been a serious under-representation of wetland resources. Much detail has been given to upland vegetation throughout the state, with many classifications of the types of grasslands, chaparral, coastal sage scrub, oak woodlands, and coniferous forests (Barbour and Major 1977, 1988; Sawyer and Keeler-Wolf 1995). At the same time, wetlands have been grouped largely into a few broad categories: "freshwater", "salt water", and "alkali" marshes; "riparian" systems; and "vernal pools". California continues to lose its natural wetland heritage, perhaps in part because we have seriously underestimated the richness of wetland types and their associated ecosystem functions and socio-economic values.

To help compensate for this underestimation of richness and to assist with the conservation of California's wetland heritage, we propose an alternative to the various classification schemes and methodologies that have been proposed to date. Our hierarchical, numerical approach, which was developed through the support of the U.S. Environmental Protection Agency, Region IX, is an extensive modification of Cowardin et al. (1979). It is presented in Part II (Ferren et al. 1996a) and Part III (Ferren et al. 1996b), as applied to the coast and coastal watersheds of central and southern California.

We are concerned for the future of California's wetlands, and in particular for those along the coast and in the coastal watersheds of Central and Southern California. The inevitable rapid urbanization of this region will necessitate continued fragmentation, isolation, and even loss of wetlands in spite of the various federal, state, and local legislation and policies to protect them. One important tool to assist in the conservation of the region's wetlands is the development of a wide base of knowledge on the diversity and importance (e.g., ecosystem functions and socio-economic values) of wetlands at all levels. Such knowledge will give us the ability to articulate accurately the need to protect, and when possible, to restore or recreate them. Recent endeavors to study, restore, purchase, or protect wetlands have contributed toward a new public interest in the importance of wetlands and the need to work actively for their conservation, including efforts by: (1) federal regulatory and resource agencies such as the U.S. Environmental Protection Agency, Fish and Wildlife Service, Army Corps of Engineers, and Forest Service; (2) California state agencies and institutions such as the State Coastal Conservancy, California Coastal Commission, State Lands Com-

mission, Department of Fish and Game, Department of Parks and Recreation, and University of California; (3) cities such as Carpinteria in Santa Barbara County; (4) organizations including the National Audubon Society, The Nature Conservancy, Campaign to Save California Wetlands, Surf Riders Association, and Urban Creeks Council; and (5) numerous local interest groups such as Friends of the Ventura River, Santa Margarita River Foundation, Land Trust for Santa Barbara County, and the Goleta Slough Management Committee.

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ANNOUNCEMENT

WETLANDS OF CALIFORNIA, PARTS I, II, AND III

The "Supplement" to Madrono 43(1) containing *Wetlands of California, Parts I, II, and III*, is available in limited numbers from author Robert Leidy at the U. S. Environmental Protection Agency. additional copies of the "Supplement" are available from authors Wayne Ferren and Peggy Fiedler @ \$5.00/copy. Individual reprints of Parts I, II, and III are not available.

ANNOUNCEMENT

WWW ADDRESS FOR FERREN, FIEDLER, AND LEIDY (1995)

Wetlands of the Central and Southern California Coast and Coastal Watersheds: A Methodology for their Classification and Description, Report to the U. S. Environmental Protection Agency, Region IX, San Francisco, CA (Ferren, Fiedler, and Leidy 1995) is available on the World Wide Web at the following address:

<http://ucjeps.herb.berkeley.edu/wetlands/>

This report is the original document from which the "Supplement" to Madroño 43(1), including *Wetlands of California, Parts I, II, and III*, has been condensed and revised. Included in this report and not available in the Supplement to Madroño 43(1) are chapters specifically dedicated to particular wetland systems, including: marine (Lafferty et al.), estuarine (Ferren et al.), riverine (Leidy et al.), lacustrine (Fiedler et al.), and palustrine (Ferren et al.) types. Also included in the report is a chapter (Mertes et al.) dedicated to the classification of wetlands and an assessment of their functions and values in the Ventura River Watershed. The electronic version of Ferren, Fiedler, and Leidy (1995) is a joint project among the UC Santa Barbara Museum of Systematics and Ecology, the SMASCH Project of the University and Jepson Herbaria, and the Museum Informatics Project at UC Berkeley.

WETLANDS OF CALIFORNIA, PART II: CLASSIFICATION
AND DESCRIPTION OF WETLANDS OF THE CENTRAL
AND SOUTHERN CALIFORNIA COAST AND COASTAL
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ABSTRACT

The modified Cowardin et al. (1979) classification described herein provides a methodology to identify all wetlands along the central and southern California coast and in the adjacent coastal watersheds from the Carmel River in Monterey County, to the Tijuana River in San Diego County. Use of classification tables in association with concepts of ecosystem context, site scale, and classification goals is intended to result in the development of a code (wetland type number) and wetland name that include information on the: (1) system, subsystem, class and subclass; (2) water regime and water chemistry; (3) hydrogeomorphic unit; and (4) substrate, dominance, or characteristic type of the wetland in question. A wetland data-page format also is proposed that provides a method for organizing information on the site location, characteristic species, ecosystem functions, socio-economic values, impacts, and conservation efforts for reference examples of the various wetland types.

Seventeen years ago Cowardin et al. (1979) presented a nationwide framework that continues today as the single best method for classifying wetlands on the national scale. Regionalization of this effort has begun in the American West because many important features of western wetlands were not covered with sufficient detail in previous efforts to identify the richness of wetland types. Specifically, in 1991, the United States Environmental Protection Agency (EPA), Region IX, funded a study to produce a classification, inventory, and description of wetland types along the coast and in coastal watersheds of the Southern Coastal, Transverse, and Peninsular Ranges in central and southern California. This region extends for approximately 400 miles, or about one-half the length of the state, from the Carmel River (ca. 36°30'N lat.) in Monterey County, south to the Tijuana River (ca. 32°30'N lat.) in San Diego County.

The investment by EPA was based upon an earlier compilation of wetland information (Ferren 1989) that was gathered in California for more than ten years and organized according to a modified version of the U.S. Fish and Wildlife Service (FWS) wetland classification (Cowardin et al. 1979). This ten-year effort was initiated because, at the time, no existing vegetation or habitat classification scheme (e.g., Munz 1959; Cheatham and Haller 1975; Holland 1986) adequately documented the great richness of wetland types in California, or attempted to incorporate the special environmental attributes that occur in the region as a result of the Mediterranean and arid climates. Ferren (1989, p. 3) “. . . found it necessary for communication purposes to categorize wetlands into some hierarchical system that would delineate the types of wetlands according to physical and biological criteria”. The Cowardin et al. (1979) system is such a hierarchical classification, “. . . progressing from system to subsystems, at the general levels, to classes, subclasses, and dominance types. . . . Modifiers for water regime, water chemistry, and soils are applied to classes, subclasses, and dominance types”.

Concern for the absence of thorough documentation of California wetlands, however, is replaced by alarm when one considers the extensive losses of wetlands (see Part I, Ferren et al. 1996a) that have occurred in the coastal watersheds without previous documentation of the habitat richness, ecosystem functions, and socio-economic values of these wetlands. Extensive agricultural development, rapid urbanization, flood control practices, and the continuing extraction of physical resources (such as petrochemicals, gravel, and water) are among the main contributors to these losses and to the degradation of many of the remaining wetlands (e.g., California Department of Parks and Recreation 1988; Dahl 1990; Leidy 1990; National Audubon Society 1992). Furthermore, changes proposed to the jurisdictional limits of wetlands as recognized by federal regulatory agencies would result in the elimination of federal jurisdiction

over many types of wetlands in western North America, and would exacerbate the potential threat of additional losses in California. Thus, this study was motivated by an urgent need for a mechanism to articulate the scope of the wetland heritage of California, particularly central and southern California, so that conservation efforts can accurately protect these resources.

Study region. California is a state of many contrasts and contradictions. Within its borders are the highest mountain (4420 m [14,495 ft]) in the lower 48 states, Mt. Whitney, and the lowest point on the continent, 85 m (276 ft) below sea level at Death Valley. The Modoc Plateau in northeastern California is a region of relatively low population density; southwestern California is one of the most densely populated regions in the world. With regard to its biotic reputation, California harbors one of the richest floras in the world (Raven and Axelrod 1978) but supports a freshwater fish fauna that is notably depauperate (Moyle 1976). Both flora (Stebbins and Major 1965; Fiedler 1995) and fauna (Moyle 1976) are renowned for their high endemism.

The study region for the proposed classification includes the coastal boundary at Point Conception, Santa Barbara County, between northern and southern California biogeographic provinces, which contributes to the many contrasts that affect wetlands. These contrasts include differences between and among: (1) northern cool and moist and southern warm and dry Mediterranean climates; (2) Mediterranean and arid climates; (3) cold, high elevations and mild, low elevations; (4) interior and coastal locations; (5) oceanic and terrestrial processes; (6) intermittent and perennial water bodies; (7) widespread and narrowly-restricted habitats and organisms; (8) coarse-scale physiographic areas and fine-scale habitat sites; (9) historic and current land use practices; (10) natural and artificial landforms; (11) pristine and degraded habitats; and (12) wilderness and urbanized regions. Additional natural elements that contribute to the region's remarkable wetland diversity include the great variation in water chemistry (e.g., fresh, salt, alkali, sulfur, petroleum) and natural processes (e.g., aeolian, fluvial, glacial, arid, volcanic, and structural). Refer to Part I of this treatise (Ferren et al. 1996a) for additional aspects of the environmental setting of the region.

Thus it is with this frame of reference—diversity, anomaly, and contrast—that the study region and its wetland resources are presented. As representative of California as a whole, the central and southern coast and coastal watersheds illustrate the complexity of the state's physical and biological diversity that contribute to the formation of the rich wetland heritage of the state.

Wetlands definition. Wetlands in California and elsewhere vary widely in topographic setting, hydrology, chemistry, substrate, veg-

etation physiognomy, and persistence. Before we proceed with the examination of the Mediterranean-climate wetlands of California, acceptance and consistent application of a wetland definition is essential. We endorse for use in California the definition proposed by Cowardin et al. (1979). At the state level, the Fish and Game Commission, Department of Fish and Game, and the Coastal Commission also accept this definition and the associated technique for the classification of wetlands (Gibbons 1992). At the regional level, the County of Santa Barbara and the City of San Diego are examples of governments that also accept this definition.

Cowardin et al. (1979) have provided some helpful insights concerning the definition of wetlands. They suggest that the term **wetlands** “. . . has grown out of a need to understand and describe the characteristics and values of all types of land, and to wisely and effectively manage wetland ecosystems. There is no single, correct, indisputable, ecologically sound definition for wetlands because of the diversity of wetlands and because the demarcation between dry and wet environments occurs along a continuum. . . . The primary objective of this classification is to impose boundaries on natural systems for the purposes of inventory, evaluation, and management” (Cowardin et al. 1979:3). Their definition follows:

Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. For the purpose of this classification, wetlands must have one or more of the following attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; (3) the substrate is nonsoil and is saturated or covered with shallow water at some time during the growing season of each year (Cowardin et al. 1979, p. 3).

This definition is broad enough to include the special nature of wetlands in the California Chaparral and Estuarine Provinces, and the Colorado Plateau and Desert Provinces in California (Bailey 1978; Cowardin et al. 1979). The National Research Council (1995), however, has offered a new definition that refines some aspects of the Cowardin et al. definition. In addition to the definition of wetlands, the following definition for **deepwater habitat** has been offered by the U.S. Fish and Wildlife Service in Cowardin et al. (1979, p. 3):

[Deepwater habitats are] permanently flooded lands lying below the deepwater boundary of wetlands. Deepwater habitats include environments where surface water is permanent and often deep, so that water, rather than air, is the principal me-

dium within which the dominant organisms live. . . . As in wetlands, the dominant plants are hydrophytes; however, the substrates are considered nonsoil because the water is too deep to support emergent vegetation. . . .

Use of these definitions in association with the modified hierarchical classification of wetlands and deepwater habitats requires some additional explanation. The FWS classification is hierarchical and progresses from systems and subsystems to classes, subclasses, dominance types, and habitat modifiers (Cowardin et al. 1979). Systems and subsystems (Table 1) are delineated according to major physical attributes such as tidal flushing, ocean-derived salts, and the energy of flowing water or waves. Classes and subclasses describe the type of substrate and habitat or the physiognomy of the vegetation or faunal assemblage. Wetland classes are divided into physical types (i.e., rock bottom, unconsolidated bottom, streambed, rocky shore, and unconsolidated shore) and biotic types (i.e., aquatic bed, reef, moss-lichen wetland, emergent wetland, scrub-shrub wetland, and forested wetland).

PRELIMINARY QUESTIONS FOR CLASSIFICATION

To provide a basis for the classification proposed herein, a series of questions can be raised and answered that will assist the classifier in collecting information that will be necessary for the development of a wetland name and numerical code. Answers to these questions provide some of the basic information needed to identify a particular wetland and to relate it to other wetlands. Below, we provide discussion for each question.

1. What are the goals of the project or task? Why is there a need to classify and describe wetlands? A clear statement and understanding of goals of a project or task will help determine the scope, scale, and detail that a wetland classification must include. If the goal of a project is to map and classify only vegetation, then some form of vegetation nomenclature and classification will be necessary. Such a project might generally ignore all of the non-vegetated wetland habitats. However, if the goal of a project is to identify hydrogeomorphic units and relate them to physical processes, then a more detailed analysis and nomenclature is necessary. Our modified Cowardin et al. approach provides the flexibility to consider various levels of detail to meet the goals of a wide variety of projects and tasks.

2. What is the ecosystem context of the wetland under construction? It is essential for most projects that include classification to determine the context in which occur the particular elements that

are to be classified. For the purposes of wetland classification it is important to identify the system of wetlands (and any associated deepwater habitats) to which a wetland belongs (e.g., Marine, Estuarine, Riverine, Lacustrine, Palustrine) or with which a wetland is associated (e.g., a Palustrine Forested Wetland on a channel bar within the Riverine System). In addition, it may also be important to identify the broader ecosystem context within which smaller wetlands occur (e.g., vernal pools occurring within grassland or chaparral), to assess the various ecosystem functions the wetland may provide.

3. At what scale will the classification be applied? Will the scale include, for example, an entire river channel or only a bar and/or back-bar channel within the main channel? The scale of a site under consideration and the detail of the classification are important factors to communicate so that it is clear what has been identified or mapped, and what the wetland relationship is to the ecosystem context as well as the goals of a project. Scale is often a perplexing issue that can result in confusion over what is being classified. Using our modified Cowardin et al. approach regarding spatial scale, it is possible to identify both the coarser-scale hydrogeomorphic or ecosystem context (e.g., type of natural lacustrine environment such as a Montane-Alkali-Lake) and the finer-scale hydrogeomorphic unit (e.g., an intermittently-flooded, unconsolidated shore), as well as the wetland associated with the latter (e.g., Emergent Nonpersistent Wetland). In general, the finer the scale, the less variable the site and easier it is to classify and name the wetland. For example, a riparian corridor may be mapped as forested wetland at a coarser-scale and yet perhaps contain four different types of forested wetland at a finer-scale, each characterized by a different water regime, hydrogeomorphic unit, dominance type, and ecosystem function. There is a degree of fineness, however, that no longer reflects a wetland type, but reflects instead, the individual organisms or substrate types of a larger-scale wetland type. It is the best professional judgement of the classifier that is generally the source of this decision, and thus the more field experience one has, the more accurate the decision becomes to split or lump hydrogeomorphic units or sites.

Temporal scale is another issue that can cause confusion, particularly in the Mediterranean climatic portions of the study region. Many wetlands types are flooded during part of the year and desiccated during another (e.g., vernal pools, vernal ponds, vernal lakes, and margins of streams and rivers), or are only intermittently flooded (e.g., playa lakes and some streams). Because a site may be characterized by different flooding regimes and dominance types during different times of the year, a single wetland site could be classified

differently depending upon the time of year, which year, project purpose, or the person doing the classifying. Such also is the case for sites that receive periodic disturbance (e.g., streambeds, floodplains, and deltas), whereby one site characterized by wetlands from a particular system, class, or subclass could be converted to wetlands of another system, class, or subclass. Such conversion is often a natural and characteristic process for the study region; thus temporal scale, like spatial scale, is important in classification and adds to the diversity and complexity of wetland types.

The modified Cowardin et al. approach provides flexibility to describe a specific wetland within the goals of a particular project. This flexibility may result in confusion or even differences of application to the same or similar sites. We believe, however, that it is more useful and a better reflection of the field experience to incorporate a series of choices than to limit scale and miss opportunities to identify particular types of wetlands. This belief has guided the development of our classification hierarchy.

4. If the context and scale have been decided, what are the class(es) and subclass(es) of wetlands that characterize the site? Is the site in question dominated by abiotic and/or biotic wetland classes? Although, in general, a particular wetland is characterized by one class and subclass, in various cases, sites of larger scale will have several attributes or mixtures of attributes at the class or subclass levels. Thus, it is important to determine the dominant characteristic of the chosen scale. In general, the finer the scale of the ecosystem or site context, the more homogeneous the wetland habitat will be. For example, a dune swale wetland is a type of hydrogeomorphic unit that, if sufficiently large and flooded seasonally, may support examples of wetland types from palustrine aquatic bed, emergent, scrub-shrub, and forested wetland classes.

In other examples, wetland sites (e.g., river channels, lake shores, and marine beaches) can be characterized by episodes of natural or artificial disturbance, and may support a mosaic of components from different abiotic classes (e.g., unconsolidated shore) and biotic classes (e.g., emergent, scrub-shrub, and forested wetlands). It is important, therefore to have some metric by which to assess dominance, and to attribute a site or portions of a site to one or more classes and subclasses of wetland (e.g., cobble-gravel, emergent-persistent, broadleaved-deciduous). Some sites, wetland types, or ecosystem contexts are problematic for other reasons (e.g., how should one classify tenajas from the Santa Rosa Plateau?) or appear to be "hybrids" (e.g., the Tijuana Estuary has characteristics of river-mouth and bay types of estuaries). Thus classification of the associated wetlands, including attribution of class and subclass, and a choice of scale or type of ecosystem context, also can be difficult to decide.

However, by having a *predetermined goal and some sense of appropriate scale* and detail of classification needed, one can reduce the number of problems encountered in the classification process.

5. What are the various hydrogeomorphic and geochemical attributes of the wetland, such as water regimes, chemistry regimes, and hydrogeomorphic units? Are more than one combination of attributes identifiable at the site? Although the system, subsystem, class, and subclass descriptors provide the context and structure to a wetland, it is the combination of hydrology, chemistry, and geomorphology that provide the distinguishing features among many wetland types. Differentiation among wetland types often is dependent upon knowledge of ecosystem processes reflected in the hydrogeomorphology and geochemistry of the ecosystem or wetland site. Differentiation of water regimes (e.g., intertidal, permanently flooded, seasonally flooded, and saturated) and chemistry regimes (e.g., alkaline, hyperhaline, and euryhaline) can be important in distinguishing among related (e.g., proximally or structurally) but functionally different wetlands. Although identification of physical attributes may require some expertise, many clues (e.g., salt crusts, rack from flooding, dried algal mats, mottled soil, etc.) can be found in the field that reveal physical characteristics of wetlands.

6. What are the dominant substrate(s) or organism(s) of the wetland that contribute to the character of the site? Descriptive terminology for wetlands often includes types of substrate (e.g., unconsolidated bottom, mud) and type of organism(s) (e.g., algae, mosses, vascular plants) or particular organisms (e.g., *Salicornia virginica* [Pickleweed]) that dominate or characterize the site or wetland. Some knowledge of substrates and organisms is essential for classification, and the level of detail in classification will depend on the specificity of the identifications. However, our modified Cowardin et al. approach allows for both generality (e.g., Class Forested Wetland) and specificity (e.g., Subclass Broadleaved Deciduous, Dominance Type *Alnus rhombifolia* [White Alder]). Animals as well as plants can be important components in the classification process, as exemplified by estuarine intertidal mud flats (Class Unconsolidated Bottom, Subclass Mud) that are dominated by horn snails (*Cerithidea californica*).

7. What are the observed or inferred ecosystem functions and socio-economic values of the wetland and/or the ecosystem context within which the wetland occurs? One important goal in the classification of wetlands is to differentiate wetland types that perform different ecosystem functions (e.g., hydrology) or groupings of functions (e.g., food chain support, habitat, and hydrology/water-quality). Some wetlands that are visually similar in hydrogeomor-

phology and dominance type may in fact perform significantly different ecosystem functions. This difference may be a reflection of the ecosystem context, disturbance history, or regional location, but nonetheless can be an important factor in the classification process. For example, wetland riparian forests occur throughout the region along rivers and streams and on margins of ponds and lakes of coastal watersheds, but some of those associated with hydrogeomorphic units that can occur in proximity (e.g., floodplains, banks, and bars) and are dominated by the same combination of tree species (e.g., alders, willows, and cottonwoods) may support different groupings of riparian-dependent migratory or resident bird species. The presence of various rare and endangered species (e.g., Least Bell's Vireo, *Vireo bellii pusillus*; Yellow-breasted Chat, *Icteria virens*; Willow Fly Catcher, *Empidonax traillii*; and Western Yellow-billed Cuckoo, *Coccyzus americanus occidentalis*) apparently reflects the importance of site characteristics that are not present in most of the riparian forests extant in the region. In this example, habitat function for riparian bird species is an important wetland feature to consider in the classification process, which can result in the differentiation of some forested wetlands from others, particularly if those sites also are nesting habitat for rare and endangered birds.

Socio-economic values are an important attribute that many wetlands have, but the value to humans (e.g., nonconsumptive types such as recreation) generally does not directly affect the classification process. However, indirectly, human land-use practices can greatly affect wetlands by transforming them from one class (e.g., Forested Wetland) to another (e.g., Emergent Wetland) as a result of deforestation, flood control, and other activities. Thus, some knowledge of ecosystem functions and socio-economic values is important for understanding the interface between wetland classification and the assessment of ecosystem functions and socio-economic values, both at site-specific and ecosystem levels. Although we do not include coding or nomenclature for ecosystem functions or socio-economic values directly in our modified Cowardin et al. approach, such information can be included with the description of wetland types (e.g., Table 10), and can be used in the rationale for separating types that otherwise are similar in classification but significantly different in ecosystem function (see Mertes et al. 1995).

A MODIFIED COWARDIN ET AL. APPROACH

Our starting point for this study was a draft classification prepared by Ferren (1989), which was a previous compilation of information on Santa Barbara regional wetlands, organized into an expanded hierarchical version of Cowardin et al. (1979). Our original goal was to locate and visit examples of all types of wetlands we would

be able to classify for the study region. From a combination of team field experience, references, assistance from others, and reconnaissance trips we compiled the information from which we developed the classification and determined the types. The scope of our project changed during the course of the three year effort, however, because we realized that the nearly limitless variation of habitats and dominance types would make it difficult for us to complete an inventory of wetland types. Thus we narrowed our focus to include: (1) the development of a methodology to identify and classify wetlands in the study region according to a modified Cowardin et al. approach; and (2) a presentation of an illustrated catalogue of examples organized according to this hierarchical classification.

Field methods. Field work was conducted from Fall 1991 to Summer 1994, and focused on: (1) visits to known sites of interest; (2) reconnaissance trips into poorly explored regions; and (3) generalized transects from the intertidal marine shoreline to the crest of the coastal watershed divides, extending from the Carmel River Watershed at the northern limit of the study region to the Tijuana River Watershed at the southern limit of the region. We designed a data sheet onto which we recorded information regarding the physical attributes (e.g., ecosystem context, hydrogeomorphology, and geochemistry) and biological attributes (e.g., vegetation physiognomy and dominant or characteristic species) from "reference site" wetlands. Obtaining answers to the questions raised above was an important part of this process. Botanical vouchers of taxa unknown to us or important records for sites or habitats were prepared and deposited at UCSB as part of the inventory of dominant and characteristic species. Photographs were taken of virtually all sites, and, along with field notes, were arranged partially for access by trip, county, and system of classification. A literature and other resource review, and interviews with regional and local specialists, contributed to the information base we have compiled. Early versions of the new classification methodology were tested by various users, and modifications were made over the course of three years.

Classification methods. To achieve the goal to classify the wetlands of the region, we developed a numerical, hierarchical presentation of the modified Cowardin et al. (1979) approach to provide a method to organize the wetland types. Our nomenclature for the wetlands is generally derived from the orderly presentation of names for the various categories of wetland information provided in the wetland type number. To describe the rich variation in wetlands of the study region, we added several categories of information to the hierarchy by Cowardin et al. that aid in the characterization of California wetlands. Perhaps the most important categories are the site-specific "geomorphic" types we designate as **hydrogeomorphic**

TABLE 1. GENERAL DESCRIPTION OF THE SYSTEMS AND SUBSYSTEMS OF WETLANDS AND DEEPWATER HABITATS (ADAPTED FROM COWARDIN ET AL. 1979).

-
- **Marine System** (Fig. 3a): The open ocean overlying the continental shelf and the adjacent coastline. Water regimes are determined by oceanic tides and salinities from NaCl (halite) exceed 30 ppt (parts per thousand). Subsystems include intertidal wetlands and subtidal deepwater habitats. See Lafferty et al. (1995).
 - **Estuarine System** (Fig. 3b): Coastal embayments that have at least occasional access to the ocean, and thus water with ocean-derived salts entering with the tides, and in which the ocean water is at least occasionally diluted by freshwater runoff from the adjacent land. Subsystems include intertidal wetlands and subtidal deepwater habitats. See Ferren et al. (1995c).
 - **Riverine System** (Fig. 3c): Wetlands and deepwater habitats within a channel that are influenced strongly by the energy of flowing water. The Riverine System excludes (1) stands of persistent vegetation such as trees, shrubs, and some forms of emergent vegetation; and (2) channels with ocean-derived salts in excess of 0.5 ppt (i.e., estuarine channels). Subsystems include tidal; upper, mid, and lower perennial; and upper, mid, and lower intermittent categories. See Leidy et al. (1995).
 - **Lacustrine System** (Fig. 3d): Wetlands and deepwater habitats located in large, at least intermittently-flooded depressions, or dammed canyons, river valleys, or montane valleys. Shoreline features and vegetation are influenced by the energy of waves and lack stands of trees, shrubs, persistent emergents, and mosses and lichens that exceed 30% cover. Total area generally exceeds 8 hectares (20 acres); in smaller examples the limnetic subsystem is not present. Subsystems include littoral (wetland) and limnetic (deepwater habitat) types. See Fiedler et al. (1995).
 - **Palustrine System** (Fig. 3e): The nontidal wetlands dominated by trees, shrubs, persistent or nonpersistent emergents, mosses or lichens, and such wetlands in tidal areas where salinity from ocean-derived salts is below 0.5 ppt. Also included are wetlands that lack vegetation but: (1) are less than 8 hectares; (2) lack wave-formed shorelines; (3) have water depths less than 2 meters (6.6 feet) at low water; and (4) have salinity due to ocean derived salts less than 0.5 ppt. Thus palustrine wetlands lack the physical and biological attributes of the other four systems but often are in proximity to examples of those systems. The Palustrine System lacks subsystems, and thus all palustrine types are classified directly into classes and subclasses. See Ferren et al. (1995b).
-

units (e.g., land forms such as flats, slopes, pools, channels, beds), many of which are defined in a glossary provided herein (Appendix I). Use of hydrogeomorphic units results in the ability to differentiate wetlands of similar hydrology, chemistry, or dominance type that occur in different topographic landforms and that may have different ecosystem functions and socio-economic values.

For the purposes of the classification and partial inventory of California wetlands, we also have provided keys to the level of wetland subclasses and a catalogue of selected types for each system (see Part III, Ferren et al. 1996b). Hierarchical information for each of the types or group of types has been organized in tabular form, and additional information (e.g., description, functions and values, characteristic species, examples, impacts, and literature) is catego-

TABLE 2. SYSTEMS, SUBSYSTEMS, CLASSES, AND SUBCLASSES OF WETLANDS AND DEEP-WATER HABITATS. Nomenclature adopted or modified from Cowardin et al. (1979). Asterisk (*) indicates new subsystem, class, or subclass added to Cowardin et al. (1979). For this classification, the user would choose one from each of the system, subsystem, class, and subclass categories. Because of potential temporal changes or issues of scale, a particular site may be classified in more than one way. However, for each purpose, a single wetland numerical code and name would be developed. See key to systems, subsystems, and classes in Part III (Ferren et al. 1996b).

I. THE SYSTEMS AND SUBSYSTEMS

- 10.000 System Marine
 - 11.000 Subsystem Intertidal (Wetlands)
 - 12.000 Subsystem Subtidal (Deepwater Habitats)
- 20.000 System Estuarine
 - 21.000 Subsystem Intertidal (Wetlands)
 - 22.000 Subsystem Subtidal (Deepwater Habitats)
- 30.000 System Riverine
 - 31.000 Subsystem Tidal (Wetlands)
 - 32.000 Subsystem Upper Intermittent (Wetlands)*
 - 33.000 Subsystem Mid Intermittent (Wetlands)*
 - 34.000 Subsystem Lower Intermittent (Wetlands)*
 - 35.000 Subsystem Upper Perennial (Wetlands)*
 - 36.000 Subsystem Mid Perennial (Wetlands)*
 - 37.000 Subsystem Lower Perennial (Wetlands)*
 - 38.000 Subsystem Limnetic (Deepwater Habitats)
- 40.000 System Lacustrine
 - 41.000 Subsystem Littoral (Wetlands)
 - 42.000 Subsystem Limnetic (Deepwater Habitats)
- 50.000 System Palustrine
 - 50.000 There are no subsystems; all habitats are wetlands.

II. THE WETLAND CLASSES AND SUBCLASSES

- 00.100 Abiotic Classes and Subclasses**
 - 00.110 Class Rock Bottom
 - 00.111 Subclass Bedrock
 - 00.112 Subclass Rubble/Boulder
 - 00.120 Class Unconsolidated Bottom
 - 00.121 Subclass Cobble-Gravel
 - 00.122 Subclass Sand
 - 00.123 Subclass Mud
 - 00.124 Subclass Organic
 - 00.125 Subclass Vegetated
 - 00.130 Class Riverbed or Streambed
 - 00.131 Subclass Bedrock
 - 00.132 Subclass Rubble/Boulder
 - 00.133 Subclass Cobble-Gravel
 - 00.134 Subclass Sand
 - 00.135 Subclass Mud
 - 00.136 Subclass Organic
 - 00.137 Subclass Vegetated Streambeds
 - 00.140 Class Rocky Shore
 - 00.141 Subclass Bedrock
 - 00.142 Subclass Rubble/Boulder
-

TABLE 2. CONTINUED

00.150	Class Unconsolidated Shore
00.151	Subclass Cobble-Gravel
00.152	Subclass Sand
00.153	Subclass Mud
00.154	Subclass Organic
00.155	Subclass Vegetated
00.200	Biotic Classes and Subclasses
00.210	Class Aquatic Bed
00.211	Subclass Attached Algal*
00.212	Subclass Floating Algal*
00.213	Subclass Aquatic Moss
00.214	Subclass Rooted Vascular
00.215	Subclass Floating Vascular
00.220	Class Reef
00.221	Subclass Coral
00.222	Subclass Mollusc
00.223	Subclass Worm
00.230	Class Moss-Lichen Wetland
00.231	Subclass Moss
00.232	Subclass Lichen
00.240	Class Emergent Wetland
00.241	Subclass Persistent
00.242	Subclass Nonpersistent
00.250	Class Scrub-Shrub Wetland
00.251	Subclass Broadleaved Deciduous
00.252	Subclass Needleleaved Deciduous
00.253	Subclass Broadleaved Evergreen
00.254	Subclass Needleleaved Evergreen
00.255	Subclass Mixed Deciduous*
00.256	Subclass Mixed Evergreen*
00.257	Subclass Mixed Deciduous and Evergreen*
00.258	Subclass Dead
00.260	Class Woodland and Forested Wetland
00.261	Subclass Broadleaved Deciduous
00.262	Subclass Needleleaved Deciduous
00.263	Subclass Broadleaved Evergreen
00.264	Subclass Needleleaved Evergreen
00.265	Subclass Mixed Deciduous*
00.266	Subclass Mixed Evergreen*
00.267	Subclass Mixed Deciduous and Evergreen*
00.268	Subclass Dead

rized and presented on a sample "wetland data page" (Table 10) for a selected wetland type.

There are six approaches to the classification technique:

- (1) use of modified Cowardin hierarchy tables for choice of wetland system, subsystem, class, and subclass and corresponding numerical code (Tables 1, 2);
- (2) use of water regime tables for choice of appropriate wetland

TABLE 3. WATER REGIMES: WETLANDS AND DEEPWATER HABITATS. Nomenclature adopted or modified from Cowardin et al. (1979). Asterisk (*) indicates new water regime added to Cowardin et al. 1979. This table provides a numerical, hierarchical listing of water regimes that are ranked by tidal water-regimes and nontidal water-regimes and from which a type would be selected for a wetland classification. All water regime terms are defined in the accompanying Glossary (Appendix I).

(10.0) Tidal Water-Regimes
(11.0) Subtidal Regime
(12.0) Irregularly-Exposed Regime
(13.0) Regularly-Flooded Regime
(14.0) Irregularly-Flooded Regime
(15.0) Seasonally-Exposed Regime*
(16.0) Seasonally-Flooded Regime*
(20.0) Nontidal Water-Regimes
(21.0) Permanently-Flooded Regime
(22.0) Intermittently-Exposed Regime
(23.0) Semipermanently-Flooded Regime
(24.0) Seasonally-Flooded Regime
(25.0) Permanently-Saturated Regime
(26.0) Seasonally-Saturated Regime*
(27.0) Temporarily-Flooded Regime
(28.0) Intermittently-Flooded Regime
(29.0) Phreatophytic Regime*

hydrology descriptor and corresponding numerical code (Table 3);

- (3) use of water/soil chemistry tables for choice of appropriate wetland chemistry descriptor and corresponding numerical code (Table 4);
- (4) use of hydrogeomorphic tables for choice of appropriate hydrogeomorphic unit and corresponding numerical code (Table 5 and Tables 6 and 7 in Appendix II);
- (5) use of dominance/substrate tables for choice of appropriate substrate or biotic dominance (or characteristic) type(s) and corresponding numerical code (Tables 8, 9 in Appendix II); and

TABLE 4. WATER/SOIL CHEMISTRY: WETLANDS AND DEEPWATER HABITATS. This table provides a numerical listing of nine alternatives for water/soil chemistry and from which a type would be selected for a wetland classification. All water/soil chemistry terms are defined in the accompanying Glossary (Appendix I).

(00.1.000) Fresh Water (Circumneutral)
(00.2.000) Fresh Water (Acidic)
(00.3.000) Fresh Water (Alkaline)
(00.4.000) Saline, Haline (Eusaline, Euhaline)
(00.5.000) Brackish (Mixosaline, Mixohaline)
(00.6.000) Eurysaline, Euryhaline
(00.7.000) Hypersaline, Hyperhaline
(00.8.000) Sulfur-Affected
(00.9.000) Petroleum-Affected

TABLE 5. HYDROGEOMORPHIC UNITS: MARINE, ESTUARINE, RIVERINE, LACUSTRINE, AND PALUSTRINE WETLANDS. This table provides an overview of the high-order categories (hundred-level series) of hydrogeomorphic (HGM) units for all wetland systems of the central and southern California coast and coastal watersheds. Specific HGM units for the combined marine and estuarine systems and the combined riverine, lacustrine, and palustrine systems are presented in Tables 6 and 7, respectively, in Appendix II.

(00.0.100.0000)	Water Bodies (Hydrogeomorphic Context)
(00.0.200.0000)	Channels, Fissures, Drainages, Inverts, Falls
(00.0.300.0000)	Shores, Beaches, Banks, Benches, Margins
(00.0.400.0000)	Beds, Bottoms, Bars, Reefs
(00.0.500.0000)	Flats, Plains, Deltas, Washes, Floodplains, Terraces
(00.0.600.0000)	Headlands, Bluffs, Slopes, Fans
(00.0.700.0000)	Seeps, Springs
(00.0.800.0000)	Pools, Ponds, Lakes, Meadows, Marshes, Swales
(00.0.900.0000)	Artificial Structures

- (6) creation of a wetland data page (Table 10) for each example that includes: (a) wetland name and numerical code; (b) the above information, nos. 1–5, in a hierarchical format; (b) list of characteristic and associated species; (d) an estimate of the wetland's ecosystem functions and socio-economic values; (e) a discussion of the impacts and conservation efforts; and (f) a list of references or available sources of additional information.

We wish to emphasize that each of the classification components can be used individually to achieve a specific goal or answer a particular question. Again, they are designed to be combined to provide a methodology for the classification of wetlands and the compilation of a catalogue of the types. The hierarchical nature of the numerical code, classification tables, and catalogue allow the approach to be open ended. This results in the ability in most cases for a user to add new elements to the classification in virtually all levels of the hierarchy. Thus, in the tradition of the Cowardin et al. approach, we have designed a classification scheme that can be tailored to the needs of the user, the complexity of the site, and the level of information available at the time the classification is applied. In other words, the classification can be "lumped-up" for less detail, a generalization of the wetland ecosystem or habitat, or for the classification of coarse-scale sites (e.g., channels or estuaries). In contrast, the classification also can be "split-down" for more detail (e.g., substrate particle size) or for the classification of fine-scale sites (e.g., channel-bars or estuarine flats).

We have modified the Cowardin et al. (1979) approach to the classification of wetlands, however, in a number of significant ways:

- (1) elements have been added to the original classification such

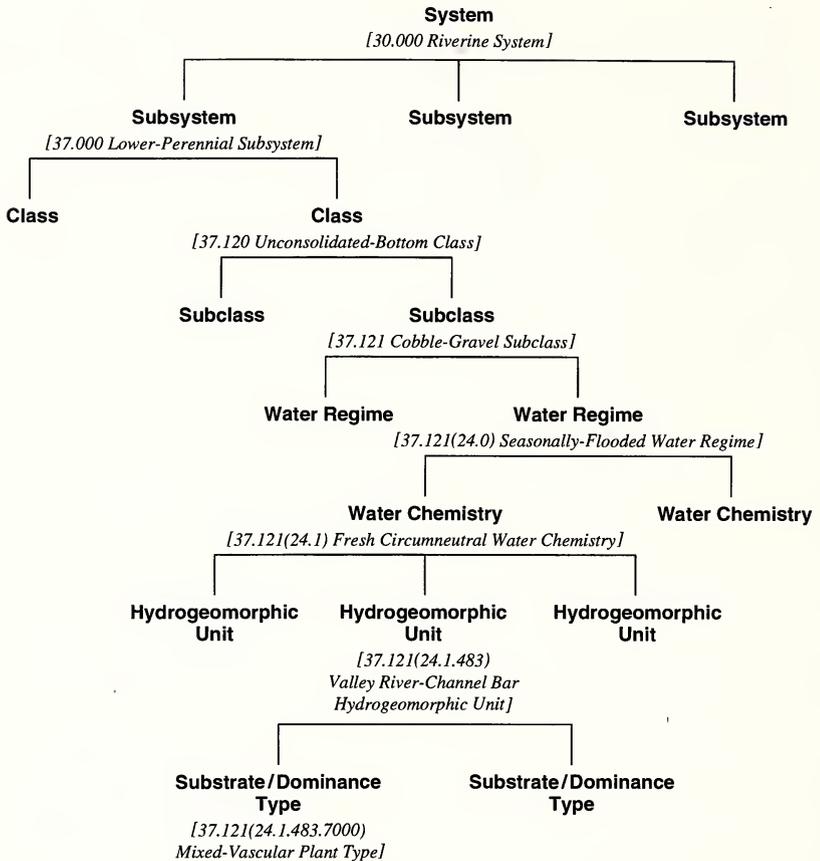


FIG. 1. Diagram of the Wetland Classification Hierarchy. Selected elements of the sample hierarchy are in bold face and examples are in small italic. The example provided demonstrates a riverine wetland with the corresponding numerical and written elements taken from the classification tables. The wetland example is identified as follows: No. 37.121 (24.1.483.7000) = Riverine Lower-Perennial Unconsolidated-Bottom (Cobble-Gravel) Seasonally-Flooded Valley River-Channel Bar Wetland. The dominance type (Mixed-Vascular Plant Type) could be added to the subclass designation (Cobble-Gravel), but this addition perhaps would be most meaningful if the wetland classification was identified as Class Vegetated, Subclass Nonpersistent. Nonetheless, the pioneering, nonpersistent vegetation on river bars could be included in this name as (Cobble-Gravel/Mixed-Vascular-Plant).

as new subsystems to the Riverine System and new subclasses to various classes;

- (2) a numerical code has been applied to the modified classification;
- (3) the original classification has been expanded to include the

Cowardin et al. modifiers and other modifiers for water regimes and soil/water chemistry;

- (4) a classification of hydrogeomorphic units (tidally-influenced and nontidally-influenced) created for this hierarchy has been added to the numerical code; and
- (5) a classification of substrate, dominance, and/or characteristic types has been created and added to the code.

The result is a hierarchical classification with multiple descriptors (elements) and descriptor states (specific examples) that includes a code generally composed of a 15 digit number, with decimal points and parentheses separating various descriptors identifying a particular type of wetland. A comma can be used to separate a series of descriptor states if more than one is used for a descriptor (see example below). An explanation of the code follows and an example is diagrammed in Figure 1:

“00.000(00.0.000.0000)”¹

“00” = the system and subsystem descriptor (Table 2)

00.“000” = the class and subclass descriptor (Table 2)

00.000.(“00”) = the water regime descriptor (Table 3)

00.000.(00.“0”) = the water chemistry descriptor (Table 4)

00.000.(00.0.“000”) = the hydrogeomorphic descriptor
(Table 5 and Tables 6 and 7 in Appendix II)

00.000.(00.0.000.“0000”) = the substrate, dominance, and/or
characteristic type descriptor (Tables 8, 9 in Appendix II)

The hydrogeomorphic descriptor (.000) includes the category level (e.g., .100), the series level (e.g., .110), and the units level (e.g., 111). Substrate/dominance/characteristic types (.0000) include hierarchies for substrates, biotic kingdoms, families, genera, species, physiognomy, and persistence.

Example Wetland Code Number: **41.125(28.3.442.1800, 5241, 5554, 5559)**

“41” = System: **Lacustrine** (40); Subsystem: **Littoral** (41)

41.“125” = Class: **Unconsolidated Bottom** (120); Subclass: **Vegetated** (125)

41.125(“28”) = Water Regime: **Intermittently-Flooded** (28)

41.125(28.“3”) = Water Chemistry: **Alkali** (3)

41.125(28.3.“442”) = Hydrogeomorphic Unit: **Montane-Lake-Bed** (442)

41.125(28.3.432.“1800, 5241, 5554, 5559”) = Substrate and Dominance Types: **Mud** (1800), *Heliotropium* (5241), *Chenopodium* (5554), and *Suaeda* (5559)

¹ Zeros = empty descriptor states.

TABLE 10. EXAMPLE OF LACUSTRINE WETLAND DATA PAGE.

LACUSTRINE WETLAND No.: 41.125(28.3.442.1800,5241,5554,5559), Fig. 2a and 2b.

NAME: LACUSTRINE-LITTORAL UNCONSOLIDATED-BOTTOM-VEGETATED (MUD, *HELIOTROPIMUM*, *CHENOPODIUM*, *SUAEDA*) INTERMITTENTLY-FLOODED ALKALI MONTANE-LAKE-BED WETLAND

CLASSIFICATION:

System: Lacustrine

Subsystem: Lacustrine littoral

Class: Unconsolidated Bottom

Subclass: Vegetated

Water Regime: Intermittently Flooded

Water Chemistry: Alkaline

HGM Unit: Montane lake-bed

Substrate/Dominance Type: Mud

Substrate/Dominance Type: *Heliotropium*

Substrate/Dominance Type: *Chenopodium*

Substrate/Dominance Type: *Suaeda*

DESCRIPTION: The unconsolidated bottom of the only natural alkali montane lake in the study region, when flooded, is represented by the subclass aquatic bed, with characteristic species that include *Zannichellia palustris*, *Ruppia cirrhosa*, *Potamogeton* spp. and others. When desiccated, as shown here, the montane lake-bed becomes vegetated with annual species.

SPECIES: Characteristic: *Suaeda calceoliformis*, *Chenopodium macrospermum*, *Heliotropium curassavicum*. Associated: *Atriplex rosea*, *Bassia hyssopifolia*.

ECOSYSTEM FUNCTIONS: Baldwin Lake serves as foraging and nesting habitat for several raptors, including the bald eagle.

REFERENCE EXAMPLE: Baldwin Lake, San Bernardino Mountains, San Bernardino Co.

IMPACTS: Proposed is a plan to raise the lake level to enhance endangered species habitat for the bald eagle and the shay meadows stickleback. Groundwater in the Big Bear Basin is being overdrafted for competing domestic and municipal uses as well as recreational and downstream commitments.

CONSERVATION EFFORTS: Lands north of Baldwin Lake have been purchased by The Nature Conservancy (TNC), and are to be designated as the "North Baldwin Lake and Holcomb Valley Special Interest Area" within the San Bernardino Forest.

LITERATURE: U.S. Forest Service 1988; Stevenson 1990.

→
FIG. 2A,B. Lacustrine-Littoral Unconsolidated-Bottom-Vegetated (Mud, *Heliotropium*, *Chenopodium*, *Suaeda*) Intermittently-Flooded Alkali Montane-Lake-Bed Wetland. San Bernardino Co., San Bernardino Mountains, Baldwin Lake. Plants dominant or characteristic of the intermittently-flooded alkali lake-bed include *Atriplex rosea*, *Bassia hyssopifolia*, *Chenopodium macrospermum*, *Heliotropium curassavicum*, and *Suaeda calceoliformis*. Wetland Type No.: 41.125(28.3.442.1800,5241,5554,5559).



Nomenclature for this wetland includes the name of the descriptor states in hierarchical order as presented in the wetland number code, except for types of substrates and dominance or characteristic species that help describe the wetland, which are placed in parentheses following the subclass names. The above example reads as follows:

**Lacustrine-Littoral Unconsolidated-Bottom-Vegetated
(Mud, *Heliotropium*, *Chenopodium*, *Suaeda*) Alkali
Montane-Lake-Bed Wetland**

This example is a type of lacustrine wetland at Baldwin Lake in the San Bernardino Mountains (Fig. 2a, b). If a user of the classification does not have information for each of the descriptors, then an abbreviated version of the classification can be employed. For example, if the lake water chemistry was unknown and the lake-bed either was: (A) not colonized by nonpersistent plants; or (B) the names of them were unknown; or (C) the user wanted only to describe the wetland class and its corresponding water regime and hydrogeomorphic unit, the classifications and nomenclature alternatives would be as follows:

Example A: **41.123(28.0.442.1800)**

**Lacustrine-Littoral Unconsolidated-Bottom (Mud) Inter-
mittently-Flooded Montane-Lake-Bed Wetland**

Example B: **41.125(28.0.442.1800,7200)**

**Lacustrine-Littoral Unconsolidated-Bottom (Mud, Mixed-
Nonpersistent Vascular-Plants) Intermittently-Flooded
Montane-Lake-Bed Wetland**

Example C: **41.120(28.0.442.0000)**

**Lacustrine-Littoral Unconsolidated-Bottom Intermittent-
ly-Flooded Montane-Lake-Bed Wetland**

The wetland classification methodology presented herein is designed to accommodate differences among classification goals, scope, and degree of detail, depending on the immediate project needs or background of the classifier. We hope the flexibility to "lump up" or "split down" in the classification will meet the needs of many users; however, we also recognize that this "fluidity" may be less suited for those who prefer fewer choices and more rigid application. We do not intend this classification to be exhaustive. We realize that the vastness of the study region and complexity of the environment limit our ability to include descriptor states for all types at this time, particularly at the rank of dominance type. Thus, we suggest this treatment be considered open-ended, as Cowardin et al. (1979) was intended to be open-ended and expandable. Additional field work and research will reveal more examples below the level of subclass, including additional hydrogeomorphic units.

CONCLUSIONS

Successful conservation of California's wetland heritage will depend on the compilation of details that enable us to identify the multitude of wetland types still found in the state. Although we may never know much about the approximately 90% of the wetland resources that have been lost, there are opportunities to conserve the richness that remain. Extensive inventory of all wetland types and documentation of their ecosystem functions are vital. Unique and vulnerable examples in particular need to be identified and protected. Furthermore, a framework with which to demonstrate wetland characteristics and relationships is needed that is sufficiently detailed to achieve the identification of the integrity and salient features of an enormous range of wetland types. We believe our classification methodology provides a regional example of such a framework.

With the great quantity of new information on wetlands being published at a national scale, and with the many alternatives to identification and classification of wetland types and their functions, we express hope that enough coordination will take place to establish standards by which at least regional priorities for wetland study and conservation can be initiated. We suggest several key opportunities that users of this classification could seize:

1. Field test this methodology and identify potential gaps in its flexibility to provide suggestions for its improvement.
2. Conduct inventories and mapping of wetlands throughout the study region in a coordinated effort to identify and conserve the diversity of wetlands and wetland resources and functions in central and southern California coastal watersheds.
3. Classify wetlands at disturbed sites and restored sites to monitor the change of particular wetlands from one type and set of functions to another type and set of functions, as a demonstration of the need for flexibility when interpreting wetlands in a Mediterranean climate.
4. Develop workshops on wetland classification, mapping, and functional assessment to broaden the participation and understanding of wetland inventory, conservation, and restoration.
5. Expand this methodology to other ecoregions in California to produce an integrated, statewide classification that can be used to identify the wetland richness at a broader scale.
6. Develop a computerized database version of the numerical, hierarchical classification of wetlands so that the potentially vast amount of information obtained through inventory and classification can be manipulated for research, conservation, and managerial purposes.

We encourage others to continue our regionalization effort, and

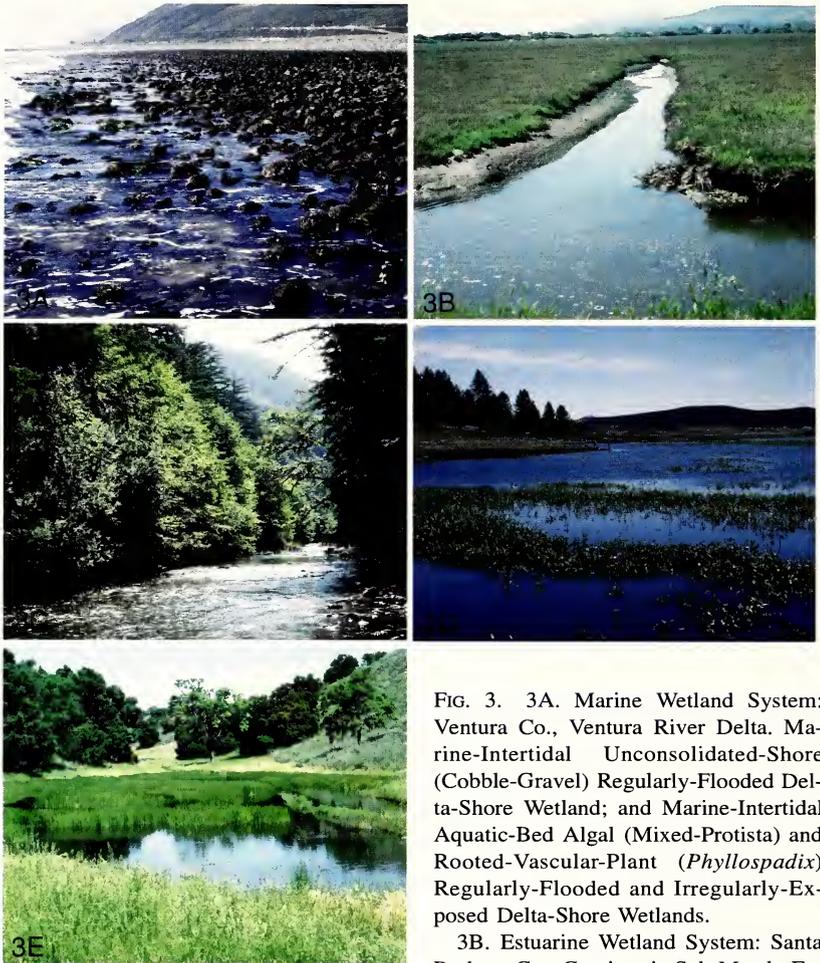


FIG. 3. 3A. Marine Wetland System: Ventura Co., Ventura River Delta. Marine-Intertidal Unconsolidated-Shore (Cobble-Gravel) Regularly-Flooded Delta-Shore Wetland; and Marine-Intertidal Aquatic-Bed Algal (Mixed-Protista) and Rooted-Vascular-Plant (*Phyllospadix*) Regularly-Flooded and Irregularly-Exposed Delta-Shore Wetlands.

3B. Estuarine Wetland System: Santa Barbara Co., Carpinteria Salt Marsh. Estuarine-Intertidal Unconsolidated-Shore (Mud) Regularly-Flooded Tidal-Marsh-Channel Wetland; and Emergent-Persistent (*Salicornia*) Irregularly-Flooded Middle-Salt-Marsh Wetland.

3C. Riverine Wetland System: Monterey Co., Big Sur River. Riverine Lower-Perennial Unconsolidated-Bottom (Cobble-Gravel) Permanently-Flooded River-Bed Wetland; and Palustrine-Forested Needleleaved-Evergreen (*Sequoia*) Temporarily-Flooded River-Bank and Broadleaved-Deciduous (*Alnus*) Seasonally-Flooded River-Bank Wetlands.

3D. Lacustrine Wetland System: San Diego Co., Cuyamacha Lake. Lacustrine-Littoral Unconsolidated-Shore (Mixed-Coarse and Mixed-Fines) Intermittently-Flooded Montane-Lake-Shore Wetland; and Emergent-Nonpersistent (*Polygonum*) Intermittently-Flooded Montane-Lake Wetland.

3E. Palustrine Wetland System: Santa Barbara Co., Foothills of the San Rafael Mountains. Palustrine Emergent-Persistent (*Eleocharis*) Seasonally-Flooded Vernal-Marsh Wetland; and Palustrine Unconsolidated-Bottom (Mud) Seasonally-Flooded Vernal-Pond Wetland.

we offer this methodology as a test to categorize the wetlands by a modified Cowardin et al. (1979) approach. An additional emphasis on hydrogeomorphic information will help differentiate wetlands based upon detailed physical as well as biological attributes. In the end, conservation of California's remaining wetlands may lie in our ability to discern the details of their form and function.

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Bob Haller has for many years given one of us in particular (WRF) much of his time and encouragement, recognizing before most California botanists the paucity of adequate information on wetland types within the state. We also wish to thank Lyndon C. Lee for providing us with much guidance on the application of this classification, and in general, for sharing his perspicacity into wetland ecosystems in the American West. Joy Zedler provided inspiration and reminders that our efforts were worthwhile.

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APPENDIX 1: GLOSSARY

Below is a listing of terms cited in this treatise, and their definitions. Sources of the definitions are listed below. Terms without a citation were defined by the authors.

SOURCES

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GLOSSARY

- algal.** Subclass in the Cowardin et al. wetland classification referring to algal communities found in the aquatic bed subclass (Cowardin et al. 1979).
- alkaline (alkali).** Pertaining to habitats or substances having a pH greater than 7; basic (Lincoln et al. 1982).
- alluvial.** Having stream deposits and sediments formed by the action of running water (California Coastal Commission 1987).
- alluvial fans.** A low, outspread, relatively flat to gently sloping mass of loose rock material, shaped like an open fan or a segment of a cone, deposited by a stream

- (esp. in a semiarid region) at the place where it issues from a narrow mountain valley upon a plain or broad valley, or where a tributary stream is near or at its junction with the main stream, or wherever a constriction in a valley abruptly ceases or the gradient of the stream suddenly decreases; it is steepest near the mouth of the valley where its apex points upstream, and it slopes gently and convexly outward with gradually decreasing gradient (Bates and Jackson 1980).
- aquatic.** Growing or living in or frequenting water; taking place in or on water (Warner and Hendrix 1984).
- aquatic bed.** Class in the Cowardin et al. wetland classification referring to wetland and deepwater habitats dominated by plants that grow principally on or below the surface of the water for most of the growing season in most years (Cowardin et al. 1979).
- aquatic moss.** Subclass in the Cowardin et al. wetland classification referring to mosses, and presumably other bryophytes, that are found in the aquatic bed subclass (Cowardin et al. 1979).
- artificially flooded.** Water regime in the Cowardin et al. wetland classification in which the amount and duration of flooding is controlled by means of pumps or siphons in combination with dikes or dams (Cowardin et al. 1979).
- backbar channel.** A channel formed behind a bar connected to the main channel but usually at a higher bed elevation than the main channel. Backbar channels may or may not contain flowing or standing water.
- backshore.** The zone of a typical beach profile above mean high water; also used for the zone covered only in exceptionally severe storms (Lincoln et al. 1982).
- backwater pools.** A pool type formed by an eddy along channel margins downstream from obstructions such as bars, rootwads, or boulders, or resulting from backflooding upstream from an obstructional blockage. Backwater pools are sometimes separated from the channel by and or gravel bars (American Fisheries Society 1985).
- bank.** The portion of the channel cross section that restricts lateral movement of water at normal levels. The bank often has a gradient steeper than 45° and exhibits a distinct break in slope from the stream bottom. An obvious change in substrate may be a reliable delineation of the bank (American Fisheries Society 1985).
- bar.** An elongated landform generated by waves and currents, usually running parallel to the shore, composed predominantly of unconsolidated sand, gravel, stones, cobbles, or rubble and with water on two sides (Cowardin et al. 1979).
- bay.** A wide, curving indentation, recess, or arm of a sea or lake into the land or between two capes or headlands, larger than a cove, and usually smaller than, but of the same general character as, a gulf (Bates and Jackson 1984).
- beach.** A sloping landform on the shore of larger water bodies, generated by waves and currents and extending from the water to a distinct break in landform or substrate type (e.g., a foredune, cliff, or bank) (Cowardin et al. 1979).
- bed.** The substrate plane, bounded by banks, over which the water column at some point in time resides (American Fisheries Society 1985).
- bedrock.** Subclass in Cowardin et al. referring to classes in which the bedrock covers 70% or more of the surface (Cowardin et al. 1979).
- bench.** A long, narrow, relatively level terrace or platform breaking the continuity of a slope. The term sometimes denotes a form cut in solid rock, as distinguished from one in unconsolidated material (Bates and Jackson 1984).
- berm.** a levee, shelf, ledge or bench along a stream bank that may extend laterally into the channel to partially obstruct the flow, or parallel to the flow to contain the flow within its stream banks. Berms may be natural or artificial (American Fisheries Society 1985).
- bluff.** A high bank or bold headland, presenting a precipitous front; a steep cliff (Bates and Jackson 1984).
- bottom.** The floor upon which any body of water rests (Bates and Jackson 1984).

- bottomland.** A lowland, usually highly fertile, along a stream; an alluvial plain (Bates and Jackson 1984).
- brackish.** Marine and estuarine waters with mixohaline salinity. The term should not be applied to inland waters (Cowardin et al. 1979).
- breakwater.** An offshore structure (such as a wall or jetty) that, by breaking the force of the waves, protects a harbor, anchorage, beach, or shore area (Bates and Jackson 1984).
- broad-leaved deciduous.** Subclass in the Cowardin wetland classification referring to wetlands in which the predominant trees or shrubs are angiosperms that lose their leaves once a year.
- broad-leaved evergreen.** Subclass in the Cowardin wetland classification referring to wetlands in which the predominant trees or shrubs are angiosperms that retain their leaves for longer than one year, and that always have some canopy.
- canyon.** A stream-cut chasm or gorge, the sides of which are composed of cliffs or a series of cliffs rising from its bed. Canyons are characteristic of arid or semiarid regions where downcutting by streams greatly exceeds weathering (Bates and Jackson 1984).
- cascades.** A habitat type characterized by swift current, exposed rocks and boulders, high gradient and considerable turbulence and surface agitation, and consisting of a stepped series of drops (American Fisheries Society 1985).
- channel.** An open conduit either naturally or artificially created which periodically or continuously contains moving water, or which forms a connecting link between two bodies of standing water (Langbein and Iseri 1960).
- channel bank.** The sloping land bordering a channel. The bank has steeper slope than the bottom of the channel and is usually steeper than the land surrounding the channel (Cowardin et al. 1979).
- circumneutral.** Term applied to water with a pH of 5.5 to 7.4 (Cowardin et al. 1979).
- cliff.** Any high, very steep to perpendicular or overhanging face of rock (Bates and Jackson 1984).
- cobble-gravel.** Subclass in the Cowardin et al. wetland classification referring to unconsolidated particles smaller than stones, sometimes intermixed with finer sediments (Cowardin et al. 1979).
- community.** An association of living organisms having mutual relationships among themselves and their environment and thus functioning, at least to some degree, as an ecological unit (Warner and Hendrix 1984).
- coral.** Subclass in the Cowardin et al. wetland classification referring to widely distributed, well-adapted, highly diverse and productive ecosystems characteristic of shallow waters in warm seas (Cowardin et al. 1979).
- cove.** A small narrow sheltered bay, inlet, creek, or recess in a coast, often inside a larger embayment; it usually affords anchorage to small craft (Bates and Jackson 1984).
- culvert.** Any covered structure, not classified as a bridge, that constitutes a transverse drain, waterway, or other opening under a road, railroad, canal, or similar structure (Bates and Jackson 1980); any covered structure that acts as a drain (Bates and Jackson, 1984).
- dam.** An artificial barrier or wall constructed across a watercourse or valley for one or more of the following purposes: creating a pond or lake for the storage of water; diverting water from a watercourse into a conduit or channel; creating a hydraulic head that can be used to generate power; improving river navigability; controlling floods; or retention of debris. It may be constructed of wood, earth materials, rocks, or solid masonry (Bates and Jackson 1980).
- dead.** Subclass in the scrub-shrub wetland and forested wetland classes of the Cowardin et al. wetland classification in which forested wetlands are dominated by dead woody vegetation (Cowardin et al. 1979).
- deepwater habitat.** Permanently flooded land below the deepwater boundary of wetland (Cowardin et al. 1979).

- delta.** A fan-shaped alluvial deposit at the mouth of a river (California Coastal Commission 1987).
- dike.** A tabular body of igneous rock that cuts across the structure of adjacent rocks or cuts massive rocks. A massive wall or embankment built around a low-lying area to prevent flooding (Bates and Jackson 1984).
- ditch.** A long, narrow excavation artificially dug in the ground; especially an open and usually unpaved waterway, channel, or trench for conveying water for drainage or irrigation, and usually smaller than a canal. Some ditches may be natural watercourses (Bates and Jackson 1980).
- dominant.** An organism or other abiotic component exerting considerable influence upon a community by its size, abundance, or coverage; the highest ranking individual in a dominance hierarchy (Lincoln et al. 1982).
- drainage.** (1) An artificial water course, such as a ditch or trench; (2) a natural watercourse modified to increase its flow (Stein 1973).
- dune pond ("lake").** A lake occupying a basin formed as a result of the blocking of the mouth of a stream by sand dunes migrating along the shore (Bates and Jackson 1980).
- dune swale.** A low place among sand dunes, typically moister and often having distinctive vegetation differing from the surrounding sand environment.
- ecosystem.** A community of organisms and their physical environment interacting as an ecological unit; the entire biological and physical content of a biotype; biosystem; holocoem (Lincoln et al. 1982).
- ecosystem context.** Environmental setting of habitats comprising an ecosystem.
- ecosystem functions.** Processes that are necessary for the self-maintenance of an ecosystem such as primary production, nutrient cycling, decomposition, etc. The term is used primarily as a distinction from values (L. C. Lee & Associates, Inc. 1994).
- emergent.** Having part of a plant aerial and the rest submersed; with parts extending out of the water (Little and Jones 1980).
- emergent hydrophytes.** Erect, rooted, herbaceous angiosperms (flowering plants) that may be temporarily to permanently flooded at the base but do not tolerate prolonged inundation of the entire plant (e.g., bulrushes, saltmarsh cordgrass) (Cowardin et al. 1979).
- emergent wetland.** Class in the Cowardin et al. wetland classification characterized by erect, rooted, herbaceous hydrophytes, excluding mosses and lichens, and which is present for most of the growing season (Cowardin et al. 1979).
- ensaline (euhaline).** Salinity approximating seawater (33‰).
- falls.** A waterfall or other precipitous descent of water (Bates and Jackson 1980).
- fault sag ponds.** A small, enclosed depression along an active or recent fault. It is caused by differential movement between slices and blocks within the fault zone or by warping and tilting associated with differential displacement along the fault, and it forms the site of a sag pond (Bates and Jackson 1980).
- flat.** A level landform composed of unconsolidated sediments—usually mud or sand. Flats may be irregularly shaped or elongate and contiguous with the shore, whereas bars are generally elongate, parallel to the shore, and separated from the shore by water (Cowardin et al. 1979).
- floating vascular.** Subclass in the Cowardin et al. wetland classification referring to a large array of vascular plants floating above a substrate and that are found in the aquatic bed subclass (Cowardin et al. 1979).
- floodplain.** The deposit of alluvium that covers a valley flat, which is the fundamental land form produced by lateral erosion of meandering streams and rivers (Thornbury 1969).
- forested wetland.** Class in the Cowardin et al. wetland classification referring to woody vegetation that is 5 m (15 ft) tall or taller found in all water regimes (Cowardin et al. 1979).

- fresh water.** Water having a salinity of less than 0.5 ppt, or, alternatively, less than 2 ppt (Lincoln et al. 1982).
- freshwater marsh.** An circumneutral ecosystem of more or less continuously water-logged soil dominated by emerged herbaceous plants, but without a surface accumulation of peat.
- fringe marsh.** A saturated, poorly drained area, intermittently or permanently water covered, close to and along the edge of a land mass.
- geomorphic.** Referring to the shape of a land surface (L. C. Lee & Associates, Inc. 1994).
- habitat.** The ecological and/or physical place determined and bounded by the needs and the presence of a specific plant or animal population, which contains a particular combination of environmental conditions sufficient for that population's survival (Warner and Hendrix 1984).
- haline.** Term used to indicate dominance of ocean salt (Cowardin et al. 1979).
- haline marshes.** A saturated, poorly drained area, intermittently or permanently water covered, having aquatic and grasslike vegetation, influenced predominately by ocean salts.
- halophyte.** A plant living in saline conditions; a plant tolerating or thriving in an alkaline soil rich in sodium and calcium salts; a seashore plant (Lincoln et al. 1982).
- headland.** A point of land, usually high and with a sheer drop, extending out into a body of water, especially the sea; a promontory (California Coastal Commission 1987).
- herbaceous.** A plant having the characteristics of an herb; having the texture and color of a foliage leaf (Little and Jones 1980).
- hogback ridge.** Any ridge with a sharp summit and steep slopes of nearly equal inclination on both flanks, and resembling in outline the back of a hog (Bates and Jackson 1984).
- hydric soil.** Soil that is wet long enough to periodically produce anaerobic conditions, thereby influencing the growth of plants (Cowardin et al. 1979).
- hydrogeomorphic unit.** A land form characterized by a specific origin, geomorphic setting, water source, and hydrodynamic.
- hydrophyte.** Any plant growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content (plants typically found in wet habitats) (Cowardin et al. 1979).
- hyperhaline.** Term used to characterize waters with salinity greater than 40 ppt (parts per thousand) due to ocean-derived salts (Cowardin et al. 1979).
- hypersaline.** Term used to characterize waters with salinity greater than 40 ppt due to land-derived salts (Cowardin et al. 1979).
- intermittently exposed.** Water regime in the Cowardin et al. wetland classification in which surface water is present throughout the year except in years of extreme drought (Cowardin et al. 1979).
- intermittently flooded.** Water regime in the Cowardin et al. wetland classification in which the substrate is usually exposed, but surface water is present for variable periods without detectable seasonal periodicity (Cowardin et al. 1979).
- intertidal zone.** The shore zone between the highest and lowest tides; eulittoral zone; littoral; tidal zone (Lincoln et al. 1982).
- irregularly exposed.** Water regime in the Cowardin et al. wetland classification in which the land surface is exposed by tides less often than daily (Cowardin et al. 1979).
- irregularly flooded.** Water regime in the Cowardin et al. wetland classification in which tidal water alternately floods and exposes the land surface less often than daily (Cowardin et al. 1979).
- islet.** A small or minor island (Bates and Jackson 1984).
- lacustrine.** Pertaining to, produced by, or inhabiting a lake or lakes (Bates and Jackson 1984).

- lagoon.** A shallow body of water separated from a larger bay or from the open ocean by a land form such as a sand spit or reef (California Coastal Commission 1987).
- lake.** Any inland body of standing water, larger and deeper than a pond [usually greater than 20 acres]. The term includes an expanded part of a river, a reservoir behind a dam, and a lake basin formerly or intermittently covered by water (Bates and Jackson 1984).
- levee.** An artificial embankment along a watercourse or an arm of the sea, to protect land from flooding (Bates and Jackson 1984).
- lichen.** Subclass in the Cowardin class moss-lichen wetland in which areas with reindeer moss (*Cladonia rangiferina*) is dominant (Cowardin et al. 1979).
- littoral.** Inhabiting bottom of sea or lake near shore, roughly within a depth to which light and wave action reach. For sea, usually taken as between high tide mark and 200 meters (i.e., approximately to limit of continental shelf). For lakes, approximately down to 10 meters (Abercrombie et al. 1983).
- macroalgae.** A large, macroscopic algae, typically referring to kelps.
- macroinvertebrate.** A large, macroscopic animal species without a spinal column, typically referring to large insects.
- macrophyte.** A large, macroscopic plant, used especially of aquatic forms such as kelp (Lincoln et al. 1982).
- main channel pool.** A pool formed by mid-channel scour that encompasses greater than sixty percent of the wetted channel (California Department of Fish and Game 1991).
- marine.** Of, or belonging to, or caused by the sea (Bates and Jackson 1984).
- marsh.** A saturated, poorly drained area, intermittently or permanently water covered; having aquatic and grasslike vegetation, especially without the formation of peat (Bates and Jackson 1984).
- mesohaline.** Term used to characterize waters with salinity of 5 to 18 ppt due to ocean-derived salts (Cowardin et al. 1979).
- mesosaline.** Term used to characterize waters with salinity of 5 to 18 ppt due to land-derived salts (Cowardin et al. 1979).
- mixohaline.** Term used to characterize water with salinity of 0.5 ppt to 30 ppt due to ocean-derived salts (Cowardin et al. 1979).
- mixosaline.** Term used to characterize water with salinity of 0.5 to 30 ppt due to land-derived salts (Cowardin et al. 1979).
- mollusk.** Subclass in the Cowardin et al. wetland classification referring to reef systems formed by members of the invertebrate phylum Mollusca (Cowardin et al. 1979).
- montane.** Of, pertaining to, or inhabiting cool upland slopes below the timber line, characterized by the dominance of evergreen trees (Bates and Jackson 1980).
- montane alkali lakes.** Lakes with a water pH greater than 7 found in cool; upland habitats below the timber line.
- montane freshwater lakes.** Circumneutral lakes found in cool, upland habitats below the timber line.
- moss.** Subclass in the Cowardin class moss-lichen wetland in which areas with mosses, typically peats, are dominant (Cowardin et al. 1979).
- moss-lichen wetland.** Class in the Cowardin et al. wetland classification that includes areas where mosses or lichens cover substrates other than rock and where emergents, shrubs, or trees make up less than 30% of the areal cover. The only water regime is saturated (Cowardin et al. 1979).
- mud.** Wet soft earth composed predominantly of clay and silt-fine mineral sediments. Also refers to a subclass within the Cowardin et al. wetland classification system (Cowardin et al. 1979).
- needle-leaved deciduous.** Subclass in the Cowardin et al. wetland classification referring to wetlands where trees or shrubs are predominantly conifers that shed their leaves once a year.
- needle-leaved evergreen.** Subclass in the Cowardin et al. wetland classification re-

- ferring to wetlands where trees or shrubs are predominantly conifers that retain their leaves for longer than one year.
- nonpersistent.** Subclass in the Cowardin et al. wetland classification referring to wetlands dominated by plants which fall to the surface of the substrate or below the surface of the water at the end of the growing season, so that, at certain seasons of the year, there is no obvious sign of emergent vegetation (Cowardin et al. 1979).
- nonpersistent emergent.** Emergent hydrophytes whose leaves and stems breakdown at the end of the growing season so that most above-ground portions of the plants are easily transported by currents, waves, or ice. The breakdown may result from normal decay or the physical force of strong waves or ice. At certain seasons of the year there are no visible traces of the plants above the surface of the water (Cowardin et al. 1979).
- organic.** Subclass in Cowardin et al. wetland classification referring to unconsolidated material smaller than stones that is predominantly organic in origin (Cowardin et al. 1979).
- palustrine.** Pertaining to wet or marshy habitats (Lincoln et al. 1982).
- permanently flooded.** Water regime in the Cowardin et al. wetland classification in which water covers the land surface throughout the year in all years (Cowardin et al. 1979).
- persistent.** Subclass in the Cowardin et al. wetland classification referring to wetland dominated by species that normally remain standing at least until the beginning of the next growing season, found only in the estuarine and palustrine systems (Cowardin et al. 1979).
- persistent emergent.** Emergent hydrophytes that normally remain standing at least until the beginning of the next growing season (e.g., bulrushes and cattails) (Cowardin et al. 1979).
- petroleum-affected.** Influenced by an oily, thick, flammable substance that is usually formed from a mixture of various hydrocarbons.
- phreatophyte.** A perennial plant which is very deeply rooted, deriving its water from a more or less permanent, subsurface water supply; it is thus not dependent upon annual rainfall for survival (Little and Jones 1980).
- phytoplankton.** The photosynthesizing organisms residing in the plankton (Levinton 1982).
- plain.** Any flat area, large or small, at a low elevation; specifically an extensive region of comparatively smooth and level or gently undulating land, having few or no prominent surface irregularities but sometimes having a considerable slope, and usually at a low elevation with reference to surrounding areas. A plain may be either forested or bare of trees, and may be formed by deposition or by erosion (Bates and Jackson 1980).
- playa lake.** A shallow, intermittent lake in an arid region, occupying a playa in the wet season but drying up in the summer; an ephemeral lake that upon evaporation leaves or forms a playa (Bates and Jackson 1984).
- polyhaline.** Term used to characterize water with salinity of 18 to 30 ppt due to ocean-derived salts (Cowardin et al. 1979).
- polysaline.** Term used to characterize water with salinity of 18 to 30 ppt due to land-derived salts (Cowardin et al. 1979).
- pond.** A natural body of standing fresh water occupying a small surface depression, usually smaller than a lake and larger than a pool (Bates and Jackson 1980).
- pool.** Channel or floodplain habitats containing water with no, or reduced current velocities; a small depression containing water at least seasonally or intermittently.
- rapids.** A part of a stream where the current is moving with a greater swiftness than usual and where the water surface is broken by obstructions but without a sufficient break in slope to form a waterfall, as where the water descends over a series of small steps. It commonly results from a sudden steepening of the stream

- gradient, from the presence of a restricted channel, or from the unequal resistance of the successive rocks traversed by the stream (Bates and Jackson 1980).
- reference wetland.** A wetland within a relatively homogeneous biogeographic region that is representative of a specific hydrogeomorphic wetland type (L. C. Lee & Associates, Inc. 1994).
- reef.** A class in the Cowardin et al. wetland classification referring to ridge-like or mound-like structures formed by the colonization and growth of sedentary invertebrates (Cowardin et al. 1979).
- regularly flooded.** Water regime in the Cowardin et al. wetland classification in which tidal waters alternately flood and expose the land surface at least once daily (Cowardin et al. 1979).
- reservoir.** A pond or lake, natural or artificial, from which water may be withdrawn for irrigation or water supply (Bates and Jackson 1984).
- revetment.** A structure built along the coast to prevent erosion and other damage by wave action; similar to a sea wall (California Coastal Commission 1987).
- riffle.** A shallow rapids where the water flows swiftly over partially or completely submerged obstructions to produce surface agitation, but standing waves are absent (American Fisheries Society 1985).
- riparian.** Pertaining to the banks and other adjacent terrestrial (as opposed to aquatic) environs of freshwater bodies, watercourses, estuaries, and surface-emergent aquifers (springs, seeps, oases), whose transported fresh waters provide soil moisture sufficiently in excess of that otherwise available through local precipitation to potentially support the growth of mesic vegetation (Warner and Hendrix 1984).
- river.** A natural or human-modified watercourse that contains water for at least part of the year.
- river banks.** The portion of the channel cross section that restricts lateral movement of water at normal discharges. Banks often have a gradient steep than 45° and exhibit a distinct break in slope from the stream bed (American Fisheries Society 1985).
- river channels.** Natural or artificial open conduits which continuously or periodically contain moving water, or which forms a connection between two bodies of water (Langbein and Iseri 1960).
- rock bottom.** Class in the Cowardin et al. wetland classification referring to all wetlands and deepwater habitats with substrates having an areal cover of stones, boulders, or bedrock 75% or greater and vegetative cover of less than 30%.
- rocky shore.** Class in the Cowardin et al. wetland classification referring to all wetland environments characterized by bedrock, stones, or boulders which singly or in combination have an areal cover of 70% or more and an areal coverage by vegetation of less than 30% (Cowardin et al. 1979).
- rooted vascular.** Subclass in the Cowardin et al. wetland classification referring to a large array of vascular plants rooted in a substrate and that are found in the aquatic bed subclass (Cowardin et al. 1979).
- rubble.** Subclass in Cowardin et al. wetland classification referring to classes with less than 70% areal cover of bedrock, but stones and boulders alone, or in combination with bedrock, cover 70% or more of the surface (Cowardin et al. 1979).
- runs.** An area of swiftly flowing water, without surface agitation or waves, which approximates uniform flow and in which the slope of the water surface is roughly parallel to the overall gradient of the stream reach (American Fisheries Society 1985).
- sag pond.** A small body of water occupying an enclosed depression or sag formed where active or recent fault movement has impounded drainage; specifically one of many ponds and small lakes along the San Andreas Fault in California (Bates and Jackson 1984).
- saline.** General term for waters containing various dissolved salts. Use of saline can be restricted to inland waters where the ratios of the salts often vary; the term

haline can be applied to coastal waters where the salts are roughly in the same proportion as found in diluted sea water (Cowardin et al. 1979).

- saline marsh.** A saturated, poorly drained area, intermittently or permanently water covered, having aquatic and grasslike vegetation whose water chemistry contains various dissolved salts.
- salinity.** The total amount of solid material in grams contained in 1 kilogram of water when all the carbonate has been converted to oxide, the bromine and iodine replaced by chlorine, and all the organic matter completely oxidized (Cowardin et al. 1979).
- sand.** Subclass in the Cowardin et al. wetland classification referring to unconsolidated particles smaller than stones, sometimes intermixed with finer sediments (Cowardin et al. 1979).
- saturated.** Water regime in the Cowardin et al. wetland classification in the substrate is saturated to the surface for extended periods during the growing season, but surface water is seldom present (Cowardin et al. 1979).
- scour pools.** A pool formed by flow directed either laterally or obliquely against a partial channel obstruction or bank (California Department of Fish and Game 1991).
- scrub-shrub wetland.** Class in the Cowardin et al. wetland classification referring to areas dominated by woody vegetation less than 5 m (15 feet) tall.
- seasonally flooded.** Water regime in the Cowardin et al. wetland classification in which surface water is present for extended periods especially early in the growing season, but is absent by the end of the season in most years (Cowardin et al. 1979).
- seasonally flooded (estuarine).** Water regime in estuaries with seasonally-closed mouths and seasonally-flooded habitats.
- sea stack.** A small, steep-sided rocky projection above sea level near a cliffed shore (California Coastal Commission 1987).
- sediment.** Fine-grain material and organic material in suspension, in transit, or deposited by air, water, or ice on the earth's surface (California Coastal Commission 1987).
- seep.** An area of minor groundwater outflow onto the land surface or into a stream channel or other waterbody. Flows are usually too small to be a spring (American Fisheries Society 1985).
- semipermanently flooded.** Water regime in the Cowardin et al. wetland classification in which surface water persists throughout the growing season in most years (Cowardin et al. 1979).
- shore.** The narrow strip of land immediately bordering any body of water, especially a sea or a large lake (Bates and Jackson 1984).
- slope.** The inclined surface of any part of the Earth's surface; also, a broad part of a continent descending toward an ocean (Bates and Jackson 1980).
- socioeconomic values (ecosystem).** Society's perceptions of the worth of an ecosystem, typically stemming from whether the system provides a form of pleasure or recreation, such as fishing, boating, etc.
- spring.** A place where ground water flows naturally from a rock or the soil into the land surface or into a body of surface water. Its occurrence depends on the nature and relationship of rocks, especially permeable and impermeable strata, on the position of the water table, and on the topography (Bates and Jackson 1980).
- cold spring.** A spring whose water has a temperature appreciably below the mean annual atmospheric temperature in the area (Bates and Jackson 1980).
- hot spring.** A thermal spring whose temperature is above that of the human body (Bates and Jackson 1980).
- stream.** Any body of running water that moves under gravity to progressively lower levels, in a relatively narrow but clearly defined channel on the surface of the ground, in a subterranean cavern, or beneath or in a glacier (Bates and Jackson 1980).

- stream bed.** Class in the Cowardin et al. wetland classification referring to wetlands contained within the intermittent subsystem of the riverine system and all channels of the estuarine system or of the tidal subsystem of the riverine system (Cowardin et al. 1979).
- stream channel.** The bed where a natural stream of water runs or may run; the long narrow depression shaped by the concentrated flow of a stream and covered continuously or periodically by water (Bates and Jackson 1980).
- submersed.** Under water, submerged (Little and Jones 1980).
- subtidal.** Water regime in the Cowardin et al. wetland classification in which the substrate is permanently flooded with tidal water (Cowardin et al. 1979).
- sulfur-affected.** Influenced by the non-metallic element sulfur.
- swamp.** Wet, spongy ground, saturated or intermittently inundated by standing water, typically dominated by woody plants but without an accumulation of surface peat (Lincoln et al. 1982).
- temporarily flooded.** Water regime in the Cowardin et al. wetland classification in which surface water is present for brief periods especially early in the growing season, but the water table usually lies well below the soil surface for most of the year (Cowardin et al. 1979).
- tenaja.** Pools in seasonal streams that may support a flora similar to vernal pools upon desiccation.
- terrace.** A relatively level bench or steplike surface breaking the continuity of a slope. The term is applied to both the lower or front slope (the riser) and the flat surface (the tread) (Bates and Jackson 1984).
- tidal.** Water regime in the Cowardin et al. wetland classification are largely determined by oceanic tides (Cowardin et al. 1979).
- tide.** The periodic rise and fall of the ocean water masses and atmosphere, produced by gravitational effects of the moon and sun on the Earth (Lincoln et al. 1982).
- tide cycle.** The duration of a given tidal sequence, as for example a lunar month or a tidal day (Lincoln et al. 1982).
- tide gate.** A gate through which water flows when the tide is in one direction and which closes automatically when the tide is in the opposite direction (Stein 1973).
- tideland.** The coastal area of land that is regularly covered and uncovered by the rise and fall of a normal daily tide (Lincoln et al. 1982).
- tide pool.** Habitat in the rocky intertidal zone that retains some water at low tide (California Coastal Commission 1987).
- tidal flat.** An extensive flat tract of land alternatively covered and uncovered by the tide, and comprising mostly unconsolidated mud and sand; tide flat (Lincoln et al. 1982).
- tidal marsh.** A low elevation marshy coastal area formed of mud and the root mat of halophytic plants, regularly inundated during high tide (Lincoln et al. 1982).
- unconsolidated bottom.** Class in Cowardin et al. wetland classification referring to all wetland and deepwater habitats with at least 25% cover of particles smaller than stones, and a vegetative cover less than 30% (Cowardin et al. 1979).
- unconsolidated shore.** Class in Cowardin et al. wetland classification referring to all wetland habitats having three characteristics: (1) unconsolidated substrates with less than 75% areal cover of stones, boulders, or bedrock; (2) less than 30% areal cover of vegetation other than pioneering plants; and (3) any of the following water regimes: irregularly exposed, regularly flooded, irregularly flooded, seasonally flooded, temporarily flooded, intermittently flooded, saturated, or artificially flooded (Cowardin et al. 1979).
- upland.** The ground above a floodplain; that zone sufficiently above and/or away from transported waters as to be dependent upon local precipitation for its water supplies (Warner and Hendrix 1984).
- vegetated.** Subclass in the Cowardin et al. wetland classification referring to nontidal

areas exposed for a sufficient period to be colonized by herbaceous annuals or seedling herbaceous perennials (pioneer plants) (Cowardin et al. 1979).

- vegetated streambed.** Subclass in the class streambed in the Cowardin et al. wetland classification referring to streambeds exposed long enough to be colonized by herbaceous annuals or seedling herbaceous perennials (pioneer plants) (Cowardin et al. 1979).
- vernal pond.** A body of water usually smaller than a true lake and larger than a pool (i.e., vernal pool), that fills with seasonal rain and usually desiccates sometime before the next rain season. All vernal ponds are wetlands.
- vernal pool.** Wetlands that occur in shallow basins that are generally underlain by an impervious subsoil layer (e.g., a "clay pan" or "hard pan") or bedrock outcrop, which produces a seasonally perched water table. Zedler (1987) defines the habitat as follows: "a vernal pool is a natural habitat of the Mediterranean climate region of the Pacific Coast [of North America] covered by shallow water for extended periods during the cool season but completely dry for most of the warm season drought." He has identified four important phases of the habitat cycle: wetting phase; aquatic phase; drying phase; and drought phase.
- wash.** A watercourse associated with an alluvial fan, stream, or river channel. Washes are often associated with arid environments and are characterized by large, high energy discharges with high bed-material load transport. Washes are often intermittent and their beds sparsely vegetated.
- watershed.** A geographical region which drains into a particular body of water (Little and Jones 1980).
- water table.** The upper surface of a zone of saturation. No water table exists where that surface is formed by an impermeable body (Cowardin et al. 1979).
- wave cut platform.** A gently sloping surface produced by wave erosion, extending far into the sea or lake from the base of the wave cut cliff (Bates and Jackson, 1984).
- wetlands.** Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. For the purposes of this classification wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year (Cowardin et al. 1979).
- worm.** Subclass in the Cowardin et al. wetland classification referring to large colonies of Sabellariid worms living in individual tubes constructed from cemented sand grains. Worm reefs are generally confined to tropical waters (Cowardin et al. 1979).

APPENDIX II: TABLES 6-9

TABLE 6. HYDROGEOMORPHIC UNITS: MARINE AND ESTUARINE SYSTEMS. This table provides a numerical, hierarchical listing of the various hydrogeomorphic (HGM) units determined by the authors to be characteristic of wetlands in the study region and that are flooded by tidal water containing ocean-derived salts. Various HGM units in this table are specific to either marine or estuarine wetlands.

(“00”) = Water Regime	(00.0.“000”) = Hydrogeomorphic Unit
(00.“0”) = Water Chemistry	(00.0.000.“0000”) = Substrate/Dominance/Characteristic Types
(00.0.100.0000) Water Bodies (Hydrogeomorphic Context)	(00.0.200.0000) Channels, Fissures, Caves
(00.0.110.0000) Oceans	(00.0.210.0000) Surge Channels
(00.0.120.0000) Exposed Bays	(00.0.211) Large (Wide/Long) Surge Channels
(00.0.120) Large Exposed Bays	(00.0.212) Small (Narrow/Short) Surge Channels
(00.0.121) Small Exposed Bays	(00.0.220.0000) Estuarine Channels
(00.0.130.0000) Estuaries	(00.0.221) Deep (Subtidal) Natural Estuarine Channels
(00.0.131) Bay-Estuaries	(00.0.222) Shallow (Intertidal) Natural Estuarine Channels
(00.0.132) Lagoonal Estuaries	(00.0.223) Deep (Subtidal) Artificial Estuarine Channels
(00.0.133) River-Mouth Estuaries	(00.0.224) Shallow (Intertidal) Artificial Estuarine Channels
(00.0.134) Canyon-Mouth Estuaries	(00.0.230.0000) Tidal-River Channels
(00.0.135) Structural-Basin Estuaries	(00.0.231) Deep (Subtidal) Main-Stem River Channels
(00.0.136) Dune-Stream Estuaries	(00.0.232) Shallow (Intertidal) Main-Stem River Channels
(00.0.137) Agricultural Drainage Mouths	(00.0.233) Deep (Subtidal) Distributary River Channels
(00.0.138) Urban Drainage Mouths	(00.0.234) Shallow (Intertidal) Distributary River Channels
(00.0.140.0000) Coves	(00.0.240.0000) Tidal-Stream Channels
(00.0.141) Coves	(00.0.241) Deep (Subtidal) Canyon-Stream Channels
(00.0.150.0000) Lagoons	(00.0.242) Shallow (Intertidal) Canyon-Stream Channels
(00.0.151) Lagoons	(00.0.243) Deep (Subtidal) Dune-Stream Channels
(00.0.160.0000) Harbors/Ports	(00.0.244) Shallow (Intertidal) Dune-Stream Channels
(00.0.161) Large Harbors/Ports	(00.0.250.0000) Tidal-Marsh Channels
(00.0.162) Small Harbors/Ports	(00.0.251) Deep (Subtidal), Large, Tidal-Marsh Channels
(00.0.170.0000) Tidal Ponds	(00.0.252) Shallow (Intertidal), Large, Tidal-Marsh Channels
(00.0.171) Tidal Dune-Swale Ponds	(00.0.253) Deep (Subtidal), Intermediate, Tidal-Marsh Channels
(00.0.172) Tidal Marsh Ponds	(00.0.254) Shallow (Intertidal), Intermediate, Tidal-Marsh Channels
(00.0.180.0000) Tide Pools	
(00.0.181) Large Tide Pools	(00.0.255) Deep (Subtidal), Small, Tidal-Marsh Channels
(00.0.182) Small Tide Pools	(00.0.256) Shallow (Intertidal), Small, Tidal-Marsh Channels

TABLE 6. CONTINUED

(00.0.260.0000) Fissures	(00.0.326) Harbor Beaches
(00.0.261) Large (Wide/Long) Fissures	(00.0.330.0000) Banks
(00.0.262) Small (Narrow/Short) Fissures	(00.0.331) Estuary Banks
(00.0.270.0000) Sea Caves	(00.0.340.0000) Benches
(00.0.271) Large Sea-Caves	(00.0.341) Ocean Benches
(00.0.272) Small Sea-Caves	(00.0.342) Exposed Bay Benches
(00.0.280.0000) Culverts	(00.0.343) Estuary Benches
(00.0.281) Large (Wide/Long) Culverts	(00.0.345) Lagoon Benches
(00.0.282) Small (Narrow/Short) Culverts	(00.0.346) Harbor Benches
(00.0.290.0000) Tidal Ditches	(00.0.350.0000) Terraces
(00.0.291) Deep (Subtidal), Large Tidal-Ditches	(00.0.351) Estuary Terraces
(00.0.292) Shallow (Intertidal), Large Tidal-Ditches	(00.0.360.0000) Ledges/Ridges
(00.0.293) Deep (Subtidal), Intermediate Tidal-Ditches	(00.0.361) Ledges
(00.0.294) Shallow (Intertidal), Intermediate Tidal-Ditches	(00.0.362) Hogback Ridges
Ditches	
(00.0.295) Deep (Subtidal), Small Tidal-Ditches	(00.0.400.0000) Bottoms, Beds, Bars, Reefs, Sea Stacks, Islets
(00.0.296) Shallow (Intertidal), Small Tidal-Ditches	(00.0.410.0000) Beds/Bottoms/Floors
(00.0.300.0000) Shores, Beaches, Banks, Benches	(00.0.411) Deep (Subtidal) Beds/Bottoms/Floors
(00.0.310.0000) Shores	(00.0.412) Shallow (Intertidal) Beds/Bottoms/Floors
(00.0.311) Ocean Shores	(00.0.420.0000) Bars
(00.0.312) Exposed Bay Shores	(00.0.421) Deep (Subtidal) Bars
(00.0.313) Estuary Shores	(00.0.422) Shallow (Intertidal) Bars
(00.0.314) Cove Shores	(00.0.430.0000) Reefs
(00.0.315) Lagoon Shores	(00.0.431) Large Reefs
(00.0.316) Harbor Shores	(00.0.432) Small Reefs
(00.0.320.0000) Beaches	(00.0.440.0000) Sea Stacks
(00.0.321) Ocean Beaches	(00.0.441) Large Sea-Stacks
(00.0.322) Exposed Bay Beaches	(00.0.442) Small Sea-Stacks
(00.0.323) Estuary Beaches	(00.0.450.0000) Islets
(00.0.324) Cove Beaches	(00.0.451) Large Islets
(00.0.325) Lagoon Beaches	(00.0.452) Small Islets

TABLE 6. CONTINUED

(00.0.500.0000) Flats, Deltas	
(00.0.510.0000) Flats	(00.0.812) Middle-Intertidal Salt Marshes
(00.0.511) Mineral (Mud, Sand) Flats	(00.0.813) High-Intertidal Salt Marshes
(00.0.512) Precipitate (Salt) Flats, Pannes	(00.0.820.0000) Brackish Marshes
(00.0.513) Vegetated-Algal Flats	(00.0.821) Low-Intertidal Brackish Marshes
(00.0.514) Vegetated-Plant Flats	(00.0.822) Middle-Intertidal Brackish Marshes
(00.0.520.0000) Deltas	(00.0.823) High-Intertidal Brackish Marshes
(00.0.521) Deltas	(00.0.830.0000) Fringe Marshes
(00.0.600.0000) Headlands, Bluffs, Slopes	(00.0.831) Low-Intertidal Fringe Marshes
(00.0.610.0000) Headlands	(00.0.832) Middle-Intertidal Fringe Marshes
(00.0.611) Large Headlands	(00.0.833) High-Intertidal Fringe Marshes
(00.0.612) Small Headlands	(00.0.840.0000) Diked Marshes
(00.0.620.0000) Cliffs/Bluffs	(00.0.841) Low-Intertidal Diked Marshes
(00.0.621) Cliffs/Bluffs	(00.0.842) Middle-Intertidal Diked Marshes
(00.0.630.0000) Slopes	(00.0.843) High-Intertidal Diked Marshes
(00.0.631) Ocean Slopes	(00.0.900.0000) Artificial Structures
(00.0.632) Exposed Bay Slopes	(00.0.910.0000) Stationary Artificial Structures
(00.0.633) Estuary Slopes	(00.0.911) Jetties/Breakwaters
(00.0.634) Cove Slopes	(00.0.912) Sea Wall/Revetment
(00.0.635) Lagoon Slopes	(00.0.913) Dams/Levees
(00.0.636) Harbor Slopes	(00.0.914) Earthen Berms/Dikes
(00.0.700.0000) Seeps, Springs	(00.0.915) Dredge Spoils
(00.0.710.0000) Seeps	(00.0.916) Piling/Piers
(00.0.711) Seeps	(00.0.917) Oil Platforms
(00.0.720.0000) Springs	(00.0.918) Boat Ramps
(00.0.721) Springs	(00.0.919) Wreckage
(00.0.800.0000) Marshes	(00.0.920.0000) Floating Artificial Structures
(00.0.810.0000) Salt Marshes	(00.0.921) Hulls
(00.0.811) Low-Intertidal Salt Marshes	(00.0.922) Docks
	(00.0.923) Buoys
	(00.0.924) Logs

TABLE 7. HYDROGEOMORPHIC UNITS: RIVERINE, LACUSTRINE, AND PALUSTRINE SYSTEMS. This table provides a numerical, hierarchical listing of the various hydrogeomorphic (HGM) units determined by the authors to be characteristic of wetlands in the study region and that are not flooded by tidal water containing ocean-derived salts. Various HGM units in this table are specific to the riverine, lacustrine, or palustrine systems.

(“00”) = Water Regime	(00.0.“000”) = Hydrogeomorphic Unit
(00.“0”) = Water Chemistry	(00.0.000.“0000”) = Substrate/Dominance/Characteristic Types
(00.0.100.0000) Water Bodies (Hydrogeomorphic Context)	
(00.0.110.0000) Pools	(00.0.152) Montane Alkali Lakes
(00.0.111) Vernal Pools	(00.0.153) Playa Lakes
(00.0.112) Tenajas	(00.0.154) Montane Reservoirs
(00.0.113) Main Channel Pools	(00.0.155) River-Valley Reservoirs
(00.0.114) Scour Pools	(00.0.156) Canyon Reservoirs
(00.0.115) Backwater Pools	(00.0.157) Caldera Lakes
(00.0.120.0000) Riffles	(00.0.160.0000) Streams
(00.0.121) Riffles	(00.0.161) Montane Streams
(00.0.122) Rapids	(00.0.162) Foothill/Terrace Streams
(00.0.123) Cascades	(00.0.163) Valley Streams
(00.0.124) Runs	(00.0.164) Coastal-Plain Streams
(00.0.125) Falls	(00.0.165) Canyon Streams
(00.0.130.0000) Springs	(00.0.170.0000) Rivers
(00.0.131) Cold Springs	(00.0.171) Montane Rivers
(00.0.132) Hot Springs	(00.0.172) Foothill Rivers
(00.0.140.0000) Palustrine Ponds, Lakes, Reservoirs	(00.0.173) Valley Rivers
(00.0.141) Dune Ponds (“Lakes”)	(00.0.174) Coastal-Plain Rivers
(00.0.142) Coastal Ponds	(00.0.175) Canyon Rivers
(00.0.143) Fault Sag Ponds	(00.0.180.0000) Drainages
(00.0.144) Glacial Ponds (“Lakes”)	(00.0.181) Montane Drainages
(00.0.145) Vernal Ponds	(00.0.182) Coastal Canyon Drainages
(00.0.146) Palustrine Vernal Lakes	(00.0.200.0000) Channels, Drainages, Inverts, Falls
(00.0.147) Agricultural Ponds, Reservoirs	(00.0.210.0000) Stream Channels
(00.0.148) Recreational Ponds, Reservoirs	(00.0.211) Montane Stream Channels
(00.0.149) Diked Estuarine Basins	(00.0.212) Foothill/Terrace Stream Channels
(00.0.150.0000) Lacustrine Lakes, Reservoirs	(00.0.213) Valley Stream Channels
(00.0.151) Montane Freshwater Lakes	(00.0.214) Coastal Plain Stream Channels

TABLE 7. CONTINUED

(00.0.0.215) Distributary Channels	(00.0.0.317) Recreational Pond Shores
(00.0.0.220.0000) River Channels	(00.0.0.320.0000) Palustrine Lake/Reservoir Shores
(00.0.0.221) Montane River Channels	(00.0.0.321) Vernal Palustrine-Lake Shores
(00.0.0.222) Foothill River Channels	(00.0.0.322) Agricultural Palustrine-Lake Shores
(00.0.0.223) Valley River Channels	(00.0.0.323) Recreational Palustrine-Lake Shores
(00.0.0.224) Coastal Plain River Channels	(00.0.0.330.0000) Lacustrine Lake/Reservoir Shores
(00.0.0.225) Distributary Channels	(00.0.0.331) Montane Freshwater Lacustrine-Lake Shores
(00.0.0.226) Canyon River Channels	(00.0.0.332) Montane Alkali Lacustrine-Lake Shores
(00.0.0.230.0000) Backbar Channels	(00.0.0.333) Playa Lake Shores
(00.0.0.231) Stream Backbar Channels	(00.0.0.334) Montane Reservoir Shores
(00.0.0.232) River Backbar Channels	(00.0.0.335) River-Valley Reservoir Shores
(00.0.0.240.0000) Drainage Channels	(00.0.0.336) Canyon Reservoir Shores
(00.0.0.241) Vernal Drainage Channels	(00.0.0.337) Caldera Lake Shores
(00.0.0.242) Montane Drainage Channels	(00.0.340.0000) Stream Shores
(00.0.0.250.0000) Inverts	(00.0.0.341) Montane Stream-Shores
(00.0.0.251) Montane Drainage Inverts	(00.0.0.342) Foothill/Terrace Stream-Shores
(00.0.0.260.0000) Falls	(00.0.0.343) Valley Stream-Shores
(00.0.0.261) Montane Stream Falls	(00.0.0.344) Coastal-Plain Stream-Shores
(00.0.0.262) Foothill Stream Falls	(00.0.0.345) Canyon Stream-Shores
(00.0.0.263) Montane River Falls	(00.0.350.0000) River Shores
(00.0.0.264) Foothill River Falls	(00.0.0.351) Montane River-Shores
(00.0.0.270.0000) Lacustrine Channels	(00.0.0.352) Foothill River-Shores
(00.0.0.280.0000) Artificial Ditches	(00.0.0.353) Valley River-Shores
	(00.0.0.354) Coastal-Plain River-Shores
	(00.0.0.355) Canyon River-Shores
(00.0.300.0000) Shores, Beaches, Banks, Margins	(00.0.360.0000) Beaches
(00.0.0.310.0000) Palustrine Pond Shores	(00.0.0.361) River Beaches
(00.0.0.311) Dune Pond Shores	(00.0.0.362) Lake Beaches
(00.0.0.312) Coastal Pond Shores	(00.0.0.370.0000) Stream Banks
(00.0.0.313) Fault Sag Pond Shores	(00.0.0.371) Montane Stream-Banks
(00.0.0.314) Glacial Pond ("Lake ⁶⁰) Shores	(00.0.0.372) Foothill/Terrace Stream-Banks
(00.0.0.315) Vernal Pond Shores	(00.0.0.373) Valley Stream-Banks
(00.0.0.316) Agricultural Pond Shores	

TABLE 7. CONTINUED

(00.0.374) Coastal-Plain Stream-Banks	(00.0.427) Recreational Pond/Reservoir Beds/Bottoms
(00.0.375) Canyon Stream-Banks	(00.0.430.0000) Palustrine Lake Beds/Bottoms
(00.0.380.0000) River Banks	(00.0.431) Palustrine Vernal Lake Beds/Bottoms
(00.0.381) Montane River-Banks	(00.0.432) Palustrine Perennial Lake Beds/Bottoms
(00.0.382) Foothill River-Banks	(00.0.433) Palustrine Agricultural Lake Beds/Bottoms
(00.0.383) Valley River-Banks	(00.0.434) Palustrine Recreational Lake/Reservoir Beds/Bottoms
(00.0.384) Coastal-Plain River-Banks	
(00.0.385) Canyon River Banks	
(00.0.390.0000) Margins	(00.0.440.0000) Lacustrine Lake/Reservoir Beds/Bottoms
(00.0.391) Stream Margins	(00.0.441) Montane Freshwater Lake Beds/Bottoms
(00.0.392) River Margins	(00.0.442) Montane Alkali Lake Beds/Bottoms
(00.0.393) Estuary Margins	(00.0.443) Playa Lake Beds/Bottoms
(00.0.394) Pool Margins	(00.0.444) Montane Reservoir Beds/Bottoms
(00.0.395) Pond Margins	(00.0.445) River-Valley Reservoir Beds/Bottoms
(00.0.396) Swale Margins	(00.0.446) Canyon Reservoir Beds/Bottoms
(00.0.397) Lake Margins	(00.0.447) Caldera Lake Beds/Bottoms
(00.0.398) Seep, Spring Margins	(00.0.450.0000) Stream Beds/Bottoms
(00.0.399) Meadow, Marsh Margins	(00.0.451) Montane Streambeds
	(00.0.452) Foothill/Terrace Streambeds
(00.0.400.0000) Beds, Bottoms, Bars	(00.0.453) Valley Streambeds
(00.0.410.0000) Pool Beds/Bottoms	(00.0.454) Coastal Plain Streambeds
(00.0.411) Vernal Pool Beds/Bottoms	(00.0.455) Canyon Streambeds
(00.0.412) Tenaja Beds/Bottoms	(00.0.460.0000) River Beds/Bottoms
(00.0.413) Main-Channel Pool Bottoms	(00.0.461) Montane Riverbeds
(00.0.414) Scour Pool Bottoms	(00.0.462) Foothill Riverbeds
(00.0.415) Backwater Pool Bottoms	(00.0.463) Valley Riverbeds
(00.0.420.0000) Palustrine Pond Beds/Bottoms	(00.0.464) Coastal-Plain Riverbeds
(00.0.421) Dune Pond ("Lake") Beds/Bottoms	(00.0.465) Canyon Riverbeds
(00.0.422) Coastal Pond Beds/Bottoms	(00.0.470.0000) Stream-Channel Bars
(00.0.423) Fault Sag Pond Beds/Bottoms	(00.0.471) Montane Stream-Channel Bars
(00.0.424) Glacial Pond ("Lake") Beds/Bottoms	(00.0.472) Foothill/Terrace Stream-Channel Bars
(00.0.425) Vernal Pond Beds/Bottoms	(00.0.473) Valley Stream-Channel Bars
(00.0.426) Agricultural Pond/Reservoir Beds/Bottoms	(00.0.474) Coastal-Plain Stream-Channel Bars

TABLE 7. CONTINUED

(00.0.475) Canyon Stream-Channel Bars	(00.0.561) River Terraces
(00.0.480.0000) River-Channel Bars	(00.0.562) Stream Terraces
(00.0.481) Montane River-Channel Bars	(00.0.563) Valley Terraces
(00.0.482) Foothill River-Channel Bars	(00.0.564) Coastal Terraces
(00.0.483) Valley River-Channel Bars	(00.0.600.0000) Headlands, Bluffs, Slopes
(00.0.484) Coastal-Plain River-Channel Bars	(00.0.610.0000) Headlands
(00.0.485) Canyon River-Channel Bars	(00.0.620.0000) Cliffs/Bluffs
(00.0.490.0000) Lake Bars	(00.0.621) Coastal Cliffs/Bluffs
(00.0.500.0000) Flats, Plains, Washes, Bottomlands, Terraces	(00.0.622) Canyon Cliffs/Bluffs
(00.0.510.0000) Flats	(00.0.630.0000) Slopes
(00.0.511) Vernal Flats	(00.0.631) Coastal Plain Slopes
(00.0.520.0000) Plains	(00.0.632) Canyon Slopes
(00.0.521) Coastal Plains	(00.0.633) Foothill Slopes
(00.0.522) Montane-Valley Vernal Plains	(00.0.634) Montane Slopes
(00.0.523) Alkali Vernal Plains	(00.0.640.0000) Alluvial Fans
(00.0.524) Haline Vernal Plains	(00.0.641) Montane Alluvial Fans
(00.0.530.0000) Deltas	(00.0.642) Foothill Alluvial Fans
(00.0.531) Stream Deltas	(00.0.643) Valley Alluvial Fans
(00.0.532) River Deltas	(00.0.700.0000) Seeps, Springs
(00.0.533) Coastal Deltas	(00.0.710.0000) Seeps
(00.0.534) Lake Deltas	(00.0.711) Drainage Head Seeps
(00.0.540.0000) Washes	(00.0.712) Bluff and Slope Seeps
(00.0.541) Stream Washes	(00.0.713) Canyon Seeps
(00.0.542) River Washes	(00.0.714) Stream Bank/Bed Seeps
(00.0.543) Alluvial Washes	(00.0.715) River Bank/Bed Seeps
(00.0.550.0000) Floodplains, Bottomlands	(00.0.716) Montane Seeps
(00.0.551) Stream Floodplains, Bottomlands	(00.0.717) Foothill Seeps
(00.0.552) River Floodplains, Bottomlands	(00.0.718) Valley and Plain Seeps
(00.0.553) Canyon Floodplains, Bottomlands	(00.0.719) Lake Seeps
(00.0.554) Montane Floodplains, Bottomlands	(00.0.720.0000) Springs
(00.0.560.0000) Terraces	(00.0.721) Drainage-Head Springs

TABLE 7. CONTINUED

(00.0.722) Bluff and Slope Springs	(00.0.832) Montane Perennial Meadows
(00.0.723) Canyon Springs	(00.0.840.0000) Marshes
(00.0.724) Stream Bank/Bed Springs	(00.0.841) Vernal Freshwater Marshes
(00.0.725) River Bank/Bed Springs	(00.0.842) Perennial Freshwater Marshes
(00.0.726) Montane Springs	(00.0.843) Saline Marshes
(00.0.727) Foothill Springs	(00.0.844) Haline Marshes
(00.0.728) Valley and Plain Springs	(00.0.845) Stream-Channel Marshes
(00.0.729) Lake Springs	(00.0.846) River-Channel Marshes
(00.0.730.0000) Hot Springs	(00.0.847) Lake-Shore Marshes
(00.0.740.0000) Artificial Seeps	(00.0.848) Diked Estuarine Marshes
(00.0.750.0000) Artificial Springs	(00.0.850.0000) Swales
	(00.0.851) Montane Drainages Swales
(00.0.800.0000) Palustrine Basins/Depressions: Pools, Ponds,	(00.0.852) Coastal Terrace Drainage Swales
Lakes, Meadows, Marshes, Swales	(00.0.853) Dune/Beach Swales
(00.0.810.0000) Vernal Pools	(00.0.854) Vernal Drainage Swales
(00.0.811) Coastal-Terrace Vernal Pools	(00.0.855) Artificial Drainage Swales
(00.0.812) Mesa Vernal Pools	(00.0.900.0000) Artificial Structures
(00.0.813) River-Terrace Vernal Pools	(00.0.910.0000) Stationary Artificial Structures
(00.0.814) Coastal-Valley/Plain Vernal Pools	(00.0.911) Jetties/Breakwaters
(00.0.815) Foothill-Valley Vernal Pools	(00.0.912) Bank Revetments
(00.0.816) Montane-Plateau Vernal Pools	(00.0.913) Dams/Levees
(00.0.820.0000) Palustrine Ponds, Lakes	(00.0.914) Earthen Berms/Dikes
(00.0.821) Coastal-Dune Ponds ("Lakes")	(00.0.915) Dredge spoils
(00.0.822) Coastal-Canyon Ponds	(00.0.916) Piling/Piers
(00.0.823) Fault-Sag Ponds	(00.0.917) Platforms
(00.0.824) Glacial Ponds ("Lakes")	(00.0.918) Boat Ramps
(00.0.825) Vernal Ponds	(00.0.919) Wreckage
(00.0.826) Palustrine Vernal Lakes	(00.0.920.0000) Floating Artificial Structures
(00.0.827) Agricultural Ponds	(00.0.921) Hulls
(00.0.828) Recreational Ponds	(00.0.922) Docks
(0.0.830.0000) Meadows	(00.0.923) Buoys
(00.0.831) Montane Vernal Meadows	(00.0.924) Logs

TABLE 8. SUBSTRATE/DOMINANCE/CHARACTERISTIC TYPES: MARINE AND ESTUARINE SYSTEMS. This table provides a numerical, hierarchical listing of major substrate categories and dominant or characteristic species of marine and estuarine wetlands (i.e., tidal-flooding with water containing ocean-derived salts). This table serves as a source of information when compiling a wetland numerical code and name. Most categories or types are either open-ended or contain open numbers for additions.

(“00”) = Water Regime	(00.0.“000”) = Hydrogeomorphic Unit
(00.“0”) = Water Chemistry	(00.0.000.“0000”) = Substrate/Dominance/Characteristic Types
SUBSTRATE/DOMINANCE/CHARACTER TYPES (Categories)	
(00.0.000.1000) Non-Organic and Non-Living Organic Dominance Types	
(00.0.000.1100) Open Water Types	(00.0.000.2240) Turf Types
(00.0.000.1200) Bedrock Types	(00.0.000.2241) <i>Bryopsis</i>
(00.0.000.1300) Boulder Types	(00.0.000.2242) <i>Cladophora</i>
(00.0.000.1400) Cobble Types	(00.0.000.2250) Encrusting Types
(00.0.000.1500) Mixed-Coarse Types	(00.0.000.2260) Filamentous Types
(00.0.000.1600) Sand Types	(00.0.000.2261) <i>Chaetomorpha</i>
(00.0.000.1700) Mixed-Fine Types	(00.0.000.2262) <i>Enteromorpha</i>
(00.0.000.1800) Mud Types	(00.0.000.2263) <i>Ullothrix</i>
(00.0.000.1900) Organic Types	(00.0.000.2300) Brown Algal Types
(00.0.000.2000) Algal (Protista-Monera) Dominance Types	(00.0.000.2310) Bladder Types
(00.0.000.2100) Diatom Types	(00.0.000.2311) <i>Cystoseira</i>
(00.0.000.2110) Estuarine Diatoms	(00.0.000.2312) <i>Egregia</i>
(00.0.000.2111) <i>Himphora</i> sp.	(00.0.000.2313) <i>Halidrys</i>
(00.0.000.2112) <i>Nittachia longissima</i>	(00.0.000.2314) <i>Sargassum</i>
(00.0.000.2113) <i>Pleurosigma estuarii</i>	(00.0.000.2320) Branching Foliose Types
(00.0.000.2200) Green Algal Types	(00.0.000.2321) <i>Desmarestia</i>
(00.0.000.2210) Bladder Types	(00.0.000.2322) <i>Eisenia</i>
(00.0.000.2220) Branching Foliose Types	(00.0.000.2323) <i>Fucus</i>
(00.0.000.2221) <i>Codium</i>	(00.0.000.2324) <i>Hesperophycus</i>
(00.0.000.2230) Non-branching Foliose Types	(00.0.000.2325) <i>Pelvetia</i>
(00.0.000.2231) <i>Ulva</i>	(00.0.000.2326) <i>Postelsia</i>
	(00.0.000.2327) <i>Zonaria</i>
	(00.0.000.2330) Non-branching Foliose Types
	(00.0.000.2331) <i>Alaria</i>
	(00.0.000.2332) <i>Colpomenia</i>

TABLE 8. CONTINUED

(00.0.000.2333) <i>Dicyota</i>	(00.0.000.2462) <i>Polysiphonia</i>
(00.0.000.2334) <i>Laminaria</i>	(00.0.000.2463) <i>Rhodochorton</i>
(00.0.000.2335) <i>Pterogophora</i>	(00.0.000.2470) Erect Coralline Types
(00.0.000.2340) Turf Types	(00.0.000.2471) <i>Bossiella</i>
(00.0.000.2341) <i>Pelvetiopsis</i>	(00.0.000.2472) <i>Corallina</i>
(00.0.000.2350) Encrusting Types	(00.0.000.2500) Mixed Protista Type
(00.0.000.2351) <i>Ralfsia</i>	(00.0.000.2600) Blue-Green Algal Type
(00.0.000.2360) Filamentous Types	(00.0.000.3000) Moss-Lichen, Fungal Types
(00.0.000.2361) <i>Giffordia</i>	(00.0.000.3100) Moss Types
(00.0.000.2362) <i>Scytosiphon</i>	(00.0.000.3200) Liverwort Types
(00.0.000.2400) Red Algal Types	(00.0.000.3300) Mixed-Bryophyte Types
(00.0.000.2410) Bladder Types	(00.0.000.3400) Lichen Types
(00.0.000.2420) Branching Foliose Types	(00.0.000.3500) Moss-Lichen Types
(00.0.000.2421) <i>Botryoglossum</i>	(00.0.000.3600) Fungal Types
(00.0.000.2422) <i>Gastroclonium</i>	(00.0.000.4000) Pteridophyte Dominance Types
(00.0.000.2423) <i>Gelidium</i>	(00.0.000.4100) Quillwort Dominance Types
(00.0.000.2424) <i>Gigartina</i>	(00.0.000.4200) Horsetail Dominance Types
(00.0.000.2425) <i>Gracilaria</i>	(00.0.000.4300) Fern Dominance Types
(00.0.000.2426) <i>Pronites</i>	(00.0.000.4310) Aquatic Bed Types
(00.0.000.2427) <i>Rhodoglossum</i>	(00.0.000.4311) <i>Azolla filiculoides</i>
(00.0.000.2428) <i>Rhodomela</i>	(00.0.000.5000) Dicot Vascular-Plant Dominance Types
(00.0.000.2430) Non-branching Foliose Types	(00.0.000.5100) Aquatic-Bed Types
(00.0.000.2431) <i>Halosaccion</i>	(00.0.000.5200) Persistent Emergent Types (Asteraceae)
(00.0.000.2432) <i>Iridaea</i>	(00.0.000.5210) <i>Jaumea</i>
(00.0.000.2433) <i>Nematon</i>	(00.0.000.5211) <i>Jaumea carnosa</i>
(00.0.000.2434) <i>Porphyra</i>	(00.0.000.5220) <i>Euthamia</i>
(00.0.000.2440) Turf Types	(00.0.000.5221) <i>Euthamia occidentalis</i>
(00.0.000.2441) <i>Endocladia</i>	(00.0.000.5300) Persistent Emergent Types (Chenopodiaceae)
(00.0.000.2450) Encrusting Types	(00.0.000.5310) <i>Arthrocnemum</i>
(00.0.000.2451) <i>Pseudolithophyllum</i>	(00.0.000.5311) <i>Arthrocnemum subterminale</i>
(00.0.000.2460) Filamentous Types	
(00.0.000.2461) <i>Bangia</i>	

TABLE 8. CONTINUED

(00.0.000.5320) <i>Atriplex</i>	(00.0.000.5600) Scrub-Shrub Types
(00.0.000.5321) <i>Atriplex watsonii</i>	(00.0.000.5610) Aizoaceae
(00.0.000.5330) <i>Salicornia</i>	(00.0.000.5611) <i>Carpobrotus edulis</i>
(00.0.000.5331) <i>Salicornia virginica</i>	(00.0.000.5612) <i>Malephora crocea</i>
(00.0.000.5340) <i>Suaeda</i>	(00.0.000.5620) Asteraceae
(00.0.000.5341) <i>Suaeda esteroa</i>	(00.0.000.5621) <i>Baccharis douglasii</i>
(00.0.000.5400) Persistent Emergent Types (Other)	(00.0.000.5622) <i>Baccharis pilularis</i>
(00.0.000.5410) Batidaceae	(00.0.000.5623) <i>Baccharis salicifolia</i>
(00.0.000.5411) <i>Batis maritima</i>	(00.0.000.5624) <i>Isocoma menziesii</i>
(00.0.000.5420) Convolvulaceae	(00.0.000.5630) Chenopodiaceae
(00.0.000.5421) <i>Cressa truxillensis</i>	(00.0.000.5631) <i>Atriplex lentiformis</i>
(00.0.000.5430) Cuscutaceae	(00.0.000.5632) <i>Suaeda californica</i>
(00.0.000.5431) <i>Cuscuta salina</i>	(00.0.000.5633) <i>Suaeda taxifolia</i>
(00.0.000.5440) Frankeniaceae	(00.0.000.5640) Salicaceae
(00.0.000.5441) <i>Frankenia salina</i>	(00.0.000.5641) <i>Salix exigua</i>
(00.0.000.5450) Plumbaginaceae	(00.0.000.5642) <i>Salix lasiolepis</i>
(00.0.000.5451) <i>Limonium californicum</i>	(00.0.000.5700) Woodland Types
(00.0.000.5500) Nonpersistent Emergent Types	(00.0.000.5800) Forest Types
(00.0.000.5510) Asteraceae	
(00.0.000.5511) <i>Cotula coronopifolia</i>	(00.0.000.6000) Monocot Vascular-Plant Dominance Types
(00.0.000.5512) <i>Lasthenia glabrata</i>	(00.0.000.6100) Aquatic-Bed Types
(00.0.000.5520) Brassicaceae	(00.0.000.6110) Lemnaceae
(00.0.000.5521) <i>Hutchinsia procumbens</i>	(00.0.000.6111) <i>Lemna gibba</i>
(00.0.000.5530) Caryophyllaceae	(00.0.000.6112) <i>Lemna minor</i>
(00.0.000.5531) <i>Spergularia marina</i>	(00.0.000.6113) <i>Lemna minuscula</i>
(00.0.000.5540) Chenopodiaceae	(00.0.000.6120) Potamogetonaceae
(00.0.000.5541) <i>Atriplex triangularis</i>	(00.0.000.6121) <i>Potamogeton pectinatus</i>
(00.0.000.5542) <i>Chenopodium macrospermum</i>	(00.0.000.6122) <i>Ruppia cirrhosa</i>
(00.0.000.5543) <i>Salicornia europaea</i>	(00.0.000.6123) <i>Ruppia maritima</i>
(00.0.000.5544) <i>Suaeda calceoliformis</i>	(00.0.000.6130) Zannichelliaceae
(00.0.000.5550) Scrophulariaceae	(00.0.000.6131) <i>Zannichellia americana</i>
(00.0.000.5551) <i>Cordylanthus maritimus</i>	(00.0.000.6140) Zosteraceae

TABLE 8. CONTINUED

(00.0.000.6141) <i>Phyllospadix scouleri</i>	(00.0.000.6521) <i>Typha domingensis</i>
(00.0.000.6142) <i>Phyllospadix torreyi</i>	(00.0.000.6600) Nonpersistent Emergent Types
(00.0.000.6143) <i>Zostera marina</i>	(00.0.000.6610) Juncaceae
(00.0.000.6200) Persistent Emergent Types (Cyperaceae— Sedges)	(00.0.000.6611) <i>Juncus bufonius</i>
(00.0.000.6210) <i>Carex</i>	(00.0.000.7000) Mixed-Vascular Types
(00.0.000.6220) <i>Eleocharis</i>	(00.0.000.8000) Animal Dominance Types
(00.0.000.6221) <i>Eleocharis macrostachya</i>	(00.0.000.8100) Sponge Types
(00.0.000.6230) <i>Scirpus</i>	(00.0.000.8110) Encrusting Types
(00.0.000.6231) <i>Scirpus americanus</i>	(00.0.000.8111) <i>Halichondria</i>
(00.0.000.6232) <i>Scirpus californicus</i>	(00.0.000.8112) <i>Haliclona</i>
(00.0.000.6233) <i>Scirpus maritimus</i>	(00.0.000.8113) <i>Hymenamphistra</i>
(00.0.000.6234) <i>Scirpus pungens</i>	(00.0.000.8114) <i>Leucetta</i>
(00.0.000.6235) <i>Scirpus robustus</i>	(00.0.000.8115) <i>Leucosolenia</i>
(00.0.000.6300) Persistent Emergent Types (Juncaceae—Rushes)	(00.0.000.8116) <i>Ophlitaspongia</i>
(00.0.000.6310) <i>Juncus</i>	(00.0.000.8120) Erect Types
(00.0.000.6311) <i>Juncus acutus</i>	(00.0.000.8121) <i>Microciona</i>
(00.0.000.6312) <i>Juncus balticus</i>	(00.0.000.8200) Coelenterate Types
(00.0.000.6400) Persistent Emergent Types (Poaceae—Grasses)	(00.0.000.8210) Hydroid Types
(00.0.000.6410) <i>Distichlis</i>	(00.0.000.8211) <i>Aglaophenia</i>
(00.0.000.6411) <i>Distichlis spicata</i>	(00.0.000.8212) <i>Anthopleura</i>
(00.0.000.6420) <i>Leymus</i>	(00.0.000.8213) <i>Corynactis</i>
(00.0.000.6421) <i>Leymus triticoides</i>	(00.0.000.8214) <i>Epiactis</i>
(00.0.000.6430) <i>Monanthochloe</i>	(00.0.000.8215) <i>Obelia</i>
(00.0.000.6431) <i>Monanthochloe littoralis</i>	(00.0.000.8216) <i>Tubularia</i>
(00.0.000.6440) <i>Spartina</i>	(00.0.000.8300) Mollusc Types
(00.0.000.6441) <i>Spartina foliosa</i>	(00.0.000.8310) Gastropod Types
(00.0.000.6500) Persistent Emergent Types (Other)	(00.0.000.8311) <i>Cerithidea</i>
(00.0.000.6510) Juncaginaceae	(00.0.000.8312) <i>Haliotis</i>
(00.0.000.6511) <i>Triglochin concinna</i>	(00.0.000.8313) <i>Littorina</i>
(00.0.000.6520) Typhaceae	(00.0.000.8314) <i>Surpulatorbis</i>
	(00.0.000.8315) <i>Tegula</i>

TABLE 8. CONTINUED

(00.0.000.8320) Oyster Types	(00.0.000.8531) <i>Emerita</i>
(00.0.000.8321) <i>Crassostrea</i>	(00.0.000.8532) <i>Hemigrapsus</i>
(00.0.000.8322) <i>Osrea</i>	(00.0.000.8533) <i>Pachygrapsus</i>
(00.0.000.8330) Mussel Types	(00.0.000.8534) <i>Pagurus</i>
(00.0.000.8331) <i>Mytilus</i>	(00.0.000.8535) <i>Uca</i>
(00.0.000.8340) Clam Types	(00.0.000.8600) Insect Types
(00.0.000.8341) <i>Donax</i>	(00.0.000.8610) Midge Types
(00.0.000.8342) <i>Macoma</i>	(00.0.000.8620) Mosquito Types
(00.0.000.8343) <i>Mya</i>	(00.0.000.8630) Blackfly Types
(00.0.000.8344) <i>Penitella</i>	(00.0.000.8640) Staphylinid beetles
(00.0.000.8345) <i>Protothaca</i>	(00.0.000.8700) Echinoderm Types
(00.0.000.8346) <i>Tagelus</i>	(00.0.000.8710) Sand Dollar Types
(00.0.000.8400) Annelid Types	(00.0.000.8711) <i>Dendroaster</i>
(00.0.000.8410) Burrow Dwelling Polychaete Types	(00.0.000.8720) Sea Urchin Types
(00.0.000.8411) <i>Euzonus</i>	(00.0.000.8721) <i>Strongylocentrotus</i>
(00.0.000.8420) Tube Building Polychaete types	(00.0.000.8800) Other Invertebrate Types
(00.0.000.8421) <i>Phragmatopoma</i>	(00.0.000.8810) Bryozoan Types
(00.0.000.8422) <i>Polydora</i>	(00.0.000.8811) <i>Bugula</i>
(00.0.000.8423) <i>Spirorbis</i>	(00.0.000.8812) <i>Thalamoporella</i>
(00.0.000.8424) <i>Surpula</i>	(00.0.000.8820) Tunicate Types
(00.0.000.8500) Crustacean Types	(00.0.000.8821) <i>Boryroides</i>
(00.0.000.8510) Amphipod Types	(00.0.000.8822) <i>Ciona</i>
(00.0.000.8511) <i>Megalorchestia</i>	(00.0.000.8823) <i>Diplosoma</i>
(00.0.000.8520) Barnacle Types	(00.0.000.8824) <i>Styela</i>
(00.0.000.8521) <i>Cithamalus</i>	(00.0.000.8900) Vertebrate Types
(00.0.000.8522) <i>Balanus</i>	(00.0.000.8910) Fish Types
(00.0.000.8523) <i>Lepas</i>	(00.0.000.8920) Bird Types
(00.0.000.8524) <i>Pollicipes</i>	(00.0.000.8230) Mammal Types
(00.0.000.8525) <i>Semibalanus</i>	(00.0.000.8931) <i>Phoca</i>
(00.0.000.8526) <i>Tetraclita</i>	(00.0.000.8932) <i>Zalophus</i>
(00.0.000.8530) Crab Types	

TABLE 9. SUBSTRATE/DOMINANCE/CHARACTERISTIC TYPES: RIVERINE, LACUSTRINE, AND PALUSTRINE SYSTEMS. This table provides a numerical, hierarchical listing of major substrate categories and dominant or characteristic species of riverine, lacustrine, and palustrine wetlands (i.e., wetlands not flooded with tidal water containing ocean-derived salts). This table serves as a source of information when compiling a wetland numerical code. Most categories or types are either open-ended or contain open numbers for additions.

