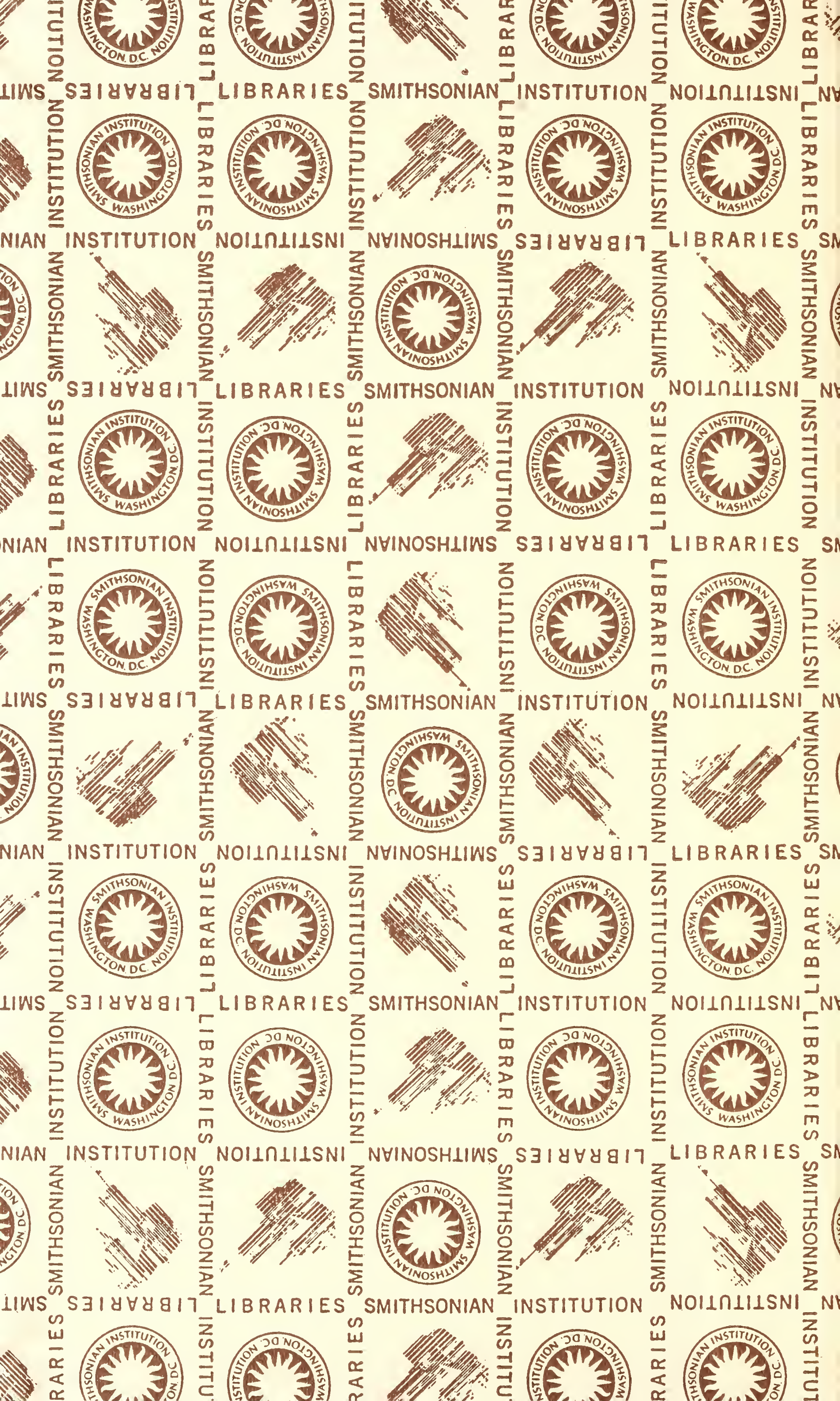
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VEGETATION CHANGE IN YOSEMITE VALLEY, YOSEMITE NATIONAL PARK, CALIFORNIA, DURING THE PROTOHISTORIC PERIOD

R. SCOTT ANDERSON
Laboratory of Palynology,
Bilby Research Center and Quaternary Studies Program,
Northern Arizona University,
Flagstaff, AZ 86011

SCOTT L. CARPENTER
Yosemite Research Center,
Yosemite National Park, CA 95389

ABSTRACT

The sediments of Woski Pond, Yosemite Valley in Yosemite National Park, record paleoenvironmental change spanning the last 1550 years. Closed conifer forest, consisting primarily of ponderosa pine, white fir, incense-cedar and Douglas-fir, existed around the pond until ca. 650 years ago. After 650 years ago more open canopy vegetation types such as oaks, sage and shrubs were found. Ethnographic records taken at the time of contact indicate that the aboriginal inhabitants regularly burned the Valley. The rapid decline in pine and increase in oak, coupled with elevated charcoal concentrations, indications of increased erosion and great expansion of aboriginal populations and cultural technologies are highly suggestive of vegetation manipulation for increased food resources by the early inhabitants of the Valley. These findings have implications for management of assumed natural vegetation types.

Until recently the number and coverage of sites with paleoecological information within the Sierra Nevada has been inadequate to answer basic questions regarding Holocene vegetation changes (Adam 1985). Adam (1967) was among the first to examine vegetation history within the central Sierra Nevada. Successive studies were not conducted for nearly two decades after his pioneering work (Cole 1983; Anderson et al. 1985; Davis et al. 1985; Davis and Moratto 1988; Smith 1989; Anderson 1990).

Though Yosemite National Park has been a focus for recent paleoecological reconstructions (Smith 1989; Anderson 1990), including palynological investigation of archeological sites at high elevations (Adam 1967), the history of vegetation change at low elevations in the more developed portions of the Park has been largely ignored. We present here the results of the first study to document long-term vegetation changes within Yosemite Valley, being part of a multidisciplinary ecological/archeological investigation. Suitable deposits for paleoecological studies are rare within Yosemite Valley, but are

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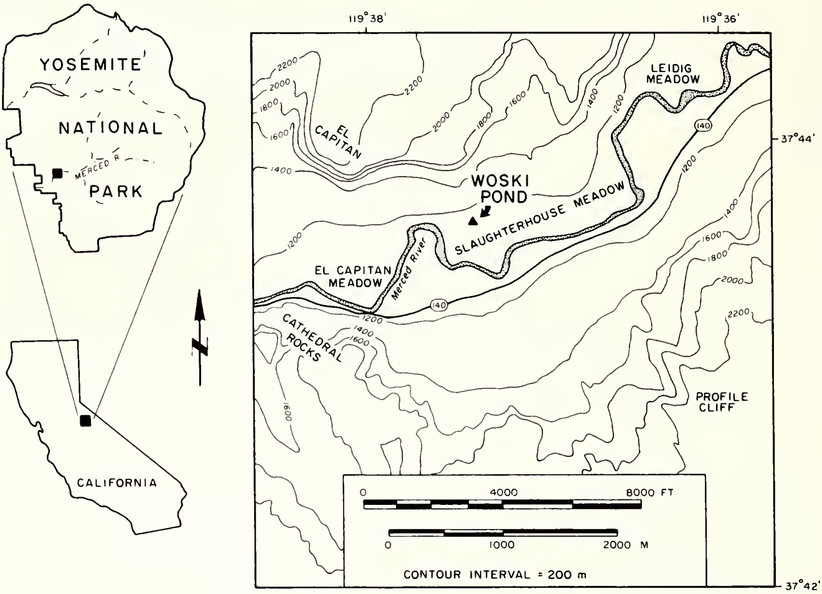

FIG. 1. Location of Woski Pond in Slaughterhouse Meadow, Yosemite National Park, California.

found at Woski Pond, a small oxbow depression on the Merced River floodplain (Fig. 1). The record covers the last ca. 1500 years, a period of considerable climatic change and expansion of human populations and related cultural systems within the area.

Three hypotheses for the major vegetation changes within Yosemite Valley that began ca. 650 yr BP will be presented. One hypothesis suggests that the forest associations were modified and exploited by the early aboriginal peoples inhabiting the Valley, subsequent to a major fire within the area. A second hypothesis relates the changes to possible climatic perturbations alone. A third alternative hypothesis suggests that geomorphic processes occurring along the floodplain of the Merced River caused the vegetation change.

STUDY AREA

The climate of the western Sierra Nevada is mediterranean, with cool, wet winters and warm, dry summers. Mean January and July temperatures in Yosemite Valley are ca. 5°C and 22°C, respectively; mean precipitation during January and July is 16.8 cm and 0.9 cm, respectively (NOAA 1980). Most precipitation comes from storms originating in the Pacific Ocean and moving eastward. However, some moisture comes from summer convection storms.

Woski Pond itself (1212 m) is a small (ca. 0.1 km) cut-off meander on the floodplain of the Merced River (Fig. 1). It is located in Slaughter House Meadow at the base of El Capitan (37°43′30″N, 119°37′30″W). In most years, the depression contains standing water through much of the summer dry season. However, when visited in September 1986 only a marshy area was apparent.

The surficial geology of the area has been studied for a long time. Much of the valley is underlain by lacustrine sediments and glacial outwash deposited in moraine-dammed lakes during the waning stages of Wisconsin and pre-Wisconsin age glaciations (Matthes 1930). Maximum thickness of these deposits approaches 600 m (Gutenberg et al. 1956).

Modern vegetation within the valley today is mixed woodland and yellow pine forest (Munz and Keck 1959). Woody species include ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), California black and scrub oaks (*Quercus kelloggii* and *Q. dumosa*), white alder (*Alnus rhombifolia*), western raspberry (*Rubus leucodermis*), and blue elderberry (*Sambucus caerulea*). Riparian woody plants include black cottonwood (*Populus trichocarpa*) and willows (*Salix* sp.). The marsh and meadow surfaces are covered by grasses, sedges and rushes, along with *Mentha arvensis, Agastache urticifolia, Rumex* cf. *angiocarpus, Alisma triviale, Viola macloskeyi, Ranunculus flammula, Equisetum arvense, Pteridium aquilinum,* several members of the Asteraceae, and others.

Woski Pond is within the immediate vicinity of several pre- and protohistoric archeological sites, occupied at various periods during the past 2000 to 3000 years. Excavations indicate a myriad of uses including habitation, resource procurement, tool manufacture, and food processing. The greater Yosemite Valley area would have provided an abundant array of plant and animal resources useful to the human populations.

METHODS

A 260-cm long sediment core was collected from the marsh surface on 13 September 1986, using a modified 5-cm ID Dachnowsky corer (Faegri and Iversen 1975). Twenty-two subsamples for pollen and microcharcoal were taken at 8–20-cm intervals along the core length. These were subjected to standard palynological processing techniques (Faegri and Iversen 1975), including addition of *Lycopodium* tracer spores for calculation of pollen concentration. The resulting pollen assemblage was mounted in silicone oil and individual grains were identified by comparison with the pollen and spore reference collection at the Department of Geosciences, University of Arizona, as well as from personal collections. Usually 300 grains exclusive of spores and aquatic pollen were counted. In most cases this consisted of counting at least 100 non-*Pinus* grains. Two size fractions of charcoal particles were tallied. Microcharcoal particles were tallied from the pollen preparations by measuring the amount of charcoal on the pollen transects (Anderson et al. 1986). Eleven half-core segments of various lengths (4–8 cm) were gently sieved with water through standard soil sieves (0.212 mm and 0.850 mm) to disaggregate the macrofossils and macrocharcoal. Macrocharcoal particles were counted from the macrofossil preparations. These were not measured but were tallied individually.

RESULTS

Sedimentology and radiocarbon dates. The top 215 cm of the core consisted of organic silts, with decreasing organic content downcore (Fig. 2). Wood fragments were abundant from 10 to 18 cm, 142 to 147 cm and at 178 cm. Silts and sands occurred between 18 and 26 cm. Coarse decomposed granitic sands with abundant muscovite occurred from 215 to 229 cm, with finer gray sands to the core bottom.

Three bulk-sediment radiocarbon dates were in stratigraphic order, with the oldest being 1440 ± 90 yr BP (Table 1). Sediment accumulation rates were calculated as follows: 0–46 cm, 0.080 cm/yr; 46–123 cm, 0.513 cm/yr; below 123 cm, 0.118 cm/yr.

Palynology and paleobotany. Two fossil assemblage zones were recognized, based on changes in the pollen (Fig. 3), plant macrofossil (Fig. 4) and aquatic fossil diagrams (Fig. 5). Zone I contained sediments deposited between ca. 650 and 1550 yr BP (between 85 cm and the core bottom), and was subdivided into two subzones. Zone II spanned the most recent ca. 650 years (the upper 85 cm of the record). At least 77 pollen and spore types were recognized, only the most common of which are shown in the diagrams. The pollen sum was composed of all upland pollen types. Pollen preservation was generally good; degraded percentages varied from 1.9 to 17.8% of the sum. However, Zone II pollen assemblages were consistently more poorly preserved than those of Zone I (see below).

Arboreal pollen types dominated during Zone I time. Pine pollen was consistently 60 to 75% of the sum. Macrofossils of ponderosa pine, lodgepole pine (*Pinus murrayana*) and Douglas-fir (*Pseudotsuga menziesii*) were found (Fig. 4). Fir (*Abies*) pollen was generally >3%, and fir needle fragments were found. TCT (Taxodiaceae-Cupressaceae-Taxaceae) pollen was variable, but centered around 6 to 7%. Leaves of *Calocedrus decurrens* were common in these sediments. Oak pollen centered around 6%, and mountain hemlock

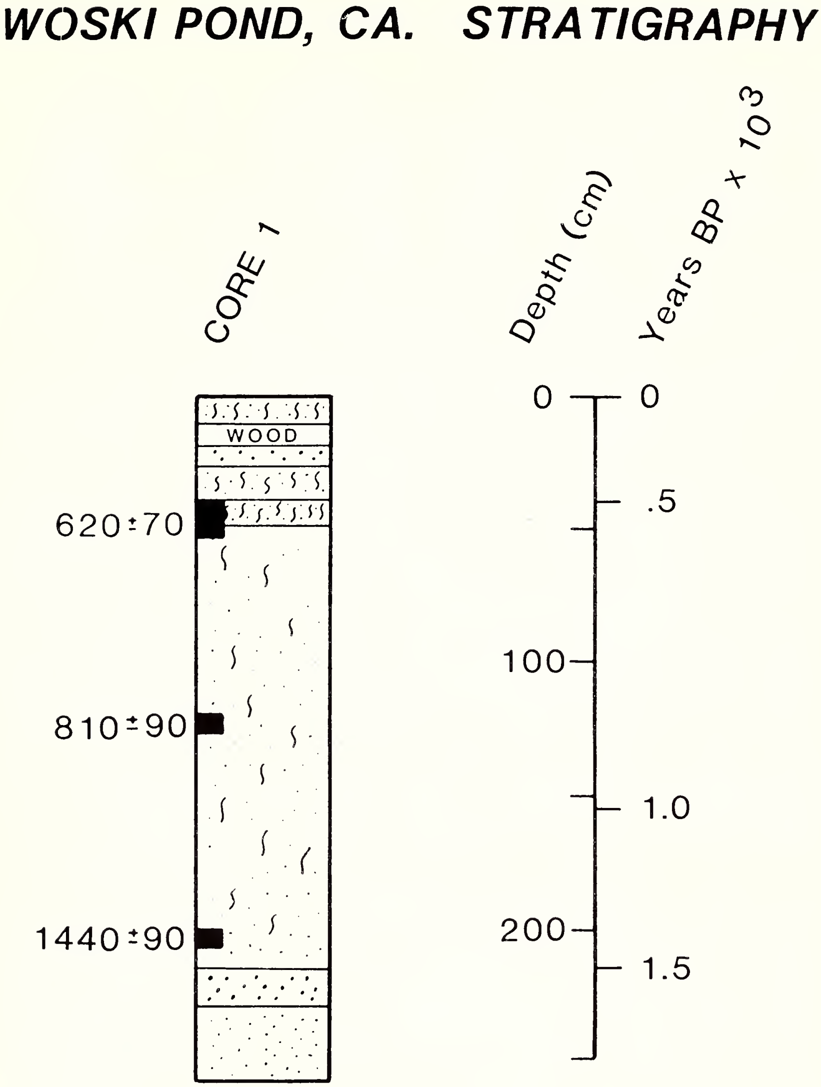

FIG. 2. Stratigraphy of the Woski Pond core. Symbols are: light dots = silts; heavier dots = sands; sigmoid symbol = organics.

(*Tsuga mertensiana*) pollen was consistently represented. A parasite primarily on conifers, mistletoe (*Arceuthobium*) pollen was found only during Zone I. Shrub pollen types were not as abundant as in the succeeding zone, with the exception of *Ceanothus*. Several herbs indicative of meadow or moist areas were common: *Gilia, Thalictrum, Polygonum bistortoides* and *Eriogonum*.

Table 1. Radiocarbon Dates on Woski Pond Sediments.

Depth (cm)	Lab no.	^{14}C Date (yr BP)	With ^{13}C adjustment (yr BP)
40–53	Beta-18362	620 ± 70	580 ± 70
120–127	Beta-18363	810 ± 90	730 ± 90
200–207	Beta-18364	1440 ± 90	1410 ± 90

Charcoal abundance was greatest within Zone I (Figs. 3 and 4). However, maximum amounts occurred at the Zone boundary, in association with a decline in coniferous elements.

Macrofossils of wetland or riparian trees and shrubs, such as *Populus, Salix* and *Alnus,* were most abundant in Zone I sediments (Fig. 5). Common herbaceous plants included *Isoetes* (subzone Ia), as well as *Potamogeton* sp. and sedges (both subzones Ia and Ib).

Arboreal pollen types also dominated the Zone II spectra, but with differing importance. Pine (35 to 52%; *P. ponderosa* macrofossils only), fir (ca. 1 to 2%), and mountain hemlock pollen types declined, with a complete absence of mistletoe pollen. Instead, increases in oak (6 to 13%) and TCT (mostly *Calocedrus* here; generally above 9%) occurred. Shrub pollen types were more abundant, including *Cercocarpus*-type, *Prunus*-type, and *Sambucus.* Common herbaceous types included *Rumex,* grasses, *Pteridium aquilinum,* and trilete spores, among others. Charcoal concentration and influx was much reduced in Zone II over values for Zone I. In the aquatic fossil assemblage, only *Alisma triviale* was more abundant during Zone II.

Discussion and Conclusions

For reconstruction of former vegetation from pollen assemblages, we utilize the modern pollen studies of Anderson and Davis (1988) and Adam (1967). The sediments of Woski Pond record paleoenvironmental change for the lower Yosemite Valley, spanning the last 1550 years. In total, the record indicates that regional vegetation has not changed significantly during the time of deposition; most fossil types identified to species can be found growing in the valley today. However, the record does suggest that significant local changes in the importance of individual species have occurred.

A closed conifer forest probably existed around Woski Pond during Zone I, based on higher pollen percentages of pine, fir, Douglas-fir, and mistletoe, along with the regular occurrence of ponderosa pine and Douglas-fir needles. The pond was surrounded by riparian species, such as *Populus trichocarpa, Salix* sp., and *Alnus rhombifolia.* After ca. 650 years ago, however, more open canopy vegetation

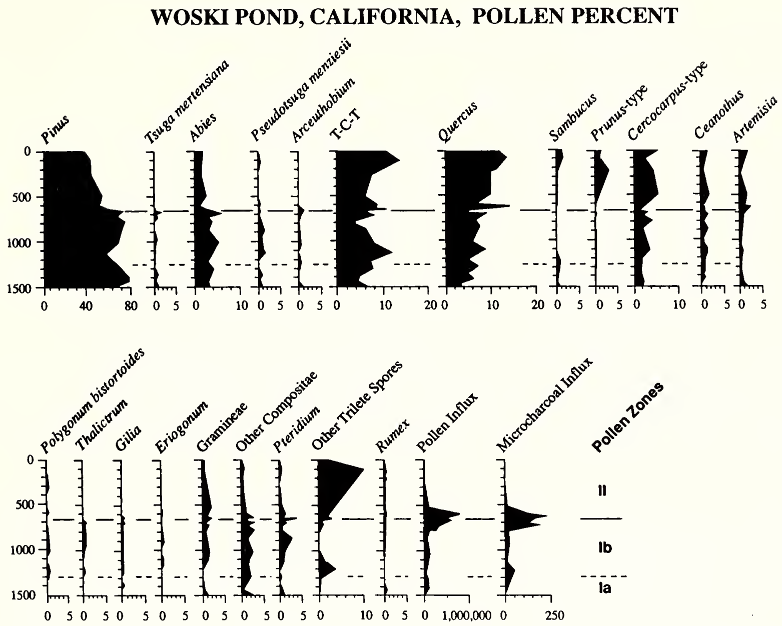

FIG. 3. Summary diagram of terrestrial pollen percentages from the Woski Pond core. Included are curves for pollen influx (grains/cm^2/year) and microcharcoal influx (mm^2/cm^2/year).

types such as oaks, sage, and the shrubs *Prunus* and *Sambucus* were favored. Few riparian trees surround the pond today, and their fossil record is diminished throughout Zone II.

The charcoal record, an indicator of fire occurrence, largely parallels the ponderosa pine macrofossil record. Abundant needle remains are associated with higher charcoal concentrations and influx in Zone I than Zone II, with maximum charcoal values at the zone boundary, ca. 650 yr BP. This suggests that the factor largely controlling the abundance of charcoal in the sediment (i.e., fire in the environment) is the local presence of this major conifer. The greater biomass provided by closed conifer forest would produce larger amounts of charcoal when burned.

The major change in pollen assemblages begins ca. 700 yr BP, with a decline in conifers and an increase in oak. Peaks in both charcoal, pollen, and sediment influx occur contemporaneously, indicating a period of erosion. These factors taken together suggest a major vegetation disturbance at that time.

Climatic change is a possible cause of the vegetation shift. Little Ice Age cooling within the Sierra Nevada (the Matthes glaciation of Burke and Birkeland 1983) commenced near that time. Evidence of

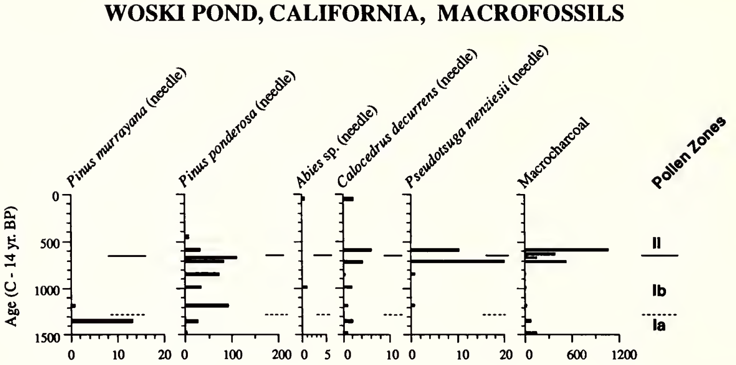

FIG. 4. Summary diagram of macrofossil influx (mm/cm^2/year) for dominant conifers found in the Woski Pond core.

lowered upper elevational tree limits (LaMarche 1973; Scuderi 1987; Anderson 1990) point to climatic change. However, the effect of climatic cooling with increased effective precipitation should have had an effect directly opposite the observed change, favoring an increase in conifers, especially fir (Anderson 1990). Somewhat conflicting evidence is indicated from tree-ring data, suggesting slightly drier winters than present near Kaiser Pass, southern Sierra Nevada (2700 m elevation), beginning by ca. 1300 AD and lasting for ca. 50 years (Graumlich 1990). Although climatic change may have been a contributing factor, neither the tree-ring nor glacialogical evidence can fully account for the abrupt vegetation changes noted at Woski Pond.

Another explanation for this rapid shift in vegetation composition is the occurrence of a local, catastrophic event caused by human or other natural factors. The effect of pre-modern human activity on the natural environment, as registered in sedimentary deposits, has been well-documented, especially for Europe (Iversen 1941; Bonatti 1970; Pilcher et al. 1971; Behre 1981), but also for North America (McAndrews 1976; Betancourt and Van Devender 1981; Burden et al. 1986; Delcourt et al. 1986; O. K. Davis and Turner 1987; Cinnamon 1988; Byrne and Horn 1989).

Yosemite Valley has been occupied by humans for at least the past 3000 years (Mundy and Hull 1987). Throughout the late Holocene, distinct changes have occurred delimiting successive cultural systems. Over 100 archeological sites are found in Yosemite Valley, spanning the Crane Flat, Tamarack and Mariposa cultural complexes (Carpenter 1984, 1985a; Mundy and Hull 1987). Changes in stone tool production and use, resource procurement, trade and other cultural traits depict a shift in lifestyle from seasonal hunting and

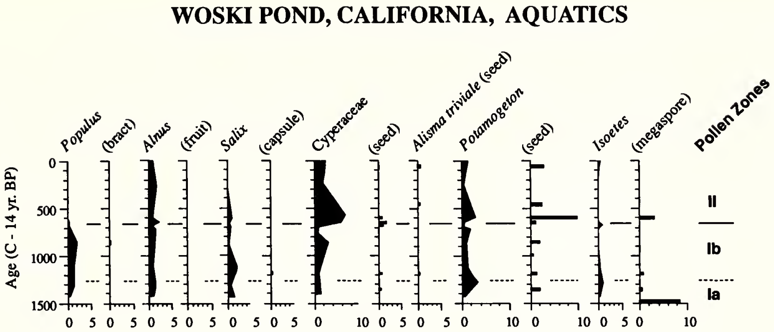

FIG. 5. Summary diagram of aquatic pollen percentages (silhouettes; outside the pollen sum) and macrofossil influx (bars; numbers/cm^2/year) for the Woski Pond core.

gathering within the Crane Flat and Tamarack complexes, to more sedentary occupation characteristic of the Mariposa complex, with increased reliance on oak acorns for consumption and trade.

If the rapid shift in vegetation composition was instigated by fire, as suggested by the large charcoal peak, it cannot be determined whether this was accomplished by aboriginal populations or lightning ignition. However, the correlation between the increase in charcoal, the change in dominant pollen from pine to oak, and the transition in cultural systems from the Tamarack to the Mariposa complex (Moratto 1984) all occur at ca. 650–750 yr BP. The Mariposa cultural sequence included an increase in population and development of specialized economic and resource-procurement systems, including the development of and reliance on various horticultural techniques (K. Anderson pers. comm. 1990). Manipulation of the natural environment by clearance of the conifers within the valley would have favored expansion of oaks, the acorns of which were a major food resource for these people.