(**00**) = Water Regime	(00.0.**000**) = Hydrogeomorphic Unit
(00.**0**) = Water Chemistry	(00.0.000.**00000**) = Substrate/Dominance/Characteristic Types
SUBSTRATE/DOMINANCE/CHARACTERISTIC TYPES (Categories)	
(00.0.000.1000) Non-Organismic Dominance Types	
(00.0.000.1100) Open Water Types	(00.0.000.2300) Brown Algal Types
(00.0.000.1200) Bedrock Types	(00.0.000.2400) Red Algal Types
(00.0.000.1300) Boulder Types	(00.0.000.2500) Mixed-Protista Types
(00.0.000.1400) Cobble Types	(00.0.000.2600) Blue-Green Algal Types
(00.0.000.1500) Mixed-Course Types	(00.0.000.3000) Moss-Lichen, Fungi Dominance/Characteristic Types
(00.0.000.1600) Sand Types	(00.0.000.3100) Moss Types
(00.0.000.1700) Mixed-Fine Types	(00.0.000.3200) Liverwort Types
(00.0.000.1800) Mud Types	(00.0.000.3300) Mixed Bryophyte Types
(00.0.000.1900) Organic Types	(00.0.000.3400) Lichen Types
	(00.0.000.3500) Moss-Lichen Types
	(00.0.000.3600) Fungi Types
(00.0.000.2000) Algal (Protista-Monera) Dominance/Characteristic Types	(00.0.000.4000) Pteridophyte Dominance/Characteristic Types
(00.0.000.2100) Diatom Types	(00.0.000.4100) Quillwort Types
(00.0.000.2200) Green Algal Types	(00.0.000.4110) <i>Isoetes</i>
(00.0.000.2210) Bladder Types	(00.0.000.4111) <i>Isoetes howellii</i>
(00.0.000.2220) Branching Foliose Types	(00.0.000.4200) Horsetail Types
(00.0.000.2221) <i>Chara</i>	(00.0.000.4210) <i>Equisetum</i>
(00.0.000.2222) <i>Nitella</i>	(00.0.000.4211) <i>Equisetum hyemale</i>
(00.0.000.2230) Non-branching Foliose Types	(00.0.000.4212) <i>Equisetum laevigatum</i>
(00.0.000.2240) Turf Types	(00.0.000.4213) <i>Equisetum telmateia</i>
(00.0.000.2250) Encrusting Types	
(00.0.000.2260) Filamentous Types	

TABLE 9. CONTINUED

(00.0.000.4300) Fern Types	(00.0.000.5211) <i>Tetragonia tetragonoides</i>
(00.0.000.4310) Aquatic Bed Types	(00.0.000.5220) Apiaceae (A-H)
(00.0.000.4311) <i>Azolla filiculoides</i>	(00.0.000.5221) <i>Apium graveolens</i>
(00.0.000.4320) Emergent Types	(00.0.000.5222) <i>Berula erecta</i>
(00.0.000.4321) <i>Adiantum capillus-veneris</i>	(00.0.000.5223) <i>Cicuta douglasii</i>
(00.0.000.4322) <i>Arhyrium filix-femina</i>	(00.0.000.5224) <i>Eryngium vaseyi</i>
(00.0.000.4323) <i>Marsilea vestita</i>	(00.0.000.5225) <i>Foeniculum vulgare</i>
(00.0.000.4324) <i>Ptilularia americana</i>	(00.0.000.5226) <i>Hydrocotyle ranunculoides</i>
(00.0.000.4325) <i>Polystichum munitum</i>	(00.0.000.5230) Apiaceae (I-Z)
(00.0.000.4326) <i>Pteridium aquilinum</i>	(00.0.000.5231) <i>Oenanthe sarmentosa</i>
(00.0.000.4327) <i>Thelypteris puberula</i>	(00.0.000.5232) <i>Perideridia</i> spp.
(00.0.000.4328) <i>Woodwardia fimbriata</i>	(00.0.000.5233) <i>Sphenostictium capitelatum</i>
(00.0.000.5000) Dicot/Conifer Vascular-Plant Dominance/Charac-	(00.0.000.5240) Apocynaceae, Asclepiadaceae
teristic Types	(00.0.000.5241) <i>Apocynum cannabinum</i>
(00.0.000.5100) Aquatic-Bed types	(00.0.000.5242) <i>Asclepias fascicularis</i>
(00.0.000.5110) Callitrichaceae	(00.0.000.5250) Asteraceae (A-L)
(00.0.000.5111) <i>Callitriche heterophylla</i>	(00.0.000.5251) <i>Artemisia douglasiana</i>
(00.0.000.5112) <i>Callitriche marginata</i>	(00.0.000.5252) <i>Artemisia ludoviciana</i>
(00.0.000.5120) Ceratophyllaceae	(00.0.000.5253) <i>Aster chilensis</i>
(00.0.000.5121) <i>Ceratophyllum demersum</i>	(00.0.000.5254) <i>Conyza canadensis</i>
(00.0.000.5130) Elatinaceae	(00.0.000.5255) <i>Euthamia occidentalis</i>
(00.0.000.5131) <i>Elatine californica</i>	(00.0.000.5256) <i>Gutierrezia sarothrae</i>
(00.0.000.5132) <i>Elatine rubella</i>	(00.0.000.5257) <i>Helentium bolanderi</i>
(00.0.000.5140) Haloragaceae	(00.0.000.5258) <i>Helentium puberulum</i>
(00.0.000.5141) <i>Myriophyllum aquaticum</i>	(00.0.000.5259) <i>Jaumea carnosa</i>
(00.0.000.5142) <i>Myriophyllum sibiricum</i>	(00.0.000.5260) Asteraceae (M-Z)
(00.0.000.5150) Hippuridaceae	(00.0.000.5261) <i>Solidago californica</i>
(00.0.000.5151) <i>Hippuris vulgaris</i>	(00.0.000.5262) <i>Solidago confinis</i>
(00.0.000.5160) Ranunculaceae	(00.0.000.5263) <i>Solidago spathulata</i>
(00.0.000.5161) <i>Ranunculus aquatilis</i>	(00.0.000.5270) Chenopodiaceae, Datisceae
(00.0.000.5200) Persistent Emergent Types (A-K Families)	(00.0.000.5271) <i>Arthrocnemum subterminale</i>
(00.0.000.5210) Aizoaceae	(00.0.000.5272) <i>Salicornia virginica</i>
	(00.0.000.5273) <i>Datisca glomerata</i>

TABLE 9. CONTINUED

(00.0.000.5280) Fabaceae	(00.0.000.5356) <i>Rumex conglomeratus</i>
(00.0.000.5281) <i>Amorpha fruticosa</i>	(00.0.000.5357) <i>Rumex crispus</i>
(00.0.000.5282) <i>Hoia macrostachya</i>	(00.0.000.5358) <i>Rumex occidentalis</i>
(00.0.000.5283) <i>Hoia orbiculata</i>	(00.0.000.5359) <i>Rumex salicifolius</i>
(00.0.000.5284) <i>Lupinus</i> sp.	(00.0.000.5400) Persistent Emergent Types (R-U Families)
(00.0.000.5285) <i>Melilotus alba</i>	(00.0.000.5410) Ranunculaceae
(00.0.000.5290) Frankeniaceae	(00.0.000.5420) <i>Delphinium glaucum</i>
(00.0.000.5291) <i>Frankenia salina</i>	(00.0.000.5421) <i>Ivesia argyrocoma</i>
(00.0.00.5300) Persistent Emergent Types (L-P Families)	(00.0.000.5422) <i>Potentilla anserina</i>
(00.0.000.5310) Hyperacaceae	(00.0.000.5430) Saururaceae
(00.0.000.5311) <i>Hypericum anagallitoides</i>	(00.0.000.5431) <i>Anemopsis californica</i>
(00.0.000.5320) Lamiaceae	(00.0.000.5440) Saxifragaceae
(00.0.000.5321) <i>Mentha arvensis</i>	(00.0.000.5441) <i>Boykinia rotundifolia</i>
(00.0.000.5322) <i>Stachys ajugoides</i>	(00.0.000.5450) Scrophulariaceae, Solanaceae
(00.0.000.5323) <i>Stachys albens</i>	(00.0.000.5451) <i>Scrophularia</i> spp.
(00.0.000.5324) <i>Stachys bullata</i>	(00.0.000.5452) <i>Datura wrightii</i>
(00.0.000.5325) <i>Stachys chamissonis</i>	(00.0.000.5453) <i>Nicoiana quadrivalis</i>
(00.0.000.5326) <i>Stachys pycnantha</i>	(00.0.000.5454) <i>Petunia parviflora</i>
(00.0.000.5330) Lythraceae, Nyphaeaceae	(00.0.000.5460) Urticaceae
(00.0.000.5331) <i>Lythrum californicum</i>	(00.0.000.5461) <i>Urtica dioica</i>
(00.0.000.5332) <i>Lythrum hyssopifolia</i>	(00.0.000.5470) Verbenaceae
(00.0.000.5333) <i>Nuphar luteum</i> ssp. <i>polysepalum</i>	(00.0.000.5471) <i>Phyla nodiflora</i>
(00.0.000.5334) <i>Nymphaea odorata</i>	(00.0.000.5472) <i>Verbena bracteata</i>
(00.0.000.5340) Onagraceae	(00.0.000.5473) <i>Verbena lasiostachys</i>
(00.0.000.5341) <i>Epilobium ciliatum</i>	(00.0.000.5500) Nonpersistent Emergent Types
(00.0.000.5342) <i>Ludwigia hexapetala</i>	(00.0.000.5510) Aizoaceae, Amaranthaceae, Apiaceae
(00.0.000.5343) <i>Oenothera elata</i> ssp. <i>hookeri</i>	(00.0.000.5511) <i>Gimus lotoides</i>
(00.0.000.5350) Polygonaceae	(00.0.000.5512) <i>Amaranthus</i> spp.
(00.0.000.5351) <i>Polygonum</i> sp.	(00.0.000.5513) <i>Berula erecta</i>
(00.0.000.5352) <i>Polygonum</i> sp.	(00.0.000.5514) <i>Eryngium aristulatum</i>
(00.0.000.5353) <i>Polygonum hydropiperoides</i>	(00.0.000.5515) <i>Hydrocoryle ranunculoides</i>
(00.0.000.5354) <i>Polygonum lapathifolium</i>	(00.0.000.5516) <i>Oenanthe armentosa</i>
(00.0.000.5355) <i>Polygonum punctatum</i>	

TABLE 9. CONTINUED

(00.0.0.000.5520)	Asteraceae (A-G)	(00.0.0.000.5559)	<i>Suaeda calceoliformis</i>
(00.0.0.000.5521)	<i>Anthemis cotula</i>	(00.0.0.000.5560)	Lamiaceae, Lythraceae
(00.0.0.000.5522)	<i>Artemisia biennis</i>	(00.0.0.000.5561)	<i>Mentha arvensis</i>
(00.0.0.000.5523)	<i>Artemisia douglasiana</i>	(00.0.0.000.5562)	<i>Mentha piperitoides</i>
(00.0.0.000.5524)	<i>Conyza coulteri</i>	(00.0.0.000.5563)	<i>Pogogyne abramsii</i>
(00.0.0.000.5525)	<i>Cotula coronopifolia</i>	(00.0.0.000.5564)	<i>Pogogyne douglassii</i>
(00.0.0.000.5526)	<i>Eclipta alba</i>	(00.0.0.000.5565)	<i>Stachys albens</i>
(00.0.0.000.5527)	<i>Gnaphalium luteo-album</i>	(00.0.0.000.5566)	<i>Ammannia coccinea</i>
(00.0.0.000.5528)	<i>Gnaphalium palustre</i>	(00.0.0.000.5567)	<i>Lythrum hyssopifolia</i>
(00.0.0.000.5530)	Asteraceae (H-X)	(00.0.0.000.5570)	Onagraceae, Malvaceae, Polygonaceae
(00.0.0.000.5531)	<i>Helentium puberulum</i>	(00.0.0.000.5571)	<i>Ludwigia peploides</i> ssp. <i>peploides</i>
(00.0.0.000.5532)	<i>Lasthenia californica</i>	(00.0.0.000.5572)	<i>Ludwigia hexapetala</i>
(00.0.0.000.5533)	<i>Lasthenia glabrata</i> ssp. <i>coulteri</i>	(00.0.0.000.5573)	<i>Epilobium ciliatum</i>
(00.0.0.000.5534)	<i>Psilocarphus brevissimus</i>	(00.0.0.000.5574)	<i>Oenothera elata</i> ssp. <i>hookeri</i>
(00.0.0.000.5535)	<i>Xanthium strumarium</i>	(00.0.0.000.5575)	<i>Malvella leprosa</i>
(00.0.0.000.5540)	Boraginaceae, Brassicaceae, Campanulaceae	(00.0.0.000.5576)	<i>Sidalcea</i> spp.
(00.0.0.000.5241)	<i>Heliotropium curassavicum</i>	(00.0.0.000.5580)	Polygonaceae, Ranunculaceae
(00.0.0.000.5542)	<i>Plagiobothrys undulatus</i>	(00.0.0.000.5581)	<i>Polygonum emersum</i> var. <i>emersum</i>
(00.0.0.000.5543)	<i>Plagiobothrys trachycarpus</i>	(00.0.0.000.5582)	<i>P. emersum</i> var. <i>stipulaceum</i>
(00.0.0.000.5544)	<i>Rorripa curvisiliqua</i>	(00.0.0.000.5583)	<i>Polygonum lapathifolium</i>
(00.0.0.000.5545)	<i>Rorripa nasturium-aquaticum</i>	(00.0.0.000.5584)	<i>Polygonum punctatum</i>
(00.0.0.000.5546)	<i>Rorripa palustris</i>	(00.0.0.000.5585)	<i>Polygonum</i> sp.
(00.0.0.000.5547)	<i>Downingia cuspidata</i>	(00.0.0.000.5586)	<i>Rumex maritimus</i>
(00.0.0.000.5548)	<i>Lobelia dunnii</i> var. <i>serrata</i>	(00.0.0.000.5587)	<i>Myosurus</i> spp.
(00.0.0.000.5550)	Chenopodiaceae	(00.0.0.000.5588)	<i>Ranunculus</i> spp.
(00.0.0.000.5551)	<i>Atriplex rosea</i>	(00.0.0.000.5590)	Scrophulariaceae
(00.0.0.000.5552)	<i>Atriplex triangularis</i>	(00.0.0.000.5591)	<i>Castilleja minor</i>
(00.0.0.000.5553)	<i>Chenopodium berlandieri</i>	(00.0.0.000.5592)	<i>Limosella aquatica</i>
(00.0.0.000.5554)	<i>Chenopodium macrospermum</i>	(00.0.0.000.5593)	<i>Lindernia dubia</i>
(00.0.0.000.5555)	<i>Chenopodium rubrum</i>	(00.0.0.000.5594)	<i>Mimulus cardinalis</i>
(00.0.0.000.5556)	<i>Kochia scoparia</i>	(00.0.0.000.5595)	<i>Mimulus guttatus</i>
(00.0.0.000.5557)	<i>Monolepis nuttalliana</i>	(00.0.0.000.5596)	<i>Mimulus</i> spp.
(00.0.0.000.5558)	<i>Salicornia europaea</i>	(00.0.0.000.5597)	<i>Veronica americana</i>

TABLE 9. CONTINUED

(00.0.000.5598)	<i>Veronica anagallis-aquatica</i>	(00.0.000.5680)	Malvaceae
(00.0.000.5599)	<i>Veronica peregrina</i>	(00.0.000.5681)	<i>Malacothamnus fasciculatus</i>
(00.0.000.5600)	Scrub-Shrub Types (A-M Families)	(00.0.000.5690)	Myriaceae, Oleaceae
(00.0.000.5610)	Alizaceae, Anacardiaceae	(00.0.000.5691)	<i>Myrica californica</i>
(00.0.000.5611)	<i>Carpobrotus edulis</i>	(00.0.000.5692)	<i>Forestiera pubescens</i>
(00.0.000.5612)	<i>Malephora crocea</i>	(00.0.000.5700)	Scrub-Shrub Types (N-Z Families)
(00.0.000.5613)	<i>Malosma laurina</i>	(00.0.000.5710)	Platanaceae
(00.0.000.5614)	<i>Toxicodendron diversilobum</i>	(00.0.000.5711)	<i>Platanus racemosa</i>
(00.0.000.5620)	Asteraceae	(00.0.000.5720)	Polygonaceae
(00.0.000.5621)	<i>Baccharis douglasii</i>	(00.0.000.5721)	<i>Eriogonum fasciculatum</i>
(00.0.000.5622)	<i>Baccharis pilularis</i>	(00.0.000.5722)	Ranunculaceae
(00.0.000.5623)	<i>Baccharis salicifolia</i>	(00.0.000.5723)	<i>Clematis ligusticifolia</i>
(00.0.000.5624)	<i>Brickellia californica</i>	(00.0.000.5730)	(P-R Families)
(00.0.000.5625)	<i>Isocoma menziesii</i>	(00.0.000.5740)	Rhamnaceae
(00.0.000.5626)	<i>Lepidospartum squamatum</i>	(00.0.000.5741)	<i>Ceanothus oliganthus</i>
(00.0.000.5627)	<i>Pluchea sericea</i>	(00.0.000.5742)	<i>Ceanothus spinosus</i>
(00.0.000.5628)	<i>Chrysothamnus nauseosus</i>	(00.0.000.5743)	<i>Rhamnus californica</i>
(00.0.000.5630)	Caprifoliaceae	(00.0.000.5750)	Rosaceae
(00.0.000.5631)	<i>Lonicera involucrata</i>	(00.0.000.5751)	<i>Prunus</i> spp.
(00.0.000.5632)	<i>Sambucus mexicana</i>	(00.0.000.5752)	<i>Rosa californica</i>
(00.0.000.5633)	<i>Symphoricarpos mollis</i>	(00.0.000.5753)	<i>Rosa gymnocarpa</i>
(00.0.000.5640)	Chenopodiaceae	(00.0.000.5754)	<i>Rosa woodsii</i>
(00.0.000.5641)	<i>Atriplex canescens</i>	(00.0.000.5755)	<i>Rubus ursinus</i>
(00.0.000.5642)	<i>Atriplex lentiformis</i>	(00.0.000.5756)	<i>Rubus</i> spp.
(00.0.000.5643)	<i>Suaeda moquinii</i>	(00.0.000.5757)	<i>Heterometes arbutifolia</i>
(00.0.000.5644)	<i>Suaeda taxifolia</i>	(00.0.000.5760)	Salicaceae
(00.0.000.5650)	Cornaceae	(00.0.000.5761)	<i>Populus balsamifera</i>
(00.0.000.5651)	<i>Cornus sericea</i> ssp. <i>occidentalis</i>	(00.0.000.5762)	<i>Salix breweri</i>
(00.0.000.5660)	Grossulariaceae	(00.0.000.5763)	<i>Salix exigua</i>
(00.0.000.5661)	<i>Ribes divaricatum</i>	(00.0.000.5764)	<i>Salix geyeriana</i>
(00.0.000.5670)	Lamiaceae	(00.0.000.5765)	<i>Salix laevigata</i>
(00.0.000.5671)	<i>Salvia mellifera</i>	(00.0.000.5766)	<i>Salix lasiolepis</i>

TABLE 9. CONTINUED

(00.0.000.5767)	<i>Salix lemmonii</i>	(00.0.000.5932)	<i>Quercus agrifolia</i> var. <i>agrifolia</i>
(00.0.000.5768)	<i>Salix lutea</i>	(00.0.000.5933)	<i>Quercus agrifolia</i> var. <i>oxydenia</i>
(00.0.000.5769)	<i>Salix scouleriana</i>	(00.0.000.5934)	<i>Quercus kelloggii</i>
(00.0.000.5770)	Solanaceae	(00.0.000.5935)	<i>Quercus lobata</i>
(00.0.000.5771)	<i>Nicotiana glauca</i>	(00.0.000.5936)	<i>Quercus wislizenii</i>
(00.0.000.5780)	Tamaritaceae	(00.0.000.5940)	Juglandaceae
(00.0.000.5781)	<i>Tamarix ramosissima</i>	(00.0.000.5941)	<i>Juglans californica</i> var. <i>californica</i>
(00.0.000.5790)	Vitaceae	(00.0.000.5942)	<i>Juglans californica</i> var. <i>hindsii</i>
(00.0.000.5791)	<i>Vitis girdiana</i>	(00.0.000.5950)	Lauraceae, Myricaceae, Oleaceae
(00.0.000.5800)	Woodland Tree Types	(00.0.000.5951)	<i>Umbellularia californica</i>
(00.0.000.5810)	Fagaceae	(00.0.000.5952)	<i>Myrica californica</i>
(00.0.000.5811)	<i>Quercus agrifolia</i> var. <i>agrifolia</i>	(00.0.000.5953)	<i>Fraxinus velutina</i>
(00.0.000.5812)	<i>Quercus agrifolia</i> var. <i>oxydenia</i>	(00.0.000.5960)	Pinaceae (Conifers)
(00.0.000.5813)	<i>Quercus lobata</i>	(00.0.000.5961)	<i>Abies concolor</i>
(00.0.000.5814)	<i>Quercus wislizenii</i>	(00.0.000.5962)	<i>Pinus contorta</i> ssp. <i>murrayana</i>
(00.0.000.5820)	Platanaceae	(00.0.000.5963)	<i>Pinus jeffreyi</i>
(00.0.000.5821)	<i>Platanus racemosa</i>	(00.0.000.5970)	Platanaceae
(00.0.000.5830)	Salicaceae	(00.0.000.5971)	<i>Platanus racemosa</i>
(00.0.000.5831)	<i>P. balsamifera</i> ssp. <i>trichocarpa</i>	(00.0.000.5980)	Salicaceae
(00.0.000.5832)	<i>Populus fremontii</i> ssp. <i>fremontii</i>	(00.0.000.5981)	<i>Populus balsamifera</i> ssp. <i>trichocarpa</i>
(00.0.000.5833)	<i>Salix laevigata</i>	(00.0.000.5982)	<i>Populus fremontii</i> ssp. <i>fremontii</i>
(00.0.000.5834)	<i>Salix lasiolepis</i>	(00.0.000.5983)	<i>Populus tremulooides</i>
(00.0.000.5835)	<i>Salix lucida</i> ssp. <i>lasianдра</i>	(00.0.000.5984)	<i>Salix goodingii</i>
(00.0.000.5900)	Forest Tree Types	(00.0.000.5985)	<i>Salix laevigata</i>
(00.0.000.5910)	Aceraceae	(00.0.000.5986)	<i>Salix lasiolepis</i>
(00.0.000.5911)	<i>Acer negundo</i>	(00.0.000.5987)	<i>Salix lucida</i> ssp. <i>lasianдра</i>
(00.0.000.5912)	<i>Acer macrophyllum</i>	(00.0.000.5990)	Taxodiaceae (Conifers)
(00.0.000.5920)	Betulaceae; Cupressaceae (Conifers)	(00.0.000.5991)	<i>Sequoia sempervirens</i>
(00.0.000.5921)	<i>Alnus rhombifolia</i>		
(00.0.000.5922)	<i>Calocedrus decurrens</i>		
(00.0.000.5930)	Fagaceae		
(00.0.000.5931)	<i>Lithocarpus densiflorus</i>		
		(00.0.000.6000)	Monocot Vascular-Plant Dominance/Characteristic Types
		(00.0.000.6100)	Aquatic-Bed types
		(00.0.000.6110)	Alismataceae

TABLE 9. CONTINUED

(00.0.000.6111) <i>Alisma plantago-aquatica</i>	(00.0.000.6213) <i>Carex multicaulis</i>
(00.0.000.6112) <i>Echinodorus berteroi</i>	(00.0.000.6220) <i>Carex</i> (o-z)
(00.0.000.6120) Cyperaceae	(00.0.000.6221) <i>Carex obnupta</i>
(00.0.000.6121) <i>Eleocharis parvula</i>	(00.0.000.6222) <i>Carex praegracilis</i>
(00.0.000.6130) Hydrocharitaceae	(00.0.000.6223) <i>Carex nutkensis</i>
(00.0.000.6131) <i>Egeria densa</i>	(00.0.000.6224) <i>Carex senta</i>
(00.0.000.6132) <i>Elodea canadensis</i>	(00.0.000.6230) <i>Cyperus</i>
(00.0.000.6133) <i>Elodea nuttallii</i>	(00.0.000.6231) <i>Cyperus</i>
(00.0.000.6134) <i>Najas guadalupensis</i>	(00.0.000.6232) <i>Cyperus eragrostis</i>
(00.0.000.6135) <i>Najas marina</i>	(00.0.000.6233) <i>Cyperus involucreatus</i>
(00.0.000.6140) Lemnaceae	(00.0.000.6234) <i>Cyperus strigosus</i>
(00.0.000.6141) <i>Lemna gibba</i>	(00.0.000.6240) <i>Eleocharis</i>
(00.0.000.6142) <i>Lemna minor</i>	(00.0.000.6241) <i>Eleocharis acicularis</i>
(00.0.000.6143) <i>Lemna minuscula</i>	(00.0.000.6242) <i>Eleocharis macrostachya</i>
(00.0.000.6144) <i>Lemna trisulca</i>	(00.0.000.6243) <i>Eleocharis montevidensis</i>
(00.0.000.6145) <i>Spirodela polyrrhiza</i>	(00.0.000.6244) <i>Eleocharis parishii</i>
(00.0.000.6146) <i>Spirodela punctata</i>	(00.0.000.6250) <i>Scirpus</i>
(00.0.000.6147) <i>Wolffia</i> spp.	(00.0.000.6251) <i>Scirpus acutus</i>
(00.0.000.6148) <i>Wolffia</i> spp.	(00.0.000.6252) <i>Scirpus americanus</i>
(00.0.000.6150) Potamogetonaceae	(00.0.000.6253) <i>Scirpus californicus</i>
(00.0.000.6151) <i>Potamogeton foliosus</i>	(00.0.000.6254) <i>Scirpus maritimus</i>
(00.0.000.6152) <i>Potamogeton pectinatus</i>	(00.0.000.6255) <i>Scirpus microcarpus</i>
(00.0.000.6153) <i>Potamogeton</i>	(00.0.000.6256) <i>Scirpus pungens</i>
(00.0.000.6154) <i>Ruppia cirrhosa</i>	(00.0.000.6257) <i>Scirpus robustus</i>
(00.0.000.6155) <i>Ruppia maritima</i>	(00.0.000.6300) Persistent Emergent Types (Juncaceae—Rushes)
(00.0.000.6160) Zannichelliaceae	(00.0.000.6310) <i>Juncus</i> (a-n)
(00.0.000.6161) <i>Zannichellia palustris</i>	(00.0.000.6311) <i>Juncus acutus</i>
(00.0.000.6200) Persistent Emergent Types (Cyperaceae—Sedges)	(00.0.000.6312) <i>Juncus balticus</i>
(00.0.000.6210) <i>Carex</i> (a-m)	(00.0.000.6313) <i>Juncus dubius</i>
(00.0.000.6211) <i>Carex alma</i>	(00.0.000.6314) <i>Juncus effusus</i>
(00.0.000.6212) <i>Carex barbarae</i>	(00.0.000.6315) <i>Juncus falcatus</i>
	(00.0.000.6316) <i>Juncus macrophyllus</i>

TABLE 9. CONTINUED

(00.0.000.6317) <i>Juncus mexicanus</i>	(00.0.000.6510) <i>Echinochloa</i>
(00.0.000.6318) <i>Juncus lesueurii</i>	(00.0.000.6511) <i>Echinochloa crus-galli</i>
(00.0.000.6319) <i>Juncus longistylis</i>	(00.0.000.6520) <i>Elymus</i>
(00.0.000.6320) <i>Juncus</i> (o-z)	(00.0.000.6521) <i>Elymus glaucus</i>
(00.0.000.6321) <i>Juncus occidentalis</i>	(00.0.000.6522) <i>E. trachycaulus</i> ssp. <i>trachycaulus</i>
(00.0.000.6322) <i>Juncus oxymetris</i>	(00.0.000.6530) <i>Festuca</i>
(00.0.000.6323) <i>Juncus patens</i>	(00.0.000.6531) <i>Festuca arundinaceae</i>
(00.0.000.6324) <i>Juncus phaeocephalis</i>	(00.0.000.6532) <i>Festuca rubra</i>
(00.0.000.6325) <i>Juncus rugulosus</i>	(00.0.000.6540) <i>Glyceria</i>
(00.0.000.6326) <i>Juncus tenuis</i>	(00.0.000.6541) <i>Glyceria elata</i>
(00.0.000.6327) <i>Juncus xiphioides</i>	(00.0.000.6550) <i>Holcus</i>
(00.0.000.6400) Persistent Emergent Types (Poaceae A-E Grasses)	(00.0.000.6560) <i>Hordeum</i>
(00.0.000.6410) <i>Agrostis</i>	(00.0.000.6561) <i>Hordeum brachyantherum</i> ssp. <i>brachyantherum</i>
(00.0.000.6411) <i>Agrostis idahoensis</i>	(00.0.000.6562) <i>Hordeum brachyantherum</i> ssp. <i>californicum</i>
(00.0.000.6412) <i>Agrostis scabra</i>	(00.0.000.6570) <i>Leptochloa</i>
(00.0.000.6413) <i>Agrostis stolonifera</i>	(00.0.000.6571) <i>Leptochloa uninerva</i>
(00.0.000.6414) <i>Agrostis viridis</i>	(00.0.000.6580) <i>Leymus</i>
(00.0.000.6420) <i>Andropogon</i>	(00.0.000.6581) <i>Leymus condensatus</i>
(00.0.000.6421) <i>Andropogon virginica</i>	(00.0.000.6582) <i>Leymus triticoides</i>
(00.0.000.6430) <i>Arundo</i>	(00.0.000.6590) <i>Muhlenbergia</i>
(00.0.000.6431) <i>Arundo donax</i>	(00.0.000.6591) <i>Muhlenbergia andina</i>
(00.0.000.6440) <i>Cortaderia</i> spp.	(00.0.000.6592) <i>Muhlenbergia asperifolia</i>
(00.0.000.6450) <i>Cynodon</i>	(00.0.000.6593) <i>Muhlenbergia filiformis</i>
(00.0.000.6451) <i>Cynodon dactylon</i>	(00.0.000.6594) <i>Muhlenbergia rigens</i>
(00.0.000.6460) <i>Danthonia</i>	(00.0.000.6600) Persistent Emergent Types (Poaceae P-Z Grasses)
(00.0.000.6461) <i>D. californica</i> var. <i>americana</i>	(00.0.000.6610) <i>Paspalum</i>
(00.0.000.6462) <i>D. californica</i> var. <i>californica</i>	(00.0.000.6611) <i>Paspalum dilatatum</i>
(00.0.000.6470) <i>Deschampsia</i>	(00.0.000.6612) <i>Paspalum distichum</i>
(00.0.000.6471) <i>D. caespitosa</i> ssp. <i>caespitosa</i>	(00.0.000.6620) <i>Pennisetum</i>
(00.0.000.6480) <i>Distichlis</i>	
(00.0.000.6481) <i>Distichlis spicata</i>	
(00.0.000.6500) Persistent Emergent Types (Poaceae F-O Grasses)	

TABLE 9. CONTINUED

(00.0.000.6621) <i>Pennisetum clandestinum</i>	(00.0.000.6910) Alismataceae
(00.0.000.6630) <i>Phalaris</i>	(00.0.000.6911) <i>Alisma plantago-aquatica</i>
(00.0.000.6631) <i>Phalaris aquatica</i>	(00.0.000.6912) <i>Echinodorus berteroi</i>
(00.0.000.6640) <i>Pipathierum</i>	(00.0.000.6920) Cyperaceae
(00.0.000.6641) <i>Piptatherum miliaceum</i>	(00.0.000.6921) <i>Cyperus erythrorhizos</i>
(00.0.000.6650) <i>Poa</i>	(00.0.000.6922) <i>Cyperus odoratus</i>
(00.0.000.6651) <i>Poa pratensis</i>	(00.0.000.6923) <i>Cyperus squarrosus</i>
(00.0.000.6700) Persistent Emergent Types (Other Families)	(00.0.000.6924) <i>Cyperus</i> sp.
(00.0.000.6710) Liliaceae	(00.0.000.6925) <i>Eleocharis bella</i>
(00.0.000.6711) <i>Smilacina racemosa</i>	(00.0.000.6926) <i>Eleocharis macrostachya</i>
(00.0.000.6712) <i>Veratrum californicum</i>	(00.0.000.6930) Juncaceae
(00.0.000.6720) Sparganiaceae	(00.0.000.6931) <i>Juncus bufonius</i>
(00.0.000.6721) <i>Sparganium eurycarpum</i>	(00.0.000.6932) <i>Juncus xiphioides</i>
(00.0.000.6730) Typhaceae	(00.0.000.6940) Juncaginaceae
(00.0.000.6731) <i>Typha angustifolia</i>	(00.0.000.6941) <i>Lilaea scilloides</i>
(00.0.000.6732) <i>Typha domingensis</i>	(00.0.000.6950) Liliaceae
(00.0.000.6733) <i>Typha latifolia</i>	(00.0.000.6960) Orchidaceae
(00.0.000.6800) Nonpersistent Emergent Types (Poaceae)	(00.0.000.6961) <i>Epipactis gigantea</i>
(00.0.000.6810) <i>Hordeum</i>	(00.0.000.7000) Mixed-Vascular Plant Dominance/Characteristic Types
(00.0.000.6811) <i>Hordeum depressum</i>	Types
(00.0.000.6820) <i>Lolium</i>	(00.0.000.8000) Animal Dominance/Characteristic Types
(00.0.000.6821) <i>Lolium multiflorum</i>	(00.0.000.8100) Sponge Types
(00.0.000.6830) <i>Orcuttia</i>	(00.0.000.8200) Colanerate Types
(00.0.000.6831) <i>Orcuttia californica</i>	(00.0.000.8300) Mollusc Types
(00.0.000.6840) <i>Paspalum</i>	(00.0.000.8400) Annelid Types
(00.0.000.6841) <i>Paspalum distichum</i>	(00.0.000.8500) Crustacean Types
(00.0.000.6850) <i>Polypogon</i>	(00.0.000.8600) Insect Types
(00.0.000.6851) <i>Polypogon monspeltensis</i>	(00.0.000.8700) Echinoderm Types
(00.0.000.6860) <i>Vulpia</i>	(00.0.000.8800) Other Invertebrate Types
(00.0.000.6900) Nonpersistent Emergent Types (Other Families)	(00.0.000.8900) Vertebrate Types

WETLANDS OF CALIFORNIA, PART III: KEY TO AND
CATALOGUE OF WETLANDS OF THE CENTRAL AND
SOUTHERN CALIFORNIA COAST AND COASTAL
WATERSHEDS

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ABSTRACT

Wetlands of the central and southern California coast and coastal watersheds belong to one of five major systems: marine, estuarine, riverine, lacustrine, or palustrine. A methodology for classifying these wetlands has been developed by Ferren et al. (1996b) as a modification of the Cowardin et al. (1979) approach. Use of this methodology during a three-year study resulted in the identification of wetlands from this region based on various abiotic and biotic descriptors and arranged in a hierarchical and numerical classification. Dichotomous keys to the higher classification rankings of system, subsystem, and class provide a way to access a catalogue of example wetland types and key additional wetlands.

The classification of wetlands of California has been evaluated (Ferren et al. 1996a) and a new classification methodology (Ferren

1989; Ferren et al. 1995, 1996b) has been proposed for use on wetlands of the central and southern California coast and coastal watersheds. This methodology is a modification of the Cowardin et al. (1979) approach, but includes a hierarchical, numerical approach that focuses on the richness of the region's physical attributes as well as its biological resources. One important addition in Ferren et al. (1996b) is a classification descriptor for hydrogeomorphic units that increases the usefulness of wetland identification because specific habitat information is included in the classification process and the wetland nomenclature.

Application of the Ferren et al. methodology has resulted in the compilation of a catalogue of wetlands from each of the five systems of wetlands and deepwater habitats (marine, estuarine, riverine, lacustrine, palustrine) that occur in the study region. This portion of California has been described in Ferren et al. (1996a, b) and extends from the Carmel River Watershed in Monterey County south to portions of the Tijuana River Watershed in San Diego County at the boundary with Mexico. The purpose of this third part of the three-part treatise by Ferren et al. is to demonstrate an application of the new classification technique. The study from which the field information was obtained was funded by the United States Environmental Protection Agency, Region IX, as part of a classification and inventory of the wetlands of the region.

In addition to the catalogue of wetlands, we also provide a key to the wetland systems, subsystems, and classes as a guide to the arrangement of the catalogue and as an approach to wetland identification to the class level that augments the classification methodology presented in Part II (Ferren et al. 1996b). A glossary to many of the terms used herein also is provided in Ferren et al. (1996b).

THE KEYS AND CATALOGUE

Keys to wetlands of the central and southern California coast and coastal watersheds are a modification of one developed by Cowardin et al. (1979) to accommodate the various abiotic and biota features of the region's wetland types. The keys (Appendix I) serve as a vehicle to: (1) locate in the catalogue (Appendix II) wetlands identified previously (see Ferren et al. 1996a, b); and (2) identify to class level additional wetlands observed in subsequent studies. The latter activity can be used in conjunction with the classification methodology presented in Ferren et al. (1996b).

The following steps provide access to the wetlands listed in the catalogue:

1. Use the "Key to the Wetland Systems" in Appendix I to determine the system of wetlands and deepwater habitats that (a) you desire to examine or (b) you want to identify.

2. Having completed the classification to a particular system, use the individual keys to classification rankings within each of the five systems to determine the subsystem and class of the wetland.
3. Once the class and subclass of a wetland have been determined, proceed to the appropriate portion of the catalogue (Appendix II) for the system, subsystem, class, and subclass within which you wish to locate an example wetland, or to which the classified wetland belongs.
4. Example wetlands occur within the ranking of subclass. All wetlands are organized according to strict numerical order, reflecting the various descriptor states derived from the classification tables provided in Part II (Ferren et al. 1996b).
5. For clarification on the nature of the five wetland systems, a brief discussion for each system precedes the listing of wetland types in the catalogue. Example wetland types also are illustrated (Figs. 1–7).

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APPENDIX I: KEY TO THE WETLANDS

To facilitate the identification and classification of wetlands of the central and southern California coast and coastal watersheds, we have constructed dichotomous keys for the systems, subsystems and classes of wetlands. These keys are modifications of those presented by Cowardin et al. (1979). Keys to several subsystems that are deepwater habitats rather than wetlands are included for the purpose of comparison. Various classes for some systems are not included here because they do not occur in coastal central and southern California. Conversely, we have expanded the classification and accompanying keys when wetlands have been found to occur in California that are not represented in the Cowardin et al. hierarchy. Refer to "Wetlands of California, Part II" (Ferren et al. 1996b) for an explanation of the methodology used to identify wetlands listed herein.

KEY TO THE WETLAND SYSTEMS

- Water regime of habitats is influenced (at least one episode seasonally or enough to establish functions of system related habitats) by oceanic tides; salinity due to ocean-derived salts (i.e., ocean-derived sodium chloride) is 0.5 ppt (parts per thousand) or greater:
- Habitats are not obstructed, or have minor obstruction, to the open ocean; halinity (concentration of sodium chloride) usually euhaline or temporarily or seasonally less near the mouths of rivers. **MARINE SYSTEM (1)**
 - Habitats are semi-enclosed by land, but are open to, partly obstructed from, or have sporadic access to the ocean and oceanic tides; halinity can vary widely within or between examples because of evaporation or because of mixing with fresh water from runoff from land. **ESTUARINE SYSTEM (2)**
- Water regime is not influenced by oceanic tides, or if water regime is influenced by ocean tides the salinity is less than 0.5 ppt (i.e., the approximate background salinity of runoff from watersheds):
- Emergent mosses, persistent emergent vascular plants, shrubs, or trees cover 30% or more of the habitat; if nonpersistent emergents, other non-plant organisms, or no organisms dominate, the wetland is not a riverine nor a lacustrine habitat. **PALUSTRINE SYSTEM (5)**
 - Emergent mosses, persistent emergent vascular plants, shrubs, or trees cover less than 30% of the substrate, but nonpersistent emergents may be widespread seasonally:

- Habitat situated in a channel or along a channel shore; water when present is flowing (e.g., streams and rivers and the vegetation when present is non-persistent). **RIVERINE SYSTEM (3)**
- Habitat situated in a basin or on level but sloping ground; water when present is usually not flowing, but if in a channel the vegetation is persistent or nonpersistent:
- Habitat area is generally 8 hectares (20 acres) or greater (e.g., large lakes). **LACUSTRINE SYSTEM (4)**
- Habitat area is less than 8 hectares (e.g., ponds and pools):
- Waved-formed or bedrock-shoreline habitat feature is present, or water depth is 2 meters (6 feet) or greater at low water. **LACUSTRINE SYSTEM (4)**
- No wave-formed or bedrock-shoreline habitat feature is present, and water is less than 2 meters deep. **PALUSTRINE SYSTEM (5)**

1. KEY TO THE MARINE SUBSYSTEMS AND CLASSES

- Marine substrate is continuously submerged (i.e., subtidal habitats, which are not included in this volume). **DEEPWATER HABITAT SUBSYSTEM**
- During the growing season of most years, cover by vegetation is less than 30%:
- Substrate formed by the colonization of sedentary (i.e., attached) invertebrates (e.g., corals, tube worms). **REEF CLASS**
- Substrate composed of rock or sediment; often colonized by invertebrates but not formed of sedentary types:
- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. **ROCK BOTTOM CLASS**
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% areal cover of bedrock, boulders, or rubble. **UNCONSOLIDATED BOTTOM CLASS**
- During the growing season of most years, percentage of habitat covered by vegetation (e.g., algae and marine aquatic flowering plants such as *Zostera*) is 30% or greater. **AQUATIC BED CLASS**
- Marine substrate is at least irregularly exposed and flooded by oceanic tides, or receives wave splash. **INTERTIDAL SUBSYSTEM**
- During the growing season of most years, cover by vegetation (algae and marine flowering plants such as *Phyllospadix*) is greater than 30%. **AQUATIC BED CLASS**
- During the growing season of most years, cover by vegetation is less than 30%:
- Substrate is formed by the colonization of sedentary invertebrates (e.g., mussels). **REEF CLASS**
- Substrate composed of rock or sediment; often inhabited by invertebrates but not formed by the colonization of sedentary types:
- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. **ROCKY SHORE CLASS**
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. **UNCONSOLIDATED SHORE CLASS**

2. KEY TO THE ESTUARINE SUBSYSTEMS AND CLASSES

- Estuarine substrate is continuously submerged (i.e., subtidal habitats, which are not included in this volume, except where emergent species dominate in subtidal channels). **DEEPWATER HABITAT SUBSYSTEM**
- During the growing season of most years, cover by vegetation is less than 30%:
- Substrate formed by the colonization of sedentary (i.e., attached) invertebrates (e.g., mussels, oysters). **REEF CLASS**
- Substrate composed of rock or sediment; often colonized by invertebrates but not formed of sedentary types:

- Substrate of bedrock, boulders, stones, or combinations of these covering 70% or more of the habitat. **ROCK BOTTOM CLASS**
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 75% cover of bedrock, boulders, or rubble.
 **UNCONSOLIDATED BOTTOM CLASS**
- During the growing season of most years, percentage of habitat covered by vegetation (e.g., algae and estuarine aquatic flowering plants such as *Ruppia*) is 30% or greater. **AQUATIC BED CLASS**
- Estuarine substrate is at least irregularly exposed and flooded by oceanic tides.
 **INTERTIDAL SUBSYSTEM**
- During the growing season of most years, cover by vegetation is less than 30%:
 Substrate formed by the colonization of sedentary invertebrates (e.g., mussels).
 **REEF CLASS**
- Substrate composed of rock or sediment; often inhabited by invertebrates but not formed by the colonization of sedentary types:
 Habitat contained within a channel bed. **STREAMBED CLASS**
- Habitat along a shoreline:
 Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. **ROCKY SHORE CLASS**
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble.
 **UNCONSOLIDATED SHORE CLASS**
- During the growing season of most years, percentage of area covered by vegetation (e.g., algae, aquatic and emergent vascular plants, or shrubs) is 30% or greater:
 Vegetation composed predominantly by macrophytic algae.
 **AQUATIC BED CLASS**
- Vegetation composed predominantly of vascular species:
 Vegetation herbaceous:
 Vegetation tidally-submerged rooted-aquatic, floating-leaved, or floating types (e.g., *Ruppia*, *Potamogeton*, *Lemna*). **AQUATIC BED CLASS**
- Vegetation emergent types:
 During the growing season of most years, the vegetation is composed largely of pioneering annuals and seedlings of perennials that occur at the time of substrate exposure:
 Vegetation occurs on unconsolidated bottom or bed habitats.
 **UNCONSOLIDATED BOTTOM (VEGETATED) CLASS**
- Vegetation occurs on unconsolidated shore or bank habitats.
 **UNCONSOLIDATED SHORE (VEGETATED) CLASS**
- During most years, the vegetation is composed largely of persistent species that dominant the substrate (e.g., *Salicornia*, *Scirpus*, *Spartina*).
 **EMERGENT WETLAND CLASS**

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FIG. 1. Marine-Intertidal Rocky-Shore (Bedrock) Regularly-Flooded Euhaline Hogback-Ridge Wetland. Santa Barbara Co., Carpinteria view from Carpinteria Bluffs. Wetland Type No.: 11.141(13.4.362.2262).

FIG. 2. Estuarine-Intertidal Emergent-Persistent (*Scirpus americanus*) Irregularly-Exposed Mixohaline Low-Brackish Fringe-Marsh Wetland (left center). San Luis Obispo Co., Morro Bay, Los Osos, Los Osos Creek. View northward across Los Osos Creek toward brackish fringe-marsh in a low flooded area supported by a seep from adjacent palustrine forested wetland (left center) but flooded by tidal water irregularly. Wetland Type No.: 21.241(12.5.821/831.6231).



Vegetation shrubs or trees:

Dominant plants less than 5 meters (15 feet) tall and composed of shrubs or stunted trees. SCRUB/SHRUB WETLAND CLASS

Dominant plants 5 meters tall or taller (does not occur in Calif.). FORESTED WETLAND CLASS

3. KEY TO THE RIVERINE SUBSYSTEMS AND CLASSES

Water gradient is low and under the influence of oceanic tides (there are no examples of this subsystem in the study area, but there are in large river systems to the north). TIDAL SUBSYSTEM

Substrates are continuously submerged (i.e., subtidal habitats):

During the growing season of most years, cover by vegetation is less than 30%:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED BOTTOM CLASS

During the growing season of most years, percentage cover by vegetation (e.g.,

algae and submerged aquatic vascular plants such as *Potamogeton*, *Zannichellia*, *Elodea*) is 30% or greater. AQUATIC BED CLASS

Substrates are at least irregularly exposed and flooded by oceanic tides (i.e., intertidal habitats):

During the growing season of most years, cover by vegetation is less than 30%:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the substrate. ROCKY SHORE CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED SHORE CLASS

During the growing season of most years, percentage of area covered by her-

baceous vegetation (e.g., algae, aquatic and emergent vascular plants) is 30% or greater:

Vegetation tidally-submerged rooted aquatic, floating-leaved, or floating types (e.g., *Zannichellia*, *Najas*, *Lemna*). AQUATIC BED CLASS

Vegetation intertidal, non-persistent emergent types (e.g., *Sagittaria*, *Isoetes*, *Elatine*). EMERGENT WETLAND CLASS

Water gradient is low, high, or intermittent, but there is no influence from oceanic tides:

Water flows in the channel for only part of the year; when water is not flowing surface water may be absent, or water may occur as isolated pools. INTERMITTENT SUBSYSTEMS

Channel occurs within a relatively high gradient (4-10%), where flows are often

flashy and closely tied to specific rainfall events, and is entrenched with steep banks and poorly defined floodplains. UPPER INTERMITTENT SUBSYSTEM

During the growing season of most years, cover by vegetation is less than 30%. RIVERBED OR STREAMBED CLASS

During the growing season of most years, percentage of area covered by vegetation is 30% or greater, composed largely of pioneering annuals and seedlings of perennials that occur at the time of substrate exposure. RIVERBED OR STREAMBED (VEGETATED) CLASS

Channel occurs within a depositional landform, with a moderate gradient (1.5-4%) and low sinuosity, and is slightly entrenched. MID INTERMITTENT SUBSYSTEM

During the growing season of most years, cover by vegetation is less than 30%. RIVERBED OR STREAMBED CLASS

During the growing season of most years, cover by vegetation is 30% or greater, composed largely of pioneering annuals and seedlings of perennials that occur at the time of substrate exposure.

. RIVERBED OR STREAMBED (VEGETATED) CLASS

Channel occurs within a depositional landform with a low gradient (1.5% or less), where the floodplain is moderate to well developed, the valley only slightly confined, and the channel only slightly entrenched.

. **LOWER INTERMITTENT SUBSYSTEM**

During the growing season of most years, cover by vegetation is less than 30%. RIVERBED OR STREAMBED CLASS

During the growing season of most years, cover by vegetation is 30% or greater, composed largely of pioneering annuals and seedlings of perennials that occur at the time of substrate exposure.

. RIVERBED OR STREAMBED (VEGETATED) CLASS

Some water flows in the channel throughout the year.

. **PERENNIAL SUBSYSTEMS**

Channel gradient is high (4–10%) and water velocity is at least seasonally or temporarily fast; substrates consist of rock, cobbles, or gravel with patches of sand; a floodplain is usually lacking or poorly developed.

. **UPPER PERENNIAL SUBSYSTEM**

During the growing season of most years, cover by vegetation is less than 30%:

Water regimes include permanently or semi-permanently flooded and intermittently exposed; substrate is usually not a soil; bottoms and beds:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. **ROCK BOTTOM CLASS**

Substrate of sand, gravel, or cobbles with less than 70% areal cover of bedrock, boulders, or rubble. **UNCONSOLIDATED BOTTOM CLASS**

Water regimes include seasonally flooded, temporarily flooded, intermittently flooded, saturated, or artificially flooded; shores and banks:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. **ROCKY SHORE CLASS**

Substrate of sand, gravel, or cobble with less than 70% cover of bedrock, boulders, or rubble. **UNCONSOLIDATED SHORE CLASS**

During the growing season of most years, cover by herbaceous vegetation is 30% or greater:

Vegetation generally permanently-flooded algae, rooted aquatic, floating-leaved, or floating types. **AQUATIC BED CLASS**

Vegetation dominated by nonpersistent emergent types:

During the growing season of most years, vegetation is composed largely of nonpersistent pioneering annuals, nonpersistent perennials, and seedlings of perennials that occur at the time of substrate exposure:

Vegetation occurs on exposed, unconsolidated bottom or bed habitats. **UNCONSOLIDATED BOTTOM (VEGETATED) CLASS**

Vegetation occurs on exposed, unconsolidated shore or bank habitats. **UNCONSOLIDATED SHORE (VEGETATED) CLASS**

During most years, vegetation is composed largely of nonpersistent perennials that dominate the substrate or flooded riverine habitat.

. **EMERGENT WETLAND CLASS**

Channel gradient is moderate (1.5–4%) and sinuosity low, and occurs in a depositional and form; substrate is variable but dominated by cobbles, gravel, and sand. **MID PERENNIAL SUBSYSTEM**

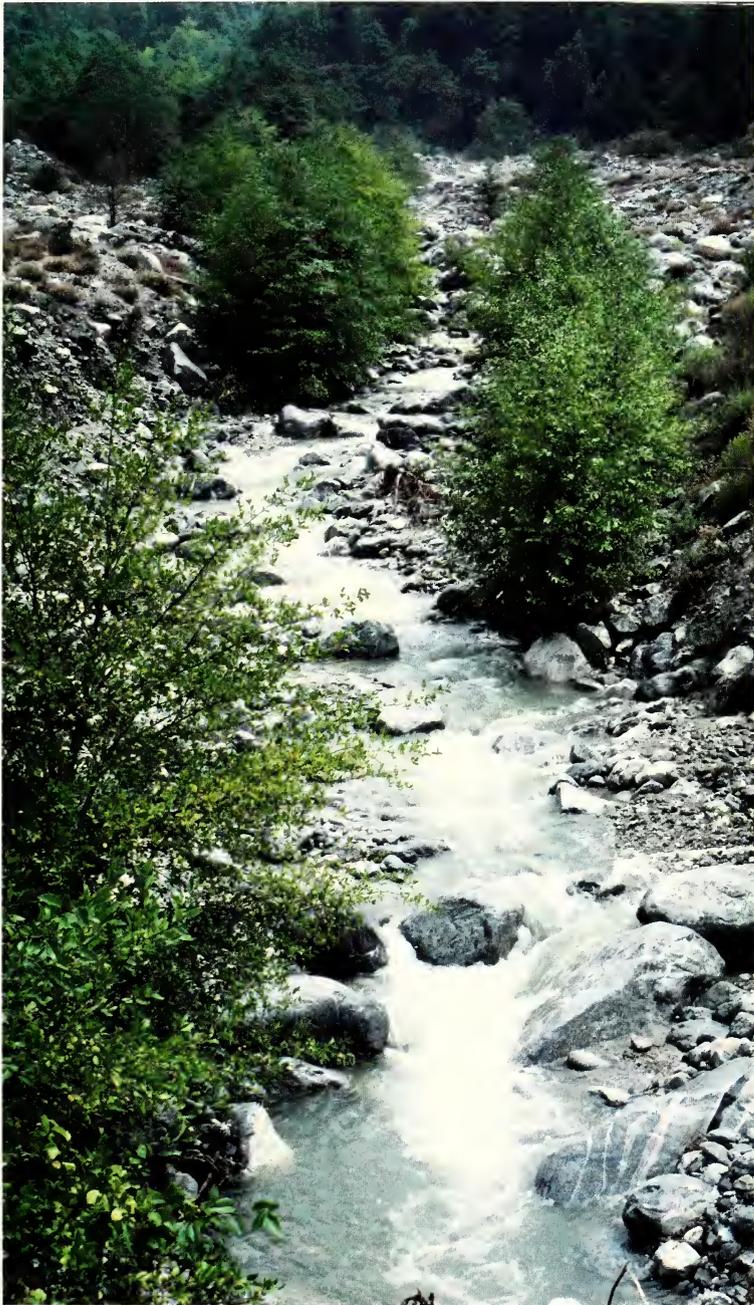
During the growing season of most years, areal cover by vegetation is less than 30%:

Water regimes include permanently or semi-permanently flooded and intermittently exposed; substrate is usually not a soil; bottoms and beds:

- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED BOTTOM CLASS
- Water regimes include seasonally flooded, temporarily flooded, intermittently flooded, saturated, or artificially flooded; shores or banks:
- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCKY SHORE CLASS
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED SHORE CLASS
- During the growing season of most years, cover by herbaceous vegetation (e.g., algae, submerged aquatic and nonpersistent emergent vascular plants) is greater than 30%:
- Vegetation generally permanently-flooded algae, rooted aquatic, floating-leaved, or floating types (e.g., *Potamogeton*, *Lemna*). AQUATIC BED CLASS
- Vegetation dominated by nonpersistent emergent types:
- During the growing season of most years, vegetation is composed largely of nonpersistent pioneering annuals, nonpersistent perennials, and seedlings of perennials that occur at the time of substrate exposure:
- Vegetation occurs on exposed, unconsolidated bottom or bed habitats. UNCONSOLIDATED BOTTOM (VEGETATED) CLASS
- Vegetation occurs on exposed, unconsolidated shore or bank habitats. UNCONSOLIDATED SHORE (VEGETATED) CLASS
- During most years, vegetation is composed largely of nonpersistent perennials that dominate the substrate or flooded riverine habitat. EMERGENT WETLAND CLASS
- Channel gradient (1.5% or less) and water velocity are low; substrates are mostly sand and mud; a floodplain is often well developed. LOWER PERENNIAL SUBSYSTEM
- During the growing season of most years, cover by vegetation is less than 30%:
- Water regimes include permanently or semi-permanently flooded and intermittently exposed; substrate is usually not a soil; bottoms and beds:
- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED BOTTOM CLASS
- Water regimes include seasonally flooded, temporarily flooded, intermittently flooded, saturated, or artificially flooded; shores and banks:
- Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCKY SHORE CLASS
- Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED SHORE CLASS

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FIG. 3. Riverine Upper-Perennial Rock-Bottom (Boulder) Permanently-Flooded Montane-Stream-Channel Wetland. San Bernardino Co., San Bernardino National Forest, San Gorgonio District, Vivian Creek. View upstream. Wetland Type No.: 35.112(21.1.211.1500).



During the growing season of most years, cover by herbaceous vegetation (e.g., algae, submerged aquatic and nonpersistent emergent vascular plants) is greater than 30%:

Vegetation generally permanently-flooded algae, rooted aquatic, floating-leaved, or floating types (e.g., *Potamogeton*, *Lemna*). AQUATIC BED CLASS

Vegetation dominated by nonpersistent emergent types:

During the growing season of most years, vegetation is composed largely of nonpersistent pioneering annuals, nonpersistent perennials, and seedlings of perennials that occur at the time of substrate exposure:

Vegetation occurs on exposed, unconsolidated bottom or bed habitats. UNCONSOLIDATED BOTTOM (VEGETATED) CLASS

Vegetation occurs on exposed, unconsolidated shore or bank habitats. UNCONSOLIDATED SHORE (VEGETATED) CLASS

During most years, vegetation is composed largely of nonpersistent perennials that dominate the substrate or flooded riverine habitat.

. EMERGENT WETLAND CLASS

4. KEY TO THE LACUSTRINE SUBSYSTEMS AND CLASSES

All habitats (i.e., deepwater habitats) in a lake extending below a depth of 2 meters (6.6 feet) below low water or below the maximum extent of nonpersistent emergent plants, if these grow below 2 meters (all such habitats are excluded from this volume, but are included in the key for the purpose of comparison). LIMNETIC SUBSYSTEM

During the growing season of most years, cover by vegetation (i.e., submerged rooted-vascular, floating-leaved, and floating such as *Najas*, *Potamogeton*, *Myriophyllum*) is 30% or greater. AQUATIC BED CLASS

During the growing season of most years, cover by vegetation is less than 30%:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% areal cover of bedrock, boulders, or rubble. UNCONSOLIDATED BOTTOM CLASS

All habitats (i.e., wetlands) in a lake extending from the shoreline boundary of the system to a depth of 6 meters (6.6 feet) below low water or to the maximum extent of nonpersistent emergent plants, if these grow at depths greater than 2 meters. LITTORAL SUBSYSTEM

During the growing season of most years, cover by vegetation is less than 30%:

Water regimes include permanently or semi-permanently flooded and intermittently exposed; substrate is usually not a soil:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED BOTTOM CLASS

Water regimes include seasonally flooded, temporarily flooded, intermittently flooded, saturated, or artificially flooded:

Substrate of bedrock, boulders, rubble of combinations of these covering 70% or more of the habitat. ROCKY SHORE CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble. UNCONSOLIDATED SHORE CLASS

During the growing season of most years, cover by herbaceous vegetation (e.g., algae, submerged aquatic and nonpersistent emergent vascular plants) is 30% or greater:

Vegetation generally consists of algae, submerged rooted aquatic, floating-leaved, or floating types (e.g., *Najas*, *Potamogeton*, *Myriophyllum*). . . .
 AQUATIC BED CLASS

Vegetation dominated by nonpersistent emergent types:

During the growing season of most years, vegetation is composed largely of nonpersistent pioneering annuals, nonpersistent perennials, and seedlings of perennials that occur at the time of substrate exposure:

Vegetation occurs on exposed, unconsolidated bottom or bed habitats. . . .
 UNCONSOLIDATED BOTTOM (VEGETATED) CLASS

Vegetation occurs on exposed, unconsolidated shore or bank habitats. . . .
 UNCONSOLIDATED SHORE (VEGETATED) CLASS

During most years, vegetation is composed largely of nonpersistent perennials that dominate the substrate or flooded littoral habitat.
 EMERGENT WETLAND CLASS

5. KEY TO THE PALUSTRINE CLASSES

(there are no subsystems)

During the growing season of most years, cover by vegetation is less than 30%:

Water regimes include seasonally flooded, temporarily flooded, saturated, or artificially flooded; substrate is often a soil. . . . UNCONSOLIDATED SHORE CLASS

Water regimes include permanently or semipermanently flooded or intermittently exposed; substrate is usually not a soil:

Substrate of bedrock, boulders, rubble, or combinations of these covering 70% or more of the habitat. ROCK BOTTOM CLASS

Substrate of organic material, mud, sand, gravel, or cobbles with less than 70% cover of bedrock, boulders, or rubble.
 UNCONSOLIDATED BOTTOM CLASS

During the growing season of most years, cover by vegetation is 30% or greater:

Vegetation composed predominantly of nonvascular plants (e.g., algae or bryophytes):

Vegetation predominantly macrophytic algae, mosses, or lichens in water or the splash zones of shores. AQUATIC BED CLASS

Vegetation predominantly mosses or lichens usually growing on organic soils and always outside the splash zone of shores.
 MOSS-LICHEN WETLAND CLASS

Vegetation composed predominantly of vascular plant species:

Vegetation herbaceous:

Vegetation generally consists of submerged rooted aquatic, floating-leaved or floating types (e.g., *Najas*, *Potamogeton*, *Myriophyllum*).
 AQUATIC BED CLASS

Vegetation dominated by emergent types:

Vegetation composed of pioneering annuals, nonpersistent perennials, or seedlings of perennials that often are not hydrophytes and occur only at the time of substrate exposure:

Vegetation occurs on exposed, unconsolidated bottom or bed habitats.
 UNCONSOLIDATED BOTTOM (VEGETATED) CLASS

Vegetation occurs on exposed, unconsolidated shore or bank habitats.
 UNCONSOLIDATED SHORE (VEGETATED) CLASS

Vegetation predominantly perennials or nonpersistent hydrophyte species occurring in natural, restored, or recreated habitats.
 EMERGENT WETLAND CLASS

Vegetation shrubs or trees:

Dominant plants generally less than 5 meters (15 feet) tall.
 SCRUB-SHRUB WETLAND CLASS

Dominant plants generally 5 meters (15 feet) tall or taller.
 FORESTED WETLAND CLASS

APPENDIX II: CATALOGUE OF WETLAND TYPES

This catalogue includes example wetland types identified during the course of this study. The catalogue is arranged to the level of subclass. Within the subclasses, the wetlands are listed according to the hierarchical wetland type number. There was no attempt on the part of the authors to include all types of wetlands from each level of the hierarchy. Instead, we include examples of types from various classes, subclasses, water regimes, chemistry, hydrogeomorphic units, and dominance types. Examples of these wetlands are illustrated for each of the five wetland systems: Marine (Fig. 1, pg. 189), Estuarine (Fig. 2, pg. 189), Riverine (Fig. 3, pg. 193), Lacustrine (Fig. 4, pg. 197), and Palustrine (Figs. 5, pg. 197, 6, pg. 201, and 7, pg. 201).

1. MARINE WETLANDS

Marine wetlands of the study region occur within the Californian Marine and Estuary Province of North America, which extends from Mendocino County southward along the coast of Baja California, Mexico, and has a shoreline strongly influenced by coastal mountains and the coasts are rocky (Cowardin et al. 1979). In this province, freshwater is limited, the climate is Mediterranean and is influenced by the Humboldt Current, and the tidal range is moderate (Cowardin et al. 1979). Point Conception in Santa Barbara County is the demarcation between northern and southern California biogeographic areas that are reflected in the marine wetlands as well as the terrestrial flora and fauna (see Lafferty et al. 1995).

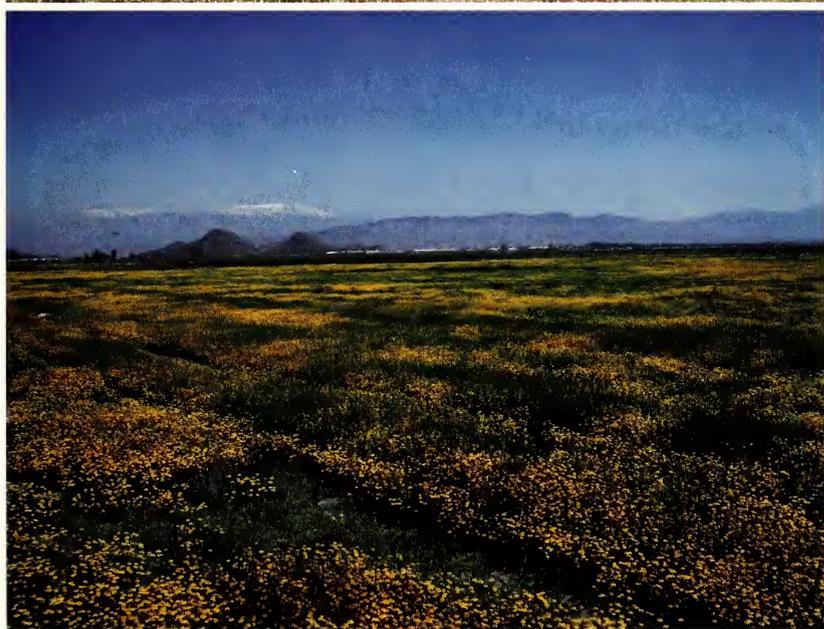
The coast of California extends along a linear length approximately 1100 miles. Although the study region covers about 400 linear miles of coastline, it is longer and richer in marine wetland types because of its fractal character. This length is studded with a rich abundance and diversity of physical attributes, renown in their scenic beauty, and unique in geologic origin. It is home to a varied and fascinating assemblage of plants and animals.

The Marine System (System No. 10.000) includes two subsystems: (1) Subsystem Intertidal (i.e., wetlands; No. 11.000); and (2) Subsystem Subtidal (i.e., deepwater habitats; No. 12.000). Cowardin et al. (1979, p. 4) define the system as follows:

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FIG. 4. Lacustrine-Littoral Unconsolidated-Shore-Vegetated (Mixed-Fines, Mixed Vascular-Plants) Seasonally-Flooded Montane-Reservoir-Shore Wetland. San Bernardino Co., San Bernardino Mountains, Big Bear Lake, Grout Bay. View northeastward from unconsolidated-shore (sand and mixed-fines) dominated by nonpersistent emergent vegetation to intermittently-exposed and permanently-flooded unconsolidated-bottom habitats. Wetland Type No.: 41.155(24.1.334.1700,7000).

FIG. 5. Palustrine Emergent-Nonpersistent (*Lasthenia californica*) Seasonally-Flooded Alkali Vernal-Plain Wetland. Riverside Co., Old Salt Creek Drainage west of Hemet, Florida Ave. and Warren Rd. View across extensive vernal plain, eastward toward the San Jacinto Mountains. Small basins forming vernal pools with different dominance types occur throughout the plain. As shown here, the disked, desiccated plain is dominated by *Lasthenia californica*, but may appear with different dominant plant species depending on the time of year, amount of rainfall in a particular year, proximity to local vernal pool areas, and degree of disturbance. Wetland Type No.: 50.242(24.3.523.5532).



The Marine System . . . consists of the open ocean overlying the continental shelf and its associated high-energy coastline. Marine habitats are exposed to the waves and currents of the open ocean and the water regimes are determined primarily by the ebb and flow of oceanic tides. Salinities exceed 30 ppt [parts per thousand], with little or no dilution except outside the mouths of estuaries. Shallow coastal indentations or bays without appreciable freshwater inflow, and coasts with exposed rocky islands that provide the mainland with little or no shelter from wind and waves, are also considered part of the Marine System because they generally support typical marine biota.

Cowardin et al. (1979) also have provided a description of the limits of this system. As a general rule, the Marine System extends from the outer edge of the continental shelf (=deepwater habitat) to one of several possible shoreline features. These features include the landward limit of tidal inundation defined as the extreme high water of spring tides (including the splash zone from breaking waves); the seaward limit of wetland emergents, shrubs, or trees; and the seaward limit of the Estuarine System.

10.000 SYSTEM MARINE

11.000 SUBSYSTEM INTERTIDAL

11.140 CLASS ROCKY-SHORE

11.141 SUBCLASS BEDROCK

Wetland Type No.: 11.141(12.4.181.2472)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) IRREGULARLY-EXPOSED LARGE-TIDE-POOL WETLAND. San Diego Co., Ocean Beach, Sunset Cliffs Park on Sunset Cliffs Blvd. at Ladera St.

Wetland Type No.: 11.141(12.4.182.2472)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) IRREGULARLY-EXPOSED SMALL-TIDE-POOL WETLAND. San Diego Co., Ocean Beach, Sunset Cliffs Park on Sunset Cliffs Blvd. at Ladera St.

Wetland Type No.: 11.141(13.4.211.2472)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LARGE-SURGE-CHANNEL WETLAND. Los Angeles Co., Palos Verdes Peninsula, San Pedro, White Point, end of Kay Fiorentino Dr.

Wetland Type No.: 11.141(13.4.261.2472)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LARGE-FISSURE WETLAND. Los Angeles Co., Palos Verdes Peninsula, San Pedro, White Point, end of Kay Fiorentino Dr.

Wetland Type No.: 11.141(13.4.271.2472)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LARGE-SEA-CAVE WETLAND. Santa Barbara Co., north side of Santa Cruz Island, Painted Cave.

Wetland Type No.: 11.141(13.4.341.8212)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED OCEAN-BENCH WETLAND. Ventura Co., Point Mugu State Park, Sycamore Cove, 9000 Pacific Coast Highway.

Wetland Type No.: 11.141(13.4.341.8331)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED OCEAN-BENCH WETLAND. Santa Barbara Co., Carpinteria, Chevron Pt.

Wetland Type No.: 11.141(13.4.342.2262)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-

FLOODED EXPOSED-BAY-BENCH WETLAND. Santa Barbara Co., Goleta, UCSB, between Campus Point and Goleta Pier.

Wetland Type No.: 11.141(13.4.361.8524)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LEDGE WETLAND. Los Angeles Co., Malibu, Leo Carrillo State Beach, 36000 Pacific Coast Hwy.

Wetland Type No.: 11.141(13.4.362.2262)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED HOGBACK-RIDGE WETLAND. Santa Barbara Co., Carpinteria Bluffs. (Fig. 1, pg. 189).

Wetland Type No.: 11.141(13.4.441.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LARGE-SEA-STACK WETLAND. Santa Barbara Co., south side of Santa Cruz Island, Willows Anchorage.

Wetland Type No.: 11.141(13.4.611.1300)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED LARGE-HEADLAND WETLAND. Los Angeles Co., Palos Verdes Peninsula, Resort Point.

Wetland Type No.: 11.141(13.4.612.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED SMALL-HEADLAND WETLAND. Santa Barbara Co., Goleta, east of Goleta Pier.

Wetland Type No.: 11.141(13.4.621.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED CLIFF WETLAND. Ventura Co., East Anacapa Island.

Wetland Type No.: 11.141(13.4.912.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED SEA-WALL WETLAND. San Diego Co., La Jolla, Marine Room, south of La Jolla Shores Beach.

Wetland Type No.: 11.141(13.4.912.2262)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED SEA-WALL WETLAND. Ventura Co., southeast from Faria County Park, Solimar Beach.

Wetland Type No.: 11.141(13.4.916.8331)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) REGULARLY-FLOODED PILING WETLAND. Orange Co., South Laguna, 31000 block of Pacific Coast Hwy., Aliso Pier.

Wetland Type No.: 11.141(14.4.451.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) IRREGULARLY-FLOODED LARGE-ISLET WETLAND. San Diego Co., Ocean Beach, on Sunset Cliffs Blvd. between Point Loma Ave. and Ladera St.

Wetland Type No.: 11.141(14.4.452.1200)

MARINE-INTERTIDAL ROCKY-SHORE (BEDROCK) IRREGULARLY-FLOODED SMALL-ISLET WETLAND. Santa Barbara Co., Goleta, More Mesa Beach.

10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.140 CLASS ROCKY-SHORE
11.142 SUBCLASS RUBBLE

Wetland Type No.: 11.142(12.4.161.1100)

MARINE-INTERTIDAL ROCKY-SHORE (RUBBLE) IRREGULARLY-EXPOSED LARGE-PORT WETLAND. Ventura Co., Port Hueneme, W. end of Hueneme Rd.

Wetland Type No.: 11.142(12.4.161.1100)

MARINE-INTERTIDAL ROCKY-SHORE (RUBBLE) IRREGULARLY-EXPOSED LARGE-HARBOR WETLAND. Orange Co., Dana Point, off Pacific Coast Hwy., 7.5 mi. S.E. of Laguna Beach.

Wetland Type No.: 11.142(12.4.311.2231)

MARINE-INTERTIDAL ROCKY-SHORE (RUBBLE) IRREGULARLY-EXPOSED OCEAN-SHORE WETLAND. Ventura Co., Old Pacific Coast Hwy. at Hwy. 101, Emma Wood State Beach.

Wetland Type No.: 11.142(13.4.920.1300)

MARINE-INTERTIDAL ROCKY-SHORE (RUBBLE) REGULARLY-FLOODED SEA-WALL WETLAND. Santa Barbara Co., Carpinteria, foot of Ash Ave., Carpinteria Beach.

* * * *

10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.150 CLASS UNCONSOLIDATED-SHORE
11.151 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 11.151(12.4.311.2231)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (COBBLE-GRAVEL) IRREGULARLY-EXPOSED OCEAN-SHORE WETLAND. Ventura Co., off old Pacific Coast Hwy., just south of Seacliff, Hobson County Park.

Wetland Type No.: 11.151(13.4.311.1400)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (COBBLE-GRAVEL) REGULARLY-EXPOSED OCEAN-SHORE WETLAND. San Diego Co., Carlsbad, West of Batiquitos Lagoon, South Carlsbad State Beach.

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FIG. 6. Palustrine Scrub-Shrub Broadleaved-Evergreen (*Pluchea sericea*) Phreatophytic River-Terrace Wetland. San Luis Obispo Co., Cuyama River Valley. View southeastward across terrace and adjacent river-channel toward the Sierra Madre Mountains. *Pluchea sericea* forms an extensive scrub-shrub wetland on alluvial soils deposited in the lower valley, up-river from the Cuyama River Gorge. Wetland Type No.: 50.253(29.1.561.5627).

FIG. 7. Palustrine Forested Broadleaved-Evergreen (*Myrica californica*) Permanently-Saturated Slope-Seep Wetland. San Luis Obispo Co., Morro Bay, Los Osos Creek, Los Osos. View southeastward across estuarine salt-marsh (foreground) dominated by *Salicornia virginica* and estuarine brackish-marsh (center and right) dominated by *Juncus acutus*, toward a headland slope-seep dominated by *Myrica californica* (Wax Myrtle), upper right. Wetland No.: 50.263(25.1.712.5952).



10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.150 CLASS UNCONSOLIDATED-SHORE
11.152 SUBCLASS SAND

Wetland Type No.: 11.152(13.4.321.1600)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED OCEAN-BEACH WETLAND. Monterey Co., Big Sur Coast, off Hwy. 1, 21 mi. S. of Carmel, Andre Molera State Park.

Wetland Type No.: 11.152(13.4.322.1600)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED EXPOSED-BAY-BEACH. Santa Barbara Co., Goleta, UCSB.

Wetland Type No.: 11.152(13.4.324.1600)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED COVE-BEACH WETLAND. San Diego Co., La Jolla, along Coast Blvd., Children's Pool.

Wetland Type No.: 11.152(13.4.324.1600)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED COVE-BEACH WETLAND. Monterey Co., Big Sur, end of Sycamore Canyon Rd., Pfeiffer Beach.

* * * *

10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.150 CLASS UNCONSOLIDATED-SHORE
11.153 SUBCLASS MUD

Wetland Type No.: 11.153(12.4.151.1800,2262)

MARINE-INTERTIDAL UNCONSOLIDATED-SHORE (MUD) IRREGULARLY-EXPOSED LAGOON WETLAND. Santa Barbara Co., Goleta, UCSB, Campus Point. The input for this lagoon is the outfall from the UCSB marine lab.

* * * *

10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.210 CLASS AQUATIC BED
11.211 SUBCLASS ATTACHED ALGAL

Wetland Type No.: 11.211(13.4.311.2323)

MARINE-INTERTIDAL AQUATIC-BED-ATTACHED-ALGAL (*FUCUS DISTICHUS*) REGULARLY-FLOODED OCEAN-SHORE WETLAND. San Luis Obispo Co., Hearst State Beach, overlook north of San Simeon Point along Hwy. 1.

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10.000 SYSTEM MARINE
11.000 SUBSYSTEM INTERTIDAL
11.210 CLASS AQUATIC BED
11.214 SUBCLASS ROOTED VASCULAR

Wetland Type No.: 11.214(12.4.521.6142)

MARINE-INTERTIDAL AQUATIC-BED-ROOTED-VASCULAR (*PHYLLOSPADIX TORREYI*) IRREGULARLY-EXPOSED DELTA WETLAND. Ventura Co., S.E. of Hwy. 101 at Hwy. 33, Ventura River Delta.

2. ESTUARINE WETLANDS

Estuaries of the study region occur within the Californian Marine and Estuarine Province of North America, which extends from Mendocino County southward along the coast of Baja California, Mexico, and has a shoreline strongly influenced by coastal mountains, and the coasts are rocky (Cowardin et al. 1979). In this province, freshwater is limited, the climate is Mediterranean and is influenced by the Humboldt Current, and the tidal range is moderate (Cowardin et al. 1979). The study region covers approximately 400 miles of this coastline and includes numerous estuaries among several major types, many of which have been studied or visited during the course of this project (see Ferren et al. 1995b).

The Estuarine System (System No. 20.000) includes two subsystems: (1) Subsystem Intertidal (i.e., wetlands; No. 21.000); and (2) Subsystem Subtidal (i.e., deepwater habitats; No. 22.000). Cowardin et al. (1979) define the system as follows:

The Estuarine System . . . consists of deepwater tidal habitats and adjacent tidal wetlands that are usually semienclosed by land but have open, partly obstructed, or sporadic access to the open ocean, and in which ocean water is at least occasionally diluted by freshwater runoff from the land. The salinity may be periodically increased above that of the open ocean by evaporation. Along some low-energy coastlines there is appreciable dilution of sea water. Offshore areas with typical estuarine plants and animals, such as mangroves . . . and eastern oysters . . . are also included in the Estuarine System.

Cowardin et al. also have provided a description of the limits of this system, including three main features: (1) the Estuarine System extends upstream or toward land to the area where salinity from ocean-derived salts (i.e., largely sodium chloride) is less than 0.5 ppt (parts per thousand) during the average annual low flow of freshwater input; (2) downstream to an imaginary line that closes the mouth of an estuary (e.g., a river, bay, or sound); and (3) extending to the seaward limit of estuarine vegetation dominated by emergents, shrubs, or trees and to the seaward limit of offshore areas continuously diluted by runoff to salinities less than those of the Marine System.

20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.110 CLASS ROCK-BOTTOM

21.112 SUBCLASS RUBBLE-BOULDER

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20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.120 CLASS UNCONSOLIDATED-BOTTOM

21.121 SUBCLASS COBBLE-GRAVEL

* * * *

20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.120 CLASS UNCONSOLIDATED-BOTTOM

21.122 SUBCLASS SAND

Wetland Type No.: 21.122(13.5.224.8342, 8346)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (SAND) REGU-

LARLY-FLOODED MIXOHALINE SHALLOW-ARTIFICIAL ESTUARINE-CHANNEL WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve.

Wetland Type No.: 21.122(13.5.422.1600)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (SAND) REGULARLY-FLOODED MIXOHALINE SHALLOW-BAR WETLAND. San Diego Co., Del Mar, San Dieguito Lagoon.

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20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.120 CLASS UNCONSOLIDATED-BOTTOM

21.123 SUBCLASS MUD

Wetland Type No.: 21.123(12.4.412.1800)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (MUD) IRREGULARLY-EXPOSED EUHALINE SHALLOW-BOTTOM WETLAND. San Luis Obispo Co., Morro Bay, Baywood Park, Sweetwater Springs Reserve.

Wetland Type No.: 21.123(13.4.412.1800)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (MUD) REGULARLY-FLOODED EUHALINE SHALLOW-BOTTOM WETLAND. Orange Co., Newport Backbay.

Wetland Type No.: 21.123(13.5.224.1700, 2110, 2200, 8311)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (MUD) REGULARLY-FLOODED MIXOHALINE SHALLOW-ARTIFICIAL ESTUARINE-CHANNEL WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve. Dominance or characteristic types include diatoms, green algae, and the gastropod *Cerithidea*.

Wetland Type No.: 21.123(13.5.256.1800)

ESTUARINE UNCONSOLIDATED-BOTTOM (MUD) REGULARLY-FLOODED MIXOHALINE SMALL-TIDAL-MARSH CHANNEL WETLAND. Ventura Co., Point Mugu Pacific Naval Air Station, Mugu Lagoon.

Wetland Type No.: 21.123(13.5.511.1800, 2200,8311)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (GREEN-ALGAE, *CERITHIDEA*) REGULARLY-FLOODED MIXOHALINE MUD-FLAT WETLAND. San Diego Co., Imperial Beach, Tijuana Estuary, Tijuana River National Estuarine Research Reserve.

Wetland Type No.: 21.123(14.7.512.1700)

ESTUARINE-INTERTIDAL UNCONSOLIDATED-BOTTOM (MIXED-FINE) IRREGULARLY-FLOODED HYPERSALINE SALT-FLAT WETLAND. San Diego Co., Camp Pendleton, San Margarita River Estuary.

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20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.140 CLASS ROCKY-SHORE

21.142 SUBCLASS RUBBLE-BOULDER

Wetland Type No.: 21.142(14.5.912.1300)

ESTUARINE-INTERTIDAL ROCKY-SHORE (RUBBLE) IRREGULARLY-FLOODED MIXOHALINE REVETMENT WETLAND. San Diego Co., Del Mar, San Dieguito Lagoon.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.150 CLASS UNCONSOLIDATED-SHORE
21.151 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 21.151(13.5.252.1500,1600)
ESTUARINE-INTERTIDAL UNCONSOLIDATED-SHORE (MIXED-COARSE AND SAND) REGULARLY-FLOODED MIXOHALINE LARGE TIDAL-MARSH-CHANNEL WETLAND. San Diego Co., Imperial Beach, Tijuana River Estuary, Tijuana River National Estuarine Research Reserve.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.150 CLASS UNCONSOLIDATED-SHORE
21.152 SUBCLASS SAND

Wetland Type No.: 21.152(13.5.313.1600)
ESTUARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED MIXOHALINE ESTUARY-SHORE WETLAND. Monterey Co., Andrew Molera State Park, Big Sur River Estuary.

Wetland Type No.: 21.152(13.5.323.1600)
ESTUARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED MIXOHALINE ESTUARY-BEACH WETLAND. Monterey Co., Andrew Molera State Park, Big Sur River Estuary.

Wetland Type No.: 21.152(13.4.323.1600)
ESTUARINE-INTERTIDAL UNCONSOLIDATED-SHORE (SAND) REGULARLY-FLOODED HALINE ESTUARY-BEACH WETLAND. Los Angeles Co., Malibu, Malibu Lagoon.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.150 CLASS UNCONSOLIDATED-SHORE
21.153 SUBCLASS MUD

Wetland Type No.: 21.153(14.7.512.8640)
ESTUARINE-INTERTIDAL UNCONSOLIDATED-SHORE (MUD) IRREGULARLY-FLOODED HYPERSALINE SALT-FLAT WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh, Carpinteria Salt Marsh Reserve.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.220 CLASS AQUATIC-BED
21.211 SUBCLASS ATTACHED-ALGAL

Wetland Type No.: 21.211(14.6.513.2600)
ESTUARINE-INTERTIDAL AQUATIC-BED ATTACHED-ALGAL (BLUE-GREEN ALGAE) IRREGULARLY-FLOODED EURYHALINE VEGETATED-FLAT WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.220 CLASS AQUATIC-BED

21.212 SUBCLASS FLOATING-ALGAL

Wetland Type No.: 21.212(13.5.224.2262)

ESTUARINE-INTERTIDAL AQUATIC-BED FLOATING-ALGAL (*ENTEROMORPHA*) REGULARLY-FLOODED MIXOHALINE SHALLOW-ARTIFICIAL ESTUARY-CHANNEL WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.210 CLASS AQUATIC-BED

21.214 SUBCLASS ROOTED-VASCULAR

Wetland Type No.: 21.214(12.4.412.6143)

ESTUARINE-INTERTIDAL AQUATIC-BED ROOTED-VASCULAR (*ZOSTERA MARINA*) IRREGULARLY-EXPOSED EUHALINE SHALLOW-BOTTOM WETLAND (lower-center). San Luis Obispo Co., Morro Bay, Baywood Park, Sweetwater Springs Reserve.

Wetland Type No.: 21.214(12.5.172.6122)

ESTUARINE-INTERTIDAL AQUATIC-BED ROOTED-VASCULAR (*RUPPIA CIRRHOSA*) IRREGULARLY-EXPOSED MIXOHALINE TIDAL-MARSH-POND WETLAND. San Diego Co., Del Mar, San Dieguito Lagoon.

Wetland Type No.: 21.214(12.5.222.6122)

ESTUARINE-INTERTIDAL AQUATIC-BED ROOTED-VASCULAR (*RUPPIA CIRRHOSA*) IRREGULARLY-EXPOSED MIXOHALINE SHALLOW-NATURAL-CHANNEL WETLAND. Santa Barbara Co., Hollister Ranch, Santa Anita Estuary.

Wetland Type No.: 21.214(15.6.412.6123)

ESTUARINE-INTERTIDAL AQUATIC-BED ROOTED-VASCULAR (*RUPPIA MARITIMA*) SEASONALLY-FLOODED EURYHALINE SHALLOW-BOTTOM WETLAND. Santa Barbara Co., Goleta Valley, University of California Santa Barbara, Coal Oil Point Reserve, Devereux Slough.

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20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.210 CLASS AQUATIC-BED

21.215 SUBCLASS FLOATING-VASCULAR

* * * *

20.000 SYSTEM ESTUARINE
21.000 SUBSYSTEM INTERTIDAL
21.240 CLASS EMERGENT WETLAND

21.241 SUBCLASS EMERGENT-PERSISTENT

Wetland Type No.: 21.241(12.5.821.6232)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SCIRPUS CALIFORNICUS*) IRREGULARLY-EXPOSED MIXOHALINE LOW-BRACKISH-MARSH WETLAND. Los Angeles Co., Malibu, Malibu Lagoon.

Wetland Type No.: 21.241(12.5.821/831.6231)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SCIRPUS AMERICANUS*) IRREGULARLY-EXPOSED MIXOHALINE LOW-BRACKISH FRINGE-MARSH WETLAND. San Luis Obispo Co., Morro Bay, Los Osos, Los Osos Creek. (Fig. 2, pg. 189).

Wetland Type No.: 21.241(12.5.821/831.6232,6233,6235)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SCIRPUS CALIFORNICUS*, *S. MARITIMUS*, *S. ROBUSTUS*) IRREGULARLY-EXPOSED MIXOHALINE LOW-BRACKISH FRINGE-MARSH WETLAND. San Luis Obispo Co., Morro Bay, Los Osos, Los Osos Creek.

Wetland Type No.: 21.241(13.5.331.5331)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*) REGULARLY-FLOODED MIXOSALINE ESTUARY-BANK WETLAND. San Luis Obispo Co., Morro Bay State Park, Morro Bay near Morro Creek; Los Angeles Co., Malibu State Beach, Malibu Lagoon.

Wetland Type No.: 21.241(13.5.811.6441)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SPARTINA FOLIOSA*) REGULARLY-FLOODED MIXOHALINE LOW-SALT-MARSH WETLAND. San Diego Co., Imperial Beach, Tijuana River Estuary, Tijuana River National Estuarine Research Reserve.

Wetland Type No.: 21.241(13.5.811.5331)

ESTUARINE EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*) REGULARLY-FLOODED MIXOHALINE LOW-SALT-MARSH WETLAND. San Diego Co., Imperial Beach, Tijuana Estuary, Tijuana River National Estuarine Research Reserve.

Wetland Type No.: 21.241(13.5.811.5331,5411)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*, *BATIS MARITIMA*) REGULARLY-FLOODED MIXOHALINE LOW-SALT-MARSH WETLAND. Ventura Co., Point Mugu Pacific Naval Air Station, Mugu Lagoon.

Wetland Type No.: 21.241(14.5.812.5331,5341)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*, *SUAEDA ESTEROA*) IRREGULARLY-FLOODED MIXOHALINE MIDDLE-SALT-MARSH WETLAND. Ventura Co., Point Mugu Pacific Naval Air Station, Mugu Lagoon.

Wetland Type No.: 21.241(14.5.812.5331,5451)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*, *LIMONIUM CALIFORNICUM*) IRREGULARLY-FLOODED MIXOHALINE MIDDLE-SALT-MARSH WETLAND. San Luis Obispo Co., Morro Bay, Morro Bay State Beach.

Wetland Type No.: 21.241(14.5.812.5332,5551)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*, *CORDYLANTHUS MARITIMUS*) IRREGULARLY-FLOODED MIXOHALINE MIDDLE-SALT-MARSH WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve. *Cordylanthus maritimus* ssp. *maritimus*, an endangered species, is a nonpersistent annual plant that seasonally can occur co-dominantly with *Salicornia virginica* and other middle and upper marsh species such as *Arthrocnemum subterminale*, *Atriplex watsonii*, and *Monanthochloe littoralis*.

Wetland Type No.: 21.241(15.5.331.5331,6232,6521)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*PLUCHEA ODORATA*, *SCIRPUS CALIFORNICUS*, *TYPHA DOMINGENSIS*) SEASONALLY-EX-

POSED MIXOHALINE ESTUARY-BANK WETLAND. San Diego Co., Buena Vista Lagoon.

Wetland Type No.: 21.241(16.5.351.5441,6235)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*FRANKENIA SALINA*, *SCIRPUS ROBUSTUS*) SEASONALLY-FLOODED MIXOHALINE ESTUARY-TERRACE WETLAND. Santa Barbara Co., Goleta Valley, University of California Santa Barbara, Coal Oil Point Reserve, Devereux Slough.

Wetland Type No.: 21.241(16.5.422.6234)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SCIRPUS PUNGENS*) SEASONALLY-FLOODED MIXOHALINE SHALLOW-BAR WETLAND. San Diego Co., Buena Vista Lagoon.

Wetland Type No.: 21.241(16.5.833.6232)

ESTUARINE-INTERTIDAL EMERGENT-PERSISTENT (*SCIRPUS CALIFORNICUS*) SEASONALLY-FLOODED MIXOHALINE HIGH-FRINGE-MARSH WETLAND. Ventura Co., San Buenaventura, Emma Wood State Beach, Ventura River Estuary.

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20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.240 CLASS EMERGENT WETLAND

21.242 SUBCLASS NONPERSISTENT

Wetland Type No.: 21.242(14.7.520.5512)

ESTUARINE-INTERTIDAL EMERGENT-NONPERSISTENT (*LASTHENIA GLABRATA*) IRREGULARLY-FLOODED EURYHALINE DELTA WETLAND. Santa Barbara Co., Carpinteria Valley, Carpinteria Salt Marsh Reserve. Emergent-Nonpersistent Wetland dominated by *Lasthenia glabrata* ssp. *coulteri* also occurs with the perennial plants *Arthrocnemum subterminale*, *Salicornia virginica*, and *Monanthochloe littoralis*. Other "winter" annuals that occur with *Lasthenia* and also can be dominant include *Juncus bufonius*, *Hutchinsia procumbens*, *Parapholis incurva*, and *Spergularia marina*. The euryhaline type is bounded by lower-elevation hyperhaline salt flats downslope and other euryhaline wetlands upslope, dominated by the annual grass *Lolium multiflorum*.

Wetland Type No.: 21.242(15.5.420.5531,5541,5542)

ESTUARINE-INTERTIDAL EMERGENT-NONPERSISTENT (*SPERGULARIA*, *ATRIPLEX*, *CHENOPODIUM*) SEASONALLY-FLOODED MIXOHALINE SHALLOW-BAR WETLAND. Ventura Co., Ventura, Seaside Wilderness Park, Ventura River Estuary. When nonpersistent vegetation is lacking, this site belongs to Class Unconsolidated-Bottom. Depending on the status of estuary mouth opening or closure and the elevation of the bars and bed, the water regime can be Irregularly-Exposed, Regularly-Flooded, Irregularly-Flooded, or Seasonally-Flooded.

* * * *

20.000 SYSTEM ESTUARINE

21.000 SUBSYSTEM INTERTIDAL

21.250 CLASS SCRUB-SHRUB WETLAND

21.253 SUBCLASS BROADLEAVED-EVERGREEN

Wetland Type No.: 21.253(14.4.313.5632)

ESTUARINE-INTERTIDAL SCRUB-SHRUB BROADLEAVED-EVERGREEN (*SUAEDA CALIFORNICA*) IRREGULARLY-FLOODED EUHALINE ESTUARY-SHORE WETLAND. San Luis Obispo Co., Morro Bay, Morro Bay State Park. A narrow band of this succulent halophyte shrub occurs in scattered locations on the

margin of the estuary adjacent to unconsolidated shore wetland or emergent (salt marsh) wetland and upland habitats. *Suaeda californica* is an endangered species that currently is known only from Morro Bay.

Wetland Type No.: 21.253(14.5.313.5611,5624,5631,5633)

ESTUARINE-INTERTIDAL SCRUB-SHRUB BROADLEAVED-EVERGREEN (CARPOBROTUS, ISOCOMA, ATRIPLEX, SUAEDA) IRREGULARLY-FLOODED MIXOHALINE ESTUARY-SHORE WETLAND. San Diego Co., Camp Pendleton, Santa Margarita River Estuary. Dominants or characteristic species include *Carpobrotus edulis* (naturalized), *Isocoma menziesii*, *Atriplex lentiformis*, *Suaeda taxifolia*.

3. RIVERINE WETLANDS

Riverine environments within the study region include most of the California Chaparral Province, as designated by Bailey (1978) and illustrated by Cowardin et al. (1979). In this province, freshwater is limited and the climate is Mediterranean. The province covers approximately 400 miles of linear coastline and the adjacent study region includes many thousands of miles of riverine hydrogeomorphic units along hundreds of streams and rivers, some of which have been studied or visited during the course of this project (see Leidy et al. 1995).

The Riverine System is characterized by unidirectional flow from upstream to downstream within a channel. Cowardin et al. (1979) define the system as follows:

The Riverine System . . . includes all wetlands and deepwater habitats contained within a channel, with two exceptions: (1) wetlands dominated by trees, shrubs, persistent emergents, emergent mosses, or lichens, and (2) habitats with water containing ocean-derived salts in excess of 0.5 ppt. A channel is "an open conduit either naturally or artificially created which periodically or continuously contains moving water, or which forms a connecting link between two bodies of standing water" (Langbein and Iseri 1960, p. 5).

Cowardin et al. (1979) also have provided a description of the limits of this system, including two major features: (1) the system terminates downstream where the concentration of ocean-derived salts in the water exceeds 0.5 ppt during the period of annual low flow (=Estuarine), or where the channel enters a lake (=Lacustrine); and (2) the system terminates upstream where tributary streams originate, or where the channel leaves a lake. On the landward side of the channel, the Riverine System is bounded by upland, or by wetland dominated trees, shrubs, persistent emergents, emergent mosses, or lichens (=Palustrine).

30.000 SYSTEM RIVERINE

32.000 SUBSYSTEM UPPER-INTERMITTENT

32.120 CLASS UNCONSOLIDATED-BOTTOM

32.122 SUBCLASS SAND

Wetland Type No.: 32.122(23.1.463.1600)

RIVERINE UPPER-INTERMITTENT UNCONSOLIDATED-BOTTOM (SAND) SEMIPERMANENTLY-FLOODED VALLEY-RIVERBED WETLAND. San Diego Co., Upper San Luis Rey River Watershed, Matagual Creek, immediately upstream from State Route 79 bridge.

30.000 SYSTEM RIVERINE**32. SUBSYSTEM UPPER-INTERMITTENT****32.130 CLASS STREAMBED****32.131 SUBCLASS BEDROCK**

Wetland Type No.: 32.131(28.1.211.1200)

RIVERINE UPPER-INTERMITTENT STREAMBED (BEDROCK) INTERMITTENTLY-FLOODED MONTANE-STREAM-CHANNEL WETLAND. Ventura Co., Dry Lakes Ridge, headwaters of the Ventura River.

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30.000 SYSTEM RIVERINE**32.000 SUBSYSTEM UPPER-INTERMITTENT****32.130 CLASS STREAMBED****32.137 SUBCLASS VEGETATED**

Wetland Type No.: 32.137(24.1.463.7000)

RIVERINE UPPER-INTERMITTENT STREAMBED-VEGETATED SEASONALLY-FLOODED VALLEY-RIVERBED WETLAND. San Diego Co., San Luis Rey River Watershed, above Lake Henshaw, Matagal Creek, upstream from State Route 79 bridge. Vegetation within river channel is dominated by native and exotic weedy annuals.

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30.000 SYSTEM RIVERINE**33.000 SUBSYSTEM MID-INTERMITTENT****33.130 CLASS STREAMBED****33.133 SUBCLASS COBBLE-GRAVEL**

Wetland Type No.: 33.133(24.1.452.1400)

RIVERINE MID-INTERMITTENT STREAMBED (COBBLE-GRAVEL) SEASONALLY-FLOODED TERRACE-STREAMBED WETLAND. San Luis Obispo Co., terrace of the Sierra Madre Mountain, Cottonwood Creek.

Wetland Type No.: 33.133 (28.1.541.1500)

RIVERINE MID-INTERMITTENT STREAMBED (COBBLE-GRAVEL) INTERMITTENTLY-FLOODED STREAM-WASH WETLAND. Los Angeles Co., Santa Clara River Watershed, Soledad Canyon, north of Santa Clarita.

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30.000 SYSTEM RIVERINE**33.000 SUBSYSTEM MID-INTERMITTENT****33.130 CLASS STREAMBED****33.134 SUBCLASS SAND**

Wetland Type No.: 33.134(28.1.543.1600)

RIVERINE MID-INTERMITTENT STREAMBED (SAND) INTERMITTENTLY-FLOODED ALLUVIAL-WASH WETLAND. Santa Barbara Co., Cuyuma River Watershed, Ballinger Canyon.

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30.000 SYSTEM RIVERINE**33.000 SUBSYSTEM MID-INTERMITTENT****33.210 CLASS AQUATIC-BED****33.211 SUBCLASS ATTACHED-ALGAL**

Wetland Type No.: 33.211(24.1.452.2200)

RIVERINE MID-INTERMITTENT AQUATIC-BED (ATTACHED-ALGAL)

SEASONALLY-FLOODED STREAMBED WETLAND. San Luis Obispo Co., terrace of the Sierra Madre Mountains, Cottonwood Creek.

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30.000 SYSTEM RIVERINE

34.000 SUBSYSTEM LOWER-INTERMITTENT

34.130 CLASS STREAMBED

34.133 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 34.133(27.1.452.1500)

RIVERINE LOWER-INTERMITTENT STREAMBED (COBBLE-GRAVEL) TEMPORARILY-FLOODED FOOTHILL-STREAMBED WETLAND. San Diego Co., San Clemente Canyon, south of State Route 52.

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30.000 SYSTEM RIVERINE

34.000 LOWER-INTERMITTENT

34.150 CLASS UNCONSOLIDATED-SHORE

34.151 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 34.151(27.1.322.1500)

RIVERINE LOWER-INTERMITTENT UNCONSOLIDATED-SHORE (COBBLE-GRAVEL) TEMPORARILY-FLOODED FOOTHILL-STREAM-SHORE WETLAND. San Diego Co., San Clemente Canyon, south of Route 52.

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30.000 SYSTEM RIVERINE

35.000 SUBSYSTEM UPPER-PERENNIAL

35.110 CLASS ROCK-BOTTOM

35.111 SUBCLASS BEDROCK

Wetland Type No.: 35.111(21.1.113.1200)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BEDROCK) PERMANENTLY-FLOODED MAIN-CHANNEL-POOL WETLAND. Santa Barbara Co., South Coast, foothills of the Santa Ynez Mountains, San Jose Creek. This pool supports the habitat function at low water for fish (trout) and amphibians (newt).

Wetland Type No.: 35.111(21.1.261.1200)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BED-ROCK) PERMANENTLY-FLOODED MONTANE-STREAM-FALL WETLAND. Santa Barbara Co., Santa Ynez Mountains, Nojoqui Falls County Park.

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30.000 SYSTEM RIVERINE

35.000 SUBSYSTEM UPPER-PERENNIAL

35.110 CLASS ROCK-BOTTOM

35.112 SUBCLASS BOULDER

Wetland Type No.: 35.112(21.1.113.1300)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BOULDER) PERMANENTLY-FLOODED MAIN-CHANNEL-POOL WETLAND. Santa Barbara Co., foothills of the San Rafael Mountains, Sedgwick Ranch, headwater of Figueroa Creek. The main-channel-pools form a series of step-pools.

Wetland Type No.: 35.112(21.1.114.1300)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BOULDER) PERMANENTLY-FLOODED SCOUR-POOL WETLAND. Ventura Co., Ventura River watershed, Matilija Creek, Wheeler Gorge.

Wetland Type No.: 35.112(21.1.121.1300)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BOULDER) PERMANENTLY-FLOODED-RIFFLE WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, Santa Ana River, South Fork.

Wetland Type No.: 35.112(21.1.211.1300)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BOULDER) PERMANENTLY-FLOODED MONTANE-STREAM-CHANNEL WETLAND. Santa Barbara County, Hollister Ranch, Santa Anita Canyon.

Wetland Type No.: 35.112(21.1.211.1500)

RIVERINE UPPER-PERENNIAL ROCK-BOTTOM (BOULDER) PERMANENTLY-FLOODED MONTANE-STREAM-CHANNEL WETLAND. San Bernardino Co., San Bernardino National Forest, San Gorgonio District, Vivian Creek. (Fig. 3, pg. 193).

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30.000 SYSTEM RIVERINE

35.000 SUBSYSTEM UPPER-PERENNIAL

35.210 CLASS AQUATIC-BED

35.211 SUBCLASS ATTACHED-ALGAL

Wetland Type No.: 35.211(21.1.261.2200)

RIVERINE UPPER-PERENNIAL AQUATIC-BED (ATTACHED-ALGAL) PERMANENTLY-FLOODED MONTANE-STREAM-FALL WETLAND. Santa Barbara Co., Santa Ynez Mountains, Nojoqui Falls County Park.

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30.000 SYSTEM RIVERINE

36.000 SUBSYSTEM MID-PERENNIAL

36.120 CLASS UNCONSOLIDATED-BOTTOM

36.121 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 36.121(21.1.124.1500)

RIVERINE MID-PERENNIAL UNCONSOLIDATED-BOTTOM (COBBLE-GRAVEL) PERMANENTLY-FLOODED RIVER-RUN WETLAND. San Diego Co., San Luis Rey River, downstream from Lake Henshaw.

Wetland Type No.: 36.121(21.1.124.1500)

RIVERINE MID-PERENNIAL UNCONSOLIDATED-BOTTOM (COBBLE-GRAVEL) PERMANENTLY-FLOODED RIVER-RUN WETLAND. Santa Barbara Co.; Los Padres National Forest, San Rafael Wilderness near Cliff Campground, Sisquoc River.

Wetland Type No.: 36.121(23.1.482.1500)

RIVERINE MID-PERENNIAL UNCONSOLIDATED-BOTTOM (COBBLE-GRAVEL) SEMIPERMANENTLY-FLOODED FOOTHILL-RIVER CHANNEL-BAR WETLAND. Santa Barbara Co., Los Padres National Forest, San Rafael Wilderness near Cliff Campground, Sisquoc River.

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30.000 SYSTEM RIVERINE

36.000 SUBSYSTEM MID-PERENNIAL

36.130 CLASS STREAMBED

36.137 SUBCLASS VEGETATED

Wetland Type No.: 36.137(21.1.214.6841)

RIVERINE MID-PERENNIAL STREAMBED-VEGETATED (*PASPALUM*)

***DISTICUM*) PERMANENTLY-FLOODED COASTAL-PLAIN STREAM-CHANNEL WETLAND.** Ventura Co., Ventura River Watershed, San Antonio Creek.

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30.000 SYSTEM RIVERINE
36.000 SUBSYSTEM MID-PERENNIAL
36.210 CLASS AQUATIC-BED
36.211 SUBCLASS ATTACHED-ALGAL

Wetland Type No.: 36.211(21.1.124.1500)
RIVERINE MID-PERENNIAL AQUATIC-BED ATTACHED-ALGAL PERMANENTLY-FLOODED MONTANE-STREAM WETLAND. Ventura Co., Piru Creek, 200 meters south of Agua Blanca and Piru Creek. Seasonally-flooded unconsolidated-shore habitat occurs adjacent to the permanently-flooded streambed.

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30.000 SYSTEM RIVERINE
37.000 SUBSYSTEM LOWER-PERENNIAL
37.110 CLASS ROCK-BOTTOM
37.112 SUBCLASS RUBBLE

Wetland Type No.: 37.112(21.1.455.1300)
RIVERINE LOWER-PERENNIAL ROCK-BOTTOM (RUBBLE) PERMANENTLY-FLOODED CANYON-STREAMBED WETLAND. Monterey Co., Santa Lucia Mountains, Los Padres National Forest, Mill Creek, canyon mouth at State Route 1. Transitional area to marine wetlands.

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30.000 SYSTEM RIVERINE
37.000 SUBSYSTEM LOWER PERENNIAL
37.120 CLASS UNCONSOLIDATED-BOTTOM
37.121 SUBCLASS COBBLE-GRAVEL

Wetland Type No.: 37.121(21.1.464.1400)
RIVERINE LOWER-PERENNIAL UNCONSOLIDATED-BOTTOM (COBBLE-GRAVEL) PERMANENTLY-FLOODED COASTAL-PLAIN RIVERBED WETLAND. Monterey Co., Andrew Molera State Park, Big Sur River, west of State Route 1.

Wetland Type No.: 37.121(24.1.474.1500)
RIVERINE LOWER-PERENNIAL UNCONSOLIDATED-BOTTOM (COBBLE-GRAVEL) SEASONALLY-FLOODED COASTAL-PLAIN STREAM-CHANNEL-BAR WETLAND. San Luis Obispo Co., Arroyo de la Cruz at State Route 1. The green alga *Enteromorpha* sp. characterizes the aquatic bed wetland in flooded portions of the channel.

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30.000 SYSTEM RIVERINE
37.000 SUBSYSTEM LOWER-PERENNIAL
37.120 CLASS UNCONSOLIDATED-BOTTOM
37.122 SUBCLASS SAND

Wetland Type No.: 37.122(24.1.464.1600)
RIVERINE LOWER-PERENNIAL UNCONSOLIDATED-BOTTOM (SAND) SEASONALLY-FLOODED COASTAL-PLAIN-RIVERBED WETLAND. Ventura Co., Santa Clara River, Southern Pacific Milling Site.

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30.000 SYSTEM RIVERINE
37.000 SUBSYSTEM LOWER-PERENNIAL
37.120 CLASS UNCONSOLIDATED-BOTTOM
37.123 SUBCLASS MUD

Wetland Type No.: 37.123(21.1.211.1700)

RIVERINE LOWER-PERENNIAL UNCONSOLIDATED-BOTTOM (MIXED FINES [MUD]) PERMANENTLY-FLOODED MONTANE-STREAM-CHANNEL WETLAND. Riverside Co., Santa Rosa Plateau. Characteristic species include *Marsilea vestita* and *Callitriche heterophylla*.

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30.000 SYSTEM RIVERINE
37.000 SUBSYSTEM LOWER-PERENNIAL
37.240 CLASS EMERGENT WETLAND
37.242 SUBCLASS EMERGENT-NONPERSISTENT

Wetland Type No.: 37.242(21.1.224.5572)

RIVERINE LOWER-PERENNIAL EMERGENT-NONPERSISTENT (*LUDWIGIA HEXAPETALA*) PERMANENTLY-FLOODED COASTAL-PLAIN RIVER-CHANNEL WETLAND. Ventura Co., San Buenaventura Main Street Bridge, Ventura River.

Wetland Type No.: 37.242(23.1.391.4323,6741,6926,6932)

RIVERINE LOWER-PERENNIAL EMERGENT-NONPERSISTENT (*MARSI-LEA VESTITA*, *PASPALUM DISTICHUM*, *JUNCUS XIPHIODES*, *ELEOCHARIS MACROSTACHYA*) SEMIPERMANENTLY-FLOODED STREAM-MARGIN WETLAND. Riverside Co., Santa Rosa Plateau.

Wetland Type No.: 37.242(24.1.474.5500,5521,5595,5766)

RIVERINE LOWER-PERENNIAL EMERGENT-NONPERSISTENT (MIXED-VASCULAR-PLANT) SEASONALLY-FLOODED COASTAL-PLAIN STREAM-CHANNEL-BAR WETLAND. San Luis Obispo Co., Morro Creek, at Morro Bay. Bar dominated by nonpersistent plants such as *Mimulus guttatus*, *Anthemis cotula*, and seedlings of *Salix lasiolepis*.

4. LACUSTRINE WETLANDS

What is most striking about the lacustrine system in central and southern California is its natural rarity. Only four natural lacustrine lakes are found in the study area, whereas a vast number of artificial lacustrine habitats (i.e., reservoirs) have been created throughout central and southern California. Each natural lake represents a unique combination of geomorphic position, flooding regime, and water chemistry, and supports a different complement of dominance types. We have identified two major types of lakes in this region—i.e., natural lakes and artificial reservoirs. These are distinguished further by their landform, topographic position, flooding regime, and water chemistry (see Fiedler et al. 1995).

The Lacustrine System (System No. 40.000) as delimited by Cowardin et al. (1979) includes two subsystems: (1) Subsystem Littoral (No. 41.000), considered here to be wetland habitats; and (2) Subsystem Limnetic (No. 42.000), considered to be deep-water habitats and not covered by this study. Cowardin et al. (1979, 11 P.) define this system as follows:

The Lacustrine System . . . includes wetlands and deepwater habitats with all of the following characteristics: (1) situated in a topographic depressions or a

dammed river channel; (2) lacking trees, shrubs, persistent emergents, emergent mosses, or lichens with greater than 30% areal coverage; and (3) total area exceeds 8 ha (20 acres). Similar wetland and deepwater habitats totaling less than 8 ha are also included in the Lacustrine System if an active wave formed or bedrock shoreline feature makes up all or part of the boundary, or if the water depth in the deepest part of the basin exceeds 2 m (6.6 feet) at low water. Lacustrine waters may be tidal or nontidal, but ocean-derived salinity is always less than 0.5 [ppt].

Cowardin et al. also have provided a description of the limits of the Lacustrine System, including: (1) landward boundaries at upland habitats or wetlands dominated by trees, shrubs, persistent emergents, emergent mosses, or lichens; and, (2) the approximate contour of the "normal" spillway or pool elevation in dammed river channels, except where palustrine wetlands extend lakeward into the lacustrine environment. The littoral or wetland habitats of the Lacustrine System extend from the shoreward boundary of the system to a depth of 2 meters (6.6 feet) below low water or to the maximum extent of nonpersistent emergents, if these grow at depths greater than 2 meters.

40.000 SYSTEM LACUSTRINE

41.000 SUBSYSTEM LITTORAL

41.120 CLASS UNCONSOLIDATED BOTTOM

41.123 SUBCLASS MUD

Wetland Type No.: 41.123(28.1.441.1800)

LACUSTRINE-LITTORAL UNCONSOLIDATED-BOTTOM (MUD) INTERMITTENTLY-FLOODED MONTANE-LAKE-BED WETLAND. San Diego Co., Cuyamacha Mountains, Cuyamacha Lake.

Wetland Type No.: 41.123(28.3.442.1800)

LACUSTRINE-LITTORAL UNCONSOLIDATED-BOTTOM (MUD) INTERMITTENTLY-FLOODED ALKALI MONTANE-LAKE-BED WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake.

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40.000 SYSTEM LACUSTRINE

41.000 SUBSYSTEM LITTORAL

41.120 CLASS UNCONSOLIDATED BOTTOM

41.125 SUBCLASS VEGETATED

Wetland Type No.: 41.125(28.3.442.1800,5541,5554,5559)

LACUSTRINE-LITTORAL UNCONSOLIDATED-BOTTOM-VEGETATED (MUD, *CHENOPODIUM*, *HELIOTROPIUM*, *SUAEDA*) INTERMITTENTLY-FLOODED ALKALI MONTANE-LAKE-BED WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake (see Part II, Fig. 2a,b, pg. 143).

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40.000 SYSTEM LACUSTRINE

41.000 SUBSYSTEM LITTORAL

41.150 CLASS UNCONSOLIDATED SHORE

41.152 SUBCLASS SAND

Wetland Type No.: 41.152(28.3.332.1600)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE (SAND) INTERMITTENTLY-FLOODED ALKALI MONTANE-LAKE-SHORE WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake.

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40.000 SYSTEM LACUSTRINE
41.000 SUBSYSTEM LITTORAL
41.150 CLASS UNCONSOLIDATED SHORE
41.153 SUBCLASS MUD (MIXED FINES)

Wetland Type No.: 41.153(28.1.331.1700)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE (MIXED-FINES) INTERMITTENTLY-FLOODED MONTANE-LAKE-SHORE WETLAND. San Diego Co., Cuyamaca Mountains, Lake Cuyamaca.

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40.000 SYSTEM LACUSTRINE
41.000 SUBSYSTEM LITTORAL
41.150 CLASS UNCONSOLIDATED SHORE
41.155 SUBCLASS VEGETATED

Wetland Type No.: 41.155(24.1.331.7000)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE VEGETATED (MIXED-VASCULAR-PLANTS) SEASONALLY-FLOODED MONTANE-LAKE-SHORE WETLAND. San Diego Co., Lake Henshaw.

Wetland Type No.: 41.155(24.1.334.1700,5544,5592,6923,6925)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE (MIXED-FINES, CYPERUS, ELEOCHARIS, LIMOSELLA, RORRIPA) SEASONALLY-FLOODED MONTANE-RESERVOIR-SHORE WETLAND. San Bernardino Co., San Bernardino Mountains, Big Bear Lake, Grout Bay (see next wetland below and Fig. 4, pg. 197).

Wetland Type No.: 41.155(24.1.334.1700,7000)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE (MIXED-FINES, MIXED-VASCULAR-PLANTS) SEASONALLY-FLOODED MONTANE-RESERVOIR-SHORE WETLAND. San Bernardino Co., San Bernardino Mountains, Big Bear Lake, Grout Bay (Fig. 4, pg. 197).

Wetland Type No.: 41.155 (28.1.334.7000)

LACUSTRINE-LITTORAL UNCONSOLIDATED-SHORE VEGETATED (MIXED-VASCULAR-PLANTS) INTERMITTANTLY-FLOODED MONTANE-LAKE-SHORE WETLAND. San Diego Co., Cuyamaca Mountains, Cuyamaca Lake.

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40.000 SYSTEM LACUSTRINE
41.000 SUBSYSTEM LITTORAL
41.210 CLASS AQUATIC BED
41.214 SUBCLASS ROOTED VASCULAR

Wetland Type No.: 41.214(23.1.446.6112)

LACUSTRINE-LITTORAL AQUATIC-BED ROOTED-VASCULAR (*ECHINODORUS BERTEROI*) SEMIPERMANENTLY-FLOODED CANYON-RESERVOIR-BOTTOM WETLAND. Ventura Co., Coyote Creek Watershed, Lake Castitas.

Wetland Type No.: 41.214(28.1.152.6152,6154,6161)

LACUSTRINE-LITTORAL AQUATIC-BED ROOTED-VASCULAR (*POTAMOGETON, RUPPIA, ZANNICHELLIA*) INTERMITTANTLY-FLOODED ALKALI MONTANE-LAKE WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake.

* * * *

40.000 SYSTEM LACUSTRINE**41.000 SUBSYSTEM LITTORAL****41.240 CLASS EMERGENT WETLAND****41.242 SUBCLASS NONPERSISTENT**

Wetland Type No.: 41.242(21.1.154.5581)

LACUSTRINE-LITTORAL EMERGENT-NONPERSISTENT (*POLYGONUM EMERSUM* VAR. *EMERSUM*) PERMANENTLY-FLOODED MONTANE-RESERVOIR WETLAND. San Bernardino Co., San Bernardino Mountains, Big Bear Lake.

Wetland Type No.: 41.242(23.1.156.6112,6912)

LACUSTRINE-LITTORAL EMERGENT-NONPERSISTENT (*ECHINODORUS BERTEROI*) SEMIPERMANENTLY-FLOODED CANYON-RESERVOIR WETLAND. Ventura Co., Coyote Creek Watershed, Lake Casitas.

Wetland Type No.: 41.242(23.1.446.6112,6912)

LACUSTRINE-LITTORAL EMERGENT-NONPERSISTENT (*ECHINODORUS BERTEROI*) SEASONALLY-FLOODED CANYON-RESERVOIR-BED WETLAND. Ventura Co., Coyote Creek Watershed, Lake Casitas.

Wetland Type No.: 41.242(28.1.151.5582)

LACUSTRINE-LITTORAL EMERGENT-NONPERSISTENT (*POLYGONUM EMERSUM* VAR. *STIPULACEUM*) INTERMITTANTLY-FLOODED MONTANE-LAKE WETLAND. San Diego Co., Cuyamaca Mountains, Cuyamaca Lake.

5. PALUSTRINE WETLANDS

The study region covers approximately 640 km (400 mi) of coast, all or portions of nine California counties, and extends from approximately sea level to over 3000 m (9000 ft). Wetlands of the Palustrine System are bounded by upland or other habitats of the four additional systems of wetlands and deepwater habitats. In central and southern California, palustrine wetlands include habitats and/or biotic communities that have been called, for example, ponds, vernal pools and lakes, freshwater marshes or palustrine emergent wetlands, alkali flats, seeps and springs, dune swales, and riparian scrub, woodlands, and forests.

The Palustrine System (System No. 50.000) contains no subsystems as considered by Cowardin et al. (1979) because there is no overwhelming physical features of the environment (e.g., oceanic tides and salinity, shoreline waves, flowing water) that influence the formation of habitats and the structure of biotic communities. All elements of this system are wetlands. Cowardin et al. define the Palustrine System as follows:

The Palustrine System . . . includes all nontidal wetlands dominated by trees, shrubs, persistent emergents, emergent mosses or lichens, and all such wetlands that occur in tidal areas where salinity due to ocean-derived salts is below 0.5 ppt [parts per thousand]. It also includes wetlands lacking such vegetation, but with all of the following four characteristics: (1) area less than 8 ha (20 acres); (2) active wave-formed or bedrock shoreline features lacking; (3) water depth in the deepest part of basin less than 2 m at low water; and (4) salinity due to ocean-derived salts less than 0.5 [ppt].

50.000 SYSTEM PALUSTRINE**50.120 CLASS UNCONSOLIDATED-BOTTOM****50.121 SUBCLASS COBBLE-GRAVEL**

Wetland Type No.: 50.121(21.1.824.1500)

PALUSTRINE UNCONSOLIDATED-BOTTOM (MIXED-COARSE) PERMANENTLY-FLOODED GLACIAL-POND WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, Dollar Lake.

* * * *

50.000 SYSTEM PALUSTRINE**50.120 CLASS UNCONSOLIDATED-BOTTOM****50.123 SUBCLASS MUD**

Wetland Type No.: 50.123(21.1.824.1700)

PALUSTRINE UNCONSOLIDATED-BOTTOM (MIXED-FINE TYPES) PERMANENTLY-FLOODED GLACIAL-POND WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, Dollar Lake.

Wetland Type No.: 50.123(24.1.823,825.1700,1800)

PALUSTRINE UNCONSOLIDATED-BOTTOM (MUD AND MIXED-FINES) SEASONALLY-FLOODED FAULT-SAG-POND AND VERNAL POND WETLANDS. Santa Barbara Co., Rancho Los Flores. Throughout the coastal mesas, foothills, plateaus, and valleys of the study region, small natural basins, which have a flooding duration that is generally longer than that of vernal pools but less than that of vernal lakes and marshes, form a group of vernal wetlands (i.e., vernal ponds) that have a distinctive combination of associated plant and animal species and that provide particular ecosystem functions. Ecosystem functions include breeding habitat for various amphibians including Western Toads and the endangered Spadefoot Toad and Tiger Salamander, and habitat for narrowly-restricted invertebrates such as Clam Shrimp.

Wetland Type No.: 50.123(24.1.825.1800)

PALUSTRINE UNCONSOLIDATED-BOTTOM (MUD) SEASONALLY-FLOODED VERNAL-POND WETLAND. Santa Barbara Co., foothill-valley of the San Rafael Mountains, Sedgwick Ranch. Persistent emergent vegetation dominated by *Eleocharis palustris* characterizes the margins of the pond and adjacent vernal marsh wetland. Nonpersistent emergent vegetation can colonize the outer margins or the center of the pond in drier years, forming a habitat with characteristics of vernal pools.

Wetland Type No.: 50.123(26.6.848.1700)

PALUSTRINE UNCONSOLIDATED-BOTTOM (MIXED-FINES) SEASONALLY-SATURATED EURYHALINE DIKED-ESTUARINE MARSH WETLAND. San Diego Co., San Eliho State Ecological Reserve.

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50.000 SYSTEM PALUSTRINE**50.150 CLASS UNCONSOLIDATED-SHORE****50.151 SUBCLASS COBBLE-GRAVEL**

Wetland Type No.: 50.151(24.1.824.1500)

PALUSTRINE UNCONSOLIDATED-SHORE (MIXED-COARSE) SEASONALLY-FLOODED GLACIAL-POND WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, Dollar Lake.

* * * *

50.000 SYSTEM PALUSTRINE**50.150 CLASS UNCONSOLIDATED-SHORE****50.153 SUBCLASS MUD**

Wetland Type No.: 50.153(24.1.824,1700,1800)

PALUSTRINE UNCONSOLIDATED-SHORE (MIXED-FINE TYPES) SEASONALLY-FLOODED GLACIAL-POND WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, Dollar Lake.

* * * *

50.000 SYSTEM PALUSTRINE**50.210 CLASS AQUATIC BED****50.212 SUBCLASS FLOATING-ALGAL**

Wetland Type No.: 50.212(21.1.141,2262)

PALUSTRINE AQUATIC-BED FLOATING-ALGAL (ENTEROMORPHA) PERMANENTLY-FLOODED DUNE-POND WETLAND. San Luis Obispo Co., Oso Flaco Lake. Dominant is the floating green alga *Enteromorpha* sp. Aquatic-Bed Rooted-Vascular species include *Potamogeton pectinatus*, *Ruppia cirrhosa*, and *Zannichellia palustris*.

Wetland Type No.: 50.212(21.1.147,2262)

PALUSTRINE AQUATIC-BED FLOATING-ALGA (ENTEROMORPHA) PERMANENTLY-FLOODED AGRICULTURAL-POND WETLAND. Santa Barbara Co., Vandenberg Air Force Base, MOD III Pond.

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50.000 SYSTEM PALUSTRINE**50.210 CLASS AQUATIC BED****50.214 SUBCLASS ROOTED-VASCULAR**

Wetland Type No.: 50.214(21.1.140,5100,6100)

PALUSTRINE AQUATIC-BED ROOTED-VASCULAR (MIXED MONOCOT AND DICOT TYPES) PERMANENTLY-FLOODED POND, "LAKE", AND RESERVOIR WETLANDS. San Luis Obispo Co., Oso Flaco Lake (dune pond); Pico Creek (canyon mouth pond). Santa Barbara Co.: Vandenberg Air Force Base (MOD III Pond); Hollister Ranch (agricultural ponds, impounded ponds). Ventura Co.: McGrath Lake (dune pond). Natural and artificial ponds often support dense growths of submerged, rooted aquatic vascular plants representing various genera and families of flower plants. Characteristic species include *Myriophyllum spicatum* spp. *exallescens*, *Najas marina*, *Potamogeton foliosus* spp. *foliosus*, *P. pectinatus*, *Ranunculus aquatilis*, *Ruppia cirrhosa*, *R. maritima*, and *Zannichellia palustris*. Associated species include attached algae such as *Chara* spp.; rooted aquatic plants such as *Egeria densa* and *Potamogeton crispus*; and floating plants such as *Azolla filiculoides*, *Hydrocotyle ranunculoides*, and *Lemna* spp. Ecosystem functions include food resources for many species of waterfowl, which disperse the characteristic plant species along the coast of California and elsewhere. The characteristic plant species are also an important component of the habitat for aquatic invertebrates and provide food, shelter, and shading for fish. These plants also contribute to water quality by absorbing pollutants and contribute to the reduction of water temperatures through shading.

Wetland Type No.: 50.214(21.1.726,5151,5161)

PALUSTRINE AQUATIC-BED ROOTED-VASCULAR (HIPURIS, RANUNCULUS) PERMANENTLY-FLOODED MONTANE-SPRING WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake Watershed, Shay Meadow. Shay Meadow near Big Bear in the San Bernardino Mountains contains a unique montane valley spring. The perennial spring supports palustrine emergent and aquatic

bed wetlands and provides habitat for the endemic and endangered fish, the Shay Meadow Stickleback (*Gasterosteus aculeatus* subsp.). Land use practices in the area threaten the quality of habitat and the surrounding palustrine wetlands that are used for residential development, pasture, and corrals. Characteristic species include *Hippuris vulgaris*, *Ranunculus aquatilis*, and associated species include *Carex* sp., *Hordeum brachyantherum*, *Juncus balticus*, *Mimulus guttatus*, *Polygonum amphibium*, and *Scirpus acutus*. Aquatic bed species are various algae, *Chara* spp., and associated floating plants such as *Lemna* spp. An important ecosystem function of this wetland is that it serves as habitat for endangered species (e.g., Shay Meadows Stickleback). Other functions include as well as breeding habitat for western toads, food chain support, and hydrology (e.g., perennial fresh water source).

Wetland Type No.: 50.214(21.1.141.6152,6154,6161)

PALUSTRINE AQUATIC-BED ROOTED-VASCULAR (*POTAMOGETON*, *RUPPIA*, *ZANNICHELLIA*) PERMANENTLY-FLOODED DUNE-POND WETLAND. San Luis Obispo Co., Oso Flaco Lake. Dominants include *Potamogeton pectinatus*, *Ruppia cirrhosa*, and *Zannichellia palustris*. Aquatic-Bed Floating-Alga dominant is *Enteromorpha* sp.

Wetland Type No.: 50.214(21.1.147.5121,5142,6152,6161)

PALUSTRINE AQUATIC-BED ROOTED-VASCULAR (*CERATOPHYLLUM*, *MYRIOPHYLLUM*, *POTAMOGETON*, *ZANNICHELLIA*) PERMANENTLY-FLOODED AGRICULTURAL-POND WETLAND. Santa Barbara Co., Vandenberg Air Force Base, MOD III Pond.

* * * * *

50.000 SYSTEM PALUSTRINE

50.210 CLASS AQUATIC BED

50.215 SUBCLASS FLOATING-VASCULAR

Wetland Type No.: 50.215(21.1.130,140,850,4311,6140)

PALUSTRINE AQUATIC-BED FLOATING-VASCULAR (*AZOLLA*, *LEMNACEAE*) PERMANENTLY-FLOODED SPRING, POND, AND SWALE WETLAND. San Bernardino Co., San Bernardino National Forest (springs). Santa Barbara Co.: La Purissima Mission State Historic Park (historic Reservoirs); Vandenberg Air Force Base (ponds, dune swales); Hollister Ranch (agricultural ponds). Floating aquatic bed plants are common in many wetland habitats that are characterized by various water regimes. Duckweed (*Lemna*) and Duckweed Fern (*Azolla*) are the most common genera. Some habitats, especially those with nutrient enrichment, can support a cover of 100% floating species. Many species of floating vascular plants also occur in wetlands dominated by emergent vascular plants. Characteristic floating vascular species include *Azolla filiculoides*, *Lemna gibba*, *L. minuscula*, *L. minor*, *L. trisulca*, *L. valdiviana*, *Spirodella polyrrhiza*, *S. punctata*, *Wolffiella ligulata*, *W. columbiana*. Associated floating and emergent vascular plants include *Hydrocotyle ranunculoides* and *Rorripa nasturtium-aquaticum*. This wetland type functions in food chain support as food for water fowl and in maintaining water quality.

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50.000 SYSTEM PALUSTRINE

50.240 CLASS EMERGENT WETLAND

50.241 SUBCLASS EMERGENT-PERSISTENT WETLAND

Wetland Type No.: 50.241(21-23.1.143.6251)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS ACUTUS*) PERMANENTLY- TO SEMIPERMANENTLY-FLOODED FAULT-SAG-POND WETLAND. Riverside Co., Temescal Wash.

Wetland Type No.: 50.241(21,23.1.214.6251,6721,6672)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS*, *SPARGANIUM*, *TYPHA*) PERMANENTLY- TO SEMIPERMANENTLY-FLOODED COASTAL-PLAIN STREAM-CHANNEL WETLAND. Santa Barbara Co., Vandenberg Air Force Base, San Antonio Creek. Dominant emergent species are *Scirpus acutus*, *Sparganium eurycarpum*, and *Typha domingensis*. The adjacent forested wetland is dominated by *Salix lasiolepis*.

Wetland Type No.: 50.241(21,25.2.563.4322,5325,6223,6255)

PALUSTRINE EMERGENT-PERSISTENT (*ATHYRIUM*, *STACHYS*, *CAREX*, *SCIRPUS*) PERMANENTLY-FLOODED TO PERMANENTLY-SATURATED ACIDIC CANYON-FLOODPLAIN WETLAND. San Luis Obispo Co., Nipomo Mesa Area, Black Lake Canyon. Dominants include *Athyrium filix-femina*, *Stachys chamissonis*, *Carex cusickii*, and *Scirpus microcarpus*.

Wetland Type No.: 50.241(21,25.2.563.6255,6733)

PALUSTRINE EMERGENT-PERSISTENT (*RORRIPA*, *SCIRPUS*, *TYPHA*) PERMANENTLY-FLOODED TO PERMANENTLY-SATURATED ACIDIC CANYON-FLOODPLAIN WETLAND. San Luis Obispo Co., Nipomo Mesa Area, Black Lake Canyon. The unusual, permanently wet, organic soils of the habitat support many rare and endangered species such as *Rorripa gambelii*, a broadleaved herbaceous species occurring among *S. microcarpus*, in addition to other species that reach their southern limits of distribution in the wetlands in Black Lake Canyon.

Wetland Type No.: 50.241(21,25.2.563.7000)

PALUSTRINE EMERGENT-PERSISTENT (MIXED VASCULAR) PERMANENTLY-FLOODED TO PERMANENTLY-SATURATED ACIDIC CANYON-FLOODPLAIN WETLAND. San Luis Obispo Co., Black Lake Canyon. Wetlands in unique canyon-bottoms in coastal central California are characterized by seasonally-flooded and permanently or semipermanently saturated hydrology. Various classes of palustrine wetlands occur in this HGM unit including a type of emergent wetland that supports many sensitive plant species. The wet, organic soils characterize a form of "bog-like" freshwater marsh where many northern plant species (e.g., *Carex cusickii*, *Calamagrostis nutkaensis*) reach their southern limits of distribution. Characteristic herbaceous species include *Arenaria paludicola*, *Athyrium filix-femina*, *Carex cusickii*, *Cladium californicum*, *Calamagrostis nutkaensis*, *Galium trifidum*, *Plantanthera leucostachys*, *Psoralea orbiculata*, *Rumex fenestratus*, *Rorripa gambelii*, *Scirpus microcarpus*, *S. americanus*, *Solidago confinis*, *Sparganium eurycarpum*, *Stachys chamissonis*, *Typha latifolia*, and *Urtica dioica*. Associated shrub species include *Baccharis douglasii*, *Lonicera involucrata*, and *Ribes divaricatum*. Associated trees include *Myrica californica* and *Salix lasiolepis*. Significant ecosystem functions include habitat for endangered species (i.e., *Arenaria paludicola*, *Rorripa gambelii*, and the Pacific Pond Turtle).

Wetland Type No.: 50.241(21.3.728.6252,6732)

PALUSTRINE PERSISTENT-EMERGENT (*SCIRPUS AMERICANUS*, *TYPHA DOMINGENSIS*) PERMANENTLY-FLOODED ALKALI VALLEY-SPRING WETLAND. San Luis Obispo Co., Cuyama Valley.

Wetland Type No.: 50.241(23.1.241.6251,6322)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS ACUTUS*, *JUNCUS OXYMERIS*) SEMIPERMANENTLY-FLOODED MONTANE-DRAINAGE-CHANNEL WETLAND. San Diego Co., Rancho Cuyamacha State Park, vicinity of Cuyamacha Lake.

Wetland Type No.: 50.241(23.1.849.6253,6732)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS CALIFORNICUS*, *TYPHA DOMINGENSIS*) SEMIPERMANENTLY-FLOODED LAGOON-SHORE WETLAND. San Diego Co., Oceanside, Buena Vista Lagoon.

Wetland Type No.: 50.241(24.1.374.6255)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS MICROCARPUS*) SEASONALLY-FLOODED COASTAL-PLAIN STREAM-BANK WETLAND. San Luis Obispo Co., Morro Bay, Morro Creek.

Wetland Type No.: 50.241(24.1.145.6242)

PALUSTRINE EMERGENT-PERSISTENT (*ELEOCHARIS MACROSTACHYA*) SEASONALLY-FLOODED VERNAL-POND WETLAND. Santa Barbara Co., foothill-valley of the San Rafael Mountains, Sedgwick Ranch. Persistent emergent vegetation dominated by *Eleocharis palustris* characterizes the margins of the pond and adjacent vernal marsh wetland. Nonpersistent emergent vegetation can colonize the outer margins or the center of the pond in drier years, forming a habitat with characteristics of vernal pools.

Wetland Type No.: 50.241(24.1.811.1100)

PALUSTRINE PERSISTENT-EMERGENT SEASONALLY-FLOODED VERNAL-POOL WETLAND. Santa Barbara Co., Goleta, Ellwood Mesa. Depending on the time of year, flooding state of the water regime, and dominant type of substrate or organisms, such vernal pools may be classified as several wetland types, including unconsolidated-bottom, aquatic bed, emergent-persistent, and emergent-nonpersistent wetlands.

Wetland Type No.: 50.241(24.1.811.5224,6241,6242)

PALUSTRINE PERSISTENT-EMERGENT (*ERYNGIUM VASEYI*, *ELEOCHARIS* SPP.) SEASONALLY-FLOODED COASTAL-MESA VERNAL-POOL WETLAND. Santa Barbara Co., Goleta, Ellwood Mesa. Although many vernal pools support nonpersistent emergent vegetation, those of the Santa Barbara area are generally characterized by persistent vegetation that is dominated by *Eryngium vaseyi*, *Eleocharis acicularis*, and *Eleocharis macrostachya*. Numerous species characteristic of nonpersistent vegetation also occur in these pools, including the annual plants *Callitriche marginata*, *Crassula aquatica*, *Elatine brachysperma*, and *Psilocarphus brevissimus*.