Ethnographic evidence provides support for the vegetation manipulation hypothesis. Once the land was cleared, the early inhabitants of Yosemite Valley (Sierra Miwok) and other California locations regularly used fire and other physical means to keep the forest in an open state (Lewis 1973; Wickstrom 1987). Galen Clark, longtime caretaker in Yosemite, wrote in 1894 that the Indian policy of management "was to annually start fires in the dry season of the year and let them spread over the whole valley to kill young trees just sprouted and keep the forest groves open and clear of all underbrush, so as to have no obscure thickets for a hiding place, or an ambush for invading hostile foes, and to have clear grounds for hunting and gathering acorns. When the forest did not thoroughly

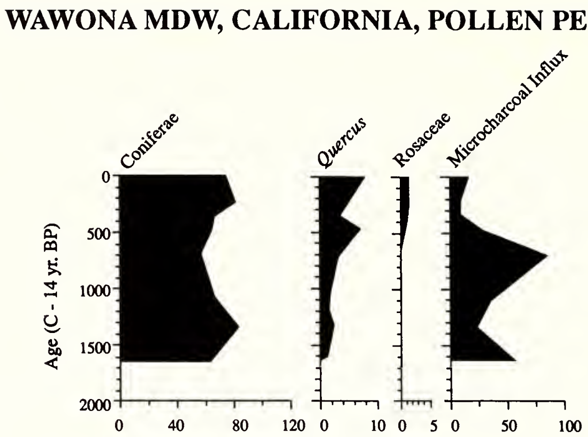

FIG. 6. Selected pollen types from the Wawona Meadow, Yosemite National Park, core. Conifers include *Pinus, Abies* and TCT (mostly *Calocedrus*); Rosaceae includes *Prunus* and *Rubus*. Microcharcoal influx is measured in mm^2/cm^2/year.

burn over the moist meadows, all the young willows and cottonwoods were pulled up by hand" (Ernst 1949). If these practices were typical also of the protohistoric Sierra Miwok, we can hypothesize a series of events leading to vegetation change within the valley. These include 1) a major fire that cleared many conifers out of the valley, and 2) subsequent regular but lighter fires and active eradication to keep the young pines from regenerating. The reduction in sedimentary charcoal during most of Zone II (Fig. 4) may be a result not of a lack of ignition but, instead, a reduction in fuel loads caused by these periodic aboriginal burns within the valley. It would also explain the major pollen changes beginning ca. 650–750 yr BP.

Additional support occurs in the pollen and charcoal stratigraphy of a core from Wawona Meadow, southeastern Yosemite National Park, at similar elevation to Woski Pond. Sampling is not as detailed as at Woski Pond; however, a major charcoal peak occurs at an interpolated age of ca. 700 yr BP (Fig. 6). Increases in pollen of oak and Rosaceae follow the charcoal peak. Over 60 archeological sites are recorded within the Wawona area, with ethnohistoric and archeological research indicating comparable cultural patterns as those known for Yosemite Valley (Hull 1989; Carpenter 1985b; Ervin 1984).

An additional alternative explanation for the changes at Woski Pond involves possible hydrological changes on the Merced River floodplain. Support for this hypothesis includes the persistence of pollen of typically higher elevation trees, such as mountain hemlock and fir, in sediments of Zone WP-Ib, possibly water-borne. The increase in oak and other pollen types in WP-II could be a result of decreased input of river-borne pollen (Adam pers. comm. 1990). This, however, does not explain similar changes in pollen stratigraphy at Wawona Meadow, where stream-borne pollen is unimportant.

This paleoecological perspective on vegetation change contains implications for management of fire and other disturbances within national parks. Heady and Zinke (1978) produced matching photographs of Yosemite Valley taken at European contact and in more modern times. At contact, much of the valley was an open oak-grassland with few conifers. However, after nearly three-quarters of a century of fire suppression or exclusion, the valley was choked with shrubs and young conifers; the sedimentary record also suggests a recent increase in coniferous elements (Fig. 4). Yet, which of the above conditions represents the more "natural" state? If we are correct in our conclusions regarding aboriginal manipulation, neither of these snapshots is representative of the vegetation conditions that would have occurred without human interference. The record from Woski Pond should provide ample incentive to modern ecologists to exercise caution when assuming that observed vegetation of a region is "natural", when in fact, the region has probably undergone significant human disturbance.

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SURVIVORSHIP AND GROWTH OF GIANT SEQUOIA (*SEQUOIADENDRON GIGANTEUM* (LINDL.) BUCHH.) SEEDLINGS AFTER FIRE

H. Thomas Harvey[1]
H. T. Harvey and Associates,
P.O. Box 1180, Alviso, CA 95002

Howard S. Shellhammer
Department of Biological Sciences, San Jose State University,
San Jose, CA 95192

Abstract

Fire has long been thought to play an important role in the reproduction of the giant sequoia (*Sequoiadendron giganteum*). In this 20 year study the efficacy of fire in promoting reproduction and growth are quantified. Findings are reported on growth and survival of seedlings that first developed in 1966 through 1968 after experimental burns in Kings Canyon National Park. Seedlings growing on substrates beneath former burn piles were significantly taller in their later years than those on scarified substrates. Seedlings that grew on substrates that had been beneath piles of burned logs had significantly higher survival rates than did those on all other substrates during the early years of seedling life.

The giant sequoia (*Sequoiadendron giganteum*) is the largest living thing known to ever exist on Earth. Formerly widely distributed, it is now restricted in its native range to the west slope of the Sierra Nevada of California. Its reproduction has long been associated with fire (Muir 1878), which is needed to remove surface litter and duff and open up the canopy (Kilgore and Biswell 1971). When hot fires burn in dense stands of mature giant sequoias as many as 100,000 seedlings per hectare may develop following heat-induced seed fall (Hartesveldt et al. 1975). It has been noted that few to no seedlings become established in unburned areas (Kilgore and Biswell 1971; Hartesveldt and Harvey 1967; Hartesveldt et al. 1975; Harvey et al. 1980). This study reports giant sequoia seedling growth and survivorship relative to fire intensity after the first experimental fires in a coniferous forest ecosystem in a western National Park.

Methods

Four study areas were established in the Redwood Mountain Grove of giant sequoias in Kings Canyon National Park in 1964, 1965, and 1966. Logs and felled snags were cut into sections, piled, and

[1] Tom Harvey died August 1, 1990; address correspondence to H. Shellhammer.

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burned in Trail Area in 1965 and in South Area in 1966. The heavy equipment used to move the logs often exposed mineral soil (scarified substrate). In other areas mineral soil was not exposed and had enough fuel to carry a surface fire (burned substrate). A few patches were a mix of scarified and heated substrates. In the first few years following these treatments thousands of giant sequoia seedlings germinated on the forest floor. Six substrates were recognized: 1) rotten logs, 2) burned surface, 3) scarified surface, 4) mixed burned and scarified surfaces, 5) fire breaks (hand cleared strips of mineral soil around the burn/manipulated portion of each study area), and 6) surface burned beneath log piles; substrates 1 and 5 are not reported on in this paper. Temperatures beneath burned log piles reached 600 degrees F from 2.5 to 7.5 cm below the soil surface (Hartesveldt and Harvey 1967).

Over 7000 seedlings were individually identified by number and then counted at each of the sites during various years (Tables 1 and 2). The survival rates of sequoia seedlings were calculated as seedling density (#/ha). The number of seedlings surviving in years when counts were not taken were interpolated from survival curves. Because the initial density of seedlings varied between substrate conditions, seedling density was standardized with a starting density of 1000 seedlings/ha.

We used a linear regression analysis to determine whether density dependent differences in survival as a result of different starting seedling density was influencing the survival between substrate conditions. The frequency distributions of the number of seedlings surviving between substrates for each cohort each year were analyzed with a G-test (Pyke and Thompson 1986). Simultaneous pairwise test procedures between substrate conditions at the Trail site followed Sokal and Rohlf (1981). Growth rate was measured as increase in seedling height.

RESULTS

There was no significant relationship between the starting density of sequoia seedlings and the average annual survival rate ($F = 0.008$, $df = 11$, $p = 0.987$) or the proportion surviving in 1986 ($F = 0.0631$, $df = 1$, $p = 0.977$). This indicated that the differences we observed in the survival of sequoia seedlings were due to differences in substrate and not to density dependent effects.

The survival of sequoia seedlings on burn piles for the Trail 1966 cohort was significantly greater than that on the other substrates each year ($p < 0.001$) (Table 1). The overall annual average survival of seedlings on burn piles was 2.5–3.5 × greater than on the other substrates ($G = 2470.3$, $df = 3$, $p < 0.0000$). The survival of seedlings on surface burn/scarified substrate was significantly greater than

Table 1. Survivability of Giant Sequoia Seedlings on Four Substrates at Trail Area, Kings Canyon National Park, 1966–1986. Seedling survival rates were calculated from seedling densities counted in 1966, 1967, 1969, 1974, 1979, and 1986 and are noted here by *. Survival rates for the intervening years were interpolated from the observed survival curve, and since the starting seedling densities varied between substrate conditions the survival rates were adjusted to a starting density of 1,000 seedlings. * = years when seedlings were counted. ** Surf. burn = surface burn, S.B./Scar. = mixture of surface burn and scarified surface, Scar. = scarified surface.

	1966 Cohort				1967 Cohort			
Year	Burn** pile	Surf. burn	S.B./ Scar.	Scar.	Burn pile	Surf. burn	S.B./ Scar.	Scar.
1966*	1000	1000	1000	1000				
1967*	273	20	69	36	1000	1000	1000	1000
1968*	273	20	64	36	190	74	65	110
1969*	273	18	61	36	171	15	22	29
1970	252	16	55	31	160	14	17	26
1971	232	15	51	27	149	13	17	22
1972	212	13	48	20	138	11	13	18
1973	212	11	43	18	126	11	9	17
1974*	212	11	41	16	115	11	4	16
1975	188	8	36	14	112	10	0	15
1976	164	6	35	13	108	9	0	14
1977	139	5	31	12	104	8	0	13
1978	115	3	30	11	100	7	0	12
1979*	91	0	25	9	97	6	0	11
1980	87	0	23	9	93	5	0	11
1981	82	0	23	8	89	5	0	10
1982	78	0	22	8	86	5	0	10
1983	74	0	20	8	82	5	0	9
1984	70	0	18	7	78	4	0	9
1985	65	0	16	7	74	3	0	9
1986*	61	0	16	7	71	3	0	8

seedlings on surface burn substrate during all years ($p < 0.0001$), and significantly greater than seedlings on scarified substrate from 1967–1986. The survival of seedlings on scarified substrate was greater than on surface burn substrate from 1967–1970 ($p < 0.0290$) and from 1978–1986 ($p < 0.0203$).

The survival of sequoia seedlings on burn piles for the Trail 1967 cohort was significantly greater than that on the other substrates each year ($p < 0.0001$) (Table 1). The overall annual average survival of seedlings on burn piles was 2.5× greater than on the other substrates ($G = 2470.3$, $df = 3$, $p < 0.0001$). The survival of seedlings on surface burn substrate was significantly greater than seedlings on surface burn/scarified substrate from 1975–1986 ($p < 0.0393$). The survival of seedlings on scarified substrate was significantly greater

TABLE 2. SURVIVABILITY OF GIANT SEQUOIA SEEDLINGS ON TWO SUBSTRATES AT SOUTH AREA, KINGS CANYON NATIONAL PARK, 1967–1986. Seedling survival rates were calculated from seedling densities counted in 1968, 1969, 1974, 1979, and 1986 and are noted here by *. Survival rates for the intervening years were interpolated from the observed survival curve, and since the starting seedling densities varied between substrate conditions the survival rates were adjusted to a starting density of 1,000 seedlings. * = years when seedlings were counted.

	1967 Cohort		1968 Cohort	
Year	Burn pile	Scarified	Burn pile	Scarified
1967*	1000	1000		
1968*	699	337	1000	1000
1969*	497	117	733	465
1970	477	79	673	333
1971	431	67	614	266
1972	386	39	554	199
1973	366	26	495	134
1974*	314	22	435	125
1975	310	20	424	119
1976	306	18	412	114
1977	301	18	401	104
1978	297	16	390	97
1979*	294	14	379	93
1980	288	14	361	92
1981	284	14	344	87
1982	279	12	325	82
1983	275	10	308	77
1984	271	10	290	72
1985	266	8	272	67
1986*	261	8	255	62

than on surface burn from 1968–1969 ($p < 0.0316$) and significantly greater than surface burn/scarified in all years except 1969–1973 ($p < 0.0001$).

For both the South 1967 and South 1968 cohorts, the survival of sequoia seedlings on burn piles was significantly greater than on scarified substrate in all years ($p < 0.0001$) (Table 2). The average annual survival of sequoia seedlings on burn piles for the South 1967 cohort was 4× greater than seedlings on scarified substrate ($G = 3758.6$, $df = 1$, $p < 0.0001$), while it was 2.5× greater for seedlings on burn piles for the South 1968 cohort ($G = 1982.2$, $df = 1$, $p < 0.0001$).

The height growth of sequoia seedlings was significantly greater on burn pile substrates than on other substrates in South Area but not in Trail Area (Figs. 1 and 2). Heights of the 1967 cohort in South Area were not measured until 1972 but by then seedlings on burn piles were significantly taller than seedlings on scarified substrates. The difference increased as time passed (Fig. 1). The 1968 cohort

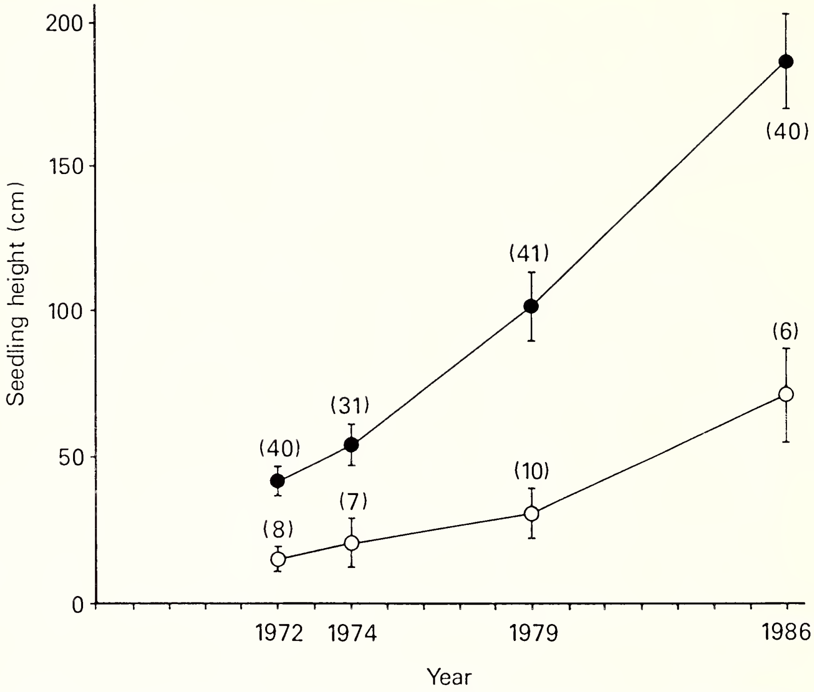

Fig. 1. Comparative growth of the South Area 1967 cohort of giant sequoia seedlings burn pile surfaces (●) versus seedlings on scarified substrate (○). Each point represents the mean height for (n) individuals ± one standard error. The results of the treatments were statistically different ($p < 0.05$) for each age class.

of South Area showed a similar pattern with a significant difference evident within four years of germination. The difference steadily increased through the years (Fig. 2).

Discussion

Results of studies of four cohorts of giant sequoia seedlings indicate that seedlings which become established on burn pile soils survive better than those on other substrates during the first few years. Our results also suggest that the hottest fires, in this case produced by logs which were piled and burned, bring about soil conditions that are most favorable to the survival and growth of giant sequoia seedlings. Most of the burn piles were placed away from the canopy of nearby giant sequoias to reduce potential damage to the trees, hence seedlings growing on burn piles received considerable sunlight. Stark (1968) noted that giant sequoia seedlings grew best in full sunlight. In general, heated soils are known to increase in wettability; heated soils are also more friable after heating than

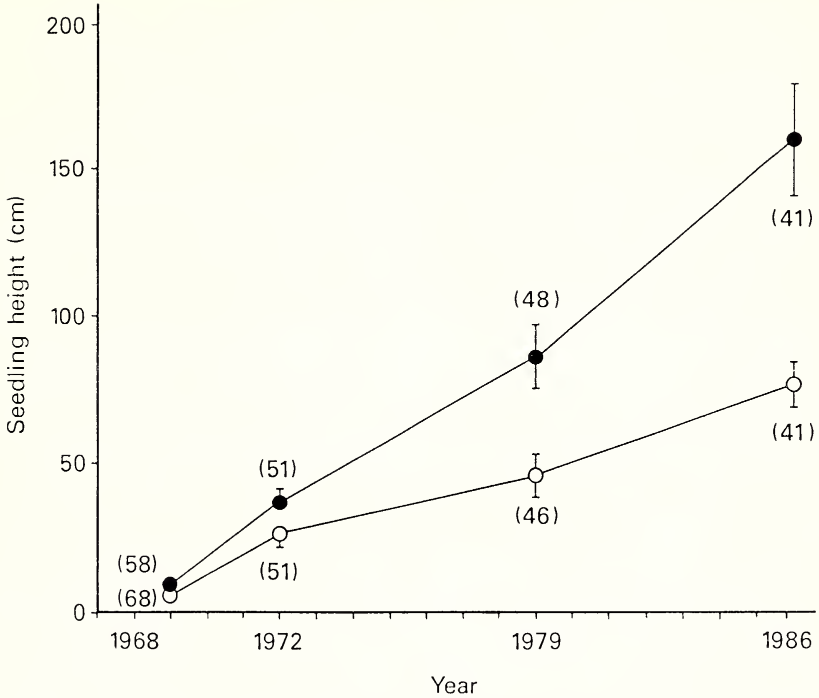

FIG. 2. Comparative growth of the South Area 1968 cohort of giant sequoia seedlings on burn pile substrates (●) versus seedlings on scarified substrates (○). Each point represents the mean height of (n) individuals ± one standard error. The results of the treatments were statistically different ($p < 0.05$) for each age class, except 1969.

before (Donaghey 1969). The killing of seeds of competing species and pathogens in the soil by heat favors the survival of giant sequoia seedlings. The giant sequoia seeds fall on the soil in large numbers after the heat of the fire has caused the serotinous cones to open (Hartesveldt et al. 1975). Thus the fire that clears the forest floor of litter and duff and kills competing species' seeds and pathogens, also kills the cone-bearing branches thus inducing a virtual rain of giant sequoia seeds from once closed cones (Harvey et al. 1980). The seeds fall upon an ideal seedbed and if the soil moisture is correct a carpet of seedlings is born.

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CHAPARRAL RESPONSE TO A PRESCRIBED FIRE IN THE MOUNT HAMILTON RANGE, SANTA CLARA COUNTY, CALIFORNIA

JIM DUNNE, ANN DENNIS, J. W. BARTOLOME,
and R. H. BARRETT
Department of Forestry and Resource Management,
University of California, Berkeley, CA 94720

ABSTRACT

Native chaparral flora showed a response to late fall prescribed burning similar to the expected effects of a summer or early fall wildfire but with some important differences. Shrub cover was temporarily reduced by burning, but *Adenostoma fasciculatum* reached preburn cover within three growing seasons. Non-sprouting shrubs recovered more slowly, and repeated prescribed fires would favor *A. fasciculatum.* Native fire-following herb response to this prescribed fire had similar cover to that expected following wildfire, but species diversity was lower than reported from wildfires.

Chaparral ecosystems occupy a large area of California and are important for wildlife habitat, watershed, and human activity (FRRAP 1988). Chaparral periodically burns, which temporarily reduces the shrub canopy and encourages herb growth (Hanes 1977). The natural fire cycle can conflict with human values, therefore land managers have long sought to manage fire occurrence in chaparral (Sampson 1944). Fire management practice since 1900 has changed from unrestricted burning to attempts at complete suppression, eventually culminating in the present policy of prescribed burning for vegetation management.

The general effects of fire on chamise chaparral are well known and have been the subject of several notable research programs (Cooper 1922; Sampson 1944; Biswell et al. 1952; Christensen and Muller 1975; Keeley et al. 1981) and extensive reviews (Hanes 1977; Keeley and Keeley 1988). The mature shrub canopy accumulates fuels, which become highly flammable in late summer and fall, beginning about ten years after burning. The accumulated fuel burns, usually within a few decades, removing woody vegetation. Within a few months after fire, sprouting shrubs begin regrowth and dormant seeds of fire-following herb and suffrutescent shrub seeds germinate. Herbs and suffrutescents dominate the chaparral for a few years until the regeneration of dominant shrubs completes the cycle.

Although the general pattern of fire effects on chaparral is documented, the variability among several important chaparral communities and some species is not (Keeley and Keeley 1988). Addi-

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tionally, the effects of prescribed fires are much more poorly known than the effects of wildfires. Because prescribed fires are usually conducted after the onset of fall rains in late fall, in winter or spring, and not during the normal wildfire season in late summer or early fall, the effects could be considerably different (Leck et al. 1989).

We describe the effects of a late fall prescribed fire on four chaparral communities in the central Coast Range of California.

STUDY AREA

The study was conducted on the 20,000 ha San Felipe Ranch, located in the Mount Hamilton Range in Santa Clara County, California. The study area, known as the Soup Bowl, is a rugged 16 km^2 basin near the confluence of Soup Bowl Creek and the Middle Fork of Coyote Creek. The basin elevation ranges from 800 meters to 1100 meters at the top of Bollinger Ridge. Annual rainfall at the nearest weather station, Mount Hamilton, averages 600 mm, mostly falling as winter rain and occasional snow in this mediterranean climate.

The soils of the area have been mapped and classified as Gaviota gravelly loam, a loamy, mixed, nonacid, themic, Lithic Xerorthent (Lindsey 1974). The vegetation is primarily chaparral, with *Quercus wislizenii* A. De Candolle dominated woodland along streams, and open grassland and *Quercus douglasii* Hook. & Arn. savannah along ridgetops. The area's fire history is poorly documented, with the exception of a wildlife that burned most of the Soup Bowl in summer 1962. No fires occurred between 1962 and the 1983 prescribed burn (Calif. Dept. Forestry and Fire Protection Records).

The plant communities of the Mount Hamilton Range are diverse and poorly described. The flora is also diverse, and species occurrence is well documented (Sharsmith 1945). The area supports a mix of distinct floristic elements from northern and southern California, including a significant (13%) proportion of endemics (Sharsmith 1945). Published studies of the response of chaparral communities in the Inner Coast Range to fire are lacking.

METHODS

Community descriptions. In summer 1983, the study area vegetation was classified into community types using dominant species composition (Dunne 1987). Using aerial photos and extensive ground checking, we mapped the types using a 625 m^2 minimum mapping unit. This map then served as the basis for allocating belt transects in a stratified random sample.

Ten community types were classified and mapped. Chaparral communities were defined as having at least 20 percent shrub cover and less than 20 percent tree cover. The four chaparral types were:

chamise chaparral, manzanita chaparral, chamise-ceanothus chaparral, and mixed chaparral.

Sampling and burning. In summer of 1983, 39 permanent belt transects were placed in chaparral types using a stratified random sample with proportional allocation. Spaced at 50 cm intervals along each 25 m transect, fifty points were measured for plant species cover and plant height, stratified into shrub and herb layers. If no plant part occurred on a point, ground surface characteristics were recorded. Each transect marked the center of a 1 m wide belt in which density of woody plant seedlings was recorded. Transects were sampled twice each year, in spring and late summer, beginning in late summer 1983 and continuing through spring 1987.

The prescribed burn was conducted by the California Department of Forestry on 3 November 1983. The treatment was typical of a post-rain, late fall fire, with moderate fuel consumption and patchy ignition. The fire was only partly successful from a management viewpoint, burning 750 of a planned 1500 hectares.

RESULTS

Preburn composition. The four chaparral community types were dominated by brush species preburn, with few herbaceous plants, and some annual grasses in a few transects (Table 1). The annual grass component represents small grassy openings too small to be mapped separately but included in the randomly placed transects.

The chamise chaparral type was dominated by *Adenostoma fasciculatum* Hook. & Arn. (60 percent cover), with lesser amounts of *Ceanothus cuneatus* (Hook.) Nutt. (6 percent cover), and *Arctostaphlos glandulosa* Eastw. (4 percent cover) (Fig. 1A). Manzanita chaparral was dominated by *A. glandulosa* (61 percent), associated with *A. fasciculatum* (29 percent) (Fig. 1B). Chamise-ceanothus chaparral consisted of *A. fasciculatum* (50 percent) and *C. cuneatus* (28 percent) (Fig. 1C). Mixed chaparral included *A. fasciculatum* (61 percent), *Arctostaphylos* spp. (17 percent), and *C. cuneatus* (14 percent) (Fig. 1D).

Fire effects on shrubs. As expected, fire greatly reduced shrub cover and increased herbs on the burned plots (Fig. 2). Patterns of recovery were clear in all four community types by the third post-fire year. In the chamise and manzanita types, the shrub cover on burned transects was insignificantly different from unburned transects after three years since both *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* were vigorous resprouters. For chamise-ceanothus and mixed chaparral types, cover was less than preburn at after three years, but would have reached preburn levels by the fourth year. Species diversity increased in all types, except for chamise chaparral, after the prescribed burn (Fig. 3).

TABLE 1. PRE-BURN PERCENTAGE COVER IN SUMMER 1983 FOR FOUR CHAPARRAL COMMUNITY TYPES.

Community type	Trees	Shrubs	Annual grasses	Perennial grasses	Annual herbs	Perennial herbs	Number of transects
Chamise	<1	73	8	0	<1	0	13
Manzanita	0	90	0	0	0	0	11
Chamise-ceanothus	0	76	7	0	1	0	9
Mixed	0	85	0	0	0	<1	6

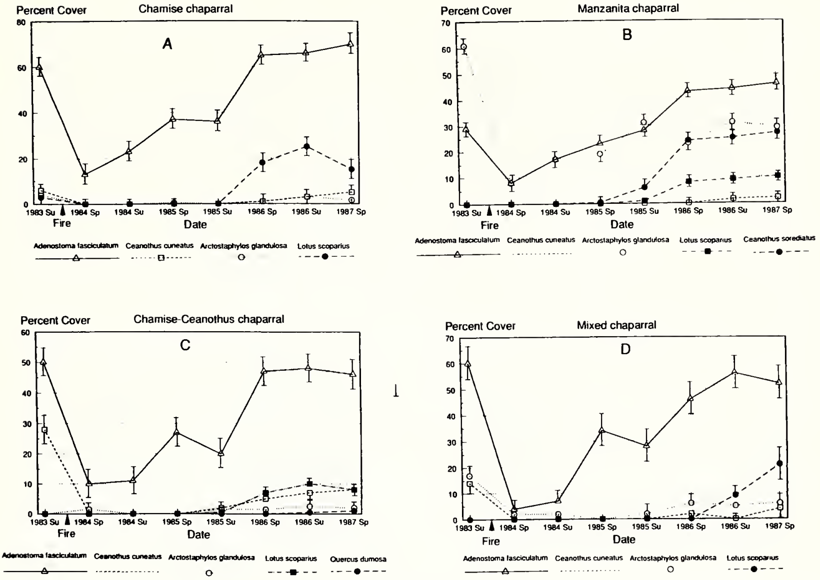

FIG. 1. Changes in cover of shrub species following a fall 1983 prescribed burn in four chaparral community types: A, chamise chaparral; B, manzanita chaparral; C, chamise-ceanothus chaparral; and D, mixed chaparral. Error bars represent ±2 SE of the mean.

Adenostoma fasciculatum showed similar patterns of seedling establishment in all four shrub community types. Increased *A. fasciculatum* cover was accompanied by establishment of an average of 35 *A. fasciculatum* seedlings/m^2 in the first post-burn spring (1984). By summer of 1987, seedling density had declined to only 2 new plants m^{-2}. *Ceanothus cuneatus* established densities of 1 to 5 plants m^{-2} by the first year in each of the four types.

Patterns of shrub recovery differed among community types. In the chamise type, *A. fasciculatum* returned to preburn cover in two years (Fig. 4A). The three most common associated shrubs had recovered by the third year (Fig. 1A). *Lotus scoparius* (Nutt. *in* Torrey & A. Gray) dramatically increased to well above preburn levels by the third spring following the fire.

In the manzanita type, although shrub cover returned to preburn levels by the third year (Fig. 4B), the fire had shifted dominance from *Arctostaphylos* spp. preburn to *Adenostoma fasciculatum* by the second spring following the fire (Fig. 1B). Several uncommon shrub species increased by the second and third years, increasing shrub diversity by the second spring.

In the chamise-ceanothus type, *Adenostoma fasciculatum* and *Lotus scoparius* recovered as in the pure chamise type, *Ceanothus cu-*

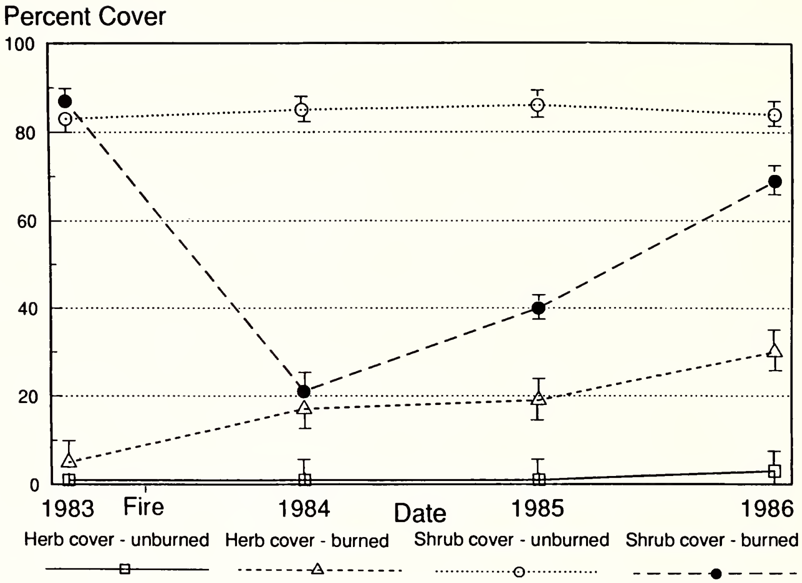

FIG. 2. Changes in cover of chaparral on burned and unburned transects. Error bars represent ±2 SE of the mean.

neatus recovered more slowly, and was at less than half preburn cover in the third spring after fire (Fig. 1C). Shrub cover after three years still had not returned to preburn levels (Fig. 4C).

In the mixed chaparral type, *Adenostoma fasciculatum* and *Lotus scoparius* showed the previously described pattern, with slow overall shrub recovery (Fig. 4D) and slower recovery of *Arctostaphylos* spp. and *Ceanothus cuneatus* (Fig. 1D).

Fire effects on herbaceous cover. Herbaceous cover increased following fire in all types (Fig. 2), least in the manzanita type (Fig. 4B). The different types displayed very different patterns of herb species diversity (Fig. 3). Herb diversity was higher in chamise and chamise-ceanothus types than in manzanita and mixed chaparral types. Few herbaceous species remained in mixed chaparral in 1987.

Fire following herbs *Anthirrhinum multiflorum* Pennell, *Emmenanthe penduliflora* Benth., *Oenothera micrantha* Hornem. ex Spreng., and *Phacelia phaceliodes* (Benth.) Brand were not found preburn, but were common in the first year post-fire. The four fire followers comprised all of the 14 percent total herbaceous cover in the manzanita type and 10 percent of the 14 percent total herbaceous cover in the mixed chaparral type in the first post-fire year. Fire followers were less dominant in the chamise and chamise-ceanothus types at 9 percent of the 22 percent total herbaceous cover and 5 percent of

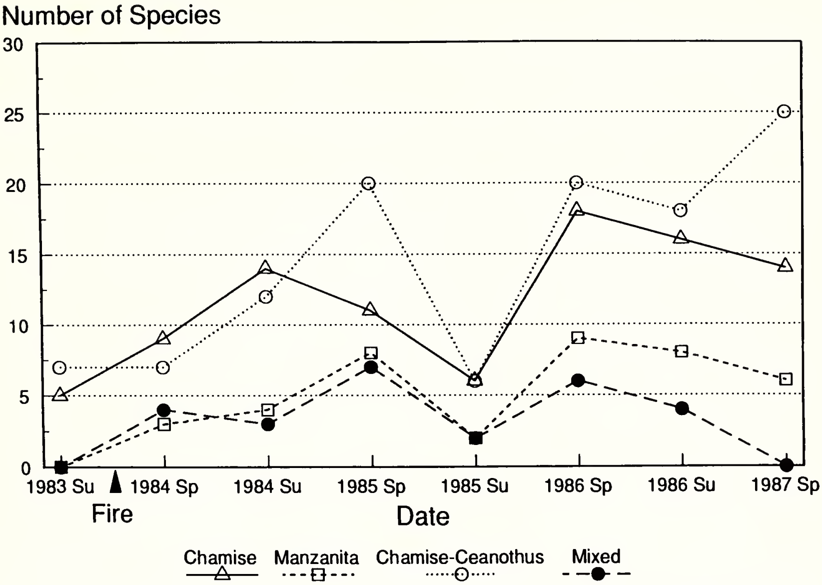

FIG. 3. Changes in number of herbaceous species found in four chaparral types following a fall 1983 prescribed burn.

the 19 percent total herbaceous cover, respectively. The non-fire follower herbaceous cover consisted primarily of the exotic annual grasses *Bromus rubens* L. and *Vulpia myuros* (L.) C. C. Gmel.

The second and third years showed similar herb cover to year one (Fig. 4), but composition shifted to increased cover of annual grasses, with few of the four fire-followers remaining. By spring 1986 fire-followers were absent from manzanita and chamise-ceanothus types, but still comprised 8 percent of the 22 percent total herbaceous cover in mixed chaparral and 3 percent of the 45 percent total herbaceous cover in the chamise-ceanothus type.

DISCUSSION

The general patterns of shrub recovery following burning were similar within the four chaparral community types and to patterns reported in wildfire studies (Keeley and Keeley 1988). However, shrub cover recovered exceptionally fast, *Adenostoma fasciculatum* returned to preburn cover within three years. *Arctostaphylos glandulosa,* where present, also recovered preburn cover within three years. Canopy recovery this rapid suggests a similarly rapid rate for fuel buildup. Under a fuel management program reburning would have to be frequent to keep shrub cover and fuel buildup below hazardous levels.

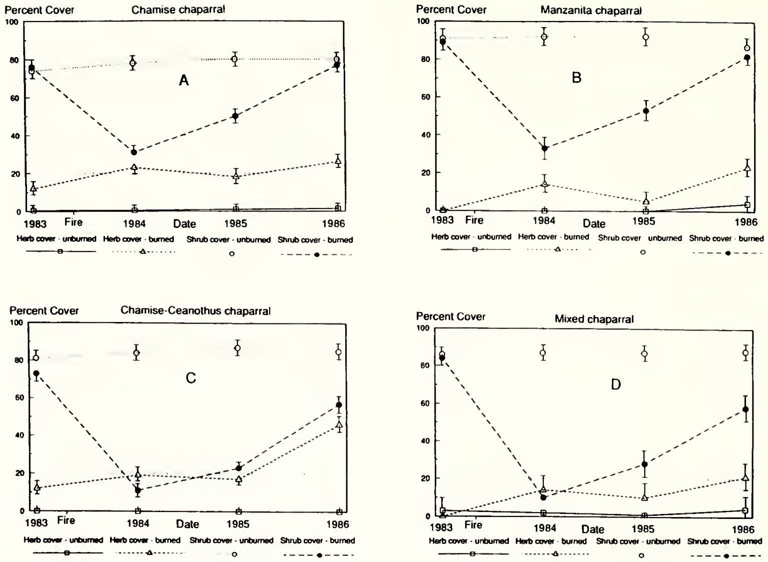

FIG. 4. Changes in relative cover of shrub and herb species following a fall 1983 prescribed burn in four chaparral community types: A, chamise chaparral; B, manzanita chaparral; C, chamise-ceanothus chaparral; and D, mixed chaparral. Error bars represent ±2 SE of the mean.

Shrubs which reproduce from seed like *Ceanothus cuneatus* recovered more slowly than sprouters, reaching only about 25 percent of preburn cover by the third year. The densities of seedling *C. cuneatus* observed in this study were low compared to other studies (Sweeney 1956). In the chamise-manzanita type, this resulted in a probably temporary *A. fasciculatum* dominance. The shorter the fire interval, the greater the expected dominance by the sprouters *A. fasciculatum* and *A. glandulosa,* therefore frequent past fires could be responsible for present *A. fasciculatum* dominance in types which can support greater shrub diversity.

Fire-following herbs appeared following this post-rain fall prescribed burn in a pattern of herb appearance similar to that reported on other chaparral sites (Hanes 1977; Keeley and Keeley 1988). Fewer species made up the fire-following herb flora in this study than reported elsewhere (Keeley and Keeley 1988) although cover was comparable. The fire-following flora is dominated by four species which were abundant in the first preburn year, declined in the second, and were scarce in the third. The pattern showed no evidence that burning in fall after the end of the normal wildfire period negatively affected the few fire-followers present on this site.

ACKNOWLEDGMENTS

We thank Amy Beaton Dunne, Carol Simmons, and Kim Lathrop for field assistance. Tom Parker and two anonymous reviewers provided helpful comments on an earlier draft. This project was funded by the California Department of Forestry and the William Hewlitt and David Packard Foundations.

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A NEW SPECIES OF *SUAEDA* (CHENOPODIACEAE) FROM COASTAL NORTHWESTERN SONORA, MEXICO

M. Carolyn Watson
Environmental Research Laboratory, The University of Arizona,
2601 E. Airport Drive, Tucson, AZ 85706

Wayne R. Ferren, Jr.
Department of Biological Sciences, University of California,
Santa Barbara, CA 93106

Abstract

Suaeda puertopenascoa, a new perennial species endemic to estuarine wetlands in northwestern Sonora, Mexico, belongs to Sect. *Heterosperma*. Distinctive characteristics include opposite branches and leaves, three flowers per dichasium, perianth lobes that are fused into a basal disk with horizontal thickenings or wings, and large brown seeds averaging 2.5 mm wide. In the vicinity of Puerto Peñasco, it grows in low marsh habitats, whereas *S. esteroa* grows in upper marsh habitats and *S. moquinii* occurs along the margins of the marsh and in upland sandy habitats and saline-alkali wetlands of the adjacent desert region.

Resumen

Suaeda puertopenascoa, perteneciente a la Sección *Heterosperma*, es una nueva especie perenne endémica en la zona de los esteros localizados en el noroeste del estado de Sonora, México. La misma se caracteriza por tener ramas y hojas opuestras, flores tres por dicasio, lóbulos del perianto fusionados para formar un disco basal con engrosaduras o alas horizontales, y grandes semillas color cafe (de un promedio de 2.5 mm de ancho). En las cercanías de Puerto Peñasco, crece en las partes bajas de las marismas dentro de los esteros, mientras que *S. esteroa* crece de las partes altas de las marismas y *S. moquinii* crece en los márgenes de las marismas y en habitats arenosos y salino-alcalinos de las áreas adyacentes a la región desertica.

In 1983, while studying *Suaeda* spp. for a halophyte research program, the senior author located small-seeded and large-seeded individuals of this genus in estuarine wetlands in the vicinity of Puerto Peñasco, Mexico. We determined the small-seeded plants to belong to *Suaeda esteroa* Ferren & Whitmore, a herbaceous perennial previously reported only from estuarine wetlands along the Pacific Ocean in southern California and Baja California (Ferren and Whitmore 1983). The large-seeded individuals were determined to belong to an undescribed species apparently restricted to estuaries of coastal northwestern Sonora, which we propose here.

Suaeda puertopenascoa C. Watson & Ferren, sp. nov. (Fig. 1).—Type: MEXICO, Sonora, Estero Cerro Prieto, 12 km NW of Puerto Peñasco, scattered along edge of tidal channel, S end of

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estuary at southern mouth, 31°24'30"N, 113°37'W, 6 Oct 1985, *Ferren and Watson 2807* (holotype, UCSB; isotypes, ARIZ, CAS, ENCB, INIF, MEXU, MO, NY, RSA, UC, US).

Suffrutex glaber usque 110 cm alti. Caulis perennis, rami erecti vel ascendentes, increbre oppositi. Folia saepe opposita ascendentia linearia sessilia glauca decidua 3–5(–7) cm longa, 2–3 mm lata; bracteae alternae 0.5–1.5 cm longae. Flores perfecti regulares et symmetrici 2–3 mm lati, 3 in quoque dichasio, per 3 bracteolas inaequales subtenti; lobi perianthii 5 cucullati inaequales, saepe disco cuneato marginibus tumidis (incrassatis), alas basales horizontales formantes; stamina 5; stigmata 2 linearia papillosa. Calyces fructiferi 3–4(–5) mm lati. Semina monomorpha horizontalia in ovario, obtusa brunnea testa tenui, (2.0–)2.5(–3.0 mm) lata. Habitat in litoribus maritimis.

Suffruticose herb, 35 to 110 cm tall, glabrous, vegetative during first year. Stems perennial, erect to ascending, to 1 cm diameter at base, generally one from a single vertical tap root, with no obvious exfoliations; branches below inflorescence few, erect to ascending, generally opposite. Leaves frequently opposite, ascending, linear, sessile, succulent, slightly glaucous, deciduous, 3–5(–7) cm long (fresh material), 2–3 mm wide, the longer ones subtending new branches, concave adaxially to terete; margins parallel; tip acute or blunt. Inflorescence compound; dichasia axillary, sessile, alternate along erect spikes. Bracts leaf-like, alternate, 0.5–1.5 cm long and 3–4 mm wide (flowers), generally becoming yellow to yellowish-orange at maturity, deciduous. Bractlets scarious, 3, unequal; margins irregular with occasional trichomes, especially near base. Flowers perfect, bilaterally symmetrical, 2–3 mm broad, 3 per dichasium; perianth lobes 5, unequal, cucullate (hooded), rarely opening, fused at base into a swollen, often cuneate disk with marginal thickenings usually drying to form basal horizontal (transverse) wings; stamens 5; stigmas 2, linear, papillose. Fruiting calyces 3–4(–5) mm wide. Seeds monomorphic, horizontal in ovary, adherent to perianth, irregularly flattened, dull, brown, with thin membranous testa, (2.0–)2.5(–3.0) mm wide.

PARATYPES: MEXICO, Sonora, Estero las Lisas, ca. 40 km N of Puerto Peñasco, 31°36'N 113°53'W, 10 Oct 1989, *Watson 973-15* (ARIZ, UCSB); Estero Cerro Prieto, 12 km NW of Puerto Peñasco, 31°24'30"N, 113°37'W, 17 Oct 1984, *Watson 973-19,20,26* (ARIZ, UCSB), 6 Oct 1985, *Ferren, Watson, and Roberts 2804* (ARIZ, UCSB); Estero Cholla, 4 km NW of Puerto Peñasco, 31°20'N, 113°36'W, 1 Mar 1985, *Watson 973-28* (UCSB), 7 Oct 1985, *Ferren, Watson, and Roberts 2829* (ARIZ, UCSB); Estero de Morua, 8 km SE of Puerto Peñasco, 31°17'N, 113°28'W, 7 October 1985, *Ferren and Roberts 2833* (ARIZ, UCSB); Estero la Pinta, ca. 25 km S of

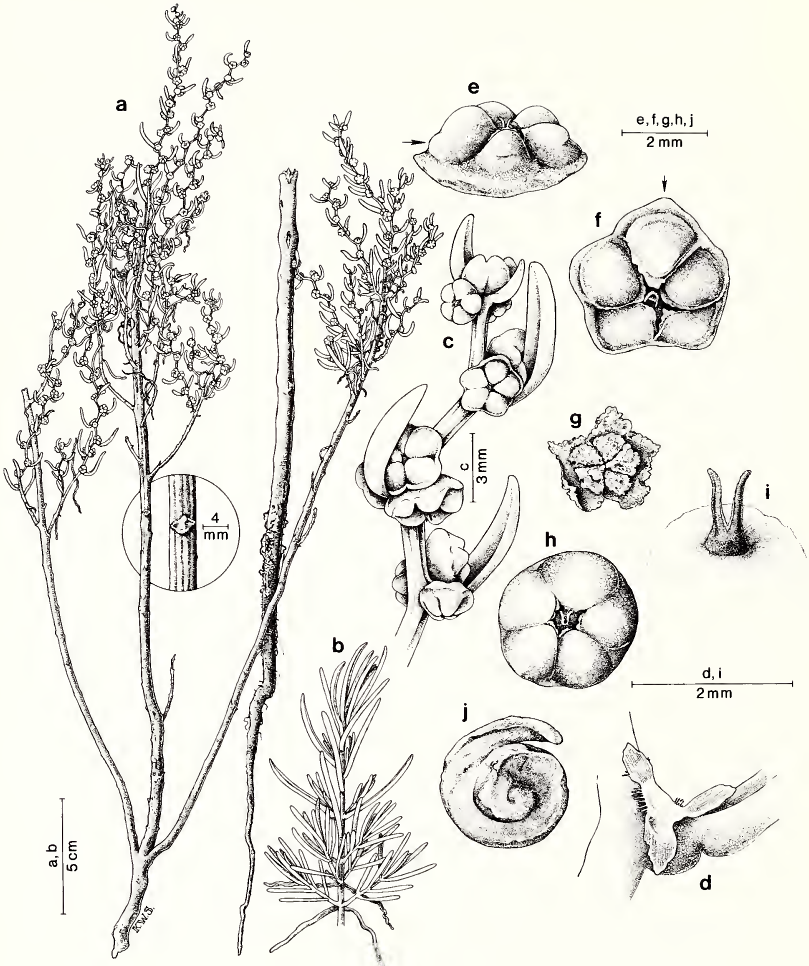

FIG. 1. *Suaeda puertopenascoa* C. Watson & Ferren. a. Habit. b. Vegetative stem. c. Portion of inflorescence. d. Bractlets and base of bract. e. Flower, fresh material, oblique view. f. Flower, fresh material, top view. g. Flower, dried material, top view. h. Flower, lower intertidal zone specimen, fresh material. i. Stigmas and crest of ovary. j. Immature seed. All illustrations are from holotype material (*Ferren 2807*) except b (fresh material) and h (paratype, *Ferren 2804*).

Puerto Peñasco, 31°16′N, 113°14′W, 9 Oct 1989, *Watson 973-12,13* (ARIZ, UCSB).

DISTRIBUTION AND HABITAT

Suaeda puertopenascoa is endemic to the northern Gulf of California and apparently is restricted to the estuaries along the northwestern coast of Sonora, where it occurs in the vicinity of Estero las Lisas, approximately 40 km N of Puerto Peñasco, and S to the vicinity of Estero la Pinto, approximately 25 km S of Puerto Peñasco. Along the northeastern gulf coast of Baja California in the vicinity of San Felipe, we have observed only *S. esteroa* in estuarine wetlands. We have no evidence that *S. puertopenascoa* occurs along the central Gulf of California from the vicinity of Bahia de Kino and southward. It appears to be restricted to estuarine wetlands northward of the occurrence of mangroves.

Suaeda puertopenascoa grows as linear groupings or scattered individuals in low marsh habitats along margins of tidal lagoons and banks of tidal channels. It colonizes open sand to silt substrates and usually occurs upslope from barren tidal flats and channel bottoms. Individuals established in lower elevations along a tidal slope are generally taller (110 versus 35 cm) and more erect in growth form than those found growing in higher elevations. It often stands taller than the frequently associated species *Batis maritima* L., *Distichlis palmeri* Fassett, *Salicornia virginica* L., and *S. bigelovii* Torr.

RELATIONSHIPS: MORPHOLOGY, PHENOLOGY, ECOLOGY

Suaeda puertopenascoa belongs to Sect. *Heterosperma* Iljin, a grouping of annuals and herbaceous perennials most frequently associated with saline and alkaline wetland habitats. This section is characterized by bilaterally symmetrical flowers, 2–3 stigmas arising directly from the top of the ovary, perianth segments often with appendages, stems which are usually not branched from the base, and seeds monomorphic or dimorphic. Species of *Suaeda* in North America that produce two distinct seed types, a dull-brown and a black-shiny type, are apparently restricted to the section. The brown seed types are relatively adherent to the perianth, light to dark brown, with a thin, membranous, testa, dull, flat to slightly plano-convex, with a prominent embryo, and generally larger than the black type. The black seed types are typically not adherent to the perianth, black to reddish-black or brown, or brownish-red, with a hard, thick testa, shiny, generally biconvex, with embryo not prominent. In North America, annuals in Sect. *Heterosperma* include *S. maritima* (L.) Dumort., *S. rolandii* Bassett & Crompton, *S. linearis* (Elliott) Moq., *S. calceoliformis* (Hook.) Moq., *S. occidentalis* Wats., *S. mexicana*

TABLE 1. COMPARISONS OF SELECTED CHARACTERS OF *SUAEDA ESTEROA* AND *SUAEDA PUERTOPENASCOA* IN SONORA, MEXICO. [1] = fresh specimens. [2] = range, mean and sample number were based on measurements of vegetative fresh specimens collected during January, 1989 and 1990.

Character	*S. esteroa*	*S. puertopenascoa*
Stature[1], cm	(15–)25–45(–60)	(35–)45–90(–110)
Branches and leaves arrangement	alternate	usually opposite
Leaf length[2], cm		
Subtending leaves	2.5–4.1, x̄ = 3.2 (n = 75)	3.0–6.8, x̄ = 4.8 (n = 75)
Branch leaves	2.0–3.3, x̄ = 2.6 (n = 95)	2.5–5.0, x̄ = 3.7 (n = 90)
Inflorescence	densely clustered	loosely spaced
No. flowers/dichasium	(3–)5–6(–8)	invariably 3
Fruiting calyx width[1], mm	2–3	3–4(–5)
Calyx lobes	without pronounced basal horizontal wings	with pronounced basal horizontal wings
Seed type	dimorphic	monomorphic
Seed width, mm	brown (1.2–)1.7(–2.0) black (1.0–)1.1(–1.2)	brown (2.0–)2.5(3.0)

(Standley) Standley and *S. jacoensis* I. M. Johnston (Hopkins and Blackwell 1977; Bassett and Crompton 1978).

Suaeda puertopenascoa appears most closely related to *S. esteroa,* the only other perennial North American species of the section. They are sympatric in estuaries of coastal northwestern Sonora but can be distinguished by ecological, morphological and phenological characteristics. *Suaeda puertopenascoa* is restricted to the low marsh zones and *S. esteroa* commonly occupies the middle to high marsh zones.

Morphological characters that can consistently be used to distinguish *S. puertopenascoa* from *S. esteroa* are listed in Table 1. Vegetatively, the most striking differences between the species are in stature, leaf length, and branch and leaf arrangement. *Suaeda puertopenascoa* is generally taller in height than *S. esteroa,* with the largest plants of both taxa being displayed in the lower-most limits of their distribution. Even though leaf size and degree of succulence appears to be variable with age and environmental extremes, in both species the subtending leaves to developing axillary branches are always larger than the leaves of branches. Average leaf length, however, is consistently longer in *S. puertopenascoa* than in *S. esteroa.* The distinguishing feature of opposite leaves in *S. puertopenascoa* is otherwise found only in *S. jacoensis,* an annual species endemic to western Coahuila, Mexico.

Reproductive characters that generally distinguish *S. puertopenascoa* from *S. esteroa* are a more loose or open inflorescence, with

FIG. 2. Habitats of *Suaeda* spp. in estuarine wetlands in the vicinity of Puerto Peñasco, Sonora, Mexico. A. *S. puertopenascoa,* low marsh zone. B. *S. esteroa,* middle marsh zone. C. *S. moquinii,* along margins of estuary.

flowers typically not congested and clusters distant, the consistent production of three flowers per dichasium, and larger fruit and seed sizes. We have never observed the black seed type in *S. puertopenascoa.* In the vicinity of Puerto Peñasco, we observed that *S. esteroa* predominantly produces the brown seed type that is consistently smaller than that of *S. puertopenascoa,* and rarely produces the black seed type in this region. Along the southern California estuarine wetlands, both seed types have been observed in *S. esteroa* plants, with the black seed type described by Ferren and Whitmore (1983). Bassett and Crompton (1978) have used seed characters as one of the morphological features to distinguish between two annual species in Canada. Likewise, seed type and size appear to be important diagnostic characters to distinguish between perennial taxon in Mexico.

Field observations and experimental field plantings at Puerto Peñasco reveal that *S. puertopenascoa* remains vegetative the first year after germination and does not flower until the second year, whereas *S. esteroa* flowers during the first growing season and then may die in some habitats or persist in others. Anthesis and seed maturation in populations of *S. puertopenascoa* appear to be more seasonally limited than that of *S. esteroa. Suaeda puertopenascoa* initiates flowering in early summer (June) and produces mature seed during late fall (October through November). In the vicinity of Puerto Peñasco, *S. esteroa* generally initiates flowering in mid-summer (July) and seed reaches maturity from late fall through winter (October through December) and occasionally through early spring (March). As seed maturity is reached, leaves and calyces of *S. puertopenascoa* turn yellow to yellowish-orange and become deciduous in late fall, generally before new vegetative material is produced; whereas those of *S. esteroa* often turn yellow to red or burgundy and can persist through winter during the same time that new vegetative portions are produced.