Wetland Type No.: 50.241(24.1.816.7000)

PALUSTRINE EMERGENT-PERSISTENT (MIXED VASCULAR) PLATEAU-VERNAL-POOL WETLAND. Riverside Co., Santa Rosa Plateau. Dominant species include *Deschampsia danthonioides*, *Blennosperma nanum*, *Alopecurus saccatus*, *Psilocarphus brevissimus*, *Plantago elongata*, *Callitriche marginata*, *Veronica peregrina*, *Lasthenia californica*, *Lilaea scilloides*, *Plagiobothrys undulatus*, *Eryngium aristulatum*, *Elatine brachysperma*, *Crassula aquatica*, *Eleocharis acicularis*.

Wetland Type No.: 50.241(24.1.826.6242,6612)

PALUSTRINE EMERGENT-PERSISTENT (*ELEOCHARIS MACROSTACHYA*, *PASPALUM DISTICHUM*) SEASONALLY-FLOODED VERNAL-LAKE WETLAND. Riverside Co., Santa Rosa Plateau, Mesa de Colorado. Vernal wetlands of the Plateau vary in size and function from vernal pools to vernal lakes and from vernal marshes to tenajas. The extensive variation and gradation among types contribute to the species richness of the plateau. Dominance types can vary depending upon the time of year, and the depth and duration of flooding. Margins of vernal lakes and pools may be dominated by *Blennosperma nanum*, whereas *Lilaea scilloides* may dominate bottoms of depressions that flood longer. As sites desiccate, dominance types also may change, whereby species characteristic of flooded conditions are replaced by species that colonize exposed soils.

Wetland Type No.: 50.241(24.1.826.5566,6111,6240)

PALUSTRINE EMERGENT-PERSISTENT (*AMMANNIA*, *ALISMA*, *ELEOCHARIS*) SEASONALLY-FLOODED VERNAL-LAKE WETLAND. Santa Barbara Co., Laguna Blanca (now seriously degraded) and historically the "lagunitas" in the Carpinteria Valley; Ventura Co., Mirror Lake in the Ojai Valley; Orange Co.,

Upper Laguna Lake in Laguna Canyon. Characteristic species include *Alisma plantago-aquatica*, *Ammannia coccinea*, *Bergia texana*, *Crassula aquatica*, *Cyperus aristatus*, *Eleocharis acicularis*, *E. macrostachya*, *Hydrocotyle ranunculoides*, *Limosella acaulis*, *Lindernia dubia* var. *anagallidea*, *Marsillea vestita*, *Pilularia americana*, *Sagittaria sanfordii*, and *Xanthium strumarium*.

Wetland Type No.: 50.241(24.1.831.5261,6210,6320,6594)

PALUSTRINE EMERGENT-PERSISTENT (*SOLIDAGO*, *CAREX*, *JUNCUS*, *MUHLENBERGIA*) SEASONALLY-FLOODED MONTANE-VERNAL-MEADOW WETLAND. San Diego Co., Cleveland National Forest, Laguna Mountains, Laguna Fire Station. These montane meadows are rich in plant species and are dominated or characterized by *Solidago californica*, *Carex* spp., *Juncus balticus*, *J. tenuis*, and *Muhlenbergia rigens*. Other characteristic genera include *Artemisia*, *Aster*, *Gnaphalium*, *Mimulus*, and *Sidalcea*.

Wetland Type No.: 50.241(24.1.851.6317)

PALUSTRINE PERSISTENT-EMERGENT (*JUNCUS MEXICANUS*) SEASONALLY-FLOODED MONTANE-DRAINAGE-SWALE WETLAND. San Diego Co., Cleveland National Forest, Laguna Mountains, Meadows Information Station.

Wetland Type No.: 50.241(24.1.851.6325)

PALUSTRINE EMERGENT-PERSISTENT (*JUNCUS RUGULOSUS*) SEASONALLY-FLOODED MONTANE-DRAINAGE-SWALE WETLAND. Riverside Co., Santa Ana Mountains, DeLuz Creek Watershed, DeLuz Rd. and Via Vaquera. This wetland can also be classified as a form of vernal-marsh that is characterized by other monocot hydrophytes such as *Eleocharis macrostachya*, *Juncus mexicanus*, and *Leymus triticoides*.

Wetland Type No.: 50.241(24,25.1.832.7000)

PALUSTRINE EMERGENT-PERSISTENT (MIXED VASCULAR) SEASONALLY-FLOODED AND PERMANENTLY SATURATED MONTANE-PERENNIAL-MEADOW WETLAND. San Bernardino Co., San Bernardino Mountains, San Geronio Wilderness Area, South Fork of the Santa Ana River. Permanently saturated meadows along the South Fork have perhaps the richest flora of the study region. This wetland type occurs in a *Abies concolor* (White Fir) and *Pinus jeffreyi* (Jeffrey Pine) forest setting. Plant genera represented include, for example, grasses (*Elymus*, *Poa*, *Glyceria*), rushes (*Juncus*, *Luzula*), sedges (*Carex*, *Eleocharis*), and many forbs (*Angelica*, *Aster*, *Berula*, *Dephningium*, *Barbarea*, *Dodecatheon*, *Heracleum*, *Geranium*, *Helonium*, *Hypericum*, *Epilobium*, *Gayophytum*, *Gentiana*, *Lilium*, *Lupinus*, *Lotus*, *Senecio*, *Stachys*, *Veratrum*, *Smilacina*, *Sidalcea*, *Solidago*, and others).

Wetland Type No.: 50.241(24,26.1.831.7000)

PALUSTRINE EMERGENT-PERSISTENT (MIXED VASCULAR) SEASONALLY-FLOODED MONTANE-VERNAL-MEADOW WETLAND. San Bernardino Co., San Bernardino Mountains, San Bernardino National Forest, meadow at Champion Lodgepole Pine. "Dry" (seasonally saturated) meadows occur in the San Bernardino Mountains in openings in forests dominated by *Abies concolor*, *Pinus contorta*, and *Pinus jeffreyi*. They are characterized by mineral rather than organic soils and are rich in plant species, although generally dominated by sedges, rushes, and grasses. Meadows in this mountain range vary considerably depending upon the depth and duration of flooding and whether they remain saturated during the dry summers or desiccate. Characteristic species include *Achillea millifolium*, *Agrostis* sp., *Aquilegia frondosa*, *Carex praegracilis*, *Carex* spp., *Castilleja* spp., *Danthonia californica* var. *americana*, *Elymus glaucus*, *Glyceria* sp., *Juncus balticus*, *Juncus* sp., *Potentilla glandulosa*, *Pteridium aquilinum*, *Smilacina racemosa*.

Wetland Type No.: 50.241(24,26.1.854,6324)

PALUSTRINE EMERGENT-PERSISTENT (*JUNCUS PHAEOCEPHALUS*)

SEASONALLY-FLOODED VERNAL-DRAINAGE-SWALE WETLAND. San Luis Obispo Co., Piedras Blancas and San Simeon State Beach.

Wetland Type No.: 50.241(24,28.3.152.6251)

PALUSTRINE EMERGENT-PERSISTENT (*SCIRPUS ACUTUS*) SEASONALLY TO INTERMITTANTLY-FLOODED MONTANE-ALKALI-LAKE WETLAND. San Bernardino Co., Baldwin Lake. Baldwin Lake in the San Bernardino National Forest is a naturally, seasonally-flooded, alkali lake that occurs on the eastern-most edge of the coastward draining watersheds of the San Bernardino Mountains. It is situated, however, in a basin without external drainage. Although it does not flood every year, the lake shore and bed supports palustrine persistent-emergent vegetation of several dominance types in addition to lacustrine wetlands such those that develop along wave-formed shorelines.

Wetland Type No.: 50.241(26.1.712,714.5453)

PALUSTRINE PERSISTENT-EMERGENT (*NICOTIANA QUADRIVALIS*) SEASONALLY-SATURATED SLOPE AND STREAM-BANK-SEEP WETLAND. San Luis Obispo Co., Cuyama Valley, Cottonwood Creek. This unique wetland occurs in a grassland setting as a seep mud-flow disturbance site, which is dominated by a dense stand of the native annual *Nicotiana quadrivalis* (Indian Tall Tobacco). *Heliotropium curassavicum* is an associated species.

Wetland Type No.: 50.241(26.1.716.6242,6325)

PALUSTRINE PERSISTENT-EMERGENT (*ELOECHARIS MACROSTACHYA*, *JUNCUS RUGULOSUS*) SEASONALLY-SATURATED PLATEAU-SEEP WETLAND. Riverside Co., Santa Rosa Plateau, Slaughterhouse Canyon area, Clinton-Keith Road. Characteristic species include *Sidalcea* sp., *Lythrum* sp., *Juncus bufonius*, *Astragalus* sp., *Cerastium* sp., *Erodium* sp., and *Bromus hordeaceus*.

Wetland Type No.: 50.241(26.1.851.6222,6242,6325,6594)

PALUSTRINE EMERGENT-PERSISTENT (*CAREX PRAEGRACILIS*, *ELOECHARIS MACROSTACHYA*, *JUNCUS RUGULOSUS*, *MUHLENBERGIA RIGENS*) SEASONALLY-FLOODED MONTANE-DRAINAGE-SWALE WETLAND. Riverside Co., Santa Rosa Plateau, Slaughterhouse Canyon Area, Clinton-Keith Rd.

Wetland Type No.: 50.241(26.1.853.6311,6317)

PALUSTRINE EMERGENT-PERSISTENT (*JUNCUS ACUTUS*, *JUNCUS MEXICANUS*) SEASONALLY-SATURATED BEACH-SWALE WETLAND. San Diego Co., Encinitas, South Carlsbad State Beach, Batiquitos Lagoon.

Wetland Type No.: 50.241(26.3.398.5252,5256,6481,6652)

PALUSTRINE EMERGENT-PERSISTENT (*ARTEMISIA*, *GUTIERREZIA*, *DISTICHLIS*, *POA*) SEASONALLY-SATURATED ALKALI SPRING-MARGIN WETLAND. San Bernardino Co., San Bernardino Mountains, Baldwin Lake Ecological Reserve. The mixed-vascular dominance types and endemic flora contribute to the species richness. Dominant or characteristic species can include *Artemisia ludoviciana*, *Gutierrezia sarothrae*, *Distichlis spicata*, and *Poa secunda*. Endemic and rare or endangered species include *Castilleja cinerea*, *Ivesia argyrocoma*, *Sidalcea pedata*, and *Thelypodium stenopetalum*.

Wetland Type No.: 50.241(26.3.831.5252,5265,6481,6652)

PALUSTRINE EMERGENT-PERSISTENT (*ARTEMISIA*, *GUTIERREZIA*, *DISTICHLIS*, *POA*) SEASONALLY-SATURATED ALKALI MONTANE-MEADOW WETLAND. San Bernardino Co., San Bernardino Mountains, Big Bear Lake, Eagle Point. Although the habitat is different than the spring-margin alkali type, this alkali meadow supports the same type of wetland dominants and the endemic, endangered flora restricted to the old deltaic sediments, which were deposited in Pleistocene lakes that once characterized the region.

Wetland Type No.: 50.241 (26.3.398.5291, 6481, 6582)

PALUSTRINE EMERGENT-PERSISTENT (*FRANKENIA*, *DISTICHLIS*, *LEYMUS*) SEASONALLY-SATURATED ALKALI SPRING-MARGIN WETLAND. San Luis Obispo Co., Cuyama Valley.

Wetland Type No.: 50.241(26.6.551.5272,5291,5552,6481)

PALUSTRINE EMERGENT-PERSISTENT (*SALICORNIA*, *FRANKENIA*, *ATRIPLEX*, *DISTICHLIS*) SEASONALLY-SATURATED EURYHALINE STREAM-FLOODPLAIN WETLAND. San Diego Co., San Elijo State Ecological Preserve.

Wetland Type No.: 50.241(26.6.848.5272.5291)

PALUSTRINE EMERGENT-PERSISTENT (*SALICORNIA VIRGINICA*, *FRANKENIA SALINA*) SEASONALLY-SATURATED EURYHALINE DIKED-ESTUARINE-MARSH WETLAND. San Diego Co., San Elijo State Ecological Preserve.

Wetland Type No.: 50.241(26.6.849.5259.6256.6311.6481)

PALUSTRINE EMERGENT-PERSISTENT (*JAUMEA CARNOSA*, *SCIRPUS PUNGENS*, *JUNCUS ACUTUS*, *DISTICHLIS SPICATA*) SEASONALLY-SATURATED EURYHALINE LAGOON-SHORE-MARSH WETLAND. San Diego Co., Oceanside, Buena Vista Lagoon.

Wetland Type No.: 50.241(27.1.833.7000)

PALUSTRINE EMERGENT-PERSISTENT (MIXED VASCULAR) TEMPORARILY-FLOODED BEACH-SWALE WETLAND. San Diego Co., Encinitas, South Carlsbad State Beach, Batiquitos Lagoon in barrow pit. Dominant species include *Xanthium strumarium*, *Cyperus eragrostis*, *Paspalum dilatatum*, *Conyza canadensis*, *Lythrum hyssopifolia*, *Chenopodium ambrosioides*, *Gnaphalium luteo-album*.

Wetland Type No.: 50.241(28.1.551.6222,6317,6582)

PALUSTRINE EMERGENT-PERSISTENT (*CAREX PRAEGRACILIS*, *JUNCUS MEXICANUS*, *LEYMUS TRITICOIDES*) INTERMITTANTLY-FLOODED STREAM-FLOODPLAIN WETLAND. Riverside Co., Santa Rosa Plateau.

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50.000 SYSTEM PALUSTRINE

50.240 CLASS EMERGENT WETLAND

50.242 SUBCLASS EMERGENT-NONPERSISTENT WETLAND

Wetland Type No.: 50.242(24.1.112.1500,5595)

PALUSTRINE EMERGENT-NONPERSISTENT (MIXED-COARSE AND *MIMULUS GUTTATUS*) SEASONALLY-FLOODED TENAJA WETLAND. Riverside Co., Ranta Rosa Plateau, Volcano Rd. at Rancho California Rd.

Wetland Type No.: 50.242(24.1.812.1500,1600,5547)

PALUSTRINE EMERGENT-NONPERSISTENT (*DOWNINGIA CUSPIDATA*, MIXED-COARSE, SAND TYPES) SEASONALLY-FLOODED MESA-VERNAL-POOL WETLAND. San Diego Co., Kearny Mesa, Miramar Mounds National Natural Monument.

Wetland Type No.: 50.242(24.1.812.5547)

PALUSTRINE EMERGENT-NONPERSISTENT (*DOWNINGIA CUSPIDATA*) SEASONALLY-FLOODED MESA-VERNAL-POOL WETLAND. San Diego Co., Kearny Mesa, Miramar Mounds National Natural Monument.

Wetland Type Nos.: 50.242(24.1.812.5532)

PALUSTRINE EMERGENT-NONPERSISTENT (*LASTHENIA CALIFORNICA*) SEASONALLY-FLOODED MESA-VERNAL-POOL WETLAND. San Diego Co., Otay Mesa, Upper O'Neil Canyon. This driest phase of the Otay vernal

pools is characterized by upland and wetland annual species and is dominated by *Lasthenia californica*.

Wetland Type No.: 50.242(24.1.812.5532)

PALUSTRINE EMERGENT-NONPERSISTENT (*LASTHENIA CALIFORNICA*) SEASONALLY-FLOODED MESA-VERNAL-POOL WETLAND. San Diego Co., Otay Mesa, Upper O'Neil Canyon.

Wetland Type No.: 50.242(24.1.826.7000)

PALUSTRINE EMERGENT-NONPERSISTENT (MIXED VASCULAR) SEASONALLY-FLOODED VERNAL-LAKE WETLAND. Riverside Co., Santa Rosa Plateau.

Wetland Type No.: 50.242(24.26.6.511,524,7000)

PALUSTRINE EMERGENT-NONPERSISTENT (MIXED VASCULAR) SEASONALLY-FLOODED OR SATURATED EURYHALINE VERNAL-FLAT OR PLAIN WETLAND. Santa Barbara Co., Santa Barbara Municipal Airport at Goleta Slough; Ventura Co., Pt. Mugu Pacific Missile Testing Center at Mugu Lagoon; San Diego Co., San Dieguito Lagoon. Coastal streams that flow into saline or hypersaline estuarine environments generally produce deltas that are characterized by seasonally-saturated nontidal palustrine wetlands as well as irregularly-flooded intertidal estuarine wetlands. The palustrine wetlands are generally seriously degraded by urbanization and often are separated from the deltaic continuum by berms, ditches, roads, runways, and other artificial structures. The palustrine habitats dominated by annual plants are classified as Palustrine Nonpersistent Emergent Wetlands, whereas those dominated by perennials or shrubs are classified as Palustrine Persistent Emergent or Scrub-Shrub Wetlands. Characteristic species include *Atriplex argentea* var. *mohavensis*, *A. triangularis*, *Hordeum depressum*, *Hutchinsia procumbens*, *Juncus bufonius*, *Lasthenia glabrata* ssp. *coulteri*, *Salicornia europaea*, *Spergularia marina*, and *Suaeda calceoliformis*.

Wetland Type No.: 50.242(24.26.1.522,7000)

PALUSTRINE EMERGENT-NONPERSISTENT (MIXED VASCULAR) SEASONALLY-FLOODED MONTANE-VERNAL-PLAIN WETLAND. Ventura Co., Upper Ojai Valley; Riverside Co., Murrietta Valley. These unique vernal plains have been heavily impacted by agriculture and grazing, and today support mostly naturalized (and native) weedy species. These include *Anthemis cotula*, *Juncus bufonius*, *Lythrum hyssopifolia*, *Lolium multiflorum*, *Polygonum monspeliensis*.

Wetland Type No.: 50.242(24.26.1.854.6821)

PALUSTRINE EMERGENT-NONPERSISTENT (*LOLIUM MULTIFLORUM*) SEASONALLY-SATURATED VERNAL-DRAINAGE-SWALE WETLAND. Santa Barbara Co., Dos Pueblos Rancho. Coastal drainage swales of the region generally occur in grassland settings and serve as rangeland for cattle. The dominant annual grass in this wetland swale is *Lolium multiflorum*.

Wetland Type No.: 50.242(26.3.523.5532)

PALUSTRINE EMERGENT-NONPERSISTENT (*LASTHENIA CALIFORNICA*) SEASONALLY-FLOODED ALKALI VERNAL-PLAIN WETLAND. Riverside Co., Old Salt Creek Drainage west of Hemet, Florida Ave. and Warren Rd. Small basins forming vernal pools with different dominance types occur throughout the plain. The disked, desiccated plain is dominated by *Lasthenia californica*, but may appear with different dominant plant species depending on the time of year, amount of rainfall in a particular year, proximity to local vernal pool areas, and degree of disturbance (Fig. 5, pg. 197).

Wetland Type No.: 50.242(26.6.848.5558)

PALUSTRINE EMERGENT-NONPERSISTENT (*SALICORNIA EUROPEA*) SEASONALLY-SATURATED EURYHALINE DIKED-ESTUARINE-MARSH WETLAND. San Diego Co., San Elijo State Ecological Reserve.

Wetland Type No.: 50.242(28.3.333.5533)

PALUSTRINE EMERGENT-NONPERSISTENT (*LASTHENIA GLABRATA*) INTERMITTENTLY-FLOODED ALKALI PLAYA-LAKE-SHORE WETLAND. Riverside Co., San Jacinto Valley, San Jacinto Wildlife Area, vicinity of Mystic Lake. Fragmentation of wetlands of the region has converted some lacustrine wetlands into palustrine types.

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50.000 SYSTEM PALUSTRINE

50.250 CLASS SCRUB-SHRUB WETLAND

50.251 SUBCLASS BROADLEAVED-DECIDUOUS

Wetland Type No.: 50.251(23.1.155.5765,5766)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*SALIX LAEVIGATA*, *SALIX LASIOLEPIS*) SEMIPERMANENTLY-FLOODED RIVER-VALLEY-RESERVOIR WETLAND. San Luis Obispo Co., Twitchell Reservoir on the Cuyama River at Alamo Creek. The willow scrub formed on alluvial deposits in the reservoir during low-water conditions.

Wetland Type No.: 50.251(24.1.482.5769)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*SALIX SCOULERIANA*) SEASONALLY-FLOODED FOOTHILL-RIVER CHANNEL-BAR WETLAND. Monterey Co., Pfeiffer Big Sur State Park, Big Sur River. Scrub-shrub wetland dominated by *Salix scouleriana* occurs on a channel-bar adjacent to riverine unconsolidated-bottom wetland.

Wetland Type No.: 50.251(24.25.1.716,726,824,5768)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*SALIX LUTEA*) SEASONALLY-FLOODED AND PERMANENTLY-SATURATED MONTANE-SPRING, SEEP AND GLACIAL POND WETLANDS. San Bernardino Co., San Geronio Wilderness Area, Dollar Lake. Scattered patches of willow-dominated scrub-shrub wetland occur at many wetland habitats in the Transverse Ranges. *Salix lutea* is common at high elevations in the study region.

Wetland Type No.: 50.251(24.25.1.375,716,726,5791)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*VITIS GIRDIANA*) PERMANENTLY AND SEASONALLY-SATURATED CANYON-STREAM-BANK, MONTANE-SEEP AND MONTANE-SPRING WETLANDS. San Bernardino Co., San Bernardino Mountains, City Canyon, along Rt. 330. Scattered dense tangles of this native grape dominate seeps and springs along rocky banks at ledges of montane canyons, such as along Rt. 330.

Wetland Type No.: 50.251(25.1.375,715,5756)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*RUBUS PARVIFLORUS*) PERMANENTLY-SATURATED RIVER-BANK-SEEP WETLAND. Monterey Co., Banks of the Big Sur River, Pfeiffer Big Sur State Park, Santa Lucia Mountains. In the central coastal portion of California, e.g., in the Santa Lucia Mountains, perennial seeps and springs generally support a rich association of hydrophytic shrubs and herbaceous plants. When shrubs dominate these conditions, *Rubus parviflorus* is frequently the shrub that characterizes the vegetation of this hydrogeomorphic unit.

Wetland Type No.: 50.251(26.1.851.5752)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-DECIDUOUS (*ROSA CALIFORNICA*) SEASONALLY-SATURATED MONTANE-DRAINAGE-SWALE WETLAND. San Diego Co., Laguna Mountains, Cleveland National Forest, Meadows Information Station. This wetland occurs on the edges of swales characterized by palustrine emergent wetland and dominated by rushes such as *Juncus mexicanus*.

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50.000 SYSTEM PALUSTRINE**50.250 CLASS SCRUB-SHRUB WETLAND****50.253 SUBCLASS BROADLEAVED-EVERGREEN**

Wetland Type No.: 50.253 (24.1.453.5623)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*BACCHARIS SALICIFOLIA*) SEASONALLY-FLOODED VALLEY-STREAMBED WETLAND. San Diego Co., Cottonwood Creek, Rt. S-1 northwest of Lake Morena.

Wetland Type No.: 50.253(24.1.453.5781)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*TAMARIX RAMOSISSIMA*) SEASONALLY-FLOODED VALLEY-STREAMBED WETLAND. San Diego Co., Cottonwood Creek, Rt. S-1 northwest of Lake Morena. This wetland is dominated by the invasive-exotic shrub *Tamarix ramosissima*.

Wetland Type No.: 50.253(26.3.398.5643)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*SUAEDA MOQUINII*) SEASONALLY-SATURATED ALKALI SPRING-MARGIN WETLAND. San Luis Obispo Co., Cuyama River Valley, Highway 166, east of Highway 33.

Wetland Type No.: 50.253(26.29.1.853.5622)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*BACCHARIS PILULARIS*) SEASONALLY-SATURATED OR PHREATOPHYTIC DUNE-SWALE WETLAND. Santa Barbara Co. San Antonio Terrace, Vandenberg Air Force Base. Dune swale wetlands in coastal dune systems are characterized by various types of wetland that largely reflect the water regime of the site. The outer zone of seasonally flooded swales and the bottom zone of the driest wetland swales are often dominated by phreatophytic shrubs, especially *Baccharis pilularis*, and usually have emergent hydrophytes, such as *Carex praegracilis*, as a dominant understory.

Wetland Type No.: 50.253(26.29.3.554.641.5628)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*CHRYSOTHAMNUS NAUSEOSUS*) SEASONALLY-SATURATED OR PHREATOPHYTIC MONTANE FLOODPLAIN AND ALLUVIAL FAN WETLAND. San Bernardino Co., San Bernardino Mountains National Forest, Fawnskin, Highway 38, Baldwin Lake. In the vicinity of Big Bear and Baldwin Lakes in the San Bernardino Mountains, exposed Pleistocene deltas and Holocene floodplains, alluvial fans, and washes support scrub-shrub wetlands that are seasonally saturated or more characteristically phreatophytic and dominated by *Chrysothamnus nauseosus*. This form of alkali scrub is often in the vicinity of seasonal seeps and springs and alkali emergent wetlands in the form of vernal meadows and vernal marshes. It occurs in the context of Jeffrey Pine and White Fir Forest.

Wetland Type No.: 50.253(27.1.385.5627)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*PLUCHEA SERICEA*) TEMPORARILY-FLOODED CANYON-RIVER-BANK WETLAND. San Luis Obispo Co., Cuyama River Gorge. *Pluchea*-dominated scrub-shrub wetland occurs on a narrow, undercut bank.

Wetland Type No.: 50.253(28.1.561.5627)

PALUSTRINE SCRUB-SHRUB BROADLEAVED-EVERGREEN (*PLUCHEA SERICEA*) PHREATOPHYTIC RIVER-TERRACE WETLAND. San Luis Obispo Co., Cuyama River Valley. *Pluchea sericea* forms an extensive scrub-shrub wetland on alluvial soils deposited in the lower valley, up-river from the Cuyama River Gorge (Fig. 6, pg. 201).

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50.000 SYSTEM PALUSTRINE**50.250 CLASS SCRUB-SHRUB WETLAND****50.257 SUBCLASS MIXED DECIDUOUS AND EVERGREEN**

Wetland Type No.: 50.257(24,28.1.480,5623,5624,5625,5626,5721)

PALUSTRINE SCRUB-SHRUB MIXED-DECIDUOUS AND EVERGREEN (BACCHARIS, BRICKELLIA, ISOCOMA, LEPIDOSPARTUM, ERIOGONUM) TEMPORARILY OR INTERMITTANTLY-FLOODED RIVER-CHANNEL-BAR WETLAND. Monterey Co., Big Sur River, Andrew Molera State Park; Santa Barbara Co., Santa Ynez and Santa Maria Rivers; Ventura Co., Santa Clara and Ventura Rivers; San Diego Co., San Luis Rey River. Wetland occurs on bars in channels of intermittent and perennial streams and rivers throughout the study region. Characteristic species include *Baccharis salicifolia*, *Brickellia californica*, *Eriogonum fascicularis*, *Isocoma veneta*, *Lepidospartum squamatum*, *Salix exigua*, *S. lasiolepis* (scrub), *Solanum douglasii*.

Wetland Type No.: 50.257(26,29.1.375,553,5614,5622,5755,5626,5661)

PALUSTRINE SCRUB-SHRUB MIXED-DECIDUOUS AND EVERGREEN (TOXICODENDRON, BACCHARIS, RUBUS, RUBES) SEASONALLY-SATURATED TO PHREATOPHYTIC CANYON-STREAM-BANK AND BOTTOMLAND WETLAND. San Luis Obispo Co., Black Lake Canyon. This scrub-shrub wetland, which often can be dominated by deciduous species, occurs on the margins of emergent and forested wetlands and ponds in canyon bottomlands and stream banks in coastal central California. At sites that can receive seasonal flooding or saturation, the vegetation tends to be characterized by greater cover of *Lonicera involucrata*, *Ribes divaricatum*, *Rosa californica*, and *Rubus ursinus*. At sites that tend to be phreatophytic rather than seasonally flooded or saturated, the vegetation is often dominated by the evergreen shrubs *Baccharis pilularis* and *Rhamnus californica*.

Wetland Type No.: 50.257(26,29.1.853,5614,5622,5691,5743,5755,5766)

PALUSTRINE SCRUB-SHRUB MIXED-DECIDUOUS AND EVERGREEN (TOXICODENDRON, BACCHARIS, MYRICA, RUBUS, SALIX, RHAMNUS) SEASONALLY-SATURATED OR PHREATOPHYTIC DUNE-SWALE WETLAND. San Luis Obispo Co., Nipomo Dunes, Guadalupe Dunes; Santa Barbara Co., San Antonio Terrace, Vandenberg Air Force Base, Coal Oil Point Reserve; Ventura Co., Emma Wood State Beach, McGrath State Beach, Mandalay Beach County Park. This wetland type occurs on margins and in bottoms of dune swales and can be quite rich in shrub species.

Wetland Type No.: 50.257(28,29.1.375,5614,5622,5743,5755,5757,5766)

PALUSTRINE SCRUB-SHRUB MIXED-DECIDUOUS AND EVERGREEN (TOXICODENDRON, BACCHARIS, RHAMNUS, RUBUS, HETEROMELES, SALIX) INTERMITTANTLY-FLOODED OR PHREATOPHYTIC CANYON-STREAM-BANK WETLAND. Santa Barbara Co., Llaga, Mission, and San Jose Creeks. This species-rich scrub-shrub wetland varies considerably in composition in coastal canyons and often is located in riparian corridors between downslope, seasonally flooded forested wetlands and upslope, non-wetland habitats and plant associations. Some classifications might consider this a mesic upland scrub rather than a type of wetland. However, its proximity to obvious wetland obligate and facultative wetland shrubs in many examples, gives support to the inclusion of the wetland into this classification. Characteristic species include *Artemisia californica*, *Baccharis pilularis*, *Clematis ligusticifolia*, *Heteromeles arbutifolia*, *Isocoma veneta*, *Keckiella cordifolia*, *Phacelia ramosissima*, *Rhamnus californica*, *Ribes* spp., *Rubus ursinus*, *Salix lasiolepis*, *Sambucus mexicanus*, *Toxicodendron diversilobum*, *Venegasia carpesioides*.

50.000 SYSTEM PALUSTRINE**50.260 CLASS FORESTED WETLAND****50.261 SUBCLASS BROADLEAVED-DECIDUOUS**

Wetland Type No.: 50.261(22.1.553.5986)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LASIOLEPIS*) INTERMITTENTLY-EXPOSED CANYON-FLOODPLAIN WETLAND. San Luis Obispo Co., Nipomo Mesa Area, Black Lake Canyon. A broad-leaved evergreen tree, *Myrica californica* (Wax Myrtle), occurs with *Salix lasiolepis* (Arroyo Willow) in these flooded conditions. This wetland is a rare, apparently natural occurrence of a permanently flooded "swamp" wetland that is located in the canyon bottomland at Black Lake Canyon. This forested wetland is part of a rich and regionally unique ecosystem that also supports palustrine aquatic bed, emergent, and scrub-shrub wetlands.

Wetland Type No.: 50.261(23.1.155.5985,5986)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LAEVIGATA*, *SALIX LASIOLEPIS*) SEMIPERMANENTLY-FLOODED RIVER-VALLEY-RESERVOIR WETLAND. San Luis Obispo Co., Twitchell Reservoir on the Cuyama River, Alamo Creek portion.

Wetland Type No.: 50.261(24.1.211.5821)

PALUSTRINE FORESTED BROAD-LEAVED DECIDUOUS (*PLATANUS RACEMOSA*) SEASONALLY-FLOODED PLATEAU-STREAM-CHANNEL WETLAND. Riverside Co., Ranta Rosa Plateau, Volcano Rd. at Rancho California Rd.

Wetland Type No.: 50.261(24,25.1.382.5921)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*ALNUS RHOMBIFOLIA*) SEASONALLY-FLOODED AND PERMANENTLY-SATURATED FOOTHILL-RIVER-BANK WETLAND. Monterey Co., Pfeiffer Big Sur State Park, Big Sur River. *Alnus*-dominated wetland occurs as a row of small trees between the riverine wetlands and needleleaved-evergreen forested wetland dominated by *Sequoia sempervirens* (Coast Redwood).

Wetland Type No.: 50.261(25.1.552.5986)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LASIOLEPIS*) PERMANENTLY-SATURATED RIVER-FLOODPLAIN WETLAND. Monterey Co., Andrew Molera State Park, Big Sur River. This forested wetland of small trees also is flooded occasionally, but the dominant hydrology that affects the vegetation is one of saturation. The understory is composed of hydrophytes such as *Scirpus microcarpus*.

Wetland Type No.: 50.261(27.1.552.5833)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LAEVIGATA*) TEMPORARILY-FLOODED RIVER-FLOODPLAIN WOODLAND WETLAND. Ventura Co., Santa Clara River Valley, Santa Clara River at Mayo Crossing. Woodland is dominated by *Salix laevigata* (Red Willow) with an understory of *Urtica dioica* (Stinging Nettle).

Wetland Type No.: 50.261(28.1.251.5912)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*ACER MACROPHYLLUM*) INTERMITTENTLY-FLOODED MONTANE-CANYON INVERT WETLAND. Monterey Co., Los Padres National Forest, Mill Creek Watershed. This forested wetland occurs as a narrow row of trees in the bottom of the shallow canyon slope drainage invert.

Wetland Type No.: 50.261(28.1.371.5833)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LAEVIGATA*) MONTANE-STREAM-BANK-WOODLAND WETLAND. San Bernardi-

no Co., San Bernardino Mountains, Fish Creek Watershed, south of junction of roads 1N05 and 1N02. Along some intermittent streams in the San Bernardino National Forest in the vicinity of the San Gorgonio Wilderness Area, narrow woodlands of *Salix laevigata* (Red Willow) occur in intermittently flooded conditions. This apparently is an uncommon wetland type that is stressed because of the intermittent nature of the streams. The woodlands occur in the context of Jeffrey Pine Forest.

Wetland Type No.: 50.261(29.1.372,562,5711)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*PLATANUS RACEMOSA*) PHREATOPHYTIC FOOTHILL-STREAM-BANK AND STREAM-TERRACE WETLAND. Santa Barbara Co., Santa Ynez Mountains, Gaviota State Park and Los Padres National Forest, Gaviota Hot Springs Area. Several tributaries to Gaviota Creek form terraces at this site, providing complex hydrogeomorphic landforms that support various wetlands, including this type of forested wetland dominated by *Platanus racemosa* (Western Sycamore).

Wetland Type No.: 50.261(29.1.532,5941,5981,5986)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*JUGLANS, POPULUS, SALIX*) PHREATOPHYTIC RIVER-DELTA WETLAND. Ventura Co., Emma Wood State Beach, Ventura River Mouth. Portions of the delta are sufficiently high in elevation to not be flooded during high water events, whereas adjacent sites of lower elevation are flooded seasonally or intermittently and support different types of forested wetland. Dominant trees include *Juglans californica* var. *californica*, *Populus balsamifera* ssp. *trichocarpa*, and *Salix lasiolepis*.

Wetland Type No.: 50.261(29.1.554,5983)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*POPULUS TREMULOIDES*) PHREATOPHYTIC MONTANE-BOTTOMLAND WETLAND. San Bernardino Co., San Gorgonio Wilderness Area, Fish Creek. The San Gorgonio Wilderness Area in the San Bernardino Mountains is the only region in southern California that supports groves of *Populus tremuloides*. These groves have smaller leaves than those to the north (e.g., Sierra Nevada), which results in loss of less water, an adaptation to hot, dry summers. The San Gorgonio population of Quaking Aspen is apparently relictual from Pleistocene time when the region was cooler and wetter than at present. In montane canyon bottomlands, the groves occur in the context of a Needleleaved-Evergreen Forested Wetland dominated by Jeffrey Pine and White Fir. In addition to occurring in these bottomlands, *P. tremuloides* also occurs in small groves along streambanks, such as along Fish Creek.

Wetland Type No.: 50.261(29.1.561,5981)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*POPULUS BALSAMIFERA*) PHREATOPHYTIC RIVER-TERRACE WETLAND. Monterey Co., Carmel Valley along the Carmel River, Carmel Valley Rd. at Miramonte Rd.

Wetland Type No.: 50.261(29.1.562,5982,5985)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*POPULUS, SALIX*) PHREATOPHYTIC STREAM-TERRACE WETLAND. San Diego Co., Kitchen and Cottonwood Creeks. This forest type occurs on narrow terraces along interior valley streams. Dominant trees include *Populus fremontii* ssp. *fremontii* and *Salix laevigata*. An associated tree is *Quercus agrifolia*, a broadleaved evergreen species

Wetland Type No.: 50.261(29.1.632,5986)

PALUSTRINE FORESTED BROADLEAVED-DECIDUOUS (*SALIX LASIOLEPIS*) PHREATOPHYTIC CANYON-SLOPE WETLAND. San Luis Obispo Co., Black Lake Canyon, Los Osos Creek, Morro Bay at Los Osos. Canyon banks can be dominated by willow forests where the water table is near the surface, particularly where there is seasonal or permanent saturation nearby caused by seeps or springs. In the example used here, there is a rich understory of mesic herbaceous

species but few obligate hydrophytes, which demonstrates the phreatophytic rather than saturated nature of the habitat.

* * * *

50.000 SYSTEM PALUSTRINE

50.260 CLASS FORESTED WETLAND

50.263 SUBCLASS BROADLEAVED EVERGREEN

Wetland Type No.: 50.263(25.1.711.5931)

PALUSTRINE FORESTED BROADLEAVED-EVERGREEN (*LITHOCARPUS DENSIFLORUS*) PERMANENTLY-SATURATED DRAINAGE-HEAD-SEEP WETLAND. Santa Barbara Co., Santa Ynez Mountains, Hollister Ranch. Forested wetland dominated by *Lithocarpus densiflorus* (Tanbark Oak). Largest trees occur in wet soils of a seep and spring and grow upslope from a willow scrub-shrub wetland along the downstream drainage.

Wetland Type No.: 50.263(25.1.712.5952)

PALUSTRINE FORESTED BROADLEAVED-EVERGREEN (*MYRICA CALIFORNICA*) PERMANENTLY-SATURATED SLOPE-SEEP WETLAND. San Luis Obispo Co., Morro Bay, Los Osos Creek, Los Osos. Headland slope-seep dominated by *Myrica californica* (Wax Myrtle) (Fig. 7, pg. 201).

Wetland Type No.: 50.263(26.1.761.5951)

PALUSTRINE FORESTED BROADLEAVED-EVERGREEN (*UMBELLULARIA CALIFORNICA*) SEASONALLY-SATURATED MONTANE-SEEP WETLAND. Santa Barbara Co., Nojoqui Falls, Nojoqui Falls County Park; Ventura Co., North Fork, Matilija Creek at Wheeler Gorge. Clay soils from decomposed bedrock in some mountain canyons may contain seasonal seeps and springs that occasionally support forested wetlands. The occurrence can be either small groves of trees as at Wheeler Gorge or relative large stands of California Bay as at Nojoqui Falls. Associated trees can include *Acer macrophyllum*, *Alnus rhombifolia*, broadleaved-deciduous species, and *Quercus agrifolia*, a broadleaved evergreen species.

Wetland Type No.: 50.263(28,29.1.212,372.5936)

PALUSTRINE FORESTED BROADLEAVED-EVERGREEN (*QUERCUS WISLIZENII*) INTERMITTENTLY-FLOODED AND/OR PHREATOPHYTIC TERRACE-STREAM-CHANNEL AND BANK WOODLAND WETLAND. San Luis Obispo Co., Sierra Madre Mountains, Cottonwood Creek Drainage, along intermittent terrace streams and drainages adjacent to Cuyama Valley. Wetland occurs as a narrow band of scattered trees in a grassland or chaparral setting.

* * * *

50.000 SYSTEM PALUSTRINE

50.260 CLASS FORESTED WETLAND

50.264 SUBCLASS NEEDLELEAVED-EVERGREEN

Wetland Type No.: 50.264(24.1.382.5991)

PALUSTRINE FORESTED NEEDLELEAVED-EVERGREEN (*SEQUOIA SEMPERVIRENS*) SEASONALLY-FLOODED FOOTHILL-RIVER-BANK WETLAND. Monterey Co., Santa Lucia Mountains, Pfeiffer Big Sur State Park, Big Sur River. *Sequoia*-dominated wetland occurs as a narrow band on the riverbank below a palustrine forested terrace and above a narrow band of *Alnus*-dominated forested wetland along the margin of the riverine wetland of the Big Sur River.

Wetland Type No.: 50.264(25.1.716,726.5962)

PALUSTRINE FORESTED NEEDLELEAVED-EVERGREEN (*PINUS CON-TORTA* VAR. *MURRAYANA*) PERMANENTLY-SATURATED MONTANE-SPRING AND SEEP WETLAND. San Bernardino Co., San Bernardino Mountains,

San Gorgonio Wilderness Area; South Fork, Santa Ana River Watershed. Lodgepole pines occur at springs, seeps, and along streams in small groves or narrow bands of forested wetland in a coniferous forest setting. Understory includes grasses (*Elymus* sp., *Poa secunda*), rushes (*Juncus xiphioides*), sedges (*Carex* spp.) and various forbs (*Geranium robertianum*, *Geum macrophyllum*, *Hypericum* sp.).

Wetland Type No.: 50.264(28.1.211,371.5991)

PALUSTRINE FORESTED NEEDLELEAVED-EVERGREEN (*SEQUOIA SEMPERVIRENS*) INTERMITTENTLY-FLOODED MONTANE-STREAM-CHANNEL AND MONTANE-STREAM-BANK WETLAND. Monterey Co., Big Sur River and Mill Creek Watersheds, Los Padres National Forest. Wetland occurs as a narrow band of trees along canyon streams usually adjacent to other forested wetland types (e.g., *Acer-Umbellularia*) or upland forest types (e.g., *Quercus* spp.).

Wetland Type No.: 50.264(29.1.554,5961,5963)

PALUSTRINE FORESTED NEEDLELEAVED-EVERGREEN (*ABIES*, *PINUS*) PHREATOPHYTIC MONTANE-BOTTOMLAND WETLAND. San Bernardino Co., San Bernardino Mountains, San Gorgonio Wilderness Area, vicinity of Fish Creek near Rd. 1N05. The San Gorgonio Wilderness Area in the San Bernardino Mountains is the only region in southern California that supports groves of *Populus tremuloides*. In montane canyon bottomlands, the groves occur in the context of this Needleleaved-Evergreen Forested Wetland dominated by *Abies concolor* and *Pinus jeffreyi*.

* * * *

50.000 SYSTEM PALUSTRINE

50.260 CLASS FORESTED WETLAND

50.267 SUBCLASS MIXED-DECIDUOUS-AND-EVERGREEN

Wetland Type No.: 50.267(27.1.371,5912,5936,5971)

PALUSTRINE FORESTED MIXED-DECIDUOUS-AND-EVERGREEN (*ACER*, *QUERCUS*, *PLATANUS*) TEMPORARILY-FLOODED MONTANE-STREAM-BANK WETLAND. San Luis Obispo Co., Sierra Madre Mountains, Cottonwood Creek Drainage. Wetland occurs as a narrow band along montane streams. Dominant species include *Acer macrophyllum*, *Platanus racemosa*, and *Quercus wislizenii*.

Wetland Type No.: 50.267(27.1.371,5921,5933,5963)

PALUSTRINE FORESTED MIXED-DECIDUOUS-AND-EVERGREEN (*ALNUS*, *QUERCUS*, *PINUS*) TEMPORARILY-FLOODED MONTANE-STREAM-BANK WETLAND. San Diego Co., Headwaters of the Sweetwater River, Cuyamaca Mountains, Cuyamaca Regional State Park. Dominant species include *Alnus rhombifolia*, a broadleaved-deciduous tree, *Quercus agrifolia* var. *oxydenia*, a broadleaved-evergreen tree, and *Pinus jeffreyi*, a needleleaved-evergreen tree. Wetland type occurs as a narrow band along streams within a *Pinus jeffreyi* forest. Often characteristic species include *Platanus racemosa*, a broadleaved-deciduous tree, and *Calocedrus decurrens*, a needleleaved-evergreen tree.

Wetland Type No.: 50.267(29.1.632,634,5912,5951)

PALUSTRINE FORESTED MIXED-DECIDUOUS-AND-EVERGREEN (*ACER*, *UMBELLULARIA*) PHREATOPHYTIC CANYON AND MONTANE-SLOPE WETLAND. Monterey Co., Mill Creek Watershed. Wetland occurs as small groves of trees on slopes above montane canyon streambanks and often adjacent to upland forests of *Quercus* spp.



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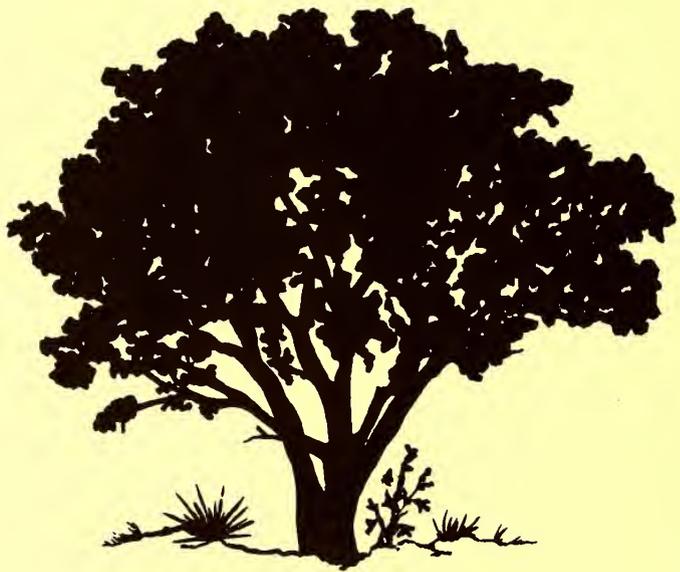
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MORPHOLOGICAL AND ELECTROPHORETIC VARIATION
AMONG THE FOUR FLORAL COLOR MORPHS OF
CLARKIA AMOENA VAR. *PACIFICA* (ONAGRACEAE)

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ABSTRACT

We examined morphological and electrophoretic variation in the four floral color morphs of *Clarkia amoena* var. *pacifica* (Peck), a plant native to grassy coastal headlands of Oregon. Mean values of morphological characters such as petal length and width, leaf length and width, fruit length, and plant height differed between the white color morph and the other three, with the white color morph being consistently larger (except for leaf width). Electrophoretic analysis at 24 loci revealed higher heterozygote frequencies and greater numbers of effective alleles in the white color morph. Nei's measure of genetic identity showed high similarity among the color variants but the white floral morph was less similar to the other morphs than they were to each other ($\bar{I} = 0.94$ versus $\bar{I} = 0.99$). Since the white morph occurs in a more isolated subpopulation at Cascade Head where the other three morphs occur sympatrically, its divergence from them in morphology and isozyme patterns might eventually lead to population differentiation and speciation.

Rapid evolutionary change often takes place in small, isolated populations and studies of such populations can lend understanding to evolutionary processes (Waser et al. 1982; Karron 1987). Examples of progenitor/derivative pairs within the genus *Clarkia* have been exceptional in this regard, providing evidence that rapid and recent speciation has occurred numerous times (Lewis 1953, 1955, 1966; Moore and Lewis 1965; Smith-Huerta 1986).

In *Clarkia*, over forty species of annuals are distributed primarily throughout the western United States. These species generally occur in small, discontinuous populations of a few to several hundred or even a thousand individuals (Smith-Huerta 1986). The genus *Clarkia* has been widely studied to determine the evolutionary relationships among various species (Lewis and Lewis 1955; Lewis and Raven 1958).

Clarkia amoena includes three varieties which range from central California northward to Vancouver Island (Hitchcock and Cronquist 1973). This study focuses on *Clarkia amoena* var. *pacifica*, a small flowered variety of the species which only occurs on grassy coastal headlands of Oregon. We are particularly interested in the possible relationships between petal color variation, morphology, and the genetics of populations occurring in a coastal prairie at Cascade Head,

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Oregon. In addition, we address the potential implications of floral color variation for the evolution of *Clarkia* in small localized populations.

MATERIALS AND METHODS

Study site. Initially, we surveyed the northern and central coast of Oregon for populations of *Clarkia amoena* var. *pacifica*. We found the variety in only two locations, Cascade Head and Cape Lookout. At Cape Lookout, we observed only one color morph (purple). Therefore, we selected Cascade Head, where four color morphs occurred, as our study site. At Cascade Head (a Nature Conservancy Preserve near Lincoln City, OR) we studied two populations of *Clarkia amoena* var. *pacifica*. One population, located in the "pinnacle" region of the headland, contained three of the four color morphs: purple spotted, white spotted and purple ("spotted" morphs contained an additional magenta spot in the center of each white or purple petal). The second population, located inland approximately 0.8 km, occurred adjacent to The Nature Conservancy trail and contained only the white morph.

Electrophoresis. To assess genetic differences among the color morphs of *Clarkia amoena* var. *pacifica*, we examined 13 enzymes using starch gel electrophoresis. We collected leaf samples from twenty individuals of each color morph from Cascade Head, and extracted enzymes from fresh material with a Tris-HCl grinding buffer (Soltis et al. 1983). Starch concentration in the gels was 12%.

Four buffer systems produced resolvable enzyme patterns. We used a lithium-borate buffer system (Werth 1985) for alcohol dehydrogenase (ADH), aspartate aminotransferase (AAT), esterase (EST), isocitrate dehydrogenase (IDH) and phosphoglucoisomerase (PGI). A tris-citrate buffer system (Soltis et al. 1983) resolved acotinase (ACO), isocitrate dehydrogenase (IDH) and phosphoglucomutase (PGM). A histidine-citrate buffer system (Stuber et al. 1977) resolved glyceraldehyde-3-phosphate (G3PDH-NAD and G3PDH-NADP forms) and 6-phosphogluconate dehydrogenase (6PGD). Finally, we used a citrate-morpholine buffer system (Wendel and Stuber 1984) for malate dehydrogenase (MDH) and shikimic dehydrogenase (SKD).

Staining followed standard recipes: AAT and ADH were stained according to Cardy et al. 1983; ACO, G3PDH, IDH, MDH, PGI, PGM, and 6PGD are provided in Shaw and Prasad 1970; EST and SKD were stained according to Soltis et al. 1983.

We made the following calculations for each color morph: the percentage of loci that are polymorphic per population (P), expected heterozygosity (H_{exp}), observed heterozygosity (H_{obs}) and effective number of alleles (A_e). Nei's genetic identities (Nei 1972) were calculated for all pairwise comparisons of the color morphs. Using

GENESTAT (Lewis and Whitkus 1989) we calculated measures of genetic diversity within and among the color morphs (H_T , H_S , G_{ST}).

Morphology. To examine possible morphological differences among the color variants within natural populations, we randomly selected 50 plants of each color morph in June 1993. We measured several morphological characters on each plant: petal length and maximum width (of first or second flower to open), leaf length and maximum width (of leaf located at the base of the flower measured), and plant height (distance from the base to the tallest bud). We also measured fruit length at maturity on ten plants of each color morph.

We established a common garden to determine whether the morphological variation we found at Cascade Head would be maintained in a common environment. We grew forty plants (12 purple spotted, 16 purple, and 12 white) in the Martha Springer Botanical Garden at Willamette University during the summer of 1993 from seeds that we collected at Cascade Head during the summer of 1992. We pooled five seeds from twenty individuals of each color morph. We germinated these seeds in the greenhouse and later transplanted them to the garden. We randomly transplanted individuals into two grids (4×5 plants) and spaced plants 30 cm apart to prevent effects of competition. Although all color morphs successfully germinated, mortality rates were high during the seedling stage and no white spotted plants survived to maturity, despite three separate attempts. We measured petal length, petal width, leaf length and leaf width on the plants grown in the garden. We examined differences among the means using analysis of variance. If the ANOVA showed significant variation among means, we used the Tukey test to identify the sets of means that were statistically distinguishable (Zar 1984).

RESULTS

Electrophoresis. The 13 enzymes encoded 24 scorable loci. Sixteen loci were monomorphic (AAT-1, ACO-1, ADH, EST-1, G3PDH-NAD-1, G3PDH-NAD-2, G3PDH-NAD-3, IDH-1, MDH-1, MDH-2, 6PGD-1, 6PGD-2, PGI-1, PGI-2, SKD-1 and SKD-2), and the eight remaining loci were polymorphic for one or more of the color morphs. In 6PGD we attributed a zone of fixed heterozygosity to a gene duplication (Odrzykoski and Gottlieb 1984).

Statistical measures of genetic variation indicate slight differences among the color morphs. P , the mean percentage of loci polymorphic per color morph was identical for the purple spotted, purple and white spotted color morphs ($P = 45.5\%$) and somewhat lower for the white ($P = 40.9\%$). The mean expected heterozygosity (H_{exp}) and the mean observed heterozygosity (H_{obs}) varied slightly among morphs and were greatest in the white color morph (Table 1). The

TABLE 1. OBSERVED HETEROZYGOSITY (H_{OBS}), EXPECTED HETEROZYGOSITY (H_{EXP}) AND EFFECTIVE NUMBER OF ALLELES (A_E) FOR POLYMORPHIC LOCI. Means are across all loci. WS = White spotted, PS = Purple spotted, P = Purple, W = White.

Locus	H_{obs}				H_{exp}				A_e			
	WS	PS	P	W	WS	PS	P	W	WS	PS	P	W
Est-2	0.20	0.55	0.10	1.00	0.18	0.40	0.10	0.50	1.22	1.66	1.11	2.00
Idh-2	0.55	0.40	0.50	0.60	0.40	0.32	0.38	0.42	1.66	1.47	1.60	1.72
Aco-2	0.15	0.15	0.15	0.05	0.14	0.22	0.29	0.35	1.16	1.28	1.41	1.54
Pgm-1	0.75	0.60	0.55	0.90	0.53	0.50	0.44	0.55	2.11	2.00	1.78	2.23
Pgm-2	1.00	0.80	0.90	1.00	0.50	0.50	0.50	0.50	2.00	1.98	2.00	2.23
Aat-2	0.11	1.00	0.56	0.00	0.48	0.50	0.40	0.00	1.91	2.00	1.67	1.00
G3pdh-nadp-1	0.10	0.30	0.10	1.00	0.10	0.26	0.10	0.50	1.11	1.34	1.11	2.00
G3pdh-nadp-2	0.00	0.00	0.00	0.00	0.65	0.68	0.68	0.75	2.82	3.13	3.08	4.00
Mean	0.12	0.16	0.12	0.19	0.12	0.14	0.12	0.15	1.25	1.29	1.24	1.35

mean number of effective alleles varied from 1.24 in the purple morph to 1.35 in the white morph (Table 1).

Frequencies of alleles at the polymorphic loci were highly variable among the color morphs (Table 2). Only three alleles were not common to all color morphs. At AAT-2, the white color morph did

TABLE 2. ALLELE FREQUENCIES OF POLYMORPHIC LOCI FOR EACH OF THE COLOR VARIANTS OF *CLARKIA AMOENA* VAR. *PACIFICA*. Abbreviations as in Table 1.

Locus	Allele	PS	WS	P	W
Est-2	1	0.72	0.88	0.95	0.50
	2	0.28	0.12	0.05	0.50
Idh-2	1	0.80	0.72	0.75	0.70
	2	0.20	0.28	0.25	0.30
Aco-2	1	0.12	0.08	0.18	0.22
	2	0.88	0.92	0.82	0.78
Pgm-1	1	0.50	0.58	0.70	0.08
	2	0.50	0.38	0.30	0.55
	3		0.05		0.38
Pgm-2	1	0.55	0.50	0.50	0.50
	2	0.45	0.50	0.50	0.50
Aat-2	1	0.50	0.39	0.28	
	2	0.50	0.61	0.72	1.00
G3pdh-nadp-1	1	0.82	0.95	0.95	0.50
	2	0.18	0.05	0.05	0.50
G3pdh-nadp-2	1	0.45	0.50	0.20	0.20
	2	0.30	0.25	0.40	0.35
	3	0.15	0.20	0.35	0.05
	4	0.05	0.05	0.05	0.25
	5	0.05			0.15

TABLE 3. NEI'S GENETIC IDENTITIES (1972) FOR THE FOUR COLOR VARIANTS OF *CLARKIA AMOENA* VAR. *PACIFICA* AT CASCADE HEAD. Abbreviations as in Table 1.

	WS	P	W
PS	0.995		0.983
WS		0.989	0.938
P			0.937

not express allele 1. At G3PDH-NADP-2, both the white spotted and purple color morphs lacked allele 5. In addition, at PGM-1, the purple spotted and purple morphs lacked allele 3. At PGM-2 and G3PDH-NADP-1 the white color morph showed no variation (all individuals were heterozygous) while individuals of the other three color morphs gave variable phenotypes, even though, on average the allele frequencies were similar.

Nei's genetic identities exceeded 90% for all color morphs (Table 3). Comparisons of purple spotted, white spotted, and purple color morphs all gave very high genetic identities ($\bar{I} = 0.99$) whereas the white color morph consistently showed less genetic similarity to the other three morphs ($\bar{I} = 0.94$).

Within population diversity (H_s) accounted for 90.0% of the electrophoretic variation, while among population diversity (D_{st}) accounted for 10.0% of the variation. For five of the polymorphic loci, G_{st} was significantly greater than zero based on chi square at $\alpha = 0.05$ (Table 4).

Morphology.

Petal length and width.—The petals of the white flowered *Clarkia* averaged 1.4 to 2.5 mm longer than those of the purple, purple spotted and white spotted flowers which had similar mean petal lengths and widths (ANOVA, Tukey test for pairwise comparisons involving the white morph at $p < 0.05$; Table 5). The mean petal

TABLE 4. NEI'S STATISTICS OF GENE DIVERSITY AND DIFFERENTIATION AT THE EIGHT POLYMORPHIC LOCI. An asterisk (*) in the G_{st} column indicates significant deviation from zero based on chi square.

	H_i	H_s	G_{st}
Est-2	0.376	0.301	0.200*
Idh-2	0.382	0.388	0.000
Aco-2	0.257	0.255	0.008
Pgm-1	0.618	0.517	0.163*
Pgm-2	0.500	0.511	0.000
Aat-2	0.436	0.363	0.167*
G3pdh-nadp-1	0.328	0.242	0.260*
G3pdh-nadp-2	0.748	0.705	0.572*

width of the white color morph was also significantly larger than the other three morphs (ANOVA, Tukey at $p < 0.05$; Table 5).

In the common garden (including the purple spotted, purple and white color morphs) the trends observed for field populations were maintained, although mean values were smaller (ANOVA, $p < 0.05$; Table 5).

Leaf length and width.—The white spotted and purple color morphs did not differ significantly from each other in either mean leaf length or width while all other comparisons of the color morphs were significant (Table 5). The purple spotted morphs had wider leaves while the white flowered plants had longer leaves (Table 5). These differences in leaf morphology did not occur in the garden plants (ANOVA, $p > 0.05$; Table 5).

Height and fruit length.—In both height and fruit length, the white morph differed significantly from all other morphs. Plants of this morph were twice as tall as the other morphs (ANOVA, Tukey at $p < 0.05$; Table 5). Mean fruit length averaged 3.8–10.5 mm greater for the white morph than for the purple, purple spotted and white spotted morphs (Tukey at $p < 0.05$) which were not significantly different from each other (Table 5).

Unfortunately, we were unable to measure height and fruit length in the common garden. Because the white morph is found in a different population from the other morphs, we cannot determine whether the observed height difference is a result of genetic differences between the morphs, environmentally induced differences, or some combination of the two. We could not effectively measure height in garden grown *Clarkia* due to the multibranching and more prostrate form of the garden plants. We presume that differences in plant form under field vs. garden conditions are related to greater light availability and the absence of competing vegetation in the garden. We did not measure fruit length because an inappropriate herbicide application led to plant death prior to fruit maturation.

DISCUSSION

A primary goal of this study was to assess the systematic and evolutionary implications of floral color variation in an endemic plant, *Clarkia amoena* var. *pacifica*. Our results provide evidence that both morphological and electrophoretic differences accompany petal color variation in coastal populations of this species.

In general, field measurements suggest that the white morph is larger than the other morphs. Lack of significant variation in leaf length and width in the garden grown plants indicates that leaf size plasticity in field grown plants may largely be a result of environmental factors. Differences in floral morphology observed in the field however, were maintained when plants were grown in the gar-

TABLE 5. MEANS AND STANDARD DEVIATIONS FOR MORPHOLOGICAL CHARACTERISTICS OF FIELD AND GARDEN PLANTS. An asterisk (*) indicates $P < 0.05$ based on ANOVA. Abbreviations as in Table 1. Different letters indicate groups which are significantly different.

Char.	WS	PS	P	W	F	df
Petal width (mm)	9.2 ± 1.3 ^a	9.2 ± 1.9 ^a	9.5 ± 2.3 ^a	11.7 ± 1.4 ^b	24.1*	196
garden	—	7.4 ± 0.9 ^c	7.8 ± 1.0 ^c	10.0 ± 1.0 ^d	26.1*	37
Petal length (mm)	11.3 ± 1.5 ^e	11.5 ± 1.8 ^e	12.2 ± 2.3 ^e	13.6 ± 2.1 ^f	14.5*	196
garden	—	9.7 ± 0.9 ^g	10.4 ± 1.3 ^g	12.5 ± 1.7 ^h	14.5*	37
Leaf width (mm)	5.3 ± 1.4 ^f	7.0 ± 1.3 ^f	5.5 ± 1.1 ^f	6.1 ± 1.3 ^g	18.4*	196
garden	—	6.0 ± 1.3 ^f	5.6 ± 0.9 ^f	5.0 ± 0.8 ^f	2.6	37
Leaf length (mm)	22.4 ± 4.5 ^m	25.7 ± 5.1 ⁿ	23.4 ± 5.9 ^m	34.3 ± 6.4 ^p	48.3*	196
garden	—	19.3 ± 3.6 ⁿ	21.1 ± 4.4 ⁿ	18.2 ± 3.5 ⁿ	1.9	37
Height (cm)	9.7 ± 3.4 ^f	12.1 ± 4.1 ^f	13.3 ± 0.8 ^f	30.6 ± 9.4 ^g	123.2*	196
Fruit length (mm)	20.1 ± 4.4 ^f	24.8 ± 4.5 ^f	26.8 ± 3.3 ^f	30.6 ± 4.5 ^g	13.2*	36

den under common conditions. This is significant because, in *Clarkia*, taxonomic separations are often based entirely on floral characters. In fact, many *Clarkia* species could not be differentiated if stripped of their flowers (MacSwain et al. 1973).

Overall, statistics of genetic diversity in *Clarkia amoena* var. *pacifica* indicate higher within than among population diversity. Among population diversity (D_{st}) accounts for 10.0% of the variation observed; the value for G_{st} is within the range of values considered indicators of moderate genetic differentiation (Hartl 1988). On average, plant species with a mixed pollination system have a G_{st} value of 0.21 (Hamrick et al. 1991). Although the G_{st} found in this study ($G_{st} = 0.10$) is somewhat lower than the average, there is still some difference among the populations.

Although no alleles were unique to a particular color morph, the white morph lacked an allele for AAT-2 that was present in all other color morphs. In addition, for two loci, PGM-1 and G3PDH-NADP-2, the white differed from the other morphs in the most frequently occurring allele. Also, the white color morph lacked variation in both PGM-2 and G3PDH-NADP-1 (it was heterozygous for all individuals) while the other color morphs were variable.

Results of electrophoresis also revealed that the white color morph shows a slightly reduced identity relative to the other more genetically similar purple and white spotted and purple morphs. On average, conspecific populations of plants have a mean genetic identity of 0.95 (Crawford 1983). In *Clarkia*, reproductively isolated populations of a single species, *C. xantiana*, had relatively high genetic identities of .91 and .89 (Gottlieb, 1984) whereas comparisons of two species, *C. speciosa* and *C. nitens* gave an identity of .94 (Soltis and Bloom 1991). Therefore, in *Clarkia*, high genetic identities between populations should not be taken as prima facie evidence that two populations are part of the same species. However, the level of genetic identity found between morphs in the two populations at Cascade Head ($\bar{I} = 0.94$) is certainly equivalent to levels found among distinct species in *Clarkia* and lower than levels found among co-occurring color morphs ($\bar{I} = 0.99$) within a single population. Thus, current levels of genetic differentiation indicate the potential for future speciation. The rapid evolutionary processes known in the genus also support the possibility that the two populations at Cascade Head may be in the initial stages of divergence.

Some pollinator and phenological differentiation are also present between the two populations. Based on field observations, the two populations have slightly staggered blooming times; the white population blooms later. In addition, the white color morph receives over one-third of its pollinator visits from vectors which have not been observed visiting the other colors (Foust and Butler pers. obs.). It is possible that these differences could be attributed to local environmen-

tal effects that influence pollinator diversity in the two populations. At Cascade Head however, there is a greater diversity of pollinators in the "pinnacle" region where the mixed population of *Clarkia amoena* var. *pacifica* occurs (Kephart personal communication), whereas we found a greater diversity of pollinators visiting the population of white morphs (Foust and Butler 1996). Additionally, most of the pollinators found visiting *Clarkia amoena* var. *pacifica* are small (Foust and Butler 1996) and are likely to have relatively short flight distances (Waser 1982). Although recent studies indicate that gene flow can occur over distances of greater than 0.5 km (Kirkpatrick and Wilson 1988; Broyles and Wyatt 1990), it is possible that the two populations of *C. amoena* var. *pacifica* are isolated from each other due to the differences in pollinators and blooming times.

Further studies of the color morphs including examination of chromosomal arrangements and hybridization experiments would provide more definitive evidence regarding the relationships of the populations of *C. amoena* var. *pacifica*. Frequent chromosomal rearrangements have occurred in this genus and the resulting arrangements have been used to differentiate species and subspecies (Lewis 1953; Gottlieb 1973). Knowledge of chromosomal arrangements along with the morphological and genetic differences found here could provide convincing evidence that speciation is occurring between the two populations of *Clarkia amoena* var. *pacifica*.

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REPRODUCTIVE FITNESS AND POLLINATION BIOLOGY
OF THE FOUR FLORAL COLOR MORPHS OF
CLARKIA AMOENA VAR. *PACIFICA*

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ABSTRACT

We studied four floral color morphs of the annual *Clarkia amoena* var. *pacifica* to determine whether variation in reproductive fitness and pollination biology accompanied floral color variation. Reproductive variables examined included insect visitation, pollen production and deposition and seed set. Pollinator visitation rates were not significantly different among color morphs in observation plots located in the two study areas. However, the white morph, which occurred in a separate population, differed from the other morphs in that it received visits from a greater variety of insects. The white morph also produced 3.3 times more pollen than the other three morphs and pollen deposition on the stigmas of the white morph was 7.2 times greater than in the other three morphs. In addition, while most within morph comparisons of the number of seeds produced by open-pollinated, self-pollinated and cross-pollinated flowers were insignificant, seed set for the white morph was significantly less in outcrossed flowers. Meanwhile, among morphs, the white flowers produced more seed per fruit ($\bar{x} = 101.1$, $SD = 16.3$) than the purple-spotted ($\bar{x} = 68.2$, $SD = 33.8$) or white-spotted ($\bar{x} = 64.2$, $SD = 27.4$) color morphs under self-pollination. This study suggests potential links between pollinator diversity, seed set, and population differentiation in a plant that appears to combine autogamous and xenogamous elements in its breeding system.

Floral color variation within and among plant populations is often related to and accompanied by other types of variation (Miller 1981; Waser and Price 1981; Galen 1989; Bosch 1992). In addition, when pollinators discriminate among floral variants, pollinator-mediated selection may play a role in the evolution of further floral variation (Miller 1981; Galen 1989; Robertson and Wyatt 1990). Discrimination among morphs by pollinators sometimes influences male reproductive characteristics, such as the number of pollen grains produced and the ability to deposit pollen on stigmas (Bosch 1992; Stanton et al. 1986). Differential pollen deposition on stigmas can also lead to variation in female fitness, measured as seed production (Waser and Price 1981; Galen 1989). Furthermore, if the spatial distribution of floral morphs is closely correlated with that of effective pollinators (Miller 1981; Galen 1989; Robertson and Wyatt 1990), pollinator-mediated selection may affect the development of distinct races (Miller 1981).

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Previous studies of the genus *Clarkia* have focused mainly on genetic variation (e.g., Soltis and Bloom 1991), evolutionary mechanisms (e.g., Lewis 1953) and pollinators of *Clarkia* (MacSwain et al 1973). Less attention has been given to the variation in reproductive fitness among floral color morphs and how this relates to pollination biology (Jones 1994). The purpose of this study was to examine whether floral color variation in *Clarkia amoena* var. *pacifica* was accompanied by variation in reproductive fitness and the ability to attract pollinators. Specific questions we addressed were: 1) Do differences in pollinator visitation rates occur among the four color morphs? 2) Are the different color morphs visited by the same insects? 3) Is variation in female reproductive fitness, pollen production and pollen deposition present?

METHODS

Clarkia amoena var. *pacifica* is an annual that occurs as four floral color morphs: white, purple, purple-spotted and white-spotted (spotted individuals have a magenta spot centrally located on each white or purple petal). We were able to locate two sites on the Oregon coast that contained *C. amoena* var. *pacifica*, Cascade Head and Cape Lookout. Cascade Head, a grassy promontory located 7 miles north of Lincoln City, Oregon, represents the only known site containing all four color morphs. We studied two populations of *C. amoena* var. *pacifica* which occur separately at Cascade Head. One site, located inland approximately 0.8 km, contains only the white morph. The second site is located along the face of the headland and contains the white-spotted, purple-spotted and purple morphs.

Pollinator study. We estimated pollinator visitation rates using 44, one meter square observation plots that were randomly located across both sites during the 1993 flowering season (May–August). Plots were observed using 20 minute time intervals. We observed plots throughout the day for all sites and color morphs, in both sunny and cloudy weather ($n = 8$ days of observation). Flowers were diurnal and therefore nocturnal pollinators were not considered. We observed 18 plots that contained only the white morph while we observed 26 plots that contained a mixture of the other three morphs. Four people assisted in pollinator studies which allowed some simultaneous observation of different plots; observers were also rotated among sites A and B. An insect was considered to be a potential pollinator if it made direct contact with the anthers. For each visit, we recorded the type of insect, the color morph visited, the number of flowers sampled, and the length of the visit.

Because we were interested in visitation rates in natural populations and since plots were randomly located in both sites, plant densities varied among plots, ranging from 3 to 57 *Clarkia* per plot.

Variability in color morph frequency among plots was monitored by recording the number of flowers of each morph per plot prior to each observation period. To determine whether flowering density affected pollinator visitation frequency we tested for a possible correlation between flower number and pollinator frequency. In addition, we compared differences in the average percentage of flowers of each morph visited per plot during the 20 minute observation periods using Chi-square.

Pollen production and deposition. To examine pollen production in the four floral color morphs we collected one flower from each of 20 randomly selected individuals of each color morph just prior to pollen release. Flowers were placed individually in glycine bags and stored temporarily in a lab desiccator. For pollen counts, we soaked individual flowers in water and placed these on a 350 μ m plankton sieve. We then washed pollen from each flower with a forceful stream of water. When microscopic examination of the sieve and anthers revealed that the pollen from all the anthers had been washed into the beaker below, the volume of water was recorded. Using a micropipetor we removed 20 (2 ml) samples from each beaker and counted the number of pollen grains using a dissecting microscope. We added glycerine drops prior to counts and pollen was stirred magnetically to ensure an even distribution and to prevent pollen grains from adhering to one another. (This was especially important because SEM photos [Phillips xl-20] revealed pollen grains to be connected by viscin threads.) The average number of pollen grains/ml was calculated and then multiplied by the total volume of water in the beaker to find the total number of pollen grains produced by each flower.

To determine the amount of pollen deposited on stigmas we sampled 10 senescent flowers (all from distinct individuals) of each color morph. Senescent flowers were defined as those that remained closed all day and appeared wilted. We removed the stigmas from these flowers and stored them individually at -85°C . For pollen counting, each stigma was placed in a depression slide with 10% hydrochloric acid and heated for about three minutes on a hot plate. Stigmas were then easily crushed between two slides, which were rubbed together to distribute the pollen across the slide. A grid placed on top of the slide aided microscope counts of the number of pollen grains.

Breeding system study.

Open-pollinated individuals.—to assess seed set under field conditions that allowed for insect pollination and autofertility, we bagged 10 green capsules from different, randomly selected plants of each color morph prior to seed release. After maturity, we re-

corded the number of filled and unfilled seed. Unfilled and filled seeds were clearly different.

Self-pollinated individuals.—In a previous study Lewis and Lewis (1955) found *C. amoena* var. *huntiana* collected in the field and grown under greenhouse conditions was self-pollinating. Thus, to determine the extent of autofertility in the absence of insects, we bagged non-emasculated flowers of each color morph with a fine nylon mesh netting prior to pollen release and stigma receptivity. Once the flowers had senesced, we removed nets and later collected the mature capsules. We recorded the number of filled and unfilled seed produced in each capsule for 10 capsules of each color morph.

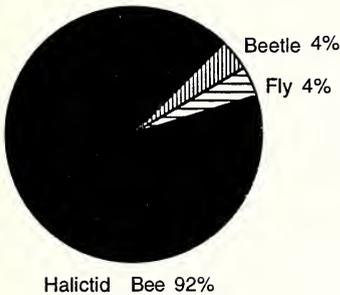
Outcrossed individuals.—We evaluated the seed set attributed to allogamy by emasculating 10 flowers on randomly selected plants of each color variant prior to stigma receptivity. Pollen left on the petals was removed by using a brush to insure that the flower would not be self-pollinated. Once flowers had senesced, we marked and bagged 10 capsules of each morph for counts of filled and unfilled seed. On average, three flowers of any given plant were simultaneously releasing pollen.

We examined variation in means among the color morphs using a two-way analysis of variance with color morph, pollination treatment and their interaction as the main effects. When variation was found to be present we applied the Tukey test (Zar 1984) to determine significant differences between means.

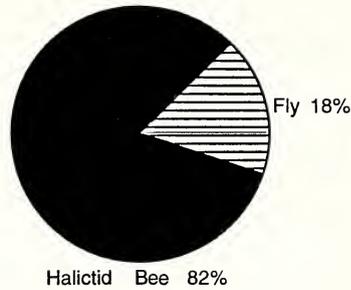
RESULTS

Pollinator visitation. The 44 observation plots contained an average of 18.8 *C. amoena* var. *pacifica* individuals. We compared the frequency of observed visits for different morphs by dividing the number of visits to each morph during the 20 minute observation interval by the number of flowers of that color morph in a given plot; we then averaged these results for all plots. Of the total number of purple-spotted flowers observed, on average 14.5% were visited during each 20 minute observation period while 9.6% of the white-spotted, 14.9% of the purple and 7.5% of the white flowers observed were visited. Visitation rates were not significantly different among the color morphs ($\chi^2 = 3.44$, $df = 3$, $P > 0.05$). However, the types of potential pollinators present on color morphs varied. Purple-spotted, purple and white-spotted flowers received 82–92% of their visits from halictid bees, whereas white flowers received visits from a greater variety of insects, including bumblebees and syrphid flies (Fig. 1). We observed pollinators visiting flowers of multiple colors on one foraging bout, however, we did not observe pollinators visiting more than one flower on an individual plant during one foraging bout. Although there was a significant difference between

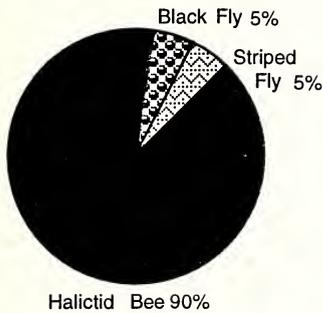
PURPLE-SPOTTED



WHITE-SPOTTED



PURPLE



WHITE

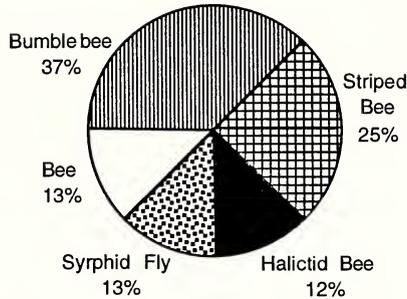


FIG. 1. Proportion of visits attributed to each of the potential pollinators for the four color morphs of *Clarkia amoena* var. *pacifica*.

plant densities in the mixed color morph plots versus the white color morph plots ($\chi^2 = 4.19$, $df = 1$, $P < 0.05$), there were no significant correlations between plant density and pollinator visitation rates ($r = 0.039$, $P = 0.85$ for the mixed plots; $r = 0.059$, $P = 0.82$ for the white plots).

Pollen production and deposition. Significant variation was present in pollen production (ANOVA, $F = 41.39$, $df = 7$, $P < 0.05$) and in the number of pollen grains deposited on stigmas among the color morphs (ANOVA, $F = 26.17$, $df = 36$, $P < 0.05$). Pollen production in the white morph ($\bar{x} = 5617$, $SD = 2118$ grains per flower) was, on average, 3.3 times greater than in the other three morphs (purple-spotted: $\bar{x} = 1574$, $SD = 859$; purple: $\bar{x} = 2134$, $SD = 1060$; white-spotted: $\bar{x} = 1415$, $SD = 725$) which were not significantly different from one another. White flowers also received significantly more pollen ($\bar{x} = 1942$, $SD = 996$ grains per stigma)

TABLE 1. MEAN NUMBER AND STANDARD DEVIATION OF SEED SET PER FRUIT AMONG OPEN-POLLINATED, SELF-POLLINATED AND OUTCROSSED INDIVIDUALS OF EACH COLOR MORPH OF *CLARKIA AMOENA* VAR. *PACIFICA*.

	Open-pollinated	Self-pollinated	Outcrossed
Purple-spotted	72.5 ± 26.2	68.2 ± 33.8	75.5 ± 17.1
Purple	69.5 ± 39.7	89.7 ± 22.7	60.0 ± 40.7
White-spotted	51.6 ± 25.0	64.2 ± 27.4	61.3 ± 21.2
White	89.8 ± 28.0	101.1 ± 16.3	59.3 ± 32.6

than the other three morphs (purple-spotted: \bar{x} = 292, SD = 190; purple: \bar{x} = 259, SD = 151; white-spotted: \bar{x} = 251, SD = 148).

Breeding system study. Pollination treatment and flower color both had a significant effect on seed production. However, there was no significant effect due to the interaction of flower color and pollination treatment. (ANOVA, F = 11.4, df = 3 for flower color, F = 3.3, df = 2 for pollination treatment, P < 0.05. For the interaction of the flower color and pollination treatment F = 1.31, df = 6, P = 0.26)

Within morph comparisons.—The only significant within color morph variation in seed production among the pollination treatments occurred in the white morph. The white morph produced significantly less seed per fruit under the outcrossing treatment (ANOVA, F = 6.64, df = 27, P < 0.05; Tukey P < 0.05; Table 1).

Between morph comparisons.—Between morphs, the only significant difference occurred under the self-pollination condition. The white morph produced significantly more seed per fruit under this treatment than both the purple-spotted and white-spotted morphs (ANOVA, F = 4.62, P < 0.05; Tukey at P < 0.05; Table 1).

DISCUSSION

Variation in seed set, pollen production and deposition, and pollinator diversity does accompany differences in floral color in *C. amoena* var. *pacifica*. Specifically, the white morph differed from the other morphs in the types of pollinators present, pollen production and deposition, and some aspects of seed set. However, visitation rates by insects did not significantly differ among the morphs, and habitat differences may account for some of the differences observed.

Pollinator visitation. Even though insect visitation rates did not differ among color morphs, a greater diversity of pollinators visited the white morph. This may have resulted from several factors. First, certain insects preferentially visit particular floral colors (Pederson 1967; Heinrich 1974; Mogford 1974). For example, Pederson (1967)

found that solitary bees visiting alfalfa selectively avoided white flowers, whereas Mogford (1974) found that bumblebees preferred white flowers of *Cirsium palustre*. In this study, visits by halictids, a type of solitary bee, represented only 12% of the visits to the white morph yet constituted between 82–92% of the visits for the other three morphs. In contrast, bumblebees were observed only on the white morph. Thus, color preferences of pollinators may play a role in visitation patterns to *C. amoena* var. *pacifica*.

Secondly, the wider array of visitors observed on the white flowered morph may be related to its greater production of pollen, an important primary attractant for many pollinators. However, whereas pollen production may have influenced the diversity of insects observed on various color morphs, the overall visitation rates were not different among morphs. Additional studies are needed to more clearly differentiate the potential effects of pollen production on both pollinator visitation rates and pollinator diversity.

Additionally, high pollen production and larger flower size often covary; in *Raphanus* and *Polemonium* the combination of these two factors may enhance the attractiveness of plants to pollinators, especially bumblebees (Stanton and Preston 1988; Galen and Newport 1987). Similarly, in *C. amoena* var. *pacifica*, the flowers of the white that produce more pollen are also significantly larger than those of the other three morphs (Butler and Foust, unpublished observation).

Finally, variation in habitat may explain some of the differences in pollinator visitation patterns. Differences among pollination systems in some species of *Clarkia* appear to be mainly ecological; where the plants are restricted to different habitats, the pollinators may differ (MacSwain et al, 1973). At Cascade Head, plants of the white morph occur among tall grasses and forbs (approximately 1m tall) while the vegetation in the mixed population is largely dominated by red fescue and a diverse array of forbs (approximately 0.3 m tall). Casual observations of pollinators from previous years (Kephart, personal communication) also suggest a greater diversity of pollinators exists in the ungrazed headland. However, if habitat rather than floral factors were responsible for the observed differences in pollinator diversity, one would predict that the biotically rich area where the mixed population occurs (consisting of ungrazed coastal prairie) would have yielded the highest pollinator diversity. Instead, the white morph in the less diverse site supported a more varied pollinator fauna. Further experimental studies are needed to distinguish among pollinator, floral, and habitat based variables.

A possible outcome of differential visitation to varied populations of a species is reproductive isolation and/or evolutionary divergence (Miller 1981; Grant 1949; Stebbins 1971). Some evidence presented here supports possible reproductive isolation for the white morph and a likelihood of considerable interbreeding among the co-occur-

ring color morphs. Observations of insect flights showed that pollen transfer readily occurs between the purple-spotted, purple, and white-spotted morphs. Similarly, Jones (1994) found that pollinators moved randomly between plants of spotted and unspotted morphs of *Clarkia gracilis*. In contrast, while pollen transfer between the white morph and the other three morphs of *C. amoena* var. *pacifica* is possible, it is likely reduced by the distance separating these populations (but see Kirkpatrick and Wilson 1988; Broyles and Wyatt 1990). In our study of *C. amoena* var. *pacifica*, reproductive isolation would be facilitated by spatial distance, differential pollinator visitation, evidence of possible autogamy in the white morph, and by the genetic differentiation for the white morph implied by electrophoretic studies (Butler and Foust 1996). These hypotheses merit further testing by combining techniques such as paternity analysis with studies of the foraging patterns of marked insects.

Pollen production and deposition. In the white morph, pollen production and deposition were higher than in the other three morphs. Theoretically, the ability to produce more pollen serves to attract more pollinators, thereby potentially increasing the number of grains deposited on stigmas (Stanton and Preston 1988). In this study, however, greater pollen production in the white morph did not result in greater insect visitation, although it was associated with greater pollinator diversity and the presence of bumblebees. Thus, the greater number of pollen grains deposited on stigmas of the white morph may instead reflect the high efficiency of bumblebees with respect to pollen transfer (Waser 1982).

Another consequence of the greater pollen production in the white morph may be enhanced self-pollination leading to higher seed set. One could argue that the significance of higher pollen deposition for reproductive success is probably somewhat limited, since stigmas of all color morphs generally received more pollen grains than the number of seed produced. However, some studies have found that increased pollen deposition may lead to increased progeny vigor (Winsor et al. 1987; Schlichting et al. 1990). Further studies on germination rates, seedling growth rate and other similar characters would give important information regarding the possible consequences of the increased pollen loads of the white morph.

Female fitness. Significant variation in female fitness within floral color variants was limited to greater seed set by the white morph in open and autogamously pollinated flowers. Because autogamy was possible only under these two conditions, the high pollen production in the white morph may influence seed set primarily via enhanced self pollination. While some inbreeding depression is likely with such a pollination system, it does not appear to compromise adequate seed set in *C. amoena* var. *pacifica*. Also, in adverse weather

(e.g. rain and high winds common at Cascade Head), a pollination system that is not pollinator-limited may be especially important (Oleson and Warncke 1992). In *C. amoena* var. *pacifica*, the equivalent heights of the anthers and stigmas and incomplete protandry also facilitate self-pollination. We observed contact of dehiscing anthers and receptive stigmas under varying weather conditions, but most commonly during rainy periods when few pollinators were present.

The increased seed set under the self-pollination condition for the white morph also highlights the potential importance of self-pollination in clarkias with mixed-mating systems. In *Clarkia gracilis* ssp. *sonomensis* self pollen deposition is common, but stigmas exposed to pure self and outcross pollen produce similar number of seeds while mixtures of self and outcross pollen produce three times more outcrossed as selfed offspring (Jones 1994). Thus, the success of self and outcross pollen in producing seed may be dependent on the presence or absence of competition, which can be influenced by the number and type of pollen grains on each stigma in *C. amoena* var. *pacifica*.

The importance of self-pollination within the white morph merits further study based on differential seed set. In other color morphs, however, filled seed set under the three different pollination conditions did not vary. The breeding system of *Clarkia amoena* var. *pacifica* overall combines both autogamy and xenogamy.

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FLORISTIC PATTERNS ON LATE TERTIARY LACUSTRINE DEPOSITS IN THE ARIZONA SONORAN DESERT

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ABSTRACT

A chain of narrow basins in the Transition Zone lies across central Arizona at the northern edge of the Sonoran Desert. They contain recently exposed late Tertiary lacustrine deposits which are infertile compared to surrounding zonal soils, forming a sharp edaphic contrast. The dominant Sonoran Desert woody species, *Larrea tridentata* (creosotebush) and *Cercidium microphyllum* (foothill palo verde), are excluded from the infertile lacustrine soils. The escape from competition for soil moisture allows an opening for disjuncts, relicts, and endemics to survive, in many cases the taxa's only occurrences in the Sonoran Desert. Floristic analysis shows these taxa to be from noncontiguous floristic areas, the Colorado Plateau to the north and the present day Chihuahuan Desert to the southeast. *Lotus mearnsii* var. *equisolensis*, a new variety endemic to one of the basins, is described.

In central Arizona the northern edge of the Sonoran Desert overlaps the Transition Zone, a geological province of closely-spaced mountain ranges with narrow basins below the Mogollon Escarpment (Tittley 1984). Most of the Sonoran Desert in Arizona, by contrast, lies within the Basin and Range Province of broad plains and isolated mountain ranges (Smiley et al. 1984). Block faulting and basin subsidence in central Arizona associated with the mid-Miocene Basin and Range Disturbance initially resulted in a series of closed basins (Fig. 1A-H) within which lacustrine deposits with interbedded ash flows were laid down into limy tuffs (Damon et al. 1984). Later, cessation of subsidence and increased precipitation during Pleistocene glacial periods caused stream throughflow between basins and erosion exposed the undeformed lacustrine deposits to plant colonization (Nations et al. 1982).

These limy tuffs were found to be comparatively infertile with very low levels of phosphorus and nitrogen (Anderson 1992). Infertile azonal soils (atypical of the surrounding common soils), including gypsum, limestone, and serpentine, have been shown to host many endemic and disjunct species by excluding the surrounding dominant species and reducing competition for soil moisture (Billings 1950; Kruckeberg 1969, 1986). The surrounding dominant shrubby species, in this case the recently arrived *Larrea tridentata* (DC) Coville (creosotebush) and *Cercidium microphyllum* (Torr.) Rose & Johnst. (foothill palo verde), have apparently not yet

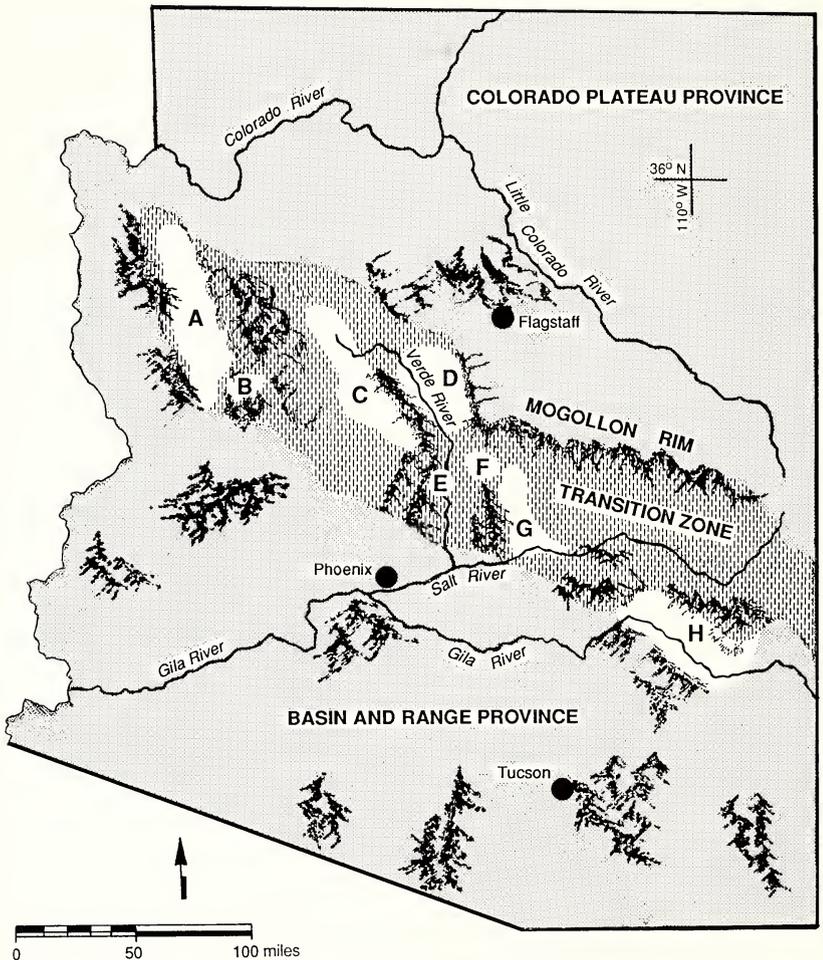


FIG. 1. Transition Zone Basins across central Arizona. A—Big Sandy Basin, B—Burro Creek, C—Chino Valley, D—Verde Valley, E—Lower Verde River (Horseshoe Reservoir), F—Payson Basin, G—Tonto Basin, and H—San Carlos Basin.

evolved ecotypes adapted to these infertile soils, but are more competitive, probably at the seedling stage, on the zonal soils (Yeaton et al 1977). There is an abrupt vegetative change across the edaphic ecotone which provides a synecological opening on the azonal soils for the less competitive disjunct, endemic, and relictual species (Fig. 2-5).

The chain of basins across central Arizona containing contrasting late Tertiary lacustrine deposits is isolated by fifty to one hundred

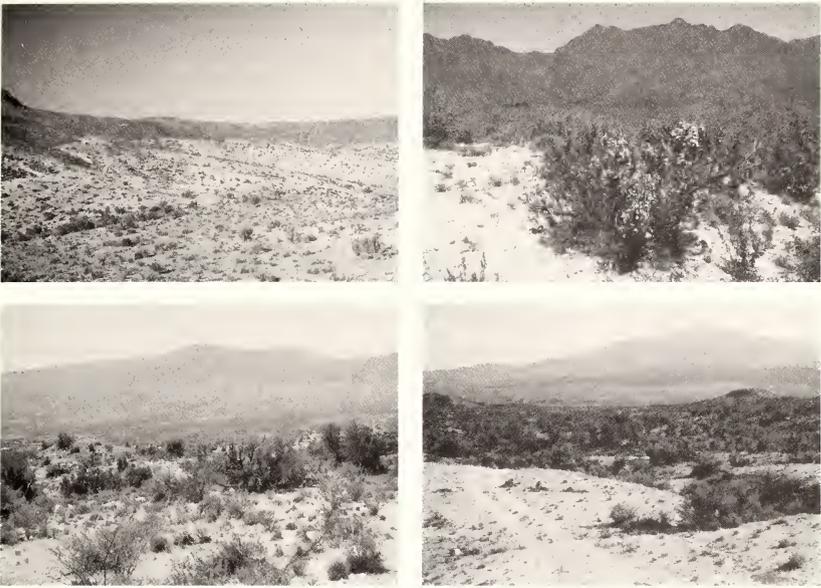


FIG. 2. (upper left) Burro Creek with late Tertiary lacustrine deposit in foreground and Aquarius Mts. in background, Mohave County. Note sharp edaphic contrast between lacustrine deposit and surrounding common soil, but similarity of lacustrine deposits in four basins in Figures 2–5.

FIG. 3. (lower left) Verde Valley with late Tertiary lacustrine deposit (Verde Formation) in foreground and Mingus Mt. in background, Yavapai County.

FIG. 4. (upper right) Lower Verde River (Horseshoe Reservoir) with late Tertiary lacustrine deposit in foreground and Humboldt Mt. in background, Maricopa County. Note *Purshia subintegra* in full bloom in foreground.

FIG. 5. (lower right) San Carlos Basin with late Tertiary lacustrine deposit in foreground and Gila River and Mt. Turnbull in background, Graham County.

miles from each other (Nations et al. 1981) and provide a similar setting for endemics and disjuncts within the Sonoran Desert (Anderson 1986). From northwest to southeast the six basins in the Sonoran Desert (Fig. 1) are the Big Sandy Basin (A) at 630 m along the Big Sandy River, small local basin deposits along Burro Creek (B) at 770 m (Fig. 2), the Verde Valley (C) at 1030 m (Fig. 3) and the Lower Verde River–Horseshoe Reservoir (E) at 630 m (Fig. 4) along the Verde River, the Tonto Basin (G) at 770 m along Tonto Creek, and the San Carlos Basin (G) at 850 m along the middle Gila River (Fig. 5). (Two other Transition Zone basins at higher elevations, the Chino (D) and Payson (F) Basins at 1300–1400 m

with plains grassland (Brown and Lowe 1980) lie outside the Sonoran Desert).

A number of species from various other floristic provinces have their only occurrences in the Sonoran Desert on these azonal edaphic sites where they are disjunct between two or more of these basins: Burro Creek, Verde Valley, Lower Verde Valley, and San Carlos. The resultant floristic patterns at these four sites thus contain unusual combinations of species that normally occur in different floristic provinces and may serve as phytogeographical clues to document past plant migrations, community types, and speciation (Anderson 1986). The other two Sonoran Desert basins, the Tonto and Big Sandy Basins, only have limited exposures of late Tertiary lacustrine deposits, however, and generally do not support disjuncts although each contains one of just three Sonoran Desert occurrence of *Stanleya pinnata* (Pursh) Britt. [Anderson 86-37 (ASU) and Butterwick and Hillyard 4577 (ASU) respectively], a species from the mountains and plains farther north and west.

FLORISTIC ANALYSIS

The Transition Zone basins in the Arizona Sonoran Desert lie within the *Larrea tridentata*-*Canotia holocantha* (creosotebush-cruifixion thorn) series of the Arizona Upland Subdivision (Brown 1982). But, the absence of the usually dominant creosotebush and foothill palo verde on the infertile lacustrine soils provides a synecological opening for the disjuncts, endemics, and relicts to occur. Other desert shrubs present in typical low densities on two or more of the basin lacustrine deposits are *Canotia holocantha* Torr., *Krameria parviflora* Benth., *Gutierrezia sarothrae* (Pursh) Britt., *Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray, *Fouquieria splendens* Engelm., *Dalea formosa* Torr., *Melampodium leucanthum* Torr. & A. Gray, *Eriogonum fasciculatum* Benth., *Simmondsia chinensis* (Link) Schneid., *Aloysia wrightii* (A. Gray) Heller, *Parthenium incanum* H.B.K., and *Dyssodia acerosa* DC. Species disjunct, endemic, and relict on the late Tertiary lacustrine deposits and their floristic affinities are listed in Table 1. Representative collections and author citations are listed in Appendix 1.

Colorado Plateau. Many of the disjuncts and endemics on the late Tertiary lacustrine deposits in the Transition Zone basins have floristic affinities to the north with the main portion of their range in the Colorado Plateau Floristic Area (McLaughlin 1986, 1989), also described as the Great Basin Desertscrub and Conifer Woodland (Brown 1982). Endemic taxa are marked with an asterisk; their affinities are with the respective typical varieties or presumed most closely related species (Reveal 1969, 1976; Isely 1983; Strachen 1982). These include *Arenaria eastwoodiae*, *Astragalus calycosus*

TABLE 1. SPECIES DISJUNCTS AND ENDEMICS ON LATE TERTIARY LACUSTRINE DEPOSITS IN CENTRAL ARIZONA AND THEIR FLORISTIC AFFINITIES. Chihuahuan Desert, Colorado Plateau, Mohave Desert, and elevational (various floristic affinities from surrounding mountains). * = endemics.

Species and Floristic Affinities	Transition Zone Basins in the Sonoran Desert			
	Burro Creek	Verde Valley	Lower Verde River	San Carlos Basin
Chihuahuan Desert				
<i>Anulocaulis leisolenus</i>		X		
<i>Polygala macradenia</i>			X	X
<i>Polygala scoparioides</i>		X	X	X
<i>Purshia subintegra</i>	X	X	X	X
<i>Thamnosma texana</i>		X	X	X
Colorado Plateau				
<i>Arenaria eastwoodiae</i>	X			X
<i>Astragalus calycosus</i> var. <i>scaposus</i>		X	X	X
<i>Astragalus newberryi</i> var. <i>aquarii</i> *	X			
<i>Astragalus newberryi</i> var. <i>newberryi</i>		X		
<i>Astragalus praelongus</i>		X		
<i>Atriplex confertifolia</i>				X
<i>Cordylanthus parviflorus</i>	X	X		
<i>Eriogonum apachense</i> *				X
<i>Eriogonum ericifolium</i> var. <i>ericifolium</i> *		X		
<i>Eriogonum ripleyi</i>		X	X	
<i>Glossopetalon spinescens</i> var. <i>aridum</i>		X		X
<i>Hymenoxys acaulis</i> var. <i>arizonica</i>		X		
<i>Penstemon thompsonae</i>		X		X
<i>Petradoria pumila</i>		X		
<i>Physaria newberryi</i>				X
<i>Polygala rusbyi</i>		X	X	
<i>Salvia dorrii</i> var. <i>mearnsii</i> *		X		
<i>Streptanthus cordatus</i>	X	X		X
Mohave Desert				
<i>Phacelia parishii</i>	X			
Elevational				
<i>Astragalus tephrodes</i> var. <i>chloridae</i>			X	
<i>Eriogonum hieracifolium</i>				X
<i>Lesquerella cinerea</i>	X	X	X	
<i>Lotus mearnsii</i> var. <i>equisolensis</i>			X	
<i>Lotus mearnsii</i> var. <i>mearnsii</i>		X		
<i>Senecio neomexicana</i>		X	X	

var. *scaposus*, *Astragalus newberryi* var. *aquarii**, *Astragalus newberryi* var. *newberryi*, *Astragalus praelongus*, *Atriplex confertifolia*, *Cordylanthus parviflorus*, *Eriogonum apacheense**, *Eriogonum ericifolium* var. *ericifolium**, *Eriogonum riplei*, *Glossopetalon spinescens* var. *aridum*, *Hymenoxys acaulis* var. *arizonica*, *Penstemon thompsonae*, *Petradoria pumila*, *Physaria newberryi*, *Polygala rusbyi*, *Salvia dorrii* ssp. *mearnsii**, and *Streptanthus cordatus*.

The Verde Valley (Fig. 3), which is closest to the Mogollon Rim and 300–450 m higher in elevation than the other basins, has the largest number of the northern disjuncts. At this higher elevation several of these taxa are not totally restricted to the Verde Formation limestone and gypsum, but have scattered occurrences along the north end of the Verde Valley: *Astragalus calycosus* var. *scaposus*, *Astragalus praelongus*, *Cordylanthus parviflora*, *Glossopetalon spinescens* var. *aridum*, *Hymenoxys acaulis* var. *arizonica*, *Lesquerella cinerea*, and *Senecio neomexicana*.

Several of the Colorado Plateau species are found all the way to the southeast on the San Carlos Basin lacustrine deposits (Fig. 5): *Arenaria eastwoodiae*, *Astragalus calycosus* var. *scaposus*, *Eriogonum apacheense* (endemic), *Glossopetalon spinescens* var. *aridum*, *Penstemon thompsonae*, *Physaria newberryi*, and *Streptanthus cordatus*. The San Carlos Basin lacustrine deposit also contains the only Sonoran Desert occurrence of *Atriplex confertifolia*, a Great Basin desertscrub species (shadscale) of alkaline soils, although it is also disjunct farther east and south into Texas (Benson and Darrow 1981). There are pollen records of *Atriplex confertifolia* from late Pleistocene packrat middens in present day Sonoran Desert mountain ranges of western Arizona documenting its southward migration during glacial periods (King and Van Devender 1977).

Chihuahuan Desert. One group of disjuncts has the main portion of their present range in the warm temperate Chihuahuan Desert in southeastern Arizona, New Mexico, Texas, and Mexico (Brown 1982). *Polygala macradenia*, *Polygala scoparioides*, and *Thamnosma texana*, which are scattered in southeastern Arizona, become disjunct and reach the northwestern margin of their ranges at the lacustrine sites along the Verde River, the former at the Lower Verde River and the latter two at the Verde Valley. None reach the Burro Creek outcrops. (There are also historical records of *Polygala scoparioides* [Collom 714 (ASC)] and *Thamnosma texana* [Collom 401 (ARIZ)] from the Payson Basin). *Anulocaulis leisolenus* is the most widely disjunct taxa, from southern New Mexico to the Verde Valley, the only one of the late Tertiary basins in which it has been found. Conversely, it does not reach its northwestern margin there as the above mentioned species do, but is then disjunct even farther northwest from the Verde Valley to limestone strata at the south rim

of the Grand Canyon and gypsum beds of the Muddy Mountains in southern Nevada (Knight 1983).

Purshia subintegra, which is endemic to the late Tertiary lacustrine deposits at all four basins: the San Carlos Basin, the Verde River sites, and Burro Creek, is a vicariant species with *Purshia ericifolia*, a Chihuahuan Desert species from over 500 miles away in the Big Bend Region of Texas and adjacent Mexico (Anderson 1992). *Purshia ericifolia* occupies a similar ecological setting there on limestone in the succulent-scrub upland of the Chihuahuan Desert (Brown 1982).

Mohave Desert. The Burro Creek site (Fig. 2) which is the smallest in size and the farthest from these floristic sources has the fewest disjuncts. It does support the only Arizona occurrence of *Phacelia parishii*, a rare annual species disjunct from the Mohave Desert in Nevada and California.

A few taxa, *Eriogonum hieracifolium*, *Lesquerella cinerea*, *Lotus mearnsii* var. *mearnsii*, and *Senecio neomexicana*, are disjunct in elevation by 300–1200 m lower to one or more of the Sonoran Desert basins from their primary distribution in the Rocky Mountain Montane Conifer Forests directly north on the Mogollon Rim or west in the Bradshaw Mountains (Brown 1982), also described as the Apachian Floristic Element of McLaughlin (1989). A new variety of *Lotus mearnsii* is described below that is endemic to the lowest elevation basin at the Lower Verde River (Fig. 4). It is related to the typical variety mentioned above. Another taxon from the Lower Verde River, *Astragalus tephrodes* var. *chloridae*, is disjunct lower from the interior chaparral in the surrounding Mazatzal Mountains; this variety also extends northwest to the higher elevation Mohave Desert between the Cerbat Mountains in Arizona and the adjacent Newberry Mountains in Nevada.

NEW VARIETY DESCRIPTION

The discovery during this study of a disjunct population of *Lotus mearnsii* from the Lower Verde River near Horseshoe Reservoir in the Sonoran Desert that differed from specimens of previously known populations led to the recognition of a new variety. It differs from typical *L. mearnsii* in longer peduncles, larger flowers, larger pods, and shorter internodes with a more compact growth habit. It is endemic to lacustrine deposits near Horseshoe Reservoir for which it is named var. *equisolensis* (horseshoe) and is separated geographically by 80 km (50 miles) from the nearest populations of *Lotus mearnsii* var. *mearnsii* in the Verde Valley.

Lotus mearnsii (Britt.) Greene var. **equisolensis** J. Anderson, var. nov.—TYPE: USA, Arizona, Maricopa County, (Lower) Verde

River, S of Horseshoe Reservoir, 0.3 miles W of road to reservoir on Forest Service Road 205, growing on white lacustrine outcrop, 2100 feet elevation, T17N, R6E, S3, with *Purshia*, *Canotia*, *Dodonea*, *Eriogonum*, *Nolina*, *Encelia*, Sonoran Desert, 3 April 1987, *J. L. Anderson 87-21* (holotype, ASU; isotypes ARIZ, BYU, ISC, NY).

A var. *mearnsii* foliis grandioribus latioribusque late obovatis minus quam duplo longioribus quam latioribus, pedunculis longioribus longitudine 25–75 mm, floribus longioribus longitudine 14–20 mm, leguminibus grandioribus 25–35 mm longis et 4–7 mm latis, internodis brevioribus et habitu condensatiore differt.

Spreading to prostrate perennial herb arising from subterranean caudex; stems clustered, procumbent, 1–3 dm long; pubescence silvery to less dense at distal end of stems, sericeous; leaves shorter than to as long as internodes, subpinnate to palmate, sericeous on both surfaces, petiole 2–5 mm, leaflets 3–5, broadly obovate or obcordate, 6–16 mm long, 4–12 mm wide, length to width ratio less than 2; peduncles prolonged beyond the leaves, 25–75(95) mm long; umbels with 2–7 flowers, 14–20 mm long; calyx tube narrowly campanulate, 4–7 mm long, teeth 2–4 mm long; corolla bright yellow, petals subequal; ovary pubescent, ovules 16–20; pod erect to ascending, oblong, 25–35 (40) mm long, 4–6 mm wide, subpersistent, dehiscent, valves strigulose, coriaceous; seeds few.

PARATYPES: same locality, 9 April 1986, *J. L. Anderson 86-33* (ASU, BYU).

Because the morphological differences between *Lotus mearnsii* var. *equisolensis* and the typical variety are quantitative rather qualitative, this new taxon has been named at the varietal level. *L. m.* var. *equisolensis* is endemic to the Lower Verde River in the Sonoran Desert at 840 m (2100 ft), whereas the range of the typical variety is separated geographically 80–240 km (50–150 miles) to the northwest, from the Verde Valley (the type locality of the typical variety (Britton 1889)), to the Bradshaw Mountains and the Chino Valley; and its habitat is described as “. . . limestone plateau, dry rocky grasslands, ca 3000–7000 ft . . .” (Isely 1981) and “. . . 3,000–7,000 feet, grassland and dry mesas and slopes . . .” (Kearney et al. 1960). Thus, the new variety is geographically isolated and largely ecologically distinct from the typical variety. Because of this populational integrity (rather than representing simply the end of a cline), taxonomic recognition of the Lower Verde River population is warranted. The varietal level is also appropriate since plants of the typical variety that are transitional to *L. m.* var. *equisolensis* occur in the Verde Valley which is intermediate in elevation and habitat between the Lower Verde River and the Chino Valley (Isely 1981). This

taxonomic situation is paralleled by *Astragalus newberryi* from the Colorado Plateau which has the geographically isolated low elevation endemic variety, *A. n. var. aquarii*, at the Burro Creek site and transitional plants of *A. n. var. newberryi* in the Verde Valley (Isely 1983).

DISCUSSION

The many floristic migrations across Arizona caused by the great climatic and topographic variability in the late Tertiary and Pleistocene have resulted in the different floristic sources of the disjuncts, relicts, and endemics occurring on the Transition Zone lacustrine basins which were formed by the late Tertiary Basin and Range Disturbance (Damon et al 1984) and which now serve as refugia as "... the edaphic environments stand as either selecting agents, or barriers imposed across the path of a migrating flora ... " (Mason 1946). Sharp edaphic boundaries can produce sharp discontinuities in plant species distribution (Gankin and Major 1964; Kruckeberg 1969). The inclusion of various types of infertile or otherwise azonal soils, for example, gypsum (Turner and Powell 1979), limestone (Wentworth 1981), and serpentine (Kruckeberg 1954; Whittaker 1954), within the surrounding, but contrasting, normal soils, can form edaphic islands that act as refugia for disjuncts, relicts, and endemics (Kruckeberg 1986). However, it is the existence of a sharp edaphic contrast itself that is more important than the specific nature of the soil differences (Gankin and Major 1964). Since Sonoran Desert soils are mainly derived from volcanics and metamorphics, limestone soils (such as the late Tertiary lacustrine deposits in the Transition Zone) form a sharp edaphic contrast here (Whittaker and Neiring 1968).

In addition, the Sonoran Desert basins along the Transition Zone contain a more equable climate compared to surrounding desert areas. The equable climatic parameters combine a moderate mean annual temperature, a small difference between mean annual high and low temperature, and a biseasonal precipitation pattern of 25 cm or more annual precipitation (Raven and Axelrod 1978; Axelrod 1979); these are the climatic parameters which are most similar to the mesic Miocene paleoclimates in the Southwest (Axelrod 1979; Brown 1882). This comparatively more mesic ecological setting at the northern edge of the Arizona Sonoran Desert is a climatic refugia similar to the Sonoran Desert/coastal chaparral ecotone in Baja California Norte at the southwestern edge of the Sonoran Desert described by Raven and Axelrod (1979) as "... an ecotonal region of equable climate that [is] inhabited by many endemics, both ancient and recently derived." Cain (1944) has termed such sites "... regions of compensation where the local conditions of microclimate

or soil allow them to resist, for a time at least, the climatic pressure and the competition from the surrounding vegetation . . . relicts are likely to occupy the most favorable sites in a region at least with respect to temperature and moisture conditions”.

In the Miocene the equable paleoclimate and low topographic relief across the Southwest supported a diverse pine-oak-juniper woodland (Axelrod 1979). Also, there was a contiguous physiographic connection of the paleoflora between central Arizona and southwestern New Mexico as the Verde and eastern Gila River drainage systems flowed eastward into New Mexico with possible connections of the Verde Valley with the Payson and Tonto Basins and the San Carlos Basin with New Mexico through the Pliocene, the opposite of their present westward courses across Arizona (Kotlowski et al. 1965; Pedersen and Royce 1970). The Pliocene uplift of the Sierra Nevada in California and the Mexican Plateau in Sonora and Chihuahua caused a rainshadow from the west and east respectively across the Southwest, resulting in a less equable climate overall with increased aridity, less summer precipitation, and a more continental climatic condition of temperature extremes (Axelrod 1979; Smiley 1984). The vegetative history of southern Arizona in the late Tertiary has reflected this progressive climatic deterioration as the pine-oak-juniper woodland has given way to the arid Sonoran Desert and Chihuahuan Desert vegetation present today (Gray 1960a, b; Axelrod 1979; Northington et al. 1981).

Along with climatic deterioration, southern Arizona and southern New Mexico were separated by uplift of the Continental Divide through southwestern New Mexico with the reversal of drainage patterns to the west across central Arizona with the westward connection of the basins and exposure of the lacustrine deposits (Nations et al. 1982). Species from the pine-oak-juniper woodlands migrated to the southeast into the present day Chihuahuan Desert of New Mexico, Texas, and Mexico; however, some left behind vicariant species pairs of paleoendemics in *Canotia*, *Castela*, *Colubrina*, and *Tetracoccus* between the Sonoran and Chihuahuan Deserts (Axelrod 1979), and including *Purshia subintegra* and *P. ericifolia* (Van Devender 1986).

A similar vicariant pattern has been documented between the Transition Zone basins in the genus *Sophora* section *Calia* (Berland) Rudd by Northington et al. (1977). *Sophora arizonica* Watson, an interior chaparral shrub called mesal bean, is disjunct between the two most widely separated basins (but in the non-limestone foothills), the Big Sandy Basin (Fig. 1A) and the San Carlos Basin (Fig. 1H), at a distance of over 300 km; it also has a few disjunct populations in southeastern Arizona mountain ranges on limestone. *Sophora arizonica*'s nearest relative is *S. gypsophila* Turner and Powell, a rare Chihuahuan Desert species of west Texas (Northington

1976). This vicariant pair is thought to be the arid remnants of a widespread mesic progenitor from the late Tertiary pine-oak-juniper woodlands with present relatives in the pine-oak-juniper woodlands of Mexico (Northington et al. 1977). Those taxa listed in Table 1 with Chihuahuan Desert floristic affinities are thus thought to really be relicts or their descendents of the late Tertiary Southwestern pine-oak-juniper woodlands which presently occur in the Chihuahuan Desert, similar to the *Sophora arizonica*/*S. gypsophila* pattern described above (Anderson 1986).

More recently, floristic migrations in Arizona have been between the south and north, rather than east and west. The presence of desert vegetation here has been interrupted by the Pleistocene glacial cycles with their colder climates that pushed pinyon-juniper woodlands and sagebrush scrublands south from the Colorado Plateau into southern Arizona as recently as 11,000 years ago, as evidenced by packrat midden studies (Van Devender 1977; Van Devender and Spaulding 1979; Betancourt 1987). Floristic remnants of the southern migration of the pinyon-juniper woodlands and sagebrush scrublands, as well as Joshua tree woodlands (Van Devender 1987), during the last Wisconsin glaciation were left behind with their subsequent retreat northward during the Holocene. These northern disjuncts have survived on the edaphic refugia of the Transition Zone Basins in various combinations, but do not occur anywhere else in the Sonoran Desert. Also, the Transition Zone receives the highest amounts of winter rainfall in the Sonoran Desert, simulating the paleoclimate of increased winter precipitation during glacial times (Van Devender 1977). Because of the parallel distribution pattern of several northern disjuncts between the Transition Zone Basins, their occurrences are probably the remnants of parallel migrations during glacial times, rather than a result of several, independent long range dispersals resulting in similar distributions (Anderson 1986). The presence of elevational disjuncts from the surrounding mountains or the Mogollon Rim onto the Sonoran Desert basins is similarly a result of the lowering of vegetation zones during the Wisconsin glaciation.

With the subsidence of southwestern Arizona during the late Tertiary Basin and Range Disturbance, these relicts have been restricted progressively northward from the lower elevations of the Sonoran Desert to the more equable climates of the basins. There they survive only on refugia of azonal edaphic islands of Late Tertiary lacustrine deposits where they also escape competition from the surrounding dominant vegetation (Anderson 1986).

Substrate switching, whereby a population disjunct from the main range of a species exhibits a different soil preference at the edge of the species' range, is well documented (Pigott and Walters 1953; Raven 1972; Mansberg and Wentworth 1984; Neely and Barkworth

1984). In a famous example, several long range disjuncts with no preference for calcareous soils elsewhere are calciphiles in Convict Basin in the Sierra Nevada where limestone soils act as an ecological island within the predominately granitic Sierra Nevada and provide a sharp edaphic contrast (Major and Bamberg 1963). Similarly, the late Tertiary lacustrine disjuncts and endemics are mostly indifferent to calcareous soils throughout their main ranges, but are calciphiles here at the edge of their range in the Sonoran Desert, for example (Kearney et al. 1960, pp. 298, 428, 459, 467, 494, 499, 501, 741, and 791; Vines 1960, pp. 426, 593, and 606).

CONCLUSIONS

In the Transition Zone basins on the northern edge of the Sonoran Desert, each set of disjuncts is independently derived and the particular combination of disjuncts and endemics is a product of the vagaries of the unique environmental history of that basin within the overall vegetative history of the Southwest. What is unusual is the resultant mix of members of normally widely separated floristic areas, the Colorado Plateau and the Chihuahuan Desert, in these climatic and edaphic refugia within another floristic area, the Sonoran Desert. Other ecotonal margins of the Sonoran Desert at the xeric/mesic boundary characterized by a more equable climate of biseasonal rainfall, the interior foothills of the Peninsular Ranges in southern California on the west and the coastal foothills of the Sierra San Pedro Mártir in northern Baja California on the southwest are also characterized by endemics and relicts (Raven and Axelrod 1978; Stebbins and Major 1965). There are more disjuncts with northern affinities because they can extend farther south wherever moisture conditions are sufficient, but frost sensitive southern species are limited sooner to the north by freezing temperatures (Shreve 1936).

A knowledge of floristic history can be used to predict where to search for other disjunct populations. For example *Anulocaulis leisolenus* might be expected on the lacustrine deposits in the San Carlos Basin or other limestones in the Chihuahuan Desert mountain ranges of southeastern Arizona, which are between its disjunct occurrences in New Mexico and the Verde Valley. A recently described species from dolomite soils in southern Nevada, *Porophyllum pygmaeum* Keil and Morefield, is postulated to be most closely related to a species from west Texas, *P. greggii* Gray (Keil and Morefield 1989). If either species occurs in Arizona, it would be expected on the late Tertiary lacustrine basin deposits.

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APPENDIX I. SPECIMEN CITATIONS FOR DISJUNCTS AND ENDEMICS

Specimen citations are listed by basin location: Burro Creek, Verde Valley, Lower Verde River (Horseshoe Reservoir), and San Carlos Basin. More specific locality data are on the herbarium labels. All voucher specimens are deposited at Arizona State University (ASU) unless otherwise indicated.

ASTERACEAE

- Hymenoxys acaulis* (Pursh) K. F. Parker var. *arizonica* K. F. Parker. - Verde Valley, 8 June 1995, *Anderson 95-17*.
- Petradoria pumila* (Nutt.) Greene. - Verde Valley, 8 June 1995, *Anderson 95-18*.
- Senecio neomexicanus* Gray. - Verde Valley, 29 May 1981, *Van Devender et al. s. n.* (ARIZ); - Lower Verde River, 7 Apr 1986, *Anderson 86-18*; 9 Apr 1986, *Anderson 86-31*.

BRASSICACEAE

Lesquerella cinerea Rollins. - Burro Creek, 10 Apr 1947, *Darrow and Gould 4251* (ARIZ); 7 Apr 1984 *Anderson s. n.*; - Verde Valley, 10 May 1967, *Rollins 67111* (ARIZ); 29 Apr 1985, *Schaack and Morefield 1474* (ASC); - Lower Verde River, 7 Apr 1986, *Anderson 86-20*.

Physaria newberryi Gray. - San Carlos Basin, 5 June 1968, *Pinkava, Keil, and Lehto 13023*; 7 Apr 1969, *Pinkava, Keil, and Lehto 15590*; 18 Mar 1985, *Anderson 85-1*; 11 Apr 1985, *Anderson 85-7*; 14 Apr 1986, *Anderson 87-9*.

Streptanthus cordatus Nutt. ex T & G. - Burro Creek, 6 Apr 1986, *Anderson 86-3*; - Verde Valley, 11 May 1968, *Patten, Pinkava, and Keil 3381*; 18 Apr 1978, *Rommingner 1743* (ASC); - San Carlos Basin, 7 Apr 1969, *Pinkava, Keil, and Lehto 15584*; 11 Apr 1985, *Anderson 85-6*.

CARYOPHYLLACEAE

Arenaria eastwoodiae Rybd. - Burro Creek, 10 Apr 1947, *Darrow and Gould 3695*; 6 Apr 1986, *Anderson 86-6*; 1 Apr 1987 *Anderson and Reichenbacher 87-1*; - San Carlos Basin, 7 Apr 1969, *Pinkava, Keil, and Lehto 15591*; 14 Apr 1986, *Anderson 86-45*; 2 May 1987, *Anderson and Reichenbacher 87-8*.

CHENOPODIACEAE

Atriplex confertifolia (Torr. & Frem.) S. Wats. - San Carlos Basin, 2 Sept 1993, *Anderson 93-17*.

CROSSOSOMATACEAE

Glossopetalon spinescens Gray var. *aridum* M. E. Jones. - Verde Valley, 2 Apr 1953, *Carter 3232 and Chisaki* (ARIZ); 16 Mar 1984, *Anderson 84-1*; San Carlos Basin, 19 Apr 1984, *Anderson s.n.*

FABACEAE

Astragalus calycosus Torr. var. *scaposus* (Gray) Jones. - Verde Valley, 10 Apr 1941, *Darrow s.n.* (ARIZ); 25 May 1947, *Gooding 5-47* (ARIZ); Lower Verde River, 8 Apr 1986, *Anderson 86-22*; - San Carlos Basin 14 Apr 1986, *Anderson 86-44*.

Astragalus newberryi Gray var. *aquarii* Isely. - Burro Creek, 18 Apr 1941, *Benson and Darrow 10898* (ARIZ); 20 Mar 1985, *Anderson 85-2*.

Astragalus newberryi var. *newberryi* Gray. - Verde Valley, 15 Apr 1977, *Lehto 25576*, *Pinkava, Parfitt, and Reeves*; 16 Apr 1978, *Gierisch 4184*.

Astragalus praelongus Sheld. - Verde Valley, 27 Mar 1959, *Deaver 5438a*; 14 Apr 1960, *Crosswhite 726*.

Astragalus tephrodes Gray var. *chloridae* (Jones) Barneby. - Lower Verde River, 3 Apr 1987, *Anderson 87-23*.

Lotus mearnsii var. *mearnsii* (Britt.) Greene. - Verde Valley, *Mearns 342* (Holotype: NY); 15 Apr 1978, *Lehto 22564*, *Pinkava, Parfitt, and Reeves*; 23 June 1979, *Ertter and Strachen 2937*; 29 Apr 1981, *Van Devender s.n.* (ARIZ); 7 May 1989, *Anderson 89-40*.

Lotus mearnsii (Britt.) Greene var. *equisolensis* J. Anderson. - Lower Verde Valley, 3 Apr 1987, *Anderson 87-21*; 9 Apr 1986, *Anderson 86-33*.

HYDROPHYLLACEAE

Phacelia parishii Gray. - Burro Creek, 2 June 1993, *Anderson 93-12*.

LAMIACEAE

Salvia dorrii (Kell.) Abrams ssp. *mearnsii* (Britt.) McClintock. - Verde Valley, 20 Apr 1985, *Schaack and Morefield 1457* (ASC); 17 May 1977, *Rommingner 1629*

(ASC); 15 Apr 1978, *Parfitt 2537, Reeves, and Pinkava*; 24 June 1979, *Ertter and Strachen 2940*; 7 May 1989, *Anderson 89-42*.

NYCTAGINACEAE

Anulocaulis leisolenus (Torr.) Standl. - Verde Valley, 24 June 1939, *Peebles 14441* (ARIZ); 19 Sept 1976, *McGill and Lehto 20699*; 24 June 1979, *Ertter and Strachen 2943*; 29 May 1981, *Van Devender s.n.* (ARIZ); *Schaack, Romminger, and Morefield S1303* (ASC); 7 May 1989, *Anderson 89-38*; - Coconino Co., Havasupai Canyon, 27 Sept 1943, *Clover 7217* (ARIZ); Grand Canyon, Little Colorado stop, 30 Apr 1970, *Holmgren and Holmgren 15494* (ARIZ); Grand Canyon National Park, along River Trail, 1/2 mile W of Phantom Ranch, 7 June 1976, *Romminger 1569* (ASC); Nevada, Clark Co., 1 mile S of Glendale, *Spaulding, Van Devender, and Tessman s.n.* (ARIZ).

POLYGALACEAE

Polygala macradenia Gray. - Lower Verde River, 8 Apr 1986, *Anderson 86-25*; San Carlos Basin, 2 Apr 1987, *Anderson with Reichenbacher 87-11*.

Polygala rusbyi Greene. - Verde Valley, 5 May 1973, *Lehto, Brown, and Pinkava 11064*; 6 May 1978, *Lehto and Pinkava 22748*; 16 Apr 1985, *Schaack 1437* (ASC); - Lower Verde River, 11 May 1979, *Harris and Lehto s.n.*; 5 Apr 1986, *Schaack 1726* (ASC); 3 Apr 1987, *Anderson 87-22*.

Polygala scoparioides Chodat. - Verde Valley, 30 Apr 1977, *Pinkava and Lehto 21345*; 18 Apr 1978, *Romminger 1744* (ASC); 27 June 1979, *Ertter and Strachen 2920*; 7 May 1989, *Anderson 89-45*; - Lower Verde River, 8 Apr 1986, *Anderson 86-24*; - San Carlos Basin, 14 Sept 1967, *Keil, Pinkava, and Lehto 10112*; 24 May 1976, *Bingham 2234*.

POLYGONACEAE

Eriogonum apachense Reveal. - San Carlos Basin, 7 Apr 1968, *Pinkava, Keil, and Lehto 13400*; 27 May 1976, *Bingham 2242*; 18 Oct 1976, *Gierisch 3837*.

Eriogonum ericifolium Torr. & Gray var. *ericifolium* Torr. & A. Gray. - Fort Verde, *Mearns 179* (Holotype: NY); Verde Valley, 19 Sept 1976, *McGill and Lehto 20720*; 24 Aug 1977, *Gierisch 3981*; 5 Oct 1984, *Schaack 1374* (ASC); 19 Oct 1984, *Schaack 1386* (ASC).

Eriogonum hieracifolium Benth. in DC. - San Carlos Basin, 24 May 1976, *Bingham 2228*; 14 Apr 1989, *Anderson and Porter 89-46*.

Eriogonum ripleyi J. T. Howell. - Verde Valley, 20 Apr 1985, *Schaack and Morefield 1458*; - Lower Verde River, 8 Apr 1986, *Anderson 86-29*; 9 Apr 1986, *Anderson 86-34*.

ROSACEAE

Purshia subintegra (Kearney) Henrickson. - Burro Creek, 4 Apr 1938, *Darrow & Crooks 3*, 18 Apr 1941 (ARIZ); *Darrow and Benson 10891* (ARIZ); 18 Apr 1977, *Geirisch 3896*; 7 Apr 1984, *Anderson 84-5* and *84-6*; - Verde Valley, 16 Mar 1984, *Anderson 84-2*; 11 Apr 1984, *Anderson 84-13*; - Lower Verde River, 7 Apr 1986, *Anderson 86-15*; 9 Apr 1986, *Anderson 86-35* and *86-36*; - San Carlos Basin, 7 Sept 1968, *Pinkava, Keil, and Lehto 13397*; 9 Apr 1984, *Anderson 84-7, 84-8, 84-10, 84-11, and 84-12*; 11 Apr 1985, *Anderson 85-5*.

RUTACEAE

Thamnosma texana (A. Gray) Torrey. - Verde Valley, 30 Apr 1977, *Pinkava and Lehto 21344*; 18 Apr 1978, *Romminger 1749* (ASC); - Lower Verde Valley, 3 Apr 1987 *Anderson 87-21*; - San Carlos Basin, 2 Apr 1987, *Anderson 87-10*.

SCROPHULARIACEAE

Cordylanthus parviflorus (Ferris) Wiggins. - Burro Creek, 5 Nov 1983, *Parfitt 3155*;
- Verde Valley, 2 Aug 1969, *Hekard and Chuang 2362* (RSA).

Penstemon thompsonae (A. Gray) Rydb. - Verde Valley, 11 May 1968, *Patten, Pinkava, and Keil 3382*; 5 May 1977, *Lehto, Brown, and Pinkava 11082*; - San Carlos Basin, 4 Sept 1967, *Keil, Pinkava, and Lehto 13022*; 4 May 1973, *Holmgren and Holmgren 7064*.

PLANT ASSOCIATIONS OF CASTLE CRAGS STATE PARK, SHASTA COUNTY, CALIFORNIA

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ABSTRACT

Vegetation types in Castle Crags State Park were classified using TWINSPLAN into 8 series and 15 associations from 237 plots. The series, in decreasing order of abundance, were *Pseudotsuga menziesii*, *Quercus kelloggii*, *Alnus rhombifolia*, *Quercus chrysolepis*, *Ceanothus cuneatus*, *Bromus tectorum*, *Quercus garryana*, and *Juncus patens*. In addition, 2 types occurring in chronically disturbed habitats (powerline corridor and mowed meadow) were described. Each vegetation type was further described using physiography, soil characteristics, species diversity, tree density by height class, and basal area of tree species. Successional interpretations were made for plant associations.

INTRODUCTION

Castle Crags State Park has several important botanical and ecological roles: a) it serves as a landscape bridge and corridor across the Sacramento River between the southern Cascades and the Klamath Mountains; b) it is host to the rare *Ivisia longibracteata*; and c) it preserves low-elevation montane forest, shrub, riparian, and herbaceous communities. Adjacent lands along the Sacramento River corridor are heavily disturbed from logging, mining, development, and construction and maintenance of transportation routes. Plant associations in this ecologically diverse and vital park have not been adequately classified and described. In this paper we present a classification and description of the park's existing plant associations, ascribe their distribution to physiographic or soil characteristics, provide data for the future management of these communities, and assess the successional potential of the forests.

The park is recovering from a series of disturbances dating from the late nineteenth and early twentieth centuries (Beat and Gut 1981). Mining, logging, and wildfires consumed nearly all of the old-growth forest, leaving behind early successional communities that were apparently characterized by sprouting hardwoods and shrubs, shrub seedlings, early seral herbaceous species, and occasional surviving conifers. Conifer seedlings and some late seral shrub and herbaceous species were undoubtedly present in these early seral communities.

Today, after approximately 125 years of succession, the plant communities in Castle Crags State Park are relatively well defined.

Much of the park is dominated by Douglas-fir and mixed conifer forest with meadows and shrublands situated on alluvial, granitic, or serpentinitic parent materials in Castle Creek Valley. Interspersed within the conifer forest are stands of California black oak.

METHODS

Study Area

Castle Crags State Park encompasses 1681 ha both east and west of the Sacramento River in the Klamath Mountains Province, California (approximately 41°9'N, 122°20'W). Elevations range from approximately 640 m to 1220 m. Slopes typically exceed 40% and have soils derived from alluvium, serpentine, granitic rock, and greenstone (Mallory and Powell 1978). The Crags lying to the northwest of the state park are what remains of a granitic pluton that has been extensively eroded and glaciated.

The McCloud weather station, situated 17 km to the northeast, receives an average of 130 cm precipitation per year. Mean high temperatures are 8°C in winter and 30°C in summer. Mean low temperatures are -7°C in winter and 8.5°C in summer (National Climatic Data Center 1990).

Forested communities conform to the Society of American Foresters cover types of Pacific ponderosa pine—Douglas-fir, California black oak, and the Sierra Nevada mixed conifer (Eyre 1980).

Study Site Selection

We used 1:12,000 color stereo aerial photography in conjunction with a U.S.G.S. orthophoto of the Dunsmuir Quadrangle to identify areas (polygons) with apparently homogeneous vegetation composition and structure. Two hundred and thirty polygons were delimited. Of these we sampled all polygons that appeared to have unique structural or species composition characteristics. Forty-eight polygons were selected for ground sampling; the remaining polygons were indistinguishable from those selected for sampling. We established approximately 5 plots per selected polygon for a total of 237 plots.

Field Measurements

Plots were subjectively placed and centrally replicated to best characterize vegetation in each polygon (Mueller-Dombois and Ellenberg 1974). No ecotone plots were established. Forested plots were 0.1 ha in area, shrub-dominated plots were 0.05 ha, and herb-dominated plots 0.01 ha. Vascular plant cover was ocularly estimated to the nearest 5% for canopy trees, 1% for small trees and shrubs, and 0.01% for herbs. On forested plots, we recorded tree

basal area and tree density by species for the 0–3 m, 3–10 m, and >10 m height classes.

Data Analysis

Species percent cover was averaged over all plots within a polygon to avoid pseudoreplication. Subsequent statistical analyses were based on the 48 polygons, and not on the 237 individual plots. Rare species, occurring in less than 3 plots, were deleted from the data matrix prior to classification because they act like outliers in multivariate classification algorithms, adding variability that obscures central tendencies (Gauch 1982).

We used TWINSpan (two-way indicator species analysis) (Hill 1979) to classify samples and species into similar groups. Pseudo-species (a type of differential species based on predetermined abundance levels) cut levels were 0, 2, 5, 10, 20, 35, and 50. Pseudo-species cut levels of 20, 35, and 50 received twice the weighting of the others in order to favor dominants. Plant associations were described using percent cover and constancy.

Species richness was determined for each classified plant association. Richness estimates were based on the cumulative number of species in 5 randomly selected plots from each plant association. We did this to avoid sampling area bias and to ensure comparability between plant associations (Magurran 1988).

Successional Inferences

Successional inferences were based on the life history attributes of potential canopy dominants: mode of persistence, species tolerance of understory conditions, fire tolerance, longevity, stature, and reproductive success in the understory.

RESULTS AND DISCUSSION

Classification and Description of Plant Associations

We interpreted 8 series and 15 plant associations from the TWINSpan output (Fig. 1). Nine associations were forested (Table 1); 3 were shrublands (Table 2); and 3 were herb-dominated (Table 3). In addition, two communities occurred in chronically disturbed sites: beneath a powerline, and in a mowed meadow. Level zero in the dendrogram (Fig. 1) divided forested from unforested plots. Level 1 separated plots according to life form, and levels 2 and 3 according to dominant overstory species, physiognomy, or parent material. Level 4 further divided plots according to physiography or parent material.

Physiographic and soil characteristics of each plant association

are presented in Table 4. Basal area, species richness, and tree density for each plant association are presented in Table 5.

Pseudotsuga menziesii Series

All plant associations within the *Pseudotsuga menziesii* series had moderately deep soils, gravely loam soil textures, and were found on greenstone, alluvium, or basaltic rock. Differences between *Pseudotsuga menziesii* associations were seen in aspect, % slope, and % rock and bare soil.

1. The *Pseudotsuga menziesii*/*Lithocarpus densiflorus* var. *echinoides* (PSME/LIDEE) association was dominated by *Pseudotsuga menziesii* with 40% cover and 100% constancy. The shrub form of *Lithocarpus densiflorus*, var. *echinoides*, was dominant in the understory with 24% cover and 94% constancy. Species richness was 27 and there were 39.7 m²/ha of basal area. This association typically occurred on north aspects. Slopes averaged 27%.
2. *Pseudotsuga menziesii* was predominant in the *Pseudotsuga menziesii*/*Cornus nuttallii*-*Toxicodendron diversilobum* (PSME/CONU-TODI) association with 51% cover and 100% constancy. *Calocedrus decurrens* and *Quercus kelloggii* were minor canopy associates. *Cornus nuttallii* and *Toxicodendron diversilobum* had the greatest cover and constancy in the understory. This association had the most biomass (basal area = 57.2 m²/ha) and the least exposed rock and bare soil. No other

←

FIG. 1. Twinspan dendrogram with interpretative annotations. Numbers beneath lines represent the number of plots prior to division. Numbers in boxes are the number of plots in each classified plant association. Labels beneath numbered boxes are plant association acronyms. QUCH/ARVI-ARPA = *Quercus garryana*/*Arctostaphylos viscida*-*Arctostaphylos patula*, ALRH-ACMA/ACCI = *Alnus rhombifolia*-*Acer macrophyllum*/*Acer circinatum*, ALRH-PSME-CADE/RUDI = *Alnus rhombifolia*-*Pseudotsuga menziesii*-*Calocedrus decurrens*/*Rubus discolor*, PSME/LIDEE = *Pseudotsuga menziesii*/*Lithocarpus densiflorus* var. *echinoides*, PSME/CONU-TODI = *Pseudotsuga menziesii*/*Cornus nuttallii*-*Toxicodendron diversilobum*, PSME-CADE-QUKE/NAPU = *Pseudotsuga menziesii*-*Calocedrus decurrens*-*Quercus kelloggii*/*Nassella pulchra*, PSME-CADE/NAPU = *Pseudotsuga menziesii*-*Calocedrus decurrens*/*Nassella pulchra*, QUKE/TODI = *Quercus kelloggii*/*Toxicodendron diversilobum*, QUKE/NAPU = *Quercus kelloggii*/*Nassella pulchra*, NAPU-SABI = *Nassella pulchra*-*Sanicula bipinnatifida*, CECU/ERLA = *Ceanothus cuneatus*/*Eriophyllum lanatum*, CECU-RHCA-ARPA = *Ceanothus cuneatus*-*Rhamnus californica*-*Arctostaphylos patula*, CECU/VUBR-BRTE = *Ceanothus cuneatus*/*Vulpia bromoides*-*Bromus tectorum*, QUGA/BRTE = *Quercus garryana*/*Bromus tectorum*, BRTE-POPR = *Bromus tectorum*-*Poa pratensis*, JUPA-POPR-LUCO = *Juncus patens*-*Poa pratensis*-*Luzula comosa*, ELEL-DACA = *Elymus elymoides*-*Danthonia californica*.

TABLE 1. AVERAGE COVER AND CONSTANCY FOR FOREST ASSOCIATIONS. Species reported are those with >50% constancy. ¹ See Figure 1 for plant association acronyms. ² COV = average cover (%). ³ CON = constancy (%).

Plant association ¹ (number of plots)	QUCH/ARVI- ARPA (5)		ALRH- ACMA/ACCI (5)		ALRH- PSME- CADE/RUDI (8)	
	COV ²	CON ³	COV	CON	COV	CON
<i>Arctostaphylos patula</i>	23	100				
<i>Arctostaphylos viscida</i>	34	100				
<i>Quercus chrysolepis</i>	19	100			2	50
<i>Smilax californica</i>			<1	80		
<i>Rubus ursinus</i>			<1	80		
<i>Rhododendron occidentale</i>			1	80		
<i>Rhamnus purshiana</i>			7	100		
<i>Montia perfoliata</i>			5	100		
<i>Lilium pardalinum</i>			<1	80		
<i>Dicentra formosa</i>			<1	60		
<i>Athyrium filix-femina</i>			<1	80		
<i>Aralia californica</i>			2	100		
<i>Adiantum pedatum</i>			<1	80		
<i>Alnus rhombifolia</i>			40	100	15	100
<i>Acer circinatum</i>			12	100	10	63
<i>Trientalis latifolia</i>			<1	80	2	75
<i>Pteridium aquilinum</i>			<1	60		
<i>Acer macrophyllum</i>			20	80	9	63
<i>Symphoricarpos albus</i>						
<i>Corylus cornuta</i>			1	60	8	63
<i>Rosa gymnocarpa</i>					3	50
<i>Rubus discolor</i>					22	63
<i>Rubus leucodermis</i>					6	50
<i>Fraxinus latifolia</i>					10	88
<i>Equisetum laevigatum</i>					5	50
<i>Danthonia pilosa</i>					7	50
<i>Carex subfusca</i>					4	63
<i>Agropyron spicatum</i>					5	75
<i>Lithocarpus densiflorus</i> var. <i>echinoides</i>						
<i>Cornus nuttallii</i>						
<i>Pseudotsuga menziesii</i>			10	80	13	75
<i>Calocedrus decurrens</i>			1	80	12	88
<i>Quercus kelloggii</i>					6	50
<i>Pinus lambertiana</i>						
<i>Pinus ponderosa</i>					4	63
<i>Toxicodendron diversilobum</i>						
<i>Viola lobata</i>						
<i>Luzula comosa</i>						
<i>Galium aparine</i>						
<i>Clarkia gracilis</i>						
<i>Carex cusickii</i>						
<i>Nassella pulchra</i>						
<i>Rhamnus californica</i>						
<i>Sanicula bipinnatifida</i>						

TABLE 1. CONTINUED.

Plant association ¹ (number of plots)	QUCH/ARVI- ARPA (5)		ALRH- ACMA/ACCI (5)		ALRH- PSME- CADE/RUDI (8)	
	COV ²	CON ³	COV	CON	COV	CON
	<i>Pinus jeffreyi</i>					
<i>Phlox speciosa</i>						
<i>Monardella odoratissima</i>						
<i>Lomatium macrocarpum</i>						
<i>Festuca californica</i>						
<i>Epilobium brachycarpum</i>						
<i>Dichelostemma multiflorum</i>						
<i>Cheilanthes gracilis</i>						
<i>Ceanothus cuneatus</i>						
<i>Agoseris retrorsa</i>						

association had as many trees taller than 10 m (208/ha). Unlike the north-loving PSME/LIDEE, PSME/CONU-TODI was found on all aspects.

3. The *Pseudotsuga menziesii*-*Calocedrus decurrens*-*Quercus kelloggii*/*Nassella pulchra* (PSME-CADE-QUKE/NAPU) association differed from the first two *Pseudotsuga menziesii* associations in that it had several co-dominant tree species in the canopy. *Pseudotsuga menziesii* was still dominant with 24% cover (100% constancy), followed by *Calocedrus decurrens* with 12% cover (97% constancy), and then by *Quercus kelloggii* with 15% cover (83% constancy). *Nassella pulchra* had the greatest understory cover. This type had more rock and bare soil (6%) than the first two *Pseudotsuga menziesii* types and was found on all aspects. It had the second highest total tree density (756 trees/ha), an average basal area of 35.8 m²/ha, and species richness of 29.
4. The *Pseudotsuga menziesii*-*Calocedrus decurrens*/*Nassella pulchra* (PSME-CADE/NAPU) association resembled PSME-CADE-QUKE/NAPU in dominant species composition, but was found at higher elevations, western aspects, and on steeper (52% versus 26%), rockier slopes (24%). This association had less biomass, with only 25.3 m²/ha of basal area and 46 trees/ha taller than 10 m. *Pinus jeffreyi* shared the sparse canopy with 9% cover and 67% constancy.

Vegetation dynamics. *Pseudotsuga menziesii* and *Calocedrus decurrens* were the most abundant reproducing species in PSME/CONU-TODI, PSME-CADE-QUKE/NAPU, AND PSME-CADE/NAPU. *Lithocarpus densiflorus* and *Pseudotsuga menziesii* were

TABLE 1. EXTENDED. CONTINUED.

PSME/ LIDEE (32)		PSME/ CONU- TODI (38)		QUKE/ TODI (31)		PSME- CADE- QUKE/NAP (30)		QUKE/ NAPU (6)		PSME- CADE/ NAPU (6)	
COV	CON	COV	CON	COV	CON	COV	CON	COV	CON	COV	CON
						8	40			9	67
										<1	50
										2	50
										1	67
										10	50
										<1	50
										1	67
										1	50
										9	67
										<1	50

TABLE 2. AVERAGE COVER AND CONSTANCY FOR SHRUB-DOMINATED ASSOCIATIONS. Species reported are those with >50% constancy. ¹ See Figure 1 for plant association acronyms. ² COV = average cover (%). ³ CON = constancy (%).

Plant association ¹ (number of plots)	CECU- RHCA- ARPA (14)		CECU/ ERLA (10)		CECU/ VUBR- BRTE (5)		NAPU- SABI (7)	
	Cov ²	Con ³	Cov	Con	Cov	Con	Cov	Con
<i>Arctostaphylos patula</i>	10	79						
<i>Hypericum perforatum</i>	1	50						
<i>Pinus jeffreyi</i>	2	79						
<i>Quercus kelloggii</i>	9	64						
<i>Rhamnus californica</i>	13	86						
<i>Calocedrus decurrens</i>			2	60				
<i>Eriophyllum lanatum</i>			2	90				
<i>Monardella odoratissima</i>			2	70				
<i>Elymus elymoides</i>			2	60				
<i>Ceanothus cuneatus</i>	39	100	22	90	10	60		
<i>Bromus mollis</i>					1	80		
<i>Bromus tectorum</i>					4	80		
<i>Draba verna</i>					<1	80		
<i>Epilobium brachycarpum</i>					<1	100		
<i>Gnaphalium</i> sp.					1	80		
<i>Rumex acetosella</i>					1	60		
<i>Scleranthus annuus</i>					2	80		
<i>Vulpia bromoides</i>					6	80		
<i>Dichelostemma multiflorum</i>					1	60	1	57
<i>Nassella pulchra</i>	1	100	8	50			22	100
<i>Agoseris retrorsa</i>							1	71
<i>Eriogonum umbellatum</i>							1	71
<i>Sanicula bipinnatifida</i>	1	57					7	100

TABLE 3. AVERAGE COVER AND CONSTANCY FOR HERB-DOMINATED ASSOCIATIONS. Species reported are those with >50% constancy. ¹ See Figure 1 for plant association acronyms. ² COV = average cover (%). ³ CON = constancy (%).

Plant association ¹ (number of plots)	JUPA- POPR- LUCO (10)		BRTE- POPR (5)		QUGA/ BRTE (20)		ELEL- DACA (5)	
	COV ²	CON ³	COV	CON	COV	CON	COV	CON
<i>Luzula comosa</i>	12	60						
<i>Juncus patens</i>	22	80						
<i>Rubus discolor</i>	5	60						
<i>Nassella pulchra</i>	7	60						
<i>Poa pratensis</i>	12	70	13	60				
<i>Dactylis glomerata</i>			1	60				
<i>Vulpia bromoides</i>			3	60				
<i>Aria caryophylla</i>					2	55		
<i>Bromus tectorum</i>			15	100	12	90		
<i>Clarkia gracilis</i>					<1	55		
<i>Lupinus argenteus</i>					1	55		
<i>Quercus garryana</i>					10	50		
<i>Rumex acetosella</i>			1	60	1	50		
<i>Scleranthus annuus</i>					2	50		
<i>Danthonia californica</i>							18	80
<i>Lotus humistratus</i>							4	100
<i>Plantago lanceolata</i>							10	80
<i>Ranunculus occidentalis</i>							<1	60
<i>Elymus elymoides</i>							21	80
<i>Tragopogon dubius</i>							<1	60
<i>Trifolium macraei</i>							3	60
<i>Triteleia hyacinthina</i>							7	60
<i>Verbascum blattaria</i>							<1	60

most abundant in PSME/LIDEE. These species were more shade tolerant than other associated tree species (Franklin and Dryness 1973; Powers and Oliver 1990) and, in the absence of fire or other disturbance, should become self-perpetuating (McDonald 1980; Sawyer 1980; Hermann and Lavender 1990). With fire, *Pinus ponderosa*, *Quercus kelloggii*, and *Pinus lambertiana* should remain within the mix of overstory dominants and co-dominants (Franklin and Dryness 1973, and Sawyer et al. 1977).

Relation to other vegetation types. PSME/CONU-TODI, PSME-CADE-QUKE/NAPU, and PSME-CADE/NAPU share elements of the warm, dry component of the mixed conifer forests found in southwestern Oregon (Franklin and Dryness 1973); of the mesic, low elevation type in the Sierra Nevada/Cascade mixed conifer forest (Rundel et al. 1977; Holland 1986); and of the Pacific ponderosa pine-Douglas-fir cover type (McDonald 1980). A *Pseudotsuga menziesii*-*Calocedrus decurrens* type has been described in southern

TABLE 4. PHYSIOGRAPHIC AND SOIL CHARACTERISTICS OF CASTLE CRAGS PLANT ASSOCIATIONS. Data are averages of plots within a plant association. ¹ See Figure 1 for plant association acronyms.

Plant associations ¹	Elevation (m)	Predominant aspect	Slope (%)	% rock and bare soil	Predominant parent material	Predominant soil depth (m)	Predominant soil texture
QUCH/ARVI-ARPA	927	S	69	15	Granite	0.3-0.5	Coarse sandy loam
ALRH-ACMA/ACCI	751	E	14	32	Alluvium	>1.5	Cobbly sandy loam
ALRH-PSME-CADE/RUDI	640	S	1	6	Alluvium	>1.5	Cobbly sandy loam
PSME/LIDEE	803	N	27	3	Greenstone	1.0-2.0	Gravelly loam
PSME/CONU-TODI	730	ALL	39	1	Greenstone, alluvium	>1.0	Gravelly loam
PSME-CADE-QUKE/NAPU	800	ALL	26	6	Greenstone, alluvium, basaltic rock	1.0-2.0	Gravelly loam
PSME-CADE/NAPU	968	W	52	24	Greenstone, alluvium, basaltic rock	1.0-1.8	Gravelly loam
QUKE/TODI	835	S	47	3	Greenstone, alluvium, basaltic rock	1.0-2.0	Gravelly loam
QUKE/NAPU	753	S	23	1	Granite	0.3-0.5	Coarse sandy loam
NAPU-SABI	735	ALL	23	26	Greenstone	1.0-2.0	Gravelly loam
CECU/ERLA	920	S	47	28	Serpentine, greenstone	0.5-1.0	Stony loam
CECU-RHCA-ARPA	762	S	42	20	Serpentine	0.5-0.76	Stony loam
CECU/VUBR-BRTE	680	S	2	23	Alluvium	>1.5	Cobbly sandy loam
QUGA/BRTE	666	FLAT	1	31	Alluvium	>1.5	Cobbly sandy loam
BRTE-POPR	658	FLAT	0	40	Alluvium	>1.5	Cobbly sandy loam
JUPA-POPR-LUCO	658	FLAT	1	0	Alluvium	>1.5	Cobbly sandy loam
ELEL-DACA	619	E	8	1	Greenstone	1.0-2.0	Gravelly loam

TABLE 5. BASAL AREA, CUMULATIVE NUMBER OF SPECIES PER 5 RANDOMLY SELECTED PLOTS, TOTAL NUMBER OF SPECIES IN ALL PLOTS, AND TREE DENSITY FOR EACH PLANT ASSOCIATION. ¹ See Figure 1 for plant associations acronyms.

Plant association ¹	Basal area (m ² /ha)	# species/ 5 plots	Total # of species in all plots	Tree density by height class (#/ha)			Total
				0-3 m	3-10 m	>10 m	
QUCH/ARVI-ARPA	2.3	9	9	22	20	0	42
ALRH-ACMA/ACCI	— ²	37	37	0	0	0	0
ALRH-PSME-CADE/RUDI	47.6	70	86	250	75	91	416
PSME/LIDEE	39.7	42	76	634	191	143	968
PSME/CONU-TODI	57.2	33	53	179	95	208	482
PSME-CADE-QUKE/NAPU	35.8	29	90	462	165	129	756
PSME-CADE/NAPU	25.3	32	37	136	62	46	244
QUKE/TODI	40.2	37	76	377	257	60	694
QUKE/NAPU	6.3	31	36	282	213	88	583
NAPU-SABI	0	56	68	0	0	0	0
CECU/ERLA	3.7	39	45	11	7	2	20
CECU-RHCA-ARPA	0.8	43	56	9	7	1	17
CECU/VUBR-BRTE	0	40	40	14	4	0	18
QUGA/BRTE	1	38	81	14	6	11	31
BRTE-POPR	0.5	19	19	0	0	2	2
JUPA-POPR-LUCO	0.9	28	42	14	6	0	20
ELEL-DACA	0	37	37	0	0	0	0

² Missing data.

Oregon by Mitchell and Moir (1976). A PSME/CONU type is found in the Cub Creek Research Natural Area in the Lassen National Forest (Taylor and Randall 1990). PSME/LIDEE is similar to the *Pseudotsuga/Lithocarpus* (shrub form) phase in the *Pseudotsuga* hardwood forest of the Klamath Mountains (Sawyer et al. 1977). *Lithocarpus densiflorus* var. *echinoides* grows in a narrow elevational band above the tree form of *L. densiflorus* on moist sites in the eastern Klamath Mountain Province (Tappeiner et al. 1990).

Quercus kelloggii Series

1. The *Quercus kelloggii/Toxicodendron diversilobum* (QUKE/TODI) association was dominated by *Quercus kelloggii* with 32% cover (94% constancy). Minor canopy associates included *Pseudotsuga menziesii* with 10% cover (94% constancy) and *Pinus ponderosa* with 13% cover (87% constancy). *Toxicodendron diversilobum* had 4% cover and 68% constancy. The 40.2 m²/ha of basal area was relatively high. Most of the 634 trees/ha shorter than 10 m tall were *Pseudotsuga menziesii*, *Calocedrus decurrens*, or some other late seral species. This association was found primarily on south aspects with slopes averaging 47%. Soil depths were between 1 and 2 m, having originated from either greenstone, alluvium, or basaltic rock.
2. Granitic parent material and shallow soils differentiate the *Quercus kelloggii/Nassella pulchra* (QUKE/NAPU) association from QUKE/TODI. This type was overwhelmingly dominated by *Quercus kelloggii*, having 63% cover and 100% constancy. *Pinus ponderosa* and *Pseudotsuga menziesii* were occasional canopy associates. The most abundant understory species were *Nassella pulchra*, *Carex cusikii*, and *Rhamnus californica*. Basal area was about 1/7th that found in QUKE/TODI.

Vegetation dynamics. *Pseudotsuga menziesii* and *Calocedrus decurrens* were the most abundant reproducing species in QUKE/TODI. This association is seral and will eventually be dominated by *Pseudotsuga menziesii* and *Calocedrus decurrens* (McDonald 1990). In the Sierra Nevada/Cascade mixed conifer forest, *Quercus kelloggii* is well adapted to light, regular surface fires and often will be succeeded by *Calocedrus decurrens* in the absence of fire (Rundel et al. 1977; McDonald 1990). QUKE/NAPU represents a self-perpetuating vegetation type largely because of the xeric conditions produced from steep, shallow, granitic soils. *Quercus kelloggii* is very drought resistant and can grow on sites too poor for other mixed conifer species (Rundel et al. 1977; McDonald 1990).

Relation to other vegetation types. *Quercus kelloggii* forests and woodlands have been reported as occurring on fire-prone, dry, warm

sites throughout southwestern Oregon (Whittaker 1960; Waring 1969) and in the northern Sierra Nevada and Cascade Mountains of California (Holland 1986; McDonald 1990). QUKE/TODI vegetation types have been described by Keeler-Wolf (1990a).

Alnus rhombifolia Series

1. The *Alnus rhombifolia*–*Pseudotsuga menziesii*–*Calocedrus decurrens*/*Rubus discolor* (ALRH-PSME-CADE/RUDI) association was found on alluvial soils along either the Sacramento River or Castle Creek. *Alnus rhombifolia* was the most common canopy species, having 15% cover (100% constancy). *Pseudotsuga menziesii* had 13% cover (75% constancy) and *Calocedrus decurrens* had 12% cover (88% constancy). *Rubus discolor* dominated the understory, having 22% cover and 63% constancy. ALRH-PSME-CADE/RUDI was structurally and floristically complex. This association had the greatest species richness (70 species) and the second highest basal area (47.6 m²/ha).
2. The *Alnus rhombifolia*–*Acer macrophyllum*/*Acer circinatum* (ALRH-ACMA/ACCI) association occurred along smaller streams like Root Creek or Indian Creek. These riparian zones typically had more shade, were cooler, and had lower species richness (37 species) than ALRH-PSME-CADE/RUDI.

Vegetation dynamics. Both ALRH-PSME-CADE/RUDI and ALRH-ACMA/ACCI are self-perpetuating. Flooding and fire are the primary disturbances expected in these types. Fire severity, though, would usually be less than surrounding upland slopes because of higher fuel moisture contents, higher relative humidities, and lower temperatures.

Relation to other vegetation types. Our riparian associations are generally similar to the white alder-dominated communities south of the Willamette Valley in Oregon (Franklin and Dryness 1973) and those scattered throughout the Klamath, northern Sierra Nevada, and Cascade Mountains. Keeler-Wolf (1990a) described a canyon riparian forest that is similar to our ALRH-ACMA/ACCI.

Quercus chrysolepis Series

The *Quercus chrysolepis*/*Arctostaphylos viscida*–*A. patula* (QUCH/ARVI-ARPA) association was the most depauperate and unproductive of all forest associations in the park. It had only 9 species and 2.3 m²/ha of basal area. *Quercus chrysolepis* was the dominant tree with 19% cover and 100% constancy. Manzanita dominated the understory. *Arctostaphylos viscida* had 34% cover

(100% constancy) and *Arctostaphylos patula* had 23% cover (100% constancy). This type was found on shallow, granitic soils on steep, south aspects in the Castle Creek Valley.

Vegetation dynamics. *Quercus chrysolepis* is climax on very steep, colluvial soils (Thornburgh 1990). When subjected to repeated fire, a *Quercus chrysolepis* chaparral type develops. With fire suppression, the chaparral should eventually revert back to a *Quercus chrysolepis*-dominated association (Mallory 1980).

Relation to other vegetation types QUCH/ARVI-ARPA is generally similar to the *Quercus chrysolepis*-*Pseudotsuga menziesii*-dominated forests found on very steep, colluvial soils throughout the Klamath Mountains Province (Mallory 1980; Thornburgh 1990). Our type, however, lacks *Pseudotsuga menziesii* and has a distinctive *Arctostaphylos* understory similar in composition to montane chaparral described by Hanes (1977). Horton (1960) described a *Q. chrysolepis*-*Arctostaphylos* spp. phase of the live oak (*Q. wislizenii*) chaparral found in the San Bernadino Mountains.

Ceanothus cuneatus Series

Ceanothus cuneatus associations were all found in Castle Creek Valley on south aspects and either on serpentine, greenstone, or alluvial soils. Serpentine soils were shallow, steep, xeric, and infertile.

1. The *Ceanothus cuneatus*-*Rhamnus californica*-*Arctostaphylos patula* (CECU-RHCA-ARPA) association was found on serpentine soils. Shrubs accounted for 62% relative cover, herbs had 24%, and trees 14%. Trees were scattered throughout the type, but species constancy was typically low. Although *Pinus jeffreyi* had the greatest tree cover, basal area was only 0.8 m²/ha and there was only 1 tree/ha taller than 10 m. *Ceanothus cuneatus* had 39% cover (100% constancy), *Rhamnus californica* had 13% cover (86% constancy), and *Arctostaphylos patula* had 10% cover (79% constancy).
2. The *Ceanothus cuneatus*/*Eriophyllum lanatum* (CECU/ERLA) association was found on serpentine and greenstone. This type had rockier soils, steeper slopes, and more herb cover than CECU-RHCA-ARPA. Shrub relative cover was 45%, herbs 42%, and trees 13%. *Nassella pulchra* had more cover than *Eriophyllum lanatum* (8% versus 2%), but had lower constancy (50% versus 90%). *Calocedrus decurrens* was widely scattered, having 3.7 m²/ha of basal area and only 2 trees/ha taller than 10 m. *Ceanothus cuneatus* dominated with 22% cover and 90% constancy.
3. The *Ceanothus cuneatus*/*Vulpia bromoides*-*Bromus tectorum* (CECU/VUBR-BRTE) association was found on gravely, cob-

bly alluvium. Herb relative cover was 58%, shrub relative cover 35%, and tree relative cover 7%. While this type had about the same species richness (40) as CECU-RHCA-ARPA (43) or CECU/ERLA (39), it had much less cover. There was only 10% *Ceanothus cuneatus* cover (60% constancy), 6% *Vulpia bromoides* cover (80% constancy), and 4% *Bromus tectorum* cover (80% constancy). There were no trees taller than 10m and no basal area.

Vegetation dynamics. CECU-RHCA-ARPA and CECU/ERLA are self-perpetuating on xeric, serpentinitic, steep slopes. CECU/VUBR-BRTE is probably self-perpetuating. Although it grows on alluvium, the soil is xeric, having been derived from a melange of coarse-textured granitic and ultramafic rocks. In the absence of fire, *Calocedrus decurrens* should increase in abundance, but should not dominate these harsh sites. With fire, *Ceanothus cuneatus* should increase in abundance.

Relation to other vegetation types. Our *Ceanothus cuneatus* associations resemble Holland's (1986) buck brush chaparral, Hane's (1977) serpentine chaparral in California, and serpentine chaparrals occurring between 860 to 980 m in the Siskiyou Mountains of southwestern Oregon (Franklin and Dryness 1973). Taylor and Teare (1990) listed a *Ceanothus cuneatus/Sitanion hystrix* association in Trinity County and Keeler-Wolf (1990b) described a *Ceanothus* scrub type in Tehama County.

Bromus tectorum series

The *Bromus tectorum*-*Poa pratensis* (BRTE-POPR) association was found on very cobbly alluvium in the Castle Creek Valley. The type is relatively depauperate, having 19 species and 40% rock and bare soil. *Bromus tectorum* had 12% cover (90% constancy) and *Poa pratensis* had 10% cover (50% constancy). *Quercus garryana* was scattered throughout the type and had 9% cover but only 20% constancy. Basal area was 0.5 m²/ha.

Vegetation dynamics. The BRTE-POPR association is an early seral stage in a yet to be determined sere. This type will probably be stable for many decades, however, because of slow soil development.

Relation to other vegetation types. This type would be similar to many other early vegetation communities dominated by *Bromus tectorum* throughout the west (Young 1994, Billings 1994).

Quercus garryana Series

The *Quercus garryana*/*Bromus tectorum* (QUGA/BRTE) association was found on flat, cobbly, alluvial soils in Castle Creek Valley.

These sites were generally similar to BRTE-POPR sites, excepting for the higher frequency and cover of *Quercus garryana*, fewer cobbles, and less bare soil that characterized QUGA/BRTE. This type had 12% cover of *Bromus tectorum* (90% constancy) and 10% cover of *Quercus garryana* (50% constancy). Species richness was twice (38) that found in BRTE-POPR. Basal area was 1.0 m²/ha and there were 11 trees/ha taller than 10 m.

Vegetation dynamics. QUGA/BRTE represents an edaphically stable plant association in Castle Crags State Park. Soil development rates on the cobbly alluvium are too slow for this woodland to succeed to another type in the foreseeable future. In some *Quercus garryana* types in northern California and southern Oregon, *Pseudotsuga menziesii* eventually overtops *Q. garryana* in the absence of recurring fire (Agee 1993).

Relation to other vegetation types. QUGA/BRTE is most similar to *Quercus garryana* communities growing on the driest sites in southern Oregon (Whittaker 1960; Riegel et al. 1992) and northern California (Griffin 1977).

Juncus patens Series

This association, *Juncus patens*-*Poa pratensis*-*Luzula comosa* (JUPA-POPR-LUCO), was found on seasonally moist soils near a pond in Castle Creek Valley. *Juncus patens* had 22% cover (80% constancy); *Poa pratensis* had 12% cover (70% constancy); and *Luzula comosa* had 12% cover (60% constancy). There were no trees taller than 10m and species richness was 28.

Vegetation dynamics We expect that the high water table on this site will perpetuate JUPA-POPR-LUCO. Other potential dominant species are intolerant of seasonally hydric soils.

Disturbed Communities

Two disturbed communities were classified: *Nassella pulchra*-*Sanicula bipinnatifida* (NAPU-SABI) and *Elymus elymoides*-*Danthonia californica* (ELEL-DACA). NAPU-SABI was found beneath the powerline corridor which transects the park in an approximately N-S orientation. It was dominated by *Nassella pulchra*, which had 22% cover and 100% constancy. Numerous shrubs and tree seedlings were present. ELEL-DACA was a mowed meadow near the campground. It was dominated by *Elymus elymoides* with 21% cover (80% constancy) and by *Danthonia californica* with 18% cover (80% constancy).

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EXCLUSION OF *ARTEMISIA TRIDENTATA* NUTT. FROM
HYDROTHERMALLY ALTERED ROCK BY LOW
PHOSPHORUS AVAILABILITY

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RESUMEN

Artemisia tridentata (sagebrush), la especie vegetal dominante en el desierto de Great Basin en Sierra Nevada (EEUU), es excluida en los suelos formados por la alteración hidrotermal de la roca madre. Para testar la hipótesis de que deficiencias nutricionales impiden el crecimiento de esta especie en este tipo de suelo, sometimos a plántulas de *Artemisia tridentata* a los siguientes tratamientos en un diseño factorial completo: media fuerza solución Hoagland's con N, media fuerza solución Hoagland's con P, ó media fuerza solución Hoagland's con pH 8.5 modificado mediante la adición de NaHCO₃. La tasa de crecimiento de las plántulas fué significativamente más alta con los tratamientos que contenían P, mientras que no tuvo ningún efecto los tratamientos con N o NaHCO₃. Nuestros resultados sugieren que *Artemisia tridentata* podía estar excluida de los suelos formados a partir de roca madre alterada hidrotermalmente debido a la baja disponibilidad de fósforo en este tipo de suelos.

ABSTRACT

Artemisia tridentata (sagebrush), the dominant plant species in the Great Basin desert of Sierra Nevada (USA), is excluded from soils derived from hydrothermally altered rock in this environment. To test for nutritional deficiencies for growth of sagebrush in this type of soil, we applied to sagebrush seedlings one of the following treatments in a full factorial design: half-strength Hoagland's plus N, half-strength Hoagland's plus P, or Hoagland's solution with pH modified to 8.5 by addition of NaHCO₃. The growth rate of seedlings was significantly highest in the P treatment, with no effect in the N or NaHCO₃ treatments. Our results suggest that sagebrush may be excluded from hydrothermally altered soil by low P availability.

A striking example of abrupt discontinuity in plant distribution is the occurrence of islands of Sierran conifers (*Pinus ponderosa* Laws. and *P. jeffreyi* Grev. and Balf) surrounded by a regional matrix of sagebrush vegetation (*Artemisia tridentata* Nutt.) in the Great Basin Desert of Sierra Nevada (Billings 1950; Schlesinger et al. 1989). These unique islands are found on soils derived from hydrothermally altered andesite. Soils on altered bedrock are shallow lithic entisols,

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which are light colored, very acid (pH 3.3–5.5) and low in exchangeable bases and phosphorus (Billings 1950; Salisbury 1954, 1964; Schlesinger et al. 1989). The adjacent soils derived from unaltered andesite are xerollic Haplargids which are brown, slightly basic, and high in exchangeable bases and phosphorus.

Sierran pines growing on these sites are excluded from the typical desert soils by competition for water with the more drought-tolerant sagebrush vegetation (DeLucia et al. 1988; DeLucia and Schlesinger 1991). Conversely, sagebrush is presumably excluded from the pine stands by intolerance of the low-nutrient conditions of soils derived from hydrothermally altered rock (Billings 1950; Schlesinger et al. 1989). We tested the response of sagebrush seedlings growing in altered soils to N and P additions and to modified pH. Our hypothesis was that sagebrush is excluded from hydrothermally altered rock zones by low phosphorus availability.

MATERIALS AND METHODS

A greenhouse experiment was carried out in the Phytotron of Duke University. Seeds of *Artemisia tridentata* were planted in 350-mL, 7-cm diameter pots containing field soils collected from an area of hydrothermally altered rock. Three seeds were planted per pot, and seedlings were thinned to one per pot soon after emergence. Seedlings were watered daily.

To test for deficiencies in the ability of the soil to supply adequate nutrients for growth of sagebrush, we designed a 3-way factorial experiment. Twelve plants were randomly assigned to each of 8 groups, and three times each week each group received one of the following treatments in a full factorial design: half-strength Hoagland's + N, half strength Hoagland's + P, or Hoagland's solution with pH modified to 8.5 by addition of NaHCO_3 . *Artemisia tridentata* seeds were also planted in unaltered soil to serve as a control. Plants were maintained at 25°C day and 15°C night temperature. After 40 days, plants were harvested, rinsed gently with distilled water to remove adhering soil particles, separated into roots and shoots, and dried at 70°C for 48 h before being weighed. Growth rate was determined by dividing the dry matter production by the duration of the growth period. Tissues of the 12 plants in each treatment were pooled to form one sample of shoot and one sample of root for N and P analysis. Tissues were digested in a Technicon block digester with a $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ flux (Lowther 1980) and analyzed for total N and P on a Traacs 800 autoanalyzer using standard methods. ANOVA (log-transformed data; type III sum of squares) was used to analyze treatment effects.

TABLE 1. SOIL CHEMICAL PROPERTIES ON ALTERED AND UNALTERED PARENT MATERIALS IN THE SAGEBRUSH ZONE OF THE GREAT BASIN. All data are means with 1 SE in parentheses; t-tests were used to distinguish differences between soil types. Asterisks indicate significance at $P < 0.05$. $\text{HCO}_3\text{-P}$ is a determination of available P from extraction at pH 8.5. (From Schlesinger et al. 1989).

Location	pH in 0.01 mol/L CaCl_2	$\text{HCO}_3\text{-P}$ ($\mu\text{g/g}$)	C (mg/g)	N (mg/g)
Unaltered	6.55* (0.17)	31.4* (4.4)	0.078 (0.012)	0.006 (0.001)
Altered	3.74 (0.15)	5.6 (2.9)	0.115 (0.015)	0.009 (0.002)

RESULTS

Some chemical properties on altered and unaltered parent materials are shown in Table 1. Average extractable P and soil pH was significantly higher in unaltered soil.

The growth rate of whole seedlings was significantly highest in the P treatment ($P < 0.0001$, Fig. 1, Table 2). Similar results were observed for root and shoot growth rate (Table 2). Total and shoot growth rate were also significantly enhanced by N additions ($P < 0.05$, Table 2), largely as a result of significantly greater growth of the seedlings when N was combined with P. When only N or NaHCO_3 was added to the soils there was no growth response. The NaHCO_3 treatment effectively increased the pH of soil solution from 3.8 to around 5.5. It is interesting to note that growth rate of sagebrush in unaltered soil was $13.54 \text{ mg/day} \pm 1.86 \text{ SE}$, significantly higher than that seen with additions of N and P to altered soil.

Although our pooling of samples precluded a statistical analysis of the differences in the N and P content of plant tissues, non P-fertilized seedlings had a P concentration ranging between 0.09% and 0.11% (Table 3). When P was added to the nutrient solution, P content ranged between 0.16% and 0.42%. Less striking differences were found in N concentration between treatments (from 1.1% to 2.3% in non N-fertilized seedlings, and from 1.91 to 3.5% in N-fertilized plants). N-to-P ratio in tissue varied between 13 and 31 in non P-fertilized and from 6.49 to 9.3 in P-fertilized plants, closer to the N-to-P ratio of 5.6 that we found in seedlings growing in unaltered soil. Even if N was not added to the watering solution, N uptake was highest in P-fertilized seedlings (Table 4).

DISCUSSION

The results indicated that P, but not N was a primary factor limiting the growth of sagebrush in altered soils. We expected that additions of NaHCO_3 might increase the availability of P in the soils

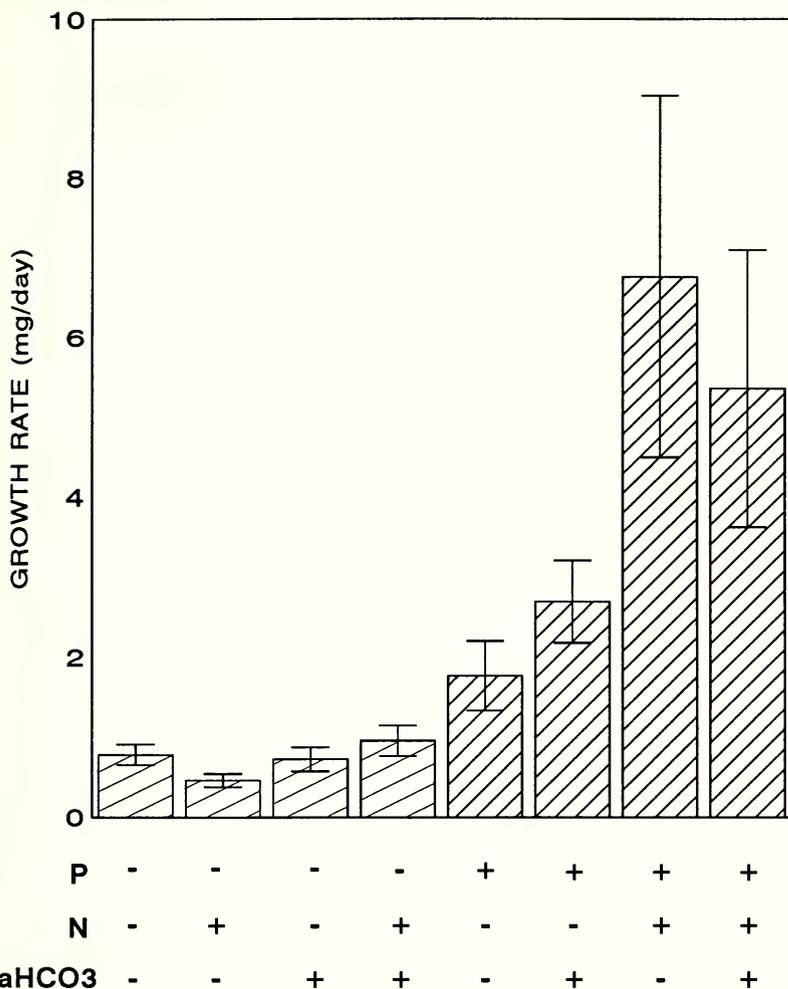


FIG. 1. Growth rate of *Artemisia tridentata* seedlings grown under N, P and NaHCO₃ treatments in soils derived from hydrothermally altered soils. Bars are 2, SE.

derived from hydrothermally altered rock, because the solubility of phosphorus is restricted by Fe and Al minerals at low pH (Schlesinger 1991). However, we found no effect of NaHCO₃ on inherent low P content in soils derived from hydrothermally altered rock. The lack of response of plant growth to our NaHCO₃ treatments suggests that low pH *per se* is not a factor that excludes *Artemisia tridentata* from soils derived from hydrothermally altered rock. A different hypothesis is that the inability of sagebrush to grow in the altered soil might be due to high Al³⁺ concentration of the soil

TABLE 2. ANALYSIS OF VARIANCE (TYPE III SUMS OF SQUARES) FOR GROWTH RATE OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOILS DERIVED FROM HYDROTHERMALLY ALTERED ROCK WITH N, P AND NaHCO_3 TREATMENTS.

Source	Sum of squares	df	F-ratio	Sig. level
Total (roots + shoots)				
Main effects				
A: Nitrogen	2.56	1	4.20	0.0440
B: Phosphorus	41.59	1	21.11	0.0000
C: NaHCO_3	1.12	1	1.83	0.1802
Interaction				
AB	3.99	1	6.53	0.0126
AC	0.08	1	0.14	0.7155
BC	0.10	1	0.17	0.6849
ABC	2.32	1	3.80	0.0550
Residual	46.44	76		
Roots				
Main effects				
A: Nitrogen	0.72	1	1.11	0.2947
B: Phosphorus	45.87	1	70.47	0.0000
C: NaHCO_3	1.20	1	1.84	0.1789
Interactions				
AB	4.68	1	7.19	0.0090
AC	0.20	1	0.31	0.5834
BC	0.13	1	0.21	0.6570
ABC	1.95	1	2.99	0.0879
Residual	49.47	76		
Shoots				
Main effects				
A: Nitrogen	5.53	1	8.89	0.0039
B: Phosphorus	38.81	1	62.42	0.0000
C: NaHCO_3	1.10	1	1.78	0.1867
Interaction				
AB	3.30	1	5.32	0.0239
AC	0.01	1	0.02	0.8850
BC	0.08	1	0.12	0.7621
ABC	2.97	1	4.78	0.0319
Residual	47.25	76		

solution. Al^{3+} concentration might be reduced by phosphate application to the acid soil. However, the solubility of Al^{3+} should have also declined precipitously with additions of NaHCO_3 alone stimulating plant growth, but this effect was not seen in our experiment. Goldberg (1985) was able to grow *bodenvag* species on soils from hydrothermally altered rock with additions of CaCO_3 . Addition of CaCO_3 increases the solution pH, but it also produces a high Ca availability that could exert important influence on some biogeo-

TABLE 3. N, P CONCENTRATION IN THE ROOT AND SHOOT TISSUE OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOIL DERIVED FROM HYDROTHERMALLY ALTERED ROCK UNDER N, P AND NaHCO_3 (C) TREATMENTS. (a) Root tissue in the +P treatment was not available for analysis.

Treatment	Concentration (%)		
	N	P	N:P
ROOT			
—	1.26	0.10	12.98
+N	2.66	0.11	24.42
+C	1.37	0.11	12.82
+N+C	2.04	0.11	19.33
+P	a	a	a
+P+C	1.06	0.16	6.49
+N+P	2.09	0.25	8.34
+N+P+C	1.91	0.22	8.51
SHOOT			
—	1.79	0.09	19.77
+N	3.03	0.10	31.03
+C	1.92	0.09	21.91
+N+C	2.47	0.10	24.39
+P	2.30	0.31	7.54
+P+C	2.23	0.30	7.55
+N+P	3.14	0.42	7.52
+N+P+C	3.48	0.37	9.30

chemical processes relevant to plant growth. For example, Lajtha and Schlesinger (1988) found that CaCO_3 directly inhibited the uptake or the availability of P to roots in *Larrea tridentata* seedlings. Additions of P reduced mortality of the seedlings grown in soils from hydrothermally altered rock. Only 2 seedlings (4%) died along the course of the experiment in P amended soils versus 9 seedlings (19%) in non-P amended soils.

TABLE 4. FINAL N AND P MASS (FINAL DRY WEIGHT * N OR P TISSUE CONCENTRATION) IN THE SEEDLINGS OF *ARTEMISIA TRIDENTATA* CULTIVATED IN SOIL DERIVED FROM HYDROTHERMALLY ALTERED ROCK UNDER N, P AND NaHCO_3 (C) TREATMENTS.

Treatment	N mass (mg)			P mass		
	Root	Shoot	Total	Root	Shoot	Total
—	0.22	0.25	0.47	0.017	0.013	0.030
+N	0.21	0.32	0.53	0.009	0.010	0.019
+C	0.21	0.26	0.47	0.017	0.012	0.029
+N+C	0.33	0.55	0.88	0.017	0.022	0.039
+P		0.70			0.093	
+P+C	0.58	1.17	1.75	0.089	0.155	0.245
+N+P	2.55	4.66	7.21	0.306	0.620	0.925
+N+P+C	1.88	4.04	5.92	0.221	0.434	0.655

There are only a few examples in which plant species are totally excluded from soils by low phosphorus availability. For example, Berliner et al. (1986) report complete exclusion of *Cistus incanus* from basaltic soils in Israel due to a failure of mycorrhizal development. Tyler and Olsson (1993) and Tyler (1994) find the calcifuge behavior of several species is due to the inability to utilize the native phosphorus of limestone soils. Our results suggest that sagebrush may be excluded from hydrothermally altered soils by low P availability which is tolerated by Sierran conifers that have higher nutrient-use efficiency and slow growth rates.

ACKNOWLEDGMENTS

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ANT-MEDIATED SEED DISPERSAL OF THE RARE
CHAPARRAL SHRUB *FREMONTODENDRON DECUMBENS*
(STERCULIACEAE)

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ABSTRACT

Ant-mediated seed dispersal is unusual for California chaparral shrubs. This study documents dispersal of the elaiosome-bearing seeds of *Fremontodendron decumbens* by the harvester ant *Messor* (= *Veromessor*) *andrei*. Seeds were released from capsules over a period of ca. 2 mo during the summer, but the timing of release varied between years. Ants were strongly attracted to the elaiosome portion of diaspores rather than the seed portion, and carried elaiosome-bearing seeds up to 12 m from *F. decumbens* shrubs. Because ant nests never occurred under shrub canopies, seeds were transported from beneath parent shrubs to nests located in gaps in the existing shrub cover. Some seeds (at least 5%) that were taken into ant nests were apparently consumed by ants, 45% were ejected intact and left on nest middens within 65 cm of nest entrances, and the remainder were not found and may have remained within the nests. The seed coat of *F. decumbens* was greatly (3-fold) thickened near the elaiosome, suggesting an adaptation to discourage ants from consuming seeds. Elaiosomes contained little moisture but significant amounts of fat, protein, and carbohydrates. Each elaiosome contained 8.8% of the total energy content of a diaspore. In energetic terms, the cost to *F. decumbens* of building elaiosomes was relatively small (an 8% reduction in seed output). Elaiosomes also were consumed by small invertebrates and decomposers, so that elaiosomes were absent from diaspores after 2 mo in the litter layer.

Chaparral is a shrub-dominated vegetation type that has long been of interest for many reasons, including its association with both a Mediterranean-type climate and periodic fires (Keeley 1989). Numerous studies of many aspects of chaparral biology have been undertaken (Keeley 1989), but detailed studies of seed dispersal mechanisms of chaparral species (particularly shrub species) are few (Hanes 1977). In some cases (e.g., Bullock 1978; Keeley 1991), dispersal mechanisms are inferred based upon morphologic characteristics of fruits or seeds.

Ant-mediated seed dispersal (myrmecochory) is relatively common in arid areas of Australia (Berg 1975; Buckley 1982) and South Africa (Milewski and Bond 1982) but seems comparatively rare in California chaparral. Conclusive documentation of the importance of myrmecochory has been demonstrated for only one chaparral shrub, *Dendromecon rigida* Benth. (Berg 1966; Bullock 1974, 1989). Myrmecochory is likely if fruits or seeds bear elaiosomes,

food bodies that attract ants and induce them to transport diaspores to their nest (Beattie 1985). Although a comprehensive study has not been conducted, few chaparral shrub species possess elaiosomes. A study by Keeley (1987) of 45 shrub species identified *Fremontodendron* (in particular *F. californicum* (Torrey) Cov., Sterculiaceae) as the only chaparral shrub other than *Dendromecon* that possesses elaiosome-bearing seeds. Keeley (1991) predicted that seeds of *Fremontodendron* were ant-dispersed.

Boyd and Serafini (1992) studied the reproductive biology of *Fremontodendron decumbens* Lloyd, a rare chaparral species with elaiosome-bearing seeds found in the foothills of the Sierra Nevada (Kelman 1991). Observations during that research indicated that ants transported seeds of *F. decumbens*. Keys and descriptions in Smith (1947) and Wheeler and Wheeler (1973) identified the ants as harvester ants of the species *Veromessor andrei* Mayr (Hymenoptera: Formicidae). The genus *Veromessor* is now included in *Messor*, so that the currently accepted name is *Messor andrei* (Mayr) (see discussion in Bolton 1982). This study documents and describes this apparent chaparral ant-plant relationship with *F. decumbens*.

METHODS

Study species. *Fremontodendron decumbens* grows only within a few km of the summit of Pine Hill in El Dorado County, California. Most plants are found within the Pine Hill Ecological Reserve, which encompasses the majority of the hill. *Fremontodendron decumbens* grows mainly on relatively rocky ridgetops, along with typical chaparral dominants such as *Arctostaphylos glauca* Lindl., *Adenostoma fasciculatum* H. & A., and *Heteromeles arbutifolia* M. Roem.

The ecologic life cycle of *F. decumbens* has been characterized by Boyd and Serafini (1992) and Boyd (1994), and will be summarized briefly here. Plants initiate flower buds in late winter. By the time flowers open in April, most of the flower buds (80%) have been destroyed by insect larvae. Flowers are efficiently pollinated by native solitary bees (Boyd 1994), but developing fruits are attacked by insect larvae and 70% are destroyed prior to maturity. Surviving fruits dehisce during summer and release seeds into the litter under shrubs. Seeds possess an orange-yellow elaiosome (technically a caruncle, Kelman 1991) on the distal end of the seed. Seeds are eaten by rodents and 90% of seeds placed into the litter under *F. decumbens* shrubs are destroyed during a one-year period (Boyd and Serafini 1992).

Messor andrei (Mayr) is found throughout the length of California (Creighton 1950). It is a group-foraging species, forming a column of workers many meters in length that explores and harvests mate-

rials from an area near the nest during a foraging period (Cook 1953). These ants typically form a midden near the nest opening in which they deposit excavated soil and discarded plant material. Harvester ants generally act as seed predators (Reichman 1979) and have been reported to decrease the effectiveness of post-fire grass seeding in California chaparral (Howard 1950), although they have been recorded to disperse elaiosome-bearing seeds (O'Dowd and Hay 1980). When handling an elaiosome-bearing seed, the elaiosome is removed and the seed is ejected onto the midden (Creighton 1950).

Study sites. Study sites were located on the main east-west ridge of Pine Hill. The ridges of Pine Hill were disturbed in 1969 by the cutting of firebreaks. Unfortunately, these ridges also contained the largest stands of *F. decumbens*. Most of the shrub species present, including *F. decumbens*, were not killed but re-sprouted from the cut stumps. They recovered to form a stand that was 13 yr old in 1982, when the studies described here began (Boyd 1994).

Both of the sites used in this study were located on the east-west ridge located east of the summit of Pine Hill. Site 1 contains the largest stand of *F. decumbens* currently known. Even so, the dominant chaparral shrub on this site was *Adenostoma fasciculatum*. Site 2 was ca. 150 m from the summit and ca. 200 m west from Site 1, in a rocky area containing a few *Pinus ponderosa* Dougl. ex P. & C. Lawson and *P. sabiniana* Dougl. Most of the shrub cover on this site was *Adenostoma fasciculatum* and *Arctostaphylos glauca*. *Fremontodendron decumbens* shrubs were scattered among shrubs of other species on both sites. Total cover of *F. decumbens* was less than 5% in both locations.

Ant activity and seed availability. Observations of ant activity patterns were made at irregular intervals during five years (1982–1986). Most of the observations were made on Site 1. I determined when seeds became available to foraging ants by monitoring the timing of fruit dehiscence on 53 branches located on 17 shrubs on Site 1. Branches were censused at approximately biweekly intervals during the late spring and summer during five years (1982–1986) to count numbers of dehiscing fruits. Precipitation records for these years were obtained from the weather station in Placerville, El Dorado County (NOAA 1982–1986). This station was the closest both geographically (16 km E of Pine Hill) and elevationally (576 m versus 627 m for Pine Hill) to the study sites.

Harvester ants as seed dispersers. I compared the attractiveness of seeds to harvester ants by a choice test, using seeds in three conditions: fresh seeds collected from Pine Hill shrubs with the elaiosomes removed, similar seeds with the elaiosomes attached, and

old seeds taken from the seed bank beneath *F. decumbens* shrubs growing in the Arboretum at the University of California, Davis. Seeds from the Arboretum seed bank were collected by hand-sifting the litter underneath the shrubs. These old seeds were weathered and their elaiosomes had disappeared (presumably by the action of decomposers, as no harvester ants were present in the Arboretum). By using seeds in these three conditions, the importance to ant attractiveness of two factors could be tested: presence of the elaiosome and freshness of the seeds. Seeds were marked with nail polish and allowed to air dry for 2 weeks before use. Subsequent handling was done with a metal spoon to minimize application of human scent to the seeds. Caches containing five seeds of each type were placed in the path of foraging columns of *M. andrei* in September 1983. A total of 20 caches were placed, using ants foraging from four nests. I counted numbers of seeds remaining in each cache at hourly intervals for 3 hours. Numbers of seeds of each type remaining were compared by the Kruskal-Wallis test, and means separation was accomplished by Tukey-type multiple comparisons as described by Zar (1984).

Active *M. andrei* middens on Sites 1 and 2 were canvassed for the presence of seeds at the end of the period of capsule dehiscence of *F. decumbens*. Most middens examined were checked in 1983, but some were checked in 1984. Any *F. decumbens* seeds present were counted and the distance from each midden to the edge of the nearest *F. decumbens* canopy was measured. All ant middens on both study sites were characterized by measuring the distance from the nest entrance to the edge of the canopy of the nearest individual of any shrub species and to the edge of the nearest *F. decumbens* canopy.

Fates of seeds taken by ants. I supplied seeds to ant nests in order to determine the fates of seeds taken into nests. Fresh seeds were marked with nail polish as above and placed in small caches in the path of foraging ant columns. Seed removal was recorded and middens of each nest were checked for discarded seeds at irregular intervals for 1–2 weeks. Discarded marked seeds (and any discarded unmarked seeds) were counted and the distance of each intact seed from the nest entrance was measured.

In early October 1983, I followed the short-term removal of *F. decumbens* seeds from ant middens on Site 1. Five marked seeds, previously recovered from middens (so that they lacked elaiosomes) were placed on each of five middens. Locations of seeds were marked with toothpicks placed within 1 cm of the seed. I counted the remaining seeds after 10, 30, 57, and 120 days.

The above studies revealed that some of the seeds taken into nests were destroyed because empty seed coats were recovered from the

middens. I hypothesized that seed coat thickness may be greater under the elaiosome to protect the seed from ants during removal of the elaiosome. To test this hypothesis, I longitudinally sectioned 45 seeds and measured seed coat thickness with the ocular micrometer of a dissecting microscope at 65 \times magnification. I measured thickness at three places: in the middle of the zone of elaiosome attachment, at the end of the seed opposite the elaiosome, and at a point on the side halfway between the first two. Data were analyzed by one-way ANOVA with pairwise comparisons using Fisher's PLSD test.

Elaiosome longevity. I determined elaiosome longevity in the litter layer under shrubs by stapling 10 fresh diaspores possessing relatively large elaiosomes into each of 45 sleeves made of 1.4-mm mesh fiberglass screen. Nine sleeves were placed under shrubs at each of five locations on Site 1 in mid-September 1983. I scraped the litter off the soil, placed the sleeves on the soil surface, covered them with a screen of 7-mm mesh hardware cloth to prevent disturbance by rodents, and replaced the litter. After weighing the elaiosomes of a sample of diaspores at the start of the experiment, I removed a sleeve from each location at irregular intervals over a 7-month period, allowed them to air-dry if the litter was wet, and removed and weighed the elaiosomes.

Nutritional analysis. Nutritional analysis of seeds and elaiosomes was performed to determine the investment of *F. decumbens* in each diaspore component, as well as the value of each to the diet of the ants. Elaiosomes and seeds from a mass collection of diaspores collected from Pine Hill shrubs were weighed individually, composited, and analyzed for nutritional quality. Subsamples of both elaiosomes and seeds were used to quantify protein, ash, fat, fiber, and soluble carbohydrate composition. Samples of about 2 g were used to determine elaiosome and seed nitrogen contents by Kjeldahl analysis and protein contents were calculated as %N multiplied by 6.25 (Jones 1984). Ash contents were determined by ignition of a 5 g sample at 600 $^{\circ}$ C for 2 hr. Fat content was measured by ether extraction of a 2 g sample followed by evaporation of the ether and weighing of the residue (Jones 1984). Crude fiber was determined as the percent of material in a 2 g sample that was insoluble in dilute acid and base (Horwitz 1965). Soluble carbohydrate was determined by subtracting the sum of protein, ash, fat and fiber from 100%. Dietary energy contents of elaiosomes and seeds were calculated from protein, fat, and carbohydrate contents by the method of Davidson and Morton (1984).

Total energy in seeds and elaiosomes was determined by bomb calorimetry, using a Gallenkamp Autobomb (automatic adiabatic bomb calorimeter). I separated a mass collection of diaspores from

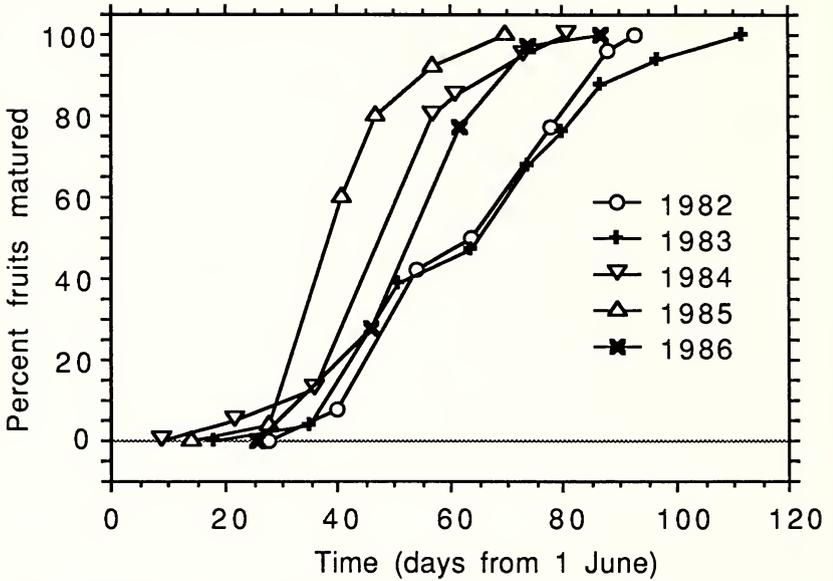


FIG. 1. Timing of fruit maturation of *F. decumbens* during 1982–1986.

Pine Hill *F. decumbens* shrubs into elaiosome and seed portions and, after drying (80°C until constant weight), used four small (1.6–2.6 g) samples of each material to measure total energy contents.

RESULTS

Ant activity and seed availability. The timing of ant activity was strongly influenced by temperature. During late winter and spring, ants were active during midday. In late spring and summer the ants switched to foraging in the early morning or at dusk, when temperatures were less extreme. An ant nest entrance usually was abandoned after several months of activity.

Capsule dehiscence spanned a period of time between 41 d (1985) and 77 d (1983). The correlation between period of dehiscence and total capsule production by the monitored branches was inverse (-0.306), indicating that the larger capsule crops tended to mature in shorter periods of time. This correlation was not statistically significant (Fisher's r to z , $n = 5$, $P = 0.655$) (Abacus Concepts 1992).

Dehiscence was first noted during late June or early July and was completed by early August or mid-September in each of the five years studied (Fig. 1). Years differed in the rapidity with which capsules matured, and the differences corresponded inversely with mean annual rainfall. Slopes of the curves in Figure 1, visually assessed from Figure 1 and listed by year from high to low have

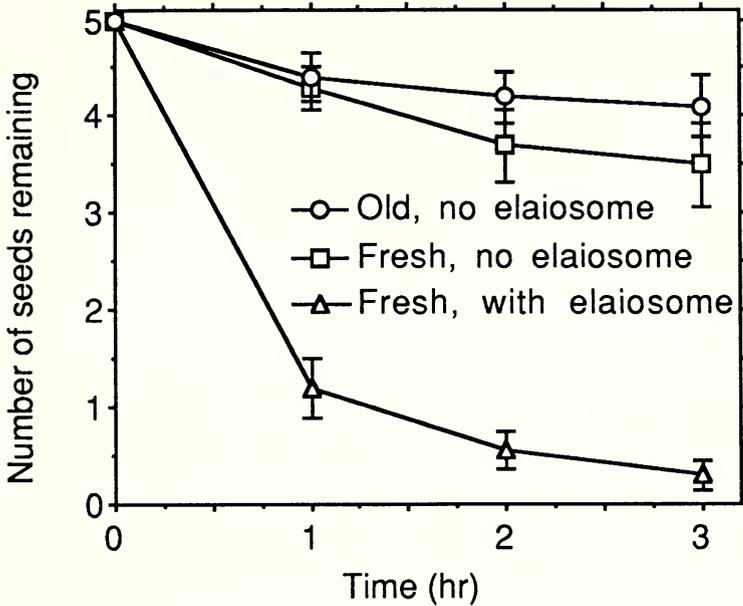


FIG. 2. Removal of *F. decumbens* seeds from caches by foraging *M. andrei* workers. Values are means with SE denoted by error bars.

the following order: 1985, 1984, 1986, 1982, and 1983. Precipitation for these years (as percent of average) and listed from low to high follows the same order of years: 1985 (71%), 1984 (74%), 1986 (105%), 1982 (165%), and 1983 (202%).

Harvester ants as seed dispersers. Harvester ants rapidly removed fresh elaiosome-bearing seeds, taking almost all intact diaspores after 3 h (Fig. 2). Seeds lacking elaiosomes were removed very slowly regardless of whether the seeds were fresh or old. Removal rates differed significantly between the three seed types at each of the census times (1, 2 and 3 hr, Kruskal-Wallis test, $P < 0.001$ for each census time). In all cases, nonparametric Tukey-type multiple comparisons (Zar 1984) revealed that the removal rate of seeds lacking elaiosomes was not significantly affected by seed freshness, whereas the removal rate of elaiosome-bearing seeds was significantly faster than that for seeds lacking elaiosomes ($P < 0.001$).

Seeds of *F. decumbens* were frequently found on ant middens, although the probability of encountering a seed decreased as the distance from the midden to the nearest *F. decumbens* shrub increased. *Fremontodendron decumbens* seeds were found on 55% of 44 ant middens examined. The majority of middens within 8 m of a *F. decumbens* shrub contained at least one *F. decumbens* seed.

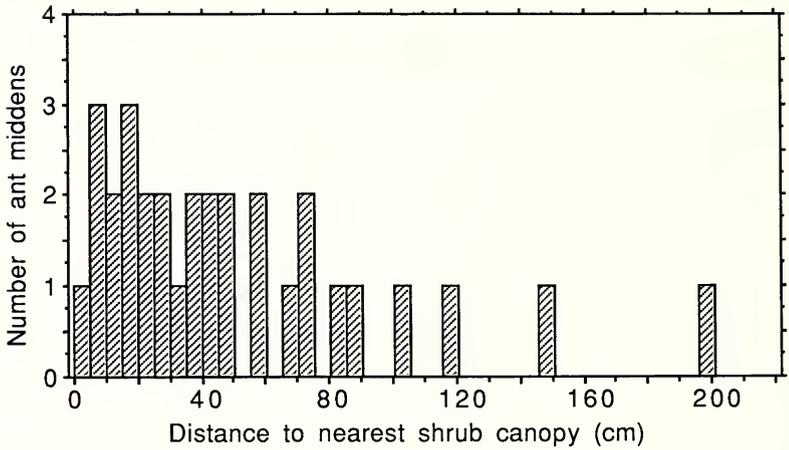


FIG. 3. Distances from the entrances of ant nests to the edge of the nearest shrub canopy.

Percentages of middens with *F. decumbens* seeds present were 86% at 0–2 m distant ($n = 7$), 60% at 2.5–4 m ($n = 15$), 58% at 4.5–6 m ($n = 12$), and 60% at 6.5–8 m ($n = 5$). At distances greater than 8 m, middens with *F. decumbens* seeds became much less frequent (14%, $n = 7$). The greatest dispersal distance measured was that of a seed found on an ant midden 12 m from the nearest *F. decumbens* shrub.

Ant middens were never found under the canopy of any shrub species. Distances from nest entrances to the edge of the nearest shrub canopy ranged from 0–200 cm, with most (87%) within 1 m (Fig. 3). All of the 39 ant middens examined were at least 35 cm from the edge of the canopy of the nearest *F. decumbens* shrub.

Numbers of seeds found on middens with at least one *F. decumbens* seed ranged widely (from 1–75), although most middens (93%) had less than 10 seeds. There was little correlation between distance from a midden to the nearest *F. decumbens* shrub canopy and the number of seeds counted on that midden. Seed numbers were log-transformed to better meet statistical assumptions underlying correlation analysis (Zar 1984). The correlation between distance and the log of seed number was only -0.16 and was not statistically significant (Fisher's r to z , $n = 20$, $P = 0.767$) (Abacus Concepts 1992).

Most seeds recovered from ant middens were relatively close to the nest entrances (Fig. 4). The greatest number of seeds was found 11–15 cm distant, but the curve was distinctly asymmetric, with a few seeds found at relatively great distances. Only 3% were found

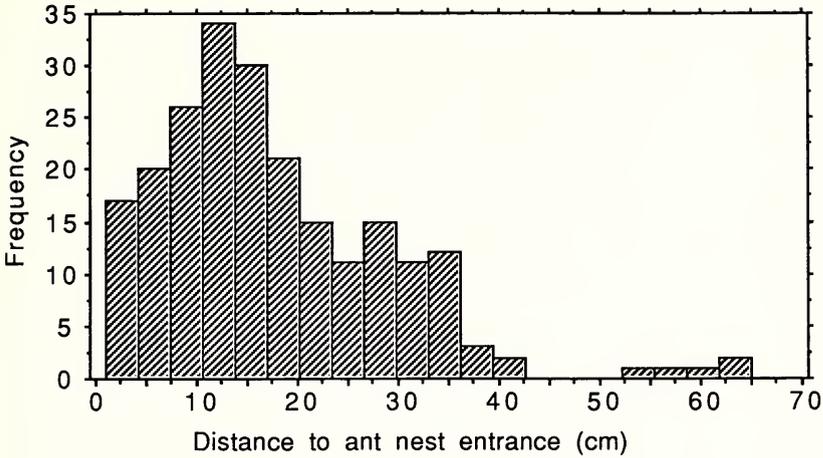


FIG. 4. Distances of *F. decumbens* seeds from the entrances of ant nests after seeds are discarded by *M. andrei* workers.

more than 50 cm from the nest entrance and none were found beyond 65 cm (Fig. 4).

Fates of seeds taken by ants. Only 47% of 785 marked diaspores taken by ants were recovered, and for most of these (45% of the total) the seed portion remained intact. The majority of recovered marked seeds, and the unmarked seeds found on the same middens, were ejected by ants after the elaiosome was completely removed (Table 1). Elaiosomes on a small percentage of both marked and unmarked seeds were intact or only partially removed. Some seeds were not recovered intact, but as empty seed coats. Nail polish marks indicated that these seed coats were from seeds supplied to the ants during the experiment. Based on these empty seed coats, at least 5% of the marked seeds were destroyed (Table 1). Almost 11% of unmarked seeds also consisted of seed coats from destroyed seeds (Table 1).

Seeds rapidly disappeared from the five middens monitored for

TABLE 1. SUMMARY OF CONDITIONS OF *F. DECUMBENS* SEEDS RECOVERED FROM *M. ANDREI* NEST MIDDENS.

Description	Marked seeds (n = 369)	Unmarked seeds (n = 120)
Seed intact, elaiosome removed	92.4%	84.2%
Seed intact, elaiosome damaged	1.1%	4.2%
Seed intact, elaiosome intact	1.6%	0.8%
Seed destroyed	4.9%	10.8%

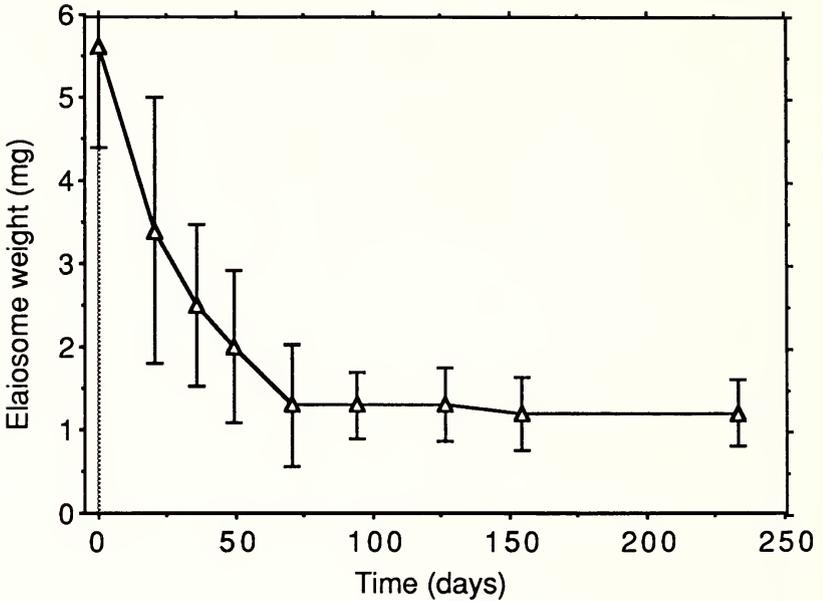


FIG. 5. Mean elaiosome weights (SD denoted by error bars) graphed against time after placement of seeds in the litter under *F. decumbens* shrubs.

seed removal. After 10 d, 48% remained and after 30 d only 16% were left. At 58 d 8% remained, and they were still present when monitoring ceased at 140 d.

Seed coat thickness under the elaiosome was 3-fold greater than at other places on the seed. Mean thicknesses (in mm, \pm SD) were 24.3 ± 3.21 , 8.07 ± 0.963 , and 7.98 ± 0.839 for the elaiosome end, opposite end, and middle measurements, respectively. Seed coat thickness varied significantly (ANOVA, $P = 0.001$), with significant pairwise comparisons for all but the comparison between the opposite end and middle measurements (Fisher PLSD test, $P < 0.05$).

Elaiosome longevity. Elaiosome weight decreased to a constant value within 70 d (Fig. 5). By the end of that period, the orange, waxy portions of the elaiosomes were gone, leaving only hard seed coat-like material at their bases. Elaiosomes declined in weight after only 19 d in the field (Fig. 5). Examination of that sample of elaiosomes showed that some had been chewed by invertebrates which were small enough to penetrate the protective screens. Significant rainfall began October 11, with 2.9 cm falling on that date (NOAA 1983). Litter moisture was relatively high after that time, and I observed elaiosomes with mold on them in the October 23 collection.

TABLE 2. WEIGHT, CALORIC CONTENT, AND NUTRITIONAL COMPOSITION OF ELAIOSOMES AND SEEDS OF *F. DECUMBENS*. Standard deviations and sample sizes are provided for replicated measurements.

Characteristic measured	Seed	Elaiosome
Fresh weight (mg)	33.7 ± 3.91 (n = 813)	3.39 ± 1.09 (n = 858)
Moisture (%)	0.96 ± 0.48 (n = 3)	4.3
Crude protein (%)	11.6	21.3
Crude fat (%)	20.4	13.7
Soluble carbohydrate (%)	40.2	45.6
Fiber (%)	23.6	15.4
Ash (%)	4.15	4.00
Total energy (J/mg)	26.3 ± 0.569 (n = 4)	23.8 ± 0.133 (n = 4)
Dietary energy/unit (J)	571	55.8
Total energy/unit (J)	878	77.1

Nutritional analysis. Elaiosomes of *F. decumbens* contained 4-fold more moisture than seeds, but because moisture contents of both were extremely low (Table 2), the dry weight of elaiosomes was 9.7% that of seeds. Elaiosomes contained almost twice as much crude protein and had less fat than seeds, but soluble carbohydrate contents were similar (Table 2). Total energy content of elaiosomes was 2.5 J/mg lower than seeds. Because of the great difference between the two in weight, seeds contained about an order of magnitude more dietary and total energy than elaiosomes (Table 2).

DISCUSSION

Harvester ants are generally viewed as seed predators (granivores) and hence negatively affect plant populations (Brown et al. 1979; Reichman 1979). Müller 1933 (in Berg 1975) suggested that the presence of harvester ants in the Mediterranean garigue explained the low percentage of myrmecochorous plant species found in that vegetation type. Since then, studies in Australia have shown a relatively large contingent of myrmecochorous plant species in an area where harvester ants are an important component of the ant fauna (Berg 1975). Studies in both Australia and South Africa have demonstrated that myrmecochory is relatively common on infertile soils in both continents (Milewski and Bond 1982). In California chaparral, only two shrub genera have been demonstrated to be ant-dispersed: *Dendromecon* (Berg 1966; Bullock 1974; 1989) and *Fremontodendron* (this study). Seeds of both species bear elaiosomes and dispersal of both involves harvester ants. Despite a relative lack of studies on dispersal mechanisms, ant-mediated dispersal of California chaparral shrub species seems a genuinely scarce phenomenon (Keeley 1991). It should be noted, however, that ants in chaparral move seeds of many species, including shrub species other than

the two noted above. For example, harvester ants have been observed transporting seeds of *Ceanothus* (Horton and Kraebel 1955; Davey 1982; Mills and Kummerow 1989), although they do so to feed upon the seeds themselves. Ant-mediated dispersal of such unspecialized seeds may occur if some seeds escape destruction by the ants. If so, then ant-mediated dispersal may be more important in chaparral than has been thought previously.

Harvester ants may be valuable ant members of a myrmecochorous mutualism with *F. decumbens* for three reasons. First, they are relatively large ants and the seeds of *F. decumbens* are also relatively large (Keeley 1987). This size correspondence allows single workers to pick up and transport single seeds (Beattie et al. 1979). Second, because these large ants may cover large distances from the nest when foraging (Cook 1953), dispersal distances may be great. For example, Gordon (1980) reported that the desert species *Messor* (= *Veromessor*) *pergandei* (Mayr) foraged up to 100 m away from the nest. In a study of dispersal of *Dendromecon*, Bullock (1989) reported that *Pogonomyrmex* harvester ants dispersed seeds "tens of meters". In this study I documented a dispersal distance of at most 12 m, but I suggest that greater dispersal distances probably can occur. In contrast, maximum dispersal distances of elaiosome-bearing seeds dispersed by small ants may be shorter. Examples include 1.5 m for *Viola* seeds (Culver and Beattie 1978) and 3.3 m for seeds of *Trillium* (Ohara and Higashi 1987). Finally, both this study and Bullock (1989) report that harvester ant nests in chaparral are typically located in openings away from the canopies of nearby shrubs. This may result in an increased probability of establishment for ant-dispersed seeds. Seedlings produced in these openings (after germination is stimulated by fire) will likely experience lessened competition from pre-existing shrubs and may have a greater likelihood of surviving to maturity.

Harvester ants also have drawbacks as seed dispersers. As discussed below, their activities as seed predators cause some loss of collected *F. decumbens* seeds. It has even been suggested that the evolution of ballistic dispersal of seeds of *Ceanothus* is an adaptation that results in lower predation of *Ceanothus* seeds by ants (Zammit and Zedler 1988). Harvester ants also leave seeds aggregated on the surface of middens, where they may be subject to increased predation. Bullock (1989) reported some rodent predation and substantial bird predation of *Dendromecon* seeds on middens. In this study, I documented rapid initial disappearance of seeds from middens. Rodent and bird predators likely were responsible.

Many authors (e.g., Berg 1975; Bond and Slingsby 1983) report that the seed portion of diaspores is not harmed when collected and processed by ants to remove the elaiosomes, although careful studies by Hughes and Westoby (1992) indicate this is not always the case.

Even harvester ants have been reported to discard seeds unharmed on their middens (O'Dowd and Hay 1980; Bullock 1989). Keeley (1991) suggested that the elaiosome of ant-dispersed seeds functions as a "bribe" that keeps ants from focussing their predatory activity on the attached seed. In this study, the elaiosome "bribe" was only partly successful. Ants destroyed some seeds taken into their nests, as evidenced by the empty *F. decumbens* seed coats found on their middens. It is possible that these seed coats had been left by another predator that encountered seeds on middens and destroyed them in place. For example, Boyd and Serafini (1992) reported that rodents consumed seeds of *F. decumbens*. However, seeds taken by rodents in that study were not consumed in place, as seed coats were not found in the feeding trays when seeds disappeared from them. This suggests that the seed coats found on the ant middens were ejected from the nests in that condition by the ants and that ants therefore did destroy these seeds.

The percentage of seeds destroyed by the ants can only be estimated. Only 4.9% of marked seeds recovered from ant middens had been destroyed, compared to 10.8% of unmarked seeds. However, these values probably under-represent losses from ant predation, as the fates of 53% of marked seeds were unknown because they were never recovered. Some of these may have remained underground, and some may have been ejected from nests but removed by rodents, but it seems likely that some were destroyed by ants and not represented by the empty seed coats I encountered on the middens. Therefore, in addition to acting as a seed disperser for *F. decumbens*, *Messor andrei* also acts as a seed predator, consuming at least 5% of the seeds transported.

The increased (3-fold) thickness of the seed coat under the point at which the elaiosome is attached to the seed suggests a defense mechanism that has evolved to limit the predatory component of the ant's activities. Because they consume seeds, harvester ants are generally viewed as having limited value to plants as seed dispersers (van der Pijl 1972). The thickened coat of *F. decumbens* seeds may be an adaptation that protects the seed and allows for successful harvester ant-mediated seed dispersal. This adaptation may not be limited to plants with seeds dispersed by harvester ants. For example, Bresinsky (1963) noted that some plant species from habitats lacking harvester ants have elaiosomes that are separated from the corresponding seed by special thick-walled tissues. It should also be noted that seeds of many plants contain toxins (Carroll and Janzen 1973), so that defense of *F. decumbens* seeds against predation by harvester ants may not be limited to the morphologic one reported here.

The elaiosome of *F. decumbens* has an important function in stimulating ants to disperse seeds. It also has a cost to the plant. Costs

of adaptations can be difficult to determine (e.g., Simms and Rausher 1987), in part due to the variety of choices regarding the "currency" in which those costs are paid. Based on energy values (Table 2), the energetic cost of building elaiosomes reduced *F. decumbens* seed output by 8%. The energetic investment of *F. decumbens* in the elaiosome portion of a diaspore is similar to that of other ant-dispersed species in arid areas. Buckley (1982) summarized Australian myrmecochores as having elaiosomes that represented 5–10% of diaspore mass and energy contents. Bullock (1989) reported that the elaiosome of *Dendromecon* represented 14% of the energetic value of the entire diaspore, an almost 2-fold greater energetic investment than that reported here for *Fremontodendron*. It should be noted that Westoby et al. (1982) suggested that the cost of elaiosomes for Australian myrmecochores may be more accurately reflected by their phosphorus content, because phosphorus was more limiting than energy in those habitats. Whether energy is the most appropriate "currency" for measuring cost of dispersal in California chaparral is not known.

The elaiosome of *F. decumbens* is colored (yellow-orange) rather than the white color typical of an ant-attractive elaiosome, and hence is similar to the arils of bird-dispersed species (Davidson and Morton 1984). Otherwise, the elaiosome of *F. decumbens* has features that are typical for an ant-dispersed species. Bresinsky (1963) qualitatively examined elaiosomes of many ant-dispersed species and reported that their elaiosomes contained significant amounts of fat, sugar, and protein. Davidson and Morton (1984) used quantitative techniques in their examination of the characteristics of arillate Australian *Acacia* species. Compared to their results, the elaiosome of *F. decumbens* is generally low in lipid, high in carbohydrate, and intermediate in protein content. Thus, it was most similar to the ant-dispersed *Acacia* species, rather than those dispersed by Australian birds. It also is very low in moisture (4.3%). This value is lower than that for any of the 19 species in Davidson and Morton's (1984) study. The low moisture content of elaiosomes in chaparral areas has been noted before for *Dendromecon*, and is explained as an adaptation that allows the elaiosome to persist in the relatively dry Mediterranean-type climate typical of these areas (Berg 1966).

The low water content of *F. decumbens* elaiosomes may aid in their longevity, but the elaiosome longevity study showed that elaiosomes disappeared from seeds within 2 months of their being placed into the litter layer. There were two reasons for this. First, elaiosomes were attacked and eaten by small invertebrates. This represents competition for elaiosomes between harvester ants and these small invertebrates. Seed dispersal probably does not result from the feeding activities of these small invertebrates. In a study of *Trillium*, Ohara and Higashi (1987) showed that ground beetles competed

with ants for elaiosomes. Damage to elaiosomes by the feeding activity of beetles seriously interfered with the ant-plant mutualism, so that 85% of seeds produced were not dispersed away from fruiting plants. Second, elaiosomes rotted when the litter had been moistened by rains. This again represents competition with harvester ants for the elaiosomes, and probably also results in dispersal failure by destroying the ant-attracting component of the diaspore. Because of the activities of these competitors, seeds of *F. decumbens* must encounter a dispersing ant fairly soon after being shed from the capsules. The release of *F. decumbens* seeds over a period of ca. 2 mo may help ensure that at least some seeds encounter dispersing ants prior to elaiosome destruction.

The function of the elaiosome in stimulating ants to disperse seeds of *F. decumbens* is clear, and corresponds with many other studies of elaiosome-bearing seeds (e.g., Marshall et al. 1979; Bond and Breytenbach 1985; Brew et al. 1989; Oostermeijer 1989; Hughes and Westoby 1992). Conversely, it can be concluded that seeds of *Fremontodendron* lacking elaiosomes would not be dispersed by ants. It is interesting to note that Kelman (1991) reported that seeds of a specimen of *F. californicum* lacked elaiosomes. Furthermore, *F. mexicanum* Davidson was reported to have either a small or (more frequently) no elaiosome on its seeds (Kelman 1991). Howard (1950) reported that many chaparral areas lack harvester ants. It would be interesting to know if harvester ants are present at the sites on which these plants grow. In addition, how (or if) *Fremontodendron* seeds lacking elaiosomes are dispersed merits investigation.

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EMERGENCE AND SURVIVAL OF *NASSELLA PULCHRA* IN A CALIFORNIA GRASSLAND

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ABSTRACT

We tested the hypothesis that prescribed burning and intense, short-duration grazing of the California annual grassland by sheep would increase emergence and survival of perennial bunchgrass seedlings at the Jepson Prairie Preserve in Solano County, California. Seeds of *Nassella (Stipa) pulchra* (Hitche.) Barkworth, either from a bulk seed collection or in three weight classes, were planted along paired transects on two topographic locations with differing soil depth. Treatment combinations that included burning or spring grazing produced higher rates of emergence than other treatments, but only in the first season after the burn. Very few seedlings (0.01%) survived in any treatment to the end of the fourth growing season. Although burning, grazing, and topography influenced the emergence of seedlings, survival to a mature stage appeared to be more strongly influenced by factors not manipulated or monitored in this study. Based on these data, we suggest that recruitment into the *N. pulchra* population may be strongly influenced by climatic variables and that the effectiveness of management techniques may be dependent on annual climatic variation. Management techniques for increasing *N. pulchra* populations must account for numerous and potentially specific habitat requirements of seedlings.

Heavy grazing by domestic animals and the introduction of invasive annual plants have been important factors in shifting community composition and dominance of California grasslands from native perennial grasses to exotic, annual grass and forb species in the last 200 years (Mack 1989). Native bunchgrasses, such as *Nassella pulchra*, tolerate light to moderate, seasonal defoliation from grazing (Painter 1995), but cannot withstand the impact of continuous defoliation by domestic livestock (Burcham 1957; Heady et al. 1992). The shift in the intensity of herbivory in the past two centuries, coupled with prolonged episodes of drought, allowed many exotic annual species to invade and dominate the California grassland in a remarkably short period of time (Burcham 1957; Mack 1989).

Experimental removal of grazing pressure has not resulted in either the return of native perennial grasses in inland California (Bartolome and Gemmill 1981; Baker 1989) or in elimination of introduced species (Biswell 1956; White 1967). The persistence of introduced annual species reflects the profound change in community

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structure that has occurred since European settlement. The rapid biomass production, dense canopy, and litter accumulation by annual species can modify many microhabitat characteristics of the grassland (Facelli and Pickett 1991). The quality of light reaching the base of perennial grasses can affect tillering rates (Derigibus et al. 1985), rate of phenological development (Weaver and Rowland 1952) and mortality of seedlings (Bartolome and Gemmill 1981). Litter accumulation can suppress grass seedling establishment by reducing temperature and humidity fluctuations that can be as important as light stimuli in controlling seed germination (Weaver and Rowland 1952; Knapp and Seastedt 1986).

Wildfire has also played an important role in grassland systems (Daubenmire 1968; Heady et al. 1992), but its influence may have been one of modifying rather than structuring the grassland community (Vogl 1974; Heady 1988). Little fire research has been done on perennial grasses in the annual-dominated system of California (Menke 1989). In the past, periodic fire helped maintain the vigor of the grassland, especially of bunchgrasses, by completely and indiscriminately removing the accumulation of litter and senescent biomass (Daubenmire 1968; Vogl 1974). Bunchgrasses experience early, vigorous regrowth and increased tillering in the growing season following a fire (Vogl 1974; Heady 1988). Resultant changes in soil temperature, soil water availability, and light penetration (Harvey 1949; Weaver and Rowland 1952; Cook 1979; Knapp and Seastedt 1986) have been implicated as important variables increasing growth and recruitment of perennial grasses.

The large seed bank and the tendency of introduced annual grasses to dominate a site can be manipulated through controlled burning, grazing, or both although the effects of such management is generally short-lived (Harvey 1949; Parsons and Stohlgren 1989). Studies have indicated a positive effect of grazing and of burning on perennial seedling establishment and survival by reducing the competitive effects of annual species (Bakker et al. 1980). Similarly, detrimental effects of competing species on seedling growth and survival have been reported (Ross and Harper 1972; Facelli and Pickett 1991).

The return of the California grassland to a perennial-grass dominated system would be desirable for improving range quality (Menke 1992), general habitat quality (Vogl 1974), and has potential for reducing the fire hazard created by annual grass litter. We hypothesize that management techniques for reducing aboveground biomass in spring and accumulated litter in summer such as controlled sheep grazing and prescribed fire will increase emergence and survival of *N. pulchra*.

MATERIALS AND METHODS

Site description. This study was conducted at the Jepson Prairie Preserve in Solano County, California, an inland grassland that is jointly managed by the University of California, Davis and The Nature Conservancy. The area is characterized by a mound and intermound topography underlain by an impervious clay layer at a depth of about 20 cm in intermound areas and of about 65 cm under mounds. The underlying clay creates a perched water table during the winter and spring months that results in a seasonally-wet, vernal pool environment in the intermound areas (Holland and Jain 1988). The soil at the preserve is classified as San Ysidro sandy loam (fine, montmorillonitic, thermic, Typic Palexeralfs).

The Mediterranean weather patterns of California's Central Valley produce long, hot, dry summers with the majority of the annual precipitation occurring in the cool, temperate winters. Annual rainfall was recorded at Davis, CA, 25 km northeast of the Jepson Prairie.

Present distribution of *N. pulchra* within the vernal pool habitat at Jepson Prairie is spatially variable. Typically, mature *N. pulchra* occur in higher numbers on top and on the slopes of mound areas with fewer occurring in the intermound areas and virtually none in the vernal pools proper. Contrasts between mounds and vernal pools include amount of vegetative cover (<30 percent vs. 100 percent), percent of native versus alien species (>70 percent vs. as low as 0 percent), and percent of alien annual species (<7 percent vs. up to 100 percent) (Holland and Jain 1988).

In December 1987, three experimental blocks of six contiguous 20-m by 20-m paddocks were established containing mature *N. pulchra* plants at densities we considered representative of the area (Fig. 1) and which contained similar amounts of mound and intermound areas. Six treatment combinations in a full factorial design of two levels of burning (burned or unburned) by three levels of grazing (spring or wet-grazed, summer or dry-grazed, and ungrazed) were randomly assigned to paddocks within each block. Seeding experiments were conducted using *N. pulchra* seed collected at the site in May 1988.

Each grazed paddock was stocked with 15 dry ewes for one short, intensive period (2–3 days) annually in March–April (wet-grazed) or in August (dry-grazed) from 1988–1992. The duration of grazing was manipulated to achieve a mean residual dry matter level of about 400–500 kg ha⁻¹ in the paddocks. Prescribed burns were applied in September of 1988 and 1991 when the senescent and dead aboveground biomass was completely dry.

In Experiment 1, four 2.5-m transects, two each in mound and intermound locations, were established in each paddock (Fig. 1).

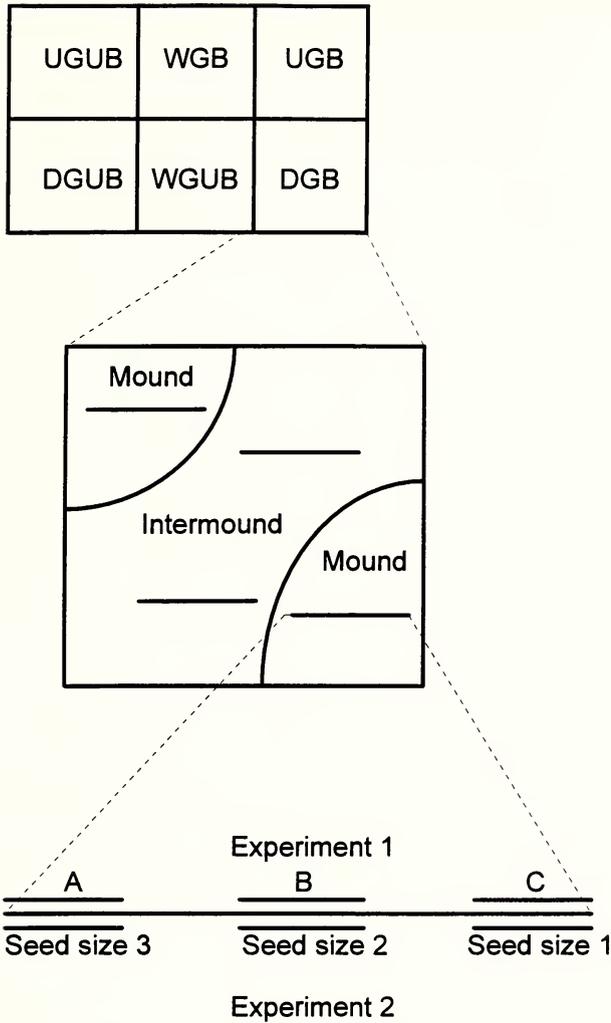


FIG. 1. Design of experimental plots with detail shown of representative blocks (top), paddocks (middle), and transects (bottom). Treatments are ungrazed (UG), wet-grazed (WG), dry-grazed (DG) and burned (B) or unburned (UB). Experiment 1 (1988) plots were located on the side of the transect closest to the center of the paddock. Sets of 20-point plots were planted on one side of the transect from left to right. Experiment 2 (1989) seeds were planted in 20-point plots according to seed size.

Each transect was permanently marked with nails and divided into three sections of 20 sample points (60 points per transect, 720 points per treatment in three replicated blocks). A 20-point wire frame (2.5 cm between points) was temporarily attached to the nails for planting accuracy and was used to relocate seedlings after emergence. One seed was planted at each sample point ($n = 4320$) from 17–22 November 1988. The seeds were planted with awns intact at a depth equal to the length of the caryopsis.

Seedling emergence was determined 6–10 weeks later from 3 January–2 February 1989 by placing the planting grid on each transect and relocating every sample point. Seedling survival/mortality was determined before grazing on 21–27 March 1989. The height of each seedling was recorded as well as the height and species of its nearest neighbor. Neighbor species were categorized into 4 functional groups (*sensu* Goldberg and Werner 1983): 1) exotic grasses, 2) native grasses (all perennials), 3) exotic forbs, and 4) native forbs. The data were analyzed using the proportion ($S_i/(S_i + NS_i)$) where S_i is the number of seedlings with species i as the nearest neighbor. The number of planting locations with no seedling, but with species i as the nearest neighbor (NS_i) was used to weight the emergence data for each functional group. The proportion represents the actual number of seedlings observed in relation to the total number possible for a given nearest neighbor species. The proportional values were transformed (arcsine-square root) and analyzed using the SAS General Linear Model (Littell et al. 1991) to determine effect of nearest-neighbor functional group on *N. pulchra* seedling emergence.

To investigate the importance of seed mass on emergence and survival, we initiated Experiment 2 one year after Experiment 1 in the same experimental plots. *N. pulchra* seeds from the same bulk collection were separated into three dry-weight categories: small (≤ 0.0054 g), medium (≥ 0.0055 g and ≤ 0.0069 g), and large (≥ 0.0070 g). Twenty seeds of each size class were planted in transects paired with all Experiment 1 transects (4320 total seeds with 1440 in each size class) from 6–14 October 1989 (Fig. 1). Seedling emergence was determined 6–10 weeks later from 17 November–8 December 1989. For both experiments, surviving seedlings were surveyed 20–26 March 1990 and 2 June 1992.

In a mixed effects, split-plot model, analysis of variance (SAS GLM) was used to detect effects of burning and grazing treatments (main-plot factors) on seedling emergence, survival, and height. Topographic location (mound or intermound) was a sub-plot factor and seed size (Experiment 2 only) was used as a covariate. A split-split plot analysis was used to assess the effect of nearest-neighbor functional group (sub-sub-plot factor) on seedlings (Little and Hills 1978). A protected LSD procedure was performed for mean sepa-

TABLE 1. EMERGENCE (%) OF *NASSELLA PULCHRA* SEEDLINGS FROM 360 SEEDS PLANTED PER TREATMENT AND LOCATION AT JEPSON PRAIRIE, CALIFORNIA, FOR TWO EXPERIMENTS INITIATED IN 1988 AND 1989. Grazing treatments within the burned and unburned plots were wet-grazed (WG), dry-grazed (DG), and ungrazed (UG). Dates indicate time of survey of seedlings. Means within rows followed by different letters are significantly different at $P = 0.05$. Differences between mound and intermound means are significant at $P = 0.05$ (1989) and $P = 0.001$ (1990).

	Treatments						Mean
	Burned			Unburned			
	UG	WG	DG	UG	WG	DG	
Emergence (%)							
Experiment 1—March 1989							
Mound	32.8a	26.4ab	18.3bc	11.1c	16.9bc	11.4c	19.5b
Intermound	28.3ab	36.4a	22.8bc	15.0c	37.5a	22.8bc	27.1a
Experiment 2—March 1990							
Mound	20.8	30.1	10.3	5.6	11.9	15.6	15.8b
Intermound	34.4	33.1	17.8	9.9	19.4	26.4	23.4a

ration of pairwise comparisons. Each block was treated as a replicate and considered a random effect.

Before making comparisons between the two experiments, we compared the coefficients of variation for Experiments 1 and 2 with a variance ratio test (Lewontin 1966) to assess the degree of variability across years. Finding low variation and similar values, we examined differences between experiments with analysis of variance using treatment combination (burning and grazing) as the main-plot factor and topographic location as the sub-plot factor.

RESULTS

Seedling emergence and survival. *N. pulchra* emergence was rapid and fairly synchronous with 23.3% ($n = 1007$) of the seedlings in Experiment 1 and 19.6% ($n = 847$) of the seedlings in Experiment 2 emerging by March of the following spring (Table 1). Mortality in the first year after emergence was very high (Fig. 2). Survival of seedlings was 1.1% ($n = 48$) after one year (Experiment 1), 0.2% ($n = 19$) after two years (Experiment 2), and 0.1% ($n = 7$) after three years (Experiment 1). Twenty-six (1.4%) of the 1854 seedlings (0.3% of the 8640 seeds planted) from the 2 experiments survived until 1992. Annual rainfall totals were below average for the duration of the study (Fig. 3).

Treatment and topographic effects. We found significant location effects on emergence in both Experiment 1 ($P = 0.05$) and in Experiment 2 ($P = 0.004$). Consistently higher mean emergence rates were recorded on intermound sites for both planting dates regardless

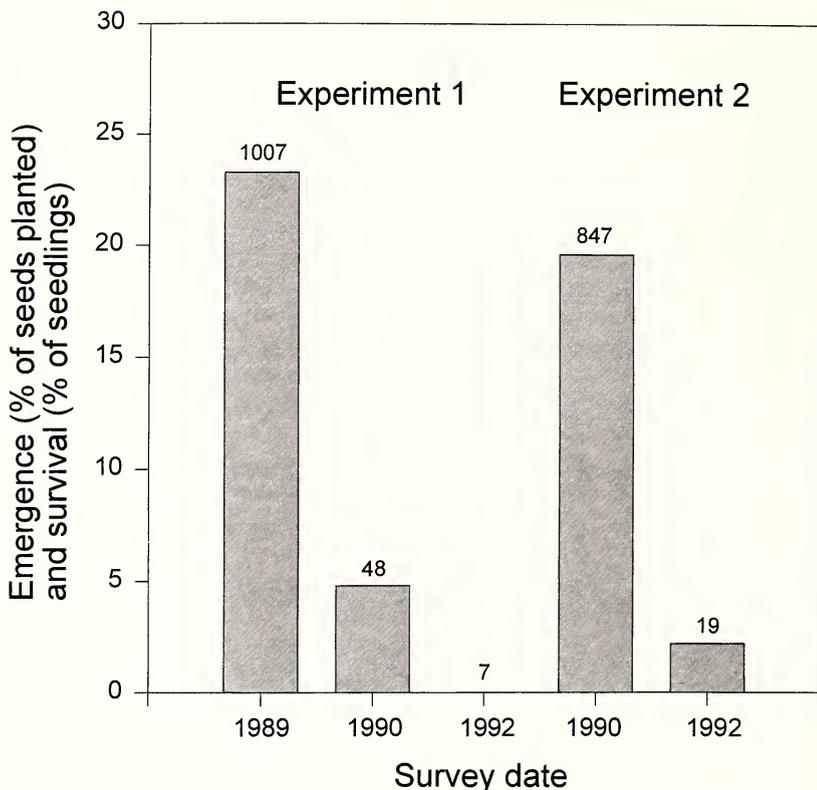


FIG. 2. Total emergence (% of seeds planted) and survival (% of seedlings) for all treatments of *Nassella pulchra* seedlings from 4320 seeds planted in 1988 and again in 1989 at jepson prairie, California. Values above each column represent numbers of seedlings recorded.

of treatment (Table 1). Seedlings were significantly taller on mound sites in Experiment 1 ($P = 0.003$) and Experiment 2 ($P = 0.0003$) (Table 2). However, for both emergence and height (Experiment 1), all significant differences between treatments disappeared by the second year.

Seedling emergence in Experiment 1 was greater in burned than in unburned plots ($P = 0.008$) and greater in wet-grazed than in ungrazed plots ($P = 0.02$). These effects were consistent across both mound and intermound locations (Table 1). A grazing by burning interaction ($P < 0.05$) was found in which dry-grazed and control plots had lower emergence than other treatments. In the second year, grazing was still a significant influence on emergence patterns ($P = 0.025$) with ungrazed plots having lower numbers of survivors. In

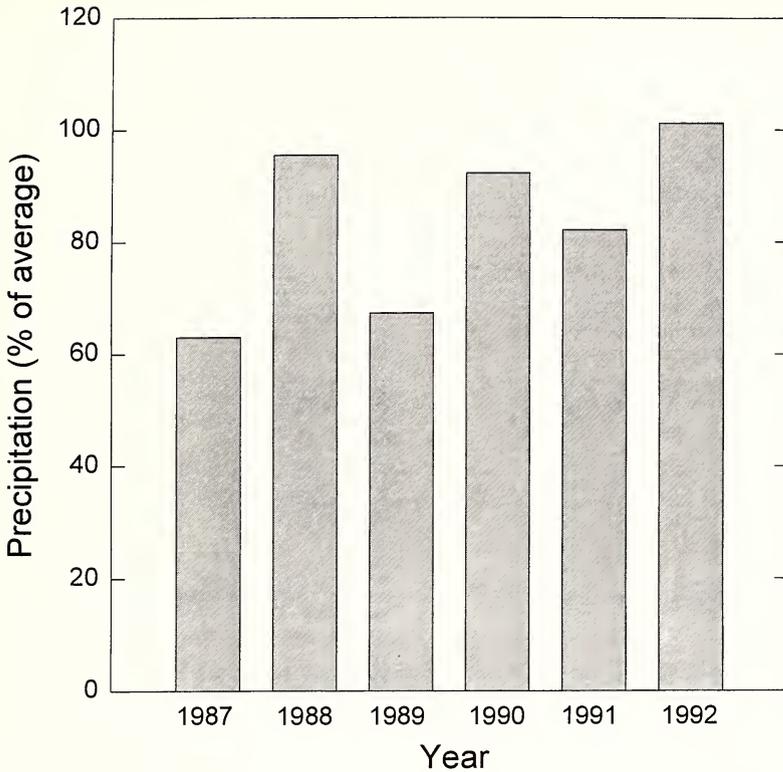


FIG. 3. Annual precipitation (% of normal) recorded at Davis, California for the years 1987–1992. The 100 year rainfall average is 43.6 cm: 7.62 cm (fall), 25.11 cm (winter), 10.41 cm (spring), and 0.46 cm (summer).

Experiment 2, no significant burning or grazing effects were found for emergence.

Experiment 1 seedlings were taller in ungrazed plots ($P = 0.04$) and in unburned plots ($P = 0.05$) while Experiment 2 seedlings showed no effect of burning or grazing on height. Topographic location of seedlings strongly influenced height in both experiments ($P = 0.003$ in Experiment 1, $P < 0.001$ in Experiment 2). Mean height of mound plants was greater than intermound plants for all treatments in both experiments.

In Experiment 2, a grazing by burning by location interaction effect was found for seedling height ($P < 0.02$) (Fig. 4). Within each treatment, mound seedlings were larger than intermound seedlings. The exception was ungrazed seedlings in unburned plots.

Nearest neighbor interactions. The plant functional group to which a nearest neighbor species belonged had no detectable effect

TABLE 2. HEIGHT (MM) OF *NASSELLA PULCHRA* SEEDLINGS FROM 360 SEEDS PLANTED PER TREATMENT AND LOCATION AT JEPSON PRAIRIE, CALIFORNIA, FOR TWO EXPERIMENTS INITIATED IN 1988 AND 1989. Grazing treatments within the burned and unburned plots were wet-grazed (WG), dry-grazed (DG), and ungrazed (UG). Dates indicate time of survey of seedlings. Means within rows followed by different letters are significantly different at $P = 0.001$. Differences between mound and intermound means are significant at $P = 0.003$ (1989) and $P = 0.001$ (1990). Empty data points indicate one-hundred percent mortality.

	Treatments						Mean	n
	Burned			Unburned				
	UG	WG	DG	UG	WG	DG		
	Height (mm)							
Experiment 1—March 1989								
Mound	22.7	19.1	19.7	28.0	16.8	23.8	21.7a	421
Intermound	16.6	17.8	14.7	23.5	18.1	17.9	18.1b	586
Experiment 2—March 1990								
Mound	53.1	36.8	42.3	41.7	49.8	43.6	44.7a	341
Intermound	39.3ab	32.1bc	33.7bc	48.3a	33.7bc	27.7c	34.8b	506
Experiment 1—March 1990								
Mound	79.3	61.0	30.5	—	51.5	26.0	56.0	15
Intermound	65.5	42.2	32.8	60.6	46.9	36.0	48.8	33

on seedling emergence. However, an interaction between time of grazing and plant functional group was noted. *N. pulchra* emergence next to native grasses (*N. pulchra*, *Distichlis spicata*, and *Melica californica*) decreased with dry-season grazing and increased when not grazed at all ($P = 0.04$) in comparison to other plant groups (Fig. 5).

Influence of seed weight on emergence and growth. Seed weight had no detectable effect on seedling emergence. Mean emergence was highest on mound sites for the medium weight category (40.6%), highest on intermound sites for the large mass category (36.0), and highest for intermound sites overall (59.7% of all seedlings) (Fig. 6). Emergence was greatest in the wet-grazed/burned treatment for all weight classes regardless of topographic location. The sole exception was for large seeds which had higher emergence in ungrazed/burned intermound sites. Seeds in ungrazed/unburned (control) plots showed the lowest emergence for all seed weight classes. However, since the power of the analysis of variance was less than 50%, this experimental design may have been ineffective for determining effects of seed weight on emergence and growth.

Year to year effects on seedlings. Treatment combination (burning and grazing) effects on emergence were found in Experiment

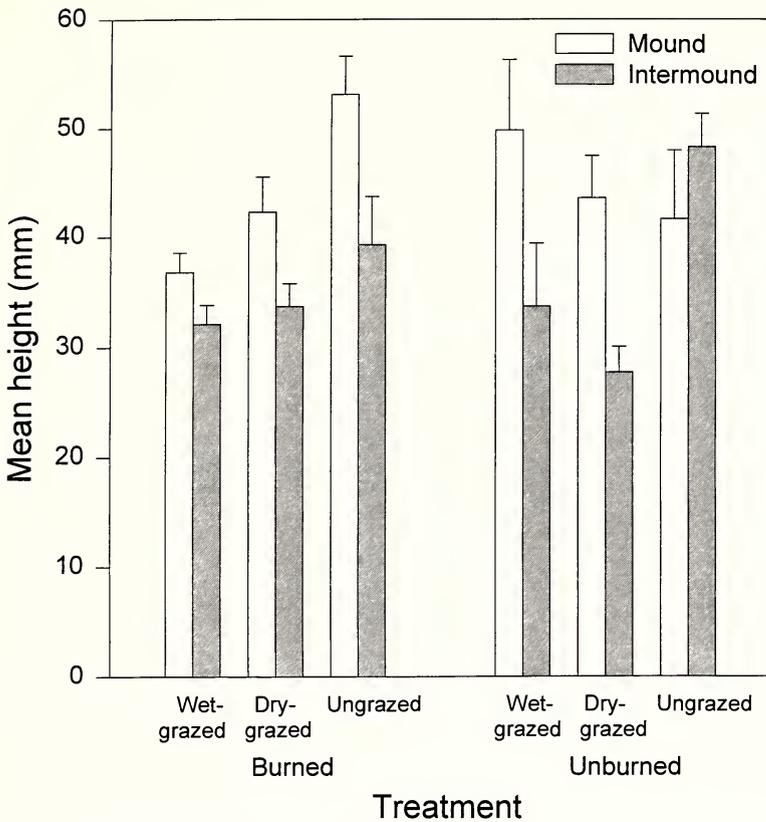


FIG. 4. Treatment interaction (grazing by burning by topographic location) ($P = 0.02$) for height (mm) of *Nassella pulchra* in 1989 plots at Jepson prairie, California. Standard error bars shown for each treatment mean.

1, but not in Experiment 2. The overall emergence means and coefficients of variation were not different for the 2 experiments when compared with a variance ratio test (Experiment 1: mean = 23.3, CV = 45.57; Experiment 2: mean = 19.8, CV = 50.43).

The mean height of Experiment 2 seedlings was significantly greater ($P = 0.001$) than Experiment 1 seedlings in both topographic locations in the first growing season (Fig. 7). A significant year by location interaction ($P = 0.02$) was found as the difference between mound and intermound plants increased from Experiment 1 to Experiment 2 (Fig. 7). However, despite the result of the variance ratio test regarding emergence, these results indicate that conditions were significantly different between years which brings into question the validity of statistical comparisons between these experiments.

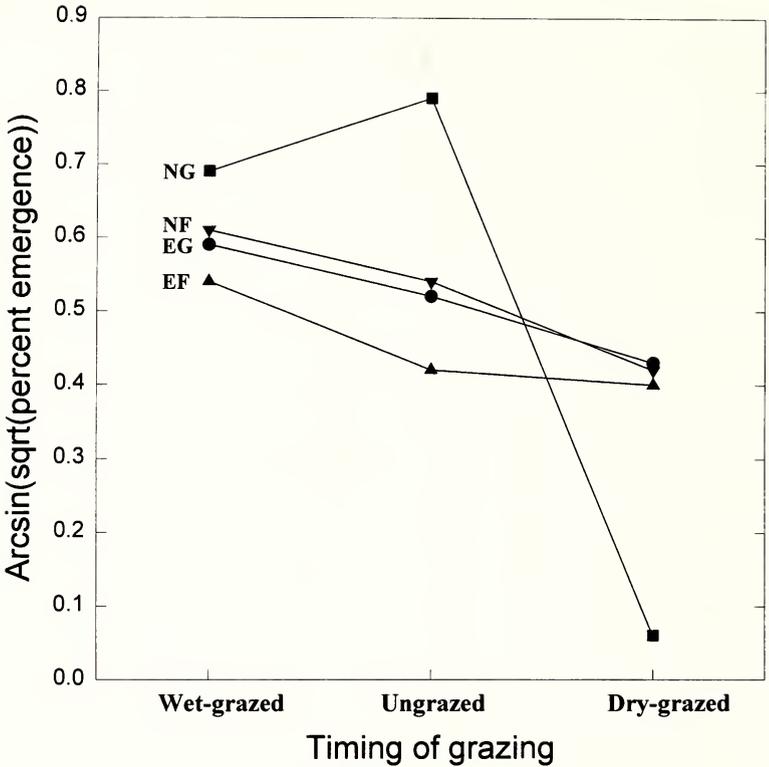


FIG. 5. Emergence of *Nassella pulchra* seedlings next to four functional plant groups in 1988 Plots at Jepson prairie, California. Values are arcsine square-root transformations of the proportion of the number of seedlings to the number of possible sample locations with a particular nearest neighbor. Nearest neighbor functional groups are 1) exotic grasses (EG), 2) native grasses (NG), 3) exotic forbs (EF), and 4) native forbs (NF).

DISCUSSION

In the first experiment, late-summer fire and short-duration grazing prior to planting strongly affected the rates of emergence of *Nassella pulchra* seedlings. Treatment combinations that included burning or wet-season grazing had the greatest positive effect on emergence although the degree was influenced by the topographic location. The effect of burning was more pronounced than grazing. In the first season following the burn, plots that were burned but not grazed had significantly higher emergence than plots that were grazed but not burned. Litter removal and thus the potential for altering the annual grass seed bank was greater with burning than with grazing. Spring grazing (i.e., defoliation of annual grasses dur-

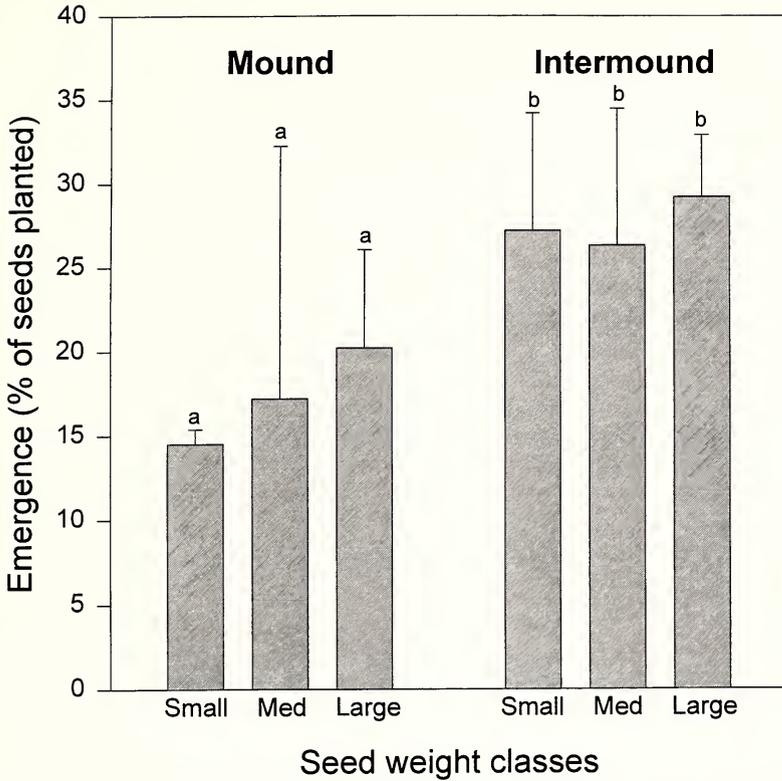


FIG. 6 Emergence (%) of *Nassella pulchra* seedlings of three seed weight categories (720 seeds per weight class) at Jepson prairie, California. Columns with different letters are different at $P = 0.001$. Standard error bars shown for each column.

ing their reproductive phase) had greater potential than summer grazing for reducing annual grass inputs to the soil seed bank.

Although fire is the most effective method for eliminating surface litter, its effect on community composition in California grasslands is short-lived and lasts 1–3 years (Hervey 1949; Cook 1979; Parsons and Stohlgren 1989). The second experiment, initiated one year after the prescribed burn, did not produce significant treatment effects on seedling emergence. Although the first experiment indicated that burning had a stronger effect than grazing, we suspect that time since burning was an important aspect of the burning effect (i.e., the period of enhanced germination appeared to be restricted to the first growing season after a fire.) Rapid reestablishment of surface litter by annual species could explain why a treatment effect was not found in the second experiment. The lack of statistical significance in the second experiment was not from a lack of statistical

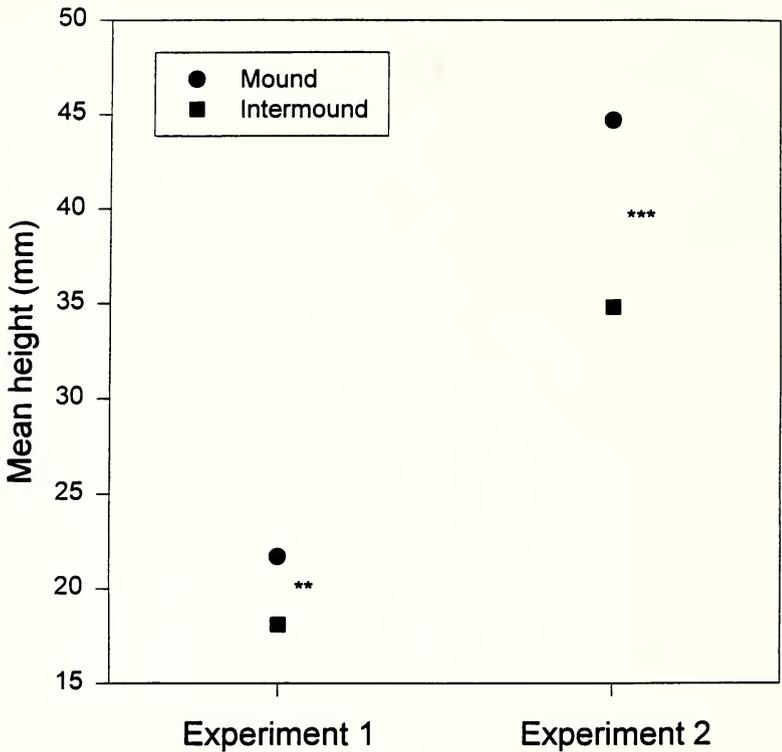


FIG. 7. Mean height (mm) of *Nassella pulchra* seedlings in mound and intermound locations at Jepson prairie, California. Experiment 1 was planted immediately following a prescribed burn and Experiment 2 was planted one year later. Significant influence of location on plant height is indicated by** ($P < 0.01$) and by*** ($P < 0.001$).

power, but from the amount of variance within the data. The error term used to test the main effects of burning and grazing in Experiment 1 was relatively small and in Experiment 2 it was relatively large and resulted in no significant effect of treatments.

Both experiments suggest that topographic location was a stronger determinant of emergence than either burning or grazing. The higher mean emergence for all treatments (except ungrazed-burned in Experiment 1) in intermound areas may reflect lower competition for light because of the lower biomass and canopy development of the intermound vegetation. In early spring, when moisture is not limiting, primary competition is for light (Grubb 1992) and the intermound would be more suitable for seedlings than the mound because of greater light penetration to the soil surface.

Grass growth rates are inversely associated with light availability (Weaver and Rowland 1952; Facelli and Pickett 1991) which is, in

turn, a function of canopy cover and stand density. Seedling height prior to grazing was a useful measurement for assessing the potential effectiveness of treatments in reducing canopy development and light competition with neighbors. A seedling in the California grassland may have several hundred to several thousand neighboring individuals of many species within a radius of 10 cm (Major and Pyott 1966; Young et al. 1981). The neighbors compete for soil moisture and available light and create a canopy as the growing season progresses. Thus, the species composition of the immediate neighborhood may be critical to seedling emergence. However, in a community as densely populated as the annual grassland, the concept of a single individual of any species having a profound effect on its nearest neighbor may be questionable (Fowler 1984). The observation in this study of the significant effects from native perennial grasses as nearest neighbors (and not from other functional groups) is therefore difficult to interpret. We can only suggest that the presence of an established perennial grass exerts a substantial influence on seedling vigor. This influence would likely be related to below-ground resource acquisition since our treatments manipulated above-ground biomass variables only.

We did not find a strong association between seed weight and emergence or survival. Although a weak relationship ($P = 0.2$) was noted between seed size and seedling height, the tallest seedlings occurred in plots exhibiting the greatest neighborhood canopy development. These results suggest an apparent, canopy-induced, etiolation effect (Weaver and Rowland 1952; Knapp and Seastedt 1986) and an interaction between treatments and topographic location. Therefore, any contribution made by seed weight to growth, competitive ability, or survival will vary in different microhabitats.

As has been noted, rates of emergence were different across treatments in both mound and intermound locations in Experiment 1, but not in Experiment 2. Conversely, seedling height was not strongly affected by treatments in Experiment 1, but was affected by treatments in the intermound in Experiment 2. Although the role of climatic variables, especially rainfall patterns, for influencing emergence and growth should not be discounted, these results suggest a diminution after one year of the effect of burning on emergence. If burning effects are short-term, the effects of the grazing treatment would be expected to be more apparent in Experiment 2. However, the significant differences in mean height between treatments in intermound, but not mound, plots seen in Experiment 2 suggest that grazing was ineffective in reducing the annual biomass on mounds. A significant grazing by location interaction term in the second year of Experiment 1 ($P < 0.04$) and our observation that sheep prefer to graze intermound areas support these results. Therefore, since our

assumption of no difference between years appeared invalid, we chose not to use the between-years statistical comparisons.

Survival after 3 to 4 growing seasons was less than 1% regardless of time since the burning treatment and despite continuation of the annual grazing treatment. We were surprised so few seedlings survived to the end of the second growing season. However, high seedling mortality in grasslands is a predictable outcome (Cook 1979; Bartolome and Gemmill 1981) and negative effects of grazing on perennial grass seedlings have been reported (Cook 1979; Salihi and Norton 1987).

The high rate of mortality at the seedling stage reflects the intensity of resource competition within the grassland community. The delayed phenological development of perennial bunchgrasses in comparison to annual grasses may put them at a competitive disadvantage (Bartolome and Gemmill 1981; Jackson and Roy 1986). Early emergence allows early access to resources and the opportunity to gain a relative competitive advantage (Ross and Harper 1972). Treatments that reduce or delay growth of the canopy-forming annual species therefore create improved conditions for establishment of perennial grasses.

Surveys of seedlings before and after the first and before the second growing season indicated that virtually all mortality occurred during or just before the summer months. Ongoing research has indicated that the vigor of the seedlings prior to the dry summer months may be an important factor for predicting subsequent survival (Dyer in preparation). The vigor of the seedling is strongly influenced by the growing environment in the preceding months. In particular, the amount of light penetrating the canopy to the seedling level may be a critical factor (Weaver and Rowland 1952; Knapp and Seastedt 1986).

The severity of post-emergence resource competition and its impact on seedling survival (low seedling survival was observed even when buildup of annual vegetation was reduced by management) was well illustrated in this study. It is possible that below-average rainfall may have intensified the severity of growing conditions. A shorter-than-average growing season and early depletion of soil moisture coupled with shallow soils may have influenced the final numbers of survivors. However, current research indicates that early-season light availability may be even more critical for *N. pulchra* seedling survival than late-season moisture availability (Dyer, in prep.). In fact, other recent work indicates that years of below-average rainfall, by reducing annual grass development, may potentially encourage pulses of recruitment of *N. pulchra* in some areas (F. T. Griggs unpublished data).

CONCLUSIONS

The use of prescribed burning and short-duration grazing for enhancing seedling recruitment into *Nassella pulchra* populations has not been supported by this study. Although emergence rates of seedlings in burned and grazed treatments appeared favorable initially, the probability of reaching a mature stage was low for a bunchgrass seedling at Jepson Prairie during the period of this study. The treatments applied were expected to alter resource availability for seedlings (e.g., the decreased biomass of annuals would result in increased resource availability for perennial seedlings.) The low overall survival indicates a failure of the treatments to modify environmental conditions sufficiently to increase *N. pulchra* seedling survival. The extended period of below-average annual rainfall and the shallow soils of Jepson Prairie may have contributed to the low survival.

The factors controlling emergence and survival of *N. pulchra* are probably more complex and integrated than can be tested by the broad treatments implemented in this study. Other environmental factors which may complicate the issue and which should be investigated in future work include a) soil depth, b) timing of and amount of annual precipitation, and c) timing of treatments within a season and throughout the year rather than intensity or frequency of treatments. We also acknowledge that recruitment likely occurs in pulses and that a "good" year for recruitment may require the simultaneous occurrence of several favorable environmental conditions (Fowler 1986). Identification of essential environmental conditions for emergence and survival of *N. pulchra* seedlings will continue to be a research goal. However, the design of experiments that simultaneously manipulate the many environmental variables involved may ultimately prove intractable.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Gwilym Lewis of the Royal Botanic Gardens, Kew, is the recipient of the 1995 Rupert Barneby Award. Mr Lewis will be working on the legumes of Ecuador.

The New York Botanical Garden also invites applications for the 1996 Rupert Barneby Award. The award of \$1000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae and a detailed letter describing the project for which the award is sought. Travel to NYBG should be planned for sometime in 1997. The letter should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126 USA, and received no later than December 1, 1996. Announcement of the recipient will be made by December 15th. Anyone interested in making a contribution to THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Luteyn.

NOTEWORTHY COLLECTIONS

CALIFORNIA

PSILOCARPHUS TENELLUS Nutt. var. *GLOBIFERUS* (DC.) Morefield (Asteraceae).—Riverside Co., base of low hills south of Winchester in roadside ditch along west side of Highway 79, about 0.25 mile north of intersection with Newport Road, Winchester 7.5' USGS quad, T5S R2W far east portion of SE 1/4 sec. 33, elevation 1520 ft, vernal flooded depression with *Veronica peregrina*, *Juncus bufonius*, *Crassula aquatica*, and *Gnaphalium palustre*, 4 May 1995, *Brian Leatherman s.n.* (RSA).

Previous knowledge. Known from vernal pools and coastal dunes, central California, especially the Central Valley, and disjunct to central Chile (J. C. Hickman [ed.], *The Jepson manual: higher plants of California*, 1993).

Significance. First report for California south of the Transverse Ranges and first record for Riverside Co.

CYPERUS ACUMINATUS Torrey & Hooker (Cyperaceae).—Riverside Co., Skunk Hollow area, 2 miles east of Murrieta Hot Springs, just west of Second San Diego Aqueduct, disturbed annual grassland above inundation area, *Eleocharis*, *Orcuttia*, *Malvella leprosa* within inundation area, common annual in damp mud around margins of pool, 14 Jun 1991, *Steve Boyd et al. 6334* (RSA), verified by R. Kral (VDB); San Jacinto River at a planned development called "Creekside" ["probably between Perris and Lakeview", A. C. Sanders, personal communication], 20 May 1992, *Karen Kirtland s.n.* (UCR), determined by A. C. Sanders.

Previous knowledge. Known from vernal pools and other wet areas from Ventura Co. and the Central Valley of California, northward to Washington and eastward through the north-central and eastern United States (Hickman, *loc. cit.*; P. A. Munz, *A flora of Southern California*, 1974).

Significance. First reports for California south of the Transverse Ranges and first records for Riverside Co.

SCIRPUS SUPINUS L. var. *SAXIMONTANUS* (Fernald) Koyama (Cyperaceae).—Riverside Co., Skunk Hollow area, 2 miles east of Murrieta Hot Springs, just west of Second San Diego Aqueduct, disturbed annual grassland above inundation area, *Eleocharis*, *Orcuttia*, *Malvella leprosa* within inundation area, annual, leaves terete, common on wet mud about margins of pool, 14 Jun 1991, *Steve Boyd et al. 6338* (RSA), determined by R. Kral (VDB).

Previous knowledge. Known from vernal pools, lake margins, and other wet areas at scattered stations from Ventura Co. through the Central Valley of California, and eastward to the central United States and northern Mexico (Hickman, *loc. cit.*).

Significance. First report for California south of the Transverse Ranges and first record for Riverside Co.

—STEVE BOYD AND TIMOTHY S. ROSS, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

ANDROSTEPHIUM BREVIFLORUM S. Watson (Liliaceae).—San Bernardino/Riverside Co. line, Cadiz Valley, T1S, R16E, boundary between sections 15 and 22, 34°4.5'N, 115°16.7'W, ca. 270 m elev., 27 May 1995, *Michael D. Wilcox* and *Stephen J. Myers*

s.n. (UCR). Ca. 12 plants in scarce, scattered patches, *Larrea tridentata* shrubland on sandy Mojave Desert bajada \pm matching Holland's (1986, Preliminary descriptions of the terrestrial natural communities of California, Calif. Dept. of Fish and Game, Sacramento, CA) description of stabilized and partially stabilized desert sand fields.

Previous knowledge. Southern Nevada, northern Arizona, Utah, to western Colorado (A. Cronquist et al. 1977, Intermountain Flora Vol. 6, New York Botanical Garden, NY). Keator (1993, *Androstaphium* in J. C. Hickman, ed., The Jepson Manual, Univ. of Calif. Press, Berkeley, CA) stated "Documentation of occurrence in CA needed," though at least three specimens and a photograph have been reported in literature and/or are housed in major herbaria. We have seen one specimen, *J. Shevock 5756* (RSA), collected in 1977 near Cronese Dry Lake in San Bernardino Co. at Interstate 15, 16 miles southwest of Baker. Rarefind (1995, Calif. Dept. of Fish and Game, Sacramento, CA) reports another specimen, *Niehaus 810* (UC), collected in 1968, also near Cronese Dry Lake and a photograph taken by K. Berry in 1978 ca. 25 km west of Cronese Dry Lake. A third specimen, *Clark 611* (CSPU), was reported by Clark et al. (1984, *Madroño* 31:192) west of Victorville, ca. 105 km. southwest of Cronese Dry Lake.

Significance. First record for Riverside Co. Bridges wide gap between California locations and distribution outside California; ca. 140 km southeast of Cronese Dry Lake, 200 km east of Victorville location, and at least 80 km west of any Mojave Co. (Arizona) locations.

CLAYTONIA LANCEOLATA Pursh (Portulacaceae).—Inyo Co., Panamint Mts., north-facing slope above Pleasant Cyn., T22S, R45E (unsurveyed sections), 36°1.5'N, 117°7'W; 2050 m elev., 19 May 1995, *Scott D. White and Steve Ogg 3170.4* (UCR). Scarce in *Pinus monophylla* woodland on very steep mountainside in loose sand and gravel. Two plants were collected, each with a single pair of leaves, 2–6 mm wide \times 10–22 mm long, widest at or just above middle; inflorescence of one plant subumbellate, pedicles 9–12 mm; the other plant with a solitary flower 20 mm above leaf axil; petals of both ca. 7 mm long.

Previous knowledge. San Gabriel Mts. (southern Calif.), disjunct from central Sierra Nevada and north through California mountain ranges to western Canada; Rocky Mts. Montana through New Mexico (Orlando Mistretta, personal communication; K. L. Chambers 1993 *Claytonia*, in J. C. Hickman, *op. cit.*). Southernmost California record in the RSA collection, other than San Gabriel Mts., is from Madera Co. Previously unknown from the Panamint Mts. (Alan Romsper, personal communication).

Significance. First record for Panamint Mts. and the Mojave Desert region as mapped by Hickman (*op. cit.*); bridges gap between Sierra Nevada and San Gabriel Mts.; ca. 190 km north of San Gabriel Mts. and ca. 260 km south of Madera Co. These plants have some, but not all, character states of the San Gabriel Mts. population (*C. lanceolata* var. *piersonii* P. A. Munz & I. M. Johnson), though Chambers (*op. cit.*) did not recognize subspecific taxa.

NICOTIANA ACUMINATA Hook. (Solanaceae).—San Bernardino Co., San Gabriel Mts., Lytle Creek Rd. $\frac{1}{4}$ mi. below Glenn Ranch, 5000 ft. elev., 12 June 1965, *John Adams 293* (UCR), chaparral on sandy soil; Santa Ana River at Riverside Ave., 34°2'N, 117°21.5'W, 840 ft. elev., 26 July 1994 A. C. *Sanders 15153* (UCR), solitary in sand of dry riverbed; San Bernardino Mts., mouth of Mill Creek Cyn., 34°4.5'N, 117°4'W, 2400 ft. elev., 19 June 1995, A. C. *Sanders 17356* (UCR), roadside in a soil stockpile of unknown origin; San Bernardino Mts., ca. 0.4 km S of Hwy. 38, T1S, R1W, SW $\frac{1}{4}$ of SW $\frac{1}{4}$, S11, 34°5.5'N, 116°57'W, 1370 m elev., 23 July 1995 *Scott D. White and Julie A. Greene 3491* (UCR) and same location 30 July 1995 *Scott D. White 3539* (UCR, duplicates to be distributed), occasional to common in disturbed soil of roadsides and parking areas.

Previous knowledge. Native of South America, known from "CA-FP (exc SW)" (M. Nee 1993, in J. C. Hickman *op. cit.*). Southernmost specimen at RSA is from Atascadero, San Luis Obispo Co.