In general, species of *Suaeda* occupy different portions of the upland to low marsh gradient along the tidal shores of estuaries of northwestern Sonora (Fig. 2). Coastal desert scrub, dunes, saline-alkali wetlands and upper margins of estuaries are often characterized by the shrub *S. moquinii* (Torrey) E. Greene, which belongs to Sect. *Limbogermen* Iljin. Upper marsh habitats often support scattered individuals or small clusters of *S. esteroa,* which rarely occupies the lower marsh zones. Lower marsh habitats often support scattered individuals or linear clusters of *S. puertopenascoa.* There are no available data to suggest that *S. puertopenascoa* and *S. esteroa* are interfertile.

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TAXONOMY AND BIOGEOGRAPHY OF *PRIMULA* SECT. *CUNEIFOLIA* (PRIMULACEAE) IN NORTH AMERICA

Sylvia Kelso
Department of Biology, Colorado College,
Colorado Springs, CO 80903

Abstract

Section *Cuneifolia* is one of the smallest but most discrete sections in the large genus *Primula.* Its three members are characterized by cuneate leaves with dentate margins, globose capsules, and involute leaf vernation, and they are geographically distributed between the Sea of Okhotsk in Asia east to the Sierra Nevada of California. The three North American taxa are *P. cuneifolia* subsp. *cuneifolia, P. cuneifolia* subsp. *saxifragifolia,* and *P. suffrutescens. Primula cuneifolia* subsp. *saxifragifolia* is redefined here on the basis of its self-fertile homostylous flowers. It probably originated in the late Pleistocene at the edge of the Alaskan ice sheets when climatic perturbations disrupted the pollinator fauna. Section *Cuneifolia* is most closely allied to the widely disjunct sect. *Auricula* found in the mountains of central Europe. Although small, sect. *Cuneifolia* may have phylogenetic significance at the generic and family level due to its developmental patterns, biogeography, and reproductive biology.

Within the large genus *Primula* L. (Primulaceae, ca. 500 species), section *Cuneifolia* Balfour is one of the smallest and most biogeographically interesting groups. The three member species are distributed from northern Japan and northeastern Asia along the Sea of Okhotsk, through southern Alaska and the coastal mountains of Canada, and in the Sierra Nevada of California. The section is defined by cuneate leaf blades with dentate margins, conspicuous glandular development, globose capsules, and by the involute vernation of emergent leaves. The latter character is common in other genera in the Primulaceae, but is shared by only three of the thirty seven currently recognized sections in *Primula,* and considered primitive for the genus (Wendelbo 1961).

Two of the three species in sect. *Cuneifolia* are found in North America. *Primula suffrutescens* A. Gray is a rhizomatous species endemic to the Sierra Nevada in California. *Primula cuneifolia* Ledebour is found commonly in the Aleutian Islands, and more rarely throughout interior Alaska and the coast ranges south to British Columbia. It is also found in Asia as far south as northern Japan, along with the third member of the section, *P. nipponica* Yatabe, an alpine endemic on the island of Honshu.

Within the section, there has been taxonomic confusion only with the widespread species, *P. cuneifolia.* Four infraspecific taxa have

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been previously described, based entirely on vegetative characters such as scape height, leaf length, and leaf dentation. In this paper I examine *P. cuneifolia* in North America and redefine two subspecies based on reproductive biology: *P. cuneifolia* subsp. *cuneifolia* which is distylous, and *P. cuneifolia* subsp. *saxifragifolia* which is homostylous.

Primula sect. *Cuneifolia* Balfour. J. Roy. Hort. Soc. 39:178. 1913.

Key to Members of Sect. *Cuneifolia* in North America

a. Plants rhizomatous, leaves in clusters, often marcescent at stem base. .... *P. suffrutescens*
a′. Plants not as above.
  b. Flowers distylous. .... *P. cuneifolia* subsp. *cuneifolia*
  b′. Flowers homostylous. .... *P. cuneifolia* subsp. *saxifragifolia*

Primula cunefolia Ledebour, Mem. Acad. Imp. Soc. St. Petersburg 5: 522. 1815. See subspecies headings for synonymy and typification.

Plants efarinose with capitate glands on vegetative parts, glabrous. Stems herbaceous, not rhizomatous. Scape to 12 cm high, densely glandular. Leaves including petiole to 6 cm long, 0.8–1 cm wide, broadly cuneate, margins coarsely dentate, blade tapering to winged petioles. Involucral bracts lanceolate, plane at the base, densely glandular, to 0.5 cm long. Umbels 2–9 flowered; pedicels 0.3–2 cm long. Calyx green, 0.4–0.6 cm long, urceolate, divided up to ⅔ the length by lanceolate teeth. Corolla deep pink to rose, rarely white, throat yellow; tube 0.5–1.2 cm long, slightly exserted from the calyx; 1.2–2.5 cm broad, deeply cleft. Stamens ca. 1.5 mm long. Stigma more or less capitate. Capsule globose at maturity, slightly shorter than the calyx. Seeds brown, 1–1.5 mm long, reticulate, angular with flanged edges.

Primula cuneifolia Ledebour subsp. **cuneifolia** (Fig. 1A)—TYPE: USSR. "in Sibiria transbaicalensis". *Tilesius s.n.*? (holotype, LE?).

P. cuneifolia var. *Dubyi* Pax in Engler, Pflanzenreich, Primulaceae 112, 4:237. 1905.—TYPE: USSR. Siberia, Ajan. *Tiling 204* (holotype, LE?).

P. cuneifolia var. *elongata* Busch, Fl. Sib. & Orient. Extrem. 4:79. 1925.—TYPE: E. Busch, Fl. Sib. and Orient. Extrem. 4:78. Fig. B. 1925.

Scapes usually greater than 5 cm in height. Leaf petioles distinct, up to 4 cm long. Umbels with 3–9 distylous flowers. Anthers in pin flowers located near the middle of the corolla tube, stigma located just above the annulus; positions reciprocal in thrum flowers. Chro-

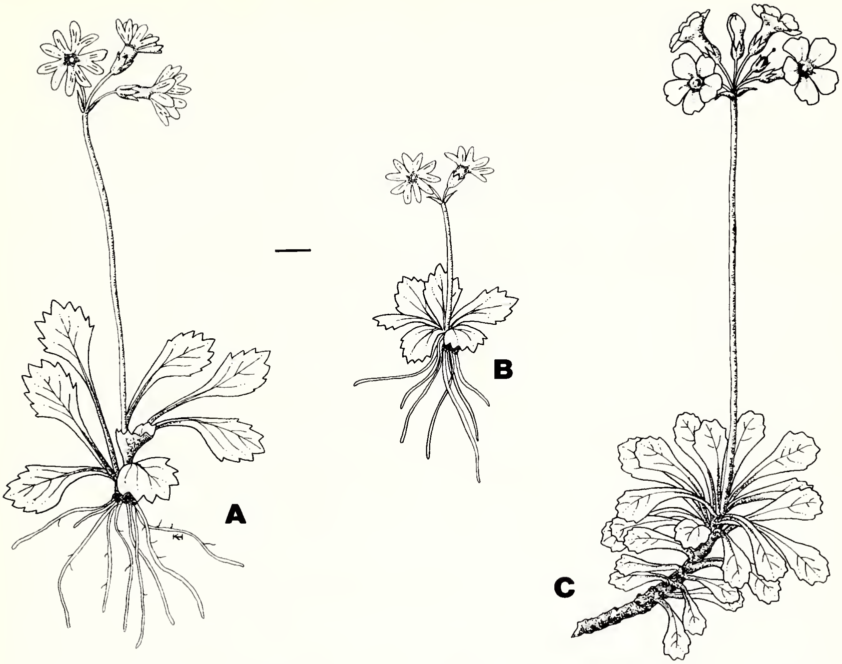

FIG. 1. A. *Primula cuneifolia* subsp. *cuneifolia.* B. *P. cuneifolia* subsp. *saxifragifolia.* C. *P. suffrutescens.* Bar indicates 1 cm.

mosome number: $2n = 22$ (Attu Island: Friedman 83-3 at ALA; Kamtschatka: Sokolovskaya 1968).

Distribution. Moist mixed herb meadows with acidic bedrock in Asia, along the Sea of Okhotsk from Hokkaido north to the Bering Strait; in North America known only from the Aleutian Islands of Attu, Agattu, and Adak (Fig. 2A).

Representative specimens. USA., Alaska, Aleutian Islands. Adak, *O'Farrell 145* (ALA), *Rausch 28* (CAS); Agattu, *Trapp 23* (COLO); Attu, *Brockner 5* (COLO), *Chandler s.n.* (GH), 28 Jun 1952, *Coe s.n.* (CAS), *Friedman 83-3* (ALA), *Hultén 6790* (CAS), *Trapp 3* (ALA), *Van Schaack 43-A* (E), *Williams 3113* (ALA).

Primula cuneifolia Ledebour subsp. **saxifragifolia** (Lehm.) Sm. & Forrest (Fig. 1B)—*Primula* nov. sp. "saxifragaefol." (nomen nudum) Langsdorff, Reise um die Welt. 1812.—*Primula saxifragifolia* Lehmann, Monograph Primulaceae 89, t. 9. 1817.—*P. cuneifolia* var. *saxifragifolia* (Lehm.)Pax *in* Engler, Das Pflanzenreich, Primulaceae 112. 1905.—*P. cuneifolia* ssp. *saxifragifolia* (Lehm.) Sm. & Forrest, Notes Roy. Bot. Garden Edinburgh 16:20. 1928.—TYPE: USA. Alaska, Aleutian Islands, Unalaska, "Herb. Fischer" Unidentified collector, possibly *Langsdorff s.n. in 1805* (holotype, LE?, isotype, K!).

Scape less than 3.5 cm in height. Leaf petioles indistinct, up to 1 cm in length. Umbels with 1–4 homostylous flowers. Anthers and stigma located adjacent to one another near upper portion of corolla tube. Chromosome number: $2n = 22$ (*Kelso 85-20* at ALA).

Distribution. Moist alpine meadows and rocky slopes in Alaska throughout the Aleutian Islands and along the Bering Sea coast north to the Seward Peninsula, throughout the interior in alpine regions N to the Alaska Range, to the S in coastal mountains to northern Vancouver Island. Distribution in Asia unclear, but apparently common along the Bering Sea coast (Fig. 2A).

Representative specimens. USA, Alaska, Aleutian Islands, Adak, 20 Jun 1945, *Chandler s.n.* (CAS); Akuktan, *Macoun 94290* (GH); Amchitka, *Erdman 551* (COLO); Atka, *Eyerdam 1316* (K); Unalaska, *Friedman 81-37* (ALA); Unimak, *Eyerdam 1841* (CAS). Alaska Peninsula, Chignik, 19 Jul 1934, *Flock s.n.* (CAS); Cold Bay, 1924, *Cladden s.n.* (CAS); Port Moller, 11 Jul 1927, *Haley s.n.* (CAS); McNeil RIver, *Taggert 12* (CAS, COLO); Ugaiushuk Island, *Lawhead 137* (ALA). Alaska Range, Copper Mountain, *Mexia 2096A* (CAS); Denali National Park, *Teare 1636* (ALA); Kantishna Hills, *Kelso 85-20, 85-21, 85-22* (ALA); Lake Nerka, *Roberson 468* (ALA); Mt. Eielson, *Viereck 1165* (ALA, COLO, GH); Peters Hills Mts., *Siplivinsky 806* (ALA); Talkeetna Mts., *Helmstetter 110-79* (ALA). Alexander Archipelago, Juneau, *Anderson 6353* (GH), *Taylor 85* (ALA); Prince of Wales Island, *Vorobik 42* (ALA). Bering Sea, Golovin, *Rynning 1025* (ALA); Goodnews Bay, *Williams 3356* (ALA); Nunivak Island, *Utermohle 32* (ALA); St. Lawrence Island, 1928, *Haley s.n.* (CAS); St. Matthew Island, 8 Jul 1927, *Haley s.n.* (CAS). Chugach Mts., Hatcher Pass, *Harms 2925* (ALA); Seward, *Calder 5638* (GH); Thompson Pass, *Cooper 85-2* (ALA).

The Alaskan *Primula saxifragifolia* was made a subspecies of *P. cuneifolia* by Smith and Forrest (1928), based on their survey of the limited material then available from Alaska. The nature of the subspecies was extensively reviewed by Hultén (1937) who concluded that the Aleutian Island material described by Lehmann differed only in height, leaf size, and number of flowers. The homostylous flowers were first noticed by Smith and Fletcher (1948) but they were unable to survey enough material to detect if this character was diagnostic.

My examination of now ample material from Alaska indicates that *Primula cuneifolia* subsp. *saxifragifolia* is homostylous. This is the only feature that consistently distinguishes it from subsp. *cu-*

neifolia, although some vegetative characters can be useful as well. Subspecies *saxifragifolia* tends to be shorter than its Asiatic counterpart, and flowers often appear before the scape develops, although scape elongation continues during and after anthesis. It also tends to have shorter petioles and fewer flowers than subsp. *cuneifolia.* Because the morphological differences between the subspecies overlap and reproductive biology is the only feature that reliably distinguishes them, it seems appropriate to retain subspecific rank for these taxa.

Primula cuneifolia is represented in Japan by two additional taxa, subsp. *hakusanensis* (Franch.) Smith & Forrest, and subsp. *heterodonta* (Franch.) Smith & Forrest. The former is distinguished by its more shallow dentation of the leaf margins, and the latter by its irregular dentation. Both are distylous, and narrowly endemic to alpine areas on the northern island of Honshu.

Primula suffrutescens A. Gray, Proc. Amer. Acad. Arts 7:371. 1868. (Fig. 1C)—TYPE: USA, California, Sierra Nevada, "trail up Silver Mt.", *Brewer 2047* (holotype, GH; isotype, US!).

Plants efarinose with capitate glands on vegetative parts, glabrous. Stems strongly rhizomatous, not woody, often densely covered with marcescent leaves. Scape to 15 cm high, bearing dense rosettes of leaves at the apex. Leaves including the petiole to 4 cm long, blade somewhat fleshy, 0.5–0.9 (11) cm wide, cuneate-spathulate, margins crenate to dentate with 3–8 teeth, tapering gradually to indistinct winged petioles. Involucral bracts lanceolate, plane at the base, densely glandular. Umbels 2–9 flowered; pedicels 0.4–1.2 cm long. Flowers distylous. Calyx green, 0.4–0.8 cm long, urceolate, divided up to ⅔ the length by lanceolate teeth. Corolla rose-pink, throat yellow, tube 0.6–1.0 cm long, twice the length of the calyx; limb 1.0–2.0 cm wide, lobes emarginate. Stamens ca. 2 mm long, located at the top of the corolla tube in thrum plants and near the middle in pin plants; stigma capitate, located in reciprocal positions to stamens. Capsule globose, ca. 5 mm in diameter, slightly shorter than the calyx. Seeds brown, 1–1.5 mm long, reticulate, angular with flanged edges. Chromosome number: $2n = 44$ (Bruun 1932).

Distribution. Rocky alpine slopes above 3300 meters, in weathered granite soils and rock fissures of the Sierra Nevada and northern mountains of California (Fig. 2B).

Representative specimens. USA, California, Alpine Co., Folger Peak, *Eggleston 9621* (GH); Fresno Co., Mt. Gould, *Sharsmith 3218* (GH); Inyo Co., Kearsarge Pass trail west of Independence, *Alexander and Kellogg 3258* (GH, US); Madera Co., volcanic ridge east of Minaret Lake, *Sharsmith 4539B* (GH); Mono Co., hill above

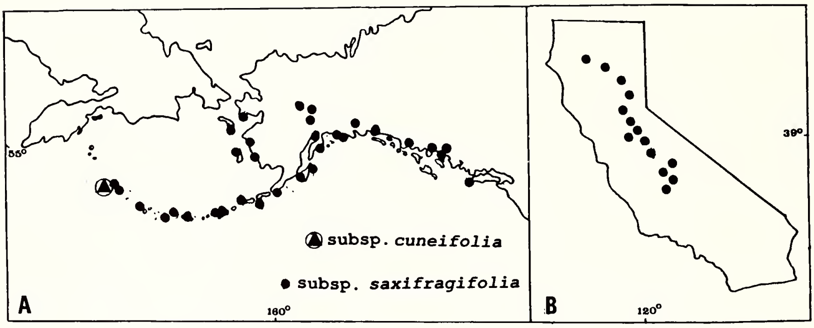

FIG. 2. A. Distribution of *Primula cuneifolia* in North America. B. Distribution of *P. suffrutescens.* Dots indicate more than 1 collection.

Mammoth, *Clausen 70-102* (GH); Nevada Co., above Troy Lake, 25 Jul 1896, *Sonne s.n.* (GH); Placer Co., Ward's Peak, *Sonne 214* (GH); Plumas Co., Luther Ridge between Wade Lake and Spencer Lake, 12 Aug 1969, *Williams s.n.* (G); Siskiyou Co., Caribou Basin near Sawtooth Ridge, *Ferlatte 1045* (K); Trinity Co., 4 miles north of Dedrick, *Hitchcock 5397* (GH); Tulare Co., Sky Blue Lake, *Howell 26007* (GH).

Primula has long been known as an example of distyly (Darwin 1884), a reproductive syndrome where two floral morphs exist with reciprocal placement of androecium and gynoecium. Distylous Primulas have a strong intramorph incompatibility system that dictates obligate outcrossing mediated by insect pollen vectors. In comparison, a simple mutation can create a self-compatible homostylous morph with juxtaposed sexual organs (Ganders 1979). Because self-compatibility and the proximity of anthers and stigma facilitate self-fertilization, homostyly is highly adaptive for colonization and may be of selective advantage when pollinator service becomes unreliable (Baker 1966).

The two subspecies of *Primula cuneifolia* described here differ principally in their reproductive biology: subsp. *cuneifolia* is distylous and subsp. *saxifragifolia* is homostylous. I believe they represent an outcrossing progenitor and a self-fertile derivative, respectively. The change in reproductive biology probably occurred during the Pleistocene when climatic perturbations and glacial fluctuations had a severe impact on the insect fauna of the Aleutian-Commander-Kurile island chain (Lindroth 1963), with presumable consequences for pollination. Selection for assured fertilization could thus promote the establishment of a mutant homostylous morph. Subspecies *saxifragifolia* probably originated near the ice margin and spread rapidly as the Aleutian glaciers began to retreat ca. 11,000 years ago (Thorson and Hamilton 1986). It may not have been able to compete with the outcrossing populations in the ice-free areas to the south, and consequently migrated only to the east as the ice retreated and left open habitats. Today subsp. *saxifragifolia* is found principally in North America except for a few locations in the Commander Islands and Kamtschatka. In North America subspecies *cuneifolia* inhabits only the western Aleutian Islands, and most of its distribution lies in Kamtschatka. This subspecies, and the additional distylous taxa found in Japan, may be limited to the Asiatic coast by contemporary pollinator and/or climatic restrictions.

The evolutionary position of *Primula suffrutescens* is problematic. As a tetraploid, it is the only polyploid in the section. Like the Asiatic members, it is found on igneous metamorphosed bedrock. Unlike *P. cuneifolia* subsp. *saxifragifolia, P. suffrutescens* is distylous and thus not an efficient colonizer. It may represent the only extant member of a more continuous preglacial extension of sect. *Cuneifolia,* surviving glaciation at low elevations on the east slope of the Sierra Nevada.

As well as indicating a biogeographic link between the California mountains and northern Japan, *Primula* sect. *Cuneifolia* also provides a disjunct link to the European Alps. Cytologically, anatomically, and morphologically, this section is most similar to sect. *Auricula* Duby which is limited to mountainous regions of Europe. Section *Auricula* is known for the narrow endemism of its members, their tendency to hybridize in cultivation, and their high levels of polyploidy. It shares with sect. *Cuneifolia* the developmental character of involute vernation, and the morphological characters of toothed leaf margins, globose capsules, deeply divided calyces, capitate glands, and flanged seed margins. Rhizomes and persistent leaf remains similar to those seen in *P. suffrutescens* are common. Section *Auricula* differs from sect. *Cuneifolia* in having more coriaceous leaves, consistently higher chromosome numbers ($4x$–$11x$) and pollen exine with three separate rather than fused colpi (Spanowsky 1962). Smith and Fletcher (1948) first noted the resemblance of the two sections, and suggested that a common ancestor must have been extirpated in the Asiatic landmass between where the two sections are found today.

In spite of its small size and limited distribution, sect. *Cuneifolia* holds an important position in the genus *Primula.* Biogeographically it links Europe, Asia, and western North America; developmentally it appears to provide a link to other genera in the Primulaceae; and reproductively it provides an example of how an outcrossing breeding system can convert to selfing with taxonomic and biogeographic implications. Section *Cuneifolia* is one of the few well-defined sections in a taxonomically complex genus, and it may well provide important phylogenetic connections both within *Primula* and within the family Primulaceae.

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ANNOTATED CHECKLIST OF CALIFORNIA MYXOMYCETES

RICHARD L. CRITCHFIELD and RICHARD S. DEMAREE
Department of Biological Sciences,
California State University, Chico
Chico, CA 95929

ABSTRACT

An annotated list of the 282 species of Myxomycetes from California was compiled from the existing literature and herbarium records. Two new state records are reported.

This list of the Myxomycetes of California is based on literature reports and herbarium specimens. Original literature has been reviewed, and specimens of most taxa reported from the state are in the herbarium of the California State University Chico (CSUC). Those taxa not in the (CSUC) Herbarium were located in the Herbarium at the University of California (UC).

In the first report on the Myxomycetes of California, Phillips (1877) listed seven genera, 26 species, and one variety. Plunkett (1934) published an annotated list of 24 genera containing 87 species including varieties, all within a 100 mile radius of Los Angeles. Pratt and Pratt (1944) prepared a list for the San Francisco region, reporting 20 genera with 75 species, including varieties. Whitney (1978, 1980, 1982), using the moist chamber technique, reported seven new state records and six new species. Cox (1981) reported four new state records and one new species. In the most comprehensive and significant accounts of the Myxomycetes in California, Kowalski (1966, 1967a, 1973a, 1987), Kowalski and Curtis (1968, 1970) reported 71 new records.

Following the names of the taxa in the list are the relative abundance, substrate, and ecological distribution based on Ornduff's classification of California woodland plant communities (Ornduff 1974). (Ornduff's classification is abbreviated as follows: C—closed pine forest, M—montane forest 4000–6500′, N—north coastal forest, P—pinion juniper woodland, S—subalpine forest 6500–11,000′, and V—valley and foothill woodland 0–4000′.) Following these brief annotations are author and date citations of the earliest report of the taxon from California so far as we have been able to determine. If an asterisk (*) follows the annotations, we have been unable to substantiate the first direct literature citation of the species for the state. The nomenclature generally follows that of Martin and Alexop-

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oulos (1969) and Martin, Alexopoulos, and Farr (1983). Varieties have not been included.

One specimen of each new record has been deposited in the Herbarium of the Department of Biological Sciences, California State University, Chico (CSUC).

Annotated Checklist of California Myxomycetes

MYXOMYCETES
CERATIOMYXOMYCETIDAE
CERATIOMYXALES

Ceratiomyxaceae

Ceratiomyxa fruticulosa (Mull.) T. Macbr.—Common; C, M, N, S, V; decaying wood, leaves, and litter. (Plunkett 1934)

MYXOGASTROMYCETIDAE
LICEALES

Cribrariaceae

Cribraria argillacea (Pers.) Pers.—Common; M, N, S, V; decaying wood. (Pratt and Pratt 1944)

Cribraria aurantiaca Schrad.—Rare; V; decaying wood. (T. Macbride 1899)

Cribraria dictyospora Martin & Lovejoy—Rare; M, S, V; decayed wood. (Kowalski 1973a)

Cribraria ferruginea Meylan—Rare; N; dead coniferous wood. (Kowalski 1987)

Cribraria intricata Schrad.—Rare; M, S; decaying wood.*

Cribraria macrocarpa Schrad.—Common; M, N, S, V; dead wood, especially conifers. (Pratt and Pratt 1944)

Cribraria microcarpa (Schrad.) Pers.—Rare; N, V; decayed wood. (Macbride and Martin 1934)

Cribraria minutissima Schw.—Rare; M, V; decayed wood, often among mosses. (Kowalski and Curtis 1970)

Cribraria oregana H. C. Gilbert—Rare; V; decaying coniferous wood. (Martin and Alexopoulos 1969)

Cribraria piriformis Schrad.—Common; N; dead coniferous wood. (Pratt and Pratt 1944)

Cribraria purpurea Schrad.—Common; N; decayed wood. (Kowalski 1967a)

Cribraria rufa (Roth) Rost.—Common; M, N, S, V; decayed wood, mainly conifers. (Pratt and Pratt 1944)

Cribraria splendens (Schrad.) Pers.—Rare; N; decaying wood, mainly conifers. (Kowalski and Curtis 1968)

Cribraria violacea Rex—Common; N, V; dead wood, bark of living and dead trees, and on mosses. (Pratt and Pratt 1944)

Dictydium cancellatum (Batsch) T. Macbr.—Common; M, N, V; rotten wood. (Plunkett 1934)

Dictydium mirabile (Rost.) Meylan—Rare; M, S; decayed coniferous wood. (Martin and Alexopoulos 1969)

Lindbladia tubulina Fries
=*Lindbladia effusa* (Ehrenb.) Rost.—Rare; M; decayed wood, usually conifers. (Kowalski 1967a)

Liceaceae

Licea alexopouli M. Blackwell—Rare; V; developed on cow dung in moist chamber. (Mock and Kowalski 1976)

Licea biforis Morgan—Rare; M; bark of living trees. (Kowalski and Curtis 1968)
Licea castanea G. Lister—Rare; V; dead wood and bark. (Kowalski 1973a)
Licea deplanata (Kow.) Kow.
=*Licea aplanata* Kow.—Rare; V; on dead *Eucalyptus* leaves. (Kowalski 1970b)
Licea kleistobolus Martin—Rare; V; decayed wood. (Kowalski 1967a)
Licea lucens Nann.-Brem.—Rare; V; developed on bark in moist chamber. (Kowalski 1987)
Licea minima Fries—Common; M, V; dead wood, mainly conifers. (Cooke 1949)
Licea operculata (Wingate) Martin—Common; V; bark of living trees. (Kowalski 1987)
Licea parasitica (Zukal) Martin—Rare; N, V; bark of living trees. (Kowalski and Curtis 1970)
Licea pedicellata (H. C. Gilbert) H. C. Gilbert—Rare; V; bark of living trees. (Kowalski 1973a)
Licea perexigua Brooks & Keller—Common; N, V; bark of living trees and grapevines. (Keller and Brooks 1977)
Licea pusilla Schrad.—Rare; M, V; decayed wood. (Kowalski 1966)
Licea scyphoides Brooks & Keller—Common; N, V; bark of living trees. (Whitney 1982)
Licea tenera Jahn—Rare; V; dead wood, bark, and dung of herbivorous animals. (Kowalski and Curtis 1968)
Licea variabilis Schrad.—Common; M, V; decayed wood. (Kowalski 1967a)
Listerella paradoxa Jahn—Rare; V; dead leaves. (Kowalski 1967a)

Enteridiaceae

(Reticulariaceae)

Dictydiaethalium plumbeum (Schum.) Rost.—Common; V; dead wood. (Plunkett 1934)
Enteridium lycoperdon Bull.—Rare; V; dead wood. (Macbride 1899)
Enteridium minutum Sturgis—Rare; M, S; decayed wood. (Kowalski 1987)
Enteridium olivaceum Ehrenb.—Rare; M, S; dead coniferous wood. (Macbride and Martin 1934)
Enteridium splendens Morgan—Rare; V; dead wood. (Plunkett 1934)
Lycogala epidendrum (L.) Fries—Common; M, N, V; decaying wood. (Macbride 1899)
Lycogala exiguum Morgan—Rare; decayed wood. (Kowalski and Curtis 1970)

ECHINOSTELIALES

Clastodermataceae

Barbeyella minutissima Meylan—Common; M, N; bryophytes on decayed wood, rarely on wood alone. (Kowalski 1973a)
Clastoderma debaryanum Blytt—Common; N; dead wood, bark, old fungal sporophores, and miscellaneous debris. (Pratt and Pratt 1944)
Clastoderma pachypus Nann.-Brem.—Common; V; in moist chamber on bark from living trees. (Whitney 1982)

Echinosteliaceae

Echinostelium apitectum Whitney—Common; P; juniper bark in moist chamber. (Whitney 1980)
Echinostelium brooksii Whitney—Common; P; juniper bark in moist chamber. (Whitney 1980)
Echinostelium coelocephalum Brooks & Keller—Rare; V; bark of living trees and grapevines in moist chamber. (Whitney 1980)

Echinostelium colliculosum Whitney & Keller—Common; M, P, V; bark of living trees and grapevines in moist chamber. (Whitney 1980)
Echinostelium corynophorum Whitney—Rare; M, P; juniper bark in moist chamber. (Whitney 1980)
Echinostelium fragile Nann.-Brem.—Common; M, P; bark of living trees and shrubs in moist chamber. (Whitney 1980)
Echinostelium lunatum Olive & Stoianovitch—Rare; V; tree bark and grapevines in moist chamber. (Whitney 1980)
Echinostelium minutum de Bary—Common; M, N, P, V; dung, dead wood, leaf litter, and bark of living trees and shrubs in moist chamber. (Kowalski and Curtis 1970)
Echinostelium paucifilum Whitney—Rare; M, P; juniper bark in moist chamber. (Whitney 1980)

TRICHIALES

Dianemaceae

Calomyxa metallica (Berk.) Nieuwl.
=*Margarita metallica* (Berk.) A. Lister—Common; M, V; rotting wood. (Plunkett 1934)
Dianema aggregatum Kow.—Common; M, S; stems of living shrubs and plant debris, near melting snow. (Kowalski 1967c)
Dianema corticatum A. Lister—Common; V; dead coniferous wood. (Martin 1948b)
Dianema depressum (A. Lister) A. Lister—Rare; M; dead wood. (Kowalski 1967a)
Dianema nivale (Meylan) G. Lister
=*Dianema andersonii* Morgan—Rare; M; twigs and debris. (Kowalski and Curtis 1968)
Dianema subretisporum Kow.—Rare; M; decaying fir twigs. (Kowalski 1967a)

Trichiaceae

Arcyodes incarnata (Alb. & Schw.) O. F. Cook—Rare; V; dead wood. (Kowalski 1966)
Arcyria cinerea (Bull.) Pers.—Common; N, V; dead wood and herbivorous animal dung. (Plunkett 1934)
Arcyria denudata (L.) Wettst.—Common; M, N, V; dead wood. (Plunkett 1934)
Arcyria elaterensis Mulleavy—Rare; V; on horse dung in moist chamber. (Mulleavy 1977)
Arcyria ferruginea Sauter—Rare; N; dead wood. (Macbride 1922)
Arcyria incarnata Pers.—Common; M, N, S, V; decayed wood. (Plunkett 1934)
Arcyria insignis Kalchbr. & Cooke—Common; N, V; dead wood and herbaceous stems. (Kowalski 1966)
Arcyria magna Rex—Rare; N, V; dead wood. (Kowalski 1987)
Arcyria nutans (Bull.) Grev.—Common; N, V; decaying wood. (Macbride 1922)
Arcyria occidentalis (T. Macbr.) Lister—Rare; V; dead wood. (Kowalski 1966)
Arcyria oerstedtii Rost.—Common; N, V; rotten wood. (Plunkett 1934)
Arcyria pomiformis (Leers) Rost.—Common; V; dead wood. (Plunkett 1934)
Arcyria versicolor Phill.—Common; M, N, S; dead coniferous wood. (Phillips 1877)
Calonema luteolum Kow.—Common; V; cow dung. (Kowalski 1969a)
Hemitrichia abietina (Wigand) G. Lister—Rare; V; dead wood. (Martin 1948b)
Hemitrichia calyculata (Speg.) Farr—Rare; S; on decayed wood.*
Hemitrichia clavata (Pers.) Rost.—Common; V; dead wood. (Plunkett 1934)
Hemitrichia karstenii (Rost.) A. Lister—Rare; V; dead wood. (Plunkett 1934)
Hemitrichia montana (Morgan) T. Macbr.—Common; M, S; dead coniferous wood. (Macbride 1899)
Metatrichia vesparium (Batsch) Nann.-Brem.
=*Hemitrichia vesparium* (Batsch) T. Macbr.—Common; V; all types of rotted wood. (Plunkett 1934)

Oligonema flavidum (Peck) Peck—Rare; V; rotted wood. (Macbride and Martin 1934)

Oligonema schweinitzii (Berk.) Martin—Common; V; decayed wood. (Martin 1948b)

Perichaena chrysosperma (Currey) A. Lister—Common; V; tree bark. (Plunkett 1934)

Perichaena corticalis (Batsch) Rost.—Common; V; dead wood and bark. (Plunkett 1934)

Perichaena depressa Libert—Common; V; dead wood and bark. (Plunkett 1934)

Perichaena minor (G. Lister) Hagelst.—Rare; V; cow dung. (Cox 1981)

Perichaena vermicularis (Schw.) Rost.—Rare; V; dead herbaceous stems, leaves, and bark. (Kowalski 1966)

Prototrichia metallica (Berk.) Massee—Common; M, S; dead coniferous wood. (Macbride 1922)

Trichia alpina (R. E. Fries) Meylan—Common; M, S; dead coniferous wood, living shrub stems, and duff. (Cooke 1949)

Trichia botrytis (Gmel.) Pers.—Common; M, S, V; dead and decaying wood. (Pratt and Pratt 1944)

Trichina brunea Cox—Rare; M; on cow dung in moist chamber. (Cox 1981)

Trichia contorta (Ditmar) Rost.—Common; V; dead wood. (Plunkett 1934)

Trichia decipiens (Pers.) T. Macbr.—Rare; V; dead wood. (Macbride 1922)

Trichia favoginea (Batsch) Pers.—Common; M, S, V; dead wood. (Pratt and Pratt 1944)

Trichia flavicoma (A. Lister) Ing—Rare; V; dead hardwood leaves. (Kowalski 1974)

Trichia floriformis (Schw.) G. Lister—Rare; N, V; dead wood. (Plunkett 1934)

Trichia lutescens (A. Lister) A. Lister—Rare; V; dead wood. (Martin 1948b)

Trichia macbridei M. E. Peck—Rare; V; dead bark. (Kowalski 1987)

Trichia scabra Rost.—Common; V; dead wood and bark. (Pratt and Pratt 1944)

Trichia subfusca Rex—Rare; N; dead wood. (Kowalski 1987)

Trichia varia (Pers.) Pers.—Common; M, S, V; dead and decaying wood. (Macbride 1899)

Trichia verrucosa Berk.—Rare; N; decaying wood. (Kowalski 1973a)

PHYSARALES

Didymiaceae

Diachea leucopodia (Bull.) Rost.—Common; V; dead leaves, sticks, and living plants. (Macbride 1899)

Diderma alpinum Meylan—Common; M, S; dead wood and twigs. (Plunkett 1934)

Diderma antarctica (Speg.) Sturgis—Rare; V; on dead leaves. (Plunkett 1934)

Diderma asteroides (A. & G. Lister) G. Lister—Common; N, V; dead wood, bark, and leaves. (Macbride 1922)

Diderma brooksii Kow.—Rare; V, M, S; decaying conifer twigs, near the melting snow. (Kowalski 1968a)

Diderma chondrioderma (de Bary & Rost.) G. Lister—Common; N, V; tree bark and mosses. (Martin 1948b)

Diderma deplanatum Fries—Rare; M, S; dead coniferous wood, twigs, and needles. (Cooke 1949)

Diderma effusum (Schw.) Morgan—Rare; V; dead leaves. (Kowalski 1987)

Diderma globosum Pers.—Common; N, V; dead wood and litter. (Pratt and Pratt 1944)

Diderma hemisphaericum (Bull.) Hornem.—Common; V; dead leaves. (Plunkett 1934)

Diderma lyallii (Massee) T. Macbr.—Common; M, S; dead coniferous wood and litter. (Cooke 1949)

Diderma montanum (Meylan) Meylan—Rare; M, S; dead coniferous wood and litter. (Martin and Alexopoulos 1969)

Diderma nigrum Kow.—Rare; M, S; dead coniferous twigs. (Kowalski 1968b)

Diderma niveum (Rost.) T. Macbr.—Common; M, S; dead coniferous wood and twigs. (Macbride 1899)

Diderma ochraceum Hoffm.—Rare; N; decaying wood. (Kowalski 1967a)
Diderma radiatum (L.) Morgan—Rare; M, S; dead wood. (Plunkett 1934)
Diderma spumarioides (Fries) Fries—Rare; V; dead leaves and litter. (Plunkett 1934)
Diderma subcaeruleum Kow.—Common; S; decaying coniferous twigs, near the melting snow. (Kowalski 1968b)
Diderma subincarnatum Kow.—Common; V; dead leaves. (Kowalski 1967b)
Diderma testaceum (Schrad.) Pers.—Rare; N, V; dead leaves and litter. (Phillips 1877)
Diderma trevelyani (Grev.) Fries—Common; V; dead wood and leaves. (Macbride 1899)
Diderma umbilicatum Pers.—Rare; V; decayed wood, leaves, and *Eucalyptus* bark. (Kowalski and Curtis 1970)
Didymium anellus Morgan—Common; N, V; dead leaves. (Plunkett 1934)
Didymium bahiense Gottsberger—Rare; N; dead leaves. (Kowalski 1987)
Didymium clavus (Alb. & Schw.) Rab.—Common; V; dead wood, leaves, and twigs. (Plunkett 1934)
Didymium difforme (Pers.) S. F. Gray—Common; N, V; dead leaves and twigs. (Plunkett 1934)
Didymium dubium Rost.—Common; M, N, S, V; dead leaves and twigs. (Pratt and Pratt 1944)
Didymium intermedium Schroet.—Rare; V; dead leaves and twigs. (Plunkett 1934)
Didymium iridis (Ditmar) Fries—Common; V; dead leaves, twigs, and wood; sometimes on mosses.*
Didymium karstensii Nann.-Brem.—Rare; V; jackrabbit dung in moist chamber. (Merrill 1969)
Didymium laxifila G. Lister
=*Didymium aurantipes* Brooks & Kow.—Rare; V; decaying leaves. (Kowalski 1973b)
Didymium megalosporum Berk. & Curt.—Rare; V; dead leaves and plant litter.*
Didymium melanospermum (Pers.) T. Macbr.—Common; V; dead wood, leaves, and twigs. (Plunkett 1934)
Didymium minus (A. Lister) Morgan—Rare; V; decaying leaves. (Kowalski 1966)
Didymium nigripes (Link) Fries—Common; N, V; dead leaves, twigs, and bark. (Pratt and Pratt 1944)
Didymium nullifilum (Kow.) Farr
=*Squamuloderma nullifila* Kow.—Rare; V; cow dung in moist chamber. (Kowalski 1972b; Farr 1982)
Didymium ovoideum Nann.-Brem.—Rare; M, S; on cow dung in moist chamber. (Cox 1981)
Didymium quitense (Pat.) Torrend—Rare; S; dead leaves and twigs. (Macbride and Martin 1934)
Didymium rugulosporum Kow.—Rare; V; on cow dung. (Kowalski 1969b)
Didymium serpula Fries—Rare; V; dead leaves. (Kowalski 1966)
Didymium squamulosum (Alb. & Schw.) Fries—Common; N, V; dead leaves. (Phillips 1877)
Didymium trachysporum G. Lister—Rare; N; dead leaves, twigs, and wood. (Pratt and Pratt 1944)
Didymium tubi-crystallinum Nann.-Brem. & Critchf.—Rare; M; on dead coniferous wood. (Nannenga-Bremekamp and Critchfield 1988)
Didymium vaccinum (Dur. & Mont.) Buchet—Rare; V; on dead leaves. (Macbride and Martin 1934)
Didymium verrucosporum Welden—Rare; V; dead leaves. (Kowalski 1987)
Lepidoderma aggregatum Kow.—Rare; M, S; decaying coniferous bark. (Kowalski 1987)
Lepidoderma carestianum (Rab.) Rost.—Common; M, S; forest litter. (Macbride & Martin 1934)
Lepidoderma chailletii Rost.—Common; M, S; forest litter and stems of living shrubs. (Macbride 1922)

Lepidoderma crustaceum Kow.—Common; M, S; leaves, twigs, and litter. (Kowalski 1967a)

Lepidoderma granuliferum (Phill.) R. E. Fries—Common; M, S; leaves, twigs, litter, and stems of living shrubs. (Macbride and Martin 1934)

Lepidoderma tigrinum (Schrad.) Rost.—Rare; V; decayed wood and on mosses. (Martin 1948b)

Mucilago crustacea Wiggers—Rare; V; stems of herbaceous plants. (Kowalski 1973a)

Trabrooksia applanata Keller—Rare; N, V; bark of living trees in moist chamber. (Whitney 1982)

Physaraceae

Badhamia affinis Rost.—Common; N, V; decayed leaves. (Kowalski and Curtis 1968)

Badhamia bispora Whitney—Rare; M; bark and decayed wood in moist chamber. (Whitney 1978)

Badhamia capsulifera (Bull.) Berk.—Rare; N, V; dead bark. (Pratt and Pratt 1944)

Badhamia crassipella Whitney & Keller—Common; N, V; dead and decaying wood. (Whitney and Keller 1982)

Badhamia goniospora Meylan
=*Badhamia dearnessii* Hagelst.—Rare; M, V; dead wood. (Kowalski 1975a)

Badhamia foliicola A. Lister—Common; N, V; dead leaves and twigs. (Plunkett 1934)

Badhamia gracilis (T. Macbr.) T. Macbr.—Common; V; dead wood. (Macbride and Martin 1934)

Badhamia macrocarpa (Ces.) Rost.—Common; V; dead wood, bark, and litter. (Plunkett 1934)

Badhamia nitens Berk.—Common; M, N, V; dead wood and bark; sometimes lichens and mosses. (Plunkett 1934)

Badhamia obovata (Peck) S. J. Smith—Rare; N, V; dead wood. (Kowalski 1973a)

Badhamia ovispora Racib.—Rare; V; dead wood, litter, and herbivorous animal dung. (Merrill 1969)

Badhamia papaveracea Berk. & Rav.—Rare; V; on *Populus* bark. (Plunkett 1934)

Badhamia populina A. & G. Lister—Rare; V; dead wood and leaves. (Martin 1948b)

Badhamia panicea (Fries) Rost.—Common; V; dead wood and leaves. (Macbride 1922)

Badhamia utricularis (Bull.) Berk.—Common; M, N, V; dead wood and leaves. (Plunkett 1934)

Badhamia versicolor A. Lister—Common; V; bark of living and dead trees, often on mosses. (Plunkett 1934)

Badhamiopsis ainoae (Yama.) Brooks & Keller
=*Badhamia ainoae* Yama.—Common; V; bark of living trees. (Kowalski and Curtis 1968)

Craterium aureum (Schum.) Rost.—Common; N, V; dead wood and leaves. (Macbride and Martin 1934)

Craterium leucocephalum (Pers.) Ditmar—Common; N, V; dead leaves. (Macbride 1922)

Craterium minutum (Leers) Fries—Common; N, V; dead leaves. (Plunkett 1934)

Fuligo cinerea (Schw.) Morgan—Rare; V; forest litter. (Plunkett 1934)

Fuligo intermedia T. Macbr.—Common; M, S, V; forest litter. (Cooke 1949)

Fuligo septica (L.) Wiggers—Common; M, V; decayed wood and litter. (Plunkett 1934)

Leocarpus fragilis (Dicks.) Rost.—Common; M, S; dead wood and forest debris, and sometimes on soil. (Macbride 1922)

Physarum albescens Ellis—Common; M, S; dead wood and forest debris. (Cooke 1949)

Physarum alpinum (A. & G. Lister) G. Lister—Rare; M, S; litter and dead twigs. (Lister 1910)

Physarum auripigmentum Martin—Common; M, S; dead coniferous wood. (Martin 1948a)

Physarum auriscalpium Cooke—Rare; V; dead wood, debris, and moss. (Plunkett 1934)

Physarum bitectum G. Lister—Common; M, V; dead leaves and twigs. (Plunkett 1934)

Physarum bivalve Pers.—Common; V; dead leaves and twigs.*

Physarum brunneolum (Phill.) Massee—Common; V; dead wood and leaves. (Macbride 1899)

Physarum carneum G. Lister & Sturgis—Common; N, V; dead wood and twigs. (Pratt and Pratt 1944)

Physarum cinereum (Batsch) Pers.—Common; V; dead leaves.*

Physarum compressum Alb. & Schw.—Common; V; dead wood, leaves and debris. (Macbride 1922)

Physarum contextum (Pers.) Pers.—Rare; M; dead leaves and twigs. (Phillips 1877)

Physarum crateriforme Petch.—Common; V; rough barked trees. (Kowalski 1967b)

Physarum decipiens Curtis—Common; M, S; dead wood. (Martin and Alexopoulos 1969)

Physarum diderma Rost.—Common; V; bark of dead wood and associated mosses. (Kowalski 1967b)

Physarum didermoides (Pers.) Rost.—Common; V; dead wood, leaves, and bark. (Plunkett 1934)

Physarum flavidum (Peck) Peck—Rare; V; mosses and dead wood.*

Physarum galbeum Wingate—Common; V; dead wood. (Martin and Alexopoulos 1969)

Physarum gilkeyanum H. C. Gilbert—Rare; V; leaf litter. (Kowalski and Curtis 1968)

Physarum globuliferum (Bull.) Pers.—Common; N, V; dead wood. (Plunkett 1934)

Physarum gyrosum Rost.—Rare; M; deer dung. (Cox 1981)

Physarum javanicum Racib.—Rare; V; dead wood and twigs. (Martin and Alexopoulos 1969)

Physarum leucophaeum Fries—Common; V; dead wood and leaves.*

Physarum leucopus Link—Common; V; dead leaves and wood. (Kowalski and Curtis 1970)

Physarum luteolum Peck—Rare; M; dead leaves. (Kowalski and Curtis 1970)

Physarum mortonii T. Macbr.—Common; V; dead leaves. (Plunkett 1934)

Physarum mutabile T. Macbr.—Rare; N, V; dead leaves. (Martin 1948b)

Physarum notabile T. Macbr. Common; N, V; dead wood and bark. (Pratt and Pratt 1944)

Physarum nutans Pers.—Common; N, V; dead wood. (Phillips 1877)

Physarum penetrale Rex—Rare; N, V; dead wood. (Plunkett 1934)

Physarum psittacinum Ditmar—Rare; M.

New California record. Butte Co., Magalia Reservoir, 731 m, on dead wood of *Cornus nutallii* Audubon, 20 Oct. 1986, (CSUC) #49871

Physarum pusillum (Berk. & Curt.) Lister—Rare; V; dead leaves.*

Physarum sessile Brandza—Rare; V; dead leaves. (Plunkett 1934)

Physarum spinisporum U. Eliass.—Rare; M, V; on cow dung. (Cox 1981)

Physarum superbum Hagelst.—Rare; M, S.

New California record. Tehama Co., Morgan Summit, 1755 m, on living leaves of *Arctostaphylos nevadensis* A. Gray, 6 May 1989, (CSUC) #49872

Physarum tenerum Rex—Rare; N; on dead wood. (Pratt and Pratt 1944)

Physarum vernum Somm.—Rare; V; dead leaves and twigs. (Plunkett 1934)

Physarum viride (Bull.) Pers.—Common; M, V; on dead wood. (Macbride 1922)

Willkommlangea reticulata (Alb. & Schw.) Farr

=*Cienkowskia reticulata* (Alb. & Schw.) Kuntze—Rare; V; dead wood. (Macbride 1922)

STEMONITOMYCETIDAE
STEMONITALES

Schenellaceae

Schenella microspora Martin—Rare; N; dead wood. (Martin 1961)
Schenella simplex T. Macbride—Rare; N, V; dead wood. (Macbride and Martin 1934)

Stemonitaceae

Amaurochaete atra (Alb. & Schw.) Rost.
=*Amaurochaete fuliginosa* (Sow.) T. Macbr.—Rare; V; dead and decaying bark. (Kowalski and Curtis 1968)
Amaurochaete comata G. Lister & Brandza—Rare; V; dead bark. (Kowalski 1987)
Amaurochaete ferruginea T. Macbr. & Martin—Rare; V; dead coniferous wood. (Macbride and Martin 1934)
Amaurochaete tubulina (Alb. & Schw.) T. Macbr.—Rare; N; dead wood. (Martin 1948b)
Colloderma oculatum (Lipert) G. Lister—Rare; N; rotting wood. (Kowalski 1987)
Comatricha acanthodes Alexop.—Rare; N, V; living tree bark in moist chamber. (Whitney 1982)
Comatricha alpina Kow.—Common; M, S; dead coniferous wood. (Kowalski 1973a, 1973b)
Comatricha anomala Rammeloo—Rare; V; decayed wood. (Kowalski and Demaree 1987)
Comatricha elegans (Racib.) G. Lister—Common; V; dead wood. (Plunkett 1934)
Comatricha ellae Harkonen—Rare; V; decayed bark and wood. (Kowalski 1987)
Comatricha fimbriata G. Lister & Cran.—Common; V; dead wood and bark of living trees. (Martin 1948b)
Comatricha fusiforme Kow.—Common; M, S; dead coniferous wood. (Kowalski 1968b)
Comatricha irregularis Rex—Common; M, N, S; dead wood. (Pratt and Pratt 1944)
Comatricha laxa Rost.—Common; V; dead wood. (Whitney 1982)
Comatricha longipila Nann.-Brem.—Rare; V; bark of living trees. (Kowalski 1987)
Comatricha lurida A. Lister—Common; N, V; on dead leaves. (Kowalski and Curtis 1970)
Comatricha nigra (Pers.) Schroet.—Common; M, N, S, V; dead wood. (Plunkett 1934)
Comatricha pencillata Nann.-Brem. & Yamam.—Rare; M; dead wood. (Kowalski 1987)
Comatricha pulchella (C. Bab.) Rost.—Common; N, V; dead wood and dead and living leaves. (Pratt and Pratt 1944)
Comatricha rubens A. Lister—Common; N, V; dead leaves and bark. (Kowalski and Curtis 1968)
Comatricha subcaespitosa Peck—Rare; V; dead wood. (Macbride and Martin 1934)
Comatricha suksdorfii Ellis & Ev.—Common; M, S; dead coniferous wood. (Plunkett 1934)
Comatricha tenerrima (M. A. Curt.) G. Lister—Rare; V; on bark. (Plunkett 1934)
Comatricha typhoides (Bull.) Rost.—Common; N, V; decayed wood. (Macbride 1899)
Diacheopsis effusa Kow.—Rare; M, S; on dead coniferous twigs near melting snow. (Kowalski 1975b)
Diacheopsis metallica Meylan—Common; M, S; living shrub stems and plant debris near melting snow. (Kowalski 1975a)
Diacheopsis spinosifila Farr & Critchf.—Rare; M; dead coniferous wood. (Farr 1988)
Enerthenema intermedium Nann.-Brem. & Critchf.—Rare; M; dead coniferous wood. (Nannenga-Bremekamp and Critchfield 1988)
Enerthenema malanospermum T. Macbr. & Martin—Common; M, S; dead coniferous wood. (Cooke 1949)
Enerthenema papillatum (Pers.) Rost.—Common; M, S; dead coniferous wood. (Kowalski 1966)

Lamproderma acanthosporum Kow.—Rare; M, S; dead coniferous twigs and living shrubs. (Kowalski 1968b)

Lamproderma arcyrioides (Sommerf.) Rost.—Common; M, S; coniferous wood, twigs, and debris; alpine. (Cooke 1949)

Lamproderma arcyrionema Rost.—Rare; M, S; dead coniferous twigs. (Kowalski 1973a)

Lamproderma atrosporum Meylan—Common; M, N, S; dead coniferous twigs and debris. (Pratt and Pratt 1944)

Lamproderma biasperosporum Kow.—Common; M, S; dead coniferous wood. (Kowalski 1968b)

Lamproderma carestiae (Ces. & de Not.) Meylan—Common; M, S; dead coniferous twigs and debris. (Cooke 1949)

Lamproderma columbinum (Pers.) Rost.—Rare; N; dead coniferous wood. (Pratt & Pratt 1944)

Lamproderma cribrarioides (Fries) R. E. Fries—Common; M; dead coniferous twigs and debris. (Kowalski 1967b)

Lamproderma disseminatum Kow.—Rare; M, S; dead coniferous wood. (Kowalski 1970b)

Lamproderma echinosporum Meylan—Common; M, S; coniferous litter, herbaceous plant debris, and living shrubs. (Kowalski 1970a)

Lamproderma fuscatum Meylan—Common; M, S; litter, wood, and twigs of conifers. (Kowalski 1968b)

Lamproderma gulielmae Meylan—Rare; M; dead leaves and twigs. (Kowalski 1967a)

Lamproderma maculatum Kow.—Common; M, S; coniferous duff and branches of living shrubs. (Kowalski 1970b)

Lamproderma muscorum (Lev.) Hagelst.—Rare; V; decaying leaves. (Kowalski 1970a)

Lamproderma sauteri Rost.—Common; M, S; coniferous debris and broadleaf shrubs and stems. (Macbride and Martin 1934)

Lamproderma scintillans (Berk. & Br.) Morgan—Common; N, V; dead branches, logs, and leaves of broadleaf trees. (Plunkett 1934)

Leptoderma iridescens G. Lister—Rare; V; plant litter. (Macbride and Martin 1934)

Macbrideola argentea Nann.-Brem. & Yamam.—Rare; V; on bark in moist chamber. (Kowalski 1987)

Macbrideola cornea (G. Lister) Alexop.—Common; N, V; variety of woody plants. (Martin and Alexopoulos 1969)

Macbrideola decapillata H. C. Gilbert—Common; V; on bark in moist chamber. (Kowalski 1973a)

Macbrideola martinii (Alexop. & Beneke) Alexop.—Rare; M; on juniper bark in moist chamber. (Kowalski 1987)

Paradiacheopsis cribrata Nann.-Brem.—Rare; N; oak bark in moist chamber. (Kowalski 1987)

Paradiacheopsis microcarpa (Meylan) Mitchell—Rare; M, V; tree bark in moist chamber. (Kowalski 1987)

Paradiacheopsis rigida (Brandza) Nann.-Brem.—Rare; N, V; tree bark in moist chamber. (Kowalski 1987)

Stemonitis axifera (Bull.) T. Macbr.—Common; M, N, V; dead wood. (Macbride 1899)

Stemonitis flavogenita Jahn—Common; V; dead wood and plant debris. (Plunkett 1934)

Stemonitis fusca Roth—Common; N, V; dead wood. (Macbride 1899)

Stemonitis herbatica Peck—Rare; N, V; dead wood and bark. (Plunkett 1934)

Stemonitis hyperopta Meylan—Rare; V; dead wood. (Kowalski 1966)

Stemonitis nigrescens Rex—Common; V; dead wood and bark. (Plunkett 1934)

Stemonitis pallida Wingate—Rare; V; dead wood. (Kowalski 1966)

Stemonitis smithii T. Macbr.—Rare; N; dead wood. (Pratt and Pratt 1944)

Stemonitis splendens Rost.—Common; N, V; dead wood. (Plunkett 1934)
Stemonitis virginiensis Rex—Rare; V; dead wood. (Plunkett 1934)

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NOTES

THE DISTRIBUTION OF LEAF MORPHS IN *ALLIUM CRATERICOLA* EASTW.—DALE W. MCNEAL, Biological Sciences Department, University of the Pacific, Stockton, CA 95211.