Significance. First records for San Bernardino Co. and southern Calif.; range extension of ca. 350 km from San Luis Obispo Co. *Sanders 15153* was collected just upstream of the San Bernardino/Riverside County boundary; the species is therefore also expected in Riverside Co. We found several *N. acuminata* specimens identified and filed as *N. attenuata* Torrey and *N. obtusifolia* Martens & Galeotti. Most were from northern Calif., but Adams's 1965 collection was among these, accounting in part for the long lapse between the species' first collection in southern Calif. and its recognition as part of the flora.

RANUNCULUS SCCELERATUS L. (Ranunculaceae).—Riverside Co., San Jacinto Mts., Lake Fulmor, 33°45'N, 116°44'W, 24 June 1969, *R. F. Thorne et. al. 38149* (RSA); same location 5 July 1978, *A. C. Sanders 575* (UCR), in wet sandy soil, ca. 1800 m elev.; Vail Lake at confluence with Temecula Ck., 33°20'N, 116°57'W, 28 August 1989, *Steve Boyd* and *Tim Ross 3807* (UCR, RSA), wet mud of recently exposed lake shore, ca. 440 m elev.; San Jacinto Valley, southeast of the Ramona Expwy./Sanderson Ave. intersection, 33°48'N, 117°0'W, 29 April 1992, *Scott D. White* and *M. Phillips s.n.* (UCR); occasional in pasture along swale carrying runoff from adjacent dairy, ca. 460 m elev.; San Jacinto Wildlife Area, T4S, R2W, S6, 1420 ft. elev., 9 July 1993, *Julie Greene et. al. 1415* (RSA), edge of drying flood area. San Bernardino Co., San Bernardino Mts., Big Bear Lake, T2N, R1E, S16, 34°15'N, 116°53'W, 5 Sept. 1990, *Chet McGaugh s.n.* (UCR); same location 1 Sept. 1992, *Scott D. White 762* (UCR), occasional on south shore of lake, northwest of Fox Farm Rd., just east of abandoned wastewater treatment ponds, ca. 2050 m elev.

Previous knowledge. Native to northern California (Cascade Ranges, Central Valley, and Modoc Plateau), to Alaska, Montana, Arizona, and eastern N. America (Wilken 1993, *Ranunculaceae* in Hickman *op. cit.*). Southernmost specimens at RSA (other than those cited here) from near Byron (Contra Costa Co.) and Oakdale (Stanislaus Co.).

Significance. First records for Riverside and San Bernardino Cos. Range extension of ca. 500 km. All specimens cited here were collected at artificial reservoirs or highly disturbed wet areas in relatively recent years. Repeated collections at Big Bear Lake and Lake Fulmor were separated by two and nine years, respectively. *R. sceleratus* has evidently been introduced in southern California and become established at several locations.

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ORCUTTIA TENUIS A. Hitchc. (Poaceae).—CA, Sacramento Co., Buffalo Creek 7.5' quadrangle at T.8N R.7E S.17 NE 1/4, 52 m, vernal pool (0.15 ha); approximately 500 plants. 20 May 1993. *Whitney 93-1a* (ARIZ), *Whitney 93-1b* (DAV). Growing with *Eleocharis macrostachya*, *Eryngium vaseyi*, *Navarretia leucocephala*. Identification confirmed by John Reeder, Herbarium, University of Arizona.

Previous Knowledge. One other population known from Sacramento Co., located approximately 9 km southwest of *Whitney 93-1* (T.7N R.6E S.11 S1/2 of NW 1/4). Other populations known from Shasta, Tehama, and Lake Counties.

Significance. The second population reported in Sacramento Co., with the next nearest Central Valley population over 160 km to the north in Vina Plains, Tehama Co.

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OREGON—WASHINGTON

LOMATIUM BRADSHAWII (Rose) Math. & CONST. (APIACEAE)—Clark Co., WA, near Lacamas Creek, 1.3 km NW of Lacamas Lake, elev. 60 m. T2N, R3E, SE¼ sect. 20, 27 May 1994, P. K. Gaddis 331897 (WTU), 9 June 1994, J. Kagan 178074 (OSC); 0.5 km NW LaCamas Lake, NW¼ s 28, 2 May 1995 L. N. Lodwick 331899 (WTU), wet prairie grassland associated with *Deschampsia cespitosa*, *Hordeum brachyantherum*, *Danthonia californica*, *Eryngium petiolatum*, *Carex densa*, *C. unilateralis*, *C. stipata*, *Juncus tenuis*, and *Camassia quamash*.

Previous knowledge. Wet prairie grasslands of southern and central Willamette Valley of Oregon (Creswell to Sublimity) where federally endangered.

Significance. Extends range N 80 km. First record for Washington state. The north subpopulation (s 20) was estimated (K. St. Hilaire 1994, unpublished report) at approximately 2,500 individuals within the property boundaries where it was originally collected. The subpopulation extends further west onto other ownerships. Preliminary survey indicates that the subpopulation covers over 20 acres and could contain several hundred thousand individuals. A population of >2000 is considered viable (U.S. Fish and Wildlife Service, 1993. *Lomatium bradshawii* (Bradshaw's lomatium) Recovery Plan). The southern sub-population may be of comparable size. The two combined sub-populations appear to represent the largest known population of the species.

—PHILIP K. GADDIS, Clark County Dept. Public Works, P.O. Box 9810, Vancouver, WA 98666.

UTAH

CALOCHORTUS EURYCARPUS S. Watson (Liliaceae).—Box Elder Co., Raft River Mts, Sawtooth National Forest, headwaters of George Creek adjacent to USFS road 022, near 41°55'25"N, 113°24'55"W, T14N R14W S26 nel/4, elev. 2680 m, open grassland with *Elymus trachycaulus*, *Stipa lettermanii*, and *Potentilla gracilis*. 18 Aug 1995, M. Curto 1639 with L. Allen & M. Hysell (UTC216695).

Previous knowledge. Indigenous to meadow margins, open grasslands, and open coniferous forest understories from e. OR and ne. NV across ID to sw. MT and nw. WY (A. Cronquist et al., Intermountain Flora V. 6, New York Botanical Garden, Bronx, 1977). The nearest documented occurrences include the East Humboldt Mts, Elko Co., NV (type locality, S. Watson 1173) and the Albion Mts, Cassia Co., ID (UTC212051).

Significance. First record in Utah, approximately 100 km (by air) northeast of the Nevada collection, and 35 km (by air) southeast of the Idaho collection.

VENTENATA DUBIA (Leers) Cosson in Durieu (Poaceae).—Cache Co., Cache Valley, northeast of the town of Paradise, near 41°35'06"N, 111°48'30"W, T10N R1E S23 sw1/4, elev. 1585 m, thousands of plants scattered over approximately 25 hectares, 14 Aug 1995, G. Ellis s.n., det. M. Curto (UTC216696).

Previous knowledge. This Eurasian annual grass is known in California from Nevada and Siskiyou Counties (J. P. Smith, The Jepson Manual, University of California Press, Berkeley, 1993), in Oregon from at least Polk county (UTC202806), in Wash-

ington state from Klickitat, Spokane and Yakima Counties (C. L. Hitchcock and A. Cronquist, *Flora of the Pacific Northwest*, Univ. of Washington Press, Seattle, 1973), in British Columbia from Coquitlam (W. J. Crins in G. W. Douglas et al., eds., *The Vascular Plants of British Columbia*, Part 4, Ministry of Forests, Victoria, 1994), and from scattered localities in Idaho, including Benewah (ID90949), Bonner (ID90915), Elmore (ID90916), Idaho (ID77868), Kootenai (ID37823), and Latah (ID97937) Counties, but has not been noted from Nevada (J. T. Kartesz, *A flora of Nevada*, Ph.D. dissertation, Univ. of Nevada, Reno, 1987). W. H. Baker first reported (*Leaflets of Western Botany* 10: 108–109, 1964) this species from Idaho; Douglass Henderson (communication with Curto) has observed population number and size increases in northern Idaho, especially upon the Camas Prairie, during the past five years. K. L. Chambers first reported (*Madroño* 32:120–121, 1985) the Polk County, Oregon collection (*Halse 2857*) and noted the difficulties in specimen identification when the typically avenoid, dorsally-awned, distal florets have disarticulated from all spikelets and only the persistent, terminally-awned, most-proximal floret remains in each.

Significance. First record in Utah, approximately 370 km (by air) southeast of the nearest Idaho collection in Elmore county. This grass has the potential to become a serious weed in Utah.

—LINDA ALLEN and MICHAEL CURTO, Intermountain Herbarium, Department of Biology, Utah State University, Logan, UT 84322-5305.

REVIEWS

A Flora of Santa Cruz Island. By STEVE JUNAK, TINA AYERS, RANDY SCOTT, DIETER WILKEN, and DAVID YOUNG (illustrated by LINDA ANN VOROBİK). 1995. Santa Barbara Botanic Garden, Santa Barbara, in collaboration with the California Native Plant Society, Sacramento. 408 pp. plus Relief Map of Santa Cruz Island by S. JUNAK & JOANN TANNER ROUNDS. Softcover, \$24.95, ISBN 0-943460-23-9.

I am not one who is eager to write book reviews. In fact, a few years ago I made extensive notes for the last book review that I was *inspired* to write, but fortunately had the foresight and will to hold my tongue and pen, else I would have acquired countless life-long enemies. On the other end of the scale, the recently published *A Flora of Santa Cruz Island* has filled me with a deep pride and inspiration that begs an audience. This floristic project has been carried out at the Santa Barbara Botanic Garden through the contributions of several staff members, past and present, and has in essence been an institutional labor of love spanning a number of years. Consequently, I was very pleased when I heard from Dieter Wilken that the book was in press and that there would be a booksigning commemorating the publication of this new flora at the Santa Barbara Botanic Garden on 28 October 1995. Hence, on the appointed day, my wife, Annette, and I made a rare trip to the SBBG to participate in this special occasion. I expected to see Steve Junak and Dieter Wilken at the event, but wondered aloud whether any of the other co-authors would be able to attend, since they now reside out of state. As it turned out, all five co-authors were present, as well as the illustrator, to proudly celebrate the completion of this important floristic work for Southern California.

Pride of the contributors is never sufficient to prove the quality of a product, however. The worth of the product must be judged on its own merits through the amount of information provided, the accuracy of the information, the completeness of the work, the utility of the work, and the aesthetic and practical presentation of the whole and its parts. All these facets considered, I have nothing but the highest praise for this new flora. From cover to cover it exhibits a care and conscientiousness for detail that is rarely paralleled in other local floras. It is refreshing in the fact that it is not a mindless collation of information from other floras. Instead, it is evident throughout the text that this work is the product of detailed historical research, thorough examination of herbarium specimens, and the authors' astute personal knowledge of the extant vascular plants on Santa Cruz Island.

An overview of the book itself is in order, although the brief words of a reviewer will not do it justice. It has been published in a convenient and appropriate size (7 × 10 inches, nearly 1 inch thick) on good quality paper stock which permits very clear reproduction of both the text and illustrations. The retail cost of this book is amazingly low considering the cumulative value of its substance and contents. I do regret that the *Flora* is only available in a paperback edition (many of us would have gladly paid ten or fifteen dollars more for a hardbound copy), but this minor complaint detracts nothing from the quality of the book itself. Before I even cracked open the *Flora*, I was impressed by the beautifully composed and aesthetically pleasing cover design by Beth Hansen. Over a muted photographic background of *Louisa argophyllus*—with its silvery-gray leaves and clusters of golden-yellow flowers—are superimposed a text block for the title and authors' names, which in turn is counterbalanced below by a dramatic topological panorama in rich earthen tones. The cover alone is a seamless composition that subtly draws the text together with the beauty of the local flora and the rugged, forbidding landscape that can seem so barren to

the uninitiated. In doing so, it provides an apt introduction to the themes and equally artful contents of the *Flora*.

While I had known that Linda Vorobik was providing the botanical illustrations for this work, I was surprised to discover that she also undertook the text layout and design. As with the cover, the text layout shows a symmetry, balance, and clarity of organization that contribute to the book's overall appeal. The type-face used in the text is formal (as it should be), but easy on the eyes. Taxon names are bolded and common names appear in all capitals for quick visual reference, but the balance of each taxonomic entry is devoid of unnecessary abbreviations, differing font-types, or other forms of visual clutter.

Beyond the aesthetic aspects of this flora, the actual content of the book is impressively solid. Introductory material is extensive (51 pages) and well presented. It begins with an overview of California's Channel Islands, turning subsequently to the unique geographic, geologic, and physiographic features of Santa Cruz Island and the associations of vascular plants upon it. Contemporary aspects of the vegetation and floristic composition are put in perspective by a discussion of historic and sub-historic changes brought about by anthropogenic influences—both conscious and accidental. A brief but excellent discussion of botanical exploration on the island is presented (pp. 41–46), which supplies notes on many of the botanists who contributed to an improved knowledge of the island's flora, either through their collections alone, or through both collections and published accounts of their observations. The introduction is fleshed-out with a numerical analysis of the flora, and three pages of orienting information for the reader/user. In addition, the introitus is supplemented with black & white historical photographs from various sources, and several additional photographs by Steve Junak (who also provided the photos for the cover) which illustrate some of the habitats, vegetation assemblages, landforms, and the essential grandeur of the island.

The heart of the book, *i.e.*, the floristic text, occupies pages 53 to 320. The major groupings are ferns and fern allies, gymnosperms, dicotyledonous angiosperms, and monocotyledonous angiosperms, within which the taxa are arranged alphabetically by family, genus, and species (as well as infraspecific taxa, where relevant). Such an arrangement is both useful and desirable from a pragmatic standpoint, since an imperfectly-known, four-dimensional phylogeny cannot be adequately represented in a linear (two-dimensional) scheme, anyway. The entire flora provides details on 648 species or lower taxa and 2 hybrids, and is provided with original keys which, like the taxon distribution data and descriptions, illustrate a personal knowledge of the taxa at hand and the range of their natural variation on the island. Each species entry is uniformly arranged with the binomial, authority, a description of the taxon, and information on phenology, abundance, habitat, plant association, elevational range, distribution pattern on the island, and distribution elsewhere if not endemic. Many entries also contain additional historical or ethnobotanical data. The accompanying botanical illustrations complement the text nicely; they are of good size, crisp in detail, and deftly display both general aspect and technical characters.

Following this taxonomic treatment is a rather extensive listing of the literature cited, which in itself will prove a valuable resource for those interested in the natural history, human history, and anthropology of California's Channel Islands and especially Santa Cruz Island; and three appendices. Appendix I (pp. 329–335) provides an overview of collecting trips on the island with dates, collectors, and localities; Appendix II (pp. 337–369), an indispensable section, cites selected herbarium specimens which substantiate the presence of the various taxa cited on the island; and Appendix III (pp. 371–375), lists those taxa that have been *reported* from the island, but for which no herbarium specimens could be located to *substantiate* their past presence on the island. Appendix III also disposes several taxa that have been reported from the island on the basis of misidentified herbarium specimens. As any conscientious floristician knows, herbarium specimens as vouchers form the basis for any and all *reliable* floristic accounts. The reliance of *this* flora on such vouchers is

one of its many strengths. Finally, the book is rounded out with a concise but clearly written glossary of botanical terms (compiled by Julie Broughton), and an index to the taxa which includes both scientific and common names.

Errors in this book are hard to find and almost non-existent. I was surprised to see the word *spicate* spelled as “spikate”. Presumably this is an Americanized spelling that was back-formed from “spike,” although I could not find it in my unabridged Webster’s dictionary or my usual assortment of botanical glossaries. At least in this case the spelling is uniform throughout the work, and the word appears in the glossary as such. I ran across a typographical error, but it too was negligible. One of my colleagues was concerned with the fact that the three appendices were not identified as to content in the Table of Contents. Overall, however, the text has the mark of a manuscript that has been read, and re-read, and refined (perhaps obsessively) in order to bring it as close to perfection as is humanly possible. I cannot fault its authors for that.

Although I do not wish to diminish to any degree the important contributions of any of the other co-authors of this excellent flora, it seems clear that this work has largely come to fruition through the efforts of its first author, Steve Junak. In recent years, Steve has conducted extensive floristic surveys not only on California’s Channel Islands, but also on numerous islands lying off the coast of the Baja California peninsula. Such floristic studies have been critical to putting insular floras—including that of Santa Cruz Island—into phytogeographic perspective. Steve has also had a profound interest in the associations between plant taxa and their geologic substrates. While for years California’s serpentine outcrops have been worshipped as the gods who solely foster “interesting plants,” Steve has made equally interesting observations on the “less glamorous” substrates upon which certain taxa restrict themselves, thrive, and live out their lives. His outstanding abilities as a field botanist have resulted in numerous documented additions to insular floras, and a concomitantly improved understanding of phytogeographic patterns in the Californian flora. His perfectionism and attention to detail have resulted in a flora infused with his observations and desire for completeness.

I have only had the privilege of visiting Santa Cruz Island once. This was in mid-September of 1992, when Steve served as a guide to Carol Galbraith, a young woman from Alaska; three entertaining and endearing Russian botanists, Amirchan Amirchanov, Yuri Gorbunov, and Peter Gorovoy, who were getting an introduction to the California flora; and myself. I made *very few* herbarium collections, my goal largely being to accompany the visiting Russian botanists and assist them with plant identifications. Consequently, when I saw my name listed as a collector in Appendix I—despite the paucity of my collections—I was amused and uttered, “that’s incredible,” when I realized just how completely Steve Junak had compiled information for this book.

One of the reasons that I am so proud of this flora, even though I have nothing to do with it, is that (in my opinion) floristic botany in Southern California has largely been in a coma in recent decades. Although there are many people who claim to be “Southern California botanists,” the number of people who are actively and systematically collecting and documenting the flora can literally be counted on the fingers of two hands, even if a couple of fingers have been lost in a shop-class accident. This is a very depressing situation when one considers the unique, irreplaceable, and still inadequately known flora of Southern California. I know that several of the active field and herbarium botanists in Southern California have regional floras as their goals, but *A Flora of Santa Cruz Island* is the first substantial new flora in Southern California in quite a few years. This particular flora clearly provides a caliber and quality that is to be aspired to in regional Californian floras, and instills in me the belief that Southern California botany is about to get up out of its hospital bed.

The diligent and competent efforts of Steve Junak, Tina Ayers, Randy Scott, Dieter Wilken, David Young, and Linda Vorobik are to be applauded. In the quality of content and execution, this book far surpasses most works of its type, and will provide

the reader an excellent introduction to this largest and most diverse of California's islands. Even if one never gets an opportunity to visit Santa Cruz Island, this book is a necessity for those interested in the flora of California and the phytogeography of the California Floristic Province.

—TIMOTHY S. ROSS, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

The Cruciferae of Continental North America: Systematics of the Mustard Family from the Arctic to Panama. By REED C. ROLLINS. 1993. Stanford University Press, Stanford. xvii plus 976 pages. Hardcover, \$125.00, ISBN 0-8047-2064-9.

As the World's preeminent authority on the family Cruciferae (Brassicaceae), Reed C. Rollins has produced his *magnum opus* with the publication of *The Cruciferae of Continental North America*. Culminating over fifty years of research and study, this monumental volume provides a comprehensive taxonomic treatment of the family for North and Central America, exclusive of Greenland, the Caribbean islands, and the other islands east of the continent. Complete coverage is provided for all genera, species, and infraspecific taxa known to occur (at least recently) on the continent. Rollins reports a total of 99 genera, 778 species, and 248 infraspecific taxa and hybrids. There has not been such a broad conspectus of the family since that of Torrey and Gray in 1838.

The requisite introductory material is presented clearly and concisely (83 pages) in the first four chapters, with the bulk of the text (837 pages) dedicated to keys and detailed descriptions of taxa. The first chapter, Introduction, provides the reader a general overview of the Cruciferae, including short discussions of geographic diversity of the family worldwide, general morphological features of the family, notable deviations from the morphological norm, and economic importance. In addition, a synopsis is provided for the directions Rollins' own research has taken over the years. Interestingly, Rollins downplays speculation on evolutionary trends and higher-level relationships within the family. Chapter Two, Phytogeography and Endemism, focuses on the phytogeographic patterns manifest in the North American taxa. The various patterns of endemism, distribution, and centers of species diversity are discussed citing numerous specific examples. Chapter Three, Taxonomic Criteria, provides an invaluable overview of the range of variation, taxonomic utility, and limitations of the principal morphological characters utilized in the description and discrimination of crucifer taxa. Discussion is also provided for pertinent cytological and breeding system characteristics of taxonomic significance. These points are amply illustrated by excellent line drawings, photographs of living and pressed plants, and photomicrographs from SEM and traditional light microscopy. Chapter Four, Methods of Treatment, provides the author's rationale for kind and style of information provided in the species treatments, intensity of coverage of native vs alien taxa, format for presentation of distributional information, etc.

The remainder of the text is largely devoted to keys and detailed descriptions of the component taxa. Those keys I have used to identify field-collected specimens proved well written and logical, providing several characters for comparison at most couplets. Following a generalized description of the family and keys to genera, the genera are arranged alphabetically. A general description is provided for each genus, including nomenclatural citation, followed by keys and detailed descriptions of the included taxa, the latter arranged alphabetically when greater than one. Species descriptions, also including nomenclatural citations, are well written, providing ample details of all portions of the plant, but emphasizing those features considered diagnostic. This is followed by general information on flowering period, habitat, range, synonyms, and in many cases, other noteworthy information about the taxa. Line drawings of selected representative taxa are provided for most genera.

An appendix provides a list of new names published in the text. These include 7 new species, one new subspecies, 11 new varieties, and 16 new combinations. The literature cited section, which is exclusive of the nomenclatural citations, runs 10 pages and is a treasure-trove for those seeking additional information on the mustards.

It is difficult to find much fault with this book. Although a number of typographical errors were noted, these are but minor distractions. I found none that seemed to alter the intended meaning of the text, or introduce confusion into the keys or technical descriptions. Perhaps my greatest complaint might be the seemingly arbitrary exclusion of Greenland and the Caribbean islands from coverage. Surely inclusion of these regions would not have added substantially to the complexity of the text, and would have rounded out coverage for an otherwise broadly circumscribed "North America". Nevertheless, Rollins' work is an outstanding piece of taxonomic literature, worthy of a place on the reference shelf of any serious botanist.

—STEVE BOYD, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711.

Remarkable Agaves and Cacti. By PARK S. NOBEL. 1994. Oxford University Press, New York and Oxford. 166 pp. Hardcover and Paperback, \$45, \$22. ISBN 0-19-508414-4, 0-19-508415-2 (pbk).

This "remarkable" book examines three aspects of agaves and cacti. The first part (Chapters 1–3) is a review of past and current uses of these desert and not-so-desert denizens. Agaves provide food, steroids, fodder, ornament, but most importantly beverages and fiber. Already, agaves produce 6% of the world's supply of precursors for corticosteroids. Certain cacti offer fruits and stems used as food, fodder, ornament, hallucinogens and carmine dye. Tells how Sicilians are able to produce larger and sweeter tuna fruits of prickly-pears. The red dye carmine, produced by cochineal scale insects farmed on prickly-pears, is a multi-use stain for arts, clothing, food, and cosmetics. In the 18th century, the value of cochineal dye exported from Mexico was second only to silver. Cheap aniline dyes largely replaced carmine, yet in 1992, 300 tons were produced, mostly in Peru; 80,000 to 130,000 female scale insects are needed to produce one kilogram of dyestuff.

The second part (Chapters 4–7) is a somewhat detailed discussion of the adaptive physiology of agaves and cacti. Explains water, CO₂ and mineral uptake, storage, and minimization of water loss by agaves and cacti. Answers such questions as: Why do roots grow better under or near rocks? How do mycorrhizae enhance growth? How is water stored? Why are prickly-pear pads oriented in certain patterns? How do these plants endure very high and low temperatures? Why do stomates open at night and close during the day? Which is the most efficient photosynthetic pathway—C₃, C₄ or CAM metabolism? How does spacing of plants affect productivity?

The third part (Chapters 7–8) alerts us to the great, useful biomass production potential of certain species of agaves and cacti, more so than nearly any other vascular plant group. The author predicts a bright future for agaves and cacti. The understanding of morphology and physiology should result in new technology that will enhance production and increase profit from farming cacti and agaves.

The author amazingly weaves his tale utilizing a couple handful of species of two diverse groups of plants, monocots and dicots. His engineering background shows through his presentation of form and physiology. This book should intrigue the grower who likes to experiment, the student who wishes to learn basic biology in a challenging way, and the visitor to arid lands to become aware of the invisible activities occurring in the common desert agaves and cacti. The advanced student can learn from Dr. Nobel's many other books and journal articles on these subjects.

—DONALD J. PINKAVA, Department of Botany, Arizona State University, Tempe, AZ 87287-1601.

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A comparative seed germination study of mainland and Channel
Island varieties of *Lotus* section *Syrmatium*.
- MARIA CLAUSS, University of Arizona, work in progress
Causes and consequences of germination cohorts in the desert
winter annual, *Plantago insularis*.
- LENA HILEMAN, San Francisco State University, work in progress
Phylogeny and biogeography of *Arbutus* (Ericaceae), a putative
Madrean-Tethyan disjunct genus.
- MARK FISHBEIN, University of Arizona, completed work
Diversity and temporal change in the effective pollinators of
Asclepias tuberosa.

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MADROÑO

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CALIFORNIA SEAWEEDS COLLECTED BY THE
MALASPINA EXPEDITION, ESPECIALLY *PELVETIA*
(FUCALES, PHAEOPHYCEAE)

PAUL C. SILVA

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ABSTRACT

When the Malaspina expedition visited Monterey in 1791, Tadeáš Haenke collected a few seaweeds which eventually were entrusted to C. A. Agardh at Lund for study. Of 28 species listed by Agardh in 1825 for the entire itinerary of the expedition, 10 were considered new. Two additional new species were described on the basis of Haenke collections by J. G. Agardh in 1847. The provenance and taxonomic placement of some of these new species have remained uncertain. A study of Haenke's collections at Prague (PR) and in the Agardh herbarium at Lund (LD) has clarified much of this uncertainty. The only name in current use for a California seaweed that is affected by the Haenke species is *Pelvetia fastigiata* (J. Agardh) De Toni. Its type was collected on the Monterey Peninsula by David Douglas and published as *Fucus fastigiatus* J. Agardh 1841 (a later homonym), but established nomenclaturally as *Fucodium fastigiatum* J. Agardh 1848. It is referable to forma *gracilis* rather than to the biologically typical form. Haenke collected the latter, which was published as *Fucus compressus* C. Agardh 1824 (also a later homonym), but established nomenclaturally as *Fucodium compressum* J. Agardh 1848. Of the two names with equal priority, *Pelvetia compressa* (J. Agardh) De Toni is herein applied to the biologically typical populations, with *f. gracilis* recognized as a minor variant.

The first scientific expedition to reach California was led by the Count de la Péyrouse (Jean François de Galaup), who visited Monterey during the period 14–24 September 1786 (McKelvey 1955). Whether seaweeds were collected at that time will never be known, since the expedition ended in shipwreck and massacre on Vanikoro, an island of the Santa Cruz group in the southwestern Pacific. The next expedition to set foot on California soil was led by Alessandro Malaspina, an Italian in the employ of Spain, commanding the corvettes *Descubierta* and *Atrevida* (McKelvey 1955). Two botanists were assigned to Malaspina, Luis Née, who was French by birth but Spanish by choice, and Tadeáš Haenke, a Czech. Haenke failed to arrive at Cádiz in time to sail with the expedition, but by taking the next available ship to Montevideo and crossing South America overland, he was able to join his fellow explorers in Chile in 1790. Leaving Valparaíso, the expedition stopped at Callao, Trujillo, Guayaquil, Panamá, and Acapulco. From Acapulco it headed for Alaska, reaching Prince William Sound before turning south to California by way of Nootka Sound, British Columbia. Remaining at Monterey during the period 13–23 September 1791, Malaspina and his ships returned to Acapulco, whence they sailed across the Pacific to Guam

and Manila. On the return voyage, they stopped in New Zealand, New South Wales, and Tonga before anchoring at Callao in 1793. At Callao, Haenke left the expedition, living the remainder of his life mostly in Cochabamba, Bolivia.

Although the Malaspina expedition, unlike its French predecessor, was not ill-fated physically, its potential for scientific accomplishments was left unfulfilled through bureaucratic neglect (Barneby 1963). Née's collections (which, because he had remained in Acapulco, did not include any material from California), together with Malaspina's journal of the expedition, were sequestered in Madrid. Née (1801) described 16 new species of *Quercus*, including *Q. agrifolia* and *Q. lobata* from Monterey (based on specimens brought back to him by ship's officers), but otherwise his collections remained unworked. Haenke's collections were first stored in a warehouse in Cádiz, then sent to Prague, where they lay deteriorating until salvaged by Count Kaspar von Sternberg, one of the founders of the Czech National Museum. Sternberg delegated responsibility for processing the Haenke collections to the Presl brothers, Jan and Karel. The algae were sent to the leading phycologist of that time, Carl Adolf Agardh in Lund. The very small number of specimens of algae indicates that they were collected only incidentally. Agardh (1825) listed 28 species for the entire itinerary of the expedition. Two were said to have come from Chile, but the provenance of the remainder was indicated vaguely, uncertainly, erroneously, or not at all, reflecting the condition of the specimens and their labels at the time that Agardh received them.

During the period 1822–1825 C. Agardh described the following new taxa of algae on the basis of Haenke's collections:

- Cystoseira australis* C. Agardh 1825:8 [no locality given].
C. caudata C. Agardh 1825:8 [no locality given].
C. expansa C. Agardh 1824:290 ["In mari australi"]; 1825:8; *Blossevillea expansa* (C. Agardh) Trevisan 1845:64; *Sirophysalis* (?) *expansa* (C. Agardh) Kützing 1849:603; *Gongolaria expansa* (C. Agardh) Kuntze 1891:895; *Cystoseira osmundacea* (Turner) C. Agardh f. *expansa* (C. Agardh) Setch. in Collins et al. 1901: no. XLVIII.
C. geminata C. Agardh 1824:286 ["In mari australi"]; *Cystophyllum geminatum* (C. Agardh) J. Agardh 1848:232; *Sirophysalis geminata* (C. Agardh) Kützing 1849:602; *Cystoseira crassipes* (Turner) C. Agardh subsp. *geminata* (C. Agardh) Yu.E. Petrov 1966: 99.
C. tuberculata C. Agardh 1824:290 ["In mari australi"]; *Blossevillea tuberculata* (C. Agardh) Trevisan 1845:66; *Gongolaria tuberculata* (C. Agardh) Kuntze 1891:895.
Fucus compressus C. Agardh 1824:279 ["In mari australi"]; 1825:

- 9; *Fucodium compressum* J. Agardh 1848:204; *Ascophylla compressa* (J. Agardh) Kuntze 1891:884; *Pelvetia* (?) *compressa* (J. Agardh) De Toni 1895:216.
- Grateloupia hystrix* C. Agardh 1822:223 [“ad caput bonae spei?”]; 1825:9; *Chaetangium hystrix* (C. Agardh) Kützing 1849:793; *Gigartina hystrix* (C. Agardh) Setchell & Gardner 1933:295.
- G. ornata* (L.) C. Agardh [var.] β *crispa* C. Agardh 1822:223 [no locality given]; 1825:9; *Chaetangium crispum* (C. Agardh) J. Agardh 1849:89; *Rissoella crispa* (C. Agardh) J. Agardh 1851:242.
- Ptilota densa* C. Agardh 1822:387 [“Ad caput bonae spei”]; 1825:11; *Neoptilota densa* (C. Agardh) Kylin 1956:393.
- Sphaerococcus canaliculatus* C. Agardh 1822:260 [“Ad litora chilensis”]; 1825:10; *Chondrus canaliculatus* (C. Agardh) Greville 1830:lv; *Gigartina chilensis* D.H. Kim 1976:39.
- S. punctatus* C. Agardh 1822:332 [“In mari Australi, ad oras Chilenses”]; 1825:10.
- S. sternbergii* C. Agardh 1822:275 [“In mari Australi”]; 1825:10; *Gelidium sternbergii* (C. Agardh) Greville 1830:lviii; *Grateloupia sternbergii* (C. Agardh) J. Agardh 1847:10; *Prionitis sternbergii* (C. Agardh) J. Agardh 1851:190; *Zanardinula sternbergii* (C. Agardh) De Toni f. 1936:[8].

In addition, Jacob Georg Agardh described two new species based on specimens that he found in his father’s herbarium without a collector’s name, but which Kylin (1941:12, 16) strongly suspected (in one case) or was certain (in another case) of having been collected by Haenke. These two species are:

- Callophyllis australis* J. Agardh 1847:13, adnot. [“Mare australe”], non *C. australis* (Harv.) Kütz.; *C. obtusifolia* J. Agardh 1851:297.
- Phyllotylus australis* J. Agardh 1847:9, adnot. [“Mar. Austral.”]; *Prionitis australis* (J. Agardh) J. Agardh 1851:188.

Eventually, as the marine algal flora of California became known, it was possible to infer that certain of Haenke’s collections were from Monterey. *Cystoseira expansa* was associated by J. Agardh (1848:226) with *C. douglasii* Harvey (1841:407), based on a collection from Monterey. This species, in turn, was considered a phenotypic variant of *C. osmundacea* by Setchell (in Collins et al. 1901: no. XLVIII). The latter species, which was described as *Fucus osmundaceus* by Turner (1809:91, pl. 105), was based on a collection made by Menzies at Trinidad, Humboldt Co., Calif., in 1793 during the Vancouver Expedition.

Kylin (1941) thought it probable that *Ptilota densa*, *Callophyllis*

obtusifolia, and *Phyllotylus australis* came from Monterey, but that *Grateloupia sternbergii* came from Acapulco. Parkinson (1980), after examining a specimen of *Grateloupia hystrix* housed at Prague, concluded that it was a cystocarpic scrap of a *Mastocarpus* (Petrocelidaceae, Gigartinales), probably *M. papillatus* (C. Agardh) Kütz. This species is common at Monterey. The remainder of the Haenke species have remained enigmatic.

In an attempt to explain these enigmas, I made a special effort to find Haenke's collections in the Agardh herbarium at Lund during a visit in 1975. A visit to the National Museum in Prague was scheduled for later that year, but was canceled because of my illness. In 1981, Dr. Jiří Soják and Miss Blanka Deylová of the National Museum in Prague kindly sent me, on loan, material representing four of the Haenke taxa, namely, *Cystoseira australis*, *Fucus compressus*, *Grateloupia ornata* [var.] β *crispa*, and *Ptilota densa*. The application of the following names has been determined.

Cystoseira australis

This name has been completely overlooked. It occurs neither in J. Agardh's monographic treatment of the brown algae (1848) nor in De Toni's *Sylloge algarum* (1895). C. Agardh described filiform branches, here and there vesiculose, ending in pinnate, torulose, filiform receptacles. The specimens at Prague (Fig. 1) and Lund show that Agardh chose the correct genus, even though he had only the tip of the fertile portion of a frond. Both specimens are accompanied by a small handwritten slip, "Regismontanae," which obviously is a translation into Latin of "Monterey." Fortified by this knowledge of the provenance of these specimens, I can say with certainty that they are referable to *Cystoseira osmundacea*.

Cystoseira tuberculata

The description of this species does not differ substantially from that of *C. australis*. It seems certain that Agardh wrote the manuscript for his contribution to Presl's book (C. Agardh 1825) prior to writing that for his own *Systema algarum* (1824) and that he changed his mind regarding the epithet of the species. Support for this reasoning is given by the specimen of *C. australis* in Lund (Agardh herbarium no. 985), which has a second label, bearing the name *Cystoseira australis*, but with the epithet crossed out and replaced by *tuberculata*. Because of the inverted sequence of publication of the two names, *C. australis* turns out to be an illegitimate substitute for *C. tuberculata*, which then becomes a taxonomic synonym of *C. osmundacea*.

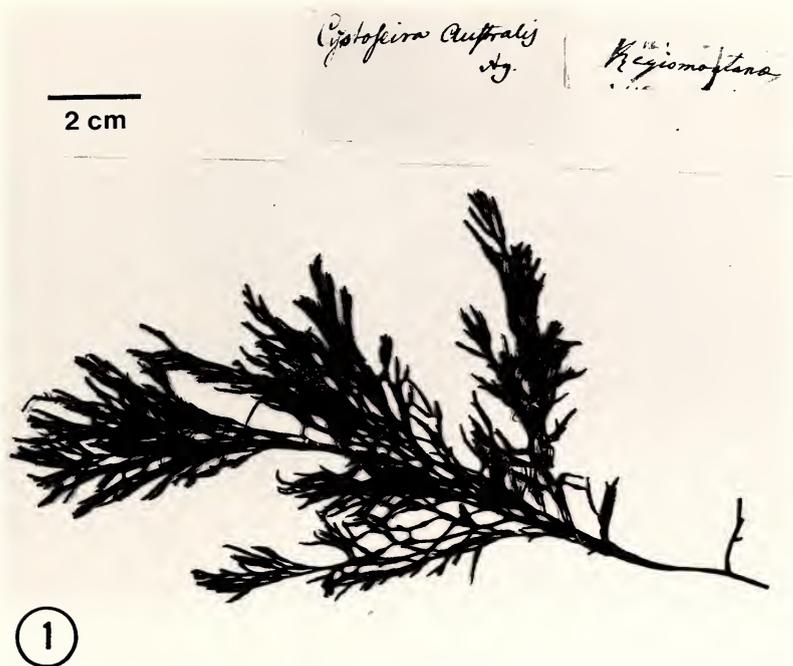


FIG. 1. *Cystoseira australis* C. Agardh. Isotype (PR).

Cystoseira caudata

The fact that specimens bearing this name were not found either at Lund or at Prague coupled with my newly found knowledge of the *C. australis*-*C. tuberculata* pair of names led to the discovery that an identical relationship existed between *C. caudata* and *C. geminata*. The two descriptions are essentially the same. Again, *caudata* was the first epithet to be conceived, but the second to be published. Specimens of *C. geminata* in the Agardh herbarium (no. 867) are labeled without an indication of change of epithet. The lack of a label indicating "Regismontanae" is in agreement with the fact that *C. geminata* does not occur at Monterey. Haenke probably made his collection at Nootka Sound on the west coast of Vancouver Island.

Grateloupia ornata [var.] β *crispa*

Whereas *Grateloupia ornata* sensu C. Agardh (not *Fucus ornatus* L., which is referable to *Suhria* in the Gelidiaceae) is representative of *Nothogenia erinacea* (Turner) Parkinson (Papenfuss 1952; Par-



FIG. 2. *Grateloupia ornata* [var.] β *crispa* C. Agardh. Isotype (PR).

kinson 1983:609), [var.] β *crispa* is quite different. No annotation "Regismontanae" accompanies the specimen at Prague (Fig. 2), suggesting that Monterey was not the provenance. The specimen, which is abundantly spermatangial, does not agree completely with any California seaweed that I know. Its anatomy, general habit, and papillae suggest *Mastocarpus*.

Ptilota densa

In the protologue is written "Ad caput bonae spei. Specimina dederunt Desfontaines, & Com. de Sternberg". No specimen of this species from the Cape of Good Hope is currently in the Agardh herbarium. Noting, however, that a specimen of this species in the Agardh herbarium (no. 20101) bears the label "e coll. Haenkeana," Kylin (1941:99) assumed that it came from the Monterey Peninsula. That Kylin was correct is borne out by the discovery that the specimen at Prague is annotated "Regismontanae." The Prague specimen of *P. densa*, but not the specimen in the Agardh herbarium, was accompanied by a small piece of *Neoptilota hypnoides* (Harv.) Kylin.

Fucus compressus

Six morphologically indistinguishable specimens, indicated as having been collected by Haenke at "Regismontanae," are available

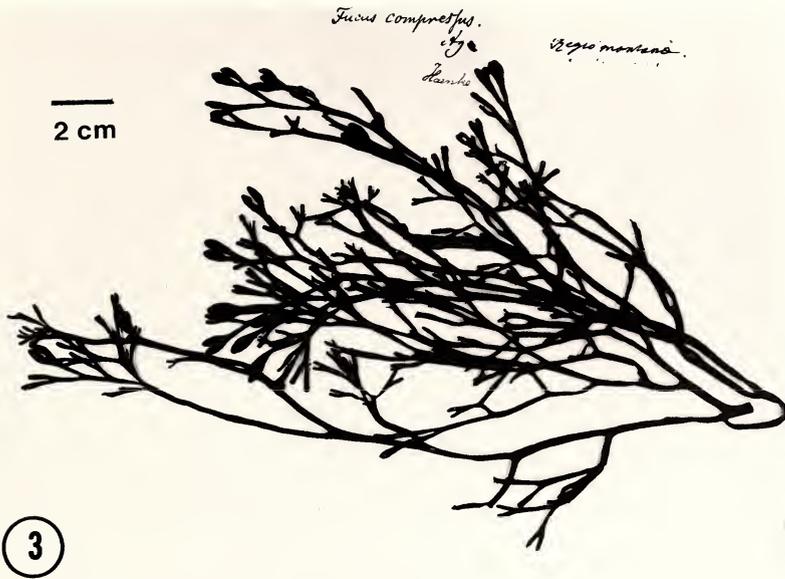


FIG. 3. *Fucus compressus* C. Agardh. Isotype (PR).

for this species. Five are in the Agardh herbarium, of which four are mounted on one sheet (no. 00093) and one is loose in a folder (no. 00094). The sixth is in Prague (Fig. 3). These specimens are in good condition and are unmistakably representative of the species currently called *Pelvetia fastigiata* (J. Agardh) De Toni. In view of the seniority of *Fucus compressus* C. Agardh (1824) over *F. fastigiatus* J. Agardh (1841), the intended basionym of *P. fastigiata*, it would seem that the correct name for this species would be *P. compressa*. The situation is complicated, however, by the fact that both of the intended basionyms are later homonyms (of *F. compressus* Esper 1799 and *F. fastigiatus* L. 1753, respectively), and hence are illegitimate and not priorable. The earliest legitimate name for each species was provided by J. Agardh (1848), who transferred both *F. compressus* and *F. fastigiatus* into his new genus *Fucodium*. Considering that the two basionyms (*Fucodium compressum* and *F. fastigiatum*) have the same date, it is appropriate to weigh other factors in deciding which name should be used.

At some time between 1831 and 1840, John Lindley, Professor of Botany at University College, London, and Assistant Secretary of the Horticultural Society of London, sent to J. Agardh some specimens collected in California in 1831 by David Douglas, a young botanical explorer in the service of the Horticultural Society. These



FIG. 4. *Fucus fastigiatus* J. Agardh. Holotype (Agardh herbarium no. 00066 in LD).

specimens were described as a new species, *Fucus fastigiatus*, by J. Agardh (1841:3), who noted that they were similar to those of *F. compressus*, but smaller and more fastigate. In 1848 J. Agardh erected the genus *Fucodium* to encompass several previously described genera of Fucaceae that differed from *Fucus* in not having a midrib. The subsumed genera, each of which was treated as a section, were *Xiphophora* Mont. 1842, *Pelvetia* Decne. & Thur. 1845, *Pycnophycus* Kütz. 1843 (now known as *Bifurcaria* Stackh. 1809), and *Ozothallia* Decne. & Thur. 1845 (now known as *Ascophyllum* Stackh. 1809).

Fucodium sect. *Pelvetia* comprised three species: *F. canaliculatum* (L.) J. Agardh (*Fucus canaliculatus* L.), the type of *Pelvetia*; *F. compressum* J. Agardh; and *F. fastigiatum* J. Agardh. After *Pelvetia* had been reestablished at the generic level by various workers in the last half of the 19th century, De Toni (1895:214) brought all the species together for the first time.

Setchell's notebooks (in UC) do not indicate that he saw either the Haenke collection or the Douglas collection when he visited the Agardh herbarium in 1903. In 1957, however, while studying types of Pacific coast algae in the Agardh herbarium, I discovered that the Douglas collection (no. 00066) (Fig. 4) is representative, not of typ-

ical *P. fastigiata*, but of *P. fastigiata* f. *gracilis*, the slender, profusely branched form described by Setchell and Gardner (in Gardner 1917:386, based on *Gardner 2997* from Pebble Beach, Carmel Bay). It can safely be assumed that the Douglas collection was made at Pebble Beach, the only locality on the Monterey Peninsula where f. *gracilis* is known to occur.

Were it not for the existence of *Fucodium compressum*, we would be in the awkward position of having to apply the name *Pelvetia fastigiata* f. *fastigiata* to f. *gracilis*, thus creating confusion and at the same time leaving the common robust form without an infra-specific epithet. By applying *Fucodium compressum* to the species as a whole, *gracilis* can be retained as the epithet for the slender, profusely branched form from Pebble Beach. Of the two competing names for this species, therefore, I choose *Pelvetia compressa* (J. Agardh) De Toni, comprising *P. compressa* f. *compressa* and *P. compressa* f. *gracilis* (Setch. & N.L. Gardner) Silva, comb. nov. (basionym = *P. fastigiata* f. *gracilis* Setch. & N.L. Gardner in Gardner 1917:386).

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MONOCOTYLEDONOUS GEOPHYTES IN THE CALIFORNIA FLORA

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ABSTRACT

Monocotyledonous geophytes form one of the most showy elements of the California spring flora, particularly in open woodlands and grasslands, and post-fire chaparral slopes. There are 262 species of such geophytes in California, comprising 5.4% of the total flora of native vascular plants. Speciation has been particularly active in the genera *Allium* and *Calochortus*, with 47 and 43 species, respectively. The majority of these species are endemic within California or the California Floristic Province in open woodland and shrubland habitats. These mediterranean-type communities are the typical habitats of 55% of California geophytes, and these species largely possess bulbs or corms as storage organs. Edaphic endemism has been an important component of speciation, with at least 35 species associated or obligately occurring on serpentine soils. Dry conifer forests and associated meadows are the characteristic habitats of 23% of the geophyte flora, followed by 13% in wet conifer forests and adjacent meadows. Forest understory geophytes commonly possess rhizomes or fleshy roots as storage organs. Only 8% of California geophytes are typical desert taxa, with the Mojave and Sonoran Desert regions particularly poor in species. Declining proportion of geophytes with increasing aridity is associated not just with the geophytes themselves, but with environmental conditions less favorable to the diversity of monocots broadly. More than one fourth of these geophytes are currently listed as rare or endangered. The overall diversity of geophytes within California is comparable to their diversity in similar climate regimes in Chile and the western Mediterranean Basin. The mediterranean-type ecosystems of Western Australia and South Africa, however, contain a far richer diversity of geophytes.

Geophytes are those vascular plants that survive unfavorable periods for growth by dying back to underground storage organs such as rhizomes, tubers, corms, or bulbs (Raunkiaer 1934; Rees 1989). While there are small numbers of geophytes with underground storage organs among dicots, this life-form is largely restricted to petaloid monocots. New aerial shoots arise from these storage organs when favorable conditions return, usually annually (Dafni et al. 1981a). Although geophytes may be present in many ecological habitats throughout the world, nowhere are they more diverse than in mediterranean-type ecosystems (Raunkiaer 1934). Such ecosystems, here defined broadly to include not only evergreen shrublands but also montane and desert habitats, have unique climatic conditions of winter rainfall, moderate winter temperatures and dry summers. These conditions occur in the five regions of the world (California,

Chile, the Mediterranean Basin, the Cape Region of South Africa, and Western and South Australia), and have been associated with dramatic evolutionary speciation within many groups of monocotyledonous geophytes.

In California, monocotyledonous geophytes form characteristic and showy components of the ephemeral spring flora in open woodlands, grasslands, wet meadows, and post-burn areas of chaparral as well as providing a significant component of the herbaceous flora in the shaded understory of coniferous forests. Despite their notable presence in such communities, there has been surprisingly little ecological study of this life-form and the ecological strategies used by geophytes to maintain their ecological success. Collaborative efforts have now been initiated by researchers from all five mediterranean-climate regions to document the biogeographic and ecological distribution of monocotyledonous geophytes in these unique areas, and to better understand similarities and differences in patterns in the biodiversity of this interesting group. This paper represents an initial contribution of study to address biogeographic patterns of species diversity of monocotyledonous geophytes in the California flora, and to explore changes in relative geophyte diversity across ecological gradients within the state.

MATERIALS AND METHODS

The species diversity of monocotyledonous geophytes within the California flora was extracted and analyzed from data presented by Hickman (1993). All species in the Liliaceae, Iridaceae, and Orchidaceae (sensu Hickman 1993), with the exclusion of species of *Agave*, *Nolina*, and *Yucca*, were identified as geophytes. In the classification system of Dahlgren et al. (1985) which is used here at the family and ordinal levels in this paper, these California geophytes are divided among 14 monocot families. Only native species were considered in calculating absolute and relative species diversity.

Geographic and ecological patterns of species distribution were largely based on the floristic regions of California delineated by Hickman (1993), while ecological distributions were determined by establishing the most characteristic habitat for each species based on data in Hickman (1993), Munz (1959), and personal observations.

The biodiversity of monocotyledonous geophytes in selected areas of other mediterranean-climate regions was extracted from the literature in a manner parallel to that used for the California species. These references are described in the discussion.

RESULTS

Phylogenetic diversity. The monocotyledonous geophyte flora of California includes 262 species (sensu Hickman 1993), divided into

five orders, fourteen families, and 44 genera (sensu Dahlgren et al. 1985; Table 1). These species comprise 5.4% of the native vascular plant flora of California.

Two genera of geophytes in California are particularly notable for their high level of diversity. The largest of these is *Allium* (Alliaceae), whose 47 species make up nearly 20% of the total geophyte flora of the state (Hickman 1993). Although this large genus is centered in distribution in the Old World (Raven and Axelrod 1978), the California species represent an important secondary area of evolution. Twenty-four of these species are endemic to the state. The Alliaceae also provide a major component of geophyte diversity for California with the related *Bloomeria*, *Brodiaea*, *Dichelostemma*, *Muilla*, and *Triteleia* totaling another 37 species. Thirty-two of these are endemic. Together they form the Tribe Brodiaeinae whose center of diversity lies in the California Floristic Province.

The second large genus of geophytes in California is *Calochortus* (Calochortaceae) with 43 species in the state. This genus has its center of diversity in California and adjacent Southwestern woodlands and shrublands (Ownbey 1940; Fiedler 1986). Thirty-five species (81%) are endemic to California or the California Floristic Province.

The Liliaceae (sensu stricto) also form an important component of the geophyte diversity of California with 43 species divided among *Erythronium* (13 species), *Fritillaria* (18 species), and *Lilium* (12 species). Endemism is high in this group with 86% of the species restricted to the California floristic province. While many of these geophytes are characteristic of open woodlands and meadows, shade-adapted species are also present and the group overall shows much less diversification into semi-arid habitats than either the Alliaceae or *Calochortus*.

Shade adaptation in relatively cool, mesic habitats is characteristic of a number of groups of geophytes in California, but these taxa have had little tendency to speciate within the state. These shade adapted taxa include the Convallariaceae (*Maianthemum* and *Smilacina*), Uvulariaceae (*Clintonia*, *Disporum*, *Scoliopus*, and *Streptopus*), and Melanthiaceae (*Stenanthium* and *Tofieldia*). Only one of the ten species in these genera is endemic to the California floristic province.

Orchids, largely consisting of shade-adapted species in California, are poor in diversity. Eleven genera and 30 species of orchids are present, forming just 11% of the geophytes. Only three of these species (10%) are endemic to the California floristic province. Orchid taxa in California are largely confined to coniferous forests of the Sierra Nevada and the moist northwestern coast, with the exception of *Piperia*. Saprophytic orchids are notably present in these forests with species of *Cephalanthera*, *Goodyera*, and *Corallorhiza*.

TABLE 1. DIVERSITY (NUMBER OF SPECIES) OF MONOCOTYLEDIOUS GEOPHYTES IN CALIFORNIA. Species level taxonomy from Hickman (1993) and family classification from Dahlgren et al. (1985).

ASPARAGALES	
Alliaceae	
<i>Allium</i>	47
<i>Androstephium</i>	1
<i>Bloomeria</i>	2
<i>Brodiaea</i>	14
<i>Dichelostemma</i>	5
<i>Muilla</i>	4
<i>Triteleia</i>	12
Amaryllidaceae	
<i>Leucocrinum</i>	1
Hyacinthaceae	
<i>Camassia</i>	1
<i>Chlorogalum</i>	5
<i>Hastingsia</i>	2
Tecophilaceae	
<i>Odontostomium</i>	1
DIOSCORIALES	
Smilacaceae	
<i>Smilax</i>	2
Trilliaceae	
<i>Trillium</i>	5
LILIALES	
Calochortaceae	
<i>Calochortus</i>	43
Convallariaceae	
<i>Maianthemum</i>	1
<i>Smilacina</i>	2
Funkiaceae	
<i>Hesperocallis</i>	1
Iridaceae	
<i>Iris</i>	13
<i>Sisyrinchium</i>	7
Liliaceae	
<i>Erythronium</i>	13
<i>Fritillaria</i>	18
<i>Lilium</i>	12
<i>Nartheceum</i>	1
Uvulariaceae	
<i>Clintonia</i>	2
<i>Disporum</i>	2
<i>Scoliopus</i>	1
<i>Streptopus</i>	1
MELIANTHALES	
Melianthaceae	
<i>Stenanthium</i>	1
<i>Tofieldia</i>	1
<i>Veratrum</i>	4
<i>Xerophyllum</i>	1
<i>Zigadenus</i>	6

TABLE 1. CONTINUED

ORCHIDALES	
Orchidaceae	
<i>Calypso</i>	1
<i>Cephalanthera</i>	1
<i>Corallorhiza</i>	4
<i>Cypripedium</i>	3
<i>Epipactis</i>	1
<i>Goodyera</i>	1
<i>Listera</i>	3
<i>Malaxis</i>	1
<i>Piperia</i>	9
<i>Platanthera</i>	4
<i>Spiranthes</i>	2

The few orchids in chaparral and desert regions are confined to mesic microsites.

Storage organs. Bulbs, corms, rhizomes and fleshy roots are all present as below-ground storage organs among monocotyledonous geophytes in the California flora. The nature of these storage organs frequently, but not invariably, follows phylogenetic lines (Table 2).

TABLE 2. PHYLOGENETIC DISTRIBUTION OF BELOW-GROUND STORAGE ORGANS IN CALIFORNIA MONOCOTYLEDONOUS GEOPHYTES.

	Total	Bulb	Corm	Rhizome	Fleshy root
Asparagales					
Alliaceae	85	47	38		
Amaryllidaceae	1				1
Hyacinthaceae	8	8			
Tecophilaceae	1		1		
Dioscoriales					
Smilacaceae	2			2	
Trilliaceae	5			5	
Liliales					
Calochortaceae	43	43			
Convallariaceae	3			3	
Funkiaceae	1	1			
Iridaceae	13			20	
Liliaceae	44	43		1	
Uvulariaceae	6			6	
Melianthales					
Melanthaceae	13	7		6	
Orchidales					
Orchidaceae	30				30

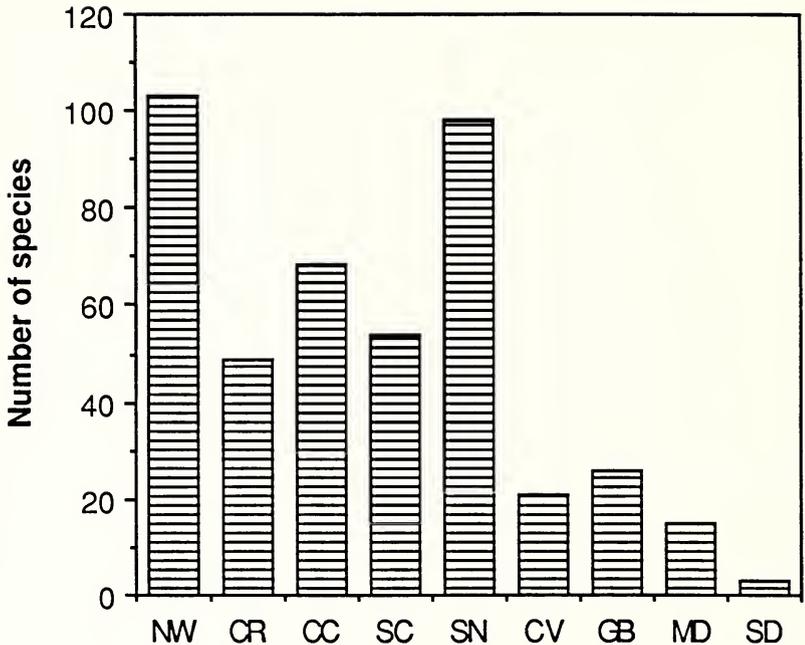


FIG. 1. Relative phylogeographic distribution of monocotyledonous geophytes within California, based on distributions described by Hickman (1993): northwest coast (NW), Cascade region (CR), central coast (CC), south coast and transverse ranges (SC), Sierra Nevada (SN), Central Valley (CV), Great Basin (GB), Mojave Desert (MD), and Sonoran Desert (SD).

Bulbs represent the most common form of organ with 149 species or 57% of these geophytes. The genus *Allium* in the Alliaceae, *Calochortus*, and 43 of 44 species of Liliaceae comprise the bulk of these taxa. Corms occur in 39 species (15%), made up of the Alliaceae outside of *Allium* and *Odontostomium* in the Tecophilaceae. Rhizomes are the characteristic storage organ in the Iridaceae and in a variety of geophytes which are characteristic of forest understory habitats. These latter include the Smilacaceae, Trilliaceae, Convallariaceae, Uvulariaceae, and Melianthaceae. Orchids and *Leucocrinum* in the Amaryllidaceae have varying types of fleshy or tuberous root systems.

Biogeographic patterns. The biogeographic distribution of monocotyledonous geophytes within California shows that the highest diversity of species occurs within the northwest coastal region (Hickman 1993) where 103 species are found, 39.6% of the total geophyte flora (Fig. 1). Second in diversity is the Sierra Nevada region whose foothill woodlands, shrublands, and coniferous forests support 98

species (37.7%). Moving southward along the coast, alpha diversity drops to 68 species in the central coast region, and then to 54 species along the south coast and associated mountain ranges.

Desert regions of California are remarkably low in geophyte diversity, with only 26 species in Great Basin communities, 15 species in the Mojave Desert flora, and just three species in the Sonoran Desert of California (Fig. 1). Such low diversity is not simply a function of a Mediterranean climate influence. The Sonoran Desert flora overall, largely occurring in summer rainfall regions, has just 24 species of geophytes, less than 1% of the total flora (Shreve and Wiggins 1964). Despite such low diversity, two endemic genera of geophytes are present. These genera are both members of the Alliaceae, *Androstephium* and *Triteleopsis* whose Baja California and Arizona desert distribution just misses California. This decline in geophyte diversity can also be seen in the flora of the Baja California peninsula (Wiggins 1980). Only 38 geophytes are present among a flora 2705 vascular plant species. Of these few geophytes, 33 are restricted in distribution to either the mediterranean-climate region of northwestern Baja California or subtropical communities of the Cape Region, leaving just five species in desert habitats.

The greatest ecological amplitude of geophyte diversity within California lies in the mediterranean-climate woodlands and chaparral of the state where 55.2% of the species are centered in their distribution (Fig. 2). Geophytes with bulbs or corms are most prominently present in these habitats. It is in woodlands and chaparral where *Allium* and *Calochortus* have developed much of their adaptive radiation. While mature chaparral stands support few herbaceous species, post-fire successional communities are rich in geophytes.

Edaphic endemism has played an important role in promoting speciation. Serpentine soils of California are notable centers of endemism for geophytes as well as other groups of ephemerals. Thirty-five California geophytes are associated with serpentine soils, many obligately (Kruckeberg 1984, Hickman 1993). Most notable of these are *Allium* (13 species), *Calochortus* (5 species), *Fritillaria* (5 species), *Brodiaea* (3 species), *Chlorogalum* (2 species), and *Erythronium* (2 species).

Dry conifer forests and associated meadows are the characteristic habitats of 23.4% of California geophytes, followed by wet conifer forests and adjacent meadows with 13.0% (Fig. 2). Forest understory habitats, as described above, typically support widespread species with rhizomes as storage organs.

Only 8.4% of California geophytes are characteristic of desert ecosystems, and the majority of these are from Great Basin communities. Very few geophytes penetrate into warm desert habitats in California. Endemic desert taxa such as *Hesperocallis undulata* or

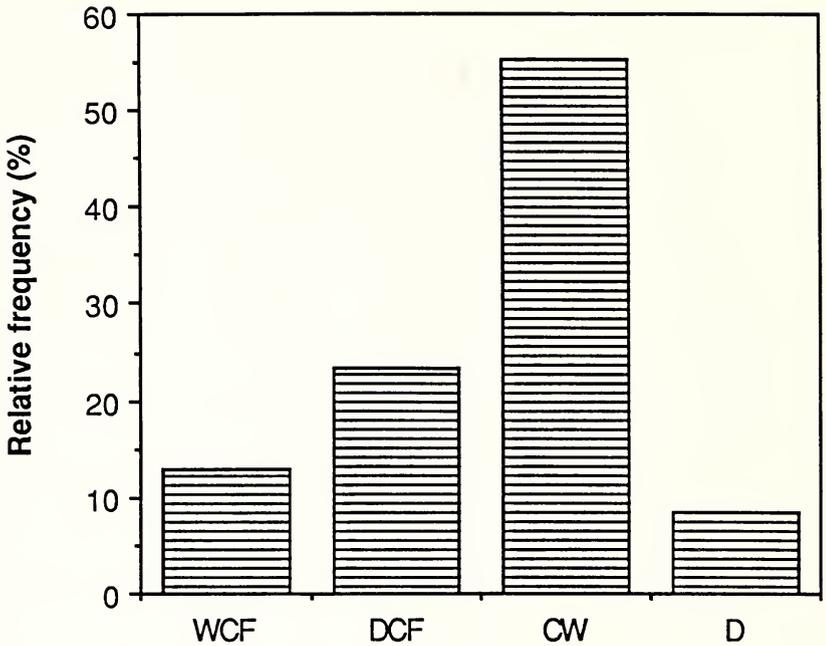


FIG. 2. Relative ecological distribution of monocotyledonous geophytes within California: wet conifer forests and associated meadows (WCF), dry conifer forests and associated meadows (DCF), chaparral and woodland (CW), and desert (D). Wide-spread species may be included in multiple communities.

Zigadenus brevibracteatus, however, may be locally abundant in sandy soils.

Rare and endangered species. Large numbers of monocotyledonous geophytes in California are classified as rare or endangered species. Recent summaries of the rare and endangered California flora include 66 species and 102 taxa of monocotyledonous geophytes (Skinner and Pavlik 1994). This is a higher proportion of such species and taxa than for the California flora as a whole. Habitat destruction is the most important factor in this threat to geophytes, although commercial collecting may be a problem with some taxa. One species, *Calochortus monanthus* from along the Shasta River is thought to now be extinct.

DISCUSSION

An analysis of the diversity of geophytes within regional floras of California can help interpret environmental correlates of relative diversity in this growth form. The highest relative importance of geophytes within regional floras of the state are present in cooler,

mesic areas of the north coast and interior where geophytes make up more than 5% of the total vascular plant flora (Table 3). This level is similar to the figure of 5.4% geophytes in the flora statewide. Increasing aridity along the coast south of the Santa Cruz Mountains is associated with a slow reduction in relative diversity of geophytes from 3.8% in San Luis Obispo County to 2.8% in the Santa Ana Mountains. This figure drops even further in the arid White Mountains (1.7%) and Eastern Mojave Desert (1.4%). The Sonoran Desert flora has less than 1% geophytes.

One correlate in these gradients of reduced geophyte diversity is a parallel decline in the relative diversity of Monocotyledonae. Monocots form 21–22% of the total vascular plant flora in the mesic Trinity Alps, north coast, and Santa Cruz Mountains, but this figure drops to 15–17% along the central and south coast of the state, and finally to just 12% in the Eastern Mojave Desert (Table 3). The relative proportion of monocotyledonous geophytes to all monocots drops only slightly along this same coastal gradient, but declines abruptly for the arid White Mountains and Eastern Mojave Desert (Table 3). This pattern suggests that while increasing aridity is associated with a decline in geophytes diversity in California, at least a portion of this decline is associated with environmental conditions that are unfavorable to monocots overall. While some monocot groups such as grasses do very well in arid habitats, many other groups are absent or poorly represented. Extreme and unpredictable drought is clearly involved in this selection against many phylogenetic and life-form groups.

There are lessons to be learned from comparing the pattern of monocotyledonous geophyte diversity in California with that of other regions of the world with mediterranean-type ecosystems. The floras of California and Chile show very similar patterns of geophyte diversity, with 5.4% of the flora as geophytes in both areas (Table 4). Gradients of diversity within the two floras, however, are somewhat different. Chile has its highest diversity of monocotyledonous geophytes in the mediterranean-climate regions of central Chile, with numbers of these geophytes dropping sharply to the north and south with drier and to the south with cooler, wetter climates (Alicia Hoffmann and Adriana Hoffmann, unpublished data). It is noteworthy that Chile possessing some of its highest relative levels of geophyte diversity in the arid Norte Chico region at the transition from mediterranean to desert environments (Armesto and Vidiella 1993). Orchids are more diverse in Chile than in California and may occur in quite xeric environments, while Chile has a lower diversity of shade-adapted geophytes in evergreen forest understories.

The western Mediterranean Basin possesses levels of geophyte diversity comparable to that of California and Chile. The flora of Alicante Province in Spain has 4.2% geophytes (Rigual 1984). Ge-

TABLE 3. ABSOLUTE AND RELATIVE DIVERSITY OF GEOPHYTES IN REGIONAL FLORAS OF CALIFORNIA. These floras are arranged roughly in a gradient from more mesic to more arid regions. Data extracted for native species from Ferlatte (1974), Smith and Wheeler (1990-1991), Howell (1970), Thomas (1961), Hoover (1970), Smith (1976), Lathrop and Thorne (1978), Wallace (1985), Raven et al. (1986), Beauchamp (1986), Lloyd and Mitchell (1973), and Thorne et al. (1981).

Region	Species total	Monocot	Geophyte	Orchid	Monocot (%)	Geophyte (%)	Orchid (%)	Geo/monocot (%)
Trinity Alps	571	121	32	11	21.2	5.6	1.9	26.4
Mendocino County	1784	—	96	19	—	5.4	1.1	—
Marin County	1004	229	51	13	22.9	5.1	1.3	22.2
Santa Cruz Mountains	1246	270	60	11	21.6	4.8	0.9	22.2
San Luis Obispo County	1287	—	49	5	—	3.8	0.4	—
Santa Barbara County	1390	211	45	2	15.2	3.2	0.01	21.3
Santa Ana Mountains	668	116	24	2	17.4	3.6	0.001	20.6
Channel Islands	621	96	18	2	14.9	2.8	0.03	19.6
Santa Monica Mountains	644	96	18	2	14.9	2.8	0.03	18.8
San Diego County	1516	229	45	7	15.1	3.0	0.05	19.6
White Mountains	763	105	13	0	13.8	1.7	0	12.4
Eastern Mojave Desert	717	85	10	0	11.9	1.4	0	11.8

TABLE 4. ABSOLUTE AND RELATIVE DIVERSITY OF GEOPHYTES IN FLORAS FROM THE FIVE REGIONS WITH MEDITERRANEAN-TYPE ECOSYSTEMS. Data for native species from Hickman (1993), Marticorena (1990), Rigual (1984), Marchant et al. (1984), and Boucher (1977).

Region	Species total	Monocot	Geophyte	Orchid	Monocot (%)	Geophyte (%)	Orchid (%)	Geo/monocot (%)
California								
Total flora	4844	823	262	30	18.2	5.4	0.6	31.7
Chile								
Total flora	4877	892	261	46	18.3	5.4	0.9	29.3
Western Mediterranean								
Alicante	1582	270	67	17	17.1	4.2	1.1	21.1
Western Australia								
Perth region	1510	462	190	92	30.6	12.6	6.1	41.1
South Africa								
Cape Hangklip	1407	460	216	55	32.7	15.4	3.9	47.0

ophyte diversity increases to the east, however. Raunkier (1934) reported high levels of geophytes diversity for Cyrenaica in Libya (8%), Ferrara in Italy (15%), and Samos Island in Greece (11%). Geophyte diversity is also rich in Turkey and Israel (Dafni et al. 1981b). As in California, geophytes diversity drops sharply in the mediterranean-climate deserts of Israel.

Remarkable levels of geophyte diversity are well documented for the mediterranean-climate floras of Western Australia and the Cape Region of South Africa. The flora of the Perth region in Western Australia possesses 12.6% geophytes, with nearly half of these orchids (Marchant et al 1987; Table 4). No other mediterranean flora exhibits such high diversity of orchids. It is noteworthy, however, that geophytes with bulbs are relatively rare in this flora (Pate and Dixon 1982). A regional flora for Cape Hangklip near Cape Town, South Africa, included 15.4% geophytes (Boucher 1977), while geophytes made up an astounding 24% and 35%, respectively, of the floras of the Stellenbosch Flats and Cape Flats (Boucher and Moll 1981). The Iridaceae, a relatively minor component of most monocot floras in other parts of the world, shows astounding diversity in the the Cape Floristic Province with 612 species (Bond and Goldblatt 1984). One genus of dicotyledonous geophytes, *Oxalis* (Oxalidaceae), is the largest single genus of geophytes in the Cape Flora with 129 species (Bond and Goldblatt 1984).

A notable characteristic of both the Western Australian and South African floras is the high diversity of geophytes relative to other monocots, and monocots relative to all vascular plants (Table 4). More than 40% of the monocots in these two floras are geophytes, significantly higher than the proportion present in the other three mediterranean-climate regions. Furthermore, monocots make up more than 30% of these floras, compared to only 17–18% in the other three regions.

While it is tempting to suggest that declining diversity of California geophytes with increasing aridity is a function of both elimination of shade habitats and increasing drought stress, the answer may not be so simple. Both the Mediterranean Basin and Western Australia share the California characteristic of a sharp decline in geophyte abundance moving into desert regions (Ozenda 1983; Jesop 1981). Most remarkable of all is South Africa where spectacularly high diversity of geophytes occurs throughout the succulent karoo. Goegap Nature Reserve in Namaqualand possesses 16.3% geophytes in its rich flora (van Rooyen et al. 1990). Relatively low interannual variation in rainfall patterns in the succulent karoo may lie at the heart of these differential patterns of geophyte abundance in arid regions. Predictable rainfall may have allowed geophytes to adapt their phenological cycles to soil moisture availability in a man-

ner impossible in the highly unpredictable precipitation regimes of other mediterranean desert regions.

Because ecological strategies and adaptations of the geophyte life-form remain poorly studied, it is difficult to formulate clear answers to questions of species diversity, abundance, and ecological strategies of adaptation in this group. The apparent correlation of storage organ type and habitat suggests that individual groups of geophytes may have highly adapted modes of ecophysiological adaptation in their modes of carbohydrate storage and growth phenology. New studies will no doubt do much to resolve such questions, and such investigations should surely take advantage of the natural ecological experiments presented by geophyte distributions in the broad mediterranean-climate regions of the world. The California Floristic Province provides excellent opportunities for studies of the ecological strategies and patterns of adaptation in monocotyledonous geophytes.

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HABITATS OF SELECTED BUTTERCUPS WITHIN THE
RANUNCULUS OCCIDENTALIS COMPLEX
(RANUNCULACEAE)

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ABSTRACT

Habitat characterization can be helpful in assigning questionable populations to a specific taxon when distinguishing morphological characteristics are obscure or debated by authorities. Such a classification problem arises in the case of the autumn buttercup, *Ranunculus aestivalis* (Benson) Van Buren and Harper. This problem has special significance since the taxon is listed as endangered (*R. acriformis* var. *aestivalis*). This paper describes and compares habitats associated with the autumn buttercup and selected relatives within the *R. occidentalis* complex and with adventive populations of *R. acris* in Utah. Two populations of *R. occidentalis* (Nevada County, California), 3 populations of *R. acriformis* var. *acriformis* (Emery and Sanpete counties, Utah), 3 populations of *R. acriformis* var. *montanensis* (Lincoln County, Wyoming), 3 populations of *R. acris* (introduced from Europe and now growing wild in Rich and Cache counties, Utah) and 2 populations of the endangered species, *R. aestivalis* (endemic to Garfield County, Utah) were sampled. Analysis of vegetal and physical environments as well as tissue chemistry associated with these taxa show that they can be separated on the basis of habitat characteristics and/or tissue chemistry. Populations of *R. occidentalis* and *R. aestivalis* are widely separated from other taxa in principal components diagrams, whereas the two varieties of *R. acriformis* occur close together in statistical space. *Ranunculus acris* populations were broadly scattered in the diagrams. Characteristics of habitats associated with these taxa differ in many ways. These results parallel those of our previous molecular study involving the same taxa and support elevation of the autumn buttercup to species level. The study provides information about the habitat of the autumn buttercup that should be useful to managers responsible for its recovery.

The autumn buttercup, *Ranunculus aestivalis* (Benson) Van Buren and Harper, is a federally listed endangered species assigned by Benson (1948) to the *R. occidentalis* group in the Section *Chrysanthe*. The group includes taxa that extend southward from the northern Yukon Territory to mountains and valleys throughout northwestern United States. The majority of species and varieties within the *R. occidentalis* group are located in the Pacific-Sierra region and the northern Rocky Mountains. Satellite species extend eastward and southward into Utah. All taxa in the *R. occidentalis* group share common morphological characteristics and selected taxa within the group share numerous DNA markers (Van Buren et al. 1994). Phenetic relationships were determined (Van Buren et al. 1994) using DNA marker analysis, which provides an estimate of

TABLE 1. LOCATIONS OF POPULATIONS OF THE FIVE *RANUNCULUS* Taxa Considered.

Taxa	No. populations	County (s)	State	Elevation (m)
<i>Ranunculus occidentalis</i> var. <i>ultramontanus</i> (ROCU)	2	Nevada; Sierra	CA	1800
<i>R. acriformis</i> var. <i>montanensis</i> (RACM)	3	Lincoln	WY	2000–2450
<i>R. acriformis</i> var. <i>acriformis</i> (RACA)	3	Sanpete; Emery	UT	2500–2900
<i>R. acris</i> (RARS)	3	Rich; Cache	UT	1700–1900
<i>R. aestivalis</i> (RAES)	2*	Garfield	UT	1950

* A site occupied by plants in 1991 but without plants in 1992 was sampled for habitat characteristics.

genetic similarity to be expected among taxa belonging to various classification levels (i. e., species and varieties) within the section.

Ranunculus aestivalis, an endemic of the Sevier River drainage in southern Utah, has been variously treated by systematists. The taxon was described by Lyman Benson in 1948 and treated as a variety of *Ranunculus acriformis* (*R. acriformis* var. *aestivalis* Benson) in the *R. occidentalis* group. In 1986, Welsh made the autumn buttercup a variety of *R. acris* [*R. acris* var. *aestivalis* (L. Benson) Welsh], a European species otherwise recognized in North America as an adventive only. The taxon is treated as *R. acris* var. *aestivalis* in the most recent edition of A Utah Flora (Welsh et al. 1993) and is considered to be an indigenous entity. It is widely disjunct from its parent species which may reach the Aleutian Islands but does not enter North America (Welsh 1974). Unique problems arise when taxonomical disagreements involve an endangered species. The autumn buttercup was listed as an endangered plant by the United States Fish and Wildlife Service under the name *Ranunculus acriformis* var. *aestivalis* L. Benson (Federal Register 1989). Based upon molecular comparisons of genomic DNA of the autumn buttercup and close congeners, this taxon was recently elevated to the species level as *R. aestivalis* (Benson) Van Buren and Harper (Van Buren et al. 1994).

To provide additional data on the relationships of the autumn buttercup to close congeners in the West, we analyzed habitat data collected at selected sites of occurrence of four perennial taxa within the *R. occidentalis* complex, and at three *R. acris* sites. These are the same sites where the authors collected leaf tissue for DNA analyses (Van Buren et al. 1994). The sample includes taxa assigned to both species and varietal levels of classification (Table 1).

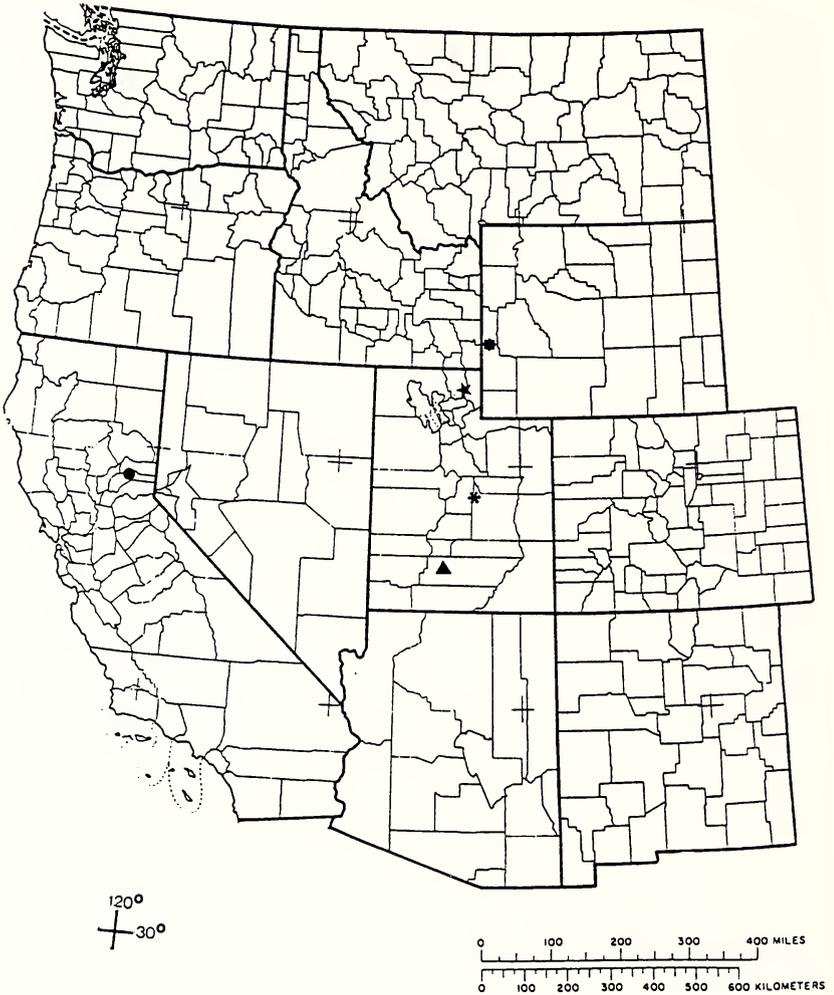
Andersson (1990) suggested that habitat characteristics should be considered when morphological characteristics do not permit un-

ambiguous classification. Van Valen's (1976) ecological species concept defines species as lineages occupying minimally different adaptive zones. This idea suggests that it is the selective pressures of the environment that result in local maintenance of unique phenotypes. Habitat selection has not been widely discussed for plant species, and supportive data are scarce. Immobility, dependence on morphological and chemical defenses, and extreme competition for resources are a few attributes unique to plants that make them less capable of assertively selecting habitat. Perhaps a more defensible view is that the habitat selects for plants with specific phenotypic or physiological characteristics. Loveless and Hamrick (1984) review ecological factors influencing genetic characteristics of plant populations. The influence of environmental and community characteristics on success of various plant species in a given habitat is beyond argument. There is thus a need for information about the characteristics of habitats that support any given plant species.

The purpose of this paper is to describe habitat conditions associated with closely related buttercups, and to identify ecological factors that may distinguish habitats congeners occupy. Habitat requirements are of particular interest to those charged with recovery efforts for endangered plant species (Menges and Gawler 1986; Buchele et al. 1989; Nelson and Harper 1991; Davis and Sherman 1992; Young 1992). Thorough descriptions of abiotic and biotic attributes of endangered species habitats may be useful for selection of potential sites for introduction and expansion of a species' range and may aid in finding remnant populations.

METHODS

Study sites. Habitat data were collected at 13 sites selected in connection with molecular (Van Buren et al. 1994) and morphological studies of these taxa (Table 1). All populations except those of *R. aestivalis* are separated by at least 1 km. On the date of collection of habitat data, all populations supported observable individuals except one site of *R. aestivalis*. However, abiotic data were collected from the site previously occupied by *R. aestivalis* which is about 0.5 km from the inhabited site. Figure 1 shows the general location of study sites for each taxon. Sites were moist, montane meadows in natural landscapes or in wet pastures in agriculturally developed areas. One population of *R. occidentalis* was located on moist, gravelly stream banks. All habitat sampling was completed during the month of July 1992. Voucher specimens of buttercups from each of the populations discussed are deposited at the Brigham Young University Herbarium, Provo, Utah (BRY), and the Arizona State University Herbarium, Tempe, Arizona (ASU).



- *Ranunculus occidentalis* var. ultramontanus
- ◆ *R. acriformis* var. montanensis
- * *R. acriformis* var. acriformis
- ★ *R. acris*
- ▲ *R. aestivalis*

FIG. 1. General locations of study sites of selected *Ranunculus* taxa.

Sampling. Soil samples were collected from each study site by inserting a 2.5-cm-diameter tube approximately 15 cm into the soil at various locations within 0.25 m²/quadrats centered over each of 10 randomly selected buttercup plants. Soil subsamples from each site were combined and the composite samples were analyzed by the Brigham Young University Soil Laboratory, Department of Agronomy and Horticulture. Soil pH, texture (% sand, silt and clay), percent organic matter, available phosphorus concentrations, and electrical conductivity were determined using methods recommended by Black et al. (1965). The presence of free soil carbonates was estimated using 10% hydrochloric acid (U. S. Salinity Laboratory Staff 1954). Soil temperature was measured by inserting a 0.4 m long steel-stem soil-thermometer into the soil at 10 random points within each study site. Soil depth was estimated by pushing a sharpened, 1.0 m steel penetrometer (rod diameter = 1.0 cm) as far as possible into the soil at ten random points at each site. Vegetal data were collected in 0.25 m² nested frequency quadrats centered over 10 randomly selected buttercup plants, and at 10 randomly chosen locations that did not support a buttercup plant but were within the area sampled at each of the 13 study sites (Smith et al. 1987). Relative frequency and percent cover for shrub, forb, grass, and cryptogamic species were estimated using the nested frequency frame to which eight points had been attached for cover estimation. Maximum height of vegetation associated with the buttercup in each quadrat was recorded. Percent cover for rock, soil, and litter were estimated using the same device. Species richness (average number of species per quadrat) in each quadrat was also calculated for each study site.

Buttercup tissue analyses were based on living leaf, stem and flower tissue of 10 randomly selected, adult individuals at each study site. Sampled individuals were at similar phenological stages. All tissue from a site was combined, quickly air-dried, and ground to pass a 0.64 mm diameter sieve. Samples were analyzed for total P, K, Ca, Mg, Na, S and % ash at the Department of Agronomy and Horticulture Tissue Analysis Lab, Brigham Young University. Analytical methods were those of the Association of Official Analytical Chemists (Horowitz 1980).

Statistical analyses. Vegetative, abiotic, and tissue chemistry data were analyzed using centered, standardized principal components analysis (STATGRAPHICS 1993) in order to visualize the relationships of the taxa as separated by variables in each data set. Discriminant analysis was employed for the larger data set consisting of vegetative characteristics of quadrats that were occupied or unoccupied by buttercup plants of the several taxa (STATGRAPHICS 1993). This analysis identified probable factors distinguishing mi-

crossites occupied and unoccupied by buttercups. Discriminant analysis would have been informative for abiotic and tissue chemistry analyses had the sample sizes been larger. Unfortunately, the collection of additional samples was beyond the resources of this study and, in the case of *R. aestivalis*, not possible.

RESULTS

Figure 2A shows the values of the first two principal components for the 13 study sites occupied by populations of the five taxa. These components are based on the abiotic habitat data reported in Table 2. The two components account for over 66% of the variation existing in this data set. Populations of *R. acriformis* (both varieties), *R. aestivalis*, and *R. occidentalis* are separated into "distinct" conspecific groups in the figure, but populations of *R. acris* are widely separated in statistical space. *R. occidentalis* and *R. aestivalis* are widely separated on the first component axis. The varieties of *R. acriformis* clump closely together on the first component axis, but they separate somewhat on the second axis. Figure 2B shows the weighting of the abiotic habitat variables along the two component axes. This diagram provides information that may be useful for interpretation of Figure 2A. Vectors connecting each variable to the origin suggest how influential individual variables might be in separating the plant taxa along an axis: vectors that closely parallel an axis are strongly correlated with that axis and may be influential factors in the relative success of the plant taxa along the axis. For example, soil electrical conductivity, depth, organic matter and free carbonate content are well correlated with component axis 1 (their vectors are nearly parallel to the axis), and may be influential factors controlling the distribution of taxa widely separated on that axis. Soil temperature, on the other hand, is the environmental variable best correlated with component axis 2. Sand and P are probably less important as their vectors are less parallel to the axis. When these habitat factors are considered in relation to placement of the several taxa in Figure 2A, the *R. occidentalis* and *R. aestivalis* sites on the first component axis are best separated using soil depth, organic matter, free carbonates and electrical conductivity. On the second component axis, the *R. acriformis* varieties and *R. acris* are apparently separated by differences in soil temperature. Table 2 shows that soil temperature values for *R. acris* vary greatly among themselves (i.e., the SE-value is large relative to the mean; Fig. 2A).

Because populations of the taxa considered in this paper were widely separated in the West, associated species differed markedly from one taxon to another. Nevertheless, the general aspect of occupied habitats was similar for all of the taxa. Although vegetative characteristics were recorded by species in the field, the data have

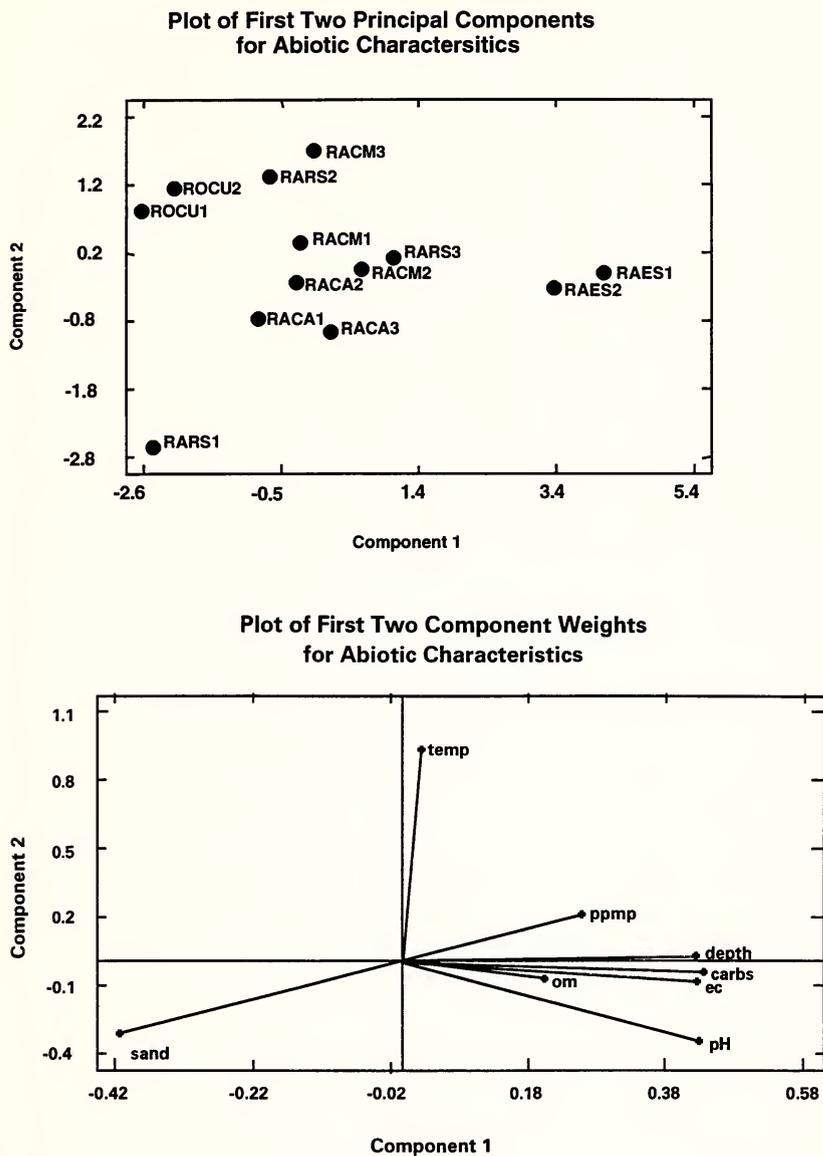


FIG. 2. A. Scattergram of the first two principal components for analysis of abiotic data collected from 13 study sites of selected *Ranunculus* taxa. Abbreviations for taxa as listed in Table 1. Populations are identified as numbers following the taxon abbreviation. B. Plot of weighting vectors for selected habitat variables on the first two principal component axes.

TABLE 2. COMPARISON OF MEAN VALUES OF HABITAT ABIOTIC CHARACTERISTICS FOR FIVE *RANUNCULUS* TAXA. ABBREVIATIONS FOR TAXA ARE AS IN TABLE 1. STANDARD ERROR FOR EACH MEAN IS IN PARENTHESES.

	Taxa					
	RACA	RACM	RARS	ROCU	RAES	
Soil pH	6.7 (0.15)	6.7 (0.21)	6.8 (0.25)	5.8 (0.20)	7.7 (0.19)	
Soil temperature	12.6 (0.21)	15.7 (1.05)	13.7 (3.95)	18.0 (0.35)	14.4 (0.75)	
Soil depth (dm)	5.7 (0.91)	3.7 (0.29)	2.5 (1.73)	3.2 (1.45)	10.0 (0)	
Soil texture (% sand)	43.8 (3.94)	40.0 (63.61)	46.6 (10.52)	57.4 (6.15)	25.1 (0)	
Organic matter (%)	7.8 (2.02)	8.1 (1.33)	5.1 (1.65)	3.2 (0.45)	12.3 (7.6)	
Electrical conductivity (mmho/cm)	1.3 (0.49)	1.3 (0.07)	1.2 (0.23)	0.7 (0.05)	2.5 (0.78)	
Free carbonates (arbitrary units)	0	0.2 (0.17)	0.7 (0.66)	0	2.5 (0.50)	
Available phosphorus (ppm)	10.9 (1.9)	103 (34.2)	17.1 (1.96)	9.1 (2.8)	87.2 (1.25)	
Sample size	3	3	3	2	2	

TABLE 3. COMPARISON OF GROSS CHARACTERISTICS OF VEGETATIONAL ENVIRONMENTS ASSOCIATED WITH THE FIVE TAXA OF *RANUNCULUS* Considered. Standard error for each mean is shown in parentheses. Abbreviations for taxa are as in Table 1.

Vegetative parameter	Taxa				
	RACA	RACM	RARS	ROCU	RAES
Species Richness (No. species/0.25 m ²)	17.5 (1.33)	20.7 (1.80)	15.6 (2.42)	14.8 (1.84)	11.5 (3.7)
Grass Cover (%)	57.6 (9.01)	41.4 (9.64)	36.2 (12.59)	44.4 (18.03)	41.3 (3.9)
Forb Cover (%)	32.5 (7.74)	46.7 (9.70)	24.1 (3.98)	15.1 (5.09)	21.9 (15.7)
Cryptogamic Cover (%)	0 (3.93)	4.5 (0.87)	0.9 (1.20)	1.2 (0.57)	0.6 —
Maximum Height of Associate plants (cm)	60.6 (1.21)	65.9 (12.6)	65.2 (8.43)	55.8 (15.98)	67.5 (1.7)
Sample size	3	3	3	2	2

been summarized here by life form class (i.e., shrubs, grasses, forbs etc.). Since site floristics differed so greatly among regions, floristic differences were not considered useful for identifying commonalities and differences among sites. Structural differences however, were considered likely to significantly alter the environments occupied by the taxa. Average characteristics of vegetational structure in meadows occupied by these taxa are reported in Table 3. The numerical values support the concept that all of the buttercup taxa have evolved in meadow environments physiognomically similar to those the species now occupy. The meadows are wet enough to remain green throughout the growing season (personal observation), but not so wet as to exclude most species and to produce communities of low diversity (e.g., *Carex* meadows, Wilson 1969). Woody plants do poorly in meadows that support these buttercups, but isolated patches of shrubs and trees may occur on drier spots. A principal components diagram (not shown here) based on the vegetational data at the 13 sites showed little tendency for sites occupied by a particular taxon to cluster into a unique group well separated from sites occupied by other taxa.

Within each sampled meadow the buttercups showed patchy distribution. To identify local factors that might control distribution of the buttercups, vegetal characteristics of quadrats occupied by buttercups (data for all species pooled) were compared with characteristics of randomly chosen unoccupied sites within the same meadows. Discriminant analysis identified vegetal differences between occupied and unoccupied sites. Although average number of species per quadrat (0.25 m²) was the only variable that differed significantly between occupied and unoccupied sites using simple t-tests (Table 4), discriminant analysis of the full data set clearly separated the

TABLE 4. COMPARISON OF MEAN VEGETATIVE DATA COLLECTED FROM SITES OCCUPIED OR UNOCCUPIED BY THE BUTTERCUP TAXA CONSIDERED IN THIS STUDY. Data for all taxa were pooled for this analysis.

% cover	Occupied	Unoccupied
	Mean (SE)	Mean (SE)
Grass	44.3 (4.9)	43.1 (4.62)
Forb	31.5 (4.37)	28.1 (4.38)
Litter	12.9 (4.16)	17.9 (5.13)
Soil	4.6 (1.71)	4.5 (1.37)
Rock	4.6 (3.91)	5.3 (3.32)
Cryptogam	1.6 (1.03)	0.6 (0.24)
Shrub	0.6 (0.25)	4.8 (2.60)
Avg. No. Species*	17.2 (1.00)	13.1 (0.80)
Avg. Height	63.0 (4.00)	67.4 (3.81)
Sample size	12	13

* Mean difference significant at 0.95 CI; all other differences between occupied and unoccupied sites are not statistically significant.

two groups (separation significant at the 0.003 probability level; Chi-Square value = 24.52). Discriminant function 1 yielded a classification percentage of 100 (i.e., occupied and unoccupied plots for all taxa were correctly placed) and a canonical correlation coefficient of over 0.85. Species richness was, as expected, shown to be the best variable for distinguishing occupied and unoccupied quadrats. Table 4 illustrates trends existing between sites occupied by buttercups and those that do not support those species in the same meadows. Microsites with greater grass, forb, and cryptogamic (moss) cover and with greater numbers of species are more likely to support buttercups, whereas sites with more litter and taller vegetation (especially woody plants) are less likely to support buttercups of this group.

Results of tissue chemistry analyses are summarized in Table 5. Unfortunately, only one tissue sample was available for the rare taxon *R. aestivalis*. However, that sample had elevated amounts of sulfur relative to values for other taxa. Sodium levels varied greatly among taxa. Relative placement of the five buttercups taxa along axes 1 and 2 of the principal components analysis of tissue chemistry is presented in Figure 3A. The first two principal components account for over 67% of the variation observed in the data set. With the exception of *R. acris*, the samples for each taxon lie close together in the figure and suggest rather similar tissue chemistry within a taxon. *Ranunculus occidentalis* is widely separated from other samples on the first axis, whereas the *R. aestivalis* sample is isolated from all other taxa on the second axis of Figure 3A. The two varieties of *R. acriformis* lie close together, suggesting considerable similarity in tissue chemistry. Figure 3B indicates the statistical

TABLE 5. MEAN VALUES FOR VARIOUS TISSUE CHEMISTRY VARIABLES FOR POPULATIONS OF EACH *RANUNCULUS* Taxon. Standard error for each mean is in parentheses. Abbreviations for taxa are as in Table 1. Elemental concentrations are reported as proportions of the oven dry tissue weights.

Tissue component	Taxa				
	RACA	RACM	RARS	ROCU	RAES
Phosphorus (%)	0.2 (0.02)	0.2 (0.05)	0.2 (0.05)	0.2 (0.02)	0.1 —
Potassium (%)	2.1 (0.17)	2.5 (0.12)	2.2 (0.39)	1.9 (0.08)	2.0 —
Calcium (%)	1.5 (0.13)	1.2 (0.04)	1.7 (0.2)	1.5 (0.13)	1.4 —
Magnesium (%)	0.2 (0.02)	0.2 (0.01)	0.3 (0.07)	0.3 (0.01)	0.2 —
Sulfur (%)	0.2 (0.03)	0.2 (0.04)	0.3 (0.03)	0.3 (0.1)	0.6 —
Ash (%)	7.9 (0.2)	7.8 (0.23)	12.0 (1.37)	12.7 (3.97)	7.6 —
Sodium (ppm)	59 (23.1)	51 (12.5)	1116 (432.0)	1899 (338.0)	915 —
Sample size	3	3	3	2	1

weighting of the several chemical elements in tissue along the two principal component axes. Sodium, ash, and calcium values are well correlated with the first component (separation of *R. acriformis* and *R. occidentalis*), whereas sulfur content is strongly correlated with separation of *R. aestivalis* from other taxa on the second component axis. *Ranunculus aestivalis* tissue contained much more sulfur and less ash content than did tissue of the other taxa considered (Table 5).

DISCUSSION

All of the buttercup taxa considered in this paper occupy floristically complex natural communities, and moist, herbaceous habitats, suggesting that they have adapted to conditions found in such sites. Discriminant analysis identified vegetal characteristics that are strongly associated with occurrence of the species considered here. These taxa are not-likely to occupy microsites with tall vegetation and heavy accumulations of litter (Table 4). The species prefer soils that are moist enough to support significant growth of mosses and lichens but not so wet that a diversity of vascular plants is precluded. Microsites dominated by woody species are rarely occupied by buttercups in this complex.

Abiotic characteristics of habitats occupied by the autumn buttercup are shown to differ strongly from those associated with other buttercup taxa studied (Figs. 2A and 2B). The unique habitat char-

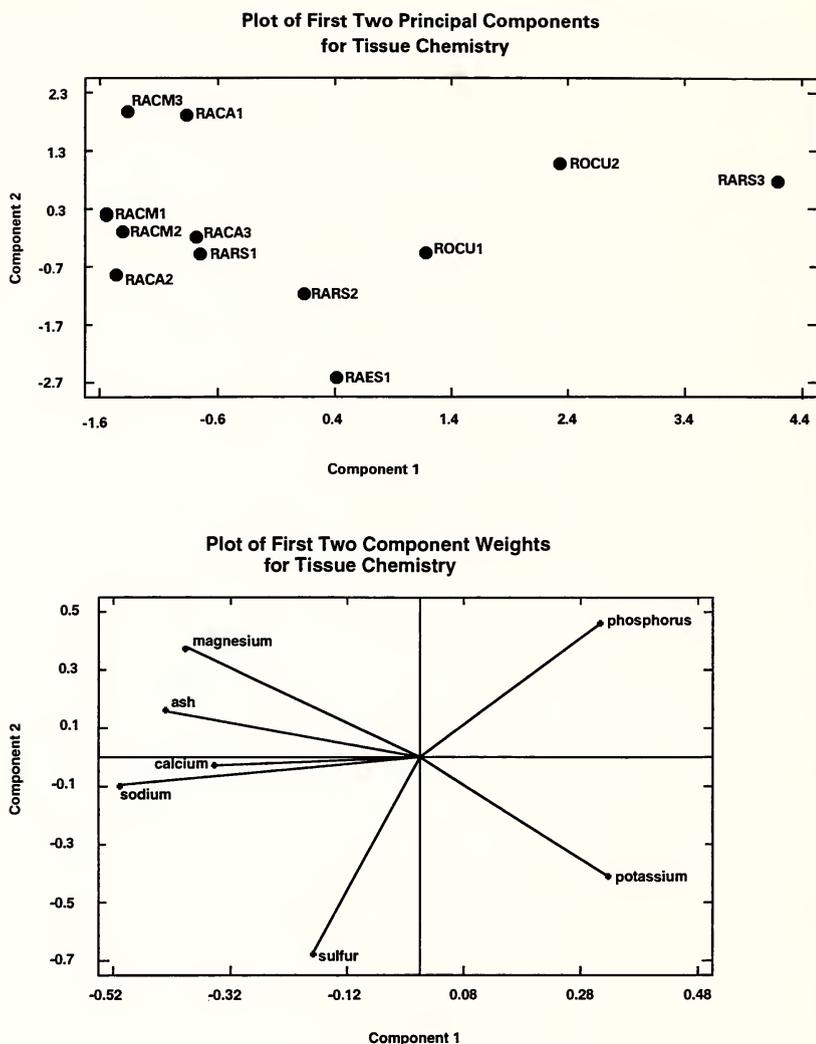


FIG. 3. A. Scattergram of the first two principal components of *Ranunculus* tissue analysis. Abbreviations for taxa as listed in Table 1. Populations are identified as numbers following the taxon. B. Plot of weighting vectors for content of selected elements in tissue of the buttercup populations shown in Figure 3A along the first two axes of the principal components analysis.

acteristics associated with *R. aestivalis* are reinforced by a geographical separation of at least 200 km (by air) from any other taxon in its generic subsection. Thus, both unique habitat features and disjunct distribution support recognition of the taxon as an independent

species, which was earlier recommended on the basis of DNA markers (Van Buren et al. 1994). In respect to both abiotic characteristics of habitat and DNA markers, *R. aestivalis* is well separated from *R. acris* and the two varieties of *R. acriformis*. *Ranunculus occidentalis* also shows unique habitat characteristics.

Based on a single sample, tissue chemistry of the autumn buttercup differs considerably from tissue of our other buttercups (Figs. 3A and 3B). Sulfur content best explains the separation of this taxon from the others, but *R. aestivalis* tissue also contained relatively less ash than other taxa considered (Table 5).

Results of this study further justify elevation of *R. aestivalis* to species status, since the varieties of *R. acriformis* with which the species had originally been allied were not strongly differentiated by abiotic or biotic habitat variables or tissue chemistry. However, *R. aestivalis* was widely separated from those and other taxa in the complex by each of the foregoing analyses. Abiotic habitat characterization appears to be especially useful for distinguishing these taxa. *Ranunculus aestivalis* occurs in habitats where soil electrical conductivity, free carbonates, organic matter and depth values differ greatly from soils occupied by other taxa.

In all of the analyses performed in this study, *R. acris* populations differ widely from each other. Figures 2A and 3A both show wide separation of *R. acris* populations in the statistical space created using environmental or tissue chemical data. Populations of *R. acris* are as widely separated from each other as species in the analyses are from each other. A possible explanation for such disparate behavior is that each *R. acris* population may represent an independent introduction from different locations in Eurasia. Multiple introductions should result in a more diverse genotype for the species a condition which does appear to be represented in molecular data for the species (Van Buren et al. 1994)] and permit it to occupy very heterogeneous habitats.

Results from this study provide managers with useful information concerning the habitat of the endangered autumn buttercup. The species has diverged from close congeners and occupies meadow habitats that are more alkaline, more saline, and drier than those occupied by other taxa in the complex and the adventive taxon, *R. acris*. The authors especially draw attention to the apparent inability of the autumn buttercup (and other taxa in the complex as well) to persist where litter is allowed to accumulate in deep layers. Since the autumn buttercup disappeared from one site following termination of grazing and accumulation of deep litter mats, it may be necessary to reinstitute grazing during the dormant season (or resort to periodic early spring burns), to restore the species to sites historically grazed in the winter where it was initially discovered. The autumn buttercup differs from all other western North American

congeners in respect to several DNA markers, kinds of habitats occupied, and tissue chemistry. It represents an accumulation of many unique qualities in the *R. occidentalis* complex and merits preservation on both genetic and aesthetic grounds.

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ANNOUNCEMENT

THE FUTURE OF ARID GRASSLANDS: IDENTIFYING ISSUES, FINDING SOLUTIONS

October 9–13, 1996 in Tucson Arizona

A solution-oriented conference for everyone interested in the future of grasslands in the American Southwest and Northern Mexico. This four-day conference will focus on understanding problems facing those grasslands and practical tools for grassland management, preservation and restoration. Attendees will be a mix of private and public land managers and owners, scientists, representatives of non-profit groups and concerned citizens. Two full days will be spent in the field, studying examples of grassland management in Southern Arizona. The other two days will include keynote speakers and panelists as well as small-group discussion and information sessions. The final day will focus on methods for preservation ranging from coordinated monitoring systems, land use and taxation tools to public involvement techniques.

Most of the speakers and panelists will be invited, but the planning committee welcomes abstracts for a few open sessions dealing with grasslands management, interrelationships between grasslands and humans or wildlife, and specific methods for preservation, especially success stories.

People are encouraged to submit abstracts for poster sessions which will be incorporated into the program featuring on-the-ground examples of problem solving to protect or restore grasslands. Both successful and unsuccessful examples are sought to illustrate what has and has not worked - and why.

The conference is organized by the Audubon Research Ranch and is cosponsored by numerous government agencies, educational institutions, and nonprofit groups.

For more information: Grasslands Conference, Tucson Audubon Society, 300 E. University # 128, Tucson AZ 85705, or the University of Arizona Water Resources Center at (520) 792-9591.

CHROMOSOME COUNTS IN MEXICAN *ERIGERON*

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ABSTRACT

Chromosome numbers are reported for 75 populations of 19 species of *Erigeron* from Mexico and 4 populations of 1 species from Arizona. First reports for the species are given for *E. fraternus*, *E. polycephalus*, *E. strigulosus*, and *E. wislizeni*, and new ploidy levels are reported for *E. coronarius* var. *durangensis*, *E. janivultus*, *E. forreri*, *E. pubescens*, and *E. versicolor*. *Erigeron gilensis* and *E. mimegletes* are treated as synonyms of *E. versicolor*, a species previously considered to be endemic to south-central Mexico. Comments on morphological variability in *E. versicolor*, *E. longipes*, *E. pubescens*, and several other species are provided.

Field studies of Mexican Asteraceae by De Jong in July–August of 1965 and Nesom in August 1977 included collections of material for chromosome number determinations of various species of *Erigeron* (Table 1). The counts, made by the respective collectors, are reported here for the first time. Almost all were determined from flower buds as meiotic counts at or near metaphase I; those of *E. griseus* (Nesom 618), *E. karvinskianus*, *E. pubescens* (De Jong 1565), and the four collections of *E. versicolor* from Arizona were determined as mitotic counts from germinating root tips. A complete set of De Jong vouchers remains with the collector; other nearly complete ones are at OS and MEXU; a partial set is at TEX. Nesom vouchers are at TEX, MEXU, and various others.

A generalization that quickly becomes apparent when assembling data on chromosome numbers in *Erigeron* is that many species of the genus, including those geographically widespread as well as those restricted in distribution, have more than one ploidy level. In some cases, polyploidy may be correlated with increased morphological variability, probably reflecting the influence of hybridization; this may be true for *E. pubescens* (as noted below), *E. calcicola*, and *E. flagellaris*. In other species, there is apparently no increased morphological variability in the polyploids and no evidence suggestive of interspecific hybridization. Variation in chromosome num-

ber is known to exist within populations of some species (e.g., *E. potosinus*: Nesom 1978). In the following comments, we discuss several of the Mexican species in which variability in chromosome number is known.

DISCUSSION

Erigeron coronarius and *E. janivultus*. Diploids and tetraploids previously have been reported for *E. coronarius* var. *coronarius* and diploids for *E. coronarius* var. *durangensis* (Nesom 1990). We report the presence of tetraploids among the populations of var. *durangensis*. Only a diploid chromosome count for the closely related *E. janivultus* has previously been available (Beaman and Turner 1962; see Nesom 1990), but this species also comprises diploids and tetraploids, as reported here.

Erigeron delphinifolius. This species appears to be diploid over its relatively wide geographic range (counts from Edo. Mexico, Tlaxcala, Durango: De Jong and Longpre 1963; Turner et al. 1961; Turner et al. 1962; Turner et al. 1973), except for a single report of a tetraploid plant from the eastern periphery of its range (San Luis Potosi: Harms 1969). Considerable morphological variability exists within the species. (Nesom 1989b).

Erigeron forreri. Diploids, hexaploids, and octoploids are reported for this species (De Jong and Longpre 1963; Keil and Stuessy 1977; the present report). Tetraploids have not been reported but should be expected. There does not appear to be notable morphological variation among populations of this species, which occurs in Durango and southern Chihuahua.

Erigeron galeottii. Diploids are known from Oaxaca, Edo. Mexico, and Michoacan; tetraploids have been reported more commonly and are known from Edo. Mexico, Distrito Federal and Michoacan (Beaman et al. 1962; De Jong and Longpre 1963; Stoutamire and Beaman 1960; Turner et al. 1961; the present report). A disjunct population of *E. galeottii* in southern Chihuahua apparently is diploid, based on an examination of pollen (Nesom unpubl.). The species is variable in growth habit, orientation of stem vestiture, leaf size, shape, and degree of marginal serration or crenation, and capitular size. The plants tend to be initially monocephalous, with a few additional heads commonly produced later.

Erigeron longipes. With the present report and previous observations on this species (Turner et al. 1961; Turner et al. 1962), diploids are known from Puebla and Oaxaca, tetraploids from Chiapas, Oaxaca, Edo. Mexico, Distrito Federal, Michoacan, Hidalgo, and San Luis Potosi, and triploids from Edo. Mexico. A report of diploid

TABLE 1. CHROMOSOME COUNTS IN MEXICAN *ERIGERON*. Collection numbers preceded by "N" are Nesom; all others are De Jong. First reports for the species are marked by an asterisk.

ERIGERON CALCICOLA Greenm.		
1807:	2n = 18II	NUEVO LEON: N of La Escondida at KMs 76-77, on hwy toward Dr. Arroyo
1817:	2n = 36II	COAHUILA: ca. 1 km W of Atenco, W of Saltillo on Hwy 140 toward Torreon (at KMs 424-425)
ERIGERON CORONARIUS Greene		
Var. CORONARIUS		
1763:	2n = 18II	CHIHUAHUA: ca. 18 mi W of Cd. Chihuahua toward Cuauhtemoc
1775:	2n = 9II	CHIHUAHUA: ca. 2 mi E of Tejolocachic toward Cd. Guerrero
Var. DURANGENSIS Nesom		
1755:	2n = 18II	DURANGO: between Canatlan and Guatimape at KM 32-33, J.G. Aguillera to Guatimape
ERIGERON DELPHINIFOLIUS Willd.		
1519:	2n = 9II	EDO. MEXICO: N side of Hwy 136 between KMs 60 and 61, on side road
1615:	2n = 9II	EDO. MEXICO: Hwy 115, between Tlalmanalco and Amecameca (KMs 50 and 51)
1749:	2n = 9II	DURANGO: KM 980 on Hwy 40, Durango to Mazatlan
1750:	2n = 9II	DURANGO: KM 968 on Hwy 45, N of Cd. Durango
1758:	2n = 9II	DURANGO: KM 26 on road from J.G. Aguillera to Guatimape
1759:	2n = 9II	DURANGO: 3.5 km NW of J.G. Aguillera, toward Guatimape
N613:	2n = 9II	DURANGO: 1 mi WSW of Cd. Durango on Hwy 40
ERIGERON FLAGELLARIS A. Gray		
1764:	2n = 27II	CHIHUAHUA: ca. 5 mi SE of Tejolocachic
1770:	2n = 9II	CHIHUAHUA: 6.3 mi NE of Madera toward San Jose Babicora
ERIGERON FORRERI (Greene) Greene		
1733:	2n = 27II	DURANGO: between KMs 1102 and 1103 on Hwy 40
N622:	2n = 9II	DURANGO: 24 mi WSW of Cd. Durango on Hwy 40
N4438:	2n = 27II	DURANGO: 10 km W of El Salto along Hwy 40
ERIGERON FRATERNUS Greene*		
N623:	2n = 9II	DURANGO: 24 mi WSW of Cd. Durango on Hwy 40
N633a:	2n = 9II	CHIHUAHUA: ca. 10 mi WSW of Madera on logging road
N633b:	2n = 9II	CHIHUAHUA: ca. 24 mi WSW of Madera on logging road
N4487:	2n = 18II	CHIHUAHUA: ca. 43 km SW of La Junta
ERIGERON GALEOTTII (A. Gray ex Hemsl.) Greene		
1468:	2n = 9II	OAXACA: Llano de las Flores, Hwy 175
1492:	2n = 18II	EDO. MEXICO: between KMs 61 and 62, old Puebla-Mexico hwy
1501:	2n = 18II	EDO. MEXICO: between KMs 54 and 55, old Puebla-Mexico hwy

TABLE 1. CONTINUED

1618:	2n = 18II	EDO. MEXICO: Puerto El Guarda (KM 24-25) on Hwy 130, Mexico to Toluca
1652:	2n = 18II	EDO. MEXICO: ca. 6 km E of Bosencheve (KM 124) on Hwy 15, Toluca to Morelia
1654:	2n = 9II	MICHOACAN: 15 km W of Cd. Hidalgo on Hwy 15
ERIGERON GRISEUS (Greenm.) Nesom		
1730:	2n = 9II	DURANGO: 2 km E of La Ciudad on Hwy 40 (between KMs 1106 and 1107)
N618:	2n = 18	DURANGO. ca. 25 mi WSW of Cd. Durango on Hwy 40
ERIGERON JANIVULTUS Nesom		
1542:	2n = 9II	HIDALGO: 2.3 mi S of Cuyamaloya
1651:	2n = 18II	EDO. MEXICO: W of Toluca on Hwy 15
1634:	2n = 18II	EDO. MEXICO: 1 km N of Marboro (KM 117-118), S of Ixtlahuaca on Hwy 55
1651:	2n = 18II	EDO. MEXICO: W of Toluca (KMs 112-113) on Hwy 15
ERIGERON KARVINSKIANUS DC.		
1443:	2n = 27	CHIAPAS: just E of San Cristobal las Casas on Hwy 190
1446:	2n = 36	CHIAPAS: E of San Cristobal las Casas on Hwy 190, KM 1135
1483:	2n = 27	OAXACA: ca. 20 km N of Ixtlan de Juarez on Hwy 175
ERIGERON LONGIPES DC.		
1403:	2n = 9II	OAXACA: N side of Cieneguillas on Hwy 190, between KMs 417 and 418
1425:	2n = 18II	CHIAPAS: 5.2 mi E of Teopisca on Hwy 190
1452:	2n = 9II	OAXACA: between KMs 36 and 37 on Hwy 175, Oaxaca to Tuxtepec
1457:	2n = 9II	OAXACA: 2 km E of Ixtlan de Juarez
1503:	2n = 18II	DIST. FEDERAL: SE of Cd. Mexico along Ixtapalapa-Los Reyes road, near XEW TV station
1575:	2n = 18II	SAN LUIS POTOSI: El Porvenir (KM 247) on Hwy 80, Cd. del Maiz to Huizache
1577:	2n = 18II	SAN LUIS POTOSI: Barbarita (KM 242) on Hwy 80, Cd. del Maiz to Huizache
1600:	2n = 9II	PUEBLA: between El Carmen and Zacatepec on Hwy 136
1624:	2n = 18II	EDO. MEXICO: N of Toluca (KM 85) on Hwy 55
1655:	2n = 18II	MICHOACAN: within city of Morelia, toward Sta. Maria
1658:	2n = 18II	MICHOACAN: 1.8 mi of Ario de Rosales, toward Villa Escalente
ERIGERON METRIUS Blake		
1781:	2n = 9II	NUEVO LEON: base of Lopez Mateos rock relief on Hwy 60, E of Iturbide toward Linares
ERIGERON POLYCEPHALUS (Larsen) Nesom*		
1686:	2n = 9II	JALISCO: 7.3 mi SW of Atenquique, lumber road above Tonila

TABLE 1. CONTINUED

ERIGERON POTOSINUS Standley		
1787:	2n = 9II	NUEVO LEON: Cerro Potosi at KMs 19-20, ca. 10,200 ft
ERIGERON PUBESCENS Kunth		
1520:	2n = 27II	EDO. MEXICO: N side of Hwy 136 between KMs 60 and 61, on side road
1565:	2n = 27	SAN LUIS POTOSI: between KMs 32 and 33 on Hwy 86 toward Rio Verde
1568:	2n = 9II	SAN LUIS POTOSI: El Milagro (at KM 37) on Hwy 86 toward Rio Verde
1586:	2n = 18II	HIDALGO: Puerto de Trancas (between KMs 216 and 217) on Hwy 85
1593:	2n = 18II	PUEBLA: 26 km S of Zacatlan on Hwy 119
1643:	2n = 36II	EDO. MEXICO: S of Ixtlahuaca on Hwy 55, at KM 98
1791:	2n = 18II	NUEVO LEON: Cerro Potosi at KMs 19-20, ca. 10,200 ft
1793:	2n = 18II	NUEVO LEON: Cerro Potosi at KMs 14-15, ca. 9500 ft
1800:	2n = 27II	NUEVO LEON: ca. 7 km N or Puerto Cieneguillas on Hwy 60, toward Dr. Arroyo
1803:	2n = 9II	NUEVO LEON: near Puerto Cieneguillas at KM 31, Hwy 60 toward Dr. Arroyo
ERIGERON SEEMANNII (Sch.-Bip.) Greene		
N624:	2n = 9II	DURANGO: ca 24 mi WSW of Cd. Durango at Rio Mimbres
ERIGERON STRIGULOSUS Greene*		
N4499:	2n = 18II	CHIHUAHUA: 12.8 km N of Madera
ERIGERON VERSICOLOR (Greenm.) Nesom		
1640:	2n = 36II	EDO. MEXICO: S of Ixtlahuaca on Hwy 55, at jct to Los Reyes
1766:	2n = 27II	CHIHUAHUA: 3 mi NW of Tejolocachic
1771:	2n = 36I	CHIHUAHUA: 3.9 mi NE of Madera toward San Jose Babicora
N628:	2n = 27I	CHIHUAHUA: 13 mi W of Cuauhtemoc on Hwy 16
N637:	2n = 27I	CHIHUAHUA: 0.5 mi E of Madera on Hwy 16
N459:	2n = 18	ARIZONA: Apache Co., 12 mi WSW of Eagar on Hwy 73
N460A:	2n = 36	ARIZONA: Apache Co., 12 mi WSW of Eagar at jct of Hwys 78 and 373
N464A:	2n = 36	ARIZONA: Apache Co., 5.2 mi SW of Alpine on Hwy 666
N466:	2n = 36	ARIZONA: Apache Co., 4.5 mi N of Alpine on Hwy 180
ERIGERON WISLIZENI (A. Gray) Greene*		
1767:	2n = 9II	CHIHUAHUA: 6.3 mi NE of Madera toward San Jose Babicora
1768:	2n = 9II	CHIHUAHUA: 6.3 mi NE of Madera toward San Jose Babicora
N635:	2n = 9II	CHIHUAHUA: 15 mi WSW of Madera
N639:	2n = 9II	CHIHUAHUA: 1 mi W of Babicora

plants of *E. longipes* from Nuevo Leon (considerably north of its known range) was based on an misidentified collection of *E. veracruzensis* Nesom (Sundberg et al. 1986).

Plants of *Erigeron longipes* produce solitary heads with numerous (up to 300), filiform ligules. The leaves may be confined to a basal rosette (= *E. scaposus* DC.) or continue up the stem relatively unreduced in size; the morphological extremes are strikingly different in habit, but intermediates are common. McVaugh (1984) and Rzedowski (1985) identified all forms of the complex as *E. longipes*, and the same course is followed here. Still, as noted by McVaugh, the scapose forms occur mostly in eastern Mexico, although leafy-stemmed plants are intermixed in that region. The limited data on chromosome numbers indicate a tendency for the scapose forms to be diploid, but some diploids have leafy stems. The plants are abundant colonizers, easily located and collected, and a broader, more intensive survey of chromosome numbers and morphological variation would probably prove to be interesting.

Erigeron pubescens. Diploids are presently known only from the northern part of the range of the species (see below); tetraploids and hexaploids are known from both the northern and southern regions, and octoploids are recorded from the southern region in the present report. In previous chromosome reports for this species (both from Hidalgo: Turner et al. 1961; De Jong and Longpre 1963), the observations were of asynaptic meiotic cells of tetraploids.

Plants of *Erigeron pubescens* are characterized as fibrous-rooted perennials that commonly produce numerous stems from the base; they are eglandular, with a strigose vestiture, relatively narrow, evenly distributed cauline leaves, solitary heads, and the ligules have a conspicuous, purple, abaxial midstripe. Plants in the southern region of the species (Puebla, Mexico, Hidalgo, and San Luis Potosi) are relatively uniform in morphology, producing a sparse vestiture, linear leaves, and relatively short peduncles. In the northern region (Tamaulipas, Nuevo Leon, and Coahuila), the phyllaries are more densely hairy, the leaves are broader, and there is a greater tendency for the stems to branch above the base. The northern plants are more variable than the southern, almost certainly reflecting the influence of hybridization with closely related species of sect. *Olygotrichium* Nutt. (Nesom 1989a) that occur commonly in the region: *E. metrius* Blake, *E. modestus* A. Gray, *E. calcicola* Greenm., and *E. divergens* Torr. & Gray. These latter species also show infraspecific variation in ploidy and form an intergradient complex in north-central Mexico (e.g., Zhao and Turner 1993).

Erigeron versicolor. Polyploids are known from populations of *Erigeron versicolor* in each of its three regions of distribution (see below). Diploid, tetraploid, and hexaploid populations are reported

within the western system (= *E. gilensis*) (Pinkava and Keil 1977; the present report); triploid and tetraploid populations are known within the eastern system (= *E. mimegletes*) (Turner and Flyr 1966; Powell and Powell 1978); the report here of an octoploid is the first available chromosome count for *E. versicolor* in the area of its typical populations (the southern system). Previous reports of triploids and tetraploids have been of completely asynaptic meiotic cells, which suggest that the polyploid populations of this species reproduce apomictically.

This species, which previously has been regarded as endemic to Hidalgo (the type locality) and Edo. Mexico, comprises three widely allopatric population systems. Those from Coahuila, Nuevo Leon, Tamaulipas, and Texas (the eastern system) have been identified as *E. mimegletes* Shinnars (the type from Texas), those from Chihuahua, Durango, Arizona, and adjacent New Mexico (the western system) as *E. gilensis* Woot. & Standl. (the type from New Mexico). Plants over the whole range characteristically occur in at least periodically wet habitats, and there are no consistent morphological differences among plants from these areas. All are annual in duration (with a tendency for a longer duration in the western populations) and vary in habit from taprooted to fibrous-rooted, single-stemmed to highly branched from the base, and from ca. 0.1 to 1.0 m in height. Plants from Chihuahua, Durango, Edo. Mexico, and Hidalgo have a greater tendency to be multiple-stemmed from the base, while those in Arizona, Texas, and Coahuila are more commonly single-stemmed. The stem vestiture varies from spreading to antrorsely appressed, the receptacles are conical, and the phyllaries are broadly lanceolate with thin-scarious margins. The pappus is reduced to a minute corona, usually lacking bristles although 1–4 short, caducous bristles are sometimes present on achenes from Arizona plants; the corona in the eastern system usually is reduced to a blunt and smooth rim, while elsewhere it tends to be slightly raised and shallowly erose.

Hybridization between *Erigeron versicolor* and *E. divergens* Torr. & Gray, which occur in close sympatry in southeastern Arizona, may explain the occurrence of bristles in the pappus of *E. versicolor* in that area. A close morphological similarity between the two taxa has been noted by Pinkava and Keil (1977), and diploid plants of the two taxa have been collected in close proximity in the White Mountains of Apache Co., Arizona (Nesom unpublished), where they also may intergrade in other features.

The nomenclature for the species in its broadened sense is summarized by the following:

ERIGERON VERSICOLOR (Greenm.) Nesom, Sida 9:225. 1982.

Achaetogeron versicolor Greenm., Proc. Amer. Acad. Arts 41:255. 1905.

Erigeron gilensis Woot. & Standl., Contr. U.S. Natl. Herb. 16:184. 1913.

Achaetogeron chihuahuensis Larsen ex Blake, J. Washington Acad. Sci. 30:470. 1940.

Erigeron mimegletes Shinnery, Wrightia 1:184. 1947.

Erigeron geiseri var. *calcicola* Shinnery, Wrightia 1:184. 1947.

Erigeron wislizeni. All populations sampled so far are diploid, but ray color, leaf morphology, and vestiture are notably variable within the species (Nesom 1989b). *De Jong 1767* and *1768* sampled morphologically divergent but immediately adjacent populations.

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REVIEW

California Plant Community Information System. By STEVEN HARTMAN. 1994. NatureBase, 3646 Fairfax, Culver City, California. Diskette Version 1.0, \$95.00.

The study of California's vegetation is beginning to enter the computer age. NatureBase of Culver City has made four treatments of the state's vegetation available for DOS users: "Preliminary descriptions of the terrestrial natural communities of California" by Robert Holland, "The map of the natural vegetation of California" by A. W. Küchler, "California plant communities" of P. Munz and D. Keck [El Aliso 2:87–105, 199–202] which also is in Munz's *A California Flora*, and summary of acreages of 32 types done by the California Department of Forestry and Fire Protection.

The Munz and Keck classification, a two-level one of nine vegetation types and 29 plant communities, is known by any botanist who has used *A California Flora*. Küchler's map was included in the *Terrestrial Vegetation of California*. The legend lists nine formations with 54 vegetation types. In 1986, Robert Holland, then vegetation ecologist for the Natural Heritage Program of the California Department of Fish and Game, prepared a vegetation classification for use in the California Natural Diversity Data Base. This classification was never published, though it has been extensively used. [A copy is available from Natural Diversity Data Base, California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814]. This classification is a four-tier one with more than 300 types at the lowest level.

The four classifications are entered separately in the computer program. The Department of Forestry scheme lists types such as Mixed conifer, Red fir, and Redwood. According to the list, Other desert covers the most area of any category in California (20%), followed by Urban-agriculture-water (16%). No descriptions beyond category names are available. For the other classifications, the user is taken through each classification, using a series of screens, to a description of a type at the lowest level. Another screen lists the characteristic species for that type. If the scientific names used in the original vegetation description differ from those used in *The Jepson Manual*, both are given.

The screens act in some ways like as set of keys, but only after the reader knows the classification. In learning a classification, sometimes a book version may be more useful, especially in the more elaborate Holland scheme where reading the descriptions is necessary to pick the appropriate category. In the computer version, the user toggles between screens. It takes seven steps to compare Interior live oak forest with Shrub interior live oak chaparral, for example.

The value of the computer form of this information is best met for those interested in working with the more complicated Holland scheme, and having synonym names for scientific names easily available for people getting use to *The Jepson Manual*. For botanists who want this material available on their computers, here is an easy way to have it.

—JOHN SAWYER, Biological Sciences Department, Humboldt State University, Arcata, CA 95521.

A NEW SPECIES OF *ACHNATHERUM* (*ORYZOPSIS*)
FROM OREGON

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ABSTRACT

A new species of *Achnatherum*, *A. wallowaensis* Maze and K. A. Robson of central and northeastern Oregon is closely related to *A. hendersonii* (Vasey) Barkworth (= *Oryzopsis hendersonii*) of central Washington and Oregon but differs from this species primarily in its lax inflorescence with drooping spikelets, *A. hendersonii* having stiff inflorescences with erect spikelets. Other differences in vegetative and reproductive features occur between these two taxa with *A. wallowaensis* tending to have longer, but thinner, parts. The two species show different relationships among their descriptive variables and are separated by a principal components analysis. Like its close relative, *A. wallowaensis* occupies small scattered areas of shallow, rocky soils that support a vegetation of small, distantly spaced plants.

Henderson's rice grass, *Achnatherum* (*Oryzopsis*) *hendersonii* (Vasey) Barkworth (nomenclature follows Barkworth [1993]) is a small bunch grass that grows in rocky shallow soils in Washington and Oregon. Until recently its distribution was known only from central Washington and central Oregon (Hitchcock et al. 1969) but, through the efforts of botanists employed by the United States Forest Service and the Nature Conservancy in Oregon, many more instances of its occurrence have been discovered (Vrilakas 1990). The greatest number of new findings of this species have been made in the Wallowa Mountains of northeastern Oregon, with some populations also discovered in the Ochoco Mountains of central Oregon and the grasslands of southern Wasco County in Oregon.

As part of a study into the nature of variation in grass species of restricted distribution, we visited the Wallowa Mountains in the summer of 1991 and noted that plants called *A. hendersonii* growing there differed from those of central Washington in their lax inflorescences and drooping spikelets. The plants of central Washington have stiff inflorescences with erect spikelets, features noted both in recent descriptions (Hitchcock et al. 1969) as well as in the original

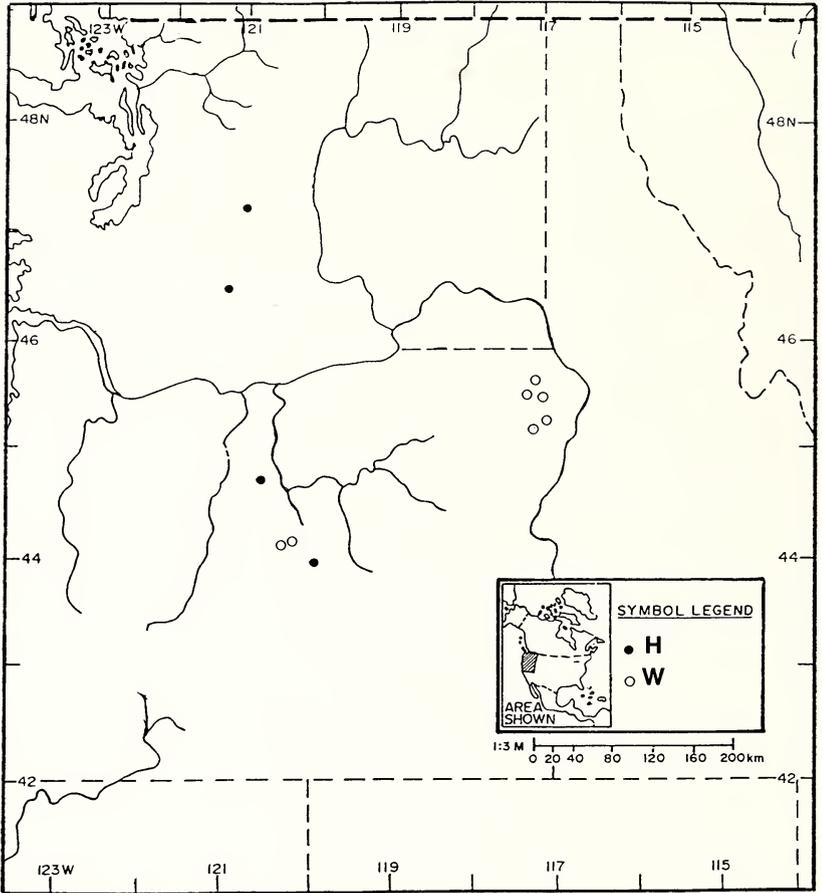


FIG. 1. Distribution of *A. hendersonii* (solid circles) and lax inflorescence forms (open circles).

species description (Vasey 1894). This stimulated a field trip in the summer of 1993 to determine the distribution and abundance of the plants bearing lax inflorescences. We wanted to know if the plants with lax inflorescences had a unique distribution and if that feature had a distinctive relationship with other morphological attributes, suggesting two unique taxa, perhaps even species.