Allium cratericola Eastw., a California endemic, is represented in the southern half of the state by several populations, all of which produce two leaves per scape. Populations from northern portions of the state tend to have one leaf per scape, though a population from Lake Co. and one from Glenn Co. have two and a population from Colusa Co. is mixed in this regard. As reported earlier (Mortola and McNeal, Aliso 11:27–35, 1985) all populations of *A. cratericola* are $n = 7$ except for a single population from volcanic soil on Table Mountain in Butte Co., which is $n = 14$. In the Coast Ranges there has been a large disjunction in the known distribution of *A. cratericola.* Several populations occur north of San Francisco Bay including the one containing both one- and two-leaved individuals on serpentine soil in Colusa Co., two-leaved populations in adjacent eastern Lake Co. on serpentine, and one-leaved populations on serpentine in western Lake Co., and on volcanic soils in Napa Co. The species next occurs in two-leaved populations on soils derived from sedimentary rock in Ventura Co.

Recently, while annotating *Allium* specimens from the herbarium at Pinnacles National Monument, I encountered a single sheet of what appeared to be *A. cratericola.* The specimen was well past anthesis and the leaves were missing, making it impossible to determine leaf number. With the permission of the National Park Service I visited the original collection site on the Balconies Formation in the Monument in late March, 1990 to re-collect the species (*McNeal 3659,* CPH), confirm its identity, determine leaf number, and obtain bud material for chromosome counts. Further, at the suggestion of the Park Service I visited a geologically similar site on the northeast side of South Chalone Peak, at the south end of the Monument, 7.5 km south of the Balconies site. Here I discovered a second population (*McNeal 3660,* CPH). Both collection sites contained populations of two-leaved individuals and were located on loose talus slopes derived from Miocene volcanic rock at 625 m and 875 m, respectively. The Monument superintendent later reported the discovery of a population of approximately 100 individuals on the north slope of North Chalone Peak in similar habitat (Selznick pers. comm.)

The chromosome number of the South Chalone Peak population was determined to be $n = 7$ from aceto-orcein squashes of pollen mother cells from fresh buds. Buds from the Balconies were too advanced to get counts. This population will be counted from bulbs grown at Stockton, CA next spring. There is no reason to suspect that the chromosome number in this population will differ from the South Chalone Peak population.

Allium cratericola is found on a variety of soils, but generally in barren areas where edaphic or other environmental factors result in reduced competition from other species. On the basis of our previous study (Mortola and McNeal loc. cit.) and these new collections I have prepared a map (Fig. 1) showing the distribution of one- and two-leaved populations of *Allium cratericola.* Because the leaves tend to break off at the soil level even after the plants have been pressed and because most collectors do not note the leaf number on their collections, this character is often difficult to determine in herbarium material. The collections represented on the map include the known distribution of the species; leaf numbers have been determined either from intact specimens or from careful counting of leaf bases where the blades were broken off.

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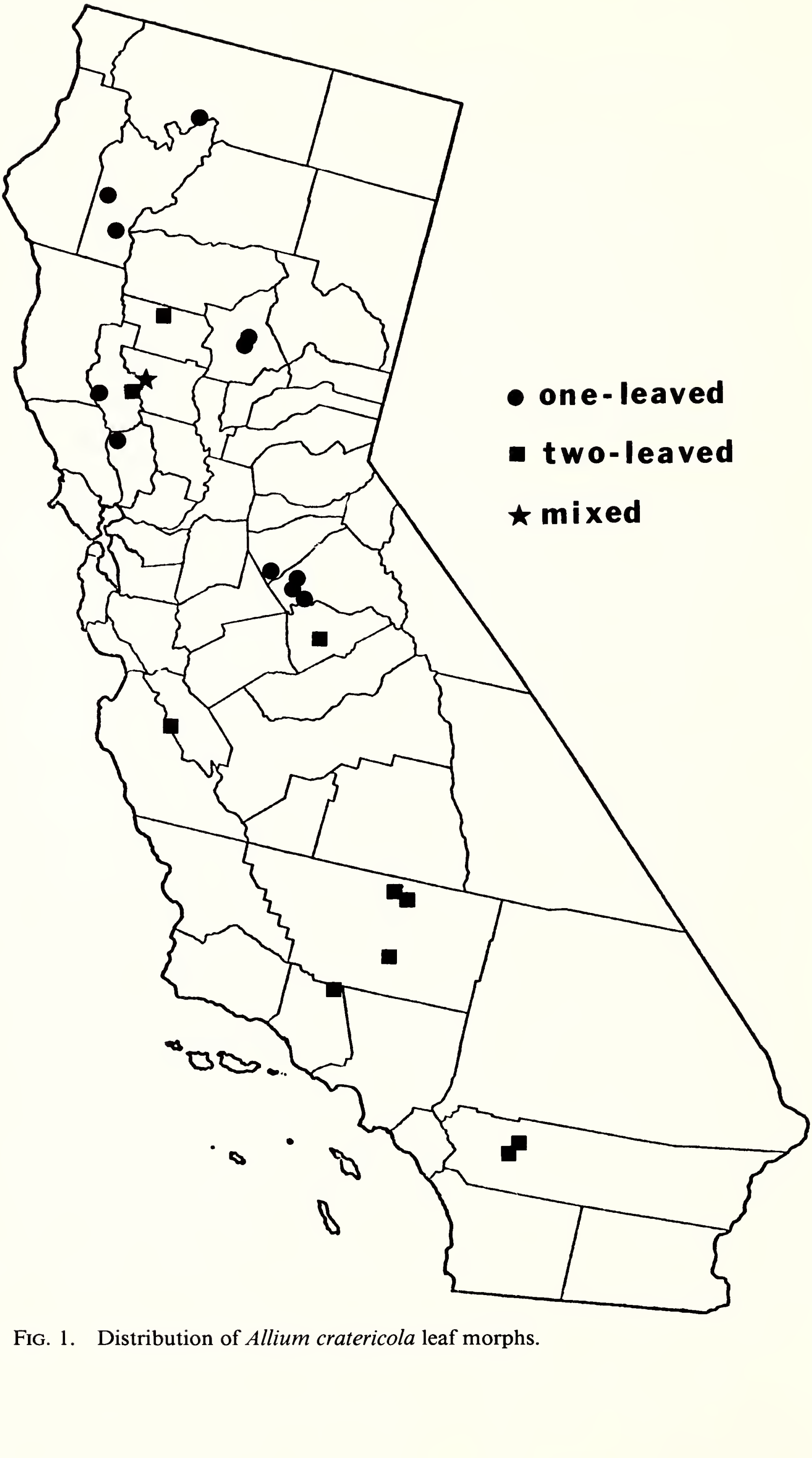

FIG. 1. Distribution of *Allium cratericola* leaf morphs.

No obvious environmental factor or combination of factors explains the distribution of one- and two-leaved forms. As the map indicates, however, the two-leaved form has the more southern distribution, with all but three of the known populations occurring south of latitude 37°30′N. Except for the mixed population in Colusa Co., several collections from Walker Ridge in eastern Lake Co., and a single sheet (*Stebbins 8003,* WS!) from Red Mountain in Glenn Co., all of the northern populations are one-leaved.

Some herbarium labels report that the eastern Lake Co. population is mixed with regard to leaf number; however, a careful field survey indicates that this is not the case. An unusual feature of this population is the frequent withering of one leaf well before the other. As this first leaf breaks off, the plant appears to have only a single leaf, and very careful observation of the leaf base is required to detect the second.

The Colusa Co. population (*Mann s.n.* DAV, WS), on the other hand, definitely has a small percentage of one-leaved individuals. These appear to be smaller and to have smaller bulbs than the two-leaved plants and may represent young plants blooming for the first time, but they are definitely present and have not been noted in any other population.

Leaf number alone does not seem to be a reliable character for recognizing taxa in *Allium* (Mortola and McNeal loc. cit.). The occurrence of a mixed population of *Allium cratericola* with regard to the number of leaves per bulb and the lack of any other consistent characters which separate the two forms argue that they are conspecific and do not deserve recognition as separate taxa, even at the varietal level.

I thank the National Park Service for their cooperation and Steve DeBenedetti for his assistance in the field. Critical reviews by R. M. Beauchamp and T. D. Jacobsen are deeply appreciated. A list of ca. 110 herbarium specimens, examined in preparing this distribution map, is available from the author.

(Received 20 Apr 1990; revision accepted 16 Aug 1990.)

TRANSFER OF *MAHONIA TRIFOLIOLATA* VAR. *GLAUCA* TO *BERBERIS.*—JOSEPH E. LAFERRIÈRE, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

While I was preparing the treatment of the Berberidaceae for the upcoming Manual of the Vascular Plants of Arizona, I learned that one of the names to be included in the work had never been formally transferred from *Mahonia* to *Berberis.* Reasons for preferring the latter generic name are discussed by Moran (Phytologia 52:221–226, 1982) and Laferrière & Marroquín (Madroño 37, in press, 1990). Validation of this transfer is as follows:

Berberis trifoliolata Moric. var. **glauca** (I. M. Johnston) M. C. Johnston ex Laferrière, comb. nov.

Berberis trifoliolata Moric. var. *glauca* (I. M. Johnston) M. C. Johnston *in* D. S. Correll & M. C. Johnston, Vascular plants of Texas 655, 1970, nomen nudum.—*Mahonia trifoliolata* (Moric.) Fedde var. *glauca* I. M. Johnston, J. Arn. Arbor. 31:190, 1950.

Berberis trifoliata Hartweg ex Lindl., Bot. Reg. 27:misc. 68, 1841.—*Mahonia trifoliata* (Hartweg ex Lindl.) Lavallée, Arboretum Segrezianum 16, 1877.

Berberis trifoliolata var. *glauca* is known from southeastern Arizona to central Texas to Hidalgo (Ahrendt, J. Linn. Soc. Bot. 57:1–410, 1961; Marroquín, Ph.D. diss., Northeastern University, Boston, 1972). It differs from var. *trifoliolata* by its glaucous, minutely pappilose epidermis. The latter is known only from southern and central Texas. M. C. Johnston (Vascular plants of Texas: a list, updating the manual of the vascular plants of Texas, 2nd ed., 1990) suggested that var. *glauca* should not be recognized at the varietal level because of mixed populations in central Texas. He does state, however, that there is no intergradation and that outside this area of overlap the two taxa are distinct. It is for these reasons that I prefer to continue to recognize the two varieties.

The oldest name for var. *glauca* is *Berberis trifoliata.* I. M. Johnston in reducing the taxon to varietal rank chose a new epithet to avoid confusion with the specific epithet "trifoliolata." According to the International Code of Botanical Nomenclature, priority rules apply only within a particular rank. The two names are based on separate types but clearly represent the same taxon.

(Received 6 Jul 1990; revision accepted 12 Oct 1990.)

REVIEW

Indicator Plants of Coastal British Columbia. By K. Klinka, V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. University of British Columbia Press, Vancouver, British Columbia. ix + 288 pages, diagrams, 183 p.p. of color photographs, references, tables, species index. ISBN 0-7748-0321-5.

This beautiful book is written for foresters, by foresters. It is also an excellent field manual for botanists in general and plant ecologists in particular. A short, succinct introductory chapter on "Concepts and methods related to indicator plants" leads into the next chapter on "Site attributes and indicator species". Plant indicators of the different climates found in coastal British Columbia, of soil moisture levels, available soil N, and soil surface materials (mull, mor, mineral, coarse rock, and surface water) are listed. That is, for the forest ecosystems of coastal British Columbia the authors set up the equation Vegetation = f(Environment), where "Vegetation" is qualitatively defined by individual species composition and the Environment is defined by a combination of climate and soil factors.

Unfortunately even the most elaborate experimental and statistical manipulations plant ecologists have so far conceived worldwide are limited to a tiny segment of this general equation—on both sides of the equal sign. But this is hardly news to plant ecologists.

The good news is that we now have an ecological guide based on a very broad and very deep field acquaintance with a most interesting forested area of North America. The guide needs testing, broadening, deepening, imitation.

A short, ecological site description for each of the 729 color-illustrated species of vascular plants, lichens, liverworts, and mosses accompanies each photograph. The description is succinct, accurate, and amazingly complete. The selected species cover a very wide range of habitats—from *Lysichitum americanum* on the wet side to *Agropyron spicatum* on the dry, from *Stellaria crispa* at low altitudes to *Leutkea pectinata* at high, from *Disporum hookeri* in shady sites to *Sedum spathulifolium* in sun-exposed sites, etc.

The book is useful, beautiful, innovative, the distillation of a very large mass of field experience.—Jack Major, Botany Department, University of California, Davis, 95816.

Madroño, Vol. 38, No. 1, p. 61, 1991

ANNOUNCEMENT

NEW PUBLICATION

SCHOENHERR, A. A. (ed.). 1990. *Endangered Plant Communities of Southern California: Proceedings of the 15th Annual Symposium.* Special Pubication No. 3 of the Southern California Botanists. Available for $10.00 plus $2.00 for tax and handling from Alan Romspert, Southern California Botanists, Department of Biological Sciences, California State University, Fullerton, CA 92634. Articles include a wealth of information on the status of southern California's endangered plant communities. Using photographs, tables, line drawings, and authoritative text, the authors have summarized the status of each of the communities and outlined plans for preservation and restoration. This should be an invaluable aid to laymen, botanists, habitat managers, and environmental consultants.

Following an introduction by the editor, Jon Keeley of Occidental College writes about California Valley Grassland. This article discusses the factors reponsible for loss of native grasses, includes a map showing the past and present distribution of native grasslands and concludes with a discussion of southern California locations where native perennial bunchgrass still occurs. Coastal Sage Scrub is covered by John Oleary from San Diego State University. He talks about species diversity, fire management, the effects of air pollution, and prospects for mitigation and restoration of this rapidly disappearing community. Ronald Quinn of Cal Poly Pomona describes the status of California Walnut Woodland and summarizes virtually all that is known of its distribution, composition, phenology, fire ecology, plant-animal relationships, and management. Wayne Ferren, Jr., manager of the University of California, Carpinteria Salt Marsh Reserve, gives a thorough review of southern California estuarine wetlands. The chapter is illustrated with fine photographs and in it Ferren characterizes a number of estuarine habitats and describes the potential impact of global warming and sea level rise on the future of these systems. Two articles are about Riparian Woodlands, one of the most endangered habitats in southern California. Peter Bowler of the University of California, Irvine, by means of a series of tables and graphics has thoroughly characterized the nature and importance of riparian habitats. Richard Zemball of the U.S. Fish and Wildlife Service has prepared a particularly thorough discussion of riparian habitat associated with the Santa Margarita and Santa Ana Rivers.

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Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

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Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum,* 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980). Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

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HERBIVORY AND THE DEMOGRAPHY OF THE CHAPARRAL SHRUB *CEANOTHUS GREGGII* (RHAMNACEAE)

STEPHEN H. BULLOCK
Department of Biology, San Diego State University,
San Diego, CA 92182-0057

and

Estación de Biología Chamela,
Universidad Nacional Autónoma de México, Apartado Postal 21,
48980 San Patricio, Jalisco, México

ABSTRACT

The distribution, size and reproduction of *Ceanothus greggii* were assessed in a six year old population, established from seed on a two hectare area burned in winter. Survivorship was an order of magnitude greater in plots fenced since the fire than in open plots. In fenced plots, height was not affected by proximity to shrubs of *Adenostoma fasciculatum* that had re-established by sprouting from lignotubers. In open plots, *C. greggii* that were located among the dense branches of *Adenostoma,* were taller than plants in uncovered microsites, where repeated clipping by *Sylvilagus bachmani* and other mammals was common. Tall and well-branched *C. greggii* were common in fenced plots and virtually absent in open plots. Flowering was restricted to taller plants, with 22% flowering in exclosures and 3% in open plots. By reversing the fencing treatment, I showed that one year's growth is affected by herbivores and *Adenostoma* cover, corresponding to the effects over six years. The size of burned areas may affect the growth and reproduction of *C. greggii* through an effect on the presence of mammalian herbivores.

The major causes of mortality in plant demography are often difficult to identify. For chaparral shrubs, the weight of opinion favors resource competition, accentuated by factors of stand structure, topography and climatic variation, as exemplified by studies of *Ceanothus* species that do not resprout after fire (Horton and Kraebel 1955; Schlesinger and Gill 1978; Montygierd-Loyba and Keeley 1987; Zammit and Zedler pers. comm.). However, herbivory by mammals can also be a major mortality factor, as shown by field experiments with plants 0–2 years old (Christensen and Muller 1975; Mills 1983, 1986; Kummerow et al. 1985). Because palatibility varies greatly among plant species (Biswell et al. 1952; Mills 1983; Rundel et al. 1987), herbivory can affect the relative abundance of species.

The major and manageable factors affecting both mortality and growth in post-seedling pre-reproductive populations are crucial subjects for basic demography (Cole 1954; Piñero et al. 1984) and

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its application (Usher 1976). For desert shrubs, the roles of interference and herbivory in population and community dynamics have been interpreted from static and dynamic aspects of size-spacing relations (McAuliffe 1984a, b; Manning and Barbour 1988). The present report focuses on a six year old population of the obligate seed-reproducing *Ceanothus greggii* A. Gray (Rhamnaceae) in chaparral dominated by resprouting *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae). The stand had been burned for experimental studies of factors influencing seedling establishment (Mills 1983, 1986; Kummerow et al. 1985). Here, the variables considered are both cumulative (density, size, spatial arrangement) and current (growth and reproduction), which are assessed for both long and short term experimental treatments.

METHODS

The study was conducted in northeastern San Diego County, California ("Sky Oaks", 33°22′N, 116°36′W) about 10.6 km NNE of Warner Springs. The site was on a westerly exposure, at an elevation of about 1500 m, with a shallow slope incline. The soil was a stony loamy sand on a micaceous schist bedrock. Mean minimum temperature from November through March was 0.4°C, and the mean maximum from June through September was 29.5°C. Mean annual precipitation (including snow) was 400 mm, with 16% falling between June and September (based on incomplete records, 1985–1987, from Sky Oaks).

The two-hectare study area was burned in December 1981, with the help of the California Department of Forestry and the U.S. Forest Service. The present report is based on twelve plots: six plots of 8 × 2 m, fenced in 1982 (Mills 1986), and six plots of 5 m radius marked out in late 1987. On these plots *Adenostoma fasciculatum* ("chamise") was the dominant, and *A. sparsifolium* Torrey ("redshank") was common on four rectangular plots but virtually absent elsewhere; *Ceanothus greggii* was a minor to co-dominant species; few other shrub species, a few herbs and no grasses were present on the plots. One side of the burned area was within 50 m of a *Quercus agrifolia* Neé woodland bordering a seasonal stream. The *Ceanothus,* established from seed in early 1982, and all *A. fasciculatum* and *A. sparsifolium* reestablished from sprouting lignotubers, were numbered, mapped in polar coordinates, and measured. Measurements included maximum height, maximum diameter, and diameter perpendicular to the maximum.

The spatial relationship of *Ceanothus* and *Adenostoma* spp. was not characterized by distances due to crown overlaps and the ambiguity of lignotuber location. Rather, the position of each *Ceanothus* plant was categorized with respect to cover by *Adenostoma* spp.

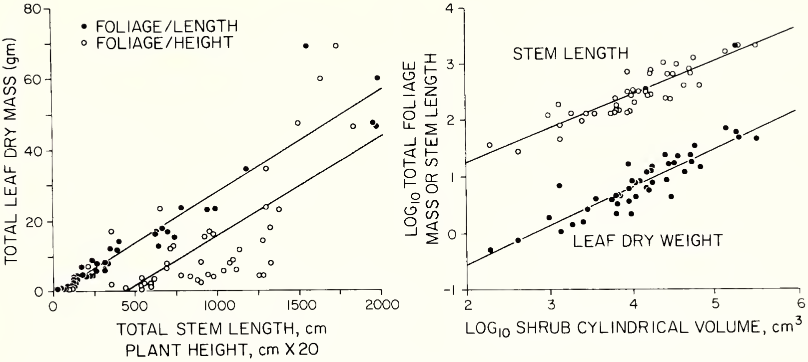

FIG. 1. Allometric relations of shrub height, total stem length, total foliage dry weight, and estimated volume for six year old *Ceanothus greggii*. (Note the scaling factor of 20 for plant height.)

bushes: 0 = completely exposed, 1 = barely shaded vertically, 2 = heavy cover, 3 = rooted among *Adenostoma* spp. sprouts or its low-lying branches. This is almost certain to have increased over six years, but with relatively less change for plants in dense cover. The growth form (density of branching) of each *Ceanothus* plant was categorized, from 1 (branching very sparse or none) to 3 (dense). Unfortunately *A. fasciculatum* could not be studied comparably to *Ceanothus,* because of the probability of post-1982 germination (Zammit and Zedler 1988), overlap of resprouts and post-burn plants, and non-uniform lateral expansion and decomposition of lignotubers (see Cox 1987).

In mid-April 1988 the fencing treatment (mammal exclosure) was modified to test the effects of introduction or exclusion of rabbits and deer after six years of regrowth. I fenced three of the open plots, and removed the fences from three old exclosures. The new fences were of 2.5 cm hexagonal mesh wire (like the 1982 fences), about 1.5 m high and placed slightly beyond the plot edge; the bottom was thoroughly staked. The fences and plots were checked repeatedly but showed no signs of rabbit or deer incursion. Censuses and measurements of the *Ceanothus* in all 12 plots were made in the subsequent period of dormancy, 14–23 February 1989. The measurements were biased against showing treatment effects, because rabbits cut many stems without affecting the single tallest or the shrubs' maximum diameters. Here, I refer to the treatments as O/O (open 1982–1988 and open 1988–1989), O/E (open/fenced), E/E and E/O. The results were compared by ANOVA's among plants (not plots), first for groups that were similar in 1982–1988 conditions, then for groups treated similarly in 1988–1989. Cover was examined as a second factor.

To quantify the relations between gross size, form, and foliage mass, plants outside the plots were selected to represent the three growth form categories in three cover categories (0, 1–2, 3), with five plants in each of the nine groups. Height and the two diameters were measured and the plants were harvested to obtain total leaf dry mass and total stem length. These plants had foliage masses of 1 to 69 g, heights from 6 to 92 cm, and total stem lengths of 28 to 1977 cm. Total dry weight of leaves had a close linear relation to total stem length (Fig. 1; $r^2 = 0.91$), which did not differ significantly among plants in different form classes. Foliage mass could be indexed more simply but less accurately by plant height ($r^2 = 0.50$). The qualitative form class 3 differed significantly from classes 1 and 2 in the slopes of both the stem length/plant height and foliage/height relations. To evaluate a volumetric size estimate, I used the height and mean of the diameters to calculate a cylindrical volume. Close relationships were found between log transformations of estimated volume and of measured foliage mass and stem length (Fig. 1; respectively, $r^2 = 0.826$ and 0.819, $F = 204.6$ and 195.1, $p < 0.0001$).

RESULTS

The average density of *Ceanothus greggii* in the exclosures was an order of magnitude higher than in the open plots (respectively, 11.6/m^2, range 4.4–24.9, and 1.0/m^2, range 0.6–2.0).