MATERIALS AND METHODS

Plants from throughout the range of *A. hendersonii* (*sensu lato*) were collected in June of 1993. The collection sites are shown in Figure 1. We collected all specimens except those from north-central

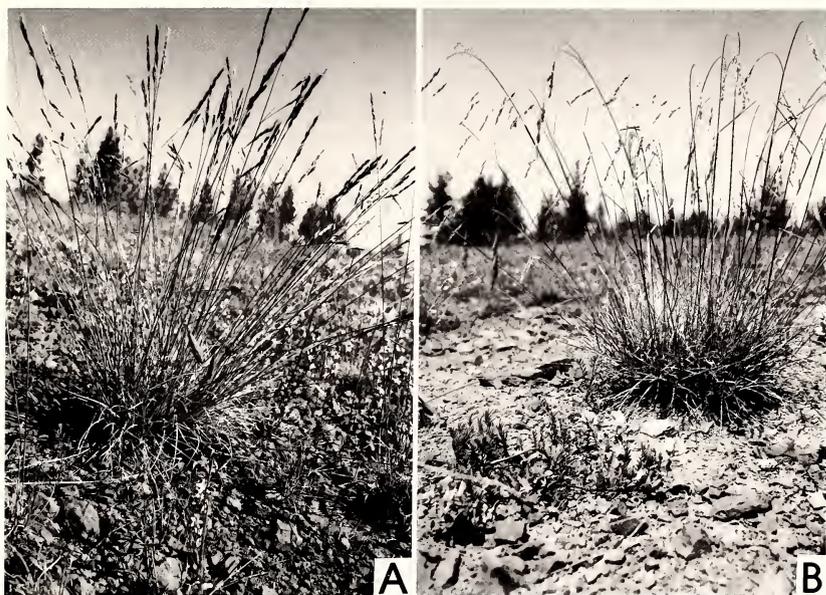


FIG. 2. Photographs of *A. hendersonii* (A) and lax inflorescence form (B) both from the Ochoco Mountains.

Oregon, which were collected by Jonathan Soll of the Nature Conservancy. We also borrowed the type of *A. hendersonii*, collected on Clemans Mt. in south-central Washington, to include in our comparisons.

Examples of both forms of what has been called *Achnatherum hendersonii* are shown in Figure 2. The plants from Washington, including the type, specimens from north-central Oregon, and some from central Oregon have stiff inflorescences with erect spikelets. Those from northeastern Oregon and some from central Oregon have lax inflorescences with drooping spikelets. These different forms do not share a common distribution (Fig. 1).

In order to quantify the variation in these grasses and to discover if the differences between them extended beyond general inflorescence features, we performed a principal components analysis (PCA) of a large set of spikelet, inflorescence, and flag leaf characters. The variables were sheath, blade, and ligule length for the flag leaf; length and width of the two glumes and the floret, and the length of the thickened portion of the lemma apex on the adaxial side of the lemma; inflorescence type (erect or drooping), the length of the lowest inflorescence branch, the total length of the inflorescence from the lowest node to the tip of the topmost spikelet, the thickness of the inflorescence axis

at its midpoint, and the thickness of the lowest inflorescence branch at its midpoint. The spikelet measurements were taken from the terminal spikelet of the lowermost inflorescence branch. All variables except inflorescence type were measured, inflorescence type was coded as either lax (1) or stiff (2). This coding was done when the plants were collected since lax inflorescences often straightened during drying in a press. We are aware of the undesirability of using coded variables in a PCA. However, the difficulty in measuring degree of laxness as other than a binary variable in the field, and the impossibility of doing so on herbarium specimens after they dried and straightened, left us little choice. And the character, to us, appears real, remaining constant within populations.

The PCA was done in two steps. First, all variables were subjected to PCA of a correlation matrix. That PCA was used to eliminate variables that were redundant (those that had very similar loadings over all eigenvectors) or those that were most weakly related to the major trends of variation in the pooled data. The latter were assessed as described in Maze et al. (1992), i.e., prorating of eigenvector values based on the percent variation for which the various axes account, and then summing over all eigenvectors. This initial comparison and adjustment of variables was made without assuming that two taxa exist. If they do then a multivariate analysis of those variables whose importance is determined independently should still reveal their existence.

As the end result of these manipulations, the variables subjected to a second PCA were INFLTYPE (inflorescence form, lax or erect), SHEATH (length of the sheath of the flag leaf), BLADE (length of blade of flag leaf), GIL (length of the first glume), FL (length of floret, including the callus), FW (width of floret), AXISTHCK (thickness of the midportion of the inflorescence axis), BRNLN (length of the lowermost inflorescence branch), and INFLN (inflorescence length). The plants used in the analysis were those collected in 1993 and the type specimen of *A. hendersonii*. Means and standard deviations for plants with different inflorescence types were calculated for the variables described above.

Another comparison based on the recognition of two species was made. The variable interrelations within each of the putative species were assessed through determinants of correlation matrices and the angle between the first principal axes from the correlation matrices and a vector of isometry. The determinant is a statistic, a generalized variance, that describes the absolute values of the off-diagonal elements in a matrix. As the elements approach 0.0, the determinant of a correlation matrix approaches 1.0, as those off-diagonals come to approximate 1.0, the determinant of a correlation matrix becomes closer to 0.0. A vector of isometry is a theoretical vector derived from a matrix in which all the off-diagonal elements are identical. As such, a vector of isometry offers a means to describe the off-

TABLE 1. COMPARISON OF VARIABLES MOST CLOSELY RELATED TO MAJOR AXES OF VARIATION BETWEEN LAX INFLORESCENCE FORM AND *A. HENDERSONII*, Mean Above, Standard Deviation Below. SHEATH, length of the sheath of the flag leaf in cm; BLADE, length of blade of flag leaf in cm; INFLN, inflorescence length in cm; AXISTHCK, thickness of the midportion of the inflorescence axis in mm; BRLN, length of the lowermost inflorescence branch in mm; G1L, length of the first glume in mm; FL, length of floret in mm; FW, width of floret in mm; *, groups significantly different at $P < 0.05$.

	<i>A. hendersonii</i>	Lax inflorescence form
Variables		
SHEATH*	6.250	8.434
	1.106	1.474
BLADE	3.113	3.080
	0.816	0.930
INFLN*	8.267	10.623
	2.069	2.033
AXISTHCK*	1.123	0.803
	0.239	0.113
BRLN*	3.368	4.785
	1.112	1.255
G1L*	4.728	5.186
	0.657	0.642
FL*	4.530	4.216
	0.542	0.533
FW	1.388	1.351
	0.232	0.181

diagonal elements of a correlation matrix derived from measured variables through calculating the angle between a vector of isometry and a first principal axis derived from measured variables. As that angle increases, to a maximum of 90 degrees, the off-diagonal elements in a correlation matrix derived from measurements become increasingly different. These statistics can also be viewed as estimators of among-variable variation (Rapson and Maze 1984). As either determinants or angles with a vector of isometry increase, the among-variable variation increases.

RESULTS

Table 1 presents the means and standard deviations for those variables, averaged for each putative taxon, that were subjected to PCA. Inflorescence type is not included in this table as it was a binary variable. Not only are there differences in inflorescence form but also in the lengths of sheaths of the flag leaf, inflorescence, lowest inflorescence branch, first glume and floret and the thickness of the axis of the inflorescence. Generally speaking, the variables for the lax inflorescence form have the higher values, aside from floret length and thickness of the inflorescence axis.

Table 2 presents the results of the PCA and the graphic results of

TABLE 2. RESULTS OF PCA. INFLTYPE, inflorescence form; SHEATH, length of the sheath of the flat leaf; BLADE, length of blade of flag leaf; G1L, length of the first glume; FL, length of floret; FW, width of floret; AXISTHCK, thickness of the mid-portion of the inflorescence axis; BRLN, length of the lowermost inflorescence branch; INFLN, inflorescence length.

Eigenvalues	3.339	1.951	1.621
Percent variance accounted for	37.097	21.679	18.008
Eigenvectors			
SHEATH	0.897	0.038	0.000
BLADE	0.452	0.355	0.559
INFLTYPE	-0.732	0.439	0.411
AXISTHCK	-0.365	0.304	0.793
INFLN	0.835	-0.114	0.432
BRLN	0.790	-0.156	0.297
G1L	0.567	0.605	-0.392
FL	0.045	0.890	-0.172
FW	0.125	0.585	-0.228

this PCA are presented in Figure 3; the two grasses are separated from each other to some degree with *A. hendersonii* occupying the left hand portion of the ordination and the lax inflorescence forms grouping to the right.

The lax inflorescence form most similar to *A. hendersonii* on the first axis, those individuals designated by solid squares in Figure 3, came from an area with a very thin soil that was grazed by cattle. Whether it is the edaphic factors, the impact of cattle, or both, that are related to the form of the plants, they tend to be smaller than others with lax inflorescences as shown in Table 3, a comparison of the measured variables and PCA axis scores among *A. hendersonii*, the lax inflorescence forms, and such designated by the solid squares in Figure 3. The grazed specimens of the lax inflorescence form are as similar to *A. hendersonii* as they are to plants with similar inflorescences on the major axis of variation, the first principal axis.

Interestingly, the *A. hendersonii* that tend to be most similar to the lax inflorescence form (there is, in fact, some overlap among these plants) are the most distantly removed geographically, coming from central Washington. The plants of *A. hendersonii* geographically closest to the lax inflorescence form, those from central and northern Oregon, are the most distantly removed from them in the scatter plot in Figure 3. The specimen designated T is the type specimen of *A. hendersonii*; it is nested within the samples of *A. hendersonii*.

Figure 3 depicts the relationship among individual plants, an assessment of among plant variation. Estimators of among-variable relationships, determinants and angles with a vector of isometry, indicate they are different for the plants with the different inflores-

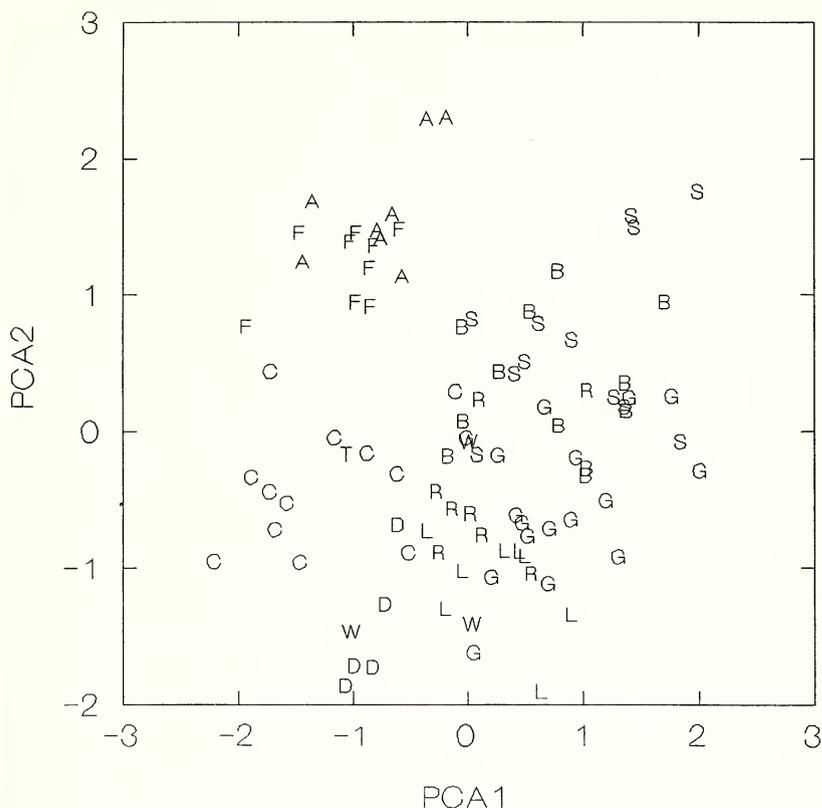


FIG. 3. PCA of length of the sheath of the flag leaf, length of blade of flag leaf, inflorescence type, inflorescence length, thickness of the midportion of the inflorescence axis, length of the first glume, length of floret, width of floret. Open stars, *A. hendersonii*; open squares, the lax inflorescence form; closed squares, the lax inflorescence form that has been grazed; PCA 1, first principal axis, 31.634% of the variation in the data; PCA 2, second principal axis, 25.921% of the variation in the data.

cence forms. *Achnatherum hendersonii* has a determinant of 0.020 and an angle between the first principal axis and a vector of isometry of 86.87 as compared to 0.003 and 15.67 respectively for the plants with lax inflorescences.

DISCUSSION

The plants of unlike inflorescence form also differ in other morphological features. As well, the two forms have unique geographic distributions and divergent patterns of among-variable relationships. The type of *A. hendersonii* has a stiff inflorescence with erect spike-

TABLE 3. COMPARISON OF *A. HENDERSONII* (AH), the Lax Inflorescence Form (AW), and the Lax Inflorescence Form that has been Grazed (AWD). Mean above, standard deviation below. SHEATH, length of the sheath of the flag leaf in cm; BLADE, length of blade of flag leaf in cm; INFLN, inflorescence length in cm; BRLN, length of lowermost inflorescence branch in cm; AXISTHCK, thickness of the midportion of the inflorescence axis in mm; GIL, length of the first glume in mm; FL, length of floret in mm; FW, width of floret in mm; PCA1-PCA3, scores on first three PCA axes; underlined means identify those that are statistically significant ($P < 0.05$).

	AH	AW	AWD
Variables			
SHEATH	6.250	8.603	6.400
	1.106	<u>1.397</u>	0.616
BLADE	3.113	3.180	1.880
	0.816	0.892	<u>0.396</u>
INFLN	8.267	<u>10.850</u>	7.900
	2.039	<u>1.940</u>	0.768
AXISTHCK	1.124	0.803	0.812
	<u>0.239</u>	0.115	0.099
BRLN	3.368	4.917	3.200
	1.112	<u>1.213</u>	0.292
GIL	4.735	5.267	4.303
	0.658	<u>0.599</u>	0.524
FL	4.537	4.267	3.681
	0.543	0.527	<u>0.276</u>
FW	1.391	1.363	1.218
	0.232	0.179	0.171
PCA1	-1.072	0.606	-0.841
	0.542	<u>0.655</u>	0.187
PCA2	0.643	-0.201	-1.450
	<u>0.992</u>	<u>0.815</u>	<u>0.484</u>
PCA3	0.602	-0.239	-0.737
	<u>1.239</u>	0.727	0.565

lets, a point noted in its species description. This suggests that the lax inflorescence form represents a new taxon. There is the question, however, of the level at which that new taxon should be recognized. Its closest relative is obviously *A. hendersonii*; both taxa share mature florets of comparable size that are shiny, brown to black at maturity, glabrous and indurate. As well, both have a thickened portion at the adaxial side of the lemma apex that extends above the base of the awn, and the palea is subequal to the lemma. The separation between *A. hendersonii* and the lax inflorescence form in the scatter plot (Figure 3) is not great; its magnitude is similar to that seen for the two subspecies of *Hesperostipa* (*Stipa*) *comata* (Trinius and Ruprecht) Barkworth, ssp. *comata* and ssp. *intermedia* (Scribner and Tweedy) Barkworth (Barkworth 1978).

In spite of strong similarities to *A. hendersonii* and a degree of separation in an ordination similar to that of subspecies of another species in the Stipeae, we decided to recognize this new taxon at

the specific level as *Achnatherum wallowaensis* Maze and K. A. Robson. There are five reasons for this decision. First, the two taxa are consistently separated by one very distinct morphological feature: drooping inflorescences for *A. wallowaensis* and erect ones for *A. hendersonii*. There are no known intermediates. Second, these two taxa differ in other features such as length of sheaths, inflorescences, longest branch of the inflorescence, first glume, and floret and thickness of the inflorescence axis. Third the two taxa, *A. wallowaensis* and *A. hendersonii*, do not occur sympatrically although they are within 20 kilometers of each other in the Ochoco Mountains in central Oregon. Fourth, the individuals of *A. hendersonii* most similar to *A. wallowaensis* are the most distant geographically. Fifth, the among variable relationships are different for the two species. The species description appears below.

A final observation we would make is that seedlings appear to be extremely rare in many of the *A. hendersonii* populations, while seedlings were numerous for at least one of the populations of *A. wallowaensis* from northeastern Oregon. Both of these species are rare and reproduction needs further study.

***Achnatherum wallowaensis* Maze and K. A. Robson sp. nov.—**

TYPE: USA, Oregon: Wallowa Co., Wallowa-Whitman National Forest, ca. 34 km N of Enterprise, near Boner Gulch along Forest Service Road 46, 1481 m, 45°43'41.16"N × 117°8'10.32"W (SW ¼ of SE ¼, section 24, T 3 N, R 45 E). *J. and E. Maze, K. A. Robson, T. Henn 1007* 26 June 1993. (holotype, US; isotypes, UTC, UBC, WTU, OCS, COLO, NMC, DAV, UC, ID).

Perenis gramen sine rhizoma, (1)1.5–4(4.5) dm altus; vegetativus lamina erectus et valde involutus; inflorescentia (6.3)8.1–12.6(14.8) cm longus, laxis cum spicula cernuus; spicula cum unus anthracinus ad brunneus induratus flosculus (3.0)3.5–5.0(5.5) cm longus, aequalis gluma; arista deciduus 8–10(11) mm longus; palea subaequalis lemma.

Non-rhizomatous perennial; culms solid to hollow, (1)1.5–4(4.5) dm tall; sheaths glabrous to puberulent; blades strongly involute, erect to sometimes reflexed in the flag leaf, glabrous ventrally, pubescent dorsally; panicle (6.3)8.6–12.6(14.8) cm long, broadly spreading with lax branches and drooping spikelets on curved pedicels; glumes obtuse to acute, first (3.5)4.5–6.0(7.0) mm long, second (3.0)4.0–4.5(6.5) mm long; floret (3.0)3.5–5.0(5.5) mm long, 1.0–1.5 mm wide, apex of dorsal side of lemma thickened, maturing black to dark brown; awn 8–10(11) mm long, readily deciduous; palea subequal to the lemma; anthers 1 mm long or less, ventral lodicule reduced.

Paratypes. USA, Oregon: Crook Co., ca. 30 km NE of Prineville, Ochoco National Forest near U. S. Forest Service Road 2730, Bull Mountain, 1481 m, 44°31'47.28" N × 120°36'56.52"W (border between SE ¼, section 7 and NE ¼, section 18, T 12 S, R 18 E), plants growing in shallow rocky soil with *Mimulus nanus*, *Astragalus whitneyi*, *Clarkia pulchella*, *Phlox hoodii*, *Eriogonum compositum* var. *compositum*, *Poa sandbergii*, *Arenaria rubella*, *Danthonia intermedia*, *Erigeron chrysopsidis* var. *chrysopsidis*, *Lomatium macrocarpum*, *Blepharipappus scaber*, *Sedum stenopetalum* (Plant names here and elsewhere follow Hitchcock and Cronquist 1973), *J. and E. Maze 1001*, 22 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC, DAV); Ochoco National Forest, ca. 30 km NE of Prineville, near U.S. Forest Service road 2730, ca. .8 km SE Skookum Rock, 1353 m; 44°33'15.12"N × 120°34'31.44"W (middle, section 9, T 12 S, R 18 E), plants growing in shallow rocky soil with *Mimulus nanus*, *Astragalus whitneyi*, *Clarkia pulchella*, *Phlox hoodii*, *Eriogonum compositum* var. *compositum*, *Poa sandbergii*, *Arenaria rubella*, *Danthonia intermedia*, *Erigeron chrysopsidis* var. *chrysopsidis*, *Lomatium macrocarpum*, *Blepharipappus scaber*, *Sedum stenopetalum*; *J. and E. Maze 1002*, 22 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC, DAV, UC, ID); Wallowa Co., ca. 15 km E of Joseph, near Cat's Back along Wallowa Co. Road 673, 7.8 km from Oregon State Highway 350, 1584 m, 45°20'45.96"N × 117°00'50.76"W (SE ¼ of NW ¼, section 36, T 2 S, R 46 E), plants growing in shallow rocky soil with *Bromus tectorum*, *Sitanion jubatum*, *Mimulus nanus*, *Lomatium cous*, *Haplopappus lanuginosus* var. *lanuginosus*, *Poa sandbergii*, *Scutellaria antirrhinoides*, *Alyssum alyssoides*, *Penstemon elegantulus*, *Eriogonum douglasii*, *Tragopogon dubius*, *Polygonum minimum*, *J. and E. Maze*, *K. A. Robson*, *T. Henn*, *M. Stein 1004*, 25 June 1993 (US, UTC); ca. 18 km ENE of Joseph, 19.7 km from Oregon State Highway 350 along Forest Service Road 900, Clear Lake Ridge, 1499 m, 44°25'10.56"N × 116°57'11.16"W (center, section 4, T 2 S, R 47 E), plants growing in shallow rocky soil with *Bromus tectorum*, *Alyssum alyssoides*, *Penstemon elegantulus*, *Eriogonum strictum* var. *strictum*, *Allium tolmei*, *Tragopogon dubius*, *Polygonum minimum*; *P. majus*, *Trifolium macrocephalum*, *Sedum stenopetalum*, *Lomatium cous*, *Poa sandbergii*, *Arabis* sp., *J. and E. Maze*, *K. A. Robson*, *T. Henn*, *M. Stein 1005*, 25 June 1993 (US, UTC, UBC, WTU, OCS, COLO, NMC); Wallowa-Whitman National Forest, ca. 24 km N of Enterprise, near Roberts Butte, along Forest Service Road 4605 near its junction with Forest Service Road 46, 1097 m, 45°38'23.64"N × 117°13'3.36"W (middle southern boundary, section 20, T 2 N, R 45 E), plants growing in shallow rocky soil with *Bromus japonicus*, *Blepharipappus scaber*, *Mimulus nanus*, *Eriogonum strictum*, *Scutellaria antirrhinoides*, *Lomatium macrocarpum*, *L. dissectum*, *L.*

triternatum, *L. ambiguum*, *L. sp.*, *Sedum stenopetalum*, *Penstemon deustus*, *Epilobium sp.*, *Clarkia pulchella*, *Allium tolmei*, *Poa scabrella*, *P. sandbergii*, *J. and E. Maze*, *K. A. Robson*, *T. Henn*, 1006, 26 June 1993 (US, UTC, UBC, WTU, OCS); Wallowa-Whitman National Forest, ca. 37 km N of Enterprise, on ridge just S East Fork of Sumac Creek, at end Forest Service Road 268 off of Forest Service Road 46, 1292 m, 45°45'27"N × 117°8'10.32"W (NE ¼ of NW ¼, section 12, T 3 N, R 45 E), plants growing in shallow rocky soil in site badly disturbed by cattle with *Poa sandbergii*, *Agropyron spicatum*, *Sedum stenopetalum*, *Chrysothamnus nauseosus*, *Polygonum majus*, *Phlox hoodii*, *J. and E. Maze*, *K. A. Robson*, *T. Henn*, 1008 26 June 1993. (US, UTC, UBC).

Distribution. Shallow rocky soils in scattered localities at 1000–1600 m in the Wallowa Mountains of northeastern Oregon and Ochoco Mountains of central Oregon.

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This work was aided immeasurably by the United States Forest Service through Paula Brooks, Marty Stein, Michael L. Simpson, and Lisa Croft, and the Nature Conservancy of Oregon through Berta Youtie and Jonathan Soll. Tom Henn and Ellie Maze were essential to the efficient collecting of specimens, Mary Barkworth, Cy Finnegan, Gordon Haas and John Reeder helped clarify some of the more esoteric phrases that appeared in early versions of this paper.

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ROMANZOFFIA THOMPSONII (HYDROPHYLLACEAE),
A NEW SPECIES FROM OREGON

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ABSTRACT

Romanzoffia thompsonii, a new species from Oregon is unique in the genus in its annual, bulbless habit, in having some lower leaves opposite, in always having some basal leaves entire and the distinct form of those that are lobed, and apparently in having throat spots or bands. This is also the smallest species of the genus in nearly every respect save seed size. Range and habitat, similarities to and differences from other members of this genus, and how this species modifies the concept of the genus are detailed.

With the addition of *Romanzoffia thompsonii*, the genus now consists of five species of temperate, western North America. All are fibrous-rooted, mesophytic herbs with helicoid inflorescences of \pm funnellform flowers arising from a basal rosette of long-petiolate, \pm ovate, orbicular or reniform, often lobed leaves; the single style is undivided or only minutely bilobed at the apex. The lobed, orbicular to reniform basal leaves of the perennials arise from bulbs or bulb-like developments; the annual is bulbless and some of its \pm ovate to orbicular basal leaves are always entire. Although none of these features is restricted to *Romanzoffia*, simple styles are absent elsewhere in the Hydrophyllaceae except for *Phacelia tetramera* J. Howell. The perennial species are an even more distinctive group; their bulbs are singular in the family. *Romanzoffia thompsonii*, although annual and bulbless, is otherwise similar to the perennials. Its greatest similarities are with *R. californica* E. Greene and *R. sitchensis* Bong., with which it shares a distinctive assortment of features.

From its first collection in 1899 to 1970 there were only six localities known for this species (South Peak, Cone Peak, Iron Mt., Lost Ck. Ranch, Spencer's Butte, and Abbott Butte). Reporting its existence at conferences on rare, threatened and endangered plants in Oregon in 1975–1977 resulted in its "rare" listing (Siddall, et al. 1979) and stimulated considerable field work and other published references (see Fitz 1979, Meinke 1982, Ross and Chambers 1988). By 1983 about 20 sites were known, most based on herbarium specimens. Since then, over 100 sites have been recorded, most based on BLM or US Forest Service Sighting Reports. Although many of these latter sites have been documented, and although both the distribution and habitat data from the Sighting Reports strongly parallel

that from the herbarium record, Sighting Report data is used here to augment understanding of this plant's habitat and for the two Coos County localities listed in the discussion of the distribution of *R. thompsonii*.

It is with great pleasure that I dedicate this new species of *Romanzoffia* to the late J. William Thompson, long a student and an assiduous collector of the Pacific Northwest flora, especially *Romanzoffia*. I have selected his collection, the first material I saw of this species, as the type.

Romanzoffia thompsonii Marttala, sp. nov. (Fig. 1).—TYPE: USA, Oregon, Douglas Co., Abbott Butte, alpine slopes, 6000', 2 Jul 1936, *J. W. Thompson 13069* (holotype, NY; isotypes, MO, ND-G, WTU).

In genere suo duratione annua, bulbis destitutis, foliis inferioribus nonnullis oppositis, foliis basalibus saepe integris (si lobatis tunc modo distincto), necnon omnium partium (praeter semina) magnitudine minima singularis.

Annual, \pm erect, gracile herb, (1.5–)2.5–10(–18) cm tall, growing singly or usually in loosely to densely aggregated mats or clumps (to ca. 50 cm across if dense); bulbless. Cotyledons usually persisting; petioles ca. 5 mm long; blade oblong-deltoid, 2–3 mm long. Leaves \pm succulent, ca. 0.5 mm thick, \pm glaucous (fresh), some of the lower leaves opposite, the upper usually alternate; petioles (3–)5–15(–25) mm long, the basal 2–5(–8) mm flattened, 0.5–1.5(–3.0) mm broad, but neither thickened (or only slightly so) nor persisting as a bulb scale, glandular-villous, especially basally; blades ovate to orbicular to obovate, entire to 3(–5)-lobed, 1–5(–10) mm long, 1–5(–9) mm broad, nearly glabrous to sparsely glandular-villous, at least the margins sparsely stipitate-glandular, base attenuate to truncate, sinus not evident in herbarium specimens but occasionally a small sinus is seen in living material whose bases are thus cordate, lobes often only small teeth, commonly unequal, triangular-ovate, broadest at or near the base of the lobe, rarely broadly ovate and broadest above the base of the lobe, 0–2(–4) mm long, apex (and that of the lobes) acute, obtuse to mucronulate; cauline leaves similar to the basal but reduced. Inflorescence ca. twice as long as or longer than the basal leaf rosette, axis often winged; terminal cyme 1, (1–)2–3(–5)-flowered; lateral cymes 1–3, each 1–2(–5)-flowered; each cyme with 1(–2) cymules of 1–2 flowers; flowering pedicels (2–)4–6(–10) mm long, fruiting pedicels (5–)7–15(–25) mm long, thus inflorescences open (see Table 1, Habit Syndromes), axis and pedicels minutely stipitate-glandular; propagules absent. Calyx lobes lanceolate to triangular, acute or obtuse to mucronulate, (1.0–)1.5–2.5(–3.0) mm long, (0.3–)0.4–0.6(–0.7) mm broad, almost gla-

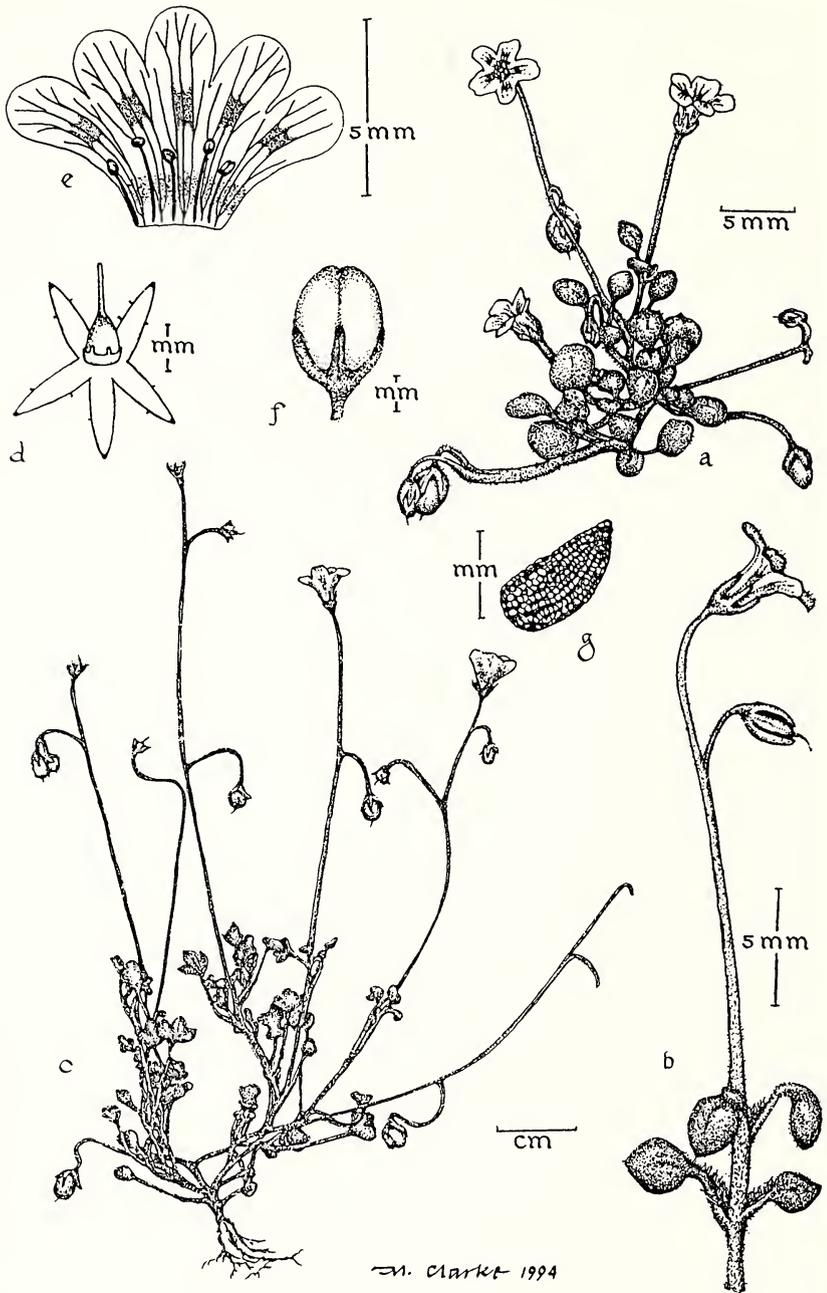


FIG. 1. *Romanzoffia thompsonii*: a-c, habit; d, calyx and gynoecium; e, corolla interior and stamens; f, capsule; g, seed. (a, b from photos; c, d, f, g from specimens;

TABLE 1. COMPARISON OF THE SPECIES OF *ROMANZOFFIA*.

>>>>>>>Bulbous perennials; only the cotyledons opposite; basal leaf blades reniform to orbicular with cordate to truncate bases, some always sinusate (sinus ~ 3/10 of blade length), some always >1 cm broad, rarely with fewer than 5 lobes; corollas mostly 5–10 mm long, without throat spots; seeds >15 per capsule, averaging 1.0–1.3 mm long

	Habit Syndrome #1	Habit Syndrome #2
	Slender, ± glabrous, glandular-villous, lax to sublux plants (inflorescences ≥ 2 × to 1.5–1 × basal rosette) with open inflorescences (flowering pedicels ≥ 2 × calyx length); calyx lobes 0.5–1.4 mm wide; styles longer; rarely coastal	± Stout, viscid-villous, very rarely glandular, condensed to sublux plants (inflorescences ~ to 1.5–2 × basal rosette) with compact inflorescences (flowering pedicels ~ calyx) calyx lobes 1.0–2.1 mm wide; styles shorter; coastal
Bulb Feature Syndromes		
Bulbs scaly; scales spirally arranged, evident, villous; styles glabrous, shorter than next; distribution more northern than next	1. <i>R. sitchensis</i> Plants lax to sublux Styles mostly >2 mm long AK to CA, ALTA, MT + ID	3. <i>R. unalascensis</i> Plants condensed to sublux Styles mostly <2 mm long AK (+ Brit. Col.?)
Bulbs tuberlike; scales distichously arranged, obscured by woolly pubescence; style base usually villous	2. <i>R. californica</i> Plants lax Styles mostly >3 mm long OR + CA	4. <i>R. tracyi</i> Plants condensed (to sublux) Styles mostly <3 mm long Brit. Col. to CA
>>>>>>>Bulbless annual; some of lower leaves as well as cotyledons opposite; basal leaves ± ovate to orbicular with cuneate to attenuate bases, rarely sinusate (then sinus ~ 1/10 of blade length), <1 cm broad, mostly entire, to 3, rarely 5-lobed; corollas mostly ≤5.5 mm long, with throat spots; seeds ≤12 per capsule, averaging 1.7 mm long; OR	5. <i>R. thompsonii</i>	

brous to sparsely glandular-villous. Corolla funnellform, (3.0–)4–5.5 (–7.0) mm long, limb eventually spreading, (2.5–)3.5–5(–6.5) mm broad, base of the corolla 1.0–1.5 mm wide, tube 1–2(–3) mm long, lobes oblong-deltoid to ovate, apex obtuse or truncate to rarely re-

←
e from photos and specimens. a from *Marttala 3097b, 3097a*; b, e–g from *Marttala 4515*; c from *Holmes 752*; d from *Marttala 3097*. Note: a and b illustrate only the above ground parts of the plants seen in the photographs, but when the plant in b was in fruit, the root system was 2/5 of the plant's total length.)

tuse, 1–2 mm long, 1.0–1.5 mm broad; tube and lower throat with a gold band about 1 mm wide, the top of which approximates the top of the calyx; throat with five gold, rarely yellow spots \pm 0.5 mm across, overlapping the base of the corolla lobes, alternating with the sinuses, or rarely a gold band \pm 0.5 mm wide at the same height; these markings seldom evident in herbarium material. Stamens 1–2.5 mm long; filaments 1.0–2.1 mm long; anthers (0.3–)0.4–0.6 mm long, (0.2–)0.3–0.5 mm broad. Disk 0.1–0.3 mm tall, appendages subulate to deltoid, 0.1–0.2 mm high. Ovary at anthesis 0.5–1.1 mm tall, 0.4–0.7 mm broad, sparsely glandular to glabrous; style (0.4–)0.7–1.3(–1.8) mm long, glabrous or the basal 0.3 mm or less sparsely villous, stipitate-glandular or glandular-villous. Capsule oblong to elliptic, (2.0–)2.8–5.0(–6.0) mm long, (1.5–)1.8–3.0(–3.4) mm broad, (1.2–)1.3–1.9(–2.1), averaging 1.6 times as long as broad, sparsely glandular to glabrous. Seeds (1–)4–8(–12); (1.4–)1.5–2.0(–2.4), averaging 1.7 mm long, 0.6–1.0(–1.2), averaging 0.8 mm broad; dull brown when mature. Blooms from March to early August, depending on site and season.

PARATYPES. USA, Oregon, Marion Co.: rock outcrop along F.S. Rd. 4685 ca. 1.6 mi S of Rd. 46, *Marttala* 4528 (NY, OSC). Linn Co.: slopes above F.S. Rd. 1003–409, ca. 0.4 mi S of Beard Saddle, *Marttala* & Poff 4515 (NY, OSC, Reed C); slopes above F.S. Rd. 2067–560 ca. $\frac{1}{4}$ mi E of start of Trail 3380, *Marttala* 4482 (NY, OSC); Cone Peak, *Antos* 485 (OSC), *Marttala* 3443 (F, HPSU, MO, NY, Reed C, RSA, TEX, U, UC, US); Iron Mt., *Eggleston* 22164 (US); Browder Ridge, T14S R6E S5, *Antos* 481 (OSC). Lane Co.: cliffs along Hwy 126, 2.3 mi S of Linn Co. line, *Marttala* 3441b (MT, NY, OSC, UBC, US, UTC, WS); cliffs along Hwy 126, 2.4 mi S of Linn Co. line, *Marttala* 3460a (CAN, CAS, ID, ISC, NY, Reed C); slope above Hwy 126, T16S R4E S23, *Close EO* # 042 (Hb. WNF); Northwest primary base of Spencer's Butte, *Verl White s.n.*, 8 May 1935 (ORE); bluffs near Lost Ck. Ranch [S of Lowell], *Andrews* 413 (ORE); rock outcrop below Rd. # 140 [not 141], T 20S R3E S6, *Pavlet* 31w (Hb. WNF). Douglas Co.: "Dome Rock", T24S R3E S35, *Everett EO* # 039 (Hb. WNF); bald, T24S R1W S18, *Holmes* 795 (ORE); rock bluff above Rd. 3806, 0.8 mi E of Siwash Ck., *Fontaine, Godfrey & LaMarr, Acc. # 4/R-6 SR # 593* (Hb. NURD: photocopy!); Medicine Ck. Rd. at Slide Ck., *Hopkins, Thiele, Fosback & Carlson M174* (Hb. DCM/RO); F.S. Rd. 28 ca. $\frac{1}{4}$ mi S of junc. with Rd. 2801 at Copeland Ck. Bridge, *Marttala & Ford* 3359 (ALA, DAO, NY, S, UC, WTU); F.S. Rd. 28 ca. 0.5 mi S of junc. with Rd. 2801 at Copeland Ck. Bridge, *Marttala & Ford* 3357 + 3557a (B, G, GH, NY, OSC, P, Reed C, UC, US, WTU); Cougar Bluffs, *Joan Fosback s.n.*, 6 Jun 1979 (OSC); bald, T26S R2W S25, *Holmes* 1073 (Hb. BLM/RD); rock outcrop $\frac{1}{4}$ mi

SW of Clover Butte, *Tighe s.n.*, 29 Jul 1993 (Hb. NURD: photocopy!); bald, T27S R3W S25, *Holmes 752* (Hb. BLM/RD, ORE); near Rd. 6510, 0.6 mi S of Flat Ck. crossing, *Loftis & Scully s.n.*, 19 Jun 1990 (OSC); Abbott Butte [topotypes?], *Leiberg 4251* (ORE, US), *Marttala 3097* (F, GH, K, LE, NY, OSC, Reed C, UC), *Marttala 3097a* (F, GH), *Marttala 3097b* (K, LE, MO); Beatty Ck. rocks, Cow Ck. canyon, *Hopkins, Thiele, Fosback & Carlson M148* (Hb. DCM/RO); Irwin Rocks, *Joan & Ollie Fosback s.n.*, 10 Apr 1978 (NY, OSC, UC, WTU); meadow ca. 14 km SE of Remote, *Sundberg 843* (Hb. BLM/RD, OSC), below Rd 33.1, T30S R9W S33, *Rittenhouse 961* (Hb. BLM/CBD: photocopy!).

Romanzoffia thompsonii is confined to Marion, Linn, Lane, Douglas and Coos (?) Counties (Fig. 2). It occurs in the Cascade Mountains and western foothills, from the upper North Santiam River drainage, south to within 0.1 mi of the Jackson County border on Abbott Butte, in the upper Rogue River and South Umpqua River drainages, west to the Southern Coast Mountains of the Middle Fork of the Coquille River drainage southeast of Remote and near Irwin Rocks in the adjacent South Umpqua River drainage, reaching Coos County at "Kenyon Mt. near Remote" (Siddall, personal communication of a Sundberg 1980 Sighting) and possibly near Bridge (Bruce Rittenhouse, personal communication). *Romanzoffia sitchensis* occurs from Alaska south to northern California, but only occasionally in Oregon and California; *R. californica* extends north from the San Francisco Bay area to the Oregon Coast Mts. of Tillamook County and Cascade Mts. of northern Lane County. Except for Marion and Linn Counties, the range of *R. thompsonii* is contained within the zone of overlap between *R. californica* and *R. sitchensis*.

Romanzoffia thompsonii grows in seasonally wet, usually open, rocky, sunny habitats. The elevation varies from approximately 230–1830 m (ca. 750–6000 feet). These sites most commonly face south to southwest (very rarely north). About two hundred plant species are known to grow with *R. thompsonii*. The most common are mosses, especially *Bryum miniatum*, *Mimulus guttatus*, *M. alsinoides*, *Plectritis congesta*, *Delphinium menziesii*, *Saxifraga integrifolia*, *S. nuttallii*, *S. marshallii* or *S. occidentalis*, *Collinsia parviflora*, *Montia parvifolia*, *M. fontana*, *Romanzoffia californica*, *Achillea millefolium*, *Cystopteris fragilis*, *Eriophyllum lanatum*, *Gilia capitata*, *Microsteris gracilis*, *Lewisia triphylla*, *Pseudotsuga menziesii*, *Holodiscus discolor*, *Calocedrus decurrens*, *Acer macrophyllum*, *Arbutus menziesii* and *Quercus garryana*. *Romanzoffia thompsonii* and *R. californica* grow together at perhaps 20% of the known *R. thompsonii* sites, at elevations of ca. 290–1370 m (960–4600 feet); at these locations the two species often grow completely intermixed in the moister parts of the habitat favored by *R. thompsonii*. Herbarium

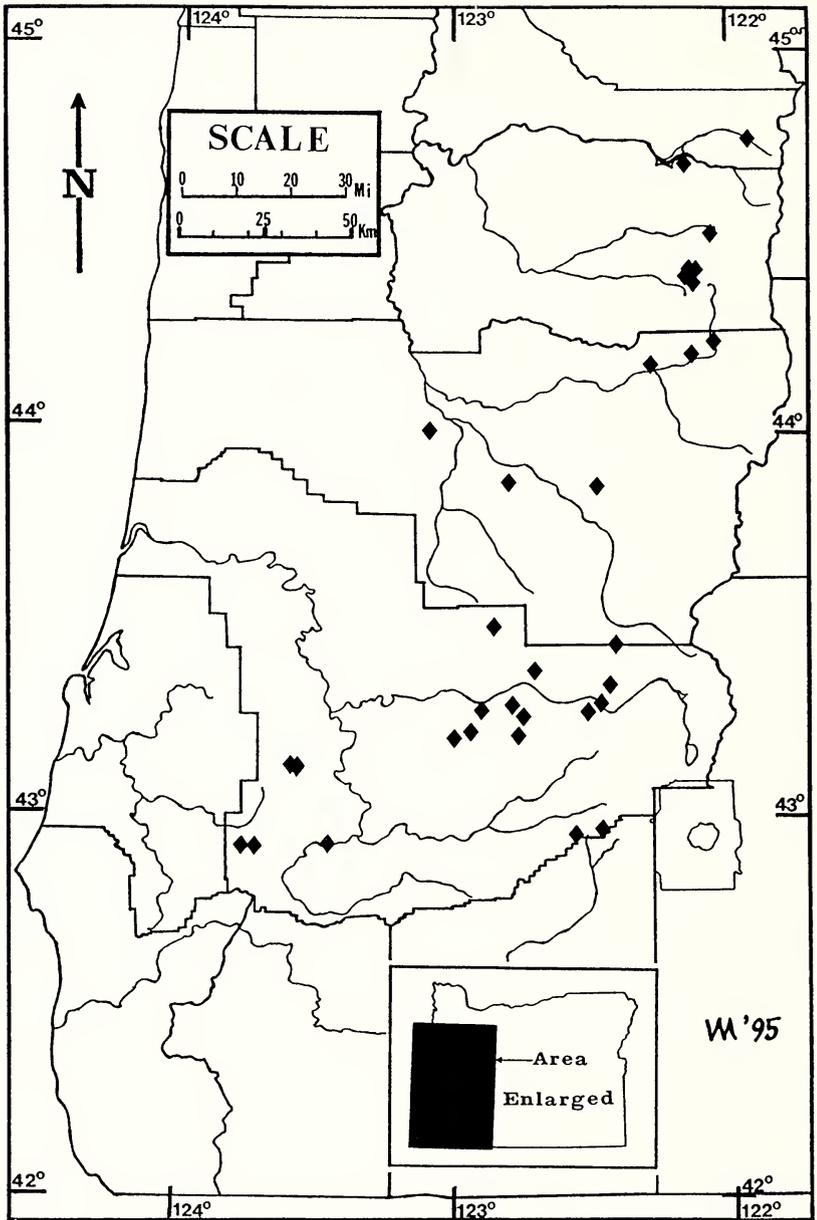


FIG. 2. Distribution of *Romanzoffia thompsonii* (solid diamonds) in western Oregon. Insert shows area enlarged.

label data and my own observations suggest that *R. thompsonii* requires saturated or inundated soil during the early part of its growing season. Later in the season these habitats experience a strong summer drought. These data suggest that this is a facultative, if not obligate, wetland plant. Site size and density vary considerably, from <10 plants in a site of a square meter to population systems estimated as tens of thousands of plants found over several acres. In larger populations the area in which *R. thompsonii* grows is often only a small part of the site in which it does occur, e.g., *Marttala 3441b* and *3460a*, Lane County sites of perhaps 50 and 75 m² on a cliff system about 0.8 km long.

Although now known from a large number of sites, the narrowness of its habitat, its annual habit and the small size of many of its populations warrant continued concern for the conservation of this species. The current status of *R. thompsonii* is Priority 1—'threatened or endangered throughout its range' (Oregon Natural Heritage Plan 1993). Probably the greatest threat to its survival are major habitat changes, e.g., erosion, loss of site water, succession converting the habitat into forest.

Table 1 and the description show that *Romanzoffia thompsonii* shares Habit Syndrome # 1 with calyx width and style length considered in proportion to flower size (see Table 2); in these respects it is unlike *R. unalaschensis* Cham. and *R. tracyi* Jepson, which share Habit Syndrome # 2. These data also show strong similarity between *R. thompsonii* and *R. sitchensis* f. *suksdorfii* (E. Greene) Brand (Brand 1913): calyx width, corolla size and style length in *R. thompsonii* approximate one half of the corresponding measurements in *R. sitchensis* f. *suksdorfii*; these taxa are also similar in corolla shape and capsule length/width ratio, but *R. sitchensis* f. *suksdorfii*, which occurs only in the Columbia River Gorge, has very different yellow eyes. In corolla shape, relative size of calyx and corolla (about twice as large as those of *R. thompsonii*), and yellow eye *R. californica* resembles *R. thompsonii*; but in longer styles and narrower capsules *R. californica* is dissimilar. While bulbless, *R. thompsonii* does share some bulb syndrome features with *R. californica*, i.e., a more southern distribution and the frequently, if inconsistently, pubescent style bases. The phase of *R. sitchensis* occurring closest to *R. thompsonii* is f. *greenei* Brand (Brand 1913, published this as f. *vulgaris*, following the American Code): it is found throughout western Oregon, but it is quite different from *R. thompsonii* in these features.

Among *Romanzoffia* the open, exposed habitats of *R. thompsonii* are most like those of the often sympatric *R. californica*. However, the habitats of *R. thompsonii* usually face \pm south (opposite the typical *R. californica* situation), and where they do grow together, *R. thompsonii* only occurs in the wetter part of their common habitat

TABLE 2. COMPARISON OF *ROMANZOFFIA THOMPSONI*, *R. SITCHENSIS*, and *R. CALIFORNICA*. Values given include 86–95% of measurements made.

Character	Taxon		
	<i>R. thompsonii</i>	<i>R. californica</i>	<i>R. sitchensis</i> f. <i>greenii</i>
Corolla Shape	long funnellform	long funnellform	broadly funnel- form/± rotate
Corolla Length	4–5.5 mm	7–10 mm	5–8 mm
Style Length	0.7–1.3 mm	3.5–6 mm	2.3–5 mm
Style Base Pubescence	present—but incon- sistently—in nearly half of populations	present, except in- consistently so in nearly half of populations near San Francisco	absent
Capsule Length/Width Ratio	1.4–1.8	1.7–2.1	1.2–1.4
Yellow Eye	gold band in upper tube and lower throat	gold band in upper tube and lower throat	gold band in lower throat
			1.4–1.75 diffuse yellow band in throat

or where the water supply persists longer. Although Leiberg also collected *R. sitchensis* on Abbott Butte (4259, ORE!, US!), his field books (US!) indicate that it was collected at a locality different from that of *R. thompsonii*. The habitat of *R. sitchensis*, as well as the ecotype of *R. californica* that Greene (1902) called *R. spergulina*, is generally more mesic, moister, and more protected (often by shade) than that of *R. thompsonii* or *R. californica*. *Romanzoffia thompsonii* is often sympatric with *R. californica* but apparently not with *R. sitchensis*, and there is no evidence of hybridization between *R. thompsonii* and either of these two species.

Overall, *Romanzoffia thompsonii* is most similar to *R. sitchensis* f. *suksdorfi* in morphology, but in habitat best fits *R. californica*, with which it is morphologically still quite similar. The habitat similarity, however, may only be a reflection of the preadaptation of *R. thompsonii* to a similar habitat.

Romanzoffia corollas have a “yellow eye”—a yellow or gold band, in the tube or throat (cf. Table 2). In addition to the yellow eye *R. thompsonii* corollas also (apparently) have five gold spots overlapping the base of the lobes, alternating with the sinuses, or a gold band at the same height, which I am calling throat spots or bands. This particular pattern—both throat markings and a yellow eye present—is rarely evident in preserved material, has not been noted by earlier collectors or observers (Fitz 1979, notes the throat spots and calls them a yellow eye, but does not mention the lower gold band; collectors note the presence of the yellow eye occasionally), and it is often not apparent in even fairly good photographs. It is evident in all thirteen of the *R. thompsonii* populations for which there is definitive photographic evidence and in the one population from which living material was available. I believe this particular pattern is a species characteristic and urge all who encounter this plant to examine the corollas for it.

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A NEW SUBSPECIES OF *LEWISIA* (PORTULACACEAE) IN CALIFORNIA

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ABSTRACT

A new subspecies of *Lewisia kelloggii* K. Brandegee is described: ssp. *hutchisonii* from Sierra Co., California.

There are two species of *Lewisia* that appear to have a 4-parted calyx, consisting, in fact, of two sepals and two similar bracts closely beneath them. One is *Lewisia brachycalyx* Engelm. ex Gray of the southwestern United States, the other *L. kelloggii* K. Brandegee, which occurs in the Sierra Nevada of California, from Plumas Co. south to Mariposa Co., and also in Elmore Co, Idaho.

In July, 1982, on a bare slate ridge in Sierra Co., Paul Hutchison collected a *Lewisia* similar to *L. kelloggii*, but much larger in all respects, somewhat less fleshy, and pink flowered. Paul and I attempted to recollect this plant in July, 1989, but found that it had produced leaves and flower buds and then dried without developing further. The plants are apparently dependent on melted snow from the knoll a little above, and this year the runoff had been insufficient to result in flowering. Enough photosynthesis probably occurred, however, before the flower buds were formed, to enable the plants to survive perhaps several dry winters. The following description is made from dried material:

Lewisia kelloggii K. Brandegee ssp. ***hutchisonii*** Dempster, ssp. nov.—TYPE: USA, California, Sierra Co., Saddleback Mountain, about 9 miles north of Downieville, July, 1982, P. C. Hutchison 8105 (holotype JEPS). West of the summit on north-facing slope, slate ridge at 1800 m.

Subspecies a typo magnitudine majore floribusque roseis differt: folia 4–10 cm longa; sepala 11–14 mm longa; bracteae 7.5–10 mm longae; petala 25–30 mm longa.

Only the type collection is known. I have seen no intermediates.

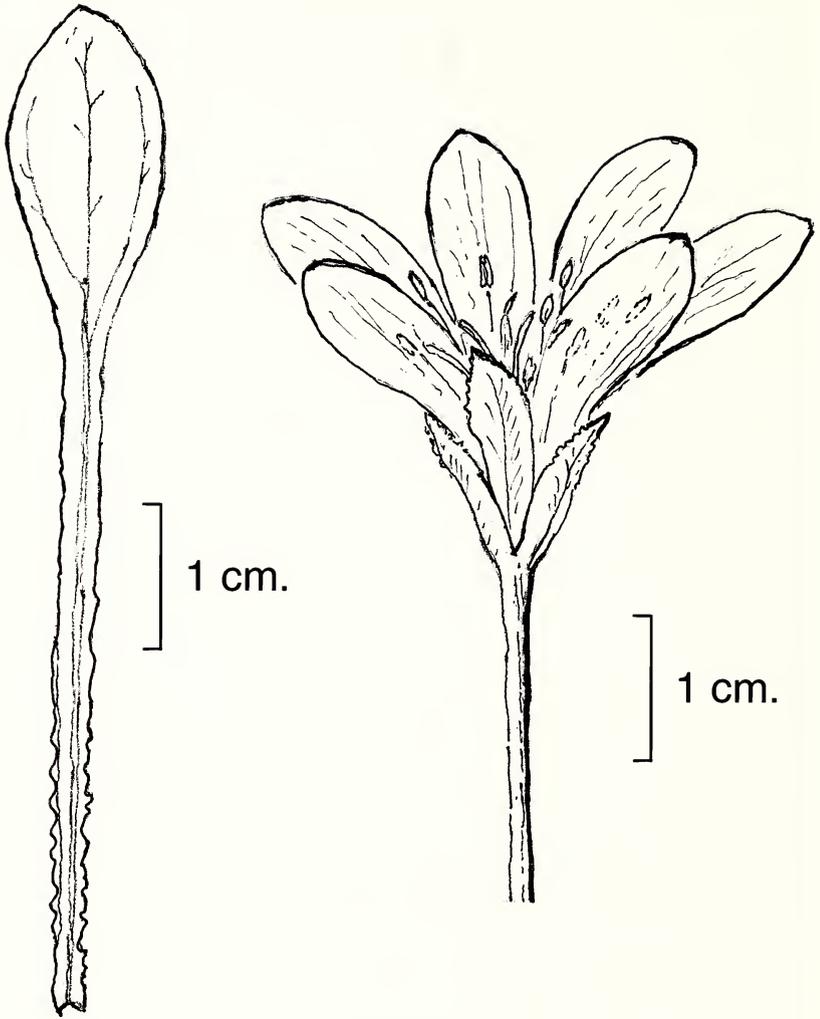


FIG. 1. Leaf and flowering stem, from *Hutchison 8105*.

KEY TO SUBSPECIES

1. Leaves 2–6 cm long; petals 10 mm long, white, off-white or pinkish
 ssp. *kelloggii*
1. Leaves 4–10 cm long; petals 25–30 mm long, pink ssp. *hutchisonii*

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A FLORISTIC STUDY OF DELTA MEADOWS RIVER PARK, SACRAMENTO COUNTY, CALIFORNIA

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ABSTRACT

A species list of 165 vascular plants was compiled for a 57 hectare park in the Sacramento River Delta. The park supports extensive, relatively undisturbed freshwater marsh habitat. Forty-four taxa occur in freshwater marsh, only 20% (9) of which are introduced. Overall, fifty percent of the taxa observed in the park are non-native, with the majority occurring in ruderal areas and annual grasslands.

Delta Meadows River Park is situated on the Sacramento River Delta east of the Sacramento River. Sacramento is located approximately 40 km north. The small town of Locke is immediately west of the park's southern portion. The 57 hectare park is composed primarily of the abandoned Southern Pacific Railroad right-of-way between Twin Cities Road and the Delta Cross Channel, just south of Locke (California Department of Parks and Recreation 1990). Snodgrass Slough defines the western boundary in the northern portion of the park. Construction of levees, on which the railroad was situated, disrupted the natural landscape. However, the park is interesting botanically because, in its northern portion, it includes a small island and portions of two peninsulas. Large portions of these areas are tidally inundated. As a result, they support extensive and relatively undisturbed freshwater marsh with strips of riparian habitat. Delta Meadows River Park is operated by the California Department of Parks and Recreation. People use the park for fishing, boating, picnicking, and swimming.

A total of 165 vascular plant species were documented within Delta Meadows River Park, 50% of which are native. Three rare plant species occur in the park's freshwater marshes: *Hibiscus lasiocarpus*, *Lathyrus jepsonii* ssp. *jepsonii*, and *Lilaeopsis masonii*. Displacement of native plant taxa has occurred in non-marsh habitat and continues due to the invasion of non-natives including *Rubus discolor*, *Centaurea solstitialis*, and *Phyla nodiflora*. These species are particularly problematic in the riparian forests and ruderal habitats within the park. *Sambucus mexicana*, host plant of the threatened *Desmocerus californicus dimorphus* (valley elderberry long-horn beetle), occurs in the park primarily along the northern levee road in the riparian forest vegetation. The vegetation patterns in the

park are correlated with hydrologic conditions. The freshwater marshes in the park are a rare ecological asset due to their relatively undisturbed nature, their native species richness, and the significant statewide loss of this habitat.

VEGETATION

Four vegetation types occur in Delta Meadows River Park: freshwater marsh, willow scrub, valley oak riparian forest, and annual grassland. The inter-tidal zone (below the mean high tideline and above the mean low tideline) supports freshwater marsh on saturated soils. The vegetation immediately adjacent to this zone on the upland side is predominantly willow scrub. The soil generally appears to be moist but not saturated. Valley oak riparian forest is established on higher ground with soils that dry out at the surface but have a ground water table generally within 1.5 to 5.5 meters. The annual grassland occurs on upland sites that were disturbed by human activity, such as agriculture and levee construction prior to state acquisition.

The zonation pattern described above is not as pronounced on levee slopes. The construction of levees in the northeast and southwest portions of the park significantly reduced the habitat available for freshwater marsh and willow scrub vegetation. These slopes are steep from top to toe. Elimination of a gradual slope altered the hydrology such that saturated soil and moist soil conditions are minimal. On levee slopes, the valley oak riparian forest often grows to the edge of the waterways. Occasionally a narrow ribbon of tules and other freshwater marsh plants establish along the water's edge at levee bases.

Although open water and ruderal habitats do not support a particular vegetation type, they support a distinctive flora. Open water adjacent to marshes supports a variety of emergent and floating aquatic plants. *Ludwigia peploides*, with its showy yellow flowers, is commonly found in the open water habitat. *Eichhornia crassipes*, also found within this habitat, is an invasive species ultimately capable of obstructing boat traffic in waterways. The ruderal habitat is found along dirt roads. Typical ruderal plants include *Foeniculum vulgare*, *Centaurea solstitialis*, and *Rubus discolor*. The majority of the non-native taxa in the park occur within the ruderal habitat (Table 1). Itemized in Table 1 are the percentages of non-native taxa represented in each of the park's habitats, including the vegetation types.

Freshwater marsh. The freshwater marsh is dominated by *Scirpus acutus* commonly in association with *Typha* spp., *Polygonum hydropiperoides*, *Verbena* spp., *Lycopus americanus*, *Ludwigia peploides*, *Sagittaria latifolia*, *Cyperus* spp., and *Juncus* spp. The three

TABLE 1. PERCENT NON-NATIVE TAXA BY HABITAT.

Habitat	Total number of taxa (a)	Percent of non-native taxa
Annual grassland (b)	23	74%
Freshwater marsh	45	20%
Open water	8	50%
Ruderal	59	81%
Valley oak riparian forest	40	33%
Willow scrub	10	20%

Notes: (a) Some taxa occur in more than one habitat.

(b) Includes taxa in the fallow agricultural field.

rare plant species occur in this habitat. The native species diversity of the marshes in the park is high, probably because the tidally inundated island and peninsulas they dominate are relatively undisturbed.

Willow scrub. The willow scrub is dominated by *Salix lasiolepis*, *S. exigua*, and *S. laevigata*. Common shrub associates include *Cephalanthus occidentalis* var. *californicus* and *Cornus sericea* ssp. *sericea*.

Valley oak riparian forest. The valley oak riparian forests within the park, although well developed, are second growth primarily on the banks of levees. *Quercus lobata* dominates the forest and is associated with several other native trees: *Q. agrifolia*, *Fraxinus latifolia*, *Juglans californica* var. *hindsii*, *Alnus rhombifolia*, *Populus fremontii*, and *Salix gooddingii*. Two other native trees are found in the valley oak riparian forest but they are uncommon within the park: *Aesculus californica* and *Platanus racemosa*. Common understory species include *Rosa californica*, *Toxicodendron diversilobum*, *Vitis californica*, *Phyla nodiflora*, *Rubus ursinus*, and *R. discolor*. *R. discolor* is an invasive, non-native which forms large mounds that exclude other plants. *Phyla nodiflora* is an invasive, non-native ground cover. *Sambucus mexicana* also occurs within this vegetation type, primarily along the levee road south of Twin Cities Road. Riparian forest is being restored at the south end of the park in an area just north of the Delta Cross Channel which was formerly under cultivation (Kerbavez personal communication).

Annual grassland. The annual grasslands are dominated by introduced grasses including *Avena barbata*, *Bromus diandrus*, *B. hordeaceus*, and the perennial *Cynodon dactylon*. A native perennial grass, *Leymus triticoides*, often occurs along the border of grasslands in the ecotone with valley oak riparian forest.

FLORA

Floristic surveys were conducted in 1992, 1993, 1994, and 1995; spring, summer, and fall trips were made. The park was surveyed on foot and by canoe. Voucher specimens are housed in the John M. Tucker Herbarium at the University of California (DAV). Voucher specimens were collected for 93% of the taxa represented in this floristic study. Vouchers were collected by the author unless otherwise noted. Nomenclature follows Hickman 1993. Common names were gleaned from several sources: Abrams 1940, 1944, and 1951, Abrams and Ferris 1960, Hickman 1993, Munz 1973, and Mason 1957. A total of 165 vascular plants were documented within Delta Meadows River Park, 50% of which are native. Fifty-eight families are represented in the flora. Further floristic work in the park will no doubt add species to the list; however, the majority are represented in this publication.

PTERIDOPHYTA

Azollaceae

Azolla filiculoides Lam. Mosquito fern. Open water and freshwater marsh. Uncommon. [1701]

Equisetaceae

Equisetum hyemale L. ssp. *affine* (Engelm.) Calder & R. H. Taylor. Common scouring rush. Uncommon. Small patch growing near southern park entrance along the road. [1726]

ANTHOPHYTA-DICOTYLEDONEAE

Aceraceae

Acer negundo L. var. *californicum* (Torrey & A. Gray) Sarg. Box elder. Valley oak riparian forest. Occasional.

Amaranthaceae

**Amaranthus albus* L. Tumble pigweed. Native to tropical America. Ruderal. Uncommon. [1733]

**Amaranthus retroflexus* L. Redroot pigweed. Native to tropical America. Ruderal. Uncommon. [1732]

Anacardiaceae

Toxicodendron diversilobum (T. & G.) Greene. Poison-oak. Valley oak riparian forest. Common.

Apiaceae

- Cicuta maculata* L. var. *bolanderi* (S. Watson) Mulligan. Water hemlock. Freshwater marsh. Uncommon. [1684]
- **Foeniculum vulgare* Mill. Sweet fennel. From Europe. Ruderal. Common. [Hrusa & Wagner 9199]
- Hydrocotyle verticillata* Thunb. Whorled marsh-pennywort. Freshwater marsh. Occasional. [1672]
- Lilaeopsis masonii* Matthias & Constance. Mason's lilaeopsis. Freshwater marsh. Rare.

Apocynaceae

- Apocynum cannabinum* L. Indian hemp. Valley oak riparian forest. Occasional. [1622]
- **Vinca major* L. Periwinkle. From Europe. Valley oak riparian forest. Occasional.

Asteraceae

- Ambrosia psilostachya* DC. Western ragweed. Ruderal. Common. [1638]
- Artemisia douglasiana* Besser. Mugwort. Valley oak riparian forest. Occasional. [1652]
- Aster lanceolatus* Willd. ssp. *hesperius* (A. Gray) Semple & J. Chmielewski. Marsh aster. Annual grassland/valley oak riparian forest ecotone. Uncommon. [1720]
- Baccharis pilularis* DC. Coyote brush. Fallow agricultural field. Uncommon. [1717]
- **Centaurea solstitialis* L. Yellowstar thistle. From Europe. Annual grassland and ruderal. Abundant.
- **Chamomilla suaveolens* (Pursh) Rydb. Pineapple weed. From nw N. America and ne Asia. Ruderal. Uncommon. [1736]
- **Cirsium vulgare* (Savi) Ten. Bull thistle. From Europe. Valley oak riparian forest. Occasional. [1657]
- **Cichorium intybus* L. Chicory. Native to Europe. Ruderal. Uncommon. [Hrusa & Wagner 9200]
- Euthamia occidentalis* Nutt. Western goldenrod. Ruderal. Uncommon. [1734]
- Grindelia camporum* E. Greene var. *camporum*. Gumweed. Ruderal. Uncommon. [1642]
- Hemizonia pungens* (Hook. & Arn.) Torrey & A. Gray. Common spikeweed. Ruderal. Uncommon. [Hrusa & Wagner 9208]
- Heterotheca grandiflora* Nutt. Telegraph weed. Ruderal. Common. [1725]
- **Lactuca serriola* L. Prickly lettuce. From the Mediterranean. Ruderal. Common. [1601]

- **Picris echioides* L. Bristly ox-tongue. Native to Europe. Ruderal. Occasional. [1676, 1718]
- **Senecio vulgaris* L. Groundsel. Native to Eurasia. Willow scrub. Uncommon. [1708]
- **Silybum marianum* (L.) Gaertn. Milk thistle. From Mediterranean region. Ruderal. Occasional.
- **Sonchus oleraceus* L. Common sow thistle. From Europe. Valley oak riparian forest. Occasional. [1655]
- **Taraxacum officinale* Wiggers. Dandelion. From Europe. Valley oak riparian forest. Uncommon. [Hrusa & Wagner 9127]
- **Tragopogon porrifolius* L. Salsify. Native to Europe. Ruderal. Uncommon. [1607]

Betulaceae

- Alnus rhombifolia* Nutt. White alder. Valley oak riparian forest. Common. [1614]

Brassicaceae

- **Brassica cf. rapa* L. Field mustard. Native to Europe. Ruderal. Occasional. [Hrusa & Wagner 9116]
- **Capsella bursa-pastoris* (L.) Medikus. Native to Europe. Ruderal. Uncommon. [1743]
- **Hirschfeldia incana* (L.) Lagr.-Fossat. Mediterranean mustard. Native to Mediterranean. Ruderal. Occasional. [1600]
- Lepidium strictum* (S. Watson) Rattan. Peppergrass. Ruderal. Uncommon. [1742]
- Rorippa palustris* (L.) Besser var. *occidentalis* (S. Watson) Rollins Marsh yellow-cress. Freshwater marsh and willow scrub. Occasional. [1705]

Caprifoliaceae

- Sambucus mexicana* C. Presl. Blue elderberry. Valley oak riparian forest. Common.

Caryophyllaceae

- **Spergularia rubra* (L.) J. S. Presl & C. Presl. Purple sand spurry. From Europe. Ruderal. Occasional. [1643]
- **Stellaria media* (L.) Villars. Common chickweed. Native to sw Europe. Annual grassland. Common. [Hrusa & Wagner 9108]

Chenopodiaceae

- **Chenopodium ambrosioides* L. Mexican tea. From tropical America. Ruderal. Uncommon. [1639]

Convolvulaceae

- Calystegia sepium* (L.) R. Br. ssp. *limnophila* (E. Greene) Brummitt.
Hedge bindweed. Freshwater marsh. Occasional. [1663]
**Convolvulus arvensis* L. Bindweed. From Eurasia. Ruderal. Occasional. [Hrusa & Wagner 9207]

Cornaceae

- Cornus sericea* L. ssp. *sericea* Creek dogwood. Freshwater marsh, valley oak riparian forest, and willow scrub. Common. [1624]

Crassulaceae

- Crassula connata* (Ruiz Lopez and Pavon) A. Berger. Annual grassland. Uncommon. [Hrusa & Wagner 9130]
**Crassula tillaea* Lester-Garl. Native to Mediterranean. Ruderal. Uncommon. [1735]

Fabaceae

- Glycyrrhiza lepidota* Pursh. Wild licorice. Ruderal. Uncommon. [1636]
Lathyrus jepsonii E. Greene var. *jepsonii*. Delta tule pea. Freshwater marsh. Rare. [1632, 2048]
**Lotus corniculatus* L. Bird's foot trefoil. Native to Eurasia. Ruderal. Occasional. [1644]
Lotus purshianus (Benth.) Clements & E.G. Clements var. *purshianus* Spanish clover. Ruderal. Common. [1640a]
**Medicago polymorpha* L. Bur-clover. From southern Europe. Ruderal. Common. [1738, 1745]
**Medicago sativa* L. Alfalfa. From Eurasia. Fallow agricultural field. Uncommon. [1714]
**Melilotus indica* (L.) All. Sourclover. From Mediterranean. Valley oak riparian forest. Occasional. [1628]
**Trifolium* sp. Clover. Ruderal. Occasional. [Hrusa & Wagner 9209]
**Vicia sativa* L. ssp. *sativa* Common vetch. Native to Europe. Annual grassland and ruderal. Occasional. [1599, 1740]
**Vicia villosa* Roth ssp. *villosa*. Native to Europe. Annual grassland and ruderal. Common. [1747]

Fagaceae

- Quercus agrifolia* Neé var. *agrifolia*. Coast live oak. Valley oak riparian forest. Common. [1610, 1646]
Quercus lobata Neé. Valley oak. Dominant tree of the riparian forest in the park. [1658]

Gentianaceae

Centaurium muehlenbergii (Griseb.) Piper. Centaury. Willow scrub along water's edge. Uncommon. [1625]

Geraniaceae

**Erodium botrys* (Cav.) Bertol. Long-beaked filaree. Native to southern Europe. Ruderal. Common. [1641]

**Erodium brachycarpum* (Godron) Thell. Native to southern Europe. Annual grassland. Occasional. [*Hrusa & Wagner 9120*]

**Erodium cicutarium* (L.) L'Her. Red-stemmed filaree. From Mediterranean region. Ruderal. Common. [*Hrusa & Wagner 9128*]

**Geranium dissectum* L. Cranesbill. From Europe. Ruderal. Common. [1608]

Haloragaceae

**Myriophyllum* sp. Water-milfoil. Open water. Uncommon. [*Hrusa & Wagner 9132*]

Myriophyllum cf. sibiricum V. Komarov. Water-milfoil. Growing in Railroad Slough. Uncommon. [1668]

Hippocastanaceae

Aesculus californica (Spach) Nutt. California buckeye. Valley oak riparian forest. Uncommon, one tree observed in park. [2057]

Hypericaceae

**Hypericum mutilum* L. Small-flowered Saint John's-wort. From e. N. America. Freshwater marsh. Uncommon. [*Hrusa & Wagner 9225*]

Juglandaceae

Juglans californica S. Watson var. *hindsii* Jepson. Northern California black walnut. Valley oak riparian forest. Occasional. [2051]

Lamiaceae

**Lamium amplexicaule* L. Henbit. From Europe. Ruderal. Annual grasslands. Uncommon. [*Hrusa & Wagner 9122*]

Lycopus americanus W. C. Barton. American bugleweed. Freshwater marsh. Common. [1649, 1680]

**Marrubium vulgare* L. Horehound. From Europe. Ruderal. Occasional. [1741]

Scutellaria lateriflora L. Blue skullcap. Freshwater marsh. Uncommon. [1648]

Stachys albens A. Gray. White hedge-nettle. Freshwater marsh. Uncommon. [1670]

Malvaceae

Hibiscus lasiocarpus Cav. Rose-mallow. Freshwater marsh. Endangered in California. Uncommon.

**Malva nicaeensis* All. Bull mallow. From Eurasia. Ruderal. Occasional. [1602]

**Malva parviflora* L. Cheeseweed. Native to Eurasia. Ruderal. Occasional. [1744]

Malvella leprosa (Ortega) Krapov. Alkali-mallow. Ruderal. Uncommon. [1727]

Moraceae

**Ficus carica* L. Edible fig. From Mediterranean area. Valley oak riparian forest. Uncommon. [2050]

**Morus alba* L. White mulberry. From China. Valley oak riparian forest. Uncommon.

Oleaceae

Fraxinus latifolia Benth. Oregon ash. Valley oak riparian forest. Occasional. [1627]

Onagraceae

Epilobium ciliatum Raf. ssp. *ciliatum*. Willow-herb. Freshwater marsh. Occasional. [1675]

Ludwigia peploides (Kunth) Raven ssp. *peploides*. Freshwater marsh and open water. Common. [1679]

Oxalidaceae

**Oxalis corniculata* L. Sorrel. From Europe. Growing on disturbed slough bank. Occasional.

Papaveraceae

Eschscholzia californica Cham. California poppy. Annual form, probably native to site. Ruderal. Occasional. [1635]

Plantaginaceae

**Plantago lanceolata* L. English plantain. From Europe. Annual grassland and ruderal. Common. [1597]

**Plantago major* L. Common plantain. Native to Europe. Annual grassland. Uncommon. [1659]

Platanaceae

Platanus racemosa Nutt. Western sycamore. Valley oak riparian forest. Uncommon. Only two western sycamores were observed in the park; they occur near the park boundary on the peninsula east of Railroad Slough and the old Southern Pacific right-of-way in the southern portion of the park.

Polygonaceae

**Polygonum arenastrum* Boreau. Common knotweed. From Eurasia. Ruderal. Common. [1596]

Polygonum hydropiperoides Michaux. Waterpepper. Freshwater marsh. Common. [1671, 1709]

**Rumex crispus* L. Curly dock. From Eurasia. Ruderal. Common. [1656, 1685]

**Rumex pulcher* L. Fiddle dock. Native to Mediterranean region. Ruderal. Uncommon. [1640b]

Rumex salicifolius J. A. Weinm. var. *transitorius* (Rech. f.) J. Hickman. Willow dock. Valley oak riparian forest along water's edge. Uncommon. [1677]

Portulacaceae

Calandrinia ciliata (Ruiz Lopez & Pavon) DC. Red maids. Annual grassland just outside of park. Uncommon. [Hrusa & Wagner 9115]

Claytonia parviflora Hook. ssp. *parviflora* Miner's lettuce. Annual grassland just outside of park. Occasional. [Hrusa & Wagner 9119]

Primulaceae

**Anagallis arvensis* L. Scarlet pimpernel. From Europe. Fallow agricultural field. Common. [1723]

Samolus parviflorus Raf. Water-pimpernel. Freshwater marsh. Uncommon. [1706]

Rosaceae

Potentilla palustris (L.) Scop. Marsh cinquefoil. Freshwater marsh. Uncommon. [1674]

**Prunus* cf. *cerasifera* Ehrh. Cherry plum. From se Europe. Valley oak riparian forest. Uncommon. [2055]

Rosa californica Cham. & Schldl. Wild rose. Valley oak riparian forest. Common. [1613]

**Rosa X hybrida* Hort. Forming a briar growing at water's edge east of the old railroad bed. Uncommon. [1629, 1662]

**Rubus discolor* Weihe & Nees. Himalayan blackberry. From Eurasia. Valley oak riparian forest. Abundant. [2049]

Rubus ursinus Cham. & Schldl. California blackberry. Valley oak riparian forest. Occasional. [1716]

Rubiaceae

Cephalanthus occidentalis L. var. *californicus* Benth. California button-willow. Freshwater marsh and willow scrub. Common. [1683]

Galium trifidum L. var. *pacificum* Wieg. Bedstraw. Freshwater marsh. Uncommon. [1682]

Salicaceae

Populus fremontii S. Watson ssp. *fremontii*. Fremont's cottonwood. Valley oak riparian forest. Common. [2056]

Salix exigua Nutt. Narrow-leaved willow. Valley oak riparian forest, willow scrub, and freshwater marsh. Common. [1645]

Salix gooddingii C. Ball. Goodding's black willow. Valley oak riparian forest. Common. [1611, 1719, 1724]

Salix laevigata Bebb. Red willow. Willow scrub. Uncommon. [1650]

Salix lasiolepis Benth. Arroyo willow. Valley oak riparian forest and willow scrub. Common. [1619, *Hrusa & Wagner 9109*]

Salix cf. lucida Muhlenb. ssp. *lasiandra* (Benth.) E. Murray. Red willow. Willow scrub. Uncommon. [*Hrusa & Wagner 9111*]

Saururaceae

Anemopsis californica (Nutt.) Hook. & Arn. Yerba manza. Valley oak riparian forest. Uncommon. [1653]

Scrophulariaceae

Mimulus guttatus DC. Common large monkey-flower. Freshwater marsh. Occasional. [1661, 1678]

Simaroubaceae

**Ailanthus altissima* (Miller) Swingle. Tree of heaven. Native to east Asia. Ruderal. Uncommon. [2057]

Solanaceae

**Solanum nigrum* L. Black nightshade. Native to Eurasia. Willow scrub on slough bank. Uncommon. [1710]

Ulmaceae

- **Ulmus pumila* L. Siberian elm. From central Asia. In habitat restoration area. Valley oak riparian forest/annual grassland ecotone. Uncommon. [1715]

Urticaceae

- Urtica dioica* L. ssp. *holosericea* (Nutt.) Thorne. Stinging nettle. Valley oak riparian forest. Occasional. [1660]

Verbenaceae

- **Phyla nodiflora* (L.) E. Greene var. *nodiflora*. Garden lippia. Valley oak riparian forest and ruderal. Native to S. America. Locally abundant. [1604, 1633, 1634]
- **Verbena bonariensis* L. Cluster-flowered verbena. Native to South America. Valley oak riparian forest along water's edge and freshwater marsh. Common. [1616, 1707]
- Verbena hastata* L. Blue vervain. Freshwater marsh. Common. [1681]

Viscaceae

- Phoradendron macrophyllum* (Engelm.) Cockerell. Big-leaf mistletoe. On cottonwoods. Valley oak riparian forest. Uncommon. [1728]

Vitaceae

- Vitis californica* Benth. California wild grape. Valley oak riparian forest. Common. [1630]
- **Vitis vinifera* L. Cultivated wine grape. From Europe. Adventive on boundary of park. Uncommon. [1620]

ANTHOPHYTA-MONOCOTYLEDONEAE

Alismataceae

- Sagittaria latifolia* Willd. Arrowhead. Freshwater marsh. Common. [1673, 1711, 1730]

Cyperaceae

- Carex barbarae* Dewey. Santa Barbara sedge. Valley oak riparian forest. Locally abundant. [1618]
- Carex comosa* Boott. Bristly sedge. Freshwater marsh. Uncommon. [1688]
- Carex praegracilis* W. Boott. Clustered field sedge. Valley oak riparian forest. Locally abundant. [1651]

- Carex* cf. *stipata* Muhlenb. var. *stipata*. Awl-fruited sedge. Freshwater marsh. Common. [1689, 1695]
Cyperus eragrostis Lam. Umbrella-sedge. Freshwater marsh. Occasional. [1615]
Cyperus strigosus L. False nutsedge. Freshwater marsh. Occasional. [1729]
Scirpus acutus Bigelow var. *occidentalis* (S. Watson) Beetle. Tule. Freshwater marsh. Abundant. [1690]

Hydrocharitaceae

- **Egeria densa* Planchon. Brazilian waterweed. Native to S. America. Freshwater marsh and open water. Locally abundant. [1667]

Juncaceae

- Juncus acuminatus* Michaux. Sharp-fruited rush. Freshwater marsh. Uncommon. [1694]
Juncus balticus Willd. Baltic rush. Freshwater marsh. Occasional. [1621]
Juncus effusus L. var. *effusus*. Bog rush. Freshwater marsh. Occasional. [1687, 1700]
Juncus xiphioides E. Meyer. Iris-leaved rush. Freshwater marsh. Occasional. [1686, 1697]

Lemnaceae

- Lemna* sp. Duckweed. Freshwater marsh and open water. Occasional. [1702]

Liliaceae

- **Asparagus officinalis* L. ssp. *officinalis*. Asparagus. From Europe. Ruderal. Uncommon. [1598]
Dichelostemma capitatum Alph. Wood. ssp. *capitatum*. Blue dicks. Annual grasslands. Uncommon. [Hrusa & Wagner 9121]

Poaceae

- **Agrostis gigantea* Roth. Giant bent grass. Native to Europe. Freshwater marsh. Uncommon. [1712]
**Agrostis stolonifera* L. Creeping bent grass. Native to Europe. Freshwater marsh. Uncommon. [1713a]
**Avena barbata* Brot. Slender wild oat. From Europe. Annual grassland and ruderal. Abundant. [1631]
**Avena fatua* L. Wild oat. From Europe. Ruderal. Common. [1605, 1739]
**Bromus catharticus* Vahl. Rescue grass. Native to South America.

- Annual grassland/valley oak riparian forest ecotone. Occasional. [1721]
- **Bromus diandrus* Roth. Ripgut. From Europe. Annual grassland and ruderal. Common.
- **Bromus hordeaceus* L. Soft chess. From Europe. Annual grassland and ruderal. Common. [Hrusa & Wagner 9118]
- **Cynodon dactylon* (L.) Pers. Bermuda grass. Native to Africa. Ruderal. Common. [2054]
- **Echinochloa crus-galli* (L.) P. Beauv. Barnyard grass. From Eurasia. Freshwater marsh. Occasional. [1731]
- **Festuca arundinacea* Schreber. Tall fescue. Native to Europe. Ruderal. Occasional. [1637]
- **Hordeum murinum* L. ssp. *leporinum* (Link) Archang. Wall barley. From Europe. Annual grassland and ruderal. Common. [1606]
- Leymus triticoides* (Buckley) Pilger. Alkali rye-grass. Valley oak riparian forest. Occasional. [1612, 1654]
- **Lolium perenne* L. Perennial ryegrass. From Europe. Ruderal. Common. [1603]
- **Paspalum dilatatum* Poir. Dallis grass. Native to South America. Valley oak riparian forest growing at water's edge. Common. [1617]
- **Phalaris arundinacea* L. Reed canary grass. From Eurasia. Ruderal. Locally abundant. [1692, 1699]
- **Phalaris aquatica* L. Harding grass. Native to Mediterranean Europe. Valley oak riparian forest. Occasional. [1623]
- **Poa annua* L. Annual bluegrass. Native to Europe. Ruderal. Occasional. [1737]
- **Polypogon interruptus* Kunth. Ditch beard grass. From S. America. Freshwater marsh. Occasional. [1713b]
- **Polypogon monspeliensis* (L.) Desf. Rabbit's-foot grass. From southern and western Europe. Freshwater marsh. Occasional. [1647]
- **Sorghum halepense* (L.) Pers. Johnson grass. Native to the Mediterranean. Fallow agricultural field. Common. [1626, 1722]
- **Vulpia myuros* (L.) C. Gmelin var. *hirsuta* (Hackel) Asch. & Graebner. Native to Europe. Ruderal. Occasional. [Hrusa & Wagner 9129]
- **Vulpia myuros* (L.) C. Gmelin var. *myuros*. Native to Europe. Annual grassland and ruderal. Common. [1745]

Pontederiaceae

- **Eichhornia crassipes* (C. Martius) Solms-Laubach. Water hyacinth. From tropical America. Freshwater marsh and open water. Locally abundant. [1693]

Potamogetonaceae

**Potamogeton crispus* L. Crispate-leaved pondweed. Native to Eurasia. Growing in Railroad Slough in open water. Uncommon. [1665]

Typhaceae

Sparganium erectum L. ssp. *stoloniferum* (Graebner) C. Cook & M. S. Nicholls. Bur-reed. Freshwater marsh. Uncommon. [1703]

Typha angustifolia L. Narrow-leaved cat-tail. Possibly naturalized in CA according to S. G. Smith (in Hickman 1993). Freshwater marsh. Occasional. [1691]

Typha latifolia L. Broad-leaved cat-tail. Freshwater marsh. Abundant. [1704]

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NOTEWORTHY COLLECTIONS

CALIFORNIA

GELIDIUM VAGUM Okamura (Gelidiaceae).—Marin Co., Tomales Bay, Marshall. 122°53'W, 38°10'N in lower intertidal, on small boulders exposed to slight wave activity, associated with *Gigartina exasperata*, 24 March 1995, J. Hughey (NCC, UC); Tomales Bay, Marshall. 17 April 1995, J. Hughey and R. Stabler (NCC, UC).

Previous knowledge. Native to the Huanghai Sea, Yellow Sea, Korea Strait, Sea of Japan, and Pacific coasts of Honshu and southern Hokkaido, Japan (D.E. Renfrew et al., CAN. J. BOT. 67: 3295-3314, 1989). It was collected for the first time from the eastern Pacific in 1986 at Hornby and Denman islands in the Strait of Georgia, British Columbia with gametophytes and tetrasporophytes being found in August, September, October, and sterile plants in April (Renfrew et al., 1989).

Significance. New for California. Juvenile plants appeared in February and tetrasporophytes in March and April. Gametophytes were abundant in April. Oyster spat was considered to be the source of introduction to British Columbia (Renfrew et al., 1989). Recently, *G. vagum* has been collected from Orcas Island and Bellingham Bay, Washington where oyster farms are also known to occur (T. Mumford, personal communication). Since the Marshall area is surrounded by oyster farms that have obtained spat and young oysters from Washington (J.T. Hollibaugh, personal communication) and since the species appeared suddenly and became abundant rapidly, it is likely that oysters or oyster spat imported from the Strait of Georgia are implicated in this introduction. The identification was verified by Prof. T. Yoshida (Univ. of Sapporo).

DAYS BINGHAMIAE A.J.K. Millar (Dasyaceae).—Marin Co., Tomales Bay, Marshall Beach. 122°55'W, 38°10'N, MLLW to -1.0 ft., on cobblestones with *Gastroclonium compressum* (see Madroño 42: 409, 1995) and *Ceramium californicum*, 21 April 1995 and 4 June 1995, J. Hughey (NCC, UC).

Previous knowledge. Listed in the Marine Algae of California as *Pogonophorella californica* (J. Ag.) P. Silva. Last collected at its northern limit near the Estero de San Antonio (3 km south of the Marin/Sonoma county line) in 1912, this alga has not been recorded north of Monterey since.

Significance. Growing profusely on cobblestones in sandy mud on a sheltered shore on the west side of Tomales Bay. Readily identified in mid April (stipitate, 2.5 cm tall, monosiphonous laterals), by June it formed dense patches that broke the water surface at low tide. Elsewhere, *D. binghamiae* grows in association with *Phyllospadix scouleri* on rocks in sandy areas exposed to high wave energy. A specimen of this alga, identified as *Dasya sinicola* var. *sinicola*, which was collected in June, 1983 by L. Remy is housed in NCC.

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GALENIA PUBESCENS. (Eckl. & Zeyh.) Druce var. *PUBESCENS* (AIZOACEAE).—Los Angeles Co.: Santa Monica Mountains, Topanga State Park near the Los Angeles City Boundary, on the W edge of the Santa Ynez Fire Road, near 34°04'18"N, 118°34'36"W, USGS Topanga 7.5' Quad., elev. ca. 1314-1325 ft [401-404 m], patch

15 or 20 feet long and about 6 or 8 feet wide, growing under a *Quercus agrifolia* and out into the sun, much smaller patches growing along the road to the south of the main patch for several hundred feet, 17 May 1995, *M. Stassforth 383* (RSA, LA), verif. by T. S. Ross.

Previous knowledge. A couple of years ago, this taxon was reported as new to the North American flora based on two collections at a disturbed site on Signal Hill, vicinity of Long Beach, Los Angeles County, where it occurred as a locally abundant weed (T. S. Ross, *Madroño* 41:226–228, 1994).

Significance. This represents documentation of this taxon as established at a second location in Southern California. The new site is ca. 50 km to the NW of Signal Hill. From the description of this occurrence it would appear to have been introduced intentionally for slope stabilization, but we do not yet know who is promoting use of this weed in Southern California. Certainly the introduction of such weeds into areas of natural vegetation needs to be vehemently discouraged.

[Margaret Stassforth, the collector of this new record, acknowledges the assistance of David S. Hollombe, who brought the original *Galenia* note to her attention.]

As an addendum to the original report (Ross, 1994), it is perhaps worth noting here some of the distinguishing characters between this taxon and *Galenia secunda* (L.f.) Sond. in Harvey. Both taxa are weeds in Australia, and the latter species has been reported from Florida. If *G. pubescens* is actually being used as a slope stabilizer in California, then there is some probability that *G. secunda* may eventually be found here as well. Both are very similar in growth habit and morphology, and examination of Australian collections indicates that misidentifications are not uncommon. The following key should assist in differentiating the two species, and has been modified from A. Prescott's fine treatment (*Galenia*, pp. 50, 52 in A. S. George [ed.], *Flora of Australia*, Vol. 4, 1984):

Leaves and stems gray-green; trichome-like scales sparse, narrowly-rhomboid, whitish and \pm opaque, closely appressed, ca. 0.3–0.8 mm long; perianth segments white to pinkish on adaxial surface; anthers often pink to \pm salmon
 *G. pubescens*

Leaves and stems gray-white; trichome-like scales dense, narrowly-rhomboid, whitish or yellowish, the longest often subulate and \pm vitreous, loosely appressed, 1–2 mm long; perianth segments white to cream-yellow on adaxial surface; anthers yellow *G. secunda*

The characters offered here are generally subtle, and may be more difficult to grasp in the absence of good comparative material. The grayish white appearance of the herbage in *G. secunda* may be compared to that of *Lotus argophyllus* (A. Gray) Greene ssp. *argophyllus* as compared to another *Lotus* in which the green of the herbage is more pronounced through the sparser pubescence. Anther color, subtle a trait as it may seem, provides a useful ancillary character in fresh material, but may also be retained in some pressed and dried collections. The specimens of *Galenia pubescens* collected in California thus far have had salmon-pink anthers.

LASIOSPERMUM BIPINNATUM (Thunb.) Druce [*L. radiatum* Trev.; *Lidbeckia b.* Thunb.] (ASTERACEAE).—Santa Barbara Co.: Goleta, dune area adjacent to the Devereaux School, apparent relic of experimental plantings by F. E. Clements, persisting after nearly 30 years, 30 April 1958, *H. M. Pollard s.n.* (RSA); Los Angeles Co., northern Claremont, just S of the intersection of Mills Avenue \times Mt. Baldy Road in disturbed but undeveloped area with sandy alluvial soil largely dominated by alluvial scrub elements such as *Artemisia californica* and *Lepidospartum squamatum*, herbaceous perennial, scattered locally amid the scrub, obviously naturalized locally, USGS Mt. Baldy 7.5' Quad., T1N R8W, NW/4 NW/4 SW/4 SW/4 SE/4 section 27; elev. ca. 1630–1640 feet [497–500 m], 26 May 1992, *T. S. Ross, S. Boyd, S. Carlquist 6427* (RSA, CAS, CDA, US), det. by Celia Kutcher, 1995.

Previous knowledge. This taxon is not currently cited for North America by John Kartesz (A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, Vol. 1, 2nd Ed., Timber Press, Portland, Oregon, 1994) and, to the best of our knowledge, has not been previously recorded in any Californian flora.

Significance. This appears to be the first formal report of this species in North America. While the first cited collection appears to have been from a locally naturalized population persisting at the site of introduction, the second was from a locally naturalized, self-disseminating occurrence. The plant from which the *Ross et al.* material was collected formed a clump ca. 50 cm broad with blow-sand accumulated around its base. Several scattered plants were noted throughout the vicinity and, although the local plants were still flowering, achenes from mature capitula were readily disarticulating and being blown about by the wind. In this herbaceous perennial species, the stem bases tend to be decumbent with adventitious roots; the showy capitula bear white rays and yellow disk florets (which may have a slight greenish cast); phyllaries are in few series (the inner one prominent); the receptacle is chaffy; and the achene is epappose, distinctively densely lanate and cocoon-like, enclosing the elliptic-turbinate brown seed. The generic name is appropriately descriptive of these achenes, and the specific epithet refers to the glabrous, bipinnatifid leaves.

This taxon is not listed in *Hortus Third* (L. H. & E. Z. Bailey, Macmillan Publishing Co., New York, 1976), or the *Sunset Western Garden Book* (Sunset Publishing Corp., Menlo Park, Calif., 1995), and is not known to be in general cultivation in California. According to Celia Kutcher, Curator and Taxonomist with the Fullerton Arboretum (personal communication), the arboretum acquired seeds from South Africa via an *Index Seminum* exchange list and offered some of the resulting plants to the public before discovering its weedy tendencies on the arboretum grounds. It is not known whether this taxon has been recently available to the Californian public through any other source. This South African species is native from the Transvaal S through the Orange Free State and Lesotho into the eastern Cape Province (A. J. Guillard, *Flora of Lesotho* [Basutoland], J. Cramer, Lehre, Germany, 1971). Various South African floristic references allude to the fact that this species is weedy and well adapted to disturbances, and some floras of adjacent areas record the taxon as adventive along roadsides. In a discussion of lowland plant ecology in Lesotho, Guillard (1971) indicates that plants (in general) around villages "are subject to severe trampling and constant grazing by the many animals which the villagers possess, so that only hardy grasses such as *Cynodon dactylon* survive there and many weed species (*Lasioppermum bipinnatum*, *Datura* species, *Chenopodium* species and tough woody types of *Helichrysum*, as well as others) are found most often." The *Lasioppermum* clearly has the attributes of a successful weed, and should be watched for in mild climate areas of the Pacific states.

STYLOCLINE MASONII Morefield (ASTERACEAE).—Los Angeles Co.: Soledad Canyon Wash (easterly extension of the Santa Clara River wash system), broad sandy wash 2600 ft ESE of Acton, USGS Acton 7.5' Quad., T5N R13W, SE/4 SE/4 section 36, elev. 2720 ft [829 m], associated with *Artemisia tridentata* ssp. *parishii*, *Ephedra nevadensis*, *Penstemon centranthifolius* [erroneously indicated on label as *P. spectabilis*], *Rumex hymenosepalus*, and numerous annuals such as *Stylocline psilocarphoides*, *Nemophila menziesii*, *Cryptantha micrantha*, *Phacelia fremontii*, *Claytonia exigua*, *C. parviflora*, *Pectocarya penicillata*, *Eriophyllum pringlei* and *E. wallacei*, 30 April 1991, T. S. Ross, S. Boyd, & L. Arnseth 4965a (RSA), det. by J. D. Morefield.

Previous knowledge. This diminutive annual species was originally described by J. D. Morefield in 1992 (Madroño 39:117) on the basis of 7 collections which spanned 1935–1971. Four of these collections were from Kern Co., two from San Luis Obispo Co., and one from Monterey Co. Morefield (1992) indicated that "visits to most of the known sites in 1989 revealed no plants (perhaps because of poor rains) but

showed ample evidence of development or disturbance.” As a result of the species’ apparent rarity, the California Native Plant Society added the taxon to its list 1B with a R-E-D Code of 3-3-3 (M. W. Skinner & B. M. Pavlik [eds.], CNPS Inventory of Rare and Endangered Vascular Plants of California, CNPS, Sacramento, 1994).

Significance. This apparently represents the only collection of this rare taxon since 1971 and extends the known range of the species to Los Angeles Co., an extension of roughly 130 km SSE from the nearest collection site in Kern Co. At present, this is the only locality where the taxon is known to be extant. Morefield, in describing *S. masonii* (1992), thought it to be most closely related to *S. psilocarphoides* M. Peck and contrasted it with that species, noting also the allopatric distribution patterns—the former in the cismontane and the latter almost exclusively transmontane. The collection cited here is the first locality where the two species have been documented together, and is near the SW margin of the Mojave Desert (interior drainage) at the head of the Santa Clara River (its coastal effluence in Ventura Co.). With the poorly known distribution of *S. masonii* now significantly broadened, it should be sought in the intervening regions as well as adjacent areas of similar habitat.

CORONILLA VALENTINA L. (FABACEAE).—Los Angeles Co.: Santa Catalina Island, 1 mi S of Avalon on rocky ridge, suffrutescent perennial, 2 ft tall [61 cm], flowers yellow, few, in shade, sandy soil at bottom of small canyon, elev. 100 ft [30.5 m], 10 April 1963, *E. R. Blakley 5607* (SBBG); Los Angeles Co.: Whittier Hills (Puente Hills, *pro parte*), Skyline Drive at the head of Turnbull Canyon, [USGS Whittier 7.5’ Quad.,] T2S R11W, center of sect. 14, elev. 1140 ft [347.6 m], shrubs to ca. 11 dm tall naturalizing at roadside, several young plants seen, 9 March 1991, *T. S. Ross 4204* (RSA); Los Angeles Co.: Rancho Palos Verdes, Abalone Cove area, old road from Palos Verdes Drive South to Abalone Cove (now just a trail), NNW of Portuguese Point and ± SSE of the Wayfarers Chapel, USGS Redondo Beach 7.5’ Quad. [near 33°44’33”N 118°22’32”W]; elev. ca. 120 ft [36.6 m], shrubs to ca. 7.5 dm tall, apparently introduced and naturalizing locally, 28 March 1992, *T. S. Ross & A. Brinkmann-Busí 6057a* [fls] *b* [frs] (RSA).

Previous knowledge. The first collection cited above was reported for Santa Catalina Island by G. D. Wallace (Vascular plants of the Channel Islands of Southern California and Guadalupe Island, Baja California, Mexico, Nat. Hist. Mus. of Los Angeles Co., Contrib. in Sci. No. 365, 1985), and has been listed for North America by Kartesz (1994). It has not, however, been listed for California in The Jepson Manual (J. C. Hickman [ed.], 1993, Univ. Calif. Press, Berkeley).

Significance. Each of the populations documented above appears to be introduced by human agency, but at least the latter two are reported by the collector as naturalizing locally outside of cultivation. While the taxon appears to lack the aggressively invasive habit of some confamilial Mediterranean shrubs (e.g., *Spartium junceum* L., *Genista linifolia* L., *G. monspessulana* (L.) L. Johnson), it should be watched for in other low elevation regions of California under maritime influence. The first collection cited apparently represents subspecies *valentina* (det. by S. Junak); the latter two collections represent subsp. *glauca* (L.) Batt. in Batt. & Trab. (det. by T. S. Ross). The species is native to the Mediterranean region and southern Portugal.

GERANIUM ROTUNDFOLIUM L. (GERANIACEAE).—Los Angeles Co.: Angeles [National] Forest, [San Gabriel Mtns.,] Trail Canyon, 14 May 1934, *L. E. Hoffman s.n.* (RSA); Los Angeles Co.: San Gabriel Mtns., Angeles National Forest, Trail Canyon, Big Cienega, elev. 3750 ft [1143 m], in dry semi-shady loose humus-rich loam in open shade of *Quercus chrysolepis*, trailing with herbage viscid glandular, 30 July 1967, *L. C. Wheeler s.n.* (RSA), both det. by T. S. Ross.

Previous knowledge. This annual species was originally reported for California by M. H. Grayum & D. L. Koutnik in 1982 (New records of vascular plants from the

Santa Monica Mountains, California, and adjacent parts of Los Angeles and Ventura counties, Aliso 10:313-320) based on a collection in the Santa Monica Range (Los Angeles Co.: abundant and well established along the lower reaches of Temescal Canyon, *Gordon et al.* 990 [SFV]).

Significance. The two specimens cited from the San Gabriel Mountains indicate that this annual species was naturalized in Trail Canyon for at least 33 years and very likely still occurs there. The taxon is listed for North America by Kartesz (1994) but is not listed for California in *The Jepson Manual* (M. S. Taylor in J. C. Hickman [ed.], 1993). The SFV herbarium is currently in a state of transition and the holdings are unavailable for study, hence we have not been able to confirm the identity of the *Gordon et al.* collection; however, the two RSA collections are currently considered correctly identified, having been previously identified as *G. molle* L. and *G. bicknellii* Britton var. *longipes* (S. Watson) Fern., respectively. It is clear that the species is not merely a "waif" in California and ultimately ought to be cited in a "complete" flora for the state. Reportedly native to most of Europe except the most northerly regions.

SCROPHULARIA PEREGRINA L. (SCROPHULARIACEAE).—Los Angeles Co.: Claremont, Rancho Santa Ana Botanic Garden, established weed throughout the garden, 2 April 1987, *A. Liston 646-1* (RSA); Los Angeles Co.: Claremont, RSABG, SE side of Indian Hill Mesa on a vernal moist clay embankment, elev. ca. 1320 ft [402 m], a common winter and spring weed in the area, annual herb 10–60 (90) cm tall, corolla dull burgundy-red, robust specimens may look similar to *Scrophularia californica* though differing in their inflorescence structure and annual habit, 24 March 1993, *T. Ross & S. Boyd 6819* (RSA).

Previous knowledge. This species is not recorded for the North American flora in Kartesz (1994) and, to the best of our knowledge, has not been previously reported in any Californian or North American floras.

Significance. First formal report of the species as naturalized in North America. This winter annual was originally cultivated by R. Shaw in his studies of the Scrophulariaceae at the Rancho Santa Ana Botanic Garden (Los Angeles Co.: Claremont, RSABG, grown in greenhouse, seed from Botanic Garden, Berlin, voucher sheet, *n* = 18, 22 April 1958, *R. J. Shaw 1105* [RSA]). The species probably escaped from cultivation here as early as the late 1950s, and has been a common weed on the garden grounds to this day. It often establishes itself in unirrigated areas, but particularly thrives amid garden plantings that receive some supplementary watering. The taxon occurs both on the clay soils of Indian Hill Mesa and on the adjacent, coarser granitic alluvial soils to the N and E of the mesa. It has also been noted amid native scrub vegetation on these alluvial soils in the Bernard Field Station immediately E of the garden grounds (Ross, personal observation 1991). Fortunately, both the garden and the field station are surrounded by suburban development and, to date, the species has not been documented outside of this general area in NE Claremont. It is native to the Mediterranean region and Portugal, and apparently is a weedy species by nature, as I. B. K. Richardson (*Scrophularia*, pp. 216–220 in Tutin et al. [eds.], *Flora Europaea* Vol. 3, 1972) cites the native habitat as "scrub, cultivated ground and waste places."

—TIMOTHY S. ROSS and STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

MONTANA

ASCLEPIAS OVALIFOLIA Dene. (Asclepiadaceae).—Carter Co., Long Pine Hills of Custer National Forest, 40 km se. of Ekalaka below Icebox Spring, T2S R61E S33,

locally common in partially burned valley opening among ponderosa pine, 1145 m, 2 July 1994, *K. H. Dueholm and B. Heidel 12217* (MONT, MONTU).

Significance. First record for MT, a range extension of 80 km n. from Crook Co., WY.

CAREX LUZULINA Olney var. *ATROPURPUREA* Dorn (Cyperaceae).—Beaverhead Co., se. shore of Waukena Lake, 2745 m, 1 August 1945, *C. L. Hitchcock and C. V. Muhlick 13042* (MONT, MONTU, RM); Deerlodge Co., wet meadow south above Storm Lake near trail, 2516 m, 13 August 1972, *K. H. Lackschewitz 3921* (MONTU), characteristic for all parts of the meadow around Warren Lake, 2582 m, 24 August 1974, *K. H. Lackschewitz 5690* (MONTU); Missoula Co., Carlton Reservoir, 21 August 1959, *C. H. MacDonald s.n.* (MONTU); Wind Lakes near Friday Pass, little lake to n., 2135 m, 20 August 1923, *J. E. Kirkwood and J. W. Severy 1657* (MONT); Ravalli Co., meadow of Lake Jerusalem, 219 m, 11 August 1968, *K. H. Lackschewitz and T. Fageraas 658* (MONTU); On moist, mossy banks of Lower Little Duffy Lake, 2226 m, 23 August 1968, *K. H. Lackschewitz and T. Fageraas 876* (MONTU); Wet pond meadow, (500') above Carlton Lake, Lolo Peak, 2532 m, 8 September 1968, *K. H. Lackschewitz and T. Fageraas 1045* (MONTU); meadow below Watchtower Trail Pass on Bitterroot-Selway Divide, 2379 m, 27 July 1969, *K. H. Lackschewitz and T. Fageraas 1538* (MONTU); Watchtower Peak, 27 July 1969, *K. H. Lackschewitz and T. Fageraas 1602* (MONTU, RM); moist run on bedrock July 1969, *K. H. Lackschewitz and T. Fageraas 1538* (MONTU); Watchtower Peak, 27 July 1969, *K. H. Lackschewitz and T. Fageraas 1602* (MONTU, RM); moist run on bedrock, July 1969, *K. H. Lackschewitz and T. Fageraas 1538* (MONTU); Watchtower Peak, no elev., 27 July 1969, *K. H. Lackschewitz and T. Fageraas 1602* (MONTU, RM); moist run on bedrock 31 July 1969, *K. H. Lackschewitz and T. Fageraas 1640* (MONTU); above Blodgett Lake, moist meadow on steep e. slope, Bitterroot-Selway Divide, 2363 m, no date, *K. H. Lackschewitz and T. Fageraas 1818* (MONTU); cirque below banks of "Crater Lake", 2225 m, 23 August 1969, *K. H. Lackschewitz 1856* (MONTU); above cirque lake, Ranger Peak, 2348–2379 m, 23 August 1969, *K. H. Lackschewitz and T. Fageraas 1857* (MONTU); Ranger Peak divide on moist terrace meadow of e. slope, 2410 m, 23 August 1969, *K. H. Lackschewitz and T. Fageraas 1925* (MONTU, RM); Chaffin Creek headwaters, 31 August 1969, *K. H. Lackschewitz and T. Fageraas 2056* (MONTU, RM); wet meadow above inlet of Nelson Lake, ¼ mile upstream along inlet, 2285 m, 2 August 1971, *K. H. Lackschewitz 3151* (MONTU); Trapper Peak, Bitterroot National Forest, T2N R22W S35 E ½ with *Larix lyallii* in wet meadows, 30 July 1968, *S. F. Arno 131* (MONTU); Chaffin Lakes Basin, e. slope in late snowpack meadow with meltwater ponds below showdrift, 2650 m, 30 Aug. 1971, *K. H. Lackschewitz 3395* (MONTU) (specimens annotated to variety by W. Fertig, Wyoming Natural Diversity Database).

Significance. This variety circumscription by Dorn (Flora of Wyoming, 1988) has not previously been applied to MT material, a range extension of over 465 km nw. from Sublette Co., WY.

CELTIS OCCIDENTALIS L. (Ulmaceae).—Big Horn Co., Chief Plenty Coups State Park, ca. 0.8 km w. of Pryor, T5S R26E S6, coulee arm off Pryor Creek at rimrock base lined with shrubs, 1250 m, 1 July 1994, *B. Heidel 1264* (MONT, MONTU, RM).

Significance. First record for MT apart from plantings, from a site historically used by Crow Indians. It is a range extension of 45 km n. from Big Horn and Sheridan cos., WY, where it is considered escaped from homestead plantings (R. L. Hartman, RM, pers. commun.), and 360 km nw. from native stations in Goshen Co., WY.

DICHANTHELIUM WILCOXIANUM (Vasey) Freckmann (Poaceae).—Custer Co., Fort Keogh Experiment Station, 8 km w. of Miles City, T7N R46E S2, 810 m, 20 July

1977, *J. Romo s.n.* (LARRL); Carter Co., Long Pines of Custer National Forest, opposite Little Noise Spring across Speelman Creek Rd., T2S R61E Sec. 28, 1105 m, 12 June 1994, *K. H. Dueholm 12194* (MONT, MONTU); Ekalaka Hills of Custer National Forest, ca. 2 km s. of McNab campground, T1N R59E S29, 1110 m, 14 June 1994, *K. H. Dueholm 12199* (MONTU)(*Romo s.n.* verified by J. H. Rumely, MONT).

Significance. First records for MT, a range extension of over 75 km w. from Perkins Co., SD and over 75 km n. from Crook Co., WY.

ELATINE BRACHYSPERMA Gray (Elatinaceae).—Gallatin Co., s. shore of Hebgen Lake, very wet mud, 2042 m, 30 October 1933, *J. C. Whitman 1433* (RM); Missoula Co., Missoula Valley, Frenchtown Pond, T15N R21W S33, rare under 25–30 cm of water, 914 m, T15N R21W S33, rare under 25–30 cm of water, 914 m, 26 September 1990, *W. E. Albert 877* (MRC)(*Whitman 1433* annotated by R. L. Hartman, RM, *Albert 877* verified by P. F. Stickney, MRC).

Significance. First record for MT, a range extension of 300 km w. from Johnson Co., WY.

EUSTOMA GRANDIFLORUM (Raf.) Shinnery (Gentianaceae).—McCone Co., private ranch w. of Circle in wet meadow, August 1994, McCone County Extension Service s.n. (MONT) (determined by J. H. Rumely, MONT).

Significance. First record for MT, a range extension of over 400 km n. from Natrona Co., WY.

EVAX PROLIFERA Nutt. ex DC. (Asteraceae).—Custer Co., U.S. Range Livestock Experiment Station, Pasture F, 12 July 1935, *L. Ellison 3247* (MRC, RM); Powder River Co., Custer National Forest app. 17 km. e. of Ashland, T3S R46E S16, base of small butte in rolling sagebrush grasslands, 1183 m, 27 June 1995, *H. Marriott 11570* (MONT)(*Ellison 3247* determined by Bureau of Plant Industry, augmented label by P. F. Stickney, MRC; *Marriott 11570* verified by R. L. Hartman, RM).

Significance. First record for MT, a range extension of over 220 km nw. from Pennington Co., SD.

GYMNOTERIS PARVULA Heller (Polemoniaceae).—Gallatin Co., near West Yellowstone on open mesa in Madison Basin, along highway among grasses on obsidian sand, 18 June 1932, 2040 m, *J. C. Whitham 1389* (MRC, MONT) (verified by J. H. Rumely, MONT; annotated and augmented label by P. F. Stickney, MRC).

Significance. First record for MT, a range extension of app. 55 km w. from Yellowstone National Park, WY.

IPOMOPSIS CONGESTA (Hook.) Grant var. *PSEUDOTYPICA* (Const. and Rollins) Day (Polemoniaceae).—Custer Co., near head of Sweeney Cr., edge of canyon under pine on sandy upland loam, 974 m, 17 May 1936, *L. Ellison 3292* (MRC, RM); T13N R47E S28, scattered distribution and fair abundance on gumbo soil on 15% slope, ne. aspect, 1067 m, 6 June 1924, *J. N. Templer 76* (RM); Powder River Co., Ft. Howes Work Center on Custer National Forest, T6S R45E S24, lower sparsely-vegetated slopes on rocky soil, 1036 m, 23 May 1995, *H. Marriott 11496* (MONT); 7.2 km s. of Camps Pass in Custer National Forest, T4S R47E S2, barren silty outcrop, 1225 m, 8 July 1995, *B. Heidel and S. Kimball 1371* (MONT)(*Ellison 3292*, *Templer 76*, *Heidel and Kimball 1371* annotated to variety by H. Marriott).

Significance. First records for MT of this variety, a range extension of 65 km n. from Campbell and Crook cos., WY.

IPOMOPSIS MINUTIFLORA V. Grant (Polemoniaceae).—Ravalli Co., Bitterroot Valley on Willoughby Cr., T8N R20W S13, steep bluff among sagebrush in loamy-clay derived from volcanic ash and in overlying alluvial sandy gravel layer, 1110 m, 20 June 1993, *J. A. Hoy 125* (MRC), *J. A. Hoy 135* (MONTU) (verified by P. F. Stickney, MRC).

Significance. First report for MT; a range extension of app. 320 km se. from Spokane Co., WA, and over 350 km n. from Bingham Co., ID.

ORYZOPSIS CONTRACTA (Johnson) Shechter (Poaceae).—Sheep Creek Ranger Stn., gravel wash in Beaverhead National Forest, 2135 m, 15 July 1921, *C. W. Griffin D6-123* (MRC, RM); Beaverhead Co., 3 km. n. of Clark Canyon Reservoir, T9S R11W S35, lower slopes of limestone ridges, 1829 m, 15 June 1995, *B. Heidel 1348* (MONT); mouth of Grasshopper Creek, T8S R10W S36, steep gravelly sagebrush slope, 1646 m, 16 June 1995, *B. Heidel 1353* (MONTU); Bannack State Park, T8N R12W S1, exposed gravelly grassland slope, 1780 m, 21 July 1995, *B. Heidel 1405* (MONT) (*Griffin D6-123* annotated by W. Fertig, Wyoming Natural Diversity Database, and location determined as Beaverhead Co., Tendency Mts., T13S R10W S36 by P. F. Stickney, MRC).

Significance. First records for MT, a range extension of app. 200 km nw. from Teton County, WY.

OXALIS STRICTA L. (Oxalidaceae).—Carter Co., Long Pine Hills of Custer National Forest, 16 km se. of Ekalaka, T2S R60E S33, occasional on dry benches in open ponderosa pine, 1150 m, 2 July 1994, *B. Heidel and K. H. Dueholm 1261* (MONTU).

Significance. Previously collected from Carter, Custer, Fallon and Toole cos., MT by Civilian Conservation Corps collectors in 1936 and 1937 as recorded in the INVADERS database (MONTU), though not published as part of the state flora. Label information and repository of the CCC collections are unknown. It is variously described as native and exotic, called a cosmopolitan weed by the Great Plains Flora Association (Flora of the Great Plains, 1986), and a species presumed to be native in much of North America by Hitchcock et al. (Flora of the Pacific Northwest, 1984).

PENSTEMON GLOBOSUS (Piper) Pennell & Keck (Scrophulariaceae).—Beaverhead Co., Trail Cr. meadows, T1S R18W S30, 14 July 1968, *D. V. Clark 162* (MONTU), 26 June 1969, *D. v. Clark 276* (MONTU); Pioneer Range, Mono Creek Park, R4S R12W S5, 20 July 1968, *D. V. Clark 170* (MONTU), 15 July 1970, *D. V. Clark 550, 552, 555, 556, 561, 564, 565, 571* (MONTU); Trail Cr. meadows, T2S R18W S5, no date, *D. V. Clark 572* (MONTU); Trail Cr. meadows, T2S R18W S4, 15 July 1970, *D. V. Clark 575* (MONTU); Trail Cr. meadows, T2S R18W S15, 15 July 1970, *D. V. Clark 578* (MONTU); 16 July 1970, *D. V. Clark 590* (MONTU); Trail Cr. 6.8 km e. of Gibbons Pass, T1S R18W S32, wet mountain meadow, 2059 m, 2 July 1960, *P. F. Stickney 387* (MONT, MRC); s. of Big Hole Natl. Battlefield entrance, T2S R17W S25, 1 July 1970, *D. V. Clark 508* (MONTU); Big Hole Battlefield, T2S R17W S24, 4 July 1980, *J. Pierce 797* (MONTU); May Creek Campground, T2S R18W S13, 15 July 1970, *D. V. Clark 582* (MONTU); below Chief Joseph Pass, T2S R18W S8, 15 July 1985, *P. Lesica 3388* (MONTU); Granite Co., Anaconda-Pintlar Range, Maloney Basin, T3N R15W S14, 20 July 1979, *K. H. Lackschewitz 9048* (MONTU); Anaconda-Pintlar Range, meadow setting, T3N R17W S11, 23 July 1993, *K. H. Lackschewitz and I. Lackschewitz 11999* (MONTU); Jefferson Co., ca. 45 km ne. (sic) of Butte along Hwy 91, 14 June 1936, *V. L. Marsh 96* (MONTU) (*Clark 170* verified by N. H. Holmgren in 1982, *Marsh 96* annotated to *P. globosus* by D. V. Clark; *Lesica 3388* annotated by K. H. Lackschewitz, MONTU).

Significance. Collected in sw. MT for doctoral research by D. V. Clark (1971) but

not recognized in floras. First records for MT, a range extension of app. 50 km n. from Custer Co., ID.

PENSTEMON GRANDIFLORUS Nutt. (Scrophulariaceae).—Custer Co., Fort Keogh Experiment Station, ca. 6.4 km w. of Miles City, T7N R46E S11 and S12, on sandy knob above Yellowstone River, 725 m, *J. Romo s.n.* (LARRL).

Significance. First record for MT, a range extension of over 150 km nw. from Butte Co., SD and 160 km n. from Crook Co., WY.

PHYSARIA BRASSICOIDES Rydb. (Brassicaceae).—Carter Co., Ekalaka Hills of Custer National Forest, ca. 2 km se. of Ekalaka, T1N R58E S2, occasional on small, steep sandstone outcrop, 1120 m, 11 June 1994, *K. H. Dueholm 12197* (MONTU).

Significance. First record for MT; a range extension of app. 100 km n. from Crook Co., WY.

PHYSARIA DIDYMOCARPA (Hook.) A. Gray var. *LANATA* A. Nels. (Brassicaceae).—Big Horn County, ca. 12.9 km nnw. of Decker, T8S R39E S14 and S22, locally abundant on steep scoria and sometimes shale slopes, 1160–1250 m, May 1993 [flowering], August 1993 [fruiting], *R. Prodgers s.n.* (MONT)(verified J. H. Rumely, MONT).

Significance. First record for MT; a range extension of less than 10 km n. from Sheridan Co., WY.

SPERGULARIA MEDIA (L.) Presl (Caryophyllaceae).—Beaverhead Co., Dillon, roadside alkaline area, 14 July 1958, *W. E. Booth 58200* (MONT); Madison Co., Twin Bridges, abundant in roadside alkaline area, 14 July 1958, *W. E. Booth 58208* (MONT); Jefferson Co., 3 km sw. of Whitehall, T1N R4W, alkaline flats of the Jefferson River valley, 1325 m., 3 August 1994, *B. Heidel 1246* (MONT, MONTU, RM, E) (*Heidel 1246* determined by J. Ratter, E; *Booth 58200* and *58208* annotated by B. Heidel, Montana Natural Heritage Program).

Significance. First record of this European species in MT, a range extension of over 590 km n. from Platte Co., WY.

SPIRANTHES DILUVIALIS Sheviak (Orchidaceae).—Jefferson Co., 3 km sw. of Whitehall in the Jefferson River valley, T1N R4W, wet meadow borders along small meander scar, 1326 m., 3 August 1994, *B. Heidel 1245* (MONTU, MONT, NYS) (determined by C. Sheviak, NYS; 2n=74).

Significance. First record for MT; a range extension of over 550 km nw. from Converse and Goshen cos., WY.

STELLARIA JAMESIANA Torrey (Caryophyllaceae).—Beaverhead Co., Centennial Mts., Odell Creek., T15S R2W S12, open conifer on 10% slope, ne. exposure, 2316 m, 17 July 1959, *D. Nelson s.n.* (RM); Centennial Mountains, ca. 16 km e. of Monida and 1.6 km s. on Price Peet Rd. near Price Cr., T14S R4W S31, 2165 m, 26 July 1993, *D. Culver 637* (MONT); Centennial Mts., Odell Creek, T14S R1W S31, 2135 m, 8 August 1993, *D. Culver 781* (MONT); (*Nelson s.n.* determined by Jane Roller; *Culver 637* and *781* determined by J. H. Rumely, MONT).

Significance. First records for MT; a range extension of app. 50 km nw. from Fremont Co., ID.

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REVIEWS

Tropical Alpine Environments: Plant Form and Function. Edited by PHILIP W. RUNDEL, ALAN P. SMITH and F. C. MEINZER. 1994. Cambridge University Press. 376 pages ISBN 0-521-42089-X.

Until recently the alpine vegetation of tropical latitudes has been neglected by tropical ecologists in favor of studies concerning the lowland forests. An approximately decade-long flurry of activity by a relatively small number of scientists has resulted in a wealth of information concerning the structure, function and population dynamics of the plants growing in this marginal environment. Unlike temperate alpine habitats where the landscape is dominated by prostrate cushion plants, much of the tropical alpine environment supports large tussock forming grasses such as *Muhlenbergia* and rosette forming plants like *Espeltia* (Asteraceae), *Puya* (Bromeliaceae) and *Lupinus* (Fabaceae) of the Andes, and *Senecio* (Asteraceae) and *Lobelia* (Campanulaceae) in Africa. This book provides a current overview of research that focuses on; 1) morphological and physiological adaptations to diurnal extremes of temperature, light and water balance along with nutrient limitation and 2) population dynamics and species interactions in a wide variety interesting and unique plants that "experience summer every day and winter every night."

The 20-chapter book begins with an overview of tropical alpine vegetation and climate. These first 2 chapters are excellent overviews that relate the unique features of the tropical alpine to more familiar habitats and are thus essential reading for those not familiar with the high elevation tropics. The next 3 chapters deal with the details of thermal and water balance and cold tolerance focused mostly, but not entirely on rosette forming plants. The chapter on anatomy is focused mostly on xylem anatomy but includes some information on leaves and covers not only rosette plants but sclerophyllous shrubs and cushion plants as well. Several chapters are devoted to single taxa, again the focus is on the common rosette forming plants such as *Puya*, *Espeletia*, *Draba* and *Polylepis*. Of particular interest is a discussion of the physiological ecology of tropical alpine Isoetes, which have no stomates, acquire CO₂ through the roots, and have CAM photosynthesis. Nutrient flow in tropical alpine habitats of Africa are discussed in two very short chapters, one of which shows that adventitious roots of *Senecio* absorb nutrients from still attached leaves that also function as insulation. Pollination ecologists will find the chapter on *Espeletia* reproductive biology interesting since it has unusually high levels of outcrossing when compared with low growing plants in the same habitats. *Espeletia* is typically an entomophilous genus except that the giant rosette forming alpine species are wind pollinated. Chapters 14, 15, and 16 discuss the population dynamics of rosette forming plants of Africa and Hawaiian silversword (*Argyroxiphium sandwicense*). The degree of demographic detail varies substantially for the different taxa but each contains important information. Other chapters pull together information concerning other habitats such as New Guinea and consider the importance and impact of herbivores in the tropical alpine. The book is loaded with ideas and background for further research. In addition, the final chapter written by the editors discusses progress and priorities for future research.

The structure of the book increases its utility to a wide audience. The book is well illustrated both with photographs showing species and habitats and with graphs and tables. The authors are based worldwide so habitats of interest and references to rare literature from around the world are included. Each chapter has a clearly identifiable and informative introduction, several chapters do not contain concluding summaries which would be helpful. References are included with each chapter. The book concludes with a usable index that will be handy for those looking for specific subjects.

Tropical Alpine Environments has the usual ups and downs associated with multiple authored volumes, perhaps unusually obvious here because of the vast differences in our depth of knowledge concerning the covered topics. All of the chapters are reasonably well written and each has information valuable to those with a direct interest in tropical alpine research. For those who teach plant structure, function, or population dynamics, this book is a treasure of interesting and thought provoking examples to share with students.

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Grasses of the Trans-Pecos and Adjacent Areas. By A. MICHAEL POWELL. Illustrations by PATRICIA R. MANNING. 1994. The University of Texas Press, Austin. xiv + 377 pp. Hardcover \$75.00. ISBN 0-292-76553-3. Paperback \$29.95. ISBN 0-292-765568-8.

Perhaps only in a state as expansive and biologically diverse as Texas is it worthwhile to publish a guide to grasses representing a portion the state. But as Texans can rightly boast, their biodiversity is vast, like the state itself. In *Grasses of the Trans-Pecos and Adjacent Areas* Dr. Powell has provided an attractive and well-written summary of the grasses of the expansive Trans-Pecos region, which will also be useful in southeastern New Mexico and the northern part of Chihuahua, Mexico.

The book treats 268 species and 24 varieties, representing 83 genera, which includes 53 endemic and 83% native taxa. About half of the species known from Texas are excluded (Gould 1975), which will expedite identifications for those working in the Trans-Pecos. The keys to tribes follow Clayton and Renvoize (1986), whereas the arrangement (order of presentation) generally follows Gould (1975). The hardback edition is an ideal size, about 6 by 9 inches, which readily fits into backpacks and attaches. The pages are neither overly cluttered nor have excessive amounts of unused space.

Beyond the *Preface* and *Acknowledgements*, the book has eleven sections. The *Introduction* is a brief overview of the region, including major landforms and climate. Figure 1 illustrates the major physiographic details of the Trans-Pecos, such as counties, mountain ranges, and major municipalities. *Grasses in Perspective* is the most cursory treatment, but will be of interest to non-specialists. *Grasslands* has a valuable discussion of the vegetation of the region, which includes 15 black and white photos. This overview will be particularly useful to those visiting the area for the first time, especially as it covers grasses and non-grasses in the descriptions. Powell has a solid command of regional history, and with more detail than many local treatments discusses how human activity has altered landforms and vegetation types; to my mind this adds significantly to the text. *Morphology of Grasses* presents the additional technical terminology needed to identify grasses. Admirable here is Powell's specific mention of local species to represent various morphological features, and his discussion of the peculiarities of the Paniceae and Andropogoneae, which will almost always confuse those who have not had specific training in agrostology. *Grasses of Trans-Pecos Texas* is a one-page numerical summary of Trans-Pecos grasses, mostly with respect to the grass flora of Texas overall. *Subfamilies, Tribes, and Genera Represented in Trans-Pecos Texas* enumerates the genera (including species number) by subfamily and tribe. Perhaps such information could have been summarized more cryptically but effectively as in Mabberley (1987). The *Key to the Tribes* should not be problematic for those with much experience in grasses. The next 300 pages is *Descriptive Grass Flora*, which provides descriptions of tribes and genera, and keys to species. Species descriptions are lacking, but the keys to species seem to present sufficient information to make identifications with reasonable certainty. Synonymy is excluded except when recent name changes have been invoked, or when there has

been historical dispute about generic boundaries, such as where Powell follows Barkworth and Dewey (1985) in splitting *Elymus* s. l. into several smaller genera. Common names are included, but curious is his citation of known localities without indicating the collector or collection number. We are told in the *Preface*, however, that most grass collections are probably those of B. H. Warnock. In scrutinizing the treatment of *Leptochloa* I found a few oversights. For example, by stating that *Leptochloa dubia* is the only perennial species in North America he has overlooked *L. virgata*. In addition, *L. dubia* can have hairs on the lemma, contrary to his key. His citation of C. Presl as the parenthetical author of *Leptochloa uninervia* should have read J. Presl. It is unfortunate that some regional agrostological treatments have been poorly edited. Careless oversights, for example the reversal of male and female inflorescences of buffalograss (Beetle 1987: 156-157), seem to be lacking. Thus, if *Leptochloa* is indicative of most genera, one need not worry about the overall reliability of the information in the present volume. The *Glossary* consists of approximately 250 entries. The *Literature Cited* is current and generally well chosen, although significant monographs (e.g., Peterson & Annable, 1991) are sometimes not cited immediately following the generic descriptions, where that information might be most useful. The volume closes with an *Index* that includes scientific and common names.

At least one species per genus is illustrated. As a general comment, I would prefer that authors be more careful in reproducing illustrations from Hitchcock (1951), since many are of dubious quality. For example, *Leptochloa uninervia* and *L. fascicularis* have much better illustrations in Correll and Correll (1972). Powell has taken an intermediate approach, using some from Hitchcock (1951) and others by Patricia Manning drawn for this volume.

Powell intended to produce a book useful to "non-scientist and scientist alike", and in my opinion he succeeded. In summary, this is a worthwhile volume, but the prices are somewhat high. My hunch is that many colleagues will not pay so much for a regional treatment of a single family. None the less, for those whose research or vacations take them to the Trans-Pecos, Powell's book is definitely recommended. I liked *Grasses of the Trans-Pecos and Adjacent Areas* and commend the author on its overall quality.

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ANNOUNCEMENT

CALIFORNIA EXOTIC PEST PLANT SYMPOSIUM '96

October 4–6, 1996

Handlery Hotel, San Diego, California

The California Exotic Pest Plant Council (CalEPPC) announces *CalEPPC Symposium '96*, its annual symposium dealing with the threat to California's natural ecosystems by invasive non-native plant species introduced from other parts of the world. The symposium will be held October 4–6, 1996 at the Handlery Hotel in beautiful San Diego.

In California, and throughout the nation, exotic pest plants pose the greatest single threat to the long term integrity of many natural areas and ecosystems. According to one estimate prepared by the Bureau of Land Management, infestations of exotic pest plants are increasing at the rate of approximately 4600 acres per day on disturbed and undisturbed public lands in the west.

The Symposium will bring together leading experts, land managers, public and non-profit agency staff, field practitioners and concerned citizens who are developing solutions to this major problem. The focus of this year's Symposium is exotic plant invasions in the western United States and Mexico. Other presentations will bring the latest information on a range of related topics from top experts in their field.

This year's keynote speaker is Dr. Michael Barbour, a widely known and respected authority on California plant communities. Barbour's extensive work on wildland vegetation across the state for over 30 years, combined with a deep passion for his subject and an award-winning teaching style, makes his appearance at CalEPPC Symposium '96 an event to look forward to. He will help us look back into history to see how non-native plant invasions have changed the state, and will help define a positive vision of the plant communities we hope to restore. Don't miss his outstanding presentation.

To receive an invitation or for more information, contact Sally Davis, P.O. Box 15575, Sacramento, CA 95852-0575. Telephone: (916) 921-5911; email: sallydavis@aol.com.

SUBSCRIPTIONS—MEMBERSHIP

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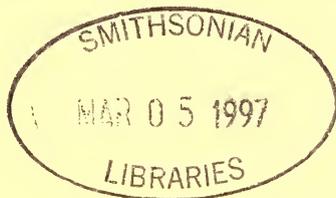
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THE ARBOL DEL TULE
(*TAXODIUM MUCRONATUM* TEN.) IS A
SINGLE GENETIC INDIVIDUAL

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ABSTRACT

El Arbol del Tule (The Tule Tree: *Taxodium mucronatum* Ten. [Taxodiaceae]), found in Santa María del Tule, Oaxaca, Mexico, is considered to have the largest trunk circumference in the world. It has been suggested, however, that this tree may be derived from the fusion of multiple individuals. Using random amplified polymorphic DNA's (RAPD's), we found evidence of genetic uniformity of the Tule tree among branches, indicating that the Arbol del Tule in all likelihood is a single genetic individual. As such, its claim to title of the tree with largest trunk circumference remains unchallenged.

RESUMEN

El Arbol del Tule (*Taxodium mucronatum* Ten. [Taxodiaceae]), localizado en Santa María del Tule, Oaxaca, México, es considerado como el árbol con el tronco más ancho del mundo. Sin embargo, se ha sugerido que este gigantesco árbol podría haberse formado por la fusión de varios individuos. Utilizando polimorfismos de DNA amplificadas al azar (RAPD's) obtuvimos evidencia de uniformidad genética entre las ramas principales del Arbol del Tule, indicando que este árbol está compuesto de un solo individuo genéticamente. Por lo tanto, el título de el árbol con el tronco más ancho del mundo, para el Arbol del Tule, permanece latente.