The height distributions were not significantly different among open plots, but these differed strongly from the exclosures (Fig. 2; respective means 25.8 ± 16.1 cm and 44.1 ± 17.0 cm; ANOVA by plots, $F = 40.6$, or treatments $F = 397.7$, $p < 0.0001$). There were some differences among the exclosures (Fisher LSD at 95%) but these did not obscure the contrast with open plots. There was a strong interaction between the exclosure treatment and cover ($F = 11.4$, $p < 0.0001$). On the open plots, the height of *Ceanothus* differed significantly between each of the cover categories, with the tallest plants rooted in the heaviest cover (Fig. 2; ANOVA by 4 cover categories $F = 25.9$, $p < 0.0001$). In the exclosures, however, there were no height differences between cover categories ($F = 1.8$, $p = 0.15$). The average diameter of the shrubs also differed between open and fenced plots (12.3 ± 7.9 cm and 18.5 ± 10.8 cm). The shape of the shrubs, as indexed by the ratio of height to the average diameter, differed between the cover categories in both the open plots and exclosures ($F = 48.5$ and 38.5, $p < 0.0001$), and among the exclosure plots themselves ($F = 5.8$, $p < 0.0001$) but not among the open plots. The calculated shrub volume did not differ among cover categories in either open or exclosure plots, but did differ among the exclosures ($F = 8.7$, $p < 0.0001$).

Flowering of the six year old *Ceanothus* plants was significantly

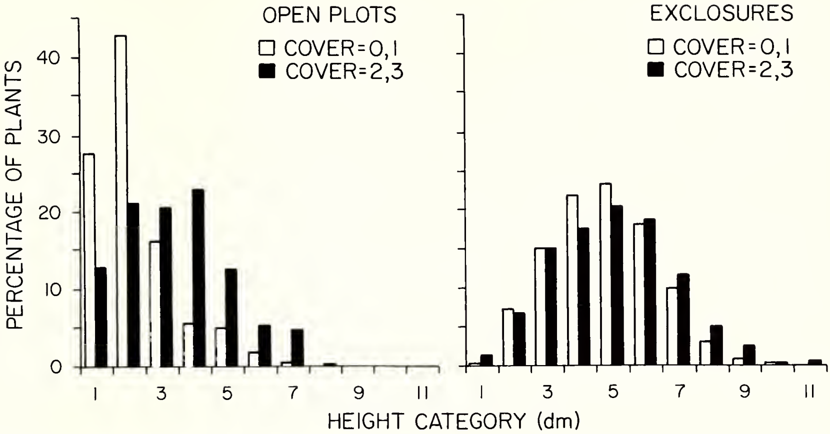

FIG. 2. Height distributions of six year old *Ceanothus greggii* on plots open or fenced since germination, with individuals categorized according to coverage by *Adenostoma* spp.

greater in exclosures (21.7%) than in the open plots (3%). Flowering plants differed in height between exclosure plots (ANOVA $F = 4.49$, $p = 0.0007$) as did non-flowering plants ($F = 5.80$, $p < 0.0001$). However, the mean height of non-flowering plants in all the exclosures taken together was 40.7 ± 15.4 cm, whereas flowering plants averaged 59.9 ± 14.7 cm (ANOVA $F = 259.9$, $p < 0.0001$). Flowering and non-flowering shrubs also differed in volume and shape (calculated from height and diameter; respectively, $F = 170.3$ and 24.5), but flowering shrubs actually had a lower height/diameter ratio. Flowering frequency in fenced plots was significantly higher at uncovered microsites (23%) than at densely covered microsites (7%; $\chi^2 = 12.7$, $p = 0.0054$). The number of plants setting fruit (17) was small, perhaps due to effects of a late April freeze.

Fresh deer tracks and pellets were occasionally found on the burned area but I did not observe characteristic feeding signs (Grinnell and Storer 1924). Evidence of rabbit feeding was abundant outside the exclosures. Accumulations of old and fresh fecal pellets were common. The many truncated stems of miniature *Ceanothus* had been cleanly clipped, not dessicated, broken, trampled, or torn. Clipped twigs were never noticed on the ground, but piles of fresh and drying leaves were common; apparently, the rabbits ate the stems and not (all) the leaves, as has been reported for *S. bachmani* with other *Ceanothus* species (Grinnell and Storer 1924; Orr 1940).

Parallel to the results for *Ceanothus,* the height of resprouting *Adenostoma* spp. "individuals" averaged less in the open plots than in the exclosures (72.9 ± 18.5 cm and 93.2 ± 29.6 cm, $F = 99.7$,

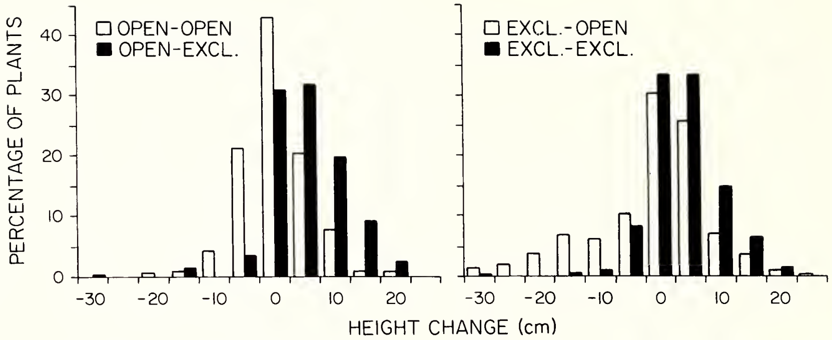

FIG. 3. Height increments for *Ceanothus greggii,* grouped by history of fencing (1982/1988–1988/1989).

$p < 0.0001$, but there were also differences among plots in each group). The respective average diameters differed similarly (75.3 ± 29.9 cm and 90.7 ± 37.1 cm).

Exclosure reversal experiment. Removal of fences (E/O plots) resulted in significant rabbit foraging by February 1989 as evidenced by the abundance of fecal pellets, piles of *Ceanothus* leaves, and cut stems on the shrubs. No new signs were found in the current exclosures (either E/E or O/E).

Height growth was three times greater in O/E than O/O *Ceanothus* (means = 6.9 cm and 2.2 cm, respectively, $F = 67.7$, $p < 0.0001$; Fig. 3). Cover by *Adenostoma* was positively associated with growth ($F = 5.0$, $p = 0.002$). Thus, in O/O plots *Ceanothus* growth increased from uncovered sites (−1.1 cm) to the densest cover (+3.7 cm). In the O/E treatment only completely uncovered plants differed.

Similarly, E/E plants grew much more than E/O plants (5.8 cm and 1.22 cm, $F = 50.0$, $p < 0.001$; Fig. 3). The interaction of cover and exclosure was also highly significant ($F = 9.5$, $p < 0.0001$), with mean increments for E/O plants increasing from −0.2 cm to 4.0 cm with increasing cover.

With regard to changes in average diameter for E/E and E/O plants, fencing in 1988 and cover were significant and interactive factors (respectively, $F = 17.8$, 10.3 and 9.0, all $p < 0.0001$). From uncovered to densely covered microsites, diameter growth of E/O plants ranged from −4.0 to 2.6 cm, whereas the opposite trend appeared for E/E plants, 0.2 to −0.02 cm. Cover was not a significant factor for O/O and O/E plants, but fencing did affect diameter growth (respectively, $F = 1.1$, $p = 0.37$, and $F = 61.6$, $p < 0.0001$).

In contrast, the O/O and E/O treatments did not differ in height growth ($p = 0.87$). For both groups, cover was a significant factor ($F = 6.7$, $p = 0.0002$). Growth was least for uncovered plants (−1.11

cm and −0.2 cm, respectively) and greatest for plants in dense cover (3.7 cm and 4.0 cm).

Comparing plants in the O/E and E/E treatments, the former grew more in height (6.9 cm and 5.8 cm, F = 6.14, p = 0.013), although they were generally smaller. Among plants in these groups, the effect of cover was marginal at best (F = 2.87, p = 0.0356), and did not interact with fencing history (p = 0.0764).

Also, in the 1989 census, 15 *Ceanothus* were found which were present only as unidentifiable stems in 1988 (73% were in E/E or O/E plots); their average height was 27.5 ± 14.8 cm. It was also notable that of the plants marked in 1988, 2.4% had all brown leaves and 1.8% had no leaves at all.

DISCUSSION

Herbivory, primarily by *Sylvilagus bachmani* was a dominant force in limiting the establishment of *Ceanothus greggii* seedlings at the Sky Oaks site (Mills 1983, 1986; Kummerow et al. 1985). This influence has continued throughout the juvenile phase, as shown by the contrast in density and size of *Ceanothus* between open and fenced plots, the relation of size to cover in open plots, and the relative recovery or depression of juvenile plants newly protected from or exposed to herbivores. Herbivory is not only the major determinant of the relative abundances, sizes and distributions of the dominant shrubs, but is also increasing the age at first reproduction in this population of *Ceanothus.*

Resprouting *Adenostoma fasciculatum* at this site actually serves as a "nurse plant" for protection of *Ceanothus* against herbivores. *Adenostoma fasciculatum* has advantages over *A. sparsifolium* and smaller shrubs in this respect, apart from its abundance. Its stiff branches are often horizontal or inclined at low angles, and the longevity of short shoots (Jow et al. 1980) assures the potential to maintain dense branching. Similarly, in the Sonoran Desert, the importance of particular species as nurse plants differs according to the density, stiffness and shape of the crown (McAuliffe 1986).

However, dense cover may also depress *Ceanothus* growth in some aspects. This is shown by results from the exclosures, where plants in heavy cover showed less lateral growth than plants in more open microsites, although there were no cover-associated differences in height. Whether this was due to shading or competitive water stress could not be determined.

I did not determine what characteristics make stems likely to be selected by the rabbits. However, individual plants were subject to repeated clipping over the years. The brush was dense enough in a few areas by 1988 that rabbits might have had forms on the burned area itself (the species is reported as nonburrowing, Orr 1940). The probable home range of individual rabbits (Connell 1954) could easily encompass part of the burned area, old chaparral, and oak woodland.

The lack of deer browsing on the Sky Oaks burn is notable, but may be due to the plants' small size, and the abundance of larger forage surrounding the plot. *Ceanothus* has been regarded as "without doubt the most important genus of forage plants for deer in California" (Dixon 1934; see also Ferrel and Leach 1950). It is also interesting to note the results from a site in the Sierra Juarez (132 km SSE from Sky Oaks; J. Sosa pers. comm.). In that case, cattle are the major herbivores in a *Adenostoma sparsifolium* chaparral stand regenerating from fire. The cows do not graze *Ceanothus* seedlings but devastate resprouting shrubs of *A. sparsifolium* and of a *Garrya* sp. Similarly, on a coastal sage–grassland boundary, Bartholomew (1970) found that mammalian herbivory had a dominant effect on vegetation structure.

Through their effect on plant growth and mortality, herbivores are important links in management problems such as watershed protection and fire potential. This study suggests that chaparral composition may diverge radically between sites comparable in physical conditions and initial flora, depending on the effect fires have on populations of resprouting shrubs (cover) and the accessibility to mammalian herbivores. Recolonization rates probably decrease as size of the burned area increases, although the relation must also differ between mammal species. The interior of very large burns (>100 km^2) often may be relatively free of small mammals for several years, while on smaller burns, typical of "controlled burning" programs, access may be immediate and frequent, resulting in reduced regeneration of preferred forage species (e.g., Biswell et al. 1952). Likewise, seed banks must be affected by the area of burns, as the foraging of granivorous rodents is influenced by distance from cover (Bradford 1976). "Brush control" has often been linked to the management goal of increasing huntable populations of deer (Bleich and Holl 1982). The herbivores, as well as seed predators and pollinators, using any stand also affect its future composition, and must be considered in management, whether the goal is maintaining diversity or preventing floods.

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A NEW SUBSPECIES AND A NEW COMBINATION IN *ESCHSCHOLZIA MINUTIFLORA* (PAPAVERACEAE)

Curtis Clark
Biological Sciences, California State Polytechnic University,
Pomona, CA 91768

Mark Faull
Red Rock Canyon State Park, P.O. Box 26, Cantil, CA 93519

Abstract

Diploid ($n=6$) poppies from the El Paso and Rand mountains of the northwestern Mojave Desert, previously referred to *Eschscholzia parishii,* are morphologically distinct from that species, with shorter, broader terminal lobes of the leaves, more oblong seeds without micropapillae, and slightly smaller corollas. In all characters but flower size the plants agree with the hexaploid *E. minutiflora* and tetraploid *E. covillei.* We believe that these plants, not *E. parishii,* represent the diploids in the series. Since the three taxa cannot be consistently distinguished by morphology, and there is no compelling reason to recognize autopolyploid levels as separate species, we describe the new diploid as *Eschscholzia minutiflora* subsp. **twisselmannii** and provide for the tetraploid the new status *E. minutiflora* subsp. **covillei.**

Resumen

Amapolas diploides ($n=6$) de las montañas El Paso y Rand del noroeste del desierto de Mojave, previamente consideradas como *Eschscholzia parishii,* son distintas morfológicamente de esa especie. Estas plantas poseen hojas con segmentos terminales más cortos y anchos, semillas más oblongas y sin micropapilas, y corolas un poco más pequeñas. En todas las características, excepto en el tamaño de las flores, las plantas se parecen más a la hexaploide *E. minutiflora* y a la tetraploide *E. covillei.* Creemos que estas plantas, y no *E. parishii,* representan las diploides en la serie. Debido a que los tres taxones no pueden reconocerse por morfología consistentemente, y no hay una razón obligada a reconocer niveles autopoliploides como especies separadas, nosotros describimos el nuevo diploide como *Eschscholzia minutiflora* subsp. **twisselmannii** y para el tetraploide proveemos el nuevo estado *E. minutiflora* subsp. **covillei.**

An affinity between *Eschscholzia parishii* E. Greene and *E. minutiflora* S. Wats. has been widely accepted since Jepson (1922) reduced the former to a variety of the latter. Lewis and Snow (1951) contended that *E. parishii* should be regarded as a separate species, since it was sympatric with *E. minutiflora* over the entire range of the former, was always morphologically distinguishable from *E. minutiflora* in areas of sympatry, never hybridized with *E. minutiflora,* and had a different chromosome number ($n=6$, versus $n=18$ in *E. minutiflora*). Nevertheless, they suggested that it was the diploid progenitor of *E. minutiflora.*

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In 1961, Mosquin applied the name *Eschscholzia covillei* E. Greene to tetraploid plants ($n=12$) previously referred to *E. minutiflora,* and strongly implied (although never explicitly stated) that the three species formed a polyploid series. He showed differences in flower size and stamen number as well as chromosome number, and pointed out that the two taxa could readily be distinguished when they grew in mixed stands. Clark (1978, 1979, and unpublished) formed greenhouse hybrids of moderate fertility between *E. covillei* and *E. minutiflora,* but was unable to cross either with *E. parishii.* Clark and Jernstedt (1978) suggested, on the basis of seed coat differences as well as hybridization, that *E. parishii* did not represent the diploid progenitor of either *E. minutiflora* or *E. covillei.*

Mosquin (1961) and Twisselmann (1967) both commented on the distinctiveness of *E. parishii* of the Rand and El Paso mountains in northeastern Kern Co. and northwestern San Bernardino Co., California. These populations are further north (120 km) and further west (125 km) than any other populations of *E. parishii.* Our investigations show that these are in fact morphologically distinct from *E. parishii,* and we believe they represent the diploid member of the *E. minutiflora* polyploid series. We have also found that morphological differences do not consistently distinguish the different ploidy levels, and so provide a taxonomic realignment at the subspecific level.

Results and Discussion

Status of the tetraploid. Eschscholzia minutiflora subsp. *minutiflora* varies greatly in its morphology (in 1905, Greene recognized six other species that can safely be synonymized with it—Clark, 1979), and subsp. *covillei* falls within this variation in all but three traits: flower size, stamen number, and number of pollen colpae. Mosquin also included bud length and stamen length, but those are correlated with flower size in all members of the genus, and thus all three constitute a single character. The number of colpae, which seems to relate to the chromosome number, shows some overlap, as does petal length. The stamen number shows considerable overlap (Mosquin 1961). In mixed stands, the taxa are generally discontinuous morphologically, but large-flowered subsp. *minutiflora* cannot be reliably distinguished from small-flowered subsp. *covillei* when specimens are taken from different populations.

Again in mixed stands, subsp. *covillei* flowers consistently earlier than subsp. *minutiflora*; differences in flowering times have been observed in other polyploid series as well (Clark 1975). However, the overlap in flowering season is almost complete, and subsp. *minutiflora* from the south end of its range will often flower much earlier than subsp. *covillei,* which occurs further north (Table 1).

TABLE 1. COMPARISON OF *ESCHSCHOLZIA MINUTIFLORA* SUBSP. *TWISSELMANNII* WITH *E. MINUTIFLORA* SUBSP. *MINUTIFLORA* SUBSP. *COVILLEI*, AND *E. PARISHII*. * Measurements of Mosquin (1961); his ranges, based on examination of a number of herbarium collections, slightly exceed what we have observed in the field.

	minutiflora	*covillei*	*twisselmannii*	*parishii*
Petal size	4–10 mm*	7–18 mm*	4–20 mm	8–22 mm*
Terminal leaf divisions	short, blunt	short, blunt	short, blunt	longer, pointed
Seed shape	oblong	oblong	oblong	spherical
Seed micropapillae	no	no	no	yes
Jugiform ridge cells	absent	rare	not seen	common
Distribution	Sonoran, Colorado, Mojave deserts, SW Great Basin	Mojave Desert	northwestern Mojave Desert	Colorado, western Sonoran deserts

The taxa hybridize in cultivation. A hybrid between subsp. *minutiflora* (collected northwest of Ocotillo in San Diego Co., California, *Clark 522,* DAV) and subsp. *covillei* (from the Newberry Mountains in San Bernardino Co., California, *Clark 561,* DAV) was of intermediate morphology. Its pollen fertility was 37% (based on a sample of 500 grains). At metaphase I, around 7–11 chromosomes were unpaired univalents. The paired chromosomes did not spread well and were thus impossible to analyze fully, but there appeared to be at least some trivalents. There is no indication that the taxa hybridize in the field.

Subspecies *twisselmannii* shows the same morphological similarities, but experimental hybrids with either subsp. *minutiflora* or subsp. *covillei* have not yet been made.

Both the morphological overlap and ability to hybridize support subspecific status, but the change in status is also supported on evolutionary grounds. Separate species are not generally recognized in autoploid complexes, because the mechanisms that created higher ploidy levels can recur, leading to gene flow between levels (Clark 1975). Even in the absence of gene flow, a lack of morphological divergence is an indication that the ploidy levels still share common evolutionary tendencies.

Thus, the differences between the taxa are not great enough either from the standpoint of morphology or of evolutionary biology to warrant their maintenance as separate species.

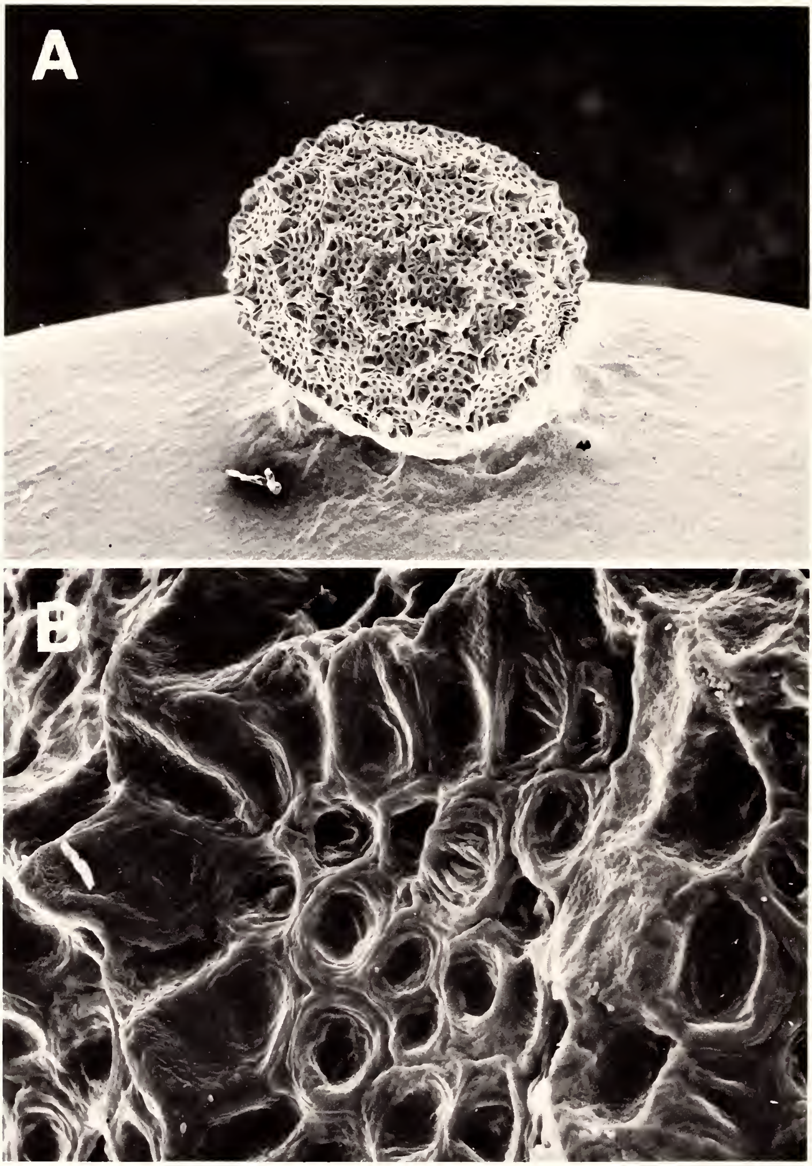

FIG. 1. Scanning electron micrographs of the seed of *Eschscholzia minutiflora* subsp. *twisselmannii.* A. ×37. B. ×360.

The new diploid. All three subspecies of *E. minutiflora* somewhat resemble *E. parishii.* However, subsp. *twisselmannii* agrees with the other two subspecies, and is clearly dissimilar from *E. parishii,* in leaf shape and three features of the seeds (Table 1, Fig. 1).

Seed coat microsculpturing is useful in many cases for distinguishing *Eschscholzia* species (Clark and Jernstedt 1978). All three subspecies of *E. minutiflora* have somewhat elongate seeds, up to 1.3 times as long as wide. They lack micropapillae on the epidermal cells, and the epidermal cells of both ridges and facets may be concave or foveate, but are almost never jugiform. The seeds of subsp. *twisselmannii* cannot be distinguished from those of the other two subspecies.

In contrast, the seeds of *Eschscholzia parishii* are nearly spherical. They always have micropapillae, and jugiform cells are common on both facets and ridges.

The taxa are also distinguished by the terminal leaf divisions. In *E. parishii,* they are pointed and 2–3 times as long as wide. In all three subspecies of *E. minutiflora,* they are blunt and 1–1.5 times as long as wide.

In addition to its morphological similarity, subsp. *twisselmannii* is well-placed geographically as the diploid member of the *E. minutiflora* complex. It is sympatric with the tetraploid subsp. *covillei,* unlike *E. parishii,* which is completely allopatric (all are sympatric with the widespread subsp. *minutiflora*). It has a much more restricted distribution than the tetraploid, and preliminary evidence suggests that it may be substrate-specific to rhyolitic tuffs, granitics, and similar rocks.

NOMENCLATURE

Eschscholzia minutiflora S. Watson subsp. **covillei** (E. Greene) C. Clark in C. Clark & Faull, comb. et stat. nov.—*Eschscholzia covillei* E. Greene, Pittonia 5:725. 1905.—TYPE: USA, California, Inyo Co., from Pete's Garden to 1000 feet below, Johnson Cañon, Panamint Mountains, April 1891, *Coville & Funston 519* (holotype, US).

Eschscholzia minutiflora S. Watson, var. **darwinensis** M. E. Jones, Contr. W. Bot. 8:2–3. 1898.—TYPE: USA, California, Inyo Co., on mesas, Darwin, 1897 (holotype, POM).

Since no name existed for the taxon at the rank of subspecies, either epithet could have been chosen. *Covillei* was chosen because it has been more commonly used in recent years as a result of Mosquin's (1961) paper. Mosquin felt that both types agreed with the morphology of the tetraploids, but there is no unequivocal evidence that either is in fact tetraploid.

Eschscholzia minutiflora S. Watson subsp. **twisselmannii** C. Clark & Faull, subsp. nov.—TYPE: USA, California, Kern County, Red Rock Canyon State Park, just E of CA Highway 14 at southern junction with Abbott Rd., on low mounds of eroded pink tuff along a streamcourse, 2 Apr 1988, *Clark 642* (holotype, CAS!; isotype, UC!).

Affinis Eschscholzia minutiflora subspecies minutiflora covilleique, floribus majoris differt. Ab Eschscholzia parishii differt divisionibus terminalibus foliorum brevioribus et seminibus oblongioribus sine micropapillis et cellulis jugiformibus. Chromosomatum gametophytorum numerus 6.

Allied to *Eschscholzia minutiflora* subsp. *minutiflora* and *covillei,* differing by its larger flowers. Differing from *Eschscholzia parishii* by shorter terminal divisions of the leaves and more oblong seeds lacking micropapillae and jugiform cells. Chromosome number $n=6$.

The subspecies is known with certainty only from the El Paso and Rand mountains of the western Mojave Desert, although large-flowered *E. minutiflora* have been reported from the Death Valley region (DeDecker 1984; listed as *E. parishii*).

PARATYPES: USA, California, Kern County, 2 mi SE of Searles Station, *Lewis and Mosquin 1117* (LA); El Paso Mountains, Mesquite Canyon, 0.6 mi N of Red Rock–Randsburg Rd. at a junction 1.1 mi W of its junction with Garlock Rd., 1 April 1988, *Clark 640* (CSPU).

The epithet honors Ernest C. Twisselmann, whose keen observations have been a source of inspiration and a stimulus for productive work for us and many other California botanists.

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BLUE OAK COMMUNITIES IN CALIFORNIA

Barbara H. Allen-Diaz and Barbara A. Holzman
Department of Forestry and Resource Management,
University of California, Berkeley, CA 94720

Abstract

Twelve blue oak plant communities at the subspecies level of classification are described for California. Community analysis was based on 1000 Vegetation Type Map plots containing information on species composition, number of trees by species and diameter class, and environmental variables including elevation, slope, aspect, and parent material. Community structure is related to environmental variables in order to understand the possible responses of blue oak communities to natural and human-caused disturbance.

Blue oak (*Quercus douglasii* Hook. & Arn.) (QUDO) woodlands occupy approximately 1.2 million hectares of California (Bolsinger 1988). They are the most extensive hardwood rangeland types, found both in the Coast Range and Sierra Nevada, as well as occupying a fairly well defined ring around the Central Valley (Griffin and Critchfield 1972). The woodlands range from 100 to 1200 meters in elevation and from northern Los Angeles County to the head of the Sacramento Valley in Shasta County (Munz 1973; Griffin and Critchfield 1972). Prominent in the foothill woodlands of the state, blue oak communities form a transitional zone between the valley grassland and the higher elevation mixed coniferous forest.

Blue oaks have become the focus of many recent studies because of the increasing awareness of the loss of blue oak habitat from land conversion and fuel wood harvesting (Ewing et al. 1988), and the lack of regeneration on many sites (Muick and Bartolome 1987). Bolsinger (1988) estimates that 75 percent of the blue oak woodlands resource is in private ownership, 14 percent in the National Forest Systems, and the remaining in other state, county, and miscellaneous federal ownerships.

Existing systems for describing and classifying hardwood rangelands are too general for planning and development of site-specific management practices (Allen et al. 1989). Existing systems also cannot provide accurate enough classification of ecological types to generalize experimental results.

Allen et al. (1989) developed an ecologically based classification system for oak woodlands in California. Seven series, based on tree dominants, and 57 subseries were identified. The subseries level of classification was developed from all species present, rather than dominants only. The classification term "association" was not used

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because all grass species were lumped into one category, thus subseries better reflects the level of detail in classification hierarchy. The system provides researchers, land managers, landowners, and the general public with a better description of the state's oak woodland resource, and unlike previous systems is based on actual plot data. Blue oak woodlands were one of seven oak woodland series identified in the Allen et al. (1989) report.

This paper describes blue oak subseries in California. It relates community structure to environmental variables, and suggests subseries appropriate for studying succession and/or management practices in blue oak woodlands. The subseries descriptions should be particularly useful for linking research to management.

METHODS

The classification system for California hardwood rangelands was based on 4300 plots surveyed in the 1920's and 1930's by the USDA Forest Service Pacific Southwest Station Vegetation Type Mapping (VTM) project (Allen et al. 1989). The data used to classify blue oak in that study were obtained from 794 VTM plots where cover of understory tree, shrub, and herbaceous species, diameter at breast height (DBH) of tree species, and environmental factors such as elevation, slope, aspect, and soil characteristics were recorded.

In this study, 1000 VTM blue oak plots, not originally used in the hardwood classification of Allen et al. (1989), were arrayed using TWINSPAN, Two-Way Indicator Species Analysis (Hill 1979), to determine if groups similar to the Allen et al. groups emerged. Multiple TWINSPAN runs were conducted using different combinations of 200 to 499 plots because the program could not simultaneously run all the plots.

The 12 blue oak subseries were plotted on the map of California by county and quad. Subseries that occurred in both the Sierra Nevada and Coast Range were analyzed separately using one way analysis of variance (Norusis 1986) to compare regional differences in elevation, dominant tree species basal area, dominant species cover, and stand density within the subseries. Subseries which occupied a wide latitudinal range were also analyzed for within group differences.

Coefficients of similarity, using Jaccard's index (Mueller-Dombois and Ellenberg 1974), were calculated for the 12 blue oak subseries. The formula used was: $IS_J = C/(A + B - C)$, where 'C' is the number of shared species, 'A' is the total number of species in subseries A, and 'B' is the total number of species found in subseries B. Based on degree of similarity, one-way analysis of variance (Norusis 1986) was used to compare mean elevation, species cover, and tree basal area between closely related subseries.

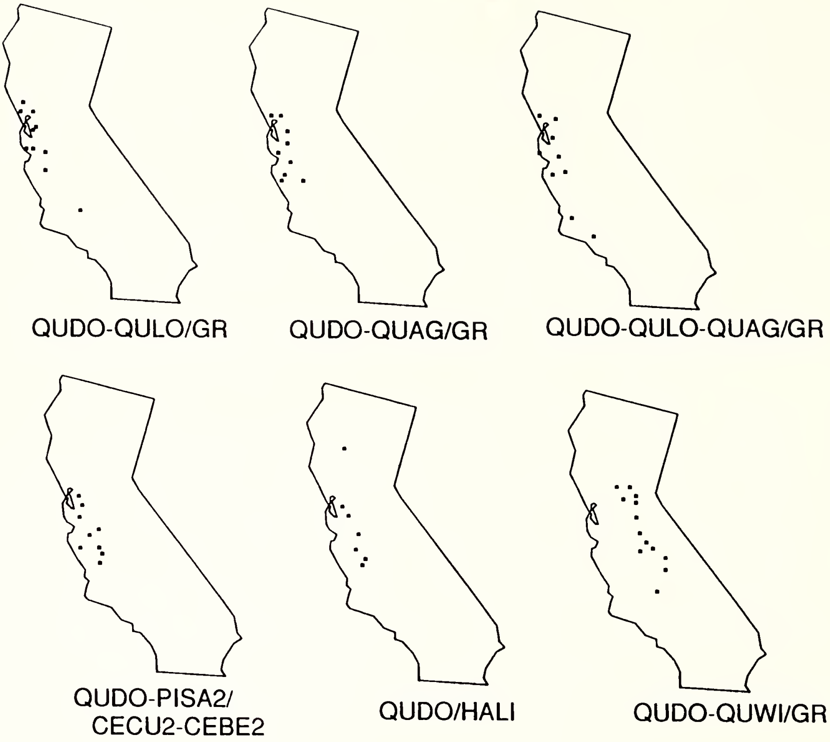
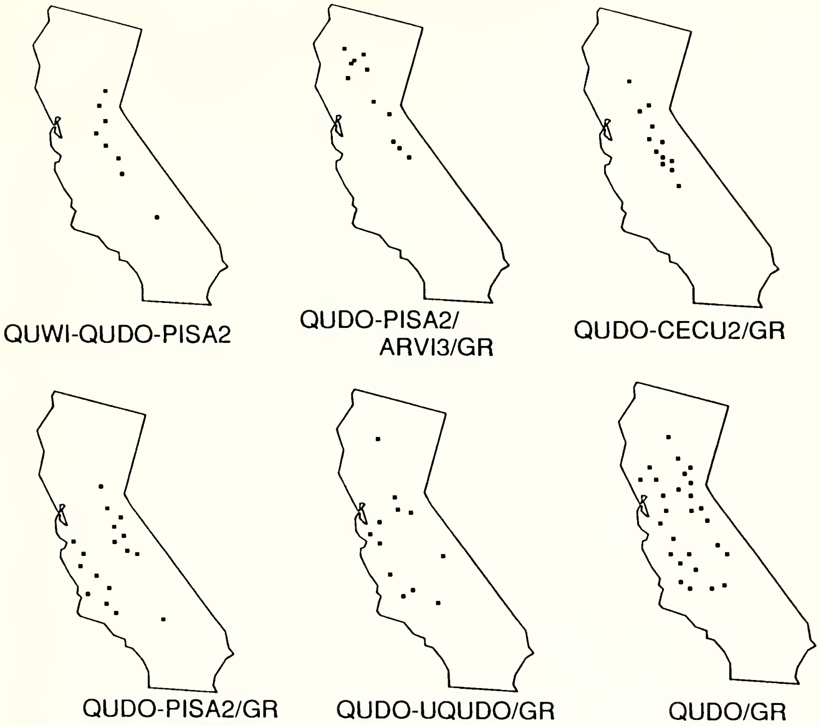


FIG. 1. Distribution of blue oak subseries in California. Dots represent the general distribution of each subseries within the state. QUDO = *Quercus douglasii,* QUWI = *Quercus wislizenii,* QUAG = *Quercus agrifolia,* QULO = *Quercus lobata,* PISA2

Stand density tables were constructed for each subseries, and comparisons of total mean number of trees and mean number by diameter class for related subseries were conducted using one-way analysis of variance. Within subseries, differences in stand structure were also examined for the three geographically extant types. Only blue oak, interior live oak (*Quercus wislizenii* A. DC.) (QUWI), valley oak (*Q. lobata* Nee) (QULO), coast live oak (*Q. agrifolia* Nee) (QUAG), and foothill pine (*Pinus sabiniana* Dougl.) (PISA2) were used in comparisons of stand density because of the lack of constancy of any of the other tree species that may occur in a type.

RESULTS

Seventy-seven species occurring in blue oak woodlands were identified in the VTM data set. Since all grass species (GR) were lumped into one category during the original survey, the subseries descriptions do not reflect the diversity of herbaceous species within the



QUWI-QUDO-PISA2

QUDO-PISA2/ARVI3/GR

QUDO-CECU2/GR

QUDO-PISA2/GR

QUDO-UQUDO/GR

QUDO/GR

= *Pinus sabiniana,* UQUDO = understory *Quercus douglasii,* ARVI3 = *Arctostaphylos viscida,* HALI = *Haplopappus linearifolius,* CECU2 = *Ceanothus cuneatus,* CEBE2 = *Cercocarpus betuloides,* GR = grass.

blue oak woodland. TWINSPAN analyses resulted in the identification of blue oak subseries similar to those defined in Allen et al. (1989). Satisfied with the repetitious emergence of the same subseries, we used the original plot data from Allen et al. to describe and compare the subseries (Fig. 1).

Blue oak/grass (QUDO/GR). This subseries occurs throughout the entire range of blue oak distribution, in the coastal and Sierran foothills, on gentle to moderate slopes. Mean elevation is 395 m. QUDO/GR is the most widespread of the blue oak subseries. It is characterized by its savanna-like appearance with sparse to moderately dense overstory of blue oak and a continuous grass understory. Basal area of blue oak averages 11 m^2/ha.

Blue oak–understory blue oak/grass (QUDO–UQUDO/GR). This subseries is similar in range and species composition to the QUDO/GR subseries. It occurs on gentle slopes with similar mean basal area for blue oak (11 m^2/ha). Mean elevation is 453 m. This subseries however, has a large number of small blue oak trees (<10 cm dbh) and can be considered woodland rather than savanna-like in nature. Grass is the dominant understory vegetation.

Blue oak–foothill pine/grass (QUDO-PISA2/GR). This subseries is also widespread, occurring throughout the state. Mean elevation is 533 m. Soils tend to be gravelly. The overstory is primarily blue oak and foothill pine with small and medium-sized trees of both species. Mean basal areas for blue oak and foothill pine are 8 m^2/ha and 6 m^2/ha, respectively. The understory is largely grass, although a sparse shrub cover can also be present.

Blue oak–valley oak/grass (QUDO-QULO/GR). This is largely a coastal subseries, occurring from Marin to Monterey counties on sandy to clay loams. Mean elevation is 450 m. The overstory is dominated by blue oak and valley oak trees of all sizes. Mean basal area for blue oak and valley oak are 7 m^2/ha and 4 m^2/ha, respectively. The understory contains little to no shrub element and is typically a continuous cover of grass.

Blue oak–coast live oak/grass (QUDO-QUAG/GR). This subseries also occurs throughout the coastal foothills. Mean elevation is 321 m. QUDO-QUAG/GR is recognized by its dominant oak species. Mean basal area for blue oak and coast live oak are 9 m^2/ha and 3 m^2/ha, respectively. There are few shrubs in the understory. Grass is the primary understory averaging 83 percent cover.

Blue oak–valley oak–coast live oak/grass (QUDO-QULO-QUAG/GR). This subseries also occurs along the coastal areas of the state. It is recognized by its dense overstory of mixed oak species with grass as the dominant understory. Total basal area for this subseries is significantly greater than the other coastal associates. Mean basal area for the individual species; blue oal, valley oak and coast live oak are 11, 14 and 5 m^2/ha, respectively.

Blue oak/narrowleaf goldenbush ((Haplopappus linearifolius) (HALI)) (QUDO/HALI). This subseries is generally restricted to the central and southern coastal foothills from Alameda to Santa Barbara counties. Mean elevation is 697 m. The overstory is blue oak and foothill pine, with California juniper ((*Juniperus californica*) (JUCA3)) and small blue oaks occurring as tree understory. Narrowleaf goldenbush is present as an understory shrub averaging 22 percent cover. Grass is present as the dominant ground cover.

Blue oak–foothill pine/buck brush ((Ceanothus cuneatus) (CECU2))–mountain mahogany ((Cercocarpus betuloides) (CEBE2)) (QUDO-PISA2/CECU2-CEBE2). This subseries is primarily a coastal subseries although it may have a central Sierran component. Although it is similar in overstory structure to the QUDO-PISA2/GR subseries it occurs at higher elevations (mean elevation is 770 m). Understory trees typically present include small blue oaks and California juniper. The shrub cover is dense and diverse, with buck brush and mountain mahogany both averaging 10 percent cover. Other common shrub associates are narrowleaf goldenbush, redberry ((*Rhamnus crocea*) (RHCR)) and California buckwheat ((*Eriogonum fasciculatum*) (ERFA)). The grass understory is less than in previous subseries and averages 59 percent cover.

Blue oak/buck brush/grass (QUDO/CECU2/GR). This is a Sierra Nevada subseries occurring from Butte to Fresno counties. Mean elevation is 534 m. The overstory is typically mixed with blue oak, foothill pine and interior live oak as dominants. Average basal area for these overstory trees are 5 m^2/ha, 4 m^2/ha, and 3 m^2/ha, respectively. There are also smaller trees (<10 cm dbh) including blue oak, interior live oak, and foothill pine present. The shrub understory is predominantly buck brush (mean percent cover is 20 percent). Other shrub associates are redberry, poison oak ((*Rhus diversiloba*) (RHDI)) and whiteleaf manzanita ((*Arctostaphylos viscida*) (ARVI3)). The grass understory averages 50 percent cover.

Blue oak–interior live oak/grass (QUDO-QUWI/GR). This subseries is also a Sierran associate. Mean elevation is 457 m. The overstory is blue oak, interior live oak, and foothill pine with mean basal areas of 5 m^2/ha, 4 m^2/ha and 2 m^2/ha, respectively. There is a sparse understory shrub component of buck brush, poison oak, and others. Grass is also present and averages 75 percent cover.

Blue oak–foothill pine/whiteleaf manzanita/grass (QUDO-PISA2/ARVI3/GR). This subseries is found in the Sierran foothills from Nevada to Calaveras counties. Mean elevation is 423 m. The overstory is blue oak and foothill pine with interior live oak occurring on some sites. Whiteleaf manzanita is the dominant understory shrub. Mean cover of whiteleaf manzanita is 21 percent. Buck brush and common manzanita ((*Arctostaphylos manzanita*) (ARMA3)) and poison oak are shrub associates on some sites. Grasses occupy about 50 percent of the understory cover.

Interior live oak–blue oak–foothill pine (QUWI-QUDO-PISA2). This subseries is a Sierran associate. Mean elevation is 467 m. The overstory is mixed oak and pine, containing a significantly higher number of trees per hectare than the other Sierran associates. Mean basal area of the three dominant trees, interior live oak, blue oak and foothill pine are 9 m^2/ha, 7 m^2/ha and 7 m^2/ha, respectively. There are few shrubs in the understory. Grass cover averages 61 percent.

Figure 1 shows the geographic distribution of the 12 blue oak

TABLE 1. MEAN ELEVATION (m) WITHIN SUBSERIES OCCUPYING DIFFERENT GEOGRAPHIC REGIONS. Different letters designate significant differences ($p \leq 0.05$) in mean elevation. QUDO = *Quercus douglasii,* PISA2 = *Pinus sabiniana,* UQUDO = understory *Quercus douglasii,* GR = grass.

	Coast Range	Sierra Nevada	F value	p value
QUDO-PISA2/GR	601	462	7.9	0.006
QUDO-UQUDO/GR	529	314	15.9	0.000

	North Coast	South Coast	Sierra Nevada	South Central Valley	F value	p value
QUDO/GR	207^{c}*	439^{b}	269^{c}	780^{a}	29.7	0.000

subseries. QUDO-PISA2/GR, QUDO/GR, and QUDO-UQUDO/GR range widely in distribution, while other subseries such as QUDO-QULO/GR, QUDO-QUAG/GR, and QUDO-QULO-QUAG/GR are relatively narrow in geographic distribution occurring in the central Coast Range. (Names of the subseries use the national standard coding system for species (Powell 1987), and are based on the dominant species in each vegetation layer).

No significant differences in tree basal area, aspect, slope or species occurred between geographic regions within a type, except for the south coast variant of the QUDO/GR subseries, which has significantly more ($p < 0.05$) basal area of blue oak (12 m^2/ha, 52 ft^2/acre). However, significant regional differences occurred in elevation within each of the 3 subseries that occur widely throughout the range of blue oak (Table 1). Coastal variants averaged higher elevation than their Sierran counterparts within a subseries, and the coastal variant of QUDO-PISA2/GR also tended to have more total shrub cover and less grass than its Sierra variant.

The similarity of floras between blue oak subseries is displayed in Table 2. The Jaccard coefficient of similarity was based on presence/absence of a species within a subseries. Results show that some subseries, such as QUDO/HALI, are distinct from any other blue oak subseries. On the other hand, some subseries appear to be very closely related to other types. For example QUDO-PISA2/CECU2-CEBE2 and QUDO-PISA2/GR ($IS_J = 0.58$), and QUDO/CECU2/GR and QUDO-QUWI/GR ($IS_J = 0.58$) are closely related. QUDO-QUWI/GR is also closely related to QUDO-PISA2/ARVI3/GR ($IS_J = 0.48$).

Table 3 provides concise descriptions of the 12 blue oak subseries and their relation to each other. Subseries that are closely related floristically often vary considerably in productivity or location. Oth-

TABLE 2. JACCARD COEFFICIENTS MEASURING SIMILARITIES OF FLORAS IN 12 BLUE OAK SUBSERIES IN CALIFORNIA. Not all comparisons are given. Similarity coefficients are based on mean presence of species for the group. Calculations do not take into account differences in sample sizes for the different groups (see Table 4 for sample sizes), and include all species listed for the type regardless of constancy. Comparison of QUDO/GR and QUDO-UQUDO/GR is most affected by the large sample size difference; if all species are used in the calculations $IS_J = 0.33$, if species present in >15% of the plots representing the type are used, $IS_J = 0.66$. QUDO = *Quercus douglasii,* QUWI = *Quercus wislizenii,* QUAG = *Quercus agrifolia,* QULO = *Quercus lobata,* PISA2 = *Pinus sabiniana,* UQUDO = understory *Quercus douglasii,* ARVI3 = *Arctostaphylos viscida,* HALI = *Haplopappus linearifolius,* CECU2 = *Ceanothus cuneatus,* CEBE2 = *Cercocarpus betuloides,* GR = grass.

Subseries comparisons	Total species	Shared species	IS_J
QUDO-QUAG/GR with QUDO-QULO/GR	17	6	0.35
QUDO-QUAG/GR with QUDO-QULO-QUAG/GR	17	6	0.35
QUDO-QULO/GR with QUDO-QULO-QUAG/GR	18	8	0.44
QUDO/HALI with QUDO-QULO-QUAG/GR	23	5	0.22
QUDO-PISA2/CECU2-CEBE2 with QUDO-QULO-QUAG/GR	36	9	0.25
QUDO-PISA2/CECU2-CEBE2 with QUDO/HALI	35	12	0.34
QUDO-PISA2/CECU2-CEBE2 with QUDO-PISA2/GR	40	23	0.58
QUDO-PISA2/GR with QUDO/CECU2/GR	46	21	0.46
QUDO-PISA2/GR with QUDO-QUWI/GR	44	19	0.43
QUDO-QUWI/GR with QUDO/CECU2/GR	43	25	0.58
QUDO-QUWI/GR with QUWI-QUDO-PISA2	42	20	0.45
QUDO-QUWI/GR with QUDO-PISA2/ARVI3/GR	40	19	0.48
QUWI-QUDO-PISA2 with QUDO/CECU2/GR	47	21	0.45

er subseries may be related successionally, or by management practices such as the suppression of fire, and are distinguished from each other by the combination of tree and shrub species on the site.

Stand density characteristics are displayed in Table 4. QUWI-QUDO-PISA2 is significantly more dense, with an average of 380 trees per ha (TPH) (154 trees per acre (TPA)), than any other blue oak type. However, the QUDO-QULO-QUAG/GR subseries also contains significantly more trees (249 TPH, 101 TPA) than any of the other blue oak types except for QUWI-QUDO-PISA2, and it

TABLE 3. COMPARISON OF MAJOR SITE CHARACTERISTICS OF 12 BLUE OAK SUBSERIES IN CALIFORNIA. Numbers in comment section refer to the numbering of subseries in this table only. "pm" in the environment section refers to parent material. QUDO = *Quercus douglasii,* QUWI = *Quercus wislizenii,* QUAG = *Quercus agrifolia,* QULO = *Quercus lobata,* PISA2 = *Pinus sabiniana,* UQUDO = understory *Quercus douglasii,* ARVI3 = *Arctostaphylos viscida,* HALI = *Haplopappus linearifolius,* CECU2 = *Ceanothus cuneatus,* CEBE2 = *Cercocarpus betuloides,* GR = grass.

Subseries	General location	Mean elevation (m)	Environment	Mean BA dominants ft²/ac (m²/ha)	Comments
1. QUDO-QUAG/GR (n = 13)	Coast Range	321	all aspects, gravelly loam	QUDO = 39 (9) QUAG = 11 (3)	very few scattered coastal shrub species
2. QUDO-QULO/GR (n = 32)	Coast Range	450	all aspects, sandy clay loams	QUDO = 31 (7) QULO = 18 (4)	grass understory, QULO on sandier soils
3. QUDO-QULO-QUAG/GR (n = 17)	Coast Range	471	all aspects, varied parent material & texture	QUDO = 46 (11) QUAG = 21 (5) QULO = 60 (14)	dense forest, maybe late seral, undisturbed mixed oak community related to 1 & 2
4. QUDO/GR (n = 298)	Sierra Nevada & Coast Range	395	all aspects, flat to gentle slope, all pm, all soils	QUDO = 47 (11)	similar to 5, but lacks understory QUDO, 47 species found at <15% constancy
5. QUDO-UQUDO/GR (n = 63)	Sierra Nevada & Coast Range	453	all aspects, flat, all pm, loam soils	QUDO = 46 (11)	differs from 5 by 95% constancy of QUDO <10 cm dbh

TABLE 3. CONTINUED.

Subseries	General location	Mean elevation (m)	Environment	Mean BA dominants ft^2/ac (m^2/ha)	Comments
6. QUDO-PISA2/GR (n = 101)	Sierra Nevada & Coast Range	533	all aspects, gravelly clay loams	QUDO = 35 (8) PISA2 = 27 (6)	related to 10, but lower elevation related to 7, but lacks QUWI
7. QUDO/CECU2/GR (n = 56)	Sierra Nevada	534	all aspects, gravelly clay loams, steep slopes	QUDO = 23 (5) QUWI = 13 (3) PISA2 = 19 (4)	related to 9, less BA of QUWI & PISA2 related to 6, but has QUWI & 100% CECU2 related to 8
8. QUDO-QUWI/GR (n = 72)	Sierra Nevada	457	all aspects, rocky sandy loams	QUDO = 22 (5) QUWI = 17 (4) PISA2 = 8 (2)	related to 9, but less dense overall with significantly less BA of QUWI & PISA2 related to 7
9. QUWI-QUDO-PISA2 (n = 42)	Sierra Nevada	467	all aspects, rocky sandy loams, relatively flat	QUDO = 29 (7) QUWI = 41 (9) PISA2 = 32 (7)	related to 7, but significantly more BA of QUWI & PISA2, fewer shrubs

TABLE 3. CONTINUED.

Subseries	General location	Mean elevation (m)	Environment	Mean BA dominants ft^2/ac (m^2/ha)	Comments
10. QUDO-PISA2/CECU2-CEBE2 (n = 23)	Coast Range	770	north to northeast, sedimentary pm gravelly to clay loams	QUDO = 25 (6) PISA2 = 17 (4)	related to 6, but higher elevation, more shrubs related to 12, but much denser & diverse shrub component
11. QUDO-PISA2/ARVI3/GR (n = 60)	Sierra Nevada	423	varied aspects, igneous pm, loam soils, flat	QUDO = 29 (7) PISA2 = 28 (6)	related to 6, 7, and 8, but high constancy of ARVI3, differences in tree dominance
12. QUDO/HALI (n = 17)	Coast Range	697	northwest to east, sandstone, shale pm sandy loam, relatively flat	QUDO = 28 (6) PISA2 = 25 (6)	related to 10, but not as diverse or dense a shrub component

TABLE 4. COMPARISON OF BLUE OAK SUBSERIES BY MEAN NUMBER OF TREES BY DIAMETER CLASS. TPH = trees per hectare, (TPA) = trees per acre, T = less than 1 TPA, * indicates significant differences ($p \geq 0.01$) from all other values in the column. Tree species used in calculations include QUDO, QUWI, QULO and PISA2 because of high constancies. QUDO = *Quercus douglasii,* QUWI = *Quercus wislizenii,* QUAG = *Quercus agrifolia,* QULO = *Quercus lobata,* PISA2 = *Pinus sabiniana,* UQUDO = understory *Quercus douglasii,* ARVI3 = *Arctostaphylos viscida,* HALI = *Haplopappus linearifolius,* CECU2 = *Ceanothus cuneatus,* CEBE2 = *Cercocarpus betuloides,* GR = grass.

	Mean total TPH (TPA)	10–29 cm dbh TPH (TPA)	30–59 cm dbh TPH (TPA)	60–89 cm dbh TPH (TPA)	89+ cm dbh TPH (TPA)
QUDO-QUAG/GR	212 (86)	180 (73)	27 (11)	5 (2)	0
QUDO-QULO/GR	143 (58)	99 (40)	37 (15)	5 (2)	T
QUDO-QULO-QUAG/GR	249 (101)	153 (62)	79 (32)*	15 (6)*	2 (1)*
QUDO/GR	173 (70)	133 (54)	35 (14)	5 (2)	T
QUDO-UQUDO/GR	183 (74)	151 (61)	27 (11)	5 (2)	0
QUDO-PISA2/GR	200 (81)	143 (58)	49 (20)	5 (2)	T
QUDO/CECU2/GR	188 (76)	153 (62)	35 (14)	2 (1)	0
QUDO-QUWI/GR	198 (80)	173 (70)	22 (9)	T	T
QUWI-QUDO-PISA2	380 (154)*	314 (127)*	59 (24)	10 (4)	0
QUDO-PISA2/CECU2-CEBE2	141 (57)	106 (43)	32 (13)	5 (2)	T
QUDO-PISA2/ARVI3/GR	151 (61)	111 (45)	30 (12)	10 (4)	T
QUDO/HALI	101 (41)	69 (28)	27 (11)	5 (2)	0

contains significantly more large diameter class trees than any of the other blue oak types. The QUDO/HALI type is the least dense containing an average of 101 TPH (41 TPA) (Table 4).

DISCUSSION

Previous statewide classification efforts provide broad series level descriptions of oak woodlands. Griffin (1977) described oak communities based on dominant tree species, and provided valuable general information on four regional blue oak types: a Great Basin transition type which includes California juniper (*Juniperus californica*), a Coast Range type, a Sierra Nevada