The intimate association between humans and nature can be identified in the cultural expressions of most civilizations. Plants, especially those with peculiar features, are closely linked to civilizations in southern Mexico. Such is the case of El Arbol del Tule (the Tule Tree: *Taxodium mucronatum* Ten. [Taxodiaceae]), found in Santa María del Tule, Oaxaca, México. This tree has the largest stem circumference (45.7 m dbh) in the world. Because of its majestic appearance this individual has played an important role in the history and culture of the local region in southern Mexico. *Taxodium mucronatum* is an abundant tree, 10–30 m tall, commonly growing along ravines and small streams. Its abundance and wide distribution in Mexico is reflected in the numerous common names applied to this plant: “ahuehuete,” “ciprés,” “pénjamu,” “sabino,” among

others (Standley 1922; McVaugh 1992). Besides the Tule tree, there are other individuals of this species that presided over relevant historic events, such as "El Arbol de la Noche Triste" (The Tree of the Sad Evening) found near Mexico City. According to some narratives, Cortés cried at the base of this tree after being defeated by the Mexica Indians in 1520 (Alvear 1976).

Hall et al. (1990) wrote a detailed literature review of the historic significance of the Tule tree and discussed the different types of studies undertaken on this tree. It has been suggested that the Tule tree may in fact represent the fusion of multiple individuals (Hall et al. 1990). Trees composed of different individuals have been reported in nature. One of the more striking examples is in the genus *Ficus* (Moraceae). Thomson et al. (1991) found that single trees of strangler figs in Panama, include multiple genotypes, and they are formed by the fusion of different individuals. The aggregate tree hypothesis of the Tule tree has been recently tested by an isozyme analysis of the main branches of this historic tree (Hall et al. 1990). Of the 16 loci surveyed in that study, all except *Skdh-2* were monomorphic, even in two neighboring trees. In addition, all samples of the Tule tree were heterozygous for *Skdh-2* (with *Skdh-2ab*) whereas both neighboring trees possessed only *Skdh-2b*. They concluded that heterozygosity of all the main branches of the Tule tree for *Skdh-2b* contrasting with the homozygosity of the two neighboring trees for this locus provides strong evidence to support the hypothesis that the Tule tree originated from a single seedling. However, the low number of loci available for comparison did not rigorously support the hypothesis that the Arbol del Tule is in fact a single tree.

Random amplified polymorphic DNA (RAPD's) has been successfully used in a great variety of applications in plants such as genetic mapping (Fauré et al. 1993; Nelson et al. 1993; Quiros et al. 1991), analysis of genetic variation (Tao et al. 1993; Wolf and Peters-Van Rijn 1993; Yu and Nguyen 1994), breeding system studies (Fritsch & Rieseberg 1992), DNA fingerprinting (Adams et al. 1993; Rieseberg et al. 1994), parentage determination (Welsh et al. 1991) and identification of molecular markers linked to specific traits (Martin et al. 1991; Chalmers et al. 1993), among others. Using RAPD's, we tested the hypothesis of genetic unity of the Tule tree. If all the main branches of this tree are identical at all RAPD loci, then the Tule tree is in all likelihood a single genetic individual. In contrast, the discovery of RAPD polymorphisms among branches of the Tule tree would support the multiple genotype hypothesis. However, for this to be a valid test of these alternative hypotheses, it is necessary to demonstrate that sampled loci are polymorphic in natural populations of *Taxodium mucronatum*. Thus, we also compared the results from the Tule tree with variation in two wild pop-

TABLE 1. POPULATIONS OF *TAXODIUM MUCRONATUM* ANALYZED FOR RAPD VARIATION. Vouchers are deposited at the herbarium of the University of Morelos (HUMO).

Population designations	Locality and collection number
Tule Tree	Santa María del Tule, Oaxaca, México, <i>Dorado 2305, Cota and Leyva.</i>
“Tule brothers” CUERNAVACA	Same locality, <i>Dorado 2306, 2307, Cota and Leyva</i> Col. Rancho Tetela, Cuernavaca, Morelos, <i>Dorado 2308, Ramírez, and Flores.</i>
TEMIXCO	Puente del Diablo, 2 km al N de Temixco, Morelos, <i>Dorado 2309, Ramírez and Flores.</i>

ulations of the same species, as well as with nearby individuals in Santa María del Tule.

MATERIALS AND METHODS

Fresh leaf tissue was collected from the six main branches of the Tule tree of Santa María del Tule, Oaxaca, Mexico. In order to detect any possible variation we sampled from both nearby populations and more distant populations. Two individuals of *Taxodium mucronatum* found in close proximity (ca. 30 m) were collected, and they were designated in this study as “Tule brothers” samples 7 and 8, respectively. In addition, 15 individuals in each of two distant populations in Cuernavaca and Temixco were sampled to assess levels of RAPD variation within wild populations of this species (Table 1). Leaves were stored on ice and total DNA was isolated from 30 mg of leaf tissue from each sample. DNA isolations followed Doyle and Doyle (1987) with three modifications. First, all volumes were reduced to allow isolations to be performed in 1.5 ml microfuge tubes. Second, sodium metabisulfite (1% w/v) was added to the CTAB buffer. Third, two chloroform extractions were performed.

Primers known to amplify strongly in plants (Fritsch et al. 1993) were used for amplification. Primers were obtained from Operon Technologies (Alameda, California) and University of British Columbia Biotechnology Center. Amplification conditions followed Williams et al. (1990) and were carried out in a MJ Research thermal cycler (Watertown, MA). Amplified products were electrophoresed through 1.5% agarose gels using TBE buffer, stained with ethidium bromide, and photographed using a UV light source. In order to standarize amplification conditions, DNA isolates were quantified with a fluorometer (Hoefer), and standardized to 10 ng/μl. We adopted a conservative approach of scoring only strongly amplified fragments.

A preliminary survey of primers in search of consistent and reliable RAPD amplifications was undertaken using five branches

from a single tree from the Cuernavaca population. Of the 104 primers analyzed, 23 primers gave uniform amplifications of all five DNA samples (Table 2). This trial was repeated with five branches from a single tree of the Temixco population. The same 23 primers were again indicated, and these primers were selected for use in the final analysis of the Tule tree and the Cuernavaca and Temixco populations.

RESULTS AND DISCUSSION

A total of 149 fragments was generated, each of which was presumed to represent a locus. Of these fragments, 31 (22.8%) were polymorphic at least within one population (Table 2). However, these polymorphisms were detected only in the Temixco and/or Cuernavaca populations. None of the six branches of the Tule tree showed variation at any of the 149 RAPD loci analyzed. An example of the amplified products from UBC primer 103 is shown in Figure 1. This primer generated variable fragments in several individuals, but the six branches of the Tule tree were invariant.

Although the Tule brothers were similar to the Tule tree, they possessed 15 loci that were different with respect to the Tule tree. In addition, 12 loci distinguished the two Tule brothers from each other. Tule brother 7 differed from the Tule tree by 10 loci, whereas 12 loci distinguished Tule brother 8 from the Tule tree. Thus, Tule brother 7 is slightly more similar to the Tule tree than to Tule brother 8, despite its close geographical distance to Tule brother 8 (ca. 5 m) and its larger distance to the Tule tree (ca. 30 m).

The lack of polymorphism found among the six branches of the Tule tree strongly supports the hypothesis that this gigantic tree represents a single genetic individual. If the Tule tree were in fact a population of several individuals, it seems likely that some of the 23 primers and 149 loci (31 polymorphic) would show variation, as they did in the Cuernavaca and Temixco populations, and as they did in the Tule brothers.

It may be argued, given the nature of cone dispersal in *Taxodium*, that a single cone may give rise to several siblings and that the Tule tree is an aggregate of siblings. However, *Taxodium* is wind pollinated, sexually reproducing, and monoembryonic (Vasil and Sahni 1964), and the ovules of a single cone would likely be, fertilized by genetically different pollen parents. That no genetic variation was detected in the Tule tree suggests that the tree is a single individual not a population of siblings.

Somatic mutation, if it exists in the Tule tree, must surely exist at a lower level than the variation found among younger individuals in the Cuernavaca and Temixco populations. The fact that we found

TABLE 2. NUMBER OF POLYMORPHIC FRAGMENTS IDENTIFIED BY EACH PRIMER IN THE ANALYSIS OF THE ARBOL DEL TULE. PRIMERS A-F ARE FROM OPERON TECHNOLOGIES; I01, I03 AND I06 ARE FROM UNIVERSITY OF BRITISH COLUMBIA BIOTECHNOLOGY CENTER.

Population	Primer																								
	A1	A8	A20	B12	B18	C1	C2	C11	C19	D3	D7	E18	E19	E20	F4	F5	F6	F10	F11	F19	I01	I03	I06		
Tule	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cuernavaca	1	3	2	1	0	0	3	1	0	2	1	0	0	0	0	2	0	0	1	0	1	0	1	3	3
Temixco	0	2	1	2	1	1	4	0	0	2	1	0	0	0	1	3	2	0	1	0	1	0	1	2	1

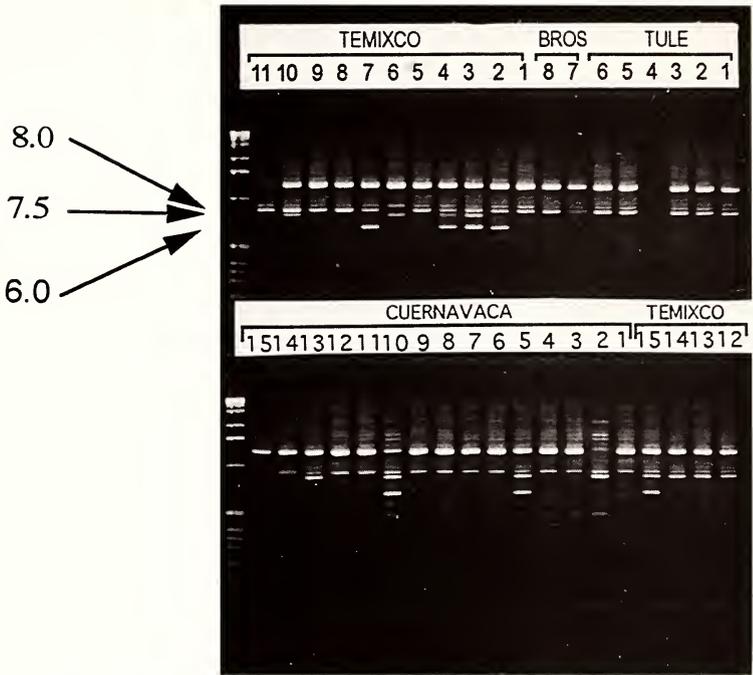


FIG. 1. Electrophoretic patterns of the RAPD products of UBC103 for the Tule tree (lanes 1–6), “Tule brothers” 7 and 8 (lanes 7–8), Temixco population (lanes 9–22), and Cuernavaca population (lanes 23–38). The fragments 8.0, 7.5 and 6.0 kb are polymorphic for several individuals of the Temixco and the Cuernavaca populations. The standard molecular marker (kb ladder: Gibco BRL) is in the last lane of both gels.

no variation *at any level* in the Tule tree samples strongly supports the conclusion that the Tule tree is a single genetic individual.

The results described in this paper show that RAPD markers are a powerful tool for the characterization of single individuals. Our data confirm that the Tule tree is a single, genetically uniform individual. As such, its claim to the title of tree with the largest trunk circumference in the world is unchallenged, and its significance to the people of Santa María del Tule is undiminished.

ACKNOWLEDGEMENTS

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NOTEWORTHY COLLECTIONS

ARIZONA

ANTHOCEROS AGRESTIS Patton (Anthocerotae).—Pinal Co., Tonto National Forest, north of Hwy 60 at Top-of-the-World, between Superior and Globe. T1S R13E, ca. 111°00'40"W, 33°24'N, growing in Mule Spring drainage, west of Power's Gulch in a wet seep area along the stream with mosses, liverworts, and orchids, 30 April 1995, J. Rebman *et al.* 2906 (ARIZ, ASC, ASU, DES, SD).

Previous knowledge. Known to be widespread but more common in the eastern parts of the United States where it can occur as a weed in cultivated areas. This species of hornwort is not well understood and does have nomenclatural problems. The taxon was long known as *A. crispulus*, but the type specimen proved to be a different race of *A. punctatus*; more recently it was placed in *Aspiromitis punctatus* var. *agrestis*, but this name is incorrect based on a typification error (Alan Whittemore personal communication 1995).

Significance. First confirmed record for Arizona and not common in the southwestern USA. The locality where this hornwort was found is part of the proposed Carlota Copper Mine project and may be destroyed as development occurs.

—JON P. REBMAN, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112 and WENDY C. HODGSON, Desert Botanical Garden, 1201 N. Galvin Parkway, Phoenix AZ 85008.

MORPHOLOGICAL AND REPRODUCTIVE
CHARACTERISTICS OF *LINANTHUS JEPSONII*
(POLEMONIACEAE), A NEWLY DESCRIBED,
GEOGRAPHICALLY RESTRICTED SPECIES FROM
NORTHERN CALIFORNIA

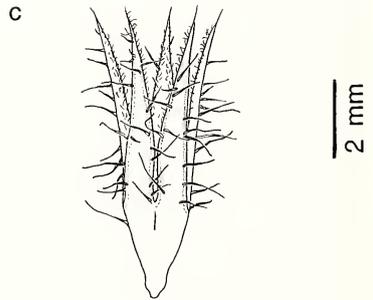
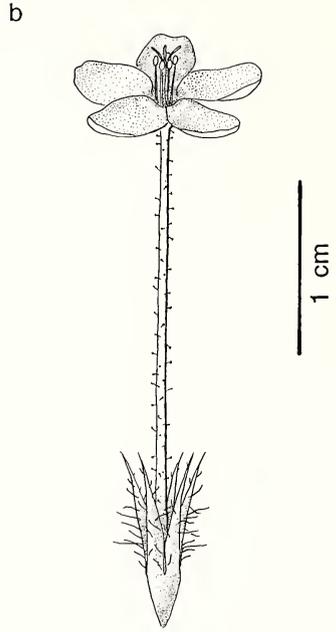
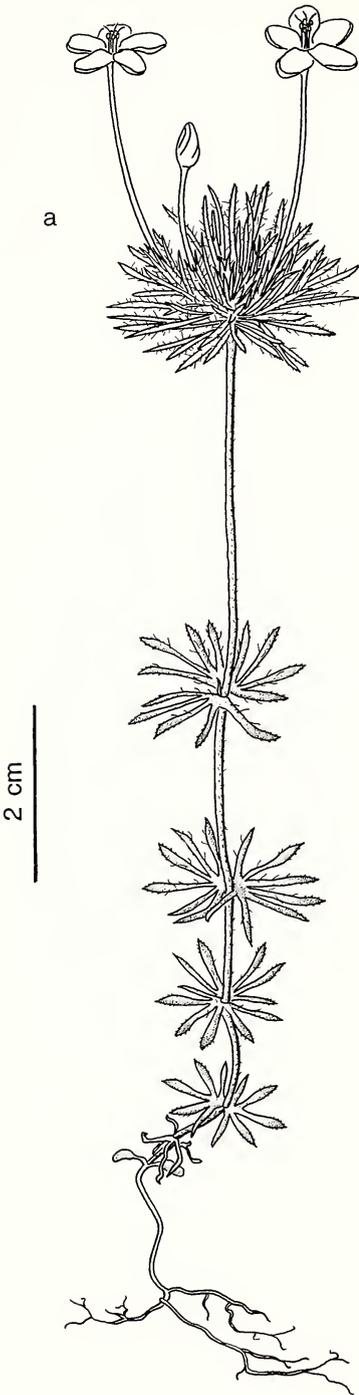
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ABSTRACT

Linanthus jepsonii is a newly described species in the *L. androsaceus* complex (sect. *Leptosiphon*) restricted to Lake, Napa and Sonoma Cos. in the California North Coast Range. Multivariate analyses of six morphological characters revealed that *L. jepsonii* is readily distinguished from the other species in the complex found in the same region. It is ecologically and morphologically most similar to *L. parviflorus*, but can be distinguished from this species by its long calyx, the long, sparse hairs on the calyx lobes and its self-compatible breeding system. Greenhouse experiments indicate that these taxa are reproductively isolated, as crosses between them produce few seeds, and hybrid plants are typically male sterile.

Field and laboratory studies to examine the evolution of a flower color polymorphism in the California annual *Linanthus parviflorus* (Benth.) Greene led to the discovery of a new species in the *Linanthus androsaceus* complex [*L. androsaceus* (Benth.) Greene, *L. parviflorus* (Benth.) Greene, *L. latisectus* Buxton, *L. bicolor* (Nutt.) Greene, *L. acicularis* Greene, and *L. serrulatus* Greene], sect. *Leptosiphon* (Endl.) V. E. Grant (Grant 1959). The new species is superficially very similar to *L. parviflorus*, and can be found in similar habitats, but differs from it in breeding system and in several distinctive morphological characters, most notably calyx pubescence. Crosses between the new species and *L. parviflorus* produce few seeds, and the few hybrids that survive are typically sterile. The morphological and reproductive characteristics of the new taxon are sufficiently distinct from other members of the section *Leptosiphon* to warrant species status. Field observations and an extensive survey of herbarium specimens indicate that the new species has a restricted geographic range, being found only in Lake, Napa and Sonoma Cos. We have chosen to name this species in honor of the renowned botanist Willis Linn Jepson, who collected the first specimen in 1893, one hundred years before publication of *The Jepson Manual* (Hickman 1993).

Linanthus jepsonii D. W. Schemske and C. Goodwillie, sp. nov.
(Fig. 1). —TYPE: USA, California, Napa County, Wantrup Wild-



life Sanctuary, on primary road 1.3 km W of Hardin Rd., and 60 m N of vernal pool on north-facing, grassy slope, elev. 256 m, 11 May 1995, *C. Goodwillie* 001 (holotype WTU; isotypes CAS, JEPS, MO, RSA, SFSU and US).

Caules erecti; raro ramosi, 4–12 cm alti; folia recta, sursum angulata, lobo medio lineari, 0.8–1.1 mm lato; calyx 6–9 mm longus, apicibus recurvis, superficie adaxiali calicis marginibusque sparse villosis, trichomatibus mollibus, 0.7–1.6 mm longis; corollae tubus 20–36 mm longus, rubellus; corollae lobi 4–6 mm, ovales, angulis rectis tubo conjuncti, sursum concavuli, rubelli vel albi; stigmata 0.8–2.0 mm longa, clavata, plerumque excedentia antheras easque superantes; inflorescentia pauci vel multiflora, floris 1–2 (3) uno tempore florentibus.

Annual. Stems erect, green or rose, pubescent, rarely branched, 4–12 cm high. Leaves opposite, straight, angled upwards, palmately divided; leaves subtending inflorescence 5–8 lobed, middle lobe linear, 0.8–1.1 mm wide, 8–13 mm long, lateral lobes similar, adaxial surface and margins sparsely villous, trichomes 1–1.5 mm long, abaxial surface glabrous; lower leaves 3–8 lobed, middle lobe linear to spatulate, lateral lobes less spatulate, trichomes shorter and less dense than on upper leaves. Inflorescence head-like, terminal, typically one per plant, 1–2 (3) flowers open at a time, 4–15 flowers per inflorescence, flowers sessile; calyx 6–9 mm long, 5-lobed with a membrane half the width of calyx lobe, tips recurved, adaxial surface and margins of calyx lobe sparsely villous, trichomes 0.7–1.6 mm long, abaxial surface glabrous. Corolla salverform; tube 20–36 mm long, 0.6 mm in diameter, glabrous to sparsely puberulent, glandular, pink; throat yellow; lobes 4–6 mm long, oval, at right angles to tube, somewhat concave upwards, pink or white. Stamens exerted, filaments 2 mm long. Style thread-like, exerted; stigmas 0.8–2.0 mm long, clavate, yellow, generally overlapping with and extending somewhat beyond anthers. Capsule obovoid with 3 locules, up to 6 seeds per locule, dehiscent. Seeds 1.2 mm long, angular, corrugated, yellowish-tan, mucilaginous when wet.

Paratypes. USA, California: Lake Co., Mt. St. Helena, 30 Apr 1933, *Mason 7217* (UC); Collayomi Valley, 19 Apr 1936, *Jepson 17417* (JEPS); Napa Co., Calistoga, 2 May 1893, *Jepson s.n.* (JEPS, UC); Pope Valley, 15 May 1920, *Ferguson 349* (JEPS, MO); Conn

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FIG. 1. *Linanthus jepsonii* D. Schemske and C. Goodwillie. **a**, habit illustrating unbranched stem, few-flowered inflorescence and long corolla tubes. **b**, calyx and corolla, with stigma lobes overlapping the anthers. **c**, calyx with recurved tips and long hairs sparsely distributed on the adaxial surface of the calyx lobes.

Valley, Napa Range, 6 Apr 1924, *Jepson 10315* (JEPS); Mt. St. Helena, 2 mi below Patten's, 21 Mar 1926, *Howell 1735* (CAS); St. Helena Grade, 3 May 1928, *Abrams 12220, 12221* (DS); 2 mi S of Hawkins Mtn. Inn Camp, 3 May 1928, *Wolf 1792* (DS); 1.5 mi W of Yountville, 22 Apr 1938, *Constance 2135* (MO, UC); Dry Creek Rd., 28 May 1960, *Ruckert 164* (CAS); Hwy. 29, 8 Apr 1971, *Shevock 920* (CAS); Sonoma Co., Cagadero, 2 May 1926, *Bacigalupi 1366* (DS); hillside opposite Maple Glen, 7 May 1927, *Baker 21441* (UC); Reibli School near springs, 13 Apr 1928, *Mason 4339* (UC); Santa Rosa, 24 Apr 1931, *Eastwood 10365* (CAS); near Mark West Springs, 15 May 1938, *Eastwood and Howell 5508* (CAS); 15 mi from Geysers, Sulfur Creek Canyon, 22 Apr 1940, *Koch 832* (UC); head of Maycama Creek, Knights Valley, 21 May 1940, *Mason 12293* (UC); vicinity of Bechtel Cabin, Pepperwood, 30 Mar 1981, *Almeda and DeNevers 4878* (CAS); Pippindale Farm, Hansel's cow pasture, Pepperwood, 8 Apr 1981, *DeNevers 664* (CAS); 4.5 mi NE of Pengrove on W slope of Sonoma Mtn., 14 May 1981, *Howell et al. 53956* (CAS); grazed shore of Hansel's cow pasture, Pepperwood, 15 May 1981, *DeNevers 1205* (CAS); Pepperwood Ranch W of Knights Valley, 11 Apr 1983, *Breedlove 58684* (CAS); 2 mi NE of Bechtel Cabin, Pepperwood, 1 May 1993, *de Geofroy 036* (SFSU).

Distribution. *Linanthus jepsonii* has a restricted distribution in the California North Coast Range, occurring only in Lake, Napa and eastern Sonoma Cos., at elevations from 200–500 m. In a sample of 2402 herbarium specimens that had been classified as *L. parviflorus*, *L. bicolor*, or *L. androsaceus* (from CAS, DS, JEPS, MO, RSA, SFSU and UC), we found only 35 that could be assigned to *L. jepsonii*, all occurring in Lake, Napa and Sonoma Cos. Extant populations were observed in Napa Co. (four populations) and Sonoma Co. (one population).

Habitat, life history and reproductive biology. *Linanthus jepsonii* is found on open or partially-shaded, grassy slopes, principally on volcanic soils, and occasionally on the periphery of serpentine soils. The seeds of *L. jepsonii* germinate during winter rains, and flowering occurs from early April through May. Fruits mature in 3 weeks, and seeds are dispersed by explosive dehiscence of the capsule. Although *L. jepsonii* is variable for flower color (pink or white corolla lobes), pink-flowered plants predominate (>95% of all plants) in three of the five populations of *L. jepsonii* we have observed, and white-flowered plants predominate in the other two populations. Despite its restricted geographic range, *L. jepsonii* often forms dense populations, with population sizes ranging from 400 to >>10,000.

Linanthus jepsonii is visited and pollinated by beeﬂies (*Bombylius*

spp.), but is fully self-compatible and capable of autogamy, as indicated by greenhouse experiments that found no significant difference in seed set in hand self-pollinations (mean = 8.7, n = 88), cross-pollinations (mean = 8.4, n = 87), and unmanipulated flowers (mean = 8.0, n = 89).

SPECIES RELATIONSHIPS

The floral characters of *L. jepsonii* place it in the section *Leptosiphon*, a group of annual *Linanthus* species first recognized by Grant (1959) and characterized by sessile flowers borne in terminal heads, with filiform tubes much exerted beyond the calyx (Buxton 1994). Although we have not made a chromosome count, electrophoretic data gathered for mating system estimation (Goodwillie and Schemske, unpublished) suggest that *L. jepsonii* is diploid, as are all other species in this section for which cytological information is known (Patterson 1979, 1993).

Morphology. Flower and calyx size, and calyx pubescence have been widely used in taxonomic treatments of the Polemoniaceae (Patterson 1993, Buxton 1994, Gordon-Reedy 1990). To compare the morphology of *L. jepsonii* to other members of the *Linanthus androsaceus* complex (sect. *Leptosiphon*) found in the same region, we measured the length of the corolla lobe, corolla tube, stigma, calyx, and calyx hairs, and counted the number of hairs on the calyx of 30 individuals for each of five populations of *L. jepsonii* (from Lake, Napa and Sonoma Cos.) and *L. parviflorus* (from Lake, Napa and Sonoma Cos.), and for each of two populations of *L. androsaceus* (from Napa County), *L. bicolor* (from Napa County) and *L. latisectus* (from Mendocino and Sonoma Cos.). The total sample comprised 480 individuals from 10 different localities. Figure 2 presents the mean value for each of the six characters for the four species examined, and provides a statistical analysis for those pairwise comparisons to *L. jepsonii*. To determine if the mean value of a character in *L. jepsonii* was significantly different from that in each of the other species, we conducted an analysis of variance (ANOVA; SAS Institute 1994) for each of the four pairwise combinations involving *L. jepsonii*, with population nested within species. Significance levels were adjusted for multiple comparisons of each character following the procedure of Rice (1989). *L. bicolor* was found to differ significantly from *L. jepsonii* for each of the six characters, and *L. latisectus* was significantly different from *L. jepsonii* for all characters except stigma length. *L. androsaceus* was significantly different from *L. jepsonii* for corolla lobe length, corolla tube length, stigma length, and calyx length, and *L. parviflorus* was significantly different from *L. jepsonii* for stigma length, number of calyx hairs, calyx hair length and calyx length (Fig. 2).

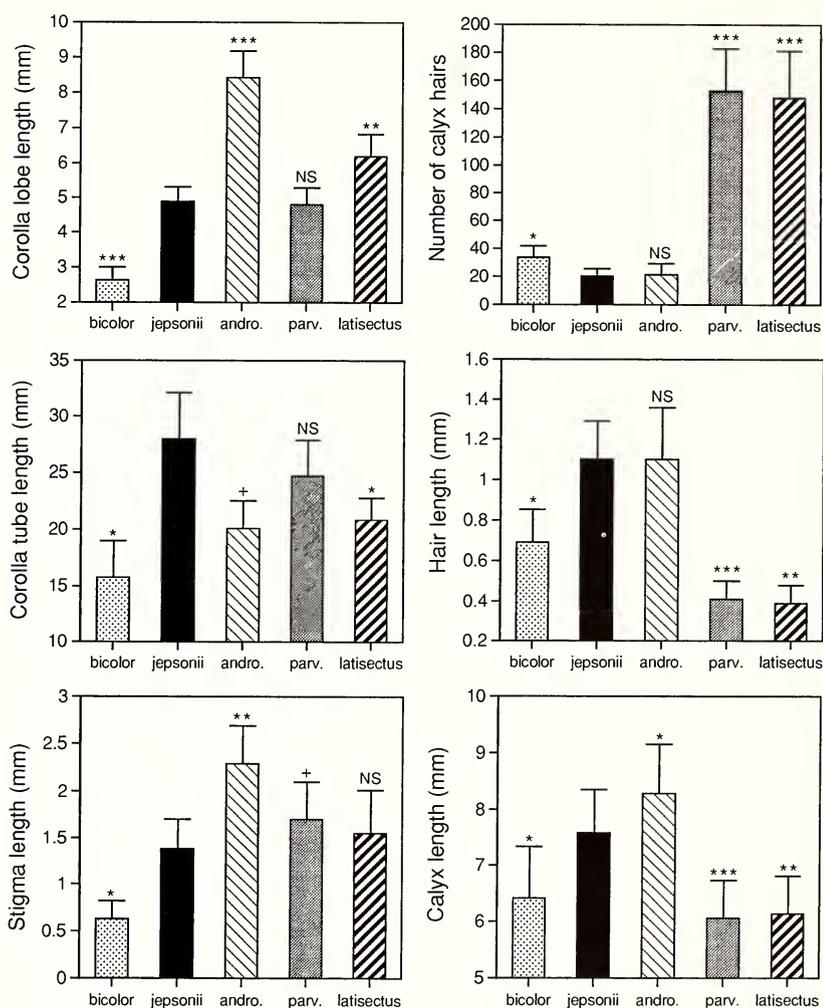


FIG. 2. Comparison of reproductive characters for five species in the *Linanthus androsaceus* complex, section *Leptosiphon*. Means and 2 SE are presented, based on a sample of 30 individuals for five populations of *L. jepsonii* and *L. parviflorus*, and two populations of *L. androsaceus*, *L. bicolor* and *L. latisectus*. The number of calyx hairs was determined for the adaxial surface of one calyx lobe (including lobe margins), and hair length represents the mean of the longest two hairs on one calyx lobe. The symbols over the bars indicate if a given species was significantly different from *L. jepsonii*; + $P < 0.06$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant.

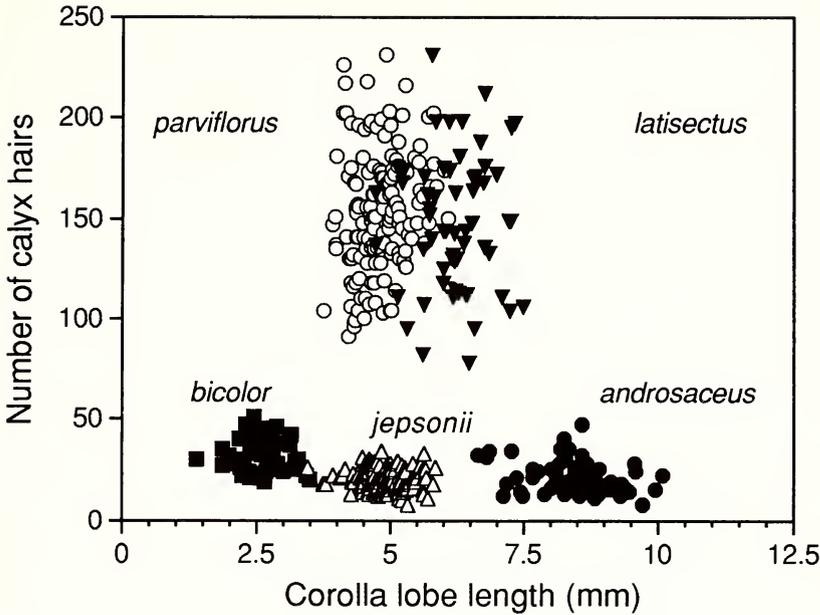


FIG. 3. Scatter plot for the number of hairs on the adaxial surface of one calyx lobe (including lobe margins) and corolla lobe length for specimens of five species of *Linanthus*. Numbers of individuals and populations are given in Figure 2.

A multivariate analysis of variance (MANOVA; SAS Institute 1994) conducted on all six characters indicated highly significant differences among species (Wilks' Lambda = 0.0016, $F = 361$, $df = 24/1641$, $P < 0.0001$). A discriminant analysis (SAS Institute 1994) was then used to determine how accurately the six characters, taken together, would classify the specimens into their correct taxon. The discriminant analysis was highly significant (Likelihood ratio = 695.6, $X^2 = 1391$, $P < 0.0001$, $R^2 = 0.96$), correctly classifying 99% of the 480 specimens, including 149 of the 150 specimens of *L. jepsonii*. A discriminant function analysis conducted with corolla lobe length and the number of hairs on the calyx lobe was the best two-character model (as judged from classification accuracy), correctly classifying 96% of all specimens, and was as efficient as the full six-character model in classifying specimens of *L. jepsonii* (MANOVA: Wilks' Lambda = 0.00997, $F = 1068$, $df = 8/948$, $P < 0.0001$; Discriminant Function Analysis: Likelihood ratio = 648.9, $X^2 = 1298$, $P < 0.0001$). A scatter plot of these two characters for all measured specimens is given in Figure 3. The number of calyx hairs divides the five species into two groups, one with many hairs, including *L. parviflorus* and *L. latisectus*, and the other

with few hairs, including *L. bicolor*, *L. jepsonii* and *L. androsaceus* (Fig. 3). In the group with sparse calyx pubescence, the corolla lobes of *L. jepsonii* are larger than those of *L. bicolor* and smaller than those of *L. androsaceus*, and the differences are sufficient to distinguish these species (Fig. 3).

Reproductive biology. In addition to the morphological characters discussed above, breeding system also varies considerably among species of the *L. androsaceus* complex. Although we do not have information on the reproductive biology of all species in the complex, our data are sufficient to make several comparisons of systematic significance. *L. bicolor* is self-compatible and appears to be highly selfing, as its diminutive flowers are rarely visited by pollinators (Goodwillie, personal observation). In contrast, both *L. jepsonii* and *L. parviflorus* are visited by bees (*Bombylus* spp.), but they differ in breeding system. *L. parviflorus* is self-incompatible (Goodwillie in press), while *L. jepsonii* is self-compatible. In greenhouse experiments with *L. parviflorus*, seed set from hand self-pollinations was less than 5% of that from cross-pollinations, indicating the presence of a strong incompatibility system. Parallel experiments with *L. jepsonii* revealed no difference in seed number for selfed and outcrossed flowers. Mating system estimates were obtained from electrophoretic loci for populations of both species in Napa County. *L. parviflorus* was found to be 79% cross-pollinated, while *L. jepsonii* appears to have an intermediate mating system, with 43% of progeny derived from cross-pollination (Goodwillie and Schemske, unpublished).

Reproductive Isolation. An additional criterion for establishing the taxonomic rank of sympatric taxa is to determine the degree to which their populations are genetically isolated from one another. Sympatric populations that fail to produce fertile hybrids in the field are reproductively isolated, and therefore represent different biological species (Grant 1981; Mayr 1982).

Linanthus jepsonii overlaps the geographic distribution of four other species in the section *Leptosiphon*: *L. androsaceus*, *L. bicolor*, *L. latisectus*, and *L. parviflorus*. Preliminary genetic data based upon molecular markers suggest that *L. jepsonii* is most closely related to *L. bicolor* (Goodwillie, unpublished), but the high selfing rate of *L. bicolor*, and our observation that *L. bicolor* and *L. jepsonii* do not co-occur at the population level, suggest that these two species are reproductively isolated in the field. Our failure to find hybrids between these taxa supports this conclusion. Nor have we observed hybrids between *L. jepsonii* and *L. androsaceus* or *L. latisectus*. In contrast, we have observed several individuals that appear to be hybrids between *L. jepsonii* and *L. parviflorus* at two localities where these species have adjacent populations ("Litto Ranch" and "Mast Hill" in Napa County). Because *L. jepsonii* and *L. parviflorus* share the same polli-

nators, are either fully (*L. parviflorus*) or partially (*L. jepsonii*) out-crossing, and often grow in close proximity, interspecific pollen flow is more likely to occur between these two species than between *L. jepsonii* and other members of the *L. androsaceus* complex.

To assess the degree of reproductive isolation between *L. jepsonii* and *L. parviflorus*, we conducted inter- and intraspecific crosses in the greenhouse on plants grown from seeds collected from three sites with populations of both *L. jepsonii* and *L. parviflorus* (Litto Ranch and Mast Hill in Napa County, and Pepperwood Ranch in Sonoma County). All pairwise combinations of inter- and intraspecific crosses were conducted, both within and among sites (including reciprocals) with 3–5 plants crossed for each taxon and site. This resulted in 18 interspecific combinations (3 sites with a given species as the male parent \times 3 sites with the other species as the female parent \times 2 species/site = 18 combinations), and 9 different intraspecific combinations for both *L. jepsonii* and *L. parviflorus* (3 sites with a given species as the male parent \times 3 sites with the same species as the female parent = 9 intraspecific combinations for each species). We counted the number of filled seeds produced for each cross, and scored germination success and survival to flowering. The number of seeds planted for inter- and intraspecific crosses, respectively, was 490 and 683. In a second experiment we scored pollen fertility for inter- and intraspecific crosses conducted on the two species collected from the Litto Ranch site. We determined the percent of plants producing some pollen, and for a subset of these plants, we used lactophenol-aniline blue stain (Maneval 1936) to quantify the percent viable pollen (100 pollen grains from 20 plants of each cross type). We combined the data for intraspecific crosses of the two species, and made statistical comparisons of the intraspecific cross type to the interspecific cross type using a Mann-Whitney U-Test for seed number (18 combinations/cross type), germination (18 combinations/cross type), survival (18 combinations/cross type), and percent viable pollen ($n = 20$ plants/cross type), and a Fisher's Exact Test for the percent of plants with good pollen ($n = 56$ plants from intraspecific crosses; $n = 32$ plants from interspecific crosses). While this analysis is based on pollen viability data for only one locality, preliminary observations of the crosses for other localities gave similar results.

The results indicate strong barriers to gene flow between *L. jepsonii* and *L. parviflorus* (Table 1). For each of the characters examined, the performance of intraspecific crosses exceeded that of interspecific crosses, and these differences were significant in four of the five comparisons (Table 1). The greatest differences were observed for seed number and percent germination, for which intraspecific crosses outperformed interspecific crosses by approximately 2 fold, and percent viable pollen production, which was 13 fold

TABLE 1. SUMMARY OF THE PERFORMANCE OF INTERSPECIFIC AND INTRASPECIFIC CROSSES INVOLVING *LINANTHUS JEPSONII* AND *L. PARVIFLORUS*.

Performance criteria	Cross type		Prob. level
	Intraspecific	Interspecific	
Mean number of seeds per fruit	4.9	1.8	<0.0001
Mean % germination	63.7	32.4	<0.05
Mean % survival	61.6	40.5	0.15
% of plants with some good pollen	100.0	84.4	<0.01
% viable pollen in fertile plants	84.0	6.4	<0.0001

higher in intraspecific crosses. The low pollen viability of hybrids produced in the greenhouse is consistent with our observation that hybrids between these taxa in the field are generally male sterile. We conclude that *L. jepsonii* and *L. parviflorus* are reproductively isolated, and that they therefore satisfy the criterion of biological species as defined by Mayr (1982).

Classification. The discontinuities in morphological and reproductive characters observed between *L. jepsonii* and other sympatric *Linanthus* species, and its reproductive isolation from *L. parviflorus*, support recognition of *L. jepsonii* as a taxonomic species. To develop a classification for *L. jepsonii* and related taxa we revised the key provided by Patterson (1993) in The Jepson Manual (Hickman 1993), incorporating information on *L. latisectus* from Buxton (1993). In so doing, we were able to keep much of Patterson's classification, adding only those sections needed to distinguish *L. androsaceus*, *L. jepsonii*, *L. latisectus* and *L. parviflorus*. We use calyx pubescence as a major character for classifying these taxa, based on our finding that it consistently distinguished *L. parviflorus* and *L. latisectus* from *L. bicolor*, *L. jepsonii* and *L. androsaceus* in the 480 specimens analyzed in our survey (Fig. 3). Calyx pubescence may not be sufficient to distinguish these two groups in all localities, as evidenced by one population of *L. parviflorus* that has glabrous calyces and one population of *L. androsaceus* with short trichomes on the calyx (Buxton, personal communication), so in some cases it may be necessary to use other characters, such as those presented in Figure 2, or discussed by Patterson (1993) or Buxton (1993). The key below is intended to replace couplet 17 in Patterson (1993):

1. Calyx sparsely hairy on lobe margins, gen glabrous elsewhere, <50 total hairs on adaxial surface (including lobe margins); hairs >1 mm long
2. Corolla tube gen <25 mm long, lobes 7–10 mm long; NCoR, SnFrB
 *L. androsaceus*
- 2' Corolla tube gen >25 mm long, lobes 4–6 mm long; NCoR . . . *L. jepsonii*
- 1' Calyx densely hairy throughout, >100 total hairs on adaxial surface (including lobe margins); hairs <0.5 mm long
 3. Middle lobe of upper leaves 2–3.5 mm wide; corolla lobe gen >6 mm long; NCoR *L. latisectus*
 - 3' Middle lobe of upper leaves <2 mm wide; corolla lobe gen <6 mm long; CA-FP *L. parviflorus*

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NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

CAREX SWANII (Fern.) Mack. (Cyperaceae).—Hernando Island, 49°59'N, 124°55'W, elevation just above sea level, undisturbed coastal prairie on southern point of island, 11 June 1995, *G.B. Straley 8510* (UBC, V, MICH), verified by A.A. Reznicek.

Previous knowledge. Widespread in eastern North America from Nova Scotia to Wisconsin, south to Alabama and Arkansas.

Significance. First record for western North America, ca 2600 km disjunct from the nearest populations in Wisconsin. In this rather remote, undisturbed location, it does not appear to be a recent weedy introduction.

—GERALD B. STRALEY, The Botanical Garden, The University of British Columbia, Vancouver, BC V6T 1Z4.

POTENTIAL ADAPTABILITY AND
CONSTRAINTS OF RESPONSE TO
CHANGING CLIMATES FOR
ENCELIA FARINOSA VAR. *PHENICODONTA* FROM
SOUTHERN BAJA CALIFORNIA, MEXICO

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ABSTRACT

To examine the physiological adaptability of *Encelia farinosa* var. *phenicodonta* from southern Baja California, plants from Todos Santos, BCS were raised in central Arizona where winter-spring precipitation is greater than typically experienced by this variety. Plants were capable of high photosynthetic rates during the cool and wet spring months and showed substantial growth and reproductive output. Winter freezes caused severe stem dieback and even plant death. These findings suggest that freezing temperatures may influence the restricted and disjunct distribution of *E. farinosa* var. *phenicodonta* in the northern part of its range. The growth and reproduction results also imply that this variety may possess the physiological adaptability to thrive under potential climatic changes in southwestern North America.

RESUMEN

Para evaluar la adaptación fisiológica de *Encelia farinosa* var. *phenicodonta* del sur de Baja California, plantas de Todos Santos, BCS, fueron cultivadas en centro Arizona donde la precipitación de invierno y primavera excede la experimentada normalmente por dicha variedad. Plantas de BCS fueron capaces de altas tasas de fotosíntesis aún durante los lluviosos y fríos meses de primavera y además mostraron un incremento substancial en crecimiento y reproducción. Sin embargo, heladas de invierno causaron la muerte de tallos y en un caso severo toda la planta. Estos resultados sugieren que frías temperaturas de invierno pueden influir la distribución de *E. farinosa* var. *phenicodonta* en la parte norte de su presente rango de distribución. Estos resultados también sugieren que esta variedad posiblemente posee la adaptabilidad fisiológica para prosperar ante los posibles cambios climatológicos en el suroeste de Norte América.

Encelia farinosa A. Gray (Compositae) is a ubiquitous drought-deciduous perennial shrub of southwestern North America. Three varieties have been described based on variation of flower color and leaf morphology (Shreve and Wiggins 1964), and the distributions of these taxa are only somewhat sympatric (Kyhos 1971; Hastings et al. 1972). *Encelia farinosa* var. *farinosa* is most common throughout the Mojave and Sonoran deserts of California, Arizona and So-

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nora. *Encelia farinosa* var. *radians* Brandegees ex S. F. Blake the rarest of these varieties, is restricted to the Cape region of Baja California. *Encelia farinosa* var. *phenicodonta* (S. F. Blake) I. M. Johnst. is widespread throughout central and southern Baja California, but its northern distribution is mostly restricted to the Colorado River drainage and tributary regions within Arizona and California (Fig. 1).

Studies of variation in ecophysiology and water use have been conducted for many years with *E. farinosa* var. *farinosa* (Shreve 1923; Cunningham and Strain 1969; Ehleringer and Mooney 1978; Smith and Nobel 1978; Ehleringer and Cook 1990; Monson et al. 1992). These studies have shown that *E. farinosa* var. *farinosa* is a highly adaptable taxon that can exhibit genetic differentiation over short topographical gradients (Monson et al. 1992) as well as local adaptation on broader geographic scales (Ehleringer 1985; Ehleringer and Cook 1990). Much less is known about the conspecific *E. farinosa* var. *phenicodonta* despite its widespread distribution in Baja California and its unusual distribution in California and Arizona.

Kyhos (1971) suggested that the scattered populations of *E. farinosa* var. *phenicodonta* in its northern range may be remnants of a once broader distribution that existed during a warmer, more mesic period. Hence, *E. farinosa* var. *phenicodonta* may be predisposed to expanding its range if, as predicted by Schlesinger and Mitchell (1987), the Mojave and Sonoran desert regions eventually experience warmer temperatures and enhanced summer rainfall. However, such range expansion would extend *E. farinosa* var. *phenicodonta* into regions with much greater winter-spring precipitation than typically found in its current range, and in these northern desert regions winter-spring rainfall is predicted to remain at present amounts or even increase in the future (Schlesinger and Mitchell 1987).

To better understand the adaptability of *E. farinosa* var. *phenicodonta*, we examined the physiology and phenology of plants from southern Baja California, Mexico, when grown under winter-spring conditions that are atypical of that region. By raising these plants in central Arizona, we could address simple questions about the lability of physiological responses and general constraints that may affect the distribution of this taxon. This study focused on the physiological capacities for exploitation of winter and spring rainfall, and growth and reproduction in these cooler seasons. In addition, we observed phenological responses to freezing because freeze-tolerance is an important climatic factor limiting the northern distribution of many desert species (Shreve 1914; Jones 1978; Bowers 1981), and *E. farinosa* varieties have been shown to be sensitive to low temperatures (Tumage and Hinckley 1938; Hastings and Turner 1965; Jones 1978).

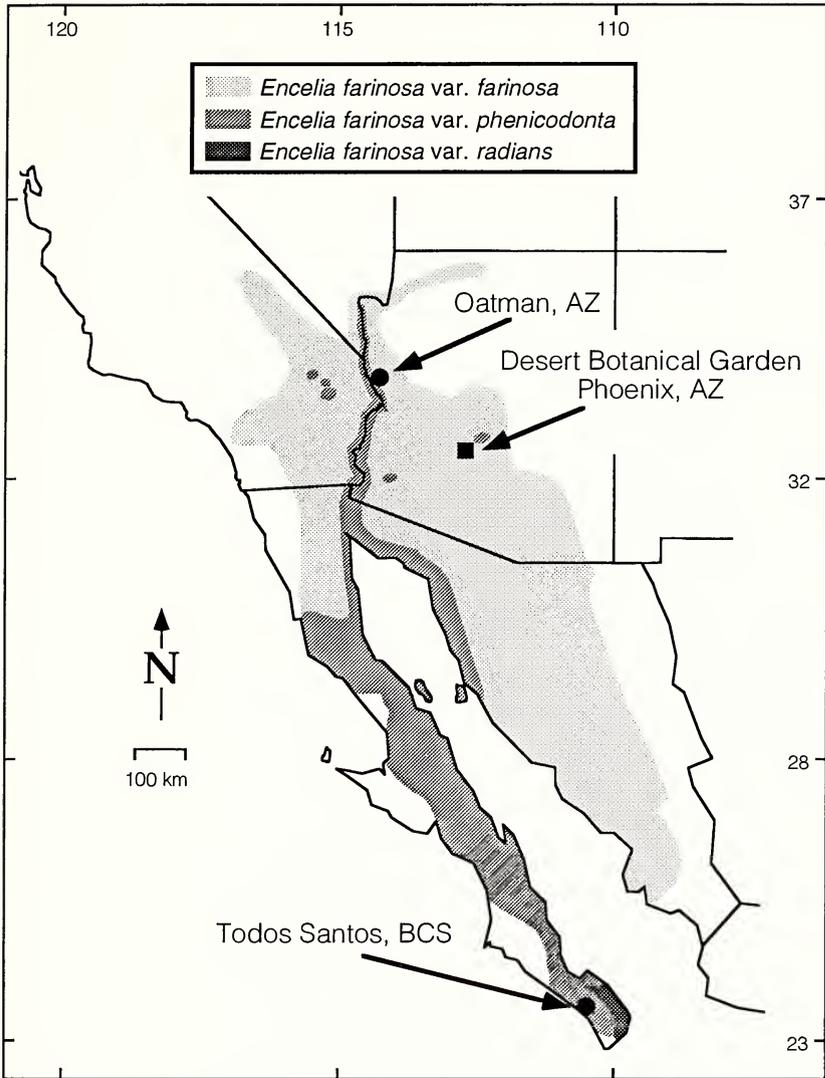


FIG. 1. The distributions of *Encelia farinosa* varieties in southwestern North America (adapted from Kyhos 1971; Hastings et al. 1972). Also shown are the sites of seed collections and the Desert Botanical Garden, where the research took place.

METHODS AND MATERIALS

Seeds and leaves of *E. farinosa* var. *phenicodonta* were collected in October 1989 from a natural population near Todos Santos, Baja California Sur, Mexico (23°26'N, 110°14'W, 18 m) (Fig. 1). The

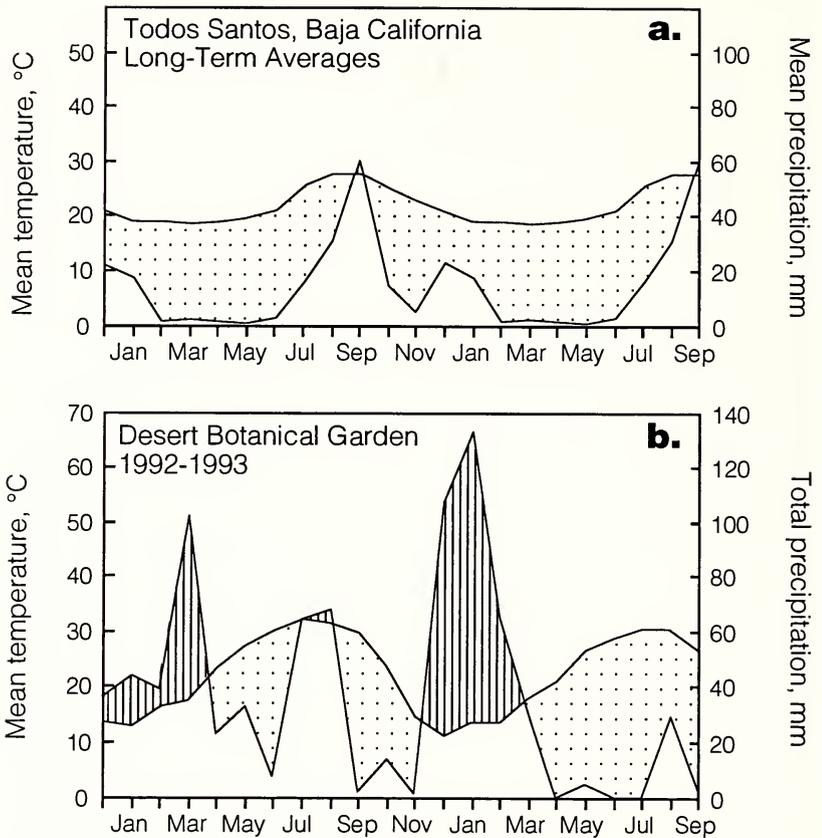


FIG. 2. Climate diagrams of monthly temperature and precipitation data. Stippled areas are periods of relative water deficit; striped are periods of water surplus. a) Long-term averages for Todos Santos, Baja California Sur, MX (1921–1967; data from Todos Santos weather station; Hastings and Humphrey 1969). b) Desert Botanical Garden monthly values from December 1991 to September 1993. Data are from the Tempe, Arizona, USA weather station, 2 km SW (Arizona Climate Summary, Office of the State Climatologist for Arizona).

long-term mean annual rainfall at Todos Santos is 170 mm (Hastings and Humphrey 1969). Of this, only 3% comes between the months of February and June (Fig. 2a), and during these months plant activity is normally very limited (Shreve 1937).

Seeds were germinated at the University of Utah greenhouse in September 1990 and transplanted to the Desert Botanical Garden in Phoenix, AZ (33°30'N, 112°00'W, 360 m) on 31 March 1991. The Desert Botanical Garden (DBG) is within the natural range of *E. farinosa* (Fig. 1) and gravelly soils at DBG are typical of *E. farinosa* habitat.

Monthly precipitation and mean temperatures at DBG during the two years of this study are shown in Figure 2b. Rainfall in the winter and spring months of 1992 and 1993 was very high. On average this input was seven times greater than normal for Todos Santos. Summer precipitation at DBG in 1992 was about the same as the long-term average at Todos Santos, but in 1993 rainfall was virtually absent from April through August (Fig. 2b).

Summer and autumn temperatures at DBG were comparable to Todos Santos averages (Fig. 2), but winter temperatures were relatively low. Recent weather records from the La Paz airport (La Paz, Baja California Sur, MX), 71 km N of Todos Santos, show that there had only been one day with a sub-freezing temperature in the past 15 years and the average minimum temperature in January, the coldest month, is 12.2°C (National Climatic Data Center, Asheville, NC). At DBG in winter 1992–1993 there were three December days with a minimum temperature below 0°C, two of which were consecutive. The average minimum temperature in December 1992 (4.3°C) was 1.9°C greater than the long-term average. The following winter had subfreezing temperatures on 26 days between 4 December 1993 and 3 February 1994, and during this period there was one seven-day period of <0°C minimum values. The average minimum temperature for December and January was 0.6°C, which, on average, was 2.7°C below the long-term mean (Arizona Climate Summary, Office of the State Climatologist for Arizona).

Twenty plants used for this study were randomly chosen from within a 26 m × 26 m plot of *E. farinosa* plants. All plants were separated by 2 m, a sufficient distance to preclude root interactions among plants (Ehleringer 1984), and the plot was bordered by a single row of non-experimental *E. farinosa*.

Surveys began with phenological and developmental measurements on 28 February 1992 and were repeated approximately every 60 to 90 days through 24 August 1993. Plant water status and gas exchange measurements were made from March through the last sample date of each year, with a few exceptions. Predawn leaf water potentials (ψ_{pd}) were measured on one or two leaves per plant with a Scholander-type pressure chamber (PMS, Corvallis, Oregon). Measurements were taken within the 3-hour period prior to sunrise. Stomatal conductance (g), which affects both water loss and carbon assimilation, was measured in conjunction with net photosynthetic rate (A) during the 2–4 hours after sunrise. These hours are during maximum photosynthetic activity for *E. farinosa* (Ehleringer 1988). Measurements of g and A were made on a single leaf or group of leaves using a LiCor 6200 portable gas exchange system (LiCor Inc., Lincoln, Nebraska). Leaves used for all measurements were from the most recent, fully expanded leaf cohort and were always in the southeast part of the upper plant canopy.

Carbon isotope composition was measured for leaves collected at Todos Santos in October 1989, and for leaf samples collected at DBG in September 1992. The carbon isotope ratio of a leaf (δ_p) is inversely related to the intercellular concentration of CO_2 during photosynthesis (c_i) (Farquhar et al. 1989), and for *E. farinosa*, c_i is genetically correlated with stomatal conductance (D. R. Sandquist, unpublished). Thus δ_p can be used to infer g values for a leaf (Farquhar et al. 1989).

Leaves were dried and ground, and carbon isotope ratios were determined relative to the Pee Dee Belemnite standard (Ehleringer and Osmond 1991). Analyses were done at the University of Utah Stable Isotope Ratio Facility for Environmental Research with Delta E and Delta S mass ratio spectrometers (Finnigan-MAT, San Jose, CA). Values are reported as isotope ratios (δ) in the per mil (‰) notation. The overall, long-term error associated with carbon isotope determination is $\pm 0.11\%$.

Plant height, maximum width and width perpendicular to the maximum width were used to calculate plant volume based on the equation for a half spheroid. Foliage density (m^2m^{-3}) of a plant was determined from a non-destructive estimation of the canopy leaf area (m^2) divided by plant volume (m^3). Canopy leaf area was estimated from an extrapolation based on the leaf areas of three leaves per each of three stems that were subjectively chosen to each represent one-third of the plant canopy (Appendix 1). The presence or absence of flowers was recorded throughout the study, and the number of flower heads produced per plant was counted in April 1992, the peak of flowering during that year.

Plant damage due to freezing during winter 1992–1993 was estimated on 30 January by visual inspection of the proportion of stems that lost apical dominance. Loss of apical dominance, if present, was very distinct since leaves near the stem tips had died and axillary branching had already started. The following winter, freeze damage was assessed in February 1994 using a different index since all plants had suffered 100% loss of apical dominance. Based on regrowth, plants were ranked as: 0) “killed”, known to have occurred over winter, 1) “extreme damage”, indicated by having only basal regrowth and no active mature stems, 2) “major damage”, indicated by regrowth on <50% of mature stems, 3) “moderate damage”, regrowth on >50% of mature stems, 4) “minor damage”, all mature stems still active. In this year 20 additional plants, raised concurrently in the DBG plot but of a different seed source, were surveyed for comparison. These plants were from a northern population of *E. farinosa* var. *farinosa* near the Colorado River drainage and the town of Oatman, Arizona (Fig. 1).

Statistical analyses were performed in JMP 3.1 (SAS Institute

Inc., Cary, NC). Plant volume and flower number were log transformed to normalize distributions.

RESULTS AND DISCUSSION

Winter and spring activity. Precipitation at the Desert Botanical Garden was high from December through March of both years (Fig. 2b), and greatly exceeded the normal winter-spring precipitation of the Todos Santos region (Fig. 2a). Additionally, temperatures at DBG were lower than those typical at Todos Santos.

In 1992, under these wet and cool winter-spring conditions at DBG, Todos Santos plants appeared to be fully active with respect to both productivity and water use parameters (Table 1). High foliage densities and photosynthetic rates indicate that Todos Santos plants have the capacity for high productivity under these conditions.

A similar pattern was seen in 1993. Foliage density and ψ_{pd} was greatest in March (Table 1) but, A and g values increased from March to April. Interpretation of this pattern should be cautious since the increases could have been a response to a late spring rain event (30 mm on 27 March), or a delayed recovery from winter freeze damages (below), or both. Nonetheless, continued growth from March to April 1993 again showed that Todos Santos plants can exploit higher rainfall, and during cooler conditions, than usually experienced in winter-spring.

Maximum photosynthetic rates for *E. farinosa* var. *phenicodonta* in this study (Table 1) were comparable to those for local *E. farinosa* var. *farinosa* measured during a greenhouse experiment (ca. 25–32 $\mu\text{mol m}^{-2}\text{s}^{-1}$, Monson et al. 1992) and in the field (Comstock et al. 1988; Sandquist 1995). Maximum stomatal conductances (Table 1) were also similar to values reported in other studies (ca. 0.4 $\text{mol m}^{-2}\text{s}^{-1}$) of *E. farinosa* var. *farinosa* in central Arizona (Ehleringer and Cook 1990; Monson et al. 1992).

Canopy development and plant sizes were also comparable to those in previous reports. Monson et al. (1992) reported a maximum leaf area per stem just greater than 300 cm^2 . The conversion of our maximum foliage density estimate (March 1992) to leaf area per stem resulted in a similar value, 309 cm^2 (± 43 , 1 SE). In addition, our results showed that plant areas (m^2) after 27 months in DBG (June 1993) were of similar size to *E. farinosa* var. *farinosa* plants grown at DBG under irrigated conditions from 1979 through 1981 (Ehleringer and Cook 1990).

The responses observed during these winter-spring conditions are not necessarily unexpected for a species that is generally water limited. Importantly, however, these results demonstrate that there is no

TABLE 1. SEASONAL CHANGE IN PHYSIOLOGICAL AND PHENOLOGICAL TRAIT MEANS (± 1 SE) FOR SOUTHERN BAJA CALIFORNIAN *ENCELIA FARINOSA* VAR. *PHENICODONTA* RAISED AT THE DESERT BOTANICAL GARDEN, PHOENIX, AZ, USA.

	Predawn water potential (MPa)	CO ₂ assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Foliage density ($\text{m}^2 \text{m}^{-3}$)	Plant volume (m^3)
Premonsoon 1992					
March	-1.14 \pm 0.06	22.0 \pm 0.9	0.50 \pm 0.04	12.7 \pm 1.1	0.034 \pm 0.010
April	-1.57 \pm 0.09	21.3 \pm 1.2	0.50 \pm 0.06	10.8 \pm 2.0	0.038 \pm 0.011
May	-1.81 \pm 0.08	19.2 \pm 1.7	0.46 \pm 0.06	10.4 \pm 1.7	na
July	-2.48 \pm 0.14	11.4 \pm 1.0	0.28 \pm 0.04	5.0 \pm 0.8	0.042 \pm 0.012
Postmonsoon 1992					
August	na	na	na	11.2 \pm 0.8	0.077 \pm 0.022
September	-1.94 \pm 0.13	11.4 \pm 0.9	0.20 \pm 0.03	5.4 \pm 0.3	0.083 \pm 0.022
October	-2.54 \pm 0.13	10.4 \pm 0.8	0.14 \pm 0.01	5.1 \pm 0.5	0.078 \pm 0.021
1993					
March	-0.61 \pm 0.03	27.1 \pm 0.9	0.67 \pm 0.04	8.7 \pm 0.8	0.262 \pm 0.058
April	-1.02 \pm 0.06	30.0 \pm 1.2	0.74 \pm 0.04	6.9 \pm 0.6	0.428 \pm 0.064
June	-1.81 \pm 0.03	21.2 \pm 0.8	0.45 \pm 0.03	6.1 \pm 0.7	0.507 \pm 0.066
July	-2.60 \pm 0.11	na	na	3.5 \pm 0.3	0.510 \pm 0.067
August	na	12.3 \pm 0.9	0.32 \pm 0.03	2.6 \pm 0.3	0.523 \pm 0.066

na = data not available.

genetic constraint on the capacity for opportunistic water use and growth under such conditions.

Spring rainfall. The response of Todos Santos plants to spring precipitation was best seen in observations after March 1992, when sporadic rainfall events persisted through the summer (Fig. 2b). In the Todos Santos region, April and May are the driest months of the year, and plant activity is most limited (Shreve 1937; Hastings and Humphrey 1969). Because temperatures at DBG during April and May were near normal for Todos Santos (Fig. 2), the April/May rains provided an opportunity to examine responses of Todos Santos plants to uncommon spring precipitation.

In these months, the downward trend of water potential and other physiological traits continued in spite of substantial water input (Table 1; Fig. 2b). It should be noted, however, that the relative change in ψ_{pd} and foliage density from April to May of 1992 was the least of any consecutive sampling periods in 1992. This may reflect a limited, albeit small, effect of spring rain. Other studies have shown that *E. farinosa* var. *farinosa* plants from the northeastern part of the range responded strongly to late spring rainfall with increased g and A values (Sandquist 1995) and greater foliage densities (Ehleringer 1985; Sandquist 1995). It has also been shown that supplemental watering, after short rainless periods, can raise plant water potential (Ehleringer and Cook 1990; Monson et al. 1992), however, plants from some populations do not respond to late spring rainfall (Ehleringer 1984; Ehleringer and Cook 1990; Sandquist 1995). While Todos Santos plants did not appear to have a substantial response to spring rain, it is clear that they were capable of sustaining activity during unfamiliar climatic conditions and at levels comparable to those reported for native *E. farinosa* plants.

Spring flowering of Todos Santos plants was not apparently constrained. In 1992 only one plant failed to produce flowers, and in 1993 all plants flowered in spring. The average number of flower heads per plant in 1992 was >200 , and flower head production was strongly related to plant size ($R^2 = 0.86$, $P < 0.001$). Because of this relationship there should be a premium on the capacity to grow whenever sufficient water is available. This may explain why there appears to be no seasonal constraint on physiological activities for *E. farinosa* var. *phenicodonta*.

Monsoon season. Pronounced response to monsoon rainfall was expected of Todos Santos plants since this is the period of greatest precipitation in their native habitat. Indeed, mean foliage density increased from a low of $5.0 \text{ m}^2\text{m}^{-3}$ in July to spring-like values of $> 11.0 \text{ m}^2\text{m}^{-3}$ in August, but by September and October the mean foliage density was again back at July levels (Table 1). No data are available for A and g in August, but during the autumn months A

and g also persisted at July-like values (Table 1). September values of Ψ_{pd} , however, remained fairly high and plant volume peaked for 1992 in this month (Table 1).

Summer rainfall is normally high in the Todos Santos region, thus foliage density and A values were expected to be greater than those observed after monsoon rainfall at DBG (Table 1). However, the values seen at DBG may be typical of *E. farinosa* var. *phenicodonta* in southern Baja, where high temperatures and associated water loss constraints could preclude greater values. Although there are no reports for A and g of naturally occurring *E. farinosa* var. *phenicodonta* in the Todos Santos area, we can make inferences from the carbon isotope composition of leaves collected from the same plants used as seed sources for this study. The carbon isotope ratios from these *in situ* plants near Todos Santos averaged -27.9‰ (SE ± 0.15) for October 1989 and were not different from those of plants at DBG in September 1992, $-27.6\text{‰} \pm 0.21$ ($t = 0.94$; $P = 0.35$).

The lack of a difference between δ_p means suggests that g values were the same among these samples; assuming that environmental conditions were similar during leaf development (Farquhar et al. 1989). This assumption is reasonable based on the comparison of climate observations recorded during collection dates in Todos Santos (by D. R. Sandquist) and weather records for DBG (Tempe, AZ weather station). Thus, it appears that Todos Santos plants at DBG were operating as they would in their native habitat—although A and g values immediately after monsoon rains could have been greater than observed (Table 1), as implied by the high foliage density and Ψ_{pd} values. Nonetheless, throughout this period, growth did continue with substantial A values during September and October (Table 1).

In summary, there did not appear to be any constraints on plant productivity or reproduction during the relatively cooler and wetter spring and summer months at DBG; conditions that are atypical of what *E. farinosa* var. *phenicodonta* would normally experience in Todos Santos. Furthermore, the seasonal changes in Ψ_{pd} , A , g , foliage density and growth were similar to those described for other *E. farinosa* populations within the northern range of this species (Ehleringer 1984, 1985; Comstock et al. 1988; Ehleringer and Cook 1990; Monson et al. 1992; Sandquist 1995). These results demonstrate that a high degree of physiological and phenological adaptability exists for these plants, which may explain, in part, the persistence of isolated *E. farinosa* var. *phenicodonta* populations within the northern range of this taxon. This also suggests that even the “biologically isolated” Cape region of Baja (Shreve 1937) has not given rise to physiologically insurgent populations of *E. farinosa* var. *phenicodonta*. Hence, if there is genetic differentiation for the above mentioned physiological traits, this apparently does not re-

TABLE 2. SUMMARY OF FREEZE DAMAGE TO TODOS SANTOS *ENCELIA FARINOSA* VAR. *PHENICODONTA* PLANTS OVER WINTER 1993–1994 (SEE TEXT FOR RANK METHODS).

	Winter 1993–1994 freeze damage index (number of plants per rank)					Average rank
	0 Killed	1 Extreme	2 Major	3 Moderate	4 Minor	
Todos Santos plants	1	19	0	0	0	0.95
Oatman plants	0	0	5	6	9	3.20

strict the species northern distribution, nor would it be implicated for doing so during past or future climate changes.

Winter freezes. All plants suffered freeze damage in the winters of 1992–1993 and 1993–1994. In 1992–1993, an average of 92.0% (± 3.5) of apical meristems were killed per plant, and there was a positive correlation between plant size and the degree of apical meristem damage (Kendall $\tau = 0.40$, $P < 0.05$). Thus, being of larger size, which was shown to be beneficial for reproduction (above), appears to be detrimental under freezing conditions. As Todos Santos plants would not normally experience freezing temperatures, selection based on this size/intolerance relationship appears to have been relaxed.

In the following winter one plant was killed and all others suffered “extreme” freeze damage (rank = 1) with the death of all stems (Table 2). By comparison, the mean rank for the twenty *E. farinosa* var. *farinosa* plants from Oatman, AZ was 3.2, or just better than “moderate damage” with less than 50% of existing stems being killed (Table 2). This difference clearly points to a mechanism that may limit the northern expansion of *E. farinosa* var. *phenicodonta*, at least for those that are genetically similar to the Todos Santos plants. It also supports the hypothesis proposed by Kyhos (1971), that *E. farinosa* var. *phenicodonta* populations in Arizona, California and parts of Sonora are relicts of a warmer and possibly wetter past climate.

Although there is evidence that summer temperatures in the Mojave and Sonoran Deserts were warmer 6000–9000 ybp (Spaulding and Graumlich 1986), it is not known if winter or annual temperatures were warm enough in the past to sustain populations of freeze-susceptible plants. Other observations, however, lend some support to the “relict populations” hypothesis. Van Devender et al. (1987) showed that the presence and abundance of *E. farinosa* in the Southwest has widely fluctuated since the late Wisconsin period (10,500 ybp). Climatic changes that affected the broad-scale floristic changes described in their study may have also influenced the distributions of *E. farinosa* varieties (Fig. 1). A different study based on a shorter

time scale described the reinvasion of *E. farinosa* into regions of Grand Canyon where the species was very rare, or absent, 100 years ago (Webb and Bowers 1993). This reinvasion, and that of other frost susceptible plants, was attributed to a decreased frequency of freezing temperatures since the late 1800's.

Presently the northern distribution of *E. farinosa* var. *phenicodonta* is within a region where freezing temperatures are common, however, freezing conditions can be spatially patchy (Jones 1978; Bowers 1981). The existence of warm microhabitats within these regions may provide a refuge for *E. farinosa* var. *phenicodonta*. This mechanism has also been proposed as the means by which very isolated individuals of *E. farinosa* and other freeze susceptible species persisted in Grand Canyon after the very cold late-1800's (Webb and Bowers 1993; see also Jones 1978). Indeed, Turnage and Hinckley (1938) reported that after a severe freeze in 1937, damage to *E. farinosa* plants was related to microhabitat, and especially to the distance above canyon or drainage bottoms where ground inversions cause very low temperatures.

CONCLUSION

The study of physiological plasticity outside of the realm of normal climatic conditions is important for understanding the genetic capacity of plants to tolerate climatic changes. With the exception of freeze intolerance, our results suggest that *E. farinosa* var. *phenicodonta* from lower Baja California has the physiological capacity for high productivity under cooler and wetter spring conditions found in its northern range. For these physiological traits it appears that there are few constraints that would preclude this taxon from exploiting pending climate changes. Thus with the possibility of a decrease in the frequency of freezing temperatures, the continuation of global warming, and a potential increase in summer monsoon rainfall (Schlesinger and Mitchell 1987), the conditions for a broader distribution of *E. farinosa* var. *phenicodonta* in the Mojave and Sonoran deserts are imminent.

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APPENDIX 1

A non-destructive estimate of individual canopy leaf area based on the following equation,

$$\text{canopy leaf area (m}^2\text{)} = \frac{S}{90000} * \sum_{i=1}^3 \left[L_i * \left(\left(0.106 * \sum_{j=1}^3 w_{ij} \right) + \left(0.006 * \sum_{j=1}^3 w_{ij}^2 \right) \right) \right].$$

S is the total number of stems, L_i is the number of leaves for stem i , and w_{ij} is the leaf width (mm) for leaf j of stem i . Three stems ($i = 1, 2, 3$) per plant and three leaves per stem ($j = 1, 2, 3$) were subjectively chosen to represent the diversity of stems on the plant and leaves on each stem. The denominator (90,000) is the product of denominators from $L/3$ (each leaf, j , representing one-third of the leaves on a stem), and $S/3$ (each stem, i , representing one-third of the stems on a plant), and the conversion for cm^2 to m^2 (10,000). The coefficients 0.106 and 0.006 are based on a binomial regression for the conversion of leaf width (mm) to leaf area (cm^2) with the intercept set to zero. This regression ($R^2 = 0.985$; $P < 0.001$) was based on measurements of leaf widths and areas for 762 leaves collected in spring 1992.

This non-destructive estimate appears to be robust, and all values fall between estimates made by two other methods based on: an LAI-2000 plant canopy analyzer (LiCor Inc., Lincoln, NE), and a destructive sample where plant leaves were removed and measured for canopy area (Sandquist 1995).

VASCULAR FLORA OF SUBALPINE PARKS IN
THE COEUR D'ALENE RIVER DRAINAGE,
NORTHERN IDAHO

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ABSTRACT

Treeless summits and ridges in the otherwise densely forested mountains of northern Idaho have a distinctive flora compared with surrounding areas. Although small in size, these subalpine parks add greatly to the biotic diversity of the regional landscape and are habitats for several plant species considered rare in Idaho. I conducted a floristic inventory of 32 parks in the mountains of the Coeur d'Alene River drainage and adjacent portions of the St. Joe drainage. The subalpine park flora contains 151 taxa representing 97 genera in 34 families. *Carex* species are surprisingly depauperate in terms of both number and cover as is the alien flora with only four species. I discovered populations of five rare plants, including *Carex xerantica*, which is here reported for Idaho for the first time. The other species considered rare in the state are *Astragalus bourgovii*, *Carex californica*, *Ivesia tweedyi*, and *Romanzoffia sitchensis*. Stevens Peak (2084 m) is the highest summit and is phytogeographically unique. It contains habitat for six species occurring nowhere else in the study area, all having high-elevation cordilleran or circumboreal affinities.

Treeless summits and ridges in the otherwise densely forested mountains of northern Idaho, have a distinctive flora compared with surrounding areas. Although small in size, these subalpine parks or balds add greatly to the biotic diversity of the regional landscape. The origin of subalpine parks was hypothesized to be a result of repeated fires (Leiberg 1897, Larson 1926) but was later shown to result from a combination of low soil moisture on slopes exposed to the wind and heavy snow accumulation on leeward slopes (Daubenmire 1944; 1968; 1981; Root and Habeck 1972). Conditions created by this interplay of topography and snow transfer are too extreme for tree seedlings to survive (Daubenmire 1981).

Floristic studies of subalpine parks in northern Idaho in general and the Coeur d'Alene River drainage in particular are sparse. The early explorations of John Leiberg (1897) and John Christ were the first to elucidate the floristic and ecologic composition of parks in the Coeur d'Alene drainage. Daubenmire (1981) described the flora of five parks between the Canadian border and the Salmon River, including one in the Coeur d'Alene drainage. These and other collectors elucidated the phytogeographic significance of subalpine parks in the area and discovered several plants with limited distribution in Idaho. Because of increasing recreational use of the north-

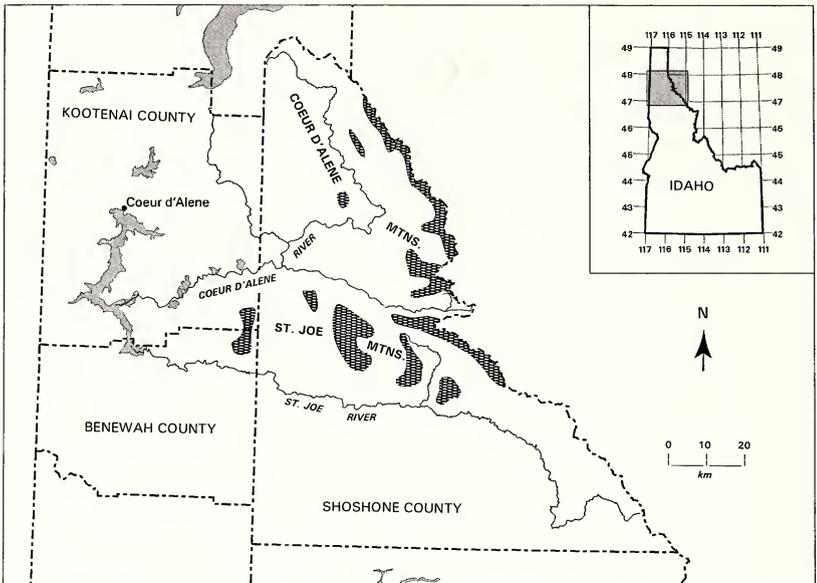


FIG. 1. Location map of the study area. Dark shading represents the general location of terrain above 1800 m where subalpine parklands in the Coeur d'Alene River drainage occur. Light shading represents lowland lakes.

ern Idaho mountains, the sensitivity of the habitat, and the preliminary nature of the floristic inventory, I undertook this study in cooperation with the Idaho Panhandle National Forests. It provides data on floristic composition and the distribution and abundance of rare plants in subalpine parks for future management.

STUDY AREA

The study area includes treeless parks above 1800 m within the Coeur d'Alene River drainage and the northern fringe of the St. Joe River drainage in Benewah, Kootenai, and Shoshone counties (Fig. 1). Stevens Peak, at 2084 m, is the highest summit. The mountains of central and northern Idaho form a nearly continuous massif. Mountains north of the Salmon River have generally been called the Bitterroot Range, with indistinct subranges named after major river drainages. In the study area, the high divide between the St. Joe and Coeur d'Alene rivers is called the St. Joe Mountains by the U.S. Geological Survey. The name Coeur D'Alene Mountains has been broadly used in the past in reference to highlands of northern Idaho that drain into Coeur d'Alene Lake (Leiberg 1897; Dort 1962), although it now appears to be more narrowly applied to mountains of the Coeur d'Alene River drainage north of its South

TABLE 1. CLIMATIC RECORDS FOR DECEPTION CREEK HQ, IDAHO, ELEVATION 933 M, 1931-1980.

	Temperature (°C)	Precipitation (mm)
Mean annual	5.5	1418
Mean October-May	1.0	1217
Mean June-September	14.9	201

Fork. I follow the latter naming convention. Latour Range and Shoshone Range are names applied to prominent mountain crests within the St. Joe and Coeur d'Alene mountains, respectively.

The area is underlain by metasedimentary rocks of the Belt Supergroup of Precambrian age. The thickness of the Belt Supergroup is estimated to be at least 6400 m and is comprised predominantly of quartzite and argillite, with minor amounts of limestone and dolomite (Bennett et al. 1989). Ridgecrests do not greatly exceed the minimum elevation necessary for formation of alpine glaciers during the Pleistocene (Dort 1962). The glaciers that did develop were relatively small, confined to the north sides of ridges and summits, resulting in relatively gentle slopes on south aspects and steep headwalls on the north.

Climate of the Coeur d'Alene River drainage is influenced primarily by prevailing westerlies which carry maritime air masses from the Pacific Ocean across the Northern Rockies during the winter and spring. This inland maritime regime extends from the Selkirk Range in British Columbia to the Clearwater River drainage in north-central Idaho. During winter and spring the inland maritime regime is characterized by gentle rains, deep snow accumulations at higher elevations, and abundant fog, cloudiness, and high humidity. Winter temperatures are 8 to 14°C warmer than continental locations at similar latitudes. Summers are relatively dry due to subtropical high pressure systems shifting northward in late June, causing the prevailing westerlies to carry dry air across northern Idaho (Ross and Savage 1967; Cooper et al. 1991).

The climate is not expressed well by any existing records, however, data from the Deception Creek HQ weather station (Finklin and Fischer 1987), located 25 km east of Coeur d'Alene at the western edge of the study area and approximately 850 m below the subalpine parks, gives an indication of climatic trends (Table 1). Temperatures in the subalpine parks are lower and precipitation is approximately 10% higher than at Deception Creek HQ. Snowpack average at 1469 m on April 1 is 183 cm (Finklin and Fischer 1987).

Dense, mixed coniferous forests cover much of the mountains in the Coeur d'Alene River drainage. *Pinus ponderosa* and *Pseudotsuga menziesii* dominate the dryer, lower elevation slopes, while *Thuja*

plicata, *Tsuga heterophylla*, *Larix occidentalis*, *Pinus monticola*, and *Abies grandis* comprise much of the forest cover at middle elevations. Upper elevation forests surrounding subalpine parks are comprised of communities dominated by *Tsuga mertensiana*, *Abies bifolia*, and *Pinus albicaulis*. *Pinus albicaulis* is represented largely by standing dead trees, as few individuals have survived the invasion of white pine blister rust (Arno and Hoff 1989). Forests at all elevations are in various stages of successional development following large wildfires of the late 1800's and early 1900's, and over a century of large-scale mining and smelting activity (Rabe and Flaherty 1974). Currently, livestock grazing does not take place in and around subalpine parks of the Coeur d'Alene drainage and, according to Leiberger (1897), was largely absent in the past.

PLANT COMMUNITIES OF SUBALPINE PARKS

Although Daubenmire was able to classify forest and steppe vegetation of the region (Daubenmire and Daubenmire 1968; Daubenmire 1970), he discontinued phytosociologic studies in subalpine parks due largely to the small-scale patterns of plant composition and dominance (Daubenmire 1981). He did, however, partition parks into two broad types, xerophytic parks on the windward slopes of ridges and summits, and snowbank parks on the lee sides. Using this classification as a basis, I recognize three types of plant habitats or communities.

Graminoid. This roughly corresponds to Daubenmire's (1981) xerophytic park. It is dominated by graminoids, largely *Festuca viridula*, but also with high cover of *Xerophyllum tenax* and *Carex geyeri* in some areas. Unlike xerophytic parks described by Daubenmire (1981), however, I found *Festuca idahoensis* and *Agropyron spicatum* to be rare. There is a high diversity, albeit low cover of forbs. Shrub cover is low and trees generally occur as scattered clumps or islands. Graminoid parks occur on southerly slopes and are exposed to prevailing winds, making them zones of snow deflation. In contrast, treeless parks occurring on south slopes in the montane zone, below about 1370 m, are dominated by *Festuca idahoensis* and *Agropyron spicatum* and lack *Festuca viridula*. These lower-elevation habitats appear to represent Daubenmire's typical xerophytic park.

Cliffs and ledges. This habitat roughly corresponds to Daubenmire's (1981) snowbank park, because it occurs on the lee sides of summits and ridges. However, unlike his sites, which had relatively gentle slopes, these northerly-facing habitats occur on steep, cirque headwalls and have considerable areas of exposed bedrock. Cliffs and ledges are generally zones of snow deposition, although in a

few places they are exposed to prevailing winds throughout the year and are relatively xeric. *Penstemon fruticosus* and *Saxifraga* spp. are characteristic of this habitat.

Talus. Talus slopes occupy only a small portion of the area, but have a distinctive flora. Talus can occur within both the graminoid community on south slopes and at the base of cliffs and ledges on north slopes (Daubenmire and Skipp 1943). This habitat is comprised of stabilized blocks of argillite or quartzite, up to 4 dm in diameter, with little soil development between the blocks. *Calamagrostis purpurascens* and *Penstemon fruticosus* are characteristic here.

METHODS

The checklist is based largely on field observations and collections that I made in 32 subalpine parks in the Coeur d'Alene River drainage between 1986 and 1993. All specimens are deposited at the University of Idaho Herbarium (ID). Other collections examined include those of John Leiberger, John Christ, W.R. Moore, Steven Brunfeldt, and Charles Wellner at ID and WS. Identification of certain *Carex* specimens were provided by J. Mastrogioseppe and M. Hurd. Following field work, three geographic abundance classes were assigned to each taxon based on the number of subalpine parks where it was present, as follows: *common*, 16 or more parks; *uncommon*, 6 to 15 parks; *rare*, 5 or fewer parks. Range-extension information for the species new to Idaho was determined from herbarium records. The Idaho Conservation Data Center database was consulted concerning the current distribution of rare species in Idaho.

RESULTS AND DISCUSSION

The vascular flora of subalpine parks in the Coeur d'Alene River drainage consists of 151 taxa representing 97 genera in 34 families of vascular plants. Only four alien species, *Centaurea maculosa*, *Rumex acetosella*, *Taraxacum officinale*, and *Trifolium repens*, were encountered. This group comprises 3% of the flora. All are rare, occurring only along roads and near electronic sites. *Carex* species are surprisingly depauperate in terms of both numbers and cover. Of the ten encountered, only *Carex geyeri* is common. Their scarcity can be attributed to the lack of late-lying snowbanks, the usual habitat for ridgeline sedges in northern Idaho. Because of the relatively low elevation of the area, few snowbanks last through an ordinary summer and fall, except in the couloirs on Stevens Peak.

My collection of *Carex xerantica* represents the first documented occurrence of this species in Idaho. Four additional species have a limited distribution and are considered rare in the state: *Astragalus bourgovii*, *Carex californica*, *Ivesia tweedyi*, and *Romanzoffia sitch-*

ensis (Conservation Data Center 1994). All five rare species have either low population levels or occupy very localized habitats in the study area, but none appear to be imminently threatened by anthropogenic disturbances. Management for their viability should be emphasized, however, and they should be periodically monitored by forest managers to assure their continued existence.

Carex xerantica. This species is distributed across the northern and central Great Plains and the high plateaus of central and southern Utah and northern Arizona (Hermann 1970). I collected it in two areas of Idaho during 1993. Two small populations were discovered on Latour Peak and nearby Mount Wiessner, Kootenai County. I discovered a second site on Mount Harrison, Cassia County, ca. 700 km south of the study area (*Moseley 2847* BOIS). The Kootenai County sites are perhaps 200 km west of the nearest known populations in Montana (*Kirkwood 1031*, *Barkley 2377*, *Ad-dor 141* all MONTU) and the Cassia County population is ca. 350 km northwest of those in Utah.

Astragalus bourgovii. Endemic to the Rocky Mountains of western Montana and adjacent areas of British Columbia and Alberta, *Astragalus bourgovii* is at the western edge of its range in Idaho (Barneby 1964), where it is represented by two populations in the study area. John Leiberger discovered the first population on Stevens Peak in 1895, and I located only one additional population on an unnamed summit 3.2 km to the east. It occurs in windswept areas of the graminoid community and on dry, ridgeline ledges.

Carex californica. Idaho populations of *Carex californica* represent disjunct locations for this otherwise Cascadian species (Hermann 1970). Five Idaho populations are known, one from the study area on the summit of Striped Peak, Shoshone County, and four from Idaho County, ca. 110 km to the south (unpublished data on file at the Idaho Conservation Data Center). The small clone on Striped Peak occurs in a graminoid community dominated by *Festuca viridula*.

Ivesia tweedyi. Another disjunct species in the mountains of northern Idaho, *Ivesia tweedyi* is also mainly a Cascadian species from Chelan and Yakima counties, central Washington. It is known from eleven populations in Idaho, with five occurring in the southeastern portion of the area (unpublished data on file at the Idaho Conservation Data Center). It occurs on exposed, rocky ridgelines and steep, dry slopes.

Romanzoffia sitchensis. This delicate member of the Hydrophyllaceae is a cordilleran species ranging from southern Alaska to northern California, and inland to Alberta (Hitchcock and Cronquist 1973). Six small populations are known from Idaho (unpublished

data on file at the Idaho Conservation Data Center), five of them from the Selkirk Mountains near the Canadian border, Boundary County, and one in the study area in Shoshone County. The study area population on Stevens Peak is disjunct ca. 160 km south of the Selkirk populations.

Results of my floristic inventory indicate that Stevens Peak occupies a unique phytogeographic position in the study area. I found that six species occur only on this summit: *Astragalus bourgovii*, *Draba lonchocarpa*, *Oxyria digyna*, *Romanzoffia sitchensis*, *Sedum roseum*, and *Smelowskia calycina*. All are high-elevation cordilleran taxa, some having circumboreal distributions. Stevens Peak is the highest summit and is one of the most heavily glaciated. The large headwall on the north face, incised by several couloirs, is where most of the unusual species occur. In addition, a large population of *Ivesia tweedyi* occurs on the peak.

ANNOTATED CHECKLIST OF VASCULAR PLANTS

The checklist is arranged by division and class (in Anthophyta), then alphabetically by family and species within these major groups. Nomenclature generally follows Hitchcock and Cronquist (1973). Exceptions include Lycophyta, Pterophyta, and Coniferophyta (Flora of North America Editorial Committee 1993) and *Poa* (Arnow 1987). Unless otherwise noted, the collection numbers are the author's, which are deposited at ID.

DIVISION LYCOPHYTA

Selaginellaceae

Selaginella scopulorum Maxon. Common on dry ledges and cliffs in graminoid community; 2715.

DIVISION PTEROPHYTA

Pteridaceae

Cheilanthes gracillima D.C. Eaton. Common on dry cliffs and ledges; 2689.

Cryptogramma acrostichoides R. Br. Common in talus and on cliffs and ledges; 2693.

Dryopteridaceae

Athyrium alpestre (Hoope) Clairville var. *americanum* Butters. Rare in talus; 2776.

Cystopteris fragilis (L.) Bernh. Common on cliffs and ledges; 2694.

Polystichum lonchitis (L.) Roth. Uncommon on moist cliffs and ledges; 2716.

Woodsia scopulina D.C. Eaton. Uncommon on cliffs and ledges; 2731.

DIVISION CONIFEROPHYTA

Cupressaceae

Juniperus communis L. var. *depressa* Pursh. Uncommon on ledges and in talus; 2662.

Pinaceae

- Abies bifolia* A. Murray. Common treeline species. No voucher.
Pinus albicaulis Engelm. Common treeline species along eastern edge of study area. Largely absent from peaks in western portion. No voucher.
Pinus contorta Dougl. var. *latifolia* Engelm. Rare in graminoid community. No voucher.
Pinus monticola Dougl. Rare in graminoid community. No voucher.
Pseudotsuga menziesii (Mirbel) Franco var. *glauca* (Mayr) Franco. Rare in south-facing graminoid community. No voucher.
Tsuga mertensiana (Bong.) Carr. Common treeline species. No voucher.

DIVISION MAGNOLIOPHYTA

CLASS MAGNOLIOPSIDA

Apiaceae

- Angelica dawsonii* Wats. Rare on moist ledges; 2740, 2754.
Angelica genuflexa Nutt. Rare on moist ledge only on Quarles Peak; 2741.
Lomatium dissectum (Nutt.) Math. & Const. var. *multifidum* (Nutt.) Math. & Const. Rare in graminoid community; 2674.
Lomatium sandbergii Coult. & Rose. Common in graminoid community and on ledges; 1265, 2673.
Lomatium triternatum (Pursh) Coult. & Rose var. *triternatum*. Rare, found only in graminoid community on Kellogg Peak; 2761.

Asteraceae

- Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper var. *lanulosa*. Common in all habitats; 2648, Wellner 674 (ID).
Agoseris aurantiaca (Hook.) Greene var. *aurantiaca*. Common in graminoid community; 2679, Wellner 672 (ID).
Anaphalis margaritacea (L.) Benth. & Hook. Rare in graminoid community; 2681.
Antennaria alpina (L.) Gaertner var. *media* (Greene) Jepson. Uncommon on moist ledges; 2764.
Antennaria microphylla Rydb. Common in graminoid community; 1273, 2653.
Antennaria racemosa Hook. Uncommon in moist graminoid community and on ledges; 2706.
Antennaria umbrinella Rydb. Common in graminoid community and on ledges; 2530, 2685.
Arnica latifolia Bong. var. *gracilis* (Rydb.) Cronq. Common in talus and on ledges; 1266, 2645, 2721.
Arnica rydbergii Greene. Rare in graminoid community; found only on an unnamed summit along eastern edge of study area; 2718.
Aster foliaceus Lindl. var. *lyallii* (Gray) Cronq. Common in graminoid community; 2845.
Centaurea maculosa Lam. Rare in graminoid community; only one vegetative rosette was observed on a mining road. No voucher.
Erigeron acris L. var. *debilis* Gray. Uncommon on cliffs and ledges; 2649.
Erigeron compositus Pursh var. *glabratus* Macoun. Common on dry ledges; 2711, 2752.
Erigeron peregrinus (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. var. *eucallianthemus* (Greene) Cronq. Uncommon on moist ledges; 2668, 2833.
Hieracium albertinum Farr. Common in graminoid community; 2768, 2836, Wellner 678 (ID).

- Hieracium gracile* Hook. Common in graminoid community and on ledges; 2684.
Microseris nigrescens Henderson. Rare in graminoid community; 2646.
Microseris nutans (Geyer) Schultz-Bip. Rare, found only on Rochat Peak; 1272.
Senecio integerrimus Nutt. var. *exaltatus* (Nutt.) Cronq. Uncommon in graminoid community; 2725.
Senecio megacephalus Nutt. Common in graminoid community; 2536, 2660, 2765.
Senecio triangularis Hook. var. *triangularis*. Rare on moist ledges. No voucher.
Solidago multiradiata Ait. var. *scopulorum* Gray. Uncommon in graminoid community; 2831.
Taraxacum officinale Weber. Alien. Rare in graminoid community; 2739.

Boraginaceae

- Mertensia paniculata* (Ait.) G. Don. var. *borealis* (Macbr.) L. O. Williams. Uncommon on moist ledges; 2743.

Brassicaceae

- Arabis holboellii* Hornem. Common in graminoid community; 2691.
Arabis nuttallii Robins. Common in all habitats; 699, 1270, 2531, 2643.
Draba lonchocarpa Rydb. var. *lonchocarpa*. Rare, found only on the north face of Stevens Peak; 2534.
Draba oligosperma Hook. var. *oligosperma*. Rare on dry cliffs and ledges; 2842.
Draba stenoloba Ledeb. Rare, found only in graminoid community on Pond Peak; Wellner 541 (ID).
Erysimum asperum (Nutt.) DC. Common in talus and on dry ledges; 2729.
Smelowskia calycina C. A. Mey. var. *americana* (Regel & Herder) Drury & Rollins. Rare, found only on the north face of Stevens Peak; 2529, 2832.
Thlaspi fendleri Gray var. *glaucum* (A. Nels.) C. L. Hitchc. Common in graminoid community; 2641.

Campanulaceae

- Campanula rotundifolia* L. Common in moist graminoid community; 2841.

Caprifoliaceae

- Lonicera utahensis* Wats. Uncommon in graminoid community; 2647.

Caryophyllaceae

- Arenaria aculeata* Wats. Common in graminoid community; 2651, 2770.
Arenaria capillaris Poir. Uncommon in graminoid community; 704, 1271, Wellner 673 (ID).
Arenaria congesta Nutt. var. *congesta*. Uncommon in graminoid community; 2830.
Cerastium arvense L. Uncommon on moist cliffs and ledges; 2537, 2838.
Silene douglasii Hook. var. *douglasii*. Common on dry ledges; 2775.
Silene scouleri Hook. var. *scouleri*. Uncommon in graminoid community; 710, 2676, 2837, Wellner 680 (ID).

Crassulaceae

- Sedum lanceolatum* Torr. var. *lanceolatum*. Common in all habitats; 2692.
Sedum roseum (L.) Scop. Rare, found only on the north face of Stevens Peak; 2527.

Ericaceae

- Phyllodoce empetriformis* (Sweet) D. Don. Uncommon in graminoid community and on ledges; 2657.
Vaccinium membranaceum Dougl. Common in graminoid community; 2699.
Vaccinium scoparium Leiberg. Uncommon in graminoid community; 2658.

Fabaceae

- Astragalus bourgovii* Gray. Rare, found only in graminoid community and on dry ledges in the vicinity of Stevens Peak; 2525, 2757, Leiberg 1470 (NY).
Hedysarum boreale Dougl. var. *boreale*. Common in all habitats; 2702, 2719.
Lupinus polyphyllus Lindl. var. *burkei* (Wats.) C.L. Hitchc. Uncommon in graminoid community; 2682.
Trifolium repens L. Alien. Rare along roads in graminoid community; 2771.

Gentianaceae

- Gentiana affinis* Griseb. Common in graminoid community; 2844.
Gentiana calycosa Griseb. Uncommon on moist ledges; 2755.

Grossulariaceae

- Ribes lacustre* (Pers.) Poir. Uncommon on moist cliffs and ledges; 2717.

Hydrophyllaceae

- Phacelia heterophylla* Pursh var. *heterophylla*. Rare in talus; 2760.
Romanzoffia sitchensis Bong. Rare, found only on the north face of Stevens Peak; 2528; Leiberg 1461 (NY). Leiberg's collection is the type for *R. leibergii* Greene, a synonym.

Hypericaceae

- Hypericum formosum* Kunth var. *nortoniae* (Jones) C.L. Hitchc. Common in graminoid community and on cliffs and ledges; 2762.

Onagraceae

- Epilobium angustifolium* L. Uncommon in talus; 2703.

Polemoniaceae

- Phlox diffusa* Benth. Common in graminoid community only along southern periphery of study area; 2726.
Phlox speciosa Pursh. Rare, found only in continuous graminoid community on Sunset and Goose peaks; 2769, Christ 51-357 (ID). This is an odd high-elevation population of an otherwise low-elevation steppe and woodland species.
Polemonium pulcherrimum Hook. var. *calycinum* (Eastw.) Brandegee. Common on cliffs and ledges; 2675.

Polygonaceae

- Eriogonum flavum* Nutt. var. *piperi* (Greene) Jones. Common in talus and uncommon in graminoid community; 2654, Wellner 675 (ID).
- Eriogonum heracleoides* Nutt. var. *minus* Benth. Uncommon in talus and graminoid community; 2655.
- Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) Jones. Rare on dry ledges; 2744, 2839.
- Eriogonum umbellatum* Torr. Uncommon in graminoid community. No voucher.
- Oxyria digyna* (L.) Hill. Rare, found only on the north face of Stevens Peak; 2538.
- Polygonum bistortoides* Pursh. Common in moist graminoid community; 2736, Wellner 538 (ID).
- Polygonum phytolaccaefolium* Meisn. Common in graminoid community; 2700.
- Rumex acetosella* L. Alien. Rare along mining roads in graminoid community; 2680.

Portulacaceae

- Claytonia lanceolata* Pursh var. *lanceolata*. Common in graminoid community and on ledges; 2687.
- Montia parvifolia* (Moc.) Greene var. *parvifolia*. Common on moist cliffs and ledges; 2535, 2690, 2706.

Primulaceae

- Dodecatheon pulchellum* (Raf.) Merr. var. *watsonii* (Tidestr.) C.L. Hitchc. Uncommon in graminoid community and on ledges; 2686.

Ranunculaceae

- Anemone multifida* Poir. var. *multifida*. Uncommon in graminoid community; 2846.
- Aquilegia flavescens* Wats. Uncommon in moist graminoid community; 2738.
- Clematis columbiana* (Nutt.) Torrey & Gray var. *columbiana*. Rare on moist ledges; 2756.
- Ranunculus eschscholtzii* Schlecht. var. *suksdorfii* (Gray) L. Benson. Uncommon on ledges; 2710.

Rosaceae

- Amelanchier alnifolia* Nutt. var. *alnifolia*. Rare in graminoid community; 2774.
- Ivesia tweedyi* Rydb. Rare in graminoid community and on dry ledges only in southeastern portion of study area; 2526, 2720, 2751, Christ 51-479 (ID), Moore 486 (WS).
- Potentilla diversifolia* Lehm. var. *diversifolia*. Uncommon in moist graminoid community; 2835.
- Potentilla glandulosa* Lindl. var. *pseudorupestris* (Rydb.) Breitung. Common on dry ledges; 705, 2714.
- Rubus idaeus* L. var. *gracilipes* Jones. Rare in talus; 2704.
- Sorbus scopulina* Greene var. *scopulina*. Rare in graminoid community; 2773.
- Spiraea densiflora* Nutt. Uncommon in talus; 2667.

Saxifragaceae

- Heuchera cylindrica* Dougl. var. *glabella* (Torrey & Gray) Wheelock. Common on cliffs and ledges, uncommon in graminoid community and talus; 1274, 2656.

- Heuchera grossulariifolia* Rydb. Rare, found only on cliffs and ledges on Ulm Peak; 706.
- Lithophragma bulbifera* Rydb. Rare in dry graminoid community; 2695.
- Mitella breweri* Gray. Uncommon on moist cliffs and ledges; 2777.
- Saxifraga bronchialis* L. var. *austromontana* (Wieg.) Jones. Common on cliffs and ledges; 2688.
- Saxifraga ferruginea* Grah. var. *macounii* Engl. & Irm. Common on cliffs and ledges; 2697, 2733.
- Saxifraga mertensiana* Bong. Common on ledges; 2532, 2696, 2732.
- Saxifraga occidentalis* Wats. var. *occidentalis*. Common in graminoid community; 2698, 2734.

Scrophulariaceae

- Castilleja longispica* A. Nels. Rare, found only on Shefoot Mountain at southern edge of area; 2724.
- Castilleja miniata* Dougl. var. *miniata*. Common in graminoid community and on ledges; 702, 2701.
- Pedicularis bracteosa* Benth. var. *latifolia* (Pennel) Cronq. Rare on moist ledges; 2735.
- Pedicularis contorta* Benth. var. *contorta*. Common in graminoid community and on ledges; 2670, Wellner 679 (ID).
- Penstemon attenuatus* Dougl. var. *attenuatus*. Common in talus; 708, 2642, 2759.
- Penstemon fruticosus* (Pursh) Greene var. *fruticosus*. Common in all habitats; 701, 1267, 2663, Wellner 539 (ID).
- Penstemon lyallii* Gray. Uncommon on dry ledges; 707, 2727.
- Synthyris missurica* (Raf.) Pennell. Rare, found only on Kellogg Peak in graminoid community; 2758.
- Veronica cusickii* Gray. Uncommon on moist ledges. 2779.

Valerianaceae

- Valeriana sitchensis* Bong. Uncommon in moist graminoid community; 2737, Wellner 540 (ID).

Violaceae

- Viola adunca* J.E.Sm. var. *bellidifolia* (Greene) Harrington. Uncommon in moist graminoid community; 1268.

CLASS LILIOPSIDA

Cyperaceae

- Carex californica* Bailey. Rare, found in graminoid community only on Striped Peak; 2669, Christ 51-419, 51-393 (WTU).
- Carex geyeri* F.Boott. Common in graminoid community, 2661, 2730.
- Carex hoodii* F.Boott. Uncommon in moist graminoid community; 2742.
- Carex microptera* Mack. Rare in graminoid community; 2728.
- Carex nigricans* C.A.Mey. Uncommon in moist graminoid community; 2772.
- Carex pachystachya* Cham. Uncommon in moist graminoid community; 2840.
- Carex paysonis* Clokey. Uncommon in graminoid community; 2763.
- Carex phaeocephala* Piper. Uncommon in graminoid community; 2707, 2766.
- Carex rossii* F.Boott. Uncommon in graminoid community; 2671.

Carex xerantica Bailey. Rare, found in graminoid community only on Latour Peak and nearby Mount Wiessner; 2778.

Juncaceae

Juncus drummondii E.Mey. Common in moist graminoid community. No voucher.

Luzula hitchcockii Hamet-Ahti. Uncommon in graminoid community; 2658.

Luzula spicata (L.) DC. Uncommon on ledges; 2709.

Liliaceae

Allium fibrillum Jones. Rare in graminoid community; 2683.

Calochortus apiculatus Baker. Common in graminoid community; 703, 1269, 2644.

Erythronium grandiflorum Pursh var. *grandiflorum*. Common in graminoid community and on ledges; 2652.

Stenanthium occidentale Gray. Common on moist cliffs and ledges; 2713.

Xerophyllum tenax (Pursh) Nutt. Common in graminoid community; 2705.

Poaceae

Agropyron caninum (L.) Beauv. ssp. *majus* (Vasey) C.L.Hitchc. var. *andinum* (Scribn. & Sm.) C.L.Hitchc. Uncommon in moist graminoid community; 2745.

Agropyron caninum (L.) Beauv. ssp. *majus* (Vasey) C.L.Hitchc. var. *latiglume* (Scribn. & Sm.) C.L.Hitchc. Uncommon in graminoid community; 2234.

Agropyron spicatum (Pursh) Scribn. & Sm. Rare in graminoid community; 2677.

Bromus carinatus Hooker & Arnott. Uncommon in moist graminoid community; 2743.

Calamagrostis purpurascens R.Br. Uncommon in graminoid community and common in talus; 709, 2650.

Danthonia intermedia Vasey. Uncommon in graminoid community; 2722.

Festuca idahoensis Elmer. Rare in graminoid community. No voucher.

Festuca viridula Vasey. Common in graminoid community; 2665, 2723, *Wellner* 537, 677 (ID).

Oryzopsis exigua Thurber. Uncommon on dry ledges; 2712.

Poa alpina L. Rare on moist ledges; 2843.

Poa fendleriana (Steudel) Vasey. Uncommon in graminoid community; 2666, 2767.

Poa glauca Vahl var. *glauca*. Uncommon in talus and on ledges; 2672.

Poa secunda Presl. Uncommon in graminoid community; 2664.

Trisetum spicatum (L.) Richter. Common on ledges and in talus; 2678.

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FIRE AND SUCCESSION IN PINYON-JUNIPER WOODLANDS OF THE SAN BERNARDINO MOUNTAINS, CALIFORNIA

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ABSTRACT

Pinyon-juniper woodlands (*Pinus monophylla*, *Juniperus californica*, *J. occidentalis*) of the San Bernardino Mountains were examined for modern and historical fire patterns, post-fire succession, and changes in mature woodlands under 20th century fire suppression management. Thirty-eight burns consisting mostly of high intensity canopy fires were identified, giving an estimated fire rotation period of 480 years. Burns were primarily colonized by Great Basin sage-scrub (*Purshia tridentata*, *Artemisia tridentata*, *Chrysothamnus nauseosus*) at higher elevations (>2000 m), and a mix of California desert chaparral (*Ceanothus greggii*, *Fremontodendron californicum*) and Great Basin sage-scrub at lower elevations (<2000 m). Chronosequence sampling shows that conifer species were absent on all burns ≤ 18 years. Shrubs increased in cover and density for 30–50 years, and were joined by *P. monophylla* recruits 25–40 years after fire. Mature shrubs acting as nurse plants appear to aid in the re-establishment of *P. monophylla* by providing a favorable microclimate for seedling survival and early growth. After 50 years, pinyon-juniper woodland development was phased with a declining shrub layer, ultimately leading to the return of a mature woodland at 100–150 years. Replication of the 1929–1935 California Vegetation Type Map survey shows only minor changes in this forest type under 20th century fire suppression management.

Pinyon pine (*Pinus monophylla*, *P. edulis*) in association with juniper (*Juniperus* spp.) occupies approximately 17 million ha in semi-arid western North America (Wright and Bailey 1982). The pinyon-juniper association typically forms open to moderately dense stands with understories of perennial grass in Arizona and New Mexico (Jameson 1962; Dwyer and Pieper 1967), sage-scrub and upland sclerophyll shrub complexes in the Great Basin and Colorado Plateau (Erdman 1970; Tueller et al. 1979; Everett and Koniak 1981), and sage-scrub and desert chaparral in California (Andre et al. 1965; Vasek and Thorne 1988).

Fire patterns and post-fire succession have been documented for much of the pinyon-juniper range, and two generalized fire and succession models have been identified: 1) surface fires with rapid post-fire perennial grass succession, and 2) canopy fires with slow post-fire shrub and tree succession. Perennial grass surface fires in pinyon-juniper woodlands result in light to moderate pinyon-juniper mortality and recovery to pre-fire conditions in <5 years (Jameson 1962; Dwyer and Pieper 1967), whereas pinyon-juniper woodlands

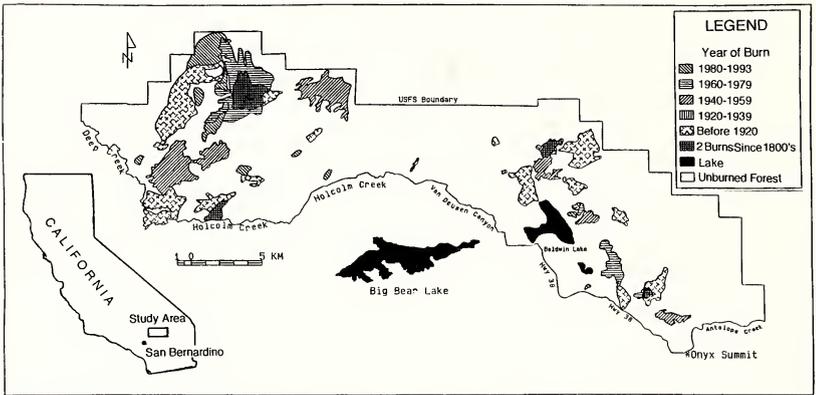


FIG. 1. Fire mosaic map for pinyon-juniper woodlands of the San Bernardino Mountains.

with sage-scrub and upland sclerophyll shrub understories commonly experience canopy fires that result in heavy pinyon-juniper mortality and >100 years for recovery to pre-fire conditions (Erdman 1970; Everett and Ward 1984; Koniak 1985).

In California, pinyon-juniper woodlands have received only cursory attention (Vasek and Thorne 1988), and the fire ecology of these woodlands has not been studied. The objective of this paper is to use a combination of temporal and spatial data from aerial photographs and field methods (chronosequence sampling, replication of the 1929–1935 California Vegetation Type Map survey) to examine the dynamics of fire and succession in pinyon-juniper woodlands of the San Bernardino Mountains in southern California. It is hypothesized that 1) pinyon-juniper woodlands experience canopy fires that result in heavy pinyon-juniper mortality; 2) post-fire succession is slow, beginning with a shrub phase that is slowly invaded by young trees, and eventually replaced by a mature woodland with a sparse understory in 100–150 years; 3) *Pinus monophylla* is dependent on perennial nurse shrubs for successful establishment during post-fire succession.

STUDY AREA

California's pinyon-juniper woodlands (*P. monophylla*, *Juniperus californica*, *J. occidentalis*) are widespread along the leeward escarpments of the Sierra Nevada, Transverse and Peninsular Ranges (Griffin and Critchfield 1976), including the San Bernardino Mountains, which are located north-east of the city of San Bernardino (Fig. 1). Pinyon-juniper woodlands occupy approximately 87,000 ha within the San Bernardino Mountains between 1300 and 2700 m

elevation along the semi-arid northern and eastern flanks of the range. Regional climate is mediterranean with winter precipitation and summer drought. Orographic effects result in strong rainshadows in the pinyon-juniper range with mean annual precipitation of 25–40 cm (U.S. Dept. of Commerce 1987).

Pinus monophylla is the dominant tree in pinyon-juniper woodlands of the San Bernardino Mountains, forming nearly monotypic stands that are sometimes mixed with California juniper (*J. californica*, <2000 m) and western juniper (*J. occidentalis*, >2000 m). Low elevation (<2000 m) woodland understories consist mostly of desert chaparral (*Ceanothus greggii*, *Fremontodendron californicum*, *Quercus wislizenii*, *Arctostaphylos glauca*, *Cercocarpus betuloides*), while at high altitudes (>2000 m), these woodlands grow with Great Basin sage-scrub (*Artemisia tridentata*, *Chrysothamnus nauseosus*, *Purshia tridentata*), as well as *Quercus chrysolepis* and *Cercocarpus ledifolius* (Minnich 1988). Herbaceous cover is sparse at all elevations as warm season moisture is limited by summer drought.

METHODS

Fire history reconstruction. With sequential aerial photographs it is possible to follow vegetation change and fire history over time (Minnich, in press; Minnich and Bahre 1995). Pinyon-juniper woodland fires leave visible scars on the landscape that persist >50 years (Minnich 1988), allowing for accurate fire history reconstruction back to the 19th century. Fire history and vegetation change were interpreted in two steps using repeat aerial photographs from 1938 and 1983. 1) stereoscopic viewing, aided by mirror and hand held stereoscopes for coverages on prints, and a Bausch and Lomb rollfilm stereoscope with 3× and 8× magnification for coverages on original negative rollfilm. Burn scars were easily recognized on aerial photographs because the removal of vegetation produces a visible contrast between bare, reflective soil and surrounding unburned vegetation. Burn scars were dated back to 1911 by matching them with fire perimeter data on file with the San Bernardino National Forest. 2) Scale matching of site-specific, repeat aerial photographs from 1938 and 1983, using a Bausch and Lomb Zoom Transfer Scope (ZTS). The ZTS permitted observation of two time-series site specific scenes visually superimposed on one another. The same vegetation features in a scene, including burns, were matched exactly from unique stand configurations, as well as from surrounding fixed features such as rock outcrops and watercourses. ZTS registration permitted the examination of post-fire succession between aerial photographs, as well as spatial and temporal changes in stand structure.

Post-fire succession. Post-fire succession was estimated by sampling burns along a chronosequence. This permits spatial vegetation patterns to be used as a surrogate for temporal vegetation change in landscapes where age is the only ecologically significant difference among sampling sites (Jackson et al. 1988; Johnson and Gutsell 1994). Twenty-three burns dating back to the 19th century were sampled between August and November, 1993. The sites were located from burn scars recorded on aerial photographs. At each site, shrub cover was estimated with a 100 m line intercept (Bauer 1943), on level or gently sloping terrain at least 100 m inside the burn perimeter. Shrub density was estimated with the point-center quarter method (Cottam and Curtis 1956), using points at 10 m intervals along the intercept. Tree density was estimated at each site with a 100 m \times 10 m belt transect (Lindsey 1956). The sites were divided into two elevational categories, >2000 m and >2000 m, to capture intersite variations due to floristic differences with altitude. Since only burn scars after 1911 could be assigned ages, it was necessary to estimate ages of older burns from their successional status. Ages of 7 undated burns (visible on 1938 aerial photographs) were estimated by obtaining tree ring counts of 10 large (old) *P. monophylla* recruits, and adding 25–40 years based on average recruitment time lags for *P. monophylla* at chronosequence sites with known ages.

Past research has indicated that perennial nurse shrubs play a vital role in the survival of *P. monophylla* recruits following fire (Erdman 1970; Everett and Ward 1984; Koniak 1985). To establish *P. monophylla* dependence on nurse shrubs, a nearest-shrub analysis of *P. monophylla* saplings was conducted. A 10 \times 100 m sampling area was established at each of 4 burned sites with abundant saplings. The distance of 51 saplings (estimated age, 5–30 years) was measured to the base of the nearest shrub. Stems <5 years that are highly susceptible to mortality were not counted (Meagher 1943). Sapling/nurse shrub distances were compared with mean inter-shrub distances from point-center quarter data to test for randomness in inter-shrub distances.

Changes in mature woodlands. In 1993, twenty-one California Vegetation Type Map (VTM) survey plots, sampled from 1929–1935, were replicated for changes in tree density and size class over a 60 year period (original VTM data on file with Dr. Barbara Allen-Diaz, Department of Forest Resources and Management, University of California, Berkeley). Within a 10 by 80 meter quadrat, trees were counted by species and dbh size class (4–11.9" = 12–33 cm; 12–23.9" = 34–67 cm; $>24"$ = >68 cm; after Minnich et al. 1995). Since the original VTM quadrats could be located only from map locations within ca. 0.5 ha, three randomly located replications were

conducted at each site, and an average was taken for a t-test comparison with the original data.

RESULTS

Fire and succession. Thirty-eight burns, covering an estimated 15,000 ha, were found in *Pinus monophylla* woodlands of the San Bernardino Mountains (Fig. 1). Approximately 17% of *P. monophylla* woodlands have burned since 1911 giving an estimated fire cycle period, or the time for the total burn area to equal total vegetation area (87,000 ha, Johnson and Gutsell 1994), of 480 years. Two general fire patterns were identified: 1) Canopy fires carried by mature *P. monophylla* woodlands (34 burns, ca. 13,750 ha); 2) Fires carried by mature post-fire shrub canopies that consume post-fire *P. monophylla* recruits (4 burns, ca. 1250 ha). All fires produced a charred landscape of standing dead trees, interspersed with small islands of unburned vegetation.

At elevations <2000 m, a shrub phase persists for ca. 50 years, followed by the slow recolonization of *P. monophylla*. Burns <10 years had resprouts of *Purshia tridentata*, and seedlings of *Artemisia tridentata*, *Chrysothamnus nauseosus*, *Ceanothus greggii*, and *Fremontodendron californicum*. These shrubs dominated throughout the shrub phase (Table 1). The shrubs *Eriodictyon trichocalyx*, *Sphaeralcea ambigua*, and *Gutierrezia microcephala*, formed sparse cover on young burns, but were absent from burns >15 years, persisting only in disturbed sites or rocky areas. Other rare species included *Malacothamnus fremontii*, *Eriogonum fasciculatum*, *Ephedra viridis*, and *Prunus fasciculata*. Total shrub cover and density increased steadily with time-since-fire (8.3% and 1988 stems ha⁻¹ at 1 year, 18.5% and 6925 stems ha⁻¹ at 8 years, and 30.2% and 7693 stems ha⁻¹ at 18 years). Cover and density peaked at 40.5% and 11,339 stems ha⁻¹ at 47 years (Figs. 2, 3).

Pinus monophylla was absent from all burns ≤18 years, and was infrequent (40–140 stems ha⁻¹) on burns 33–90 years (Table 3). Stand densities were >250 stems ha⁻¹ on burns ≥130 years. On burns >47 years, total shrub cover and density decreased rapidly from 21.4% and 7670 stems ha⁻¹ at 90 years, to 6.3% and 1215 stems ha⁻¹ at 160 years (Figs. 2, 3). *Pinus monophylla* density increased from 170 stems ha⁻¹ at 90 years, to 360 stems ha⁻¹ at 160 years (Table 3). Although skeletons of *C. greggii* and *F. californicum* were often seen, living stems were absent on burns >47 years. *Prunus fasciculata*, *A. tridentata*, and *Purshia tridentata* were the only shrubs consistently found on burns >90 years.

Post-fire recovery on burns >2000 m was similar to that at lower elevations. Burns ≤14 years were dominated by seedlings of *G. microcephala*, *S. ambigua*, *E. trichocalyx*, as well as *A. tridentata*

TABLE 1. ESTIMATED SHRUB COVER (%) AND DENSITY (STEMS HA⁻¹) ON BURNED SITES < 2000 M ELEVATION.)

Species	Years since fire											
	1	8	9	13	18	33	38	47	90*	130*	140*	160*
Estimated cover												
<i>Artemisia tridentata</i>	1.3	3.1	1.9	4.2	9.5	4.3	19.3	17.4	6.5	6.2	3.7	4.6
<i>Ceanothus greggii</i>	1.7	3.5	11.1	10.3	13.1	10.3	3.7	3.4	—	—	—	—
<i>Chrysothamnus nauseosus</i>	0.7	1.7	3.2	3.2	2.6	8.3	1.2	5.2	2.7	—	0.6	—
<i>Ephedra viridis</i>	—	—	—	—	—	—	—	1.6	—	1.1	0.4	—
<i>Eriodictyon trichocalyx</i>	—	1.5	2.9	—	—	—	2.9	—	2.3	—	—	—
<i>Eriogonum fasciculatum</i>	—	—	—	1.3	1.0	—	—	—	1.8	—	—	—
<i>Fremontodendron californicum</i>	—	2.1	6.5	3.3	3.2	3.5	1.1	3.2	—	—	—	—
<i>Gutierrezia microcephala</i>	—	1.2	—	—	—	—	1.5	2.1	0.7	—	—	—
<i>Malacothamnus fremontii</i>	4.6	—	—	—	—	—	—	—	—	—	—	—
<i>Prunus fasciculata</i>	—	—	—	—	—	—	—	2.7	—	—	1.2	—
<i>Purshia tridentata</i>	—	4.7	—	—	0.8	0.7	—	4.2	6.1	2.5	1.6	1.7
<i>Sphaeralcea ambigua</i>	—	0.7	—	2.1	—	—	—	0.7	1.3	—	—	—
Total	8.3	18.5	25.6	24.4	30.2	27.1	29.7	40.5	21.4	9.8	7.5	6.3
Estimated density												
<i>Artemisia tridentata</i>	398	557	336	1564	2439	2174	8711	3849	2314	2050	1312	972
<i>Ceanothus greggii</i>	299	3098	2449	1810	3232	4094	1523	2250	—	—	—	—
<i>Chrysothamnus nauseosus</i>	199	278	995	844	969	4711	1523	1313	1017	—	94	—
<i>Ephedra viridis</i>	—	—	—	—	—	—	—	566	—	153	47	—
<i>Eriodictyon trichocalyx</i>	—	811	1836	—	—	—	1523	—	1473	—	—	—
<i>Eriogonum fasciculatum</i>	—	—	—	564	242	—	—	—	933	—	—	—
<i>Fremontodendron californicum</i>	—	556	1026	422	484	1754	508	1022	—	—	—	—
<i>Gutierrezia microcephala</i>	1092	202	—	—	—	—	508	783	311	—	—	—
<i>Malacothamnus fremontii</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Prunus fasciculata</i>	—	—	—	—	—	—	—	632	—	—	280	—
<i>Purshia tridentata</i>	—	1221	—	—	327	313	—	783	1311	153	140	243
<i>Sphaeralcea ambigua</i>	—	202	—	422	—	—	—	141	311	—	—	—
Total	1988	6925	6642	5626	7693	13,046	14,296	11,339	7670	2356	1873	1215

* Estimated burn ages dated from tree cores.

$$\circ < 2000 \text{ m}; y = 11.98 + 1.12x - .02x^2 + 5.93E-5x^3; r^2 = .865$$

$$\blacksquare > 2000 \text{ m}; y = -8.87 + 2.59x - .04x^2 + 1.54E-4x^3; r^2 = .919$$

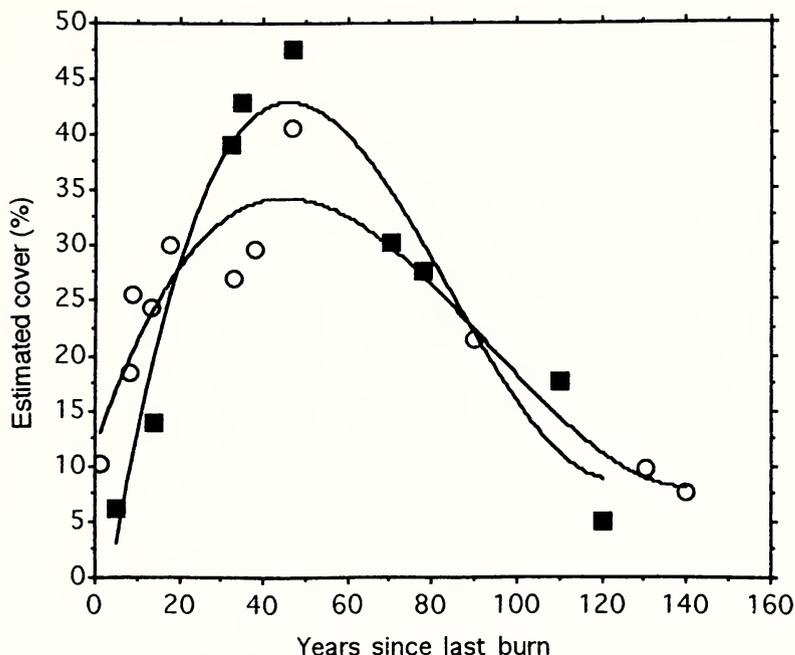


FIG. 2. Third order polynomial regressions for total shrub cover (%) on chronosequence sites.

and *C. nauseosus*. The dominant resprouters were *P. tridentata* and *E. viridis*. *A. tridentata* and *C. nauseosus* co-dominated on burns <30 years, with *A. tridentata* becoming solely dominant on burns >40 years (Table 2). Total shrub cover and density increased to 39.1% and 14,375 stems ha^{-1} at 32 years (Figs. 2, 3), and maintained maximum levels of 38.2–47.7% and 12,063–16,199 stems ha^{-1} at 32–47 years.

Pinus monophylla was absent from burns ≤ 35 years, but was present on all burns ≥ 47 years (Table 3). *Pinus monophylla* density varied from 80 stems ha^{-1} at 47 years to 544 stems ha^{-1} at 160 years. Total shrub cover and density decreased from 30.0% and 10,423 stems ha^{-1} at 70 years, to 17.6% and 3968 stems ha^{-1} at 110 years (Figs. 2, 3). *Pinus monophylla* density increased from 180 stems ha^{-1} at 70 years, to 404 stems ha^{-1} at 110 years (Table 3). At 120–160 years, total shrub cover and density decreased to 5.8–6.2% and 1343–1423 stems ha^{-1} , and *P. monophylla* density increased to

$$\circ < 2000 \text{ m}; y = 1631.43 + 545.73x - 7.89x^2 + .03x^3; r^2 = .923$$

$$\blacksquare > 2000 \text{ m}; y = -2224.98 + 873.49x - 13.36x^2 + .05x^3; r^2 = .951$$

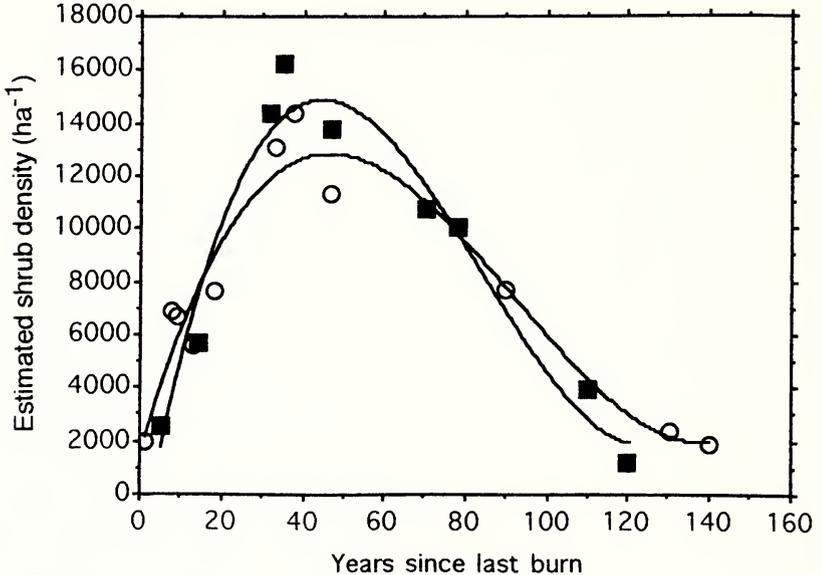


FIG. 3. Third order polynomial regressions for total shrub density (ha^{-1}) on chronosequence sites.

451–544 stems ha^{-1} . *Chrysothamnus nauseosus* was rare on burns >47 years and *A. tridentata* formed only sparse cover on burns >70 years. *Cercocarpus ledifolius*, a nonsprouter, established sparingly on burns >47 years, and persisted on burns ≥ 78 years along with *Amelanchier utahensis*, *E. viridis*, *A. tridentata* and *P. tridentata*.

At all sites, *P. monophylla* saplings were commonly seen emerging through shrub canopies with stems located near shrub root axes. Ninety percent of the saplings were rooted within 26 cm of the nearest shrub root axis, with 50% of individuals ≤ 5 cm (Fig. 4). Perennial nurse shrubs consisted primarily of *A. tridentata*, *C. nauseosus*, *F. californicum*, and *C. greggii*. The mean inter-shrub distance for all sites was 114 cm.

Mature woodlands. Original data from the 1929–1935 VTM field quadrats show that pinyon-juniper woodlands consisted of open to moderately dense stands with a relatively open shrub understory dominated by *A. tridentata*, *Cercocarpus ledifolius*, and *C. betuloides* (Table 4), similar to modern old growth stands (Tables 1–3). *Pinus monophylla* formed mixed-aged woodlands that varied in den-

TABLE 2. ESTIMATED SHRUB COVER (%) AND DENSITY (STEMS HA⁻¹) ON BURNED SITES (>2000 M ELEVATION).

Species	Years since fire										
	5	14	32	35	43	47	70	78	110*	120*	160*
Estimated cover											
<i>Amelanchier utahensis</i>	—	—	—	—	—	—	—	—	—	—	—
<i>Arctostaphylos patula</i>	—	—	—	—	—	—	10.7	—	—	—	—
<i>Artemisia tridentata</i>	—	2.1	18.4	22.3	19.3	19.1	14.6	4.2	10.3	3.2	3.7
<i>Ceanothus greggii</i>	—	1.4	—	—	—	11.4	—	—	—	—	—
<i>Cercocarpus ledifolius</i>	—	—	—	—	5.1	—	—	1.3	—	0.8	—
<i>Chrysothamnus nauseosus</i>	1.1	3.0	12.1	12.1	7.2	6.1	—	—	0.8	—	—
<i>Ephedra viridis</i>	0.9	0.4	—	1.5	1.8	—	—	7.7	—	—	—
<i>Eriodictyon trichocalyx</i>	—	2.6	—	—	3.2	4.4	2.1	—	—	—	—
<i>Fremontodendron californicum</i>	—	—	—	—	—	6.7	2.6	—	—	—	—
<i>Gutierrezia microcephala</i>	0.6	—	1.1	1.2	—	—	—	1.2	—	—	0.4
<i>Purshia tridentata</i>	2.2	4.5	5.3	3.6	1.6	—	—	13.2	4.5	1.8	2.1
<i>Sphaeralcea ambigua</i>	3.6	—	2.2	2.3	—	—	—	—	0.6	—	—
Total	8.4	14.0	39.1	43.0	38.2	47.7	30.0	27.6	17.6	5.8	6.2
Estimated density											
<i>Amelanchier utahensis</i>	—	—	—	—	—	—	—	—	—	—	—
<i>Arctostaphylos patula</i>	—	—	—	—	—	—	1416	—	199	—	—
<i>Artemisia tridentata</i>	—	638	7531	7822	5142	6302	6411	1293	2074	980	875
<i>Ceanothus greggii</i>	—	638	—	—	—	2342	—	—	—	—	—
<i>Cercocarpus ledifolius</i>	—	—	—	—	—	—	—	258	—	121	—
<i>Chrysothamnus nauseosus</i>	515	2208	4907	6091	1872	2278	—	—	399	—	—
<i>Ephedra viridis</i>	192	159	—	—	624	—	—	2328	399	—	—
<i>Eriodictyon trichocalyx</i>	—	319	—	—	780	2342	1631	—	—	—	—
<i>Fremontodendron californicum</i>	—	—	—	—	—	468	965	—	—	—	—
<i>Gutierrezia microcephala</i>	192	—	176	228	—	—	—	258	—	—	110
<i>Purshia tridentata</i>	1143	1753	1509	1602	624	—	—	3879	698	242	438
<i>Sphaeralcea ambigua</i>	515	—	252	456	—	—	—	—	199	—	—
Total	2557	5715	14,375	16,199	12,063	13,732	10,423	8016	3968	1343	1423

* Estimated burn ages dated from tree cores.

TABLE 3. ESTIMATED TREE DENSITIES (STEMS HA⁻¹) ON BURNED SITES.

Species	Years since fire																							
	1	8	9	13	18	33	38	47	90*	130*	140*	160*	5	14	32	35	43	47	70	78	110*	120*	160*	
<2000 meters elevation																								
<i>Juniperus californica</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pinus monophylla</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Years since fire																							
>2000 meters elevation																								
<i>Juniperus occidentalis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pinus jeffreyi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pinus monophylla</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* Estimated burn ages dated from tree cores.

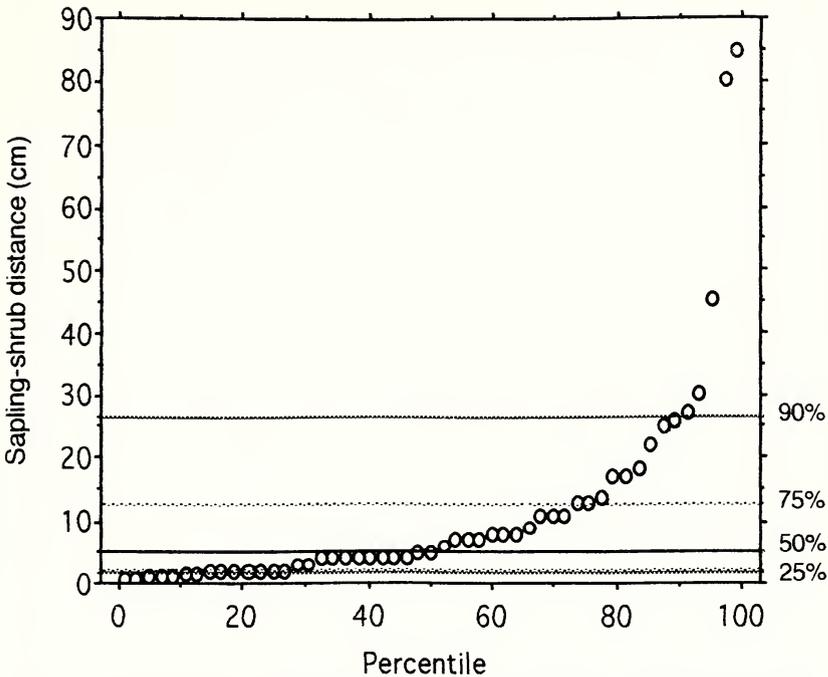


FIG. 4. Cumulative frequency graph for *P. monophylla* sapling-nearest shrub analysis.

sity from 50 to 450 stems ha^{-1} with an average of 192.3 ± 24.5 stems ha^{-1} (Fig. 5a). Eighty percent of stems, averaging 155.4 ± 21.3 stems ha^{-1} , had dbh's < 33 cm, while most remaining trees had dbh's of 34–67 cm. Few trees exceeded 67 cm. *Juniperus occidentalis* density ranged from 0 to 62 stems ha^{-1} (average, 8.9 ± 4.1 ha^{-1}), with most stems falling in the 34–67 cm size class (average, 5.4 ± 3.1 stems ha^{-1} , Fig. 6a).

Replication of VTM plots in 1993 show that modern *P. monophylla* stand density ranges from 75 to 475 stems ha^{-1} with an average of 220.8 ± 26.1 stems ha^{-1} (Fig. 5b), an insignificant increase of 15% since 1929–1935 ($P > 0.05$, $\text{df} = 20$, Table 5). Average stand density for dbh < 33 cm did not change significantly ($P > 0.05$, $\text{df} = 20$), but did increase significantly for dbh 34–67 cm ($P \leq 0.05$, $\text{df} = 20$). Few trees exceed 67 cm. Modern *Juniperus occidentalis* density ranges from 0 to 50 stems ha^{-1} with an average of 9.5 ± 3.5 stems ha^{-1} (Fig. 6), an insignificant increase of 6% ($P > 0.05$, $\text{df} = 20$, Table 6). Size classes underwent little change.

DISCUSSION

The fire regime of pinyon-juniper woodlands in the San Bernardino Mountains is dominated by long-period canopy fires and slow

TABLE 4. SHRUB COVER (%) AS REPORTED BY 1929-1935 VTM SURVEY FOR PINYON-JUNIPER WOODLANDS.

Plot #	Altitude (m)	Ag	Ap	Apn	Atr	Cg	Cb	Cl	Fc	Pi	Qc	Qcm	Qw	Total
Deep Creek Zone														
B-1-14	1189	5	—	—	—	6	10	—	—	6	—	—	—	27
B-1-15	1265	7	—	—	—	6	11	—	1	—	—	—	6	31
B-2-9*	1615	—	—	—	24	21	9	—	15	—	—	—	—	69
B-3-2	1783	—	—	—	—	—	—	—	—	—	—	—	—	0
B-3-3	1753	—	—	—	12	—	—	—	—	—	—	—	—	12
B-3-11	1814	—	—	—	2	1	—	—	—	—	—	—	—	3
B-3-14	1814	—	—	—	41	—	—	—	—	—	—	—	—	41
B-3-15	1768	—	—	—	6	3	3	—	1	—	—	—	—	13
B-3-17	2012	—	—	—	3	—	—	22	—	—	42	—	—	67
B-3-18*	2286	—	4	—	7	34	—	—	13	—	16	—	—	74
C-1-10	1341	—	—	—	—	7	16	—	—	—	—	—	12	35
C-2-9	1448	—	—	—	—	2	12	—	—	—	—	—	—	14
C-2-10	1570	—	—	—	—	—	3	—	4	—	1	—	—	8
C-2-12	1387	—	—	—	—	4	5	—	7	—	—	—	—	16
C-3-1	1798	—	—	—	9	2	9	—	—	—	—	—	—	20
C-3-8	1875	—	—	—	—	—	—	—	—	—	—	—	—	0
San Gorgonio Zone														
B-3-1	1890	—	—	—	—	—	—	8	—	—	—	—	—	8
C-2-6*	2286	—	2	—	14	22	—	25	2	—	—	—	—	65
C-2-8	2423	—	—	—	—	—	—	5	—	—	—	—	—	5
C-2-9	2286	—	—	—	—	—	—	6	—	—	—	—	—	6
C-2-10	2377	—	9	—	—	—	—	12	—	—	—	—	—	21
C-2-11	2225	—	—	—	—	—	—	9	—	—	—	—	—	9
C-2-12	2103	—	—	—	4	—	—	4	—	—	—	—	—	8
C-3-1	1859	—	—	—	19	—	—	—	—	—	—	—	—	19
C-3-4	2072	—	—	—	3	—	—	—	6	—	—	—	—	9
C-3-6	2118	—	—	—	17	—	—	—	—	—	2	—	—	19
C-3-7	2103	—	—	—	17	—	—	—	—	—	—	—	—	17
C-3-9	2164	—	—	—	—	—	—	—	—	—	24	—	—	24
C-3-11	2195	—	—	—	10	—	—	20	3	—	—	—	—	33
C-4-1	1890	—	—	—	—	—	—	—	—	—	—	—	—	0
C-4-2	1981	—	—	—	12	—	—	—	—	—	—	—	—	12
D-3-2	2286	—	—	—	—	—	—	—	1	—	3	—	—	4
D-4-2	2347	—	—	—	1	—	—	7	—	—	—	—	—	8
D-4-4	2195	—	—	—	—	—	—	6	—	—	16	—	—	22
D-4-5	2103	2	—	—	—	—	—	—	—	—	21	—	—	23
D-5-2	1646	—	—	—	—	—	—	—	—	—	—	14	—	14
D-5-3	1951	—	—	—	—	—	—	—	—	—	—	1	—	1
D-5-5	2073	—	—	—	—	—	—	—	—	—	39	—	—	39

* Sampled within 19th century burn perimeters.

Ag: *Arctostaphylos glauca*; Ap: *Arctostaphylos patula*; Apn: *Arctostaphylos pungens*; Atr: *Artemisia tridentata*; Cg: *Ceanothus greggii*; Cb: *Cercocarpus betuloides*; Cl: *Cercocarpus ledifolius*; Fc: *Fremontodendron californicum*; Pi: *Prunus ilicifolia*; Qc: *Quercus chrysolepis*; Qcm: *Quercus cornelius-mulleri*; Qw: *Quercus wislizenii*.

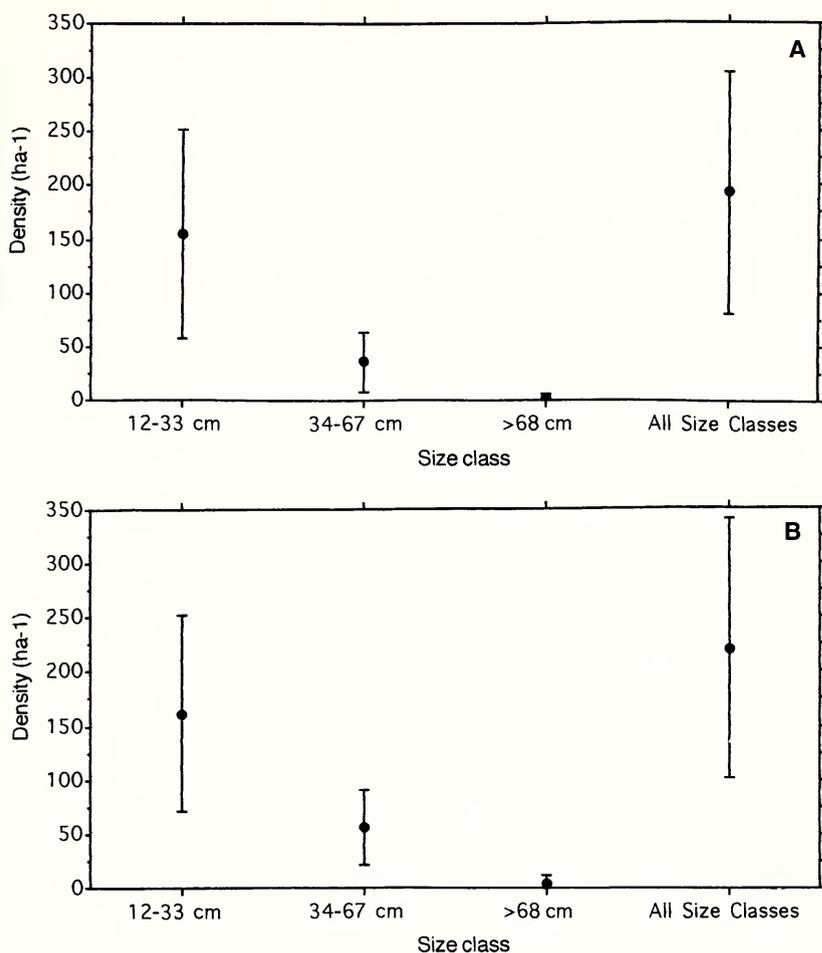


FIG. 5. A) Average *P. monophylla* density by size class for 1929-1935 VTM survey. B) Average *P. monophylla* density by size class for 1993 survey.

post-fire succession. These woodlands are restricted to rain shadows at middle and high altitudes where production of woody fuels, litter and flashy herbaceous cover are limited by cold winters and prolonged warm season drought (Minnich 1988). The open fuel arrangement of stands tends to restrict burns to severe weather (high winds and low relative humidity), resulting in intense stand replacement fires. Tree mortality is high because of pitchy foliage and basal canopies that are contiguous with ground fuels (Minnich 1988). Fires are brief because extreme weather necessary for fire spread is

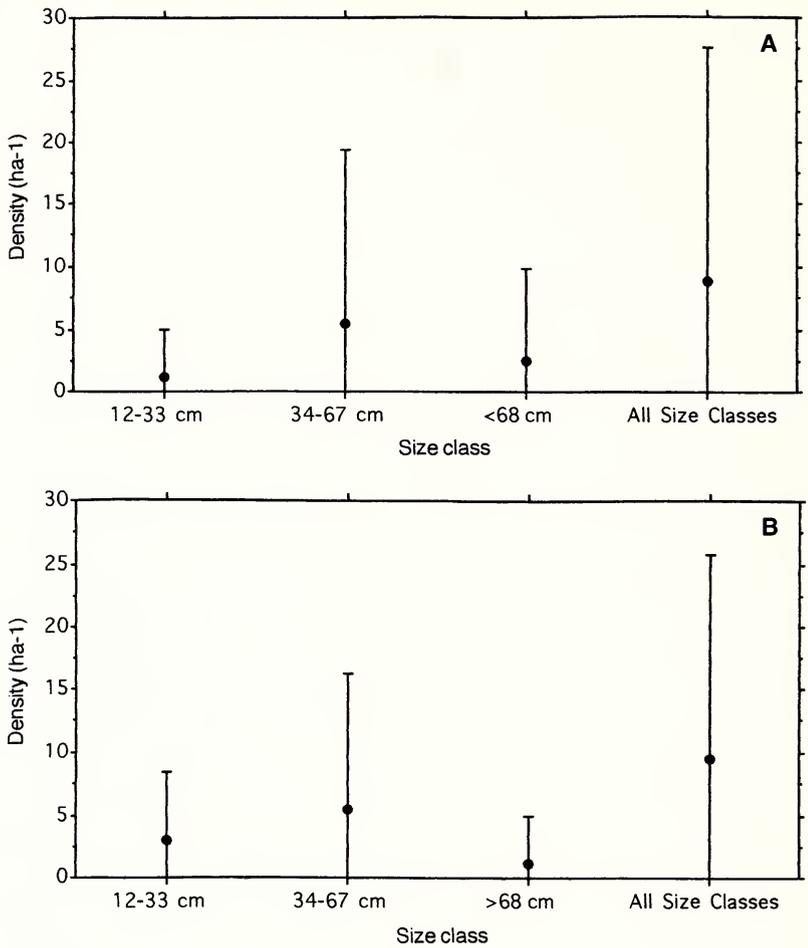


FIG. 6. A) Average *J. occidentalis* density by size class for 1929-1935 VTM survey. B) Average *J. occidentalis* density by size class for 1993 survey.

TABLE 5. COMPARISON OF AVERAGE *PINUS MONOPHYLLA* DENSITY (HA⁻¹) BY SIZE-CLASS FOR 1929-1935 VTM SURVEY AND 1993 REPLICATION.

(DBH in cm) size class	(Stems ha ⁻¹ ± standard error)		P value
	1929-1935	1993	
12-33	155.4 ± 21.3	161.3 ± 19.7	0.384
34-67	35.7 ± 6.0	55.9 ± 7.5	0.007
>68	1.2 ± 0.8	3.6 ± 1.8	0.096
All sizes	192.3 ± 24.5	220.8 ± 26.1	0.143

TABLE 6. COMPARISON OF AVERAGE *JUNIPERUS OCCIDENTALIS* DENSITY (HA-1) BY SIZE-CLASS FOR 1929-1935 VTM SURVEY AND 1993 REPLICATION.

(DBH in cm) size class	Stems ha ⁻¹ ± standard error)		P value
	1929-1935	1993	
12-33	1.2 ± 0.8	2.9 ± 1.2	0.076
34-67	5.4 ± 3.1	5.4 ± 2.4	0.493
>68	2.4 ± 1.6	1.2 ± 0.8	0.078
All sizes	8.9 ± 4.1	9.5 ± 3.5	0.431

usually short-lived, resulting in a mosaic of mostly small, scattered patches within uniform old growth stands across the landscape.

Pinyon-juniper succession is characterized by the colonization of opportunistic shrubs into disturbed, mineral soil habitats in full sun as the result of canopy burns. While initial *P. monophylla* recruitment appears to be autogenically dependent on nurse shrubs, the development of mixed-aged stands with canopy closure suggests that nurse shrub dependence eventually ceases in later succession. Canopy closure also causes die-back in most understory shrub species, reducing the probability of short-period understory fires breaching the developing *P. monophylla* woodland.

The shrub phase is dominated by species adapted for efficient colonization of burns (Noble and Slatyer 1980), including re-sprouting (*P. tridentata*, *E. viridis*, pers. obs.), wind-blown seed establishment (*A. tridentata*, *C. nauseosus*, *G. microcephala*, *E. trichocalyx*, *S. ambigua*, Burkhardt and Tisdale 1976), and establishment from *in situ* refractory seed banks (*C. greggii*, *F. californicum*, Keeley 1991). Once established, individual species must rely on longevity and/or the ability to continuously recruit to survive later into succession.

The disappearance of *G. microcephala* and *S. ambigua* in early succession suggests they are short-lived. They persist locally by recruiting continuously on permanently disturbed sites such as washes, road cuts and rock outcrops. *Ceanothus greggii* and *F. californicum* establish even-aged stands from seed banks immediately following fire. *Ceanothus* spp. are known to continuously cache seeds in the soil from the time of reproductive maturity (ca. 5 years) until senescence (usually <50 years) and to germinate only in the presence of ash (Mooney and Miller 1985). Both shrubs disappear after ca. 50 years. These shrubs may also suffer photosynthetic decline in the shade of *P. monophylla* (Campbell 1977). Continuous recruitment of *A. tridentata* and *C. nauseosus* accounts for most of the increase in shrub density during the shrub phase (Tables 1, 2). However, *A. tridentata* and *C. nauseosus* also decline late in succession, forming a discontinuous understory with other shade-tolerant species (*P. tridentata*, *C. ledifolius*) in mature *P. monophylla* woodlands. Al-

though the shrub phase is dominated by desert chaparral (*C. greggii*, *F. californicum*) at lower elevations, and Great Basin sage-scrub (*A. tridentata*, *C. nauseosus*) above 2000 m, total shrub cover and densities are similar across all elevations (Figs. 2, 3).

The establishment of *P. monophylla* after 25–40 years appears to be autogenic as specific environmental conditions may be necessary for successful establishment (Weaver and Clements 1938). Although *P. monophylla* seeds are large and heavy, and do not survive fire directly, establishment during early succession is not limited by dispersal, because jays, nutcrackers, and small mammals such as ground squirrels continuously cache seed (Van der Wall and Balda 1976). Instead, a combination of several environmental factors appear to inhibit early establishment of *P. monophylla*. In early succession, unshaded seedlings are susceptible to mortality from exposure to direct solar radiation. Phillips (1909) observed that *P. monophylla* recruits best in the shade of mature woodlands. Meagher (1943) reported high *P. monophylla* mortality due to insolation on exposed sites one year after germination.

Pinus monophylla recruitment may also be deterred by cold nights and frost heaving. Clear windless nights combined with low relative humidities result in rapid nocturnal radiational cooling favorable for ground inversions, with minimum temperatures below freezing between October and May (Minnich 1971). Because snow cover is limited most years (Minnich 1986), seedlings are frequently exposed to frost, and the upper soils to frost heaving which may uproot newly established seedlings. Meagher (1943) reported that frost and frost heaving account for greater seedling mortality on exposed sites than on shaded or shrub covered sites. Indeed, heavy *P. monophylla* seedling mortality was observed at restoration plantings on recent burns east of Baldwin Lake.

Pinus monophylla saplings are typically rooted in the shade of mature shrubs, often next to their root axes (Fig. 4). Apparently the shrub canopy provides a regulated microclimate that gives seedlings the best chance for survival. This is supported by average sapling-shrub distances that are an order of magnitude less than mean inter-shrub distances. Above 2000 m, the initial establishment of *P. monophylla* is delayed 10–15 years longer than at lower elevations (Table 3). Still, mature stand densities are greater at high elevations due perhaps to a wetter climate (Fig. 7). Establishment of *Juniperus* spp. is thought to be similar (Meagher 1943), but the low frequency of these trees in the San Bernardino Mountains precluded their examination.

Once *P. monophylla* begins to dominate a site, it appears that the developing tree canopy moderates environmental conditions so that seedlings establish in the shade of older trees without the aid of nurse shrubs. In the field we observed little heaving in mature stands

$$\circ < 2000 \text{ m}; y = 2.21x - 9.91; r^2 = .856$$

$$\blacksquare > 2000 \text{ m}; y = 4.61x - 154.70; r^2 = .915$$

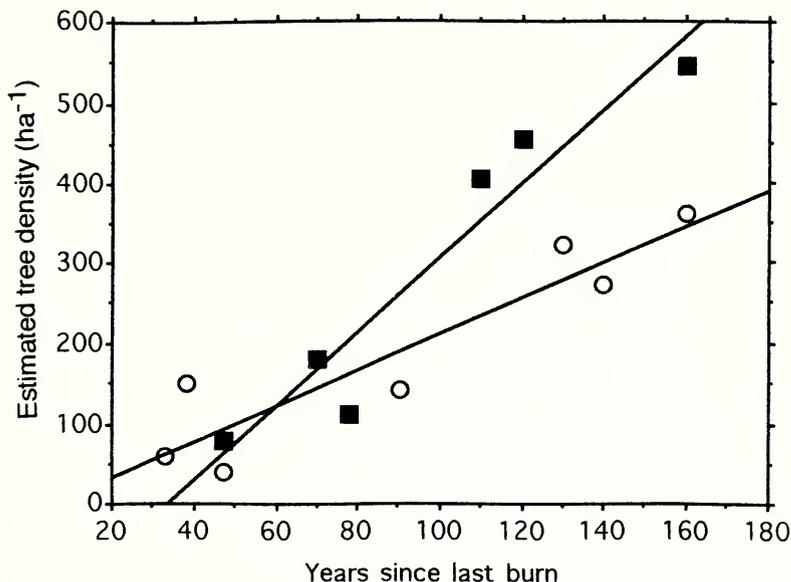


FIG. 7. Linear regressions for total tree density (ha^{-1}) on chronosequence sites.

immediately adjacent to burns where heaving is active. The local change in microclimate is probably related to nocturnal long-wave radiant energy fluxes associated with tree canopies (Miller 1981). During clear, windless nights (ca. 200 year^{-1} , Minnich 1971), equivalent downward long-wave radiant fluxes (sky radiation) are $20\text{--}40^\circ\text{C}$ below ambient (Miller 1981), resulting in intense ground inversions and soil freezing. In mature woodlands, nocturnal ground level air temperatures reflect radiant emissions of tree canopies whose temperatures are close to ambient.

The broad homogeneity of pinyon-juniper woodlands in the San Bernardino Mountains, as indicated by VTM data, suggests that this vegetation type may achieve some old-growth equilibrium in species composition and stand structure. Canopy closure initiates a period of continuous recruitment of *P. monophylla*, as suggested by uneven-aged dbh size distributions. This is typical of white pines which recruit best in shade (Fowells 1965). Stand densities of $150\text{--}300 \text{ ha}^{-1}$ are achieved by 100 years after fire. Whether densities continue to increase with stand age, or reach some equilibrium between recruitment and mortality is unclear.

Comparison with pinyon-juniper woodlands in the Southwestern United States. Fire and succession patterns in pinyon-juniper woodlands of the San Bernardino Mountains are similar to those reported in the Great Basin and Colorado Plateau. In these regions, sparse understories and open tree canopies restrict burning to times of severe weather, resulting in a mosaic of small, stand-replacement burns within a uniform old-growth landscape (Erdman 1970; Everett and Ward 1984; Koniak 1985). Overall productivity is limited by cold winters and low annual precipitation that reduce photosynthetic activity during much of the year (Caldwell, 1985). Post-fire succession begins with a shrub phase that is followed by the gradual establishment of trees in the shade of nurse shrubs. Koniak (1985) recorded conifer establishment in dense stands of Great Basin sage scrub 20–30 years after fire, and reported tree canopies topping the shrub layer 60 years after fire. Erdman (1970) concluded that shrub densities gradually decline in the shade of tree canopies, resulting in mature woodlands with sparse shrub understories 200–300 years after fire.

Studies in Arizona and New Mexico report that pinyon-juniper woodlands with perennial grass understories experience short interval, low intensity fires that cause high mortality among young recruits <2 m tall, but rarely kill mature trees. In Arizona, Jameson (1962) found that young trees <2 m tall accounted for >70% of *J. monosperma* mortality, and in New Mexico, Dwyer and Pieper (1967) reported that all trees <1.5 m tall were fire-killed, but total tree mortalities were only 24% for *J. monosperma* and 13.5% for *P. edulis*. In both regions, perennial grasses (*Bouteloua gracilis* and *B. eriopoda*) resprouted from undamaged root crowns, resulting in rapid recovery of herbaceous biomass within 2 years.

In the San Bernardino Mountains, short-interval surface fires seldom occur due to lack of herbaceous cover, and slow rates of post-fire succession. Understory fires in successional Great Basin sage-scrub and desert chaparral communities result in high mortality among both shrub and tree layers. Fires are usually short-lived, and rarely spread beyond the successional community into adjacent mature pinyon-juniper woodlands. Evidence against short-interval fires is the marginal overlap between contiguous burns. This pattern indicates that stands seldom reburn during early successional stages. Hence, the spread of fire is system-regulated and influenced by previous fire history (Loucks 1970; Heinselman 1981), similar to chaparral (Minnich 1983, in press).

It is asserted that fire intervals have been lengthened in pinyon-juniper woodlands of the Great Basin and Colorado Plateau during the 20th century due to the combined effects of fire suppression management and removal of herbaceous cover due to heavy livestock grazing (Cottam and Stewart 1940; Johnsen 1962; Arnold et al. 1964; Blackburn and Tueller 1970; Nabi 1978; Tausch et al.

1981; Wright and Bailey 1982). The shift toward longer fire intervals appears to encourage pinyon and juniper expansion in these regions (Arnold et al. 1964; Blackburn and Tueller 1970; Nabi 1978; Tausch et al. 1981; Wright and Bailey 1982). In the San Bernardino Mountains, pinyon-juniper woodlands were grazed in the late 19th and early 20th centuries (Minnich 1988). However, low overall productivity and limited herbaceous cover during the warm season may have mitigated the impact of grazing on fire intervals.

Pinyon-juniper woodlands of the San Bernardino Mountains have remained unchanged since the late 19th century, before fire control was initiated. Past and present fires have been most frequent in mesic stands at the highest elevations, but rare in woodlands adjacent to the Mojave Desert (Leiberg 1899, 1900; Minnich 1988). Leiberg described the pinyon-juniper association as consisting of moderately dense woodlands interspersed with a mosaic of different aged canopy burns across the landscape. Leiberg (1900) saw little evidence of surface fires, reporting that bole scars were noticeably absent. In northern Baja California, Mexico, where little fire intervention exists, pinyon-juniper woodlands also experience long-period canopy fires at intervals of centuries (Minnich in press). Replication of VTM quadrats in the San Bernardino Mountains show that stand densities and size class distributions have experienced only minor changes since 1932. This is in sharp contrast to Californian mixed-conifer forests where pre-suppression forests of open old growth trees of large size classes have shifted to dense stands of shade-tolerant sapling and pole size trees (Vankat 1977; Vankat and Major 1978; Minnich et al. 1995). Moreover, site-specific scale matching of 1938–1983 aerial photographs show that recent stand turnover by canopy burns has been paralleled by recolonization of trees on 19th century burns, and that pinyon-juniper distributions have remained unchanged.

CONCLUSION

In the pinyon-juniper woodlands of the San Bernardino Mountains, infrequent canopy fires result in a mosaic of mostly small, scattered patches within uniform old-growth stands across the landscape. Post-fire succession to mature woodlands proceeds over a span of a century, beginning with the colonization of Great Basin sage-scrub (*P. tridentata*, *A. tridentata*, *C. nauseosus*) at higher elevations (>2000 m), and a mix of California desert chaparral (*C. greggii*, *F. californicum*) and Great Basin sage-scrub at lower elevations (>2000 m). The shrub phase increases in cover and density for 30–50 years, and is joined by *P. monophylla* recruits at 25–40 years. Initial recruits appear to be dependent on perennial nurse shrubs which provide a regulated microclimate suitable for *P. mon-*

ophylla establishment. After 50 years, increases in *P. monophylla* densities are phased with a decline in the shrub layer, and the development of a self-regulating micro-climate that favors *P. monophylla* recruitment without the aid of nurse shrubs. Mature woodlands with sparse understories return at 100–150 years. Lengthened fire intervals and pinyon-juniper expansion, as reported in the Great Basin and Colorado Plateau, have not occurred in the San Bernardino Mountains, even under fire suppression management.

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POST-MANUAL ADJUSTMENTS IN CALIFORNIAN
LOMATIUM (APIACEAE)

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ABSTRACT

Lomatium observatorium, described herein from Mount Hamilton, California, is the southernmost link in a chain of morphologically similar entities extending through the Coast Ranges to southern Oregon. The first of these to receive taxonomic recognition was *L. ciliolatum*; its former variety is herein raised to specific rank as *L. hooveri* to demonstrate its parity with other members of the alliance. Outside of the alliance, two species of *Lomatium* not included in the Jepson Manual are now known to occur in California: *L. grayi* and *L. hendersonii*.

Even before *The Jepson Manual: Higher Plants of California* appeared in print, it was evident that the text on *Lomatium*, with some 48 taxa the largest genus of California Apiaceae (Constance 1993), was already in need of revision. This article examines the new species and records in preparation for an upcoming second edition.

NEW SPECIES

In 1991, photographer Nigel J. Hancock observed a yellow-flowered umbel growing among the University of California observatory buildings atop Mount Hamilton, Santa Clara Co., California, and brought an excellent photographic slide and fragmentary material to our attention. In his treatment of Apiaceae for the new Jepson Manual, Constance (1993) had previously provided for the three existing voucher specimens from this locality, plus another from nearby Del Puerto Canyon, Stanislaus Co., under *L. ciliolatum* Jepson, with which they more or less agreed in pubescence, by extending the species' range southward. This differed from Sharsmith (1945), who had used at least some of the same specimens as the basis for her inclusion of *L. caruifolium* (Hook. & Arn.) J. Coulter & Rose in her *Flora of the Mount Hamilton Range of California*. As a result of Hancock's discovery of extant populations on Mount Hamilton, new and better material has come to hand. Features of the leaves, fruit, and habitat, as indicated in the accompanying key, make it apparent that a previously undescribed entity is concerned.

Lomatium observatorium Constance & Ertter, sp. nov. (Fig. 1)—
TYPE: USA, California, Santa Clara Co., partly open rocky

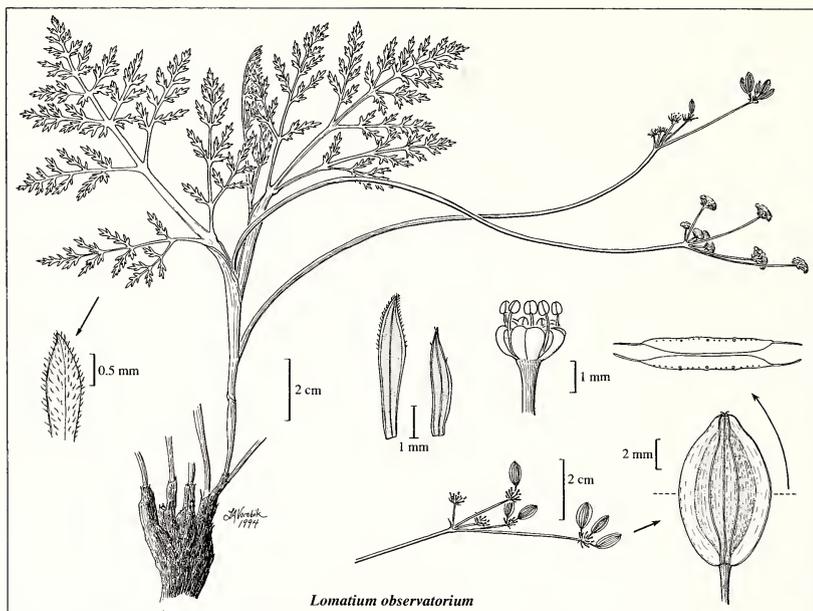


FIG. 1. *Lomatium observatorium*: habit in flower with enlargement of leaf segment showing vestiture; involucel bractlets; flower; infructescence; fruit with cross-section. From type collection, *Constance and Constance 3902*.

ridge on San Antonio Valley road 1.2 miles below (east of) summit of Mount Hamilton, ca. 1219 m., 23 May 1993, *L. and W. C. Constance 3902* (holotype UC; isotypes to be distributed).

Plantae acaulescentes vel brevicaulescentes puberulae vel dense hirtellae interdum glabratae e radice palari elongatae, scapis florescentibus 1–2; lamina foliorum glauco-viridis late ovata, ternato-bipinnata, divisionibus ultimis lineari-lanceolatis acutis; petioli purpureo-vaginantes; pedunculi folia excedentes; radii fertiles valde inaequales, patenti vel patento-ascendentes; umbellularum flores 6–12, 1–8 fertilibus; involucellae bracteolae lanceolatae vel obovatae \pm ciliolatae, quam flores breviores, basi confluentes; petala et antherae obscure citrinae, ovariis glabris; fructus ovalis glabrous apice basique vix angustatus, costis dorsalibus filiformibus inconspicuis alis quam corpore multo angustioribus; vittae minimae in intervallis et in commissuris pluribus; seminis superficie plana; chromosomatum numerus $n=11$.

Plants acaulescent or subacaulescent, 10–30 cm tall, the herbage puberulent to densely hirtellus, rarely glabrate, from an elongated

taproot up to 15 cm long and bearing 1–8 flowering shoots at summit; leaves inserted at ground level and spreading laterally or ascending, grayish-green, the blade broadly ovate, 4–12 cm long and broad, ternate-bipinnate, the ultimate divisions linear-lanceolate, acute, mucronulate, 1–8 mm long, ca 1 mm broad; petiole 3–6 cm long, wholly sheathing, the sheaths purplish with membranous margins ca 1 mm wide; peduncles 0.8–20 cm long, rather slender, axillary, usually decumbent at base and spreading laterally or spreading-ascending, exceeding the leaves; involucre 0; rays 4–16, only 1–3(–7) developing, 0.8–5(–8) cm long; umbellets usually 8–12-flowered, 1–8 flowers fertile; involucre of 5–10 lanceolate to obovate, venose, very narrowly scarious, \pm ciliolate bractlets 3–4 mm long, usually slightly confluent at base; fruiting pedicels 1–3(–5) mm long; petals dull yellow with a darker central stripe, oblong to obovate, the anthers yellow, the ovaries glabrous; carpophore bipartite, filiform, persistent; fruit oval, 7–10 mm long, 3.5–5 mm broad, scarcely narrowed at apex and base, purplish dorsally, ashy-white on the commissural surface, the ribs filiform, inconspicuous, the lateral wings inconspicuous, ca. 0.6 mm wide, much narrower than the body; vittae very small, several in the intervals and on the commissure, the seed face nearly plane; chromosome number $n=11$.

PARATYPES: USA: CALIFORNIA, Santa Clara Co., type locality, 4 Apr 1993, *Constance, Ertter & Olson 3901* (UC); Mt. Hamilton, 29 Apr 1923, *Eastwood 11675* (CAS), 18 Jun 1941, *Eastwood & Howell 9667* (CAS); rocks near Aquarius road, NE slope at summit of Mt. Hamilton, 10 Mar 1934, *H. K. Sharsmith 583* (UC); Mt. Hamilton, behind 120-inch telescope, rocky flat, 31 May 1993, *Ertter & Willingham 11081* (UC). Stanislaus Co., near head of Del Puerto Canyon, rocky N-facing slope, 20 Apr 1941, *R. F. Hoover 4892* (UC).

Open or partly shaded rocky openings in *Pinus coulteri-Quercus wislizenii-Q. chrysolepis* woodland adjoining *Quercus-Garrya-Ceanothus-Arctostaphylos* chaparral. Substrate consisting of partly metamorphosed sedimentary Franciscan rocks and intruded volcanics, in the Mount Hamilton Range, at an altitude of ca. 1280–1330 m. Blooming March to May; fruiting May to June.

THE *LOMATIUM CILIOLATUM* GROUP

Lomatium observatorium represents a fifth and southernmost member of the *L. ciliolatum* group, which extends from the Lakeview District of south-central Oregon into and southward in the Coast Ranges of northern California (Fig. 2). The northernmost species is *L. peckianum* Mathias & Constance, from Lake and Klamath counties, Oregon, and Siskiyou Co., California. *Lomatium tracyi*

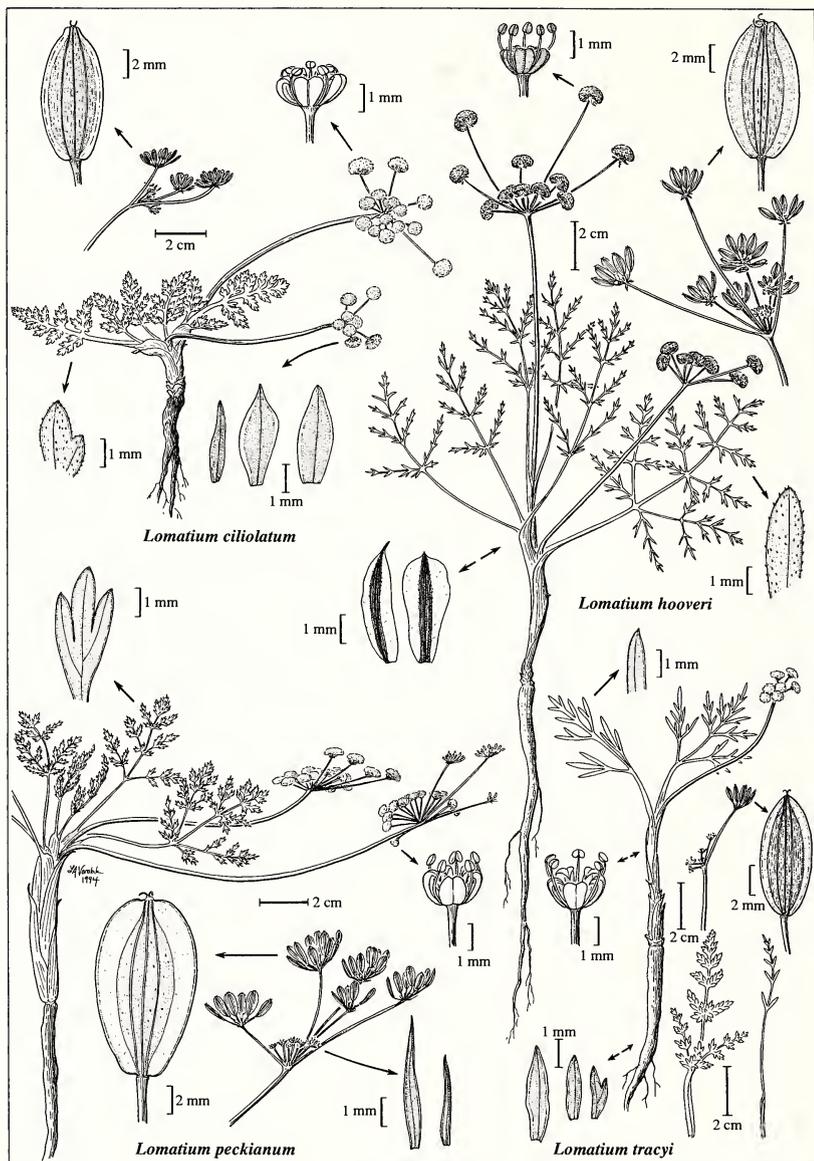


FIG. 2. Clockwise from upper righthand corner: *Lomatium ciliolatum*, *L. hooveri*, *L. tracyi*, and *L. peckianum*. Each showing habit in flower with enlargements of leaf segment showing vestiture, involucre bractlets, and flower; infructescence with enlargement of fruit.

Mathias & Constance is a rare ultramafic endemic of Humboldt, Trinity, Shasta, and Lassen counties, California, while *Lomatium ciliolatum* itself, described by Jepson in 1924, occurs from Trinity Co. to Colusa Co., chiefly in the inner north Coast Ranges. The final element, *L. ciliolatum* var. *hooveri* Mathias & Constance, is herein raised to specific status since its distinctiveness is equivalent to that of the other species. It occurs in Napa, Lake, and Colusa counties.

Lomatium hooveri (Mathias & Constance) Constance & Ertter, comb. et stat. nov. Based upon *Lomatium ciliolatum* var. *hooveri* Mathias & Constance, Bulletin of the Torrey Botanical Club 69: 153. 1942.

In its preference for a volcanic habitat, *L. observatorium* is similar to *L. peckianum*, but that species has glabrous to sparsely scaberulous foliage, broader leaf divisions, and nearly cream flowers. The other three species are all serpentine endemics, *L. hooveri* usually occurring in chaparral while *L. ciliolatum* and *L. tracyi* are mostly found in coniferous forests. *Lomatium hooveri* is further distinctive in its broad white scarious bractlets contrasting sharply with the red-purple petals. *Lomatium ciliolatum* differs from *L. observatorium* in its crowded ciliolate to densely hirsutulous and broad leaf divisions, with flowers either yellow or occasionally (as on Snow and Sheet-iron mountains) bright red. Finally, *L. tracyi* is quite glabrous, with few and generally more slender leaf divisions, narrower bractlets, and mostly only one or very few fertile rays.

In the Jepson Manual, the key to *Lomatium* (Constance 1993) on p. 152 can be modified to include *L. observatorium* as follows:

- 50. Corolla gen yellow; bractlets very narrowly scarious-margined
 - 50a. Ultimate lf divisions broad, obtuse, overlapping; fr oblong, the wings thick; serpentine substrates, inner north Coast Ranges . . . *L. ciliolatum*
 - 50a'. Ultimate lf divisions narrow, gen acute, less crowded; fr oval, the wings thin; volcanic substrates, Mt. Hamilton range *L. observatorium*
- 50'. Corolla purple; bractlets scarious throughout *L. hooveri*

Lomatium ciliolatum, *L. observatorium*, *L. hooveri*, *L. peckianum*, and *L. tracyi* are all low, essentially stemless, taprooted perennials of open or lightly shaded rocky ridges, slopes, or flats. The leaves are frequently glaucous, bluish, or purplish, varying from strictly glabrous to densely hirtellous; they generally either lie flat on the ground or ascend gradually. The inflorescence consists of one or more divergent or spreading flowering scapes bearing few-rayed compound umbels. The flowers vary from pale yellow to bright purplish-red and may be set off by a more or less scarious involucrel, although the latter may be only weakly developed in some instances. The fruits are often shining and narrowly thin- to strikingly thick-

winged. All have been examined cytologically and determined to be diploid with a chromosome number of $n=11$.

We therefore believe that the five species do indeed constitute a natural grouping, even though this conclusion derives no support from unpublished phenetic and cladistic analyses that have been kindly brought to our attention. Karen S. Simmons (1985), working with the late Amy Jean Gilmartin in her pioneering numerical studies of *Lomatium*, set out "to examine the entire genus and to establish putatively closely related groups of *Lomatium* species", admitting, however, that she "was not seeking a fully resolved tree of all *Lomatium* species". In pursuit of her goals, she subjected 13 binary characters, mostly drawn from existing monographs and species descriptions, to phenetic and cladistic analyses, using *Polytaenia* as an outgroup. Other than one well-defined clade that Simmons used as a focus for further studies, the resultant trees failed to agree on the clustering of most other species, including those in the *L. ciliolatum* group.

NEW RECORDS

Bruce Bartholomew (CAS), in conjunction with his work on a flora of Modoc County, has called our attention to the occurrence of two species of *Lomatium* in California which are not currently in the Jepson Manual. These are the Great Basin species *L. grayi* (J. Coulter & Rose) J. Coulter & Rose and *L. hendersonii* (J. Coulter & Rose) J. Coulter & Rose. Both were ostensibly collected in Modoc Co., California, by Mrs. C. C. Bruce in 1899, and re-collected nearly a century later by Bartholomew.

Lomatium grayi is abundant and widespread in the northern Great Basin. In the Jepson Manual it would key to *L. torreyi* (J. Coulter & Rose) J. Coulter & Rose, from which it differs in its broader leaves, the possession of an involucl, longer pedicels, and broader fruit. It is vouchered in California by *Bruce 73* (Modoc Co., Jun 1899; DS) and *Bartholomew 6634* (Surprise Valley, 13 Jun 1993; CAS, UC).

Lomatium hendersonii, largely restricted to central Oregon, belongs to the tuberous group of species monographed by Schlessman (1984). It does not fare well in the Manual key, but would probably place near *Lomatium stebbinsii* Schlessman & Constance, from which it may be differentiated by its much more numerous leaf segments, the presence of an involucl, its longer pedicels, and its much thicker (corky) fruit wings. It is vouchered in California by *Bruce 2491* (high mts., Goose Lake, Aug 1899; DS) and *Bartholomew et al. 6533* (road to West Valley Reservoir, 13 May 1993; CAS, UC).

According to both Schlessman (1984) and Mathias & Constance

(1945), *L. hendersonii* has as a synonym *Leptotaenia leibergii* J. Coulter & Rose (not to be confused with *Lomatium leibergii* J. Coulter & Rose, 1900). Cronquist (1992), however, suspected that more than one entity is involved and proposed the name *Lomatium roseanum* Cronq. as a nomen novum for *Leptotaenia leibergii*. Schlessman (1984) comments that *L. hendersonii* is poorly collected and that it is the only member of the tuberous group of *Lomatium* for which two different chromosome numbers have been reported. Further field work is obviously needed.

ACKNOWLEDGMENTS

The writers are particularly grateful to Linda Vorobik, who designed and executed the excellent illustrations. We are indebted to Mr. Hancock for calling the Mount Hamilton population to our attention, and to Bruce Bartholomew for alerting us to the Modoc County records. We acknowledge the assistance and fellowship of our field companions: William C. Constance, Lynne Hosley, Brad Olson, and Joe Wiltingham. We thank the staff of UC/JEPS and CAS/DS for materials.

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NOTE

CHROMOSOME NUMBER IN *NEVIUSIA* (ROSACEAE: KERRIEAE).—Peter Goldblatt, Missouri Botanical Garden, P. O. Box. 299, St. Louis, MO 63166-0299.

In 1992 a new species of the genus *Neviusia* was discovered in northern California, later named *N. cliftonii* Shevock, Ertter & Taylor (Shevock et al. 1992, Novon 2: 285–289). This new addition to the California flora was particularly interesting because it was a second species of a genus that, until then, included just *N. alabamensis* Gray from the southeastern United States. Renewed interest in *Neviusia* prompted this study of the chromosome cytology of the genus, an undertaking suggested by Stebbins (Fremontia 22(3):11–13, 1993). *Neviusia alabamensis* had first been reported as having a diploid chromosome number of $2n=16$ (Sax, Journal of the Arnold Arboretum 12:3–22, 1931), a count later corrected to $2n=18$ (Sax, Journal of the Arnold Arboretum 13:363–367, 1932). A second count for the species, $2n=14$, was made by Taylor & Deramus (Rhodora 66:274, 1964). The count of $2n=18$ was confirmed by Baldwin (Rhodora 53:203–206, 1951).

New chromosome numbers were obtained for both species of *Neviusia* from mitotic metaphase in root tips harvested from actively growing plants. The methods for the counts were the same as described elsewhere in detail (Goldblatt & Takei, Annals of the Missouri Botanical Garden 80:961–973, 1993): tips were pretreated in aqueous m-bromonaphthalene for four hours at room temperature, then hydrolyzed in 10% HCl at 60° for six minutes after which the excised apical meristems were squashed on glass slides in lactopropionic orcein.

Both species proved to be diploid, $2n=18$, thus with a basic chromosome number of $x=9$. Chromosomes are relatively small and similar in size, (ca.) 2 μm long, and submetacentric to metacentric. Owing to their small size chromosomes could not be matched in pairs and I could not distinguish any karyotypic details. Observations here for *N. alabamensis* suggest that the count of $2n=14$ for the species by Thomas & Deramus is erroneous, or at best atypical of the species. Counts for the immediately related genera *Kerria* and *Rhodotypos*, which together with *Neviusia*, comprise the tribe Kerrieae, are also $2n=18$ (Sax, Journal of the Arnold Arboretum, 13:363–367, 1932). It now seems beyond reasonable doubt that $x=9$ is the basic chromosome number for Kerrieae and that all members of the tribe are diploids with $2n=18$.

Although *Neviusia* is traditionally placed in subfamily Rosoideae of the Rosaceae (e.g., Melchior, A. Engler's Syllabus der Pflanzenfamilien, 1964; Robertson, Journal of the Arnold Arboretum 55:344–401, 1974), the basic chromosome number, $x=9$ for the genus and for Kerrieae, at first appears at odds with this treatment. The most

TABLE 1. CHROMOSOME NUMBER AND VOUCHER DATA FOR SPECIES OF *NEVIUSIA* COUNTED.

Species	Diploid number $2n$	Vouchers
<i>N. alabamensis</i>	18	USA, without precise locality, cultivated at the Missouri Botanical Garden, St. Louis, <i>Dietrich et al.</i> 120 (MO)
<i>N. cliftonii</i>	18	USA, California, Shasta Co., <i>Taylor & Clifton</i> 12513 (JEPS)

common base number in the subfamily is $x=7$ (e.g., Raven, *Annals of the Missouri Botanical Garden* 62:724–764, 1975). A base of $x=9$ does, however, characterize at least the tribes Dryadeae as well as Kerriae of the subfamily, as well as the entire subfamily Spiraeoideae (Raven, *Annals of the Missouri Botanical Garden* 62:724–764, 1975; Goldblatt, 63:200–206, 1976). Although the chromosome number in *Neviusia* thus at first seems discordant in Rosoideae, it is not for Kerriae. There seems no reason to dispute the subfamilial position of Kerriae but it seems worth pointing out that although the traditional view is that $x=7$ is basic for Rosoideae, this number is merely the most common chromosomal base in the subfamily. Most likely the ancestral base number for Rosoideae is $x=9$. Dysploid reduction of the chromosome number to $x=8$ and then to 7 most likely occurred early in the differentiation and radiation of the subfamily.

NOTEWORTHY COLLECTIONS

CALIFORNIA

BRASSICA FRUTICULOSA Cyrillo (BRASSICACEAE).—Los Angeles Co., southern base of the San Gabriel Mtns. in Evey Canyon, just north of San Antonio Dam and Potato Mtn., alt. 700 m, 11 Jun 1993, *Steve Boyd et al.* 8190 (RSA); Riverside Co., Box Springs Mountains, E edge of Riverside, Two Trees Canyon, ca. 20 individuals in a large stand of wildflowers on a one year old burn, 5 Apr 1989, *A. C. Sanders & O. F. Clarke* 9035 (UCR); San Bernardino Co., Ontario, N side of Holt Blvd. just NE of the Ontario Airport, sandy soil in a waste area, 26 Jan 1992, *A. C. Sanders* 12017 (RSA, UCR); Redlands, Santa Ana River Wash, between Orange St. and Church St., 34°06'N, 117°11'W, T1S, R3W, S15, alt. 1200 ft., 18 Jun 1993, *Scott White* 1565D (UCR); San Gabriel Mountains, Cucamonga Creek, T1N R7W S20, alt. 2140 ft., 26 Jan 1994, *Dick Swinney* 2705 (RSA, UCR); San Gabriel Mountains, N of 19th St. in Rancho Cucamonga, ca. ½ mi W of Sapphire St., alt. 1624 ft., 26 Jan 1994, *Dick Swinney* 2713 (RSA, UCR); Muscoy, Hwy 30 (Highland Ave.) at Cajon Wash, 34°10'N, 117°20'W, alt. 365 m, 2 Dec 1994, *A. C. Sanders* 15893 (UCR & to be distributed)

Previous knowledge. Native to Europe, previously introduced into Australia.

Significance. First records for California. Not reported anywhere in North America by R. C. Rollins (*The Cruciferae of Continental North America*, 1993).

This species will key to *Brassica juncea* (L.) Czernov in the *Brassica* treatment in *The Jepson Manual* (R. C. Rollins, in, J. C. Hickman, ed., 1993). It differs from *B. juncea* in that the leaves, especially the upper, are more deeply and consistently lobed; the beak of the fruit is shorter (3–4 mm versus 6–7 mm); the fruits have a strongly “beaded” appearance caused by bulges created by the seeds; and the flowers are smaller (sepals only 3–4 mm versus 5–6 mm). It is also similar to *B. elongata* Ehrh., which has been introduced into Nevada, but differs in that the fruit is not stipitate and the inflorescence is much less highly branched. *B. elongata* looks like a tumbleweed, such as *Sisymbrium altissimum*, whereas *B. fruticulosa* has longer, little-branched, racemose, inflorescence branches.

Brassica fruticulosa is apparently well established along the south foot of the San Gabriel and San Bernardino Mountains and in adjacent interior valleys to the south.

It was first collected in 1989, but was soon thereafter found at scattered localities by several collectors. It appears to have spread rapidly beginning in the late 1980's. The species may also be present, but overlooked, elsewhere in southern California.

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ACHRACHNE RACEMOSA (Roem. & Schult.) Ohwi (Poaceae).—Riverside Co., Palm Springs, Tahquitz debris basin at base of Tahquitz Canyon, off Sunny Dunes Rd., 9 Sep 1991, L. LaPré & M. Phillips 91-18 (UCR). (Determined by J. R. & C. G. Reeder.)

Previous knowledge. Native to the Old World tropics from Africa to Australia, previously introduced to the West Indies (S. Phillips 1974; pg. 258–260, in R. M. Polhill, ed., *Flora of Tropical East Africa.*, illustrated).

Significance. First record for California and the U.S. of this monotypic genus. This annual grass, up to 75 cm tall and resembling *Eleusine* or *Chloris*, should be watched for in moist areas in the Coachella and Imperial Valleys and along the Colorado River.

AEGILOPS CYLINDRICA Host. (Poaceae).—San Bernardino Co., San Bernardino Mtns., Waters Rd. just W of Fernwood Dr., Cedarpines Park, 117°17'W, 34°15'N, T2N R4W S20, alt. 1325 m, locally abundant on roadside in yellow pine forest, 26 Jun 1994, A. C. Sanders 14933 (UCR, & to be distributed).

Previous knowledge. Native to the Middle East, but previously recorded in northern California, on Santa Cruz Island, and at Santa Barbara (G. D. Barbe, *Noxious Weeds of California, Distribution Maps*, CA Dept. of Food and Ag., 1990).

Significance. First record for San Bernardino Co., second for mainland southern California, and a 250 km E range extension.

ATRIplex MUELLERI Benth. (Chenopodiaceae).—Riverside Co., solitary plant on roadside 20 miles west of Blythe, 17 Oct 1965, J. C. Roos s.n. (CAS, COLO, RSA, UCR). (Determined by W. A. Weber.)

Previous knowledge. Native to Australia.

Significance. First record for California; apparently reported from the U.S. only by Kartesz (*A Synonymized Flora of the United States, Canada and Greenland*, Timber Press, 1994), but on what basis and from where is unknown. Recent searching of the collection area has not revealed the species.

BAILEYA MULTIRADIATA Harv. & Gray (Asteraceae).—Riverside Co., Coachella Valley, Indio, remnant dune patch at the edge of the lawn of a commercial strip mall, just SW of the Whitewater River channel at Auto Center Dr., 33°43.3'N, 116°12.3'W, T5S R7E S24, alt. 7 m, almost certainly introduced at this site, probably came with turf grown in Arizona, 12 Mar 1995, A. C. Sanders et al. 16019 (UCR); San Bernardino Co., NE foot of the San Bernardino Mtns., below Terrace Spring, locally common in an open disturbed area near the road, fairly common on an adjacent undisturbed slope, T3N R2E S16, alt. 1375 m, 7 May 1995, A. C. Sanders et al. 16943 (UCR); San Diego Co., Borrego Valley, Hwy S-3, opposite entrance to Ram's Hill Country Club, alt. 230 m, irrigated area, [weed] growing among landscape plants, 3 Apr 1991, R. D. Goeden & J. Teerink s.n. (UCR).

Previous knowledge. Eastern Mojave Desert of San Bernardino Co., W to near Kelso, and to UT, TX and northern Mexico.

Significance. First records for Riverside and San Diego Counties and a range extension within San Bernardino Co. of 130 km SW from Kelso. The Riverside and San Diego Co. populations are associated with landscaped areas and are certainly introduced, but the Terrace Spring population appears native; there is no landscaping or irrigation in the area.

BROMUS SECALINUS L. (Poaceae).—San Bernardino Co., San Bernardino Mtns., Waters Rd. just W of Fernwood Dr., Cedarpines Park, 117°17'W, 34°15'N, T2N R4W S20, alt. 1325 m, yellow pine forest, fairly common along old roads in partial to full sun, 26 Jun 1994, A. C. Sanders 14922 (ARIZ, UCR, & to be distributed); Lake Silverwood, Cleghorn Day Use Area, south side of the lake near mouth of Sawpit Canyon, T2N R4W S6, alt. 1100 m, 12 Jun 1994, A. C. Sanders & P. MacKay 14774 (ARIZ, UCR, & to be distributed). (Det. confirmed by J. R. Reeder.)

Previous knowledge. Native to Europe but introduced widely in N America, previously reported from the central Sierra Nevada and northern California.

Significance. First records for San Bernardino Co. and southern California, and a range extension of about 400 km.

CENCHRUS CILIARIS L. (Poaceae).—Orange Co., along the Newport Freeway (55) at its intersection with Chapman Ave., City of Orange, locally common and vigorous, scattered at least as far south as the Garden Grove Freeway (22), 8 Oct 1983, J. West s.n. (RSA, UCR); Riverside Co., roadside 20 miles west of Blythe, 17 Oct 1965, J. C. Roos s.n. (RSA, UCR).

Previous knowledge. First reported in California by Webster (in J. C. Hickman, ed., *The Jepson Manual*, 1993), but only from Los Angeles Co. Native to Africa, but widely planted as a pasture grass in Mexico and Texas. Fairly common on roadsides in Arizona, including sites along I-10 less than 10 miles E of Blythe.

Significance. First records for Orange and Riverside Counties. This species is well established, though quite uncommon, in southern California. It seems to require summer moisture and so may never become widespread, except in irrigated areas. It is common at the West collection site, but I have been unable to relocate it at the Roos site. In addition to the above specimens, I have seen fragmentary material (not preserved) collected near Indio, Riverside Co. Oddly, both the West and Roos specimens at RSA were annotated by Webster in 1991, but Orange and Riverside were not counties he reported. I don't know the basis for the report from Los Angeles Co. and wonder if it might be an error.

CENTAUREA DIFFUSA Lam. (Asteraceae).—San Bernardino Co., San Bernardino Mtns., Arrowbear Lake, 34°12.69'N, 117°04.61'W, T2N R2W S34., alt. 1890 m, locally common on disturbed slope between lake and parking lot, 21 Aug 1994, A. C. Sanders et al. 15356 (UCR, & to be distributed).

Previous knowledge. A noxious weed introduced from Europe, known from scattered locations in northern California, mostly north of San Francisco, but with one site in Monterey Co. (Barbe 1990).

Significance. First record for San Bernardino Co. and southern California; a range extension of ca. 450 km.

CENTAUREA MACULOSA Lam. (Asteraceae).—San Bernardino Co., San Bernardino Mtns., Hwy 18, turnout ¼ mi. W of Big Bear Lake dam, T2N R1W SE ¼ S21, roadside in mixed yellow pine and canyon live oak forest, alt. 2065 m, 14 Aug 1994, A. C. Sanders et al. 15283 (UCR, & to be distributed).

Previous knowledge. A noxious weed from Europe, known from scattered locations

in California, primarily in northern third of the state; the only known southern population in Julian, San Diego Co. (Barbe 1990).

Significance. First record for San Bernardino Co.

CERATONIA SILIQUA L. (Fabaceae).—Los Angeles Co., Ballona wetlands, adventive in area 1, also seen in area 3, 16 Sep 1980, *R. Gustafson 1927* (RSA); San Jose Hills west of California State Polytechnic University, Pomona, 34°03'32"N, 117°49'53"W, adventive on slopes with *Quercus agrifolia*, *Juglans californica*, *Eriogonum fasciculatum*, *Opuntia littoralis*, *Salvia apiana*, etc., alt. ca. 300 m, 3 Jun 1991, *T. S. Ross & A. H. Ross 5553* (RSA); Riverside Co., Riverside, UCR Botanic Garden, fairly common weed in the Australian section, most plants cut to the ground and resprouting, not allowed to mature sufficiently to flower, T2S R4W SE/4 S29, alt. 400 m, 19 Dec 1995, *A. C. Sanders 17937* (UCR); San Bernardino Co., Santa Ana River wash between Orange St. and Church St., Redlands, 34°06'N, 117°11'W, T1S R3W S15, associated with *Lepidospartum squamatum*, *Eriogonum fasciculatum*, *Sambucus mexicana*, *Brickellia californica*, etc., alt. 365 m, 18 Jun 1993, *Scott White 1565E* (UCR).

Previous knowledge. Native to the Mediterranean and Middle East, commonly cultivated in California.

Significance. First report of naturalized plants in California. Apparently reported from the U. S. only by Kartesz (1994), but from where and on what basis is unknown. This species is commonly spontaneous in urban areas in southern California and is now, for example, one of the worst woody weeds in the UCR and RSA Botanic Gardens. It only rarely escapes into undisturbed habitats, but should be watched for along washes and in other moist places. Also observed naturalized by T. S. Ross (personal communication) on a relatively steep easterly slope in Loop Cyn., W end San Gabriel Mtns., Angeles Nat. Forest (Los Angeles Co.), T3N R15W SE 1/4 S14, alt. 610 m, May 1993.

The fruits are commonly eaten by coyotes which disperse the seeds. In urban areas it germinates in great numbers following application of mulch made from street trees. Spread into natural habitats may be retarded by jackrabbits which eat the foliage and can create a "browse-line" on unprotected trees (O. F. Clarke personal communication), though this effect is not noticable with cottontail rabbits at the UCR Botanic Garden.

CHLORIS TRUNCATA R. Br. (Poaceae).—Riverside Co., Temecula, Drake Enterprises vinyard at Buck Rd. and Berenda Rd., common around the emitters for the drip irrigation system, also present in the adjacent Calaway vinyard, 6 Nov 1995, *V. McAfee-Jacobs & B. R. Drake 1* (RSA, UCR, & to be distributed). (Determined by Travis Columbus.)

Previous knowledge. Native to Australia. Previously reported from Hawaii, but apparently rare there (W. L. Wagner et al., *Manual of the Flowering Plants of Hawai'i*, 1990).

Significance. First record for California and North America. This appears to be an established member of California's growing weed flora; has been present at this location for 7–8 years and becoming common.

CYNANCHUM LOUISEAE Kartesz & Gandhi (Asclepiadaceae).—Riverside Co., Riverside, weed of unknown origin in the UCR Botanic Garden, 5 Sep 1985, *A. C. Sanders 5951* (RSA, UCR).

Previous knowledge. Native of Europe; common as a weed in the eastern U. S.

Significance. First record for California, but has been in Riverside for ca. 20 years. Known as *C. nigrum* (L.) Pers., but see Kartesz & Gandhi (*Phytologia* 71:270, 1991).

EPHEDRA FUNEREA Cov. & Mort. (Ephedraceae).—San Bernardino Co., Hesperia, alt. 915 m, 12 Apr 1919, *P. A. Munz 2517* (POM); ca. 19 miles ESE of Barstow in Newberry Mts., up canyon just W of Newberry, frequent in red rhyolite, alt. 600–900 m, 6 May 1978, *James Henrickson 16805* (RSA); lower slopes of Newberry Mt., just S. of town of Newberry, off Interstate Highway 40, 31 Jul 1984, *Sherwin Carlquist 15821* (RSA); Twentynine Palms Marine Corps Air-Ground Combat Center, NW end of the Lava Bed Mountains, UTM: 11S, NJ-5036, alt. 1000 m, fairly common (1.75% cover) on rocky slopes, 24 Apr 1989, A. C. Sanders & J. Lyman 9049 (RSA, UCR); Twentynine Palms MCACC, W side of Hidalgo Mountain, 34°26.2'N, 116°19.2'W, alt. 915 m, 19 May 1991, *B. Pitzer 1572* (UCR).

Previous knowledge. Death Valley region of California and Nevada and the eastern Mojave Desert of California (H. Cutler, *Ann. Mo. Bot. Gard.* 26:373–428, 1939; P. Munz, *A Flora of Southern California*, 1974). Griffin (in Hickman 1993) reports this from “DMoj” without specific detail, but given the vague range descriptions in the Jepson Manual that is not evidence of records away from the N and E Mojave; it is not known from the W Mojave Desert.

Significance. Range extensions of 100–165 km S and SW from the Avawatz Mtns. in the N Mojave Desert and first reports for the central and southern Mojave Desert. *Munz 2517* was annotated “*Ephedra funerea* Cov. & Mort.?” by Cutler in 1939, but was not cited in his monograph, and it did not influence Munz in range description in his floras (*A California Flora*, 1959; 1974). It was collected so far from the species' known range that it may not have been trusted; additional collections reported here solidify the record.

ERAGROSTIS CURVULA (Schrad.) Nees var. *CONFERTA* Nees (Poaceae).—Riverside Co., Riverside, weed in the UCR Botanic Garden, 27 Jul 1992, *S. Morgan 92-7* (ARIZ, UCR); Riverside, Santa Ana River between the Hwy 60 bridge and Mission Blvd. bridge, 117°23'W, 33°59'N, scarce in sand among rocks in rip-rap, alt. 243 m, 28 Jul 1994, A. C. Sanders & S. Ogg 15183 (ARIZ, RSA, UCR). (Determined by J. R. Reeder).

Previous knowledge. Native to Africa.

Significance. First records in California of this distinctive variety; plantlets in leaf axils make recognition easy.

FATOUA VILLOSA (Thunb.) Nakai (Moraceae).—Riverside Co., Riverside, UCR Botanic Garden, weed in potted plants in the lath house, 7 Oct 1994, A. C. Sanders & S. Morgan 15832 (F, UCR, & to be distributed); same location, scattered and uncommon in potted plants, common until the last few weeks when most were pulled, 30 Nov 1995, A. C. Sanders & S. Morgan 17926 (UCR, & to be distributed); same location, abundant in greenhouse on mist bench, though mostly small seedlings because of weeding of larger plants, A. C. Sanders & S. Morgan 17927 (RSA, UCR).

Previous knowledge. Native to China, Japan and the Ryukyu Islands (J. Liao, *Moraceae*, in *Flora of Taiwan*, 1976). Previously reported from N America as a greenhouse and garden weed in Louisiana (J. Thieret, *Sida*: (4):248, 1964).

Significance. First record for California. Though the specimens were from a lath house and a greenhouse, the plant will doubtless be found outside, probably in irrigated gardens. First noticed in the greenhouse about 1992 (W. Gary personal communication). It has increased considerably despite attempts to eliminate it by hand weeding and is particularly aggressive and fast growing in the greenhouse.

Fatoua resembles some non-stinging Urticaceae, but is placed in Moraceae primarily because of a vestigial second style (A. Cronquist, *An Integrated System of Classification of Flowering Plants*, 1981), but it lacks laticifers. The seeds are shot from the fruits in a manner similar to *Dorstenia* (I've not seen this noted in the literature); this fact might suggest affinities to that herbaceous member of Moraceae, and will certainly be of assistance in identification when live material is available.

LINANTHUS ORCUTTHI (Perry & Gray) Jeps. (Polemoniaceae).—San Bernardino Co. [all eastern San Bernardino Mtns.], Burns Reserve in piñon woodland on rocky, desert, hills, alt. ca. 1225 m, 22 Apr 1973, *O. F. Clarke s.n.* (UCR); Broom Flats, T2N R2E S25, alt. 2140 m, in open pinyon woodland on hills surrounding meadow, 20 May 1980, *T. Krantz s.n.* (UCR); Pioneertown Rd., 1.9 mi. N of Yucca Valley, 2.1 mi. S of Pioneertown, 34°08'N, 116°28'W, T1N R5E S ½ S29 & N ½ S33, alt. 1125 m, sandy wash, 30 Apr 1995, *A. C. Sanders, G. & L. Helmkamp 16843* (UCR). (Clarke and Krantz collections determined by R. W. Patterson and T. P. Krantz).

Previous knowledge. San Diego Co. and northern Baja California, and perhaps just entering Riverside Co. near Mt. Palomar.

Significance. First records for San Bernardino Co. and a range extension of 100 km NNE from Mt. Palomar. These records also extend the elevation limits given by Patterson (in Hickman 1993) by 320 m; from 1300–2000 to 1125–2145 m. This plant, listed as rare and endangered by CNPS (*Inventory of Rare and Endangered Vascular Plants of California*, Skinner & Pavlik, 1994), should be sought in the San Jacinto Mtns., Riverside Co.

MATRICARIA GLOBIFERA (Thunb.) Fenzl in Harv. & Sond. (Asteraceae).—Riverside Co., Lake Perris State Recreation Area, Moreno Beach Rd., 1.75 mi. from northern entrance gate, alt. 490 m, coastal sage scrub, 19 May 1981, *P. Schiffman 2* (UCR); same area, south side of lake, opposite Allesandro Island, 490 m, 9 May 1989, *D. Concannon s.n.* (UCR); Box Springs Mountains, alt. 735 m, coastal sage scrub, 19 May 1981, *K. M. Kummer s.n.* (UC, UCR); San Jacinto Wildlife Area, ca. 1 km northwest of Lakeview [E of Lake Perris], T4S R2W SE ¼ S6, alkali playa community, alt. 433 m, 6 May 1992, *D. Branlet 2265* (UCR); San Jacinto Wildlife Area, ca. 2 km northeast of Lakeview, T4S R2W NW ¼ S5, alt. 433 m, 8 Jun 1995, *D. Branlet 2434* (RSA, UCR). (Kummer collection determined by John Strother.)

Previous knowledge. Native to southern Africa.

Significance. First records for California and N America. Well established and common at Lake Perris, especially in campgrounds and on roadsides. Given high visitor use of this area, it appears probable that this plant will be dispersed widely in southern California. I believe the Kummer collection to be mislabeled; it almost certainly came from Lake Perris and may be part of the Schiffman collection (same date). I've not found this plant in the Box Springs Mtns. despite years of collecting.

MELICA CALIFORNICA Scribn. (Poaceae).—San Bernardino Co., San Bernardino Mtns., Pisgah Peak Rd., ca. 1.5 km above Oak Glen Rd., NW foot of Pisgah Peak, T1S R1W SW ¼ S33, alt. 1100 m, edge of chaparral, 14 May 1993, *A. C. Sanders & E. J. Lott 14041* (UCR).

Previous knowledge. Northern California, south to the mountains of Kern Co. and the Sespe Creek area of Ventura and Santa Barbara Counties (C. F. Smith, *A Flora of the Santa Barbara Region, California*, 1976).

Significance. First record for San Bernardino Co. and a range extension 250 km SE from the Tehachapi Mtns. and 300 km ESE from the Sespe Cr. area. The plants found fit var. *nevadensis* Boyle as described by Munz (1959) and Barkworth (in Hickman 1993).

MELISSA OFFICINALIS L. (Lamiaceae).—San Bernardino Co., San Bernardino Mtns., Miller Cyn. (Mojave River) below Pilot Rock Camp, T2N R4W S10, alt. 1200 m, fairly commonly naturalized on banks of the stream, 19 Jun 1994, *A. C. Sanders 14814* (UCR).

Previous knowledge. Native to Europe. Cultivated garden herb in California. Reported naturalized only in N California by Wilken (in Hickman 1993) and by Munz

(1959; 1974), but recently reported from the Santa Ana Mtns. (Boyd et al., *Aliso*, 14: 105-108, 1995).

Significance. First record for San Bernardino Co. and second locality for southern California. Also reproduces spontaneously in gardens, as in Riverside.

PANICUM ANTIDOTALE Retz. (Poaceae).—Inyo Co., China Ranch along the Amargosa River near the San Bernardino Co. line, alt. 460 m, 16 Oct 1973, *G. Helmkamp, O. F. Clarke, & J. Derby s.n.* (UCR). (Determined by J. R. Reeder.)

Previous knowledge. A noxious weed, introduced from India. Naturalized in TX, AZ, and at three scattered localities in irrigated areas in the deserts of southern California, one each in Imperial, Riverside and San Bernardino Counties (Barbe 1990).

Significance. First Inyo County locality and a 150 km range extension NE from the vicinity of Barstow. This locality is very close to the county line, the label actually reads "San Bernardino Co." but the China Ranch buildings are in Inyo County, and George Helmkamp's recollection is that none of the collections were made south of the ranch buildings. Helmkamp is doubtless correct and an error was evidently made when the label was prepared. Other collections at UCR, from the same trip, have labels reading "China Ranch, San Bernardino-Inyo Co. line", or some variant of that. Labels were typed at different times by different typists; formats vary.

PANICUM MAXIMUM Jacq. (Poaceae).—Riverside Co., Riverside, UCR Botanic Garden, alt. 500 m, locally common perennial weed, 3 Sep 1991, *A. C. Sanders & O. F. Clarke 11159* (ARIZ, RSA, UCR). (Determined by John R. Reeder.)

Previous knowledge. Presumed native to Africa, but widely cultivated in the tropics, notably Mexico, as a pasture grass.

Significance. First record for California. Well established at this location, had been present for several years at the time of collection, and still present and common in 1996.

PISTACIA ATLANTICA Desf. (Anacardiaceae).—Riverside Co., Riverside, scattered on NE facing granitic slopes of Mt. Rubidoux, 33°59'N, 117°23'W, alt. 400 m, coastal sage scrub, 15 May 1994, *A. C. Sanders 14480* (UCR, & to be distributed); Cherry Valley, naturalized in landscaping at Edward-Dean Museum on Oak Glen Rd., 1 mi. N of Orchard St., 33°59'N, 116°58'W, alt. 1000 m, no cultivated individuals in the immediate area, dispersed from elsewhere, 11 Jul 1994, *A. C. Sanders 15060* (UCR); San Bernardino Co., Oak Glen Creek wash, ca. 0.5 mi S of Oak Glen Rd. and 1.4 mi E of Bryant St., 34°02'N, 117°01'W, alt. 915 m, coastal sage scrub, 25 Apr 1987, *B. Pitzer 502* (UCR).

Previous knowledge. Native from N Africa to the eastern Mediterranean and Pakistan. Fairly commonly cultivated in California as an ornamental and as a rootstock for *Pistacia vera* L. Reported naturalized in northern California ("ScV") by Wilken (in Hickman 1993). Not reported for N America by Kartesz (1994).

Significance. First records of naturalized plants in Riverside and San Bernardino Counties, and in southern California. Becoming naturalized on dry slopes in interior southern California. Also common at the margins of cultivated areas and is one of the worst woody weeds in the UCR Botanic Garden. Reproduces readily from seed and is apparently dispersed by birds. Most plants are relatively young, vigorous, and reproducing freely. They appear to represent the incipient stages of a biological invasion that may well have an influence on the structure of the vegetation on the coastal slope of southern California. This species occurs at much higher elevations, 400–1000 m, in southern California than reported by Wilken (in Hickman 1993) for northern California (<100 m).

SCHINUS POLYGAMUS (Cav.) Cabr. (Anacardiaceae).—Los Angeles Co., Claremont, Rancho Santa Ana Botanic Garden, spontaneous on east edge of Indian Hill Mesa, alt. 410 m, 24 Nov 1991, *T. Ross & S. Boyd s.n.* (RSA); same area, T1S R8W SW 1/4 S3, alt. 415 m, weedy shrub occurring sporadically around the grounds, 15 Nov 1991, *T. Ross s.n.* (RSA); Riverside Co., Riverside, UCR campus, common weedy shrub in hedges and on brushy slopes at the margins of cultivated areas, 33°58'N, 117°19'W, T2S R4W S29, alt. 335 m, 5 Dec 1995, *A. C. Sanders & G. Helmkamp 17929* (UCR, & to be distributed); Riverside, common in an abandoned orange orchard on Spruce St. just E of Rustin Av., 33°59'N, 117°20'W, T2S R4W S18, alt. 300 m, 5 Dec 1995, *A. C. Sanders & G. Helmkamp 17930* (UCR, & to be distributed); Riverside, 4081 Glenwood, shrubby small tree, "perhaps spontaneous", Oct 1985, *Alden Kelly s.n.* (RSA, UCR); San Bernardino Co., Chino Hills, naturalized on roadside of Hwy 142 (Carbon Canyon Rd.), 33°56'N, 117°45'W, alt. ca. 300 m, Apr 1992, *K. Kirtland s.n.* (UCR); Ontario, volunteer in yard, alt. 320 m, 24 Nov 1991, *T. S. Ross 6028* (RSA).

Previous knowledge. Native to Chile and Argentina. Cultivated as an ornamental in California.

Significance. First records of naturalized plants in California, but widely established in urban areas in inland southern California. This species is probably more common as an escapee than it is as an ornamental; not commonly grown because it is somewhat spiny but otherwise nondescript. Tends to occur in slightly moist sites and is frequently found in abandoned groves and at untended margins of disturbed or cultivated areas receiving irrigation runoff. This is among the worst woody weeds in the UCR Botanic Garden. It may become a problem in natural communities in the moister areas toward the coast and in the northern parts of the state, but it has so far shown little tendency to invade the drier hillsides around Riverside. It appears less well adapted to aridity than *S. molle* L., which is fairly common. Conversely, it naturalizes in the Riverside area much more commonly than *S. terebinthifolia*. Raddi., which is infrequent as an escapee, but common as an ornamental. Apparently reported in the U. S., only in the checklist of Kartesz (1994).

SCHOENUS NIGRICANS L. (Cyperaceae).—San Bernardino Co., Avawatz Mtns., abundant at a spring 3 miles SE of peak 1876, 30 Sep 1994, *G. F. Pratt & C. Pratt s.n.* (UCR, & to be distributed); Arrowhead Hot Springs, 34°11.5'N, 117°16'W, T1N R4W S11, alt. 600 m, 27 Apr 1993, *A. C. Sanders et al. 13832* (UCR).

Previous knowledge. Widespread in the northern hemisphere, but rare and spotty in N America, and especially so in California. In California known only from scattered springs in the Death Valley region of Inyo Co., from Arrowhead Hot Springs, San Bernardino Mtns., and from a single marshy spring in Lone Pine Cyn., San Gabriel Mtns. The latter two locations are in SW San Bernardino Co. on the coastal slope of southern California. Reported by Dedecker (*Flora of the Northern Mojave Desert, California*, 1984) from the Grapevine, Black and Inyo Mtns., and has also been collected in the Funeral Mtns.

Significance. First report for Mojave Desert south of Inyo Co., range extension of ca. 80 km SSE from the Black Mtns.; first collection since 1924 at Arrowhead Hot Springs, a location where most local botanists thought it extirpated. This species is not listed in the CNPS Inventory (Skinner and Pavlik 1994) but should probably be included in list 2 (rare and endangered in California, more common elsewhere).

SCRIBNERIA BOLANDERI (Thurb.) Hack. (Poaceae).—San Bernardino Co., San Bernardino Mtns., Summit Valley on Hwy 173, 1 mi. S of the Grass Valley Cr. crossing, 117°16'W, 34°19'N, T3N R4W SW/4 S26, alt. 1000 m, moist gully in an opening in chaparral, 24 Apr 1993, *A. C. Sanders & H. Spilman 13775* (MO, RSA, SBBG, SD, UC, UCR); same location, dried seep on roadside bank, 23 Apr 1993, *A. C. Sanders et al. 13767* (ARIZ, CAS, RSA, SBBG, SD, UCR, US).

Previous knowledge. Washington to northern California, south to Santa Barbara Co., also reported from San Diego Co. (Zedler et al., *Madroño* 34(4):381, 1987), very recently from the Santa Ana Mtns (Boyd et al. 1995), and from one locality in Baja California (Zedler et al. 1987).

Significance. First records for San Bernardino Co. and a range extension of 220 km E from the Santa Ynez Mountains near Santa Barbara and 90 km NNE of the recently reported Santa Ana Mtns. locality. Worley (in Hickman 1993) says this is a species of "dry, disturbed areas," but based on its habitat in San Bernardino Co., and on the available label data at RSA and UCR, it appears instead to favor vernal moist seeps and ephemeral streams. Zedler et al. (1987) report it from the margins of vernal pools. Many specimens from northern California (e.g., *L. C. Wheeler 3500*, Siskiyou Mts, Siskiyou Co.—"low sunny site wet in spring, soil heavy") were taken in habitats very similar to those occupied in southern California. Local floras, if they give ecological notes on this species, make similar observations (e.g., R. F. Hoover, *The Vascular Plants of San Luis Obispo County, California*, 1970; J. T. Howell, *Marin Flora*, 1970; Smith 1976).

SENNA OBTUSIFOLIA (L.) Irwin & Barneby. (Fabaceae).—Riverside Co., south of Blythe in Paloverde Valley, 1 mi. N of the Imperial Co. line, 2 sterile plants in a 40 acre cotton field, 25 Jul 1989, *Les Ede s.n.* (RSA, UCR); same area, scarce weed in cotton fields, 19 Aug 1989, *Les Ede s.n.* (MO, NY, RSA, SD, UCR). (Determined by R. Barneby.)

Previous knowledge. A widespread weed of the neotropics, common in tropical and subtropical Mexico, occurring as far north as Baja California and Sonora. Occurs in Hawaii and the central and eastern U.S.

Significance. First records for California. Plants, while few in number, were vigorous and obviously doing well under the environmental conditions of the Colorado River Valley. The collector noted that they were up to 2 m tall and had a habit similar to *Sesbania*. The sterile plants found in July were destroyed at the time of collection and pieces sent to UCR. Better material was requested and a few more plants, with flowers and fruits, were found a month later. Agricultural areas along the Colorado River receive very little attention from collectors and doubtless support undetected populations of this and other tropical weeds.

SOLANUM MAURITIANUM Scop. (Solanaceae).—Riverside Co., Riverside, edge of an orange orchard and a light industrial area on Rustin Av., T2S R4W SE ¼ S18, alt. 300 m, 30 Nov 1995, *A. C. Sanders 17928* (UCR, & to be distributed); San Bernardino Co., Redlands, abandoned orange orchard on the NW side of Hillside Cemetery, T2S R3W S3, small tree scattered through the orchard, alt. 490 m, 29 Dec 1984, *A. C. Sanders 5355* (MO, RSA, UCR). (5355 determined by W. G. D'Arcy).

Previous knowledge. Native to Argentina. Uncommonly cultivated as an ornamental in southern California. Widely naturalized in warm regions, including southern Asia, Australia, Hawaii, and Florida.

Significance. First records of spontaneous plants in California. This weak tree is occasionally naturalized in moist untended areas in the vicinity of Riverside and San Bernardino. It is particularly characteristic of neglected citrus orchards, but also appears in yards and hedges. It has been observed as an urban weed in Pasadena, Los Angeles Co. (O. F. Clarke personal communication). It should be watched for in riparian areas in southern California, where it might become established. Probably dispersed by fruit-eating birds.

TRITELEIA HYACINTHINA (Lindl.) E. Greene (Liliaceae).—San Bernardino Co., San Bernardino Mtns., Water Canyon off Wildwood Canyon, T2S R1W N ½ S9, alt. 1000

m, scarce at edge between oak woodland and annual grassland, 14 May 1993, A. C. Sanders & E. J. Lott 14036 (UCR).

Previous knowledge. Northern California, south in the coast ranges to about the San Luis Obispo/Monterey Co. line.

Significance. First record for San Bernardino Co. and a range extension of 400 km SE.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany & Plant Sciences, University of California, Riverside, CA 92521.

SINALOA

MICROMERIA BROWNEI (Sw.) Benth. (Lamiaceae).—Uncommon annual in mud in irrigation runoff, vic. Bacorehuis, 4.5 km (by air) SE of Agiabampo, 26°14'55"N, 109°06'25"W, 10 m, *Friedman 062-94* (17 March 94, ASU, det. B. L. Turner).

Previous knowledge. Widespread in tropical america in woods and along ditches in US from southern Texas to Florida, in Mexico from Nuevo Leon, Tamaulipas, south to Yucatan, Dominican Republic, West Indies.

Significance. First Sinaloan locality.

SONORA

BRICKELLIA BRANDEGEI B. L. Rob. (Asteraceae).—Steep rocky slopes, Sierra Bojihua-came, SE of Obregón, 270–650 m, *H. S. Gentry 14508* (17–25 Oct 1954, ARIZ); N of Sierra de la Cebollita, 1.9 km NW of Nuri, *Sanders 2695* (8 Apr 1982, ARIZ, UC, UCR, UTEP, ann. from *B. Californica* by R. K. Van Devender); rock quarry, Cerro Bayajuri, ca. 18 km ESE of Villa Juarez, 27°04'40"N, 109°40'20"W, 100 m, *P. S. Martin s. n.* (28 Dec 1985, ARIZ, det. R. K. Van Devender); common on roadside cliffs, Cerro Onteme, 3.5 km S of Vicam, 27°36'20"N, 110°17'W, 100 m, *Sanders 8777* (13 Dec 1988, ARIZ, DAV, MO, RSA, SD, UCLA, UCR, TEX, ann. from *B. californica* (T. & G.) A. Gray by R. K. Van Devender); common on rocky roadcut, Cerro Prieto, ca. 14.5 km E Navojoa, in foothills thornscrub, 27°05'N, 109°17'05"W, 300 m, *Van Devender 92-725*, *Friedman* (4 Jul 1992, ARIZ, ASU, TEX, UCR); solitary shrub on rock face in tropical deciduous forest, Cerro Piedra Boluda, ca. 1 km NE of El Rincon Viejo, ca. 4.5 km N of Alamos, 27°04'10"N, 108°56'15"W, 720 m, *Van Devender, López E., Yetman* (13 Apr 1994, ARIZ, TEX, UCR, USON, det. B. L. Turner); In foothills thornscrub, Cerro La Antena, 1 km N of Microondas La Cabaña, 27°27'45"N, 109°46'20"W, 450 m, *Van Devender 94-612*, *Yetman* (19 Sept 1994, ARIZ, ASU); common 0.5 m tall subshrub on roadside cliffs in tropical deciduous forest, 4 km NW of Tepoca on Mex. 16, Mpio. de Yécora, *Van Devender 95-499*, *Reina G.* (7 May 1995, TEX, USON, det. B. L. Turner).

Previous knowledge. Baja California.

Significance. First Sonoran records.

CORDIA GLOBOSA (Jacq.) H. B. K. (Boraginaceae).—Solitary shrub in periodically flooded flats, Arroyo Jeberojacquia at Camahuiroa-Estero Bamocha road, 6.5 km S Camahuiroa, 26°29'20"N, 109°15'15"W, 5 m, *Friedman 245-94* (15 Aug 1994, ARIZ, ASU, BCMEX, UCR).

Previous knowledge. Sinaloa and Durango to Oaxaca, Veracruz and Yucatán, West Indies, Central and South America.

Significance. First Sonoran record.

BROMELIA ALSODES St. John (Bromeliaceae).—Colony in narrow canyon bottom,

hills W of Piedras Verdes, S of Presa Mocúzari (Adolpho Ruíz Cortínez), 27°08'06"N, 109°01'07"W, ca. 350 m, *Jenkins 89-124* (25 Dec 1989, ARIZ, MEXU); colony ca. 4 m across beneath *Celtis pallida* and *Ziziphus amole* in dense thornscrub on fine-textured soil, 22.3 km SE of Alamos on rd to El Zapote, 26°52'53.9"N, 108°50'48.7"W, 210 m, *Felger 94-140* (20 Mar 1994, ARIZ, MEXU).

Previous knowledge. Sinaloa, S Nayarit, Oaxaca, Veracruz, San Luis Potosí, Tamaulipas, Yucatán and Central America.

Significance. First Sonoran records.

SELENICEREUS VAGANS (K. Brandegee) Britt. & Rose (Cactaceae).—Dense epiphytic clumps 2–3 m above ground in *Havardia sonorae* and *Sideroxylon occidentale*, Huasaguarí, Arroyo Las Rastras between Masiaca and San Antonio de Las Ibarras, 26°50'55"N, 109°09'05"W, 140 m, *Van Devender 93-991*, López E., Yetman (22 Sept 1993, ARIZ, ASU, TEX, UCR, USON, det. A. D. Zimmerman); a few in *Prosopis glandulosa*, 2.0 km S of Arroyo El Mentidero on San Vicente road, 13 km (by air) S of Alamos, 26°54'N, 108°55'25"W, 240 m, *Van Devender 94-823* (30 Oct 1994, ARIZ); El Paso on Río Cuchujaqui, 26°40'35"N, 108°49'30"W, 150 m, *Van Devender 95-104A*, Reina G., Yetman (25 Feb 1995, USON); dense clump 4 m above ground in *Diospyros sonorae*, Arroyo Camahuiroa, 2.2 km (by air) NE Camahuiroa, 26°33'N, 109°15'30"W, 15 m, *Friedman 264-95* (7 Aug 1995, ASU, DES).

Common names are *sina volador* (Spanish) and *cuenoji* (Mayo).

Previous knowledge. W coast of México, type from Mazatlán, Sinaloa.

Significance. First Sonoran collections.

CAPPARIS FLEXUOSA (L.) L. (Capparidaceae).—Rare tall shrub on sandy yellow soil, Masiaca, Mpio. de Navojoa, 26°46'N, 109°13'W, 10 m, *P. Tenorio L. 13685* (28 May 1987, ARIZ, MEXU); uncommon shrub in coastal thornscrub, Arroyo Jeberojaquia, 6.8 km S of Camahuiroa, 26°29'20"N, 109°15'15"W, 5 m, *Friedman 162-94* (25 Jun 1994, ARIZ, ASU, BCMEX); common sprawling shrub in coastal thornscrub, Arroyo Camahuiroa, 2.2 km (by air) NE of Camahuiroa, 26°33'N, 109°15'30"W, 15 m, *Friedman 170-94* (26 Jun 1994, ARIZ, ASU, BCMEX, USON).

Mayo common name is *tabareca*.

Previous knowledge. Widely distributed in tropical America, in México from Tamaulipas to Sinaloa, Colima, and Yucatán.

Significance. First Sonoran records.

IPOMOEA IMPERATI (Vahl.) Griseb. (Convolvulaceae).—Prostrate perennial vine common in beach sand, Camahuiroa, 26°31'N, 109°16'W, *Van Devender 92-1067* (8 Oct 1992, ARIZ, FAU, UCR, det D. F. Austin).

Previous knowledge. Pantropical distribution, along beaches.

Significance. First Sonoran record.

OPERCULINA PENNATIFIDA (H.B.K.) O'Don. (Convolvulaceae).—Uncommon perennial vine in *Erythrina flabelliformis* to 6 m, 6.8 km S Camahuiroa to jct. with Arroyo Jeberojaquia, 10 km W-SW Melchor Ocampo, 26°29'20"N 109°15'15"W, 10m, *Friedman 435-94* (20 Oct. 1994, ASU, FAU), Det. D. Austin.

Previous knowledge. Texas through eastern Mexico, south to Guatemala, and in Sinaloa, and Michoacan.

Significance. First Sonoran record.

DOYEREA EMETOCATHARTICA Gros. (Cucurbitaceae).—Rocky hillside, vic. Cerrillos,

26°29'N, 109°07.5'W, 40–70 m, *H. S. Gentry 14399* (3 Oct 1954, ARIZ); uncommon vine to 2 m, vic. Sirebampo, 9.5 km S on Mex 15 from Las Bocas Road turnoff, 3.5 km W on Sirebampo Road, 26°38'45"N, 109°15'15"W, 35 m, *Friedman 372-93* (26 Dec 1993, ASU); coastal flats 0.35 km S of road to Las Bocas at a point 8.6 km W of Hwy 15, 26°46'N, 109°17'W, 60 m, *Sanders 14476* (9 Apr 1994, UCR); rocky slope at base of Cerro Tasiroguojo in foothills thornscrub, 1 km W Francisco Sarabia, 26°30'40"N, 109°07'35"W, 80 m, *Friedman 157-94* (24 Jun 1994, ASU).

Previous knowledge. México (Oaxaca, Guerrero, Sinaloa, Veracruz), Guatemala, Columbia, Dominican Republic, West Indies, Nicauragua, Puerto Rico, Venezuela, Virgin Isles, St. Croix, Lesser Antilles, and Netherlands Antilles.

Significance. First records for Sonora.

MOMORDICA CHARANTIA L. (Cucurbitaceae).—Common herbaceous perennial vine with bright orange fruits, 2–3 m high in shrubs along Río Mayo, Chihuahita Park at Mex. 159, 3 km (by air) WNW of Navojoa, 27°06'15"N, 109°29'W, 40 m, *Friedman 463-94* (21 Oct 1994, ARIZ, ASU).

Previous knowledge. An Old World native widely introduced in the New World tropics.

Significance. First Sonoran record.

BERGIA TEXANA (Hook.) Seub. (Elatinaceae).—Dried pools 6 km SW of Hwy 15 on road to Camahuira, 8 km E of Camahuira, 26°33'N, 109°12.5'W, 30 m, *Sanders 13525* (21 Mar 1993, UCR).

Previous knowledge. Southern US from California to Texas, Baja California and Nuevo Leon in México.

Significance. First record for Sonora.

CAESALPINIA SCLEROCARPA Standl. (Fabaceae).—Occasional tree, Arroyo Camahuira, 2.2 km NE of Camahuira, 23°33'05"N, 109°15'10"W, 15 m, *Friedman 168-94* (26 Jun 1994, ARIZ, ASU, NY, det. R. C. Barneby) and *Friedman 337* (21 Sept 1994, ARIZ, ASU).

Common names are *éban*, *palo freno* (Spanish), and *tubchi* (Mayo).

Previous knowledge. Sinaloa to Oaxaca.

Significance. First Sonoran record.

MIMOSA ASPERATA L. (Fabaceae).—Common in moist ditch, W edge of Talamante, 2 mi E of Bacobampo, 30 m, *Sanders 8957* (17 Dec 1988, RSA, UCR); rare 3 m tall shrub along coastal canal, 3.2 km N of Jecopaco on Calle 24, 13.5 km NE of Villa Juarez, 27°13'35"N, 109°46'30"W, *Friedman 005-94* (13 March 94, ARIZ, ASU, BCMEX); common in remnant marsh, NE side of Cerro Bayajuri, 27°05'N, 109°39'W, 30 m, *Sanders 14412* (6 Apr 1994, UCR); 3 m shrub in dense thickets on banks of Río Mayo, Chihuahita Park at Mex 159, 3 km (by air) WNW of Navojoa, 27°06'15"N, 109°29'W, 40 m, *Friedman 415-94* (21 Oct 94, ASU); 1.8 mi S Huatabampo on road to Etchoropa, 0.6 mi S of jct Hwy 178, 26°47.5'N, 109°39'W, 5 m *M. Fishbein 1973* (26 Dec 94, ARIZ); edge of Río Mayo, Etchojoa, 26°54'55"N, 109°39'30"W, ca. 10 m, *Van Devender 95-282*, *Reina G.*, *Yetman* (14 Apr 1995, ARIZ, ASU, NY, UCR, USON), dets. P. D. Jenkins & R. C. Barneby.

Spanish common names are *rama dormilera*, or *rama dormilona*.

Previous knowledge. Atlantic coast from Texas to Nicaragua, Sinaloa, Nayarit, Michoacán, Guatemala, and Cuba. Collections from México have generally been called *M. pigra* L.

Significance. First Sonoran records.

PHOLISMA CULIACANUM (Dressler & Kuijt) Yatskievych (Lennoaceae).—Tropical deciduous forest, La Higuera, N of Alamos, 27°6.7'N, 108°57.5'W, 300 m, *Meyer s. n.* (6 Jul 1990, ARIZ); mixed oak-tropical deciduous forest, Ranchito, Arroyo Santa Barbara, 27°07'N, 108°43.2'W, 1000 m, *Jenkins 90-162* (6 Oct 1990, ARIZ); scattered on volcanic slope, in foothills thornscrub, Cerro Terucuchi, ca. 3 km N of Teachive de Masiaca, Mpio. de Navojoa, 26°48'50"N, 109°12'55"W, 120 m, *Van Devender 93-894*, *López E.*, *Yetman* (21 Sept 1993, ARIZ, ASU, MO, UCR, USON); rare in tropical deciduous forest, El Rincón Viejo, ca. 3.4 km N of Alamos, 27°03'55"N, 109°56'W, 480–520 m, *Van Devender 93-1074*, *López E.*, *Yetman* (23 Sept 1993, ARIZ, ASU); in sandy-clay soil under *Prosopis* along Arroyo Masiaca, Teachive, Mpio. de Navojoa, 26°47'10"N, 109°14'W, 75 m, *Van Devender 94-677*, *Yetman* (21 Sept 1994, ARIZ, CAS, TEX); rare in coastal thornscrub, 1.0 km S of Sirebampo, 23°37'30"N, 109°15'30"W, 40 m, *Van Devender 95-1071*, *Reina G.* (26 Sept 1995, ARIZ, RSA); in sandy flat, possibly on *Ambrosia* roots on sandy flat in *Prosopis-Sabal* community, Mpio. Ures, Rancho La Noria Aguilareña, ca. 20 km N of Ures, 29°35'N, 110°23'W, 530 m, *E. Joyal 2577* (20 Oct 1995, ASU).

Called *hongo* and *lilita* (Spanish). Mayo Indians do not eat this species unlike the O'odham (Papago) of northwestern Sonora who formerly ate *P. sonorae*.

Previous knowledge. Endemic to the W slope of the Sierra Madre Occidental from 50–500 m, in Sinaloa and Sonora.

Significance. New records and elevational extension for a little-known holorrhizoparasitic species.

NESAEA LONGIPES A. Gray (Lythraceae).—Dried pools 6 km SW of Hwy 15 at Ejido Diez de Abril on road to Camahuiroa, 8 km E of Camahuiroa, 26°33'N, 109°12.5'W, 30 m, *Sanders 13530* (21 Mar 1993, UCR, det. S. Graham) and *Friedman 295-94* (19 Sep 1994, ARIZ, ASU, det. S. Graham); vic. Sirebampo, from a point 9.5 km S on Mex 15 from Las Bocas Road turnoff, 3.7 km SW of Mex 15, 26°38'N, 109°14.5'W, 30 m, *Friedman 079-95* (19 Jan 1995, ASU).

Previous knowledge. South central Texas, southeastern New Mexico, and Coahuila.

Significance. First records for Sonora.

MALPIGHIA GLABRA L. (Malpigiaceae).—Uncommon sprawling shrub, 2.5 mi W Mexico Hwy 15 on Hwy 176 in coastal thornscrub, 26°50'N, 109°24'W, 40 m, *Van Devender 92-1050*, *Sanders*, *Meyers* (7 Oct. 1992, ARIZ, CAS, TEX, UCR), dets. P. D. Jenkins and B. Anderson.

Previous knowledge. Known from Nuevo Leon and Tamaulipas to Tabasco and Yucatan. Southern Texas, Central America, West Indies, and northern South America.

Significance. New record for Sonora.

BASTARDIA VISCOSA (L.) H.B.K. (Malvaceae).—Locally common subshrub in sandy wash in coastal thornscrub, near Camahuiroa, 26°31'N, 109°16'W, 10 m, *Van Devender 93-276*, *Friedman* (15 Mar 1993, ARIZ, ASU, TEX, UCR, det. P. A. Fryxell).

Previous knowledge. From S Texas to the Gulf Coast in México, the West Indies and Perú.

Significance. First Sonoran records.

OKENIA HYPOGEA Schl. & Cham. (Nyctaginaceae).—Common perennial herb with subterranean fruits, in beach sand at Camahuiroa, 26°31'N, 109°16'W, *Van Devender 92-1069*, *Friedman*, *Meyer* (8 Oct 1992, ARIZ, NMSU, UCR, det. R. Spellenberg); 11 km WNW of Melchor Ocampo, Mpio. de Huatabampo, 26°32'45"N, 109°17'25"W, *Friedman 344-93*, *Steinmann*, *Van Devender* (24 Nov 1993, ASU, BCMEX); and *Friedman 200-93* (20 Jul 1993, ASU, BCMEX).

Previous knowledge. In Florida, Sinaloa, Colima, Oaxaca, Veracruz, and Nicauragua.
Significance. First Sonoran locality.

OENOTHERA DRUMMONDII Hook. var. *THALASSAPHILA* (Brandege) Munz (Onagraceae).—Fairly common perennial herb on sandy beach, Camahuiroa, 26°32';35"N, 109°17'31"W, *Van Devender 92-1069 Friedman, Meyer* (23 Jul 1992, ARIZ, ASU, CAS, MO, SD, TEX, UCR), and *Friedman 202b-93* (20 Jul 1993, ASU).

Previous knowledge. This species occurs along the coast of Gulf of México from Florida and Texas S to Veracruz; widely introduced elsewhere. *O. drummondii* var. *thalassaphila* occurs only in S Baja California.

Significance. First Sonoran locality.

OPHIOGLOSSUM NUDICAULE L. f. (Ophioglossaceae).—Locally common in moist depression on steep volcanic ash slopes, Palm Canyon, 25 km SE of Magdalena on Cucurpe road, Cerro Cinta de Plata, 30°21'N, 111°48'W, ca. 1200 m, *Van Devender s. n.* (14 Aug 1983, ARIZ, det. W. H. Wagner, Jr.); locally common in 5 m² area in coastal thornscrub, 3.3 km SSE of Camahuiroa, Laguna Barochipa, 26°31'N, 109°16'20"W, near sea level, *Steinmann 93-372, Friedman, Meyer, Van Devender* (23 Nov 1993, ARIZ, MO, det. W. H. Wagner, Jr., & G. Yatskievych); locally common in 2 m² area on red clay soil in tropical deciduous forest along trail from Parque El Chalotón to La Huerta, N side of Sierra de Alamos, ca. 2–3 km SW of Alamos, 27°00'N, 108°57'30"W, ca. 700 m, *Steinmann 94-63* (20 Aug 1994, ARIZ, MEXU); uncommon in moist soil depression on open rocky slope in tropical deciduous forest, Las Piedras Canyon, NE corner of Sierra de Alamos, 3.2 km (by air) S of Alamos, 26°59'20"N, 108°56'45"W, 550 m, *Van Devender 95-1136, Reina G.* (3 Oct 1995, ARIZ).

Previous knowledge. Southeastern US south to Central and South America, West Indies, South Africa, Australia, and tropical Asia. Widespread in México as far north as Sinaloa and Durango.

Significance. First Sonoran localities.

LUZULA GRACILLIMA Prodoehl (Poaceae).—Locally common emergent from shallow water in scattered pools and in wet sand in broad boulder-filled wash, Arroyo El Tigre, 2.8 km SE of Rancho El Tigre, ca. 1.5 km E of México 15 at 11 km N of junction with road to Bahía San Carlos, 28°05'N, 110°56'30"W, ca. 35 m, *Felger 85-1486* (22 Nov 1985, ARIZ, MEXU); locally abundant perennial in muddy depression in coastal thornscrub, 2.5 km W of Tierra y Libertad, 26°30'N, 109°30'W, 15 m, *Friedman 292-94* (19 Sept 1994, ARIZ, ASU, BCMEX); dets. J. R. Reeder.

Previous knowledge. Wet places in Sonora and Jalisco.

Significance. Second and third Sonoran localities.

PANICUM ANTIDOTALE Retz. (Poaceae).—Perennial grass to 3 m tall, Arroyo Camahuiroa, 2.2 km NE of Camahuiroa, 26°33'05"N, 109°15'10"W, 15 m, *Friedman 036-95* (17 Jan 95, ASU, det. J. R. Reeder).

Previous knowledge. Cultivar widely escaped throughout México.

Significance. First Sonoran locality.

TRIDENS ERAGROSTOIDES (Vasey & Scribner) Nash (Poaceae).—Rare perennial in shade under shrub in coastal thornscrub near Las Bocas, ca. 60 km S of Navojoa, 26°35'30"N, 109°20'30"W, near sea level, *Van Devender 92-130, Friedman, Meyer* (1 Feb 1992, ARIZ); rare in coastal thornscrub in center of *Stenocereus alamosensis*,

Camahuiroa, 26°31'N, 109°16'W, near sea level, *Van Devender 93-302* (15 Mar 1992, ARIZ); dets. J. R. Reeder.

Previous knowledge. Florida to Texas, Arizona, also reported from N México and Cuba.

Significance. Three previous Sonoran localities are close to US border. These collections represent a southern range extension of 400 km.

AMYRIS BALSAMIFERA L. (Rutaceae).—Common 3 m tree, 0.8 km S of Camahuiroa, on road to Tierra y Libertad road, 26°32'15"N, 109°16'30"W, 5 m, *Friedman 043-94* (16 Mar 1994, ARIZ, ASU); common along arroyo in coastal thornscrub, Arroyo Camahuiroa, 1.5 km NE of Camahuiroa, 9.5 km WNW of Melchor Ocampo, 26°33'05"N, 109°16'15"W, 15 m, *Friedman 174-94* (26 Jun 1994, ARIZ, ASU); Cañon Las Barajitas, Sierra Aguaje, ca. 18 km NW San Carlos, 28°03'12"N, 111°10'57.7" W, 70 m, *Felger 95-191* (18 Feb 1995, ARIZ, CAS, MEXU, MO, NY, RSA, TEX, US).

Previous knowledge. Sinaloa to Guerrero, S Florida to the West Indies, and South America.

Significance. First Sonoran records and first record of this tropical genus in a mesic desert canyon habitat.

CAPRARIA BIFLORA L. (Scrophulariaceae).—Two 0.8 m tall subshrubs on river bank, El Paso on the Río Cuchujaqui, 26°40'35"N, 108°49'30"W, 150 m, *Van Devender 95-90*, *Reina G.*, *Yetman* (25 Feb 1995, ARIZ, UCR, det. P. D. Jenkins).

Previous knowledge. Florida, West Indies, Central and South America, México.

Significance. First Sonoran locality.

SOLANUM AZUREUM Fern. (Solanaceae).—Scattered in sparse coastal thornscrub, Camahuiroa, 26°31'N, 109°16'W, near sea level, *Van Devender 92-1078*, *Sanders* (8 Oct 1992, ARIZ, ASU, CAS, MO, UCR, USON, det M. Fishbein); *Van Devender 93-304*, *Meyer* (15 Mar 1993, ARIZ, MO), *Van Devender 93-1254*, *Friedman*, *Steinmann* (23 Nov 1993, ARIZ, ASU, MO, USON); uncommon, 2.3 km NW of Camahuiroa, 4.2 km SE of Las Bocas, 26°33'45"N, 109°17'45"W, 5 m, *Friedman 176-93* (18 July 1993, ASU); common on coastal flats, near Arroyo Muerto, 1.5 km NNW of Camahuiroa on road to Las Bocas, Mpio. de Huatabampo, 26°33'25"N, 109°17'25"W, 5 m, *Friedman 329-93*, *Steinmann*, *Van Devender* (23 Nov 1993, ASU); common in sparse thornscrub, vic. Bacorehuis, 4.5 km SE of Agiabampo, 26°14'55"N, 109°06'25"W, 15 m, *Friedman 050-94* (17 Mar 1994, ASU).

Previous knowledge. Known only from the type locality at Topolobampo, Sinaloa.

Significance. First Sonoran records for a species endemic to coastal thornscrub.

CITHAREXYLUM SCABRUM Sessé & Moc. (Verbenaceae).—Rare sprawling shrub at arroyo margin in coastal thornscrub, Arroyo Nescotahuca, 0.8 km (by air) SW Rancho Nescotahuca, 26°36'15"N, 109°16'15"W, 25 m, *Friedman 359-94* (22 Sep 1994, ASU); solitary 7 m tall tree, Arroyo Masiaca, W side of Masiaca; 26°45'55"N, 109°14'25"W, 65 m, *Van Devender 94-712*, *Yetman* (22 Sep 1994, ARIZ, ASU, TEX, UCR, USON, det. G. Nesom); common shrub at arroyo margin, Jopopaco vicinity, 26°44'20"N, 109°16'W, 55 m, *Friedman 371-94* (23 Sept 1994, ASU).

Previous knowledge. Sinaloa.

Significance. First Sonoran records.

LIPPIA GRAVEOLENS H.B.K. (Verbenaceae).—Locally common shrub along road in

tropical deciduous forest, Microondas La Luna, Cerro Las Tatemas, 13.8 km NW of Alamos, 27°07'N, 109°02'W, 720 m, *Sanders 9434* (6 Sept 1989, ARIZ, UCR), *Jenkins 90-270* (10 Oct 1990, ARIZ), and *Van Devender 93-342* (16 Mar 1993, ARIZ, ASU, CAS, det. G. Nesom); uncommon shrub, Naopatia, Estero Bamocha, Mpio. de Huatabampo, 26°45'N, 109°15'W, *Van Devender 93-1271*, *Friedman, Meyer, Steinmann* (23 Nov 1993, ARIZ, ASU, TEX, UCR, USON); common at Arroyo Las Rastras, SW edge of Sierra de Alamos, 26°56'30"N, 109°30"W, 380 m, *Van Devender 93-1480*, *López E., Yetman* (9 Dec 1993, ARIZ, ASU, TEX, UCR, USON); uncommon 1.5 m tall shrub in foothills thornscrub-tropical deciduous forest transition, Tres Marias limestone quarry, 28 km E of Navojoa, 27°06'46"N, 109°09'45"W, 220 m, *Van Devender 95-1108*, *Reina G., Yetman* (27 Sep 1995, ARIZ, USON).

Spanish common names are *burro mariola*, or *oregano del burro*.

Previous knowledge. Dry, rocky hills, arroyos, and valleys from central Texas and New Mexico south to Central America.

Significance. Previous Sonoran collections (*F. Shreve 6150 & 6173*), between Tesopaco and Cedros reported as *L. berlandieri* Schauer were not deposited into ARIZ with either the Gentry or Shreve collections, and could not be rechecked.

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REVIEWS

Trees of the California Sierra Nevada. (Backpacker Field Guide Series). By GEORGE A. PETRIDES and OLIVIA PETRIDES. 1996. Explorer Press, Michigan. 80 pages. \$9.95, ISBN 0-9646674-0-1.

No backpacker in the mountain range of Sierra Nevada will want to be without his/her *Trees of the California Sierra Nevada* field guide. This handy, lightweight book is small enough to fit easily inside a pants' pocket or even an overpacked backpack. It is very practical and easy to use, especially for the beginning botany student or any person with a slight interest in identification.

The field guide provides guidelines for identifying 95 tree species that grow at anytime of the year in the California Sierra Nevada. The book is divided into five sections based on leaf arrangement, composition, and morphology. Once you have reached the correct section for the tree selected for identification, a non-technical description of the habitat, seed, leaf and flower morphologies and sizes are appropriately provided along with a good illustration of distinct characteristics of the particular tree. Other tree species that are similar to each other are also described together and includes illustrations of each for comparison. Although some pencil drawings of described trees are dark and the details are not very clear, the overall clarity is nicely conveyed and beautifully illustrated.

Occasionally, natural history, medicinal and edible uses are mentioned in the tree descriptions to further intrigue the user. Both scientific and common names are given, although there is emphasis on common names as well as an avoidance of technical terms. This type of presentation will probably be more appealing for the user who is not interested in technicalities, may further invite the user to appreciate the natural world and perhaps increase the desire to learn more about plants.

As best expressed by the author himself, "[the field guide is] a new and simple way to identify and enjoy some of the world's most beautiful and impressive forest trees in a mountain setting of incomparable majesty." I will be sure to bring along my field guide on my next hike so that my non-botanists friends may share in the wonderful experience of identifying the stunning trees in Sierra Nevada mountain.

—YOLANDA MOLETTE, Department of Biology, San Francisco State University, San Francisco, CA 94132.

The Biophilia Hypothesis. Edited by STEPHEN R. KELLERT and EDWARD O. WILSON. A Shearwater Book, published by Island Press, Washington D.C., 1993, 439 pages. \$29.95(cloth), ISBN 1-55963-148-1; \$17.95(paper), ISBN 1795-147-3.

As the technological age rolls on, creating undreamed of wonders and conveniences for humanity (or at least for the privileged parts of it), so the natural resources that fuel it are being depleted. The exact cost is not yet known, and there is a wide range of opinion about what the bottom line might be. Unlike the optimism generated by engineers with vision, an understanding of biology, and familiarity with ecological and evolutionary processes tends to give one a rather dark view of the outcome. *The Biophilia Hypothesis* is hopefully one of the lights on the distant horizon for developing a rational approach to what is often seen by our technologically blinkered societies as unqualified progress.

E.O. Wilson is already a recognized and respected thinker engaged in constructing a rationale for biological realism, and biophilia is one of the conceptual tools that he has developed for this purpose. He explored the idea in some detail more than a

decade ago in his highly introspective book by the same name (Wilson 1984), and explains it in the currently reviewed volume as “. . . the innately emotional affiliation of human beings to other living organisms.” This he claims gives rise to a complex of learning rules that mould feelings that range “. . . from attraction to aversion, from awe to indifference, from peacefulness to fear-driven anxiety.” Wilson, together with co-editor Stephen Kellert, has taken biophilia into a new realm by producing this diverse collection of essays on the topic. Drafts of these chapters were presented at a meeting at the Woods Hole Oceanographic Institute in Massachusetts in 1992, and the book appeared in the following year. The final product aspires to Renaissance breadth, and 20 authors are from widely varying fields, including: mathematical modelling, population biology, psychology, psychiatry, behavioral geography, veterinary science, anthropology, microbial evolution, human evolution, animal welfare, and philosophy, not to mention the contributors from the expected branches of ecology, environmental science, and conservation biology. In spite of this breadth, the central message of the book is one clearly identifiable with the name of E.O. Wilson—promotion of the conservation of global biodiversity.

The basic tenet of the biophilia hypothesis is that natural selection molds our worldview, and can be used to explain some of our attitudes towards nature. It suggests that there is some important self-knowledge just below the conscious surface that can be used to our advantage as we face the future in a heavily human-impacted environment, or perhaps more correctly, which we can ignore at our peril. Natural selection has put us where we are, and our descent from savanna-dwelling hominids must carry with it the mechanisms to generate biophilia, as well as its complement, biophobia—such as the feelings of well-being in open environments where we can see both our prey and our predators, or the innate fear of snakes, spiders and high places. Without these responses, future generations are more likely to be selected against, or were until our environment became so transformed by culturally driven changes, that selective forces for humans ceased to be vipers, lions and lightning. Does an innate response formula still reside somewhere in our psyche? If it does, are our responses genetically programmed, or are they transferred from one generation to the next by cultural mechanisms? These are just a couple of the questions raised by the biophilia hypothesis.

For readers with a natural science background, the information and ideas put forward in the book make fascinating and challenging reading, and offer some good handles for hypothetical-deductive thinking about natural selection and the influence of disturbed environments on the behavior of *H. sapiens*. The heart of the debate, however, is not whether biophilia exists, but rather how powerful it is, what its component parts are, and how certain we can be that it (and the love of life it alludes to) will persist to guide the management of our environment. The arguments and opinions of the chapter authors cover a lot of ground. There are many accounts, some backed by statistics, others just anecdotal, that support the idea that humans have some distinct preferences, and possibly some real needs, in their relationship to the environment. Even the use of animals as cultural symbols in language, mythology and literature is given extensive coverage. A thought provoking chapter that addresses the phenomenon of human alienation from nature is one that centers on human artifacts, and the role that they may play in supplanting our reverence for natural elements of the environment. In this essay, Madhav Gadgil of the Indian Institute of Science, suggests that some elements of biophilia can possibly be squeezed out by transferral of our attention to artifacts, causing a breakdown of the innate kinship and reciprocity relationships which are important both in social behavior, and in our attitudes towards the natural environment. Jared Diamond, in his fascinating account of indigenous New Guinean knowledge about natural species and their habitats, puts forward the view that there is little to suggest a genetic basis for biophilia.

To accommodate the wide spectrum of perspective offered by the authors, the book is divided into six parts, each with two or three chapters. These divisions are: (1) clarification of the concept of biophilia, in which the editors each contribute a back-

ground chapter to set the scene; (2) the influence of biophilia on human aesthetics regarding landscapes; (3) human cultures and their relationship to nature (dealing for the most part with indigenous, non-technological cultures); (4) the reflection of the natural world (non-human animals and their behavior mainly) as symbols in human thought processes; (5) the evolutionary perspective (with some reference to Gaia and the ultimate helplessness of humans in the face of evolutionary processes); and (6) the ethical and political actions which might be appropriate to solve the real world problems that are arising from our increasing separation from nature.

If the purpose of the biophilia debate is to persuade humans that their existence is inseparable from the natural world, and that they are subject to a whole range of influences beyond their conscious control, then the book has made a good contribution. If, however, the purpose is to translate the realization of biophilia into actions that will conserve the elements of the natural world that most natural historians believe intuitively that we need for humanity to survive, then there is plenty yet to be said and done. It is Michael Soulé in his summary chapter who puts his finger on an important pulse. He remarks that while all of the contributions are implicitly neo-Darwinian, this is not the perspective or language of political action—of the arena where policy for effective conservation of biodiversity will be forged. The radically different policies needed for environmental protection in the face of escalating human impacts will not be guided by a knowledge of natural selection, but are much more likely to be done according to an economic paradigm challenged by new-Marxist concepts. Biophysical principles, it follows, need to be politicized to the point that ecological idealists can parley as effectively with political wolves as they can understand natural ones. Until then the cause of biological sustainability will not be satisfactorily addressed. The closest that the book comes to dealing with these practicalities of conserving biodiversity in the face of need-driven human impacts, is in the three-chapter section on human culture. In order to tease apart the subtle components of biophilia, however, these chapters concentrate for the most part on pre-technological human communities living in relative harmony with nature. In reality, the greater threats to natural systems and the biodiversity they contain, come from the messy mixture of cultures that one finds in the countless impoverished rural communities around the world. As an ecologist living and working close to the developing world of southern Africa, where natural resources are buckling under the pressure created by human needs, I perceive conservation concerns to overlap significantly with those of resource management. From this angle, the book has a distinctly “developed world” feel to it. It concentrates on issues such as nature’s contribution to the quality of life, and the opportunity for self-fulfillment through reverence and protection of biological species and natural systems. Relative to the rural poor, these are considerations of the comfort-zone. Biophilia as described here will not convince peasant farmers in the Zambesi River Valley that the elephants plundering their crops are more valuable as icons of a better quality of life, than they are as a source of meat and black-market ivory.

Having made my “southern perspective” objection to a perceived omission, I need to finish off this review with a comment that reflects my overall delight with the book. I feel that this book, apart from providing some absorbing reflections on the natural history of humans, is an important contribution to the awareness of the connectivity between people and the rest of nature that must precede a global strategy for conserving biodiversity.

LITERATURE CITED

WILSON, E. O. 1984. *Biophilia*. Harvard University Press, Cambridge, Massachusetts. 157 p.

—GEORGE DAVIS, Stress Ecology Research Unit, National Botanical Institute, Private Bag X7, Claremont 7735, South Africa.

The Rare and Endangered Plants of San Mateo and Santa Clara County. By T. CORELLI and Z. CHANDIK. 1995. Monocot Press, Half Moon Bay, CA. 139 pp

Until now there has never been a book with photographs or other illustrations of rare and endangered plants listed by county in California. Toni Corelli and Zoe Chandik have produced such a book. It will be useful not only to the interested public but also to environmental consultants, city and county planners, and public land managers. The species included are those which may enjoy some level of protection by the federal and state governments, i.e., special-status species.

Most of the information has been obtained from the CNPS's *Inventory of Rare and Endangered Species*, fifth edition (Skinner and Pavlik 1994). In addition, the authors have included a description of each species, with distinguishing characteristics underlined for quick reference, as well as lists of associated species and local habitat notes. Taxa are arranged alphabetically, starting at the family level. The book includes a general index by scientific name, common name, and family as well as a table arranged by scientific name with a description of the habitat of each species. A bibliography is also included.

One hundred and six species, constituting approximately 10% of the total number of species listed in *The Inventory*, are discussed in the book. Species are illustrated by either a drawing, a picture of herbarium specimens, or by photographs usually showing a close-up of the flower and the habitat. Unfortunately, the illustrations are of uneven quality. In many instances, the pictures poorly depict the plant and/or the habitat. Some pictures appear superfluous in that there is little difference between the close-up and the habitat shot for a specific species. Some species, including San Joaquin spearscale (*Atriplex joaquiniana*), a relatively common plant, are illustrated with only a drawing and three species are not illustrated at all. The inconsistency in illustration quality is somewhat of a disappointment.

This first publication in California, using a format that includes photographs of rare and endangered plants, not only acquaints the public with the local flora, but is also a visual tool for identifying sensitive plant species by those who document the occurrence and location of these species. Books like *The Rare and Endangered Plants of San Mateo and Santa Clara County* (sic) for other counties in California would be welcome supplements to state and local manuals.

—EVA G. BUXTON, LSA Associates, Inc., Point Richmond, CA 94801.

PRESIDENT'S REPORT FOR VOLUME 43

Welcome to the 1996–1997 program year for the California Botanical Society! We have completed another successful year, and I look forward to the coming year of events. On behalf of the Society, there are a number of Council members I want to thank for their contributions. Bob Patterson completes his term as Editor of *Madroño* with issue 43(4). Bob has provided great guidance for the journal over the past three years and has made many important contributions including the editing of the Jepson Symposium issue and review of the first supplement issue. Thanks Bob! We are very pleased to welcome Beth Painter as the new Editor, and we look forward to working with her. I also thank Margriet Wetherwax and Holly Forbes for their many contributions as Corresponding Secretary and Treasurer, respectively. During the last four years, they have provided important team work in dealing with the many aspects of membership, subscriptions, dues, and back issues of *Madroño*. The Society could not function without the contributions of Council members such as Margriet and Holly. We welcome Sue Bainbridge, Corresponding Secretary, and Mary Butterwick, Treasurer, who have worked closely with Margriet and Holly during the transition between board members.

As Graduate Student Representative, Lisa Schultheis demonstrated her many talents in helping to coordinate the monthly, post-meeting receptions and in organizing the Graduate Student Meeting, held this year at the Claremont Graduate Schools and co-sponsored by the Rancho Santa Ana Botanic Garden. The meeting was a grand success by all accounts thanks to Lisa's thorough efforts and the efforts of her assistants. The Society is proud to sponsor this event biennially and we look forward to working with Staci Markos, our new graduate student representative, to organize the next meeting in February 1998. I also thank Mark Porter, the past Second Vice-President, for organizing the Annual Banquet, which also was co-sponsored by the Rancho Santa Ana Botanic Garden and held on the Pitzer College Campus in Claremont. The Council appreciates the tremendous effort that went in to organizing this very successful event. We thank Ken Berg for his many insightful comments during the evening's address entitled *Conservation of Native California Plants in the Changing Political Landscape*. I am pleased to welcome Mona Bourell back to the Council as the new Second Vice-President who will organize this year's Annual Banquet to be held at the California Academy of Sciences in San Francisco. We are fortunate to have Reid Moran as the banquet speaker. The title of his talk is *Guadalupe Island Flora, and what's left of it!* I look forward to seeing many of you at the Academy on February 22!

Many others also have made important contributions to the Society. I thank Roxanne Bittman, Recording Secretary, for preparing minutes of the monthly Council meetings; Dean Taylor, First Vice-President, for organizing the annual program of speakers; Past-President Peggy Fiedler and Council members Mary Butterwick, John Little, and Tony Morosco for their assistance, advice, and attendance at meetings; and Brent Mischler and the University and Jepson herbaria for co-sponsoring the receptions that followed the presentations at the regular meetings. The presentations and receptions were a great success last year and I encourage more members and friends to attend. I thank John Little for continuing on the Council for a second term, and I welcome Margriet Wetherwax for her first term as a Council member. I am pleased to announce that John Little and Sycamore Associate have been working on an index to all issues of *Madroño*, which will be available in the near future. Thanks John for undertaking this large effort.

Various new and lingering issues and topics will be addressed by the Council in the coming year. We are continually mindful of the need to keep the Society finan-

cially sound and at the same time continue to publish a high-quality journal. We look to a growth in membership as one way to assist in this. I courage all members to request their botanical colleagues and friends to become members. I am always amazed at how many academic, agency, and applied botanists in California and the West are not members of the California Botanical Society, and thus do not receive Madroño. We also will work to have Madroño listed henceforth with Current Contents so that papers published in the journal are cited more frequently. This action alone may help increase membership. We have been gradually increasing dues as another way to keep pace with rising costs. We still have a relatively low dues fee at \$27 for regular membership.

This is my final year of a three-year term as President. It has been an honor to serve in this capacity for such an important organization, and I am pleased to have participated in the continuing evolution of the Society and in the many significant events we have sponsored during the past two years. During the next few months, the Society's Nominating Committee will be proposing a slate for President (3-yr), First Vice-President (3-yr), and Second Vice-President (1-yr). Please send to me the names of individuals you would like to have considered for these positions and I will be happy to forward them to the Committee.

In closing, I note with great sadness the passing of George Clark, President of the California Native Plant Society. George died in June the week before the convening of the *Conference on the Ecology, Conservation, and Management of Vernal Pool Ecosystems*, which CNPS co-sponsored. In addition to being a wonderful person, George made many contributions over a long and distinguished period to the understanding and conservation of the flora and vegetation of California, and to the stewardship of CNPS. We want to express our gratitude to George for his dedication, enthusiasm, and scholarship.

—WAYNE R. FERREN, JR.

EDITOR'S REPORT FOR VOLUME 43

This report serves to tell members of the Society the status of *Madroño* from manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 42[4]) the journal received 73 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 35 of these have since been accepted for publication. Average turn-around time for articles from submission to acceptance was 5 months. Notes generally took less time, and Noteworthy Collections generally appeared in the first issue available. Time between acceptance and appearing in print ranged from 3 to 15 months. As was the case over the last two years, very few manuscripts were rejected outright or after review. Authors of *Madroño* articles did a good job of responding to reviewers' suggestions.

This year volume 42(1) included a special supplement of the Wetlands of California, which should serve as a major reference for botanists and environmental consultants. The color figures were particularly well done and added a new and dynamic dimension to *Madroño*. The production of the supplement was funded by the authors, for which the Society is most grateful.

As usual I must thank those persons who have made my job as editor easier: Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who continues to assemble the Index and Table of Contents; Sheila Johnson, my student assistant who keeps me and *Madroño* on schedule; Jim Kelley, Dean of the College of Science at SFSU, who provided the funds to support Sheila; once again, Annielaurie Seifert at Allen Press for making the editor's job so easy; members of the CBS executive council for supporting the level of *Madroño* productivity in the face of increasing publication costs; and of course the reviewers upon whom I depend so much for their counsel - their names appear on a separate page of this issue.

As I finish my third and final year as editor of *Madroño*, I look back to 1993 to what seems like yesterday, sitting with John Keeley in his office, listening to his good counsel about how he functioned as editor. Soon I will look forward to sitting with Beth Painter and sharing with her the enjoyable experience of receiving manuscripts, sending them out to review, and ultimately writing to authors that their paper has been accepted for publication in *Madroño*. Everyone should have such a rewarding experience. It has been fun. I am pleased to leave *Madroño* in Beth's able hands.

—Robert Patterson

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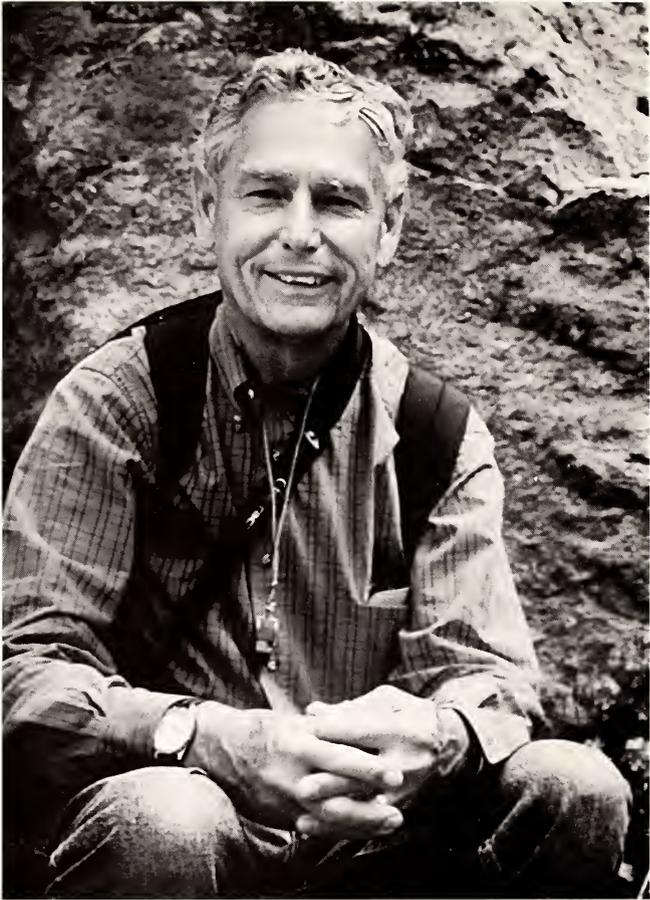
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DEDICATION

J. R. (Bob) Haller, professor of botany at UCSB for 35 years, retired in 1993. He made lasting contributions as a taxonomist and educator. He received his graduate training under the direction of Harlan Lewis in the rich botanical atmosphere of UCLA in the 1950's. Bob specialized in systematic relationships of yellow pines, which remained the center of his research interests throughout his career. Bob shared the first George Cooley Award for the best paper presented at the annual meeting of the American Society of Plant Taxonomists, in recognition of his innovative studies on hybridization in pines. Bob joined the faculty of biology at UCSB in 1957. He had an array of graduate students of his own, and he was an oft-sought member of many graduate committees.

His interest in systematics also extended to the preservation and management of collections, horticulture, and natural reserves. Many of his pine voucher specimens

are deposited at the UCSB herbarium, where he served as associate curator until 1986, and then director until his retirement. Bob also was interested in the preservation of the natural areas at UCSB and the development of quality horticultural plantings at UCSB for teaching and research. He served as chair of the landscape committee and even after his retirement continues as a member of the subcommittee on architecture, planning, and environment. Perhaps one of his more important administrative contributions was his involvement in the founding of the UC Natural Reserve System and his many contributions to the NRS over the years, including serving as faculty advisor to the Sierra Nevada Aquatic Reserve Lab and Valentine Camp and chair or member of various NRS committees.

One of Bob's main assignments at UCSB was to teach the California Flora Course (Botany 103, née Botany 3). It was in this capacity that he may have had the greatest effect on the botanical community, for he trained an enormous number of students, introducing them to the diversity of plant life in California. For many future botanists their first field experience was a Haller field trip. Long drives over long weekends during spring terms became a way of life for generations of botanists. For many of us who have followed in his footsteps as educators, the style, the pace, and even the routes of our field trips are decidedly Hallerian. Bob's dedication to sharing the flora of California was reflected in his famous slide show—a three-screen, six-projector production, set to music, that for an hour took the audience on a botanical tour of the state. Typical of Bob's taste toward personalizing things, he wove into the show candid slides of the instructors of his course, and many a student saw their own picture in the version of the show that Bob would run at the end of the course. Bob's course became so popular that at one time, non-botany majors had to submit proposals to enroll.

The students that Bob taught and influenced form an extensive collection of professors and teachers, federal, state, and local agency biologists, private consultants, and dedicated amateur botanists. He inspired us all to explore the fascinating floras of California and of the world, and to share our fascination with others. Following retirement from UCSB, Bob joined the staff of the Santa Barbara Botanic Garden, where he continues his devotion to education through specialized courses and instructional field trips. In this spirit we dedicate Madroño volume 43 to J. R. Haller, botanist, educator, and friend.

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ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY
ANNUAL DINNER

Saturday, 22 February

California Academy of Sciences, San Francisco

5:15 Socializing—No-host Bar

6:30 Dinner

8:00 Evening Talk

“Guadelupe Island and Its Flora, what’s left of it!”

Dr. Reid Moran

Dr. Moran’s book on the Guadelupe Island Flora will be available for sale.

Cost: \$37.00 regular, \$25.00 students

For more information call the 2nd vice president, Mona Bourell, at (415) 750-7195, or email her at: mbourell@cas.calacademy.org

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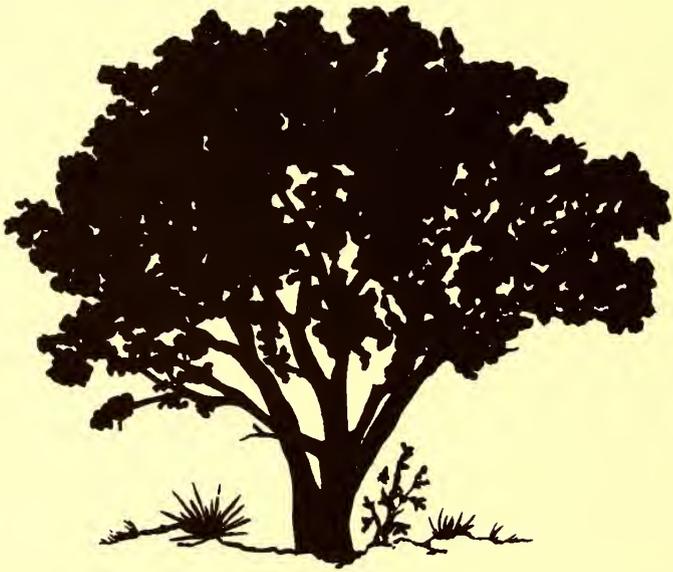
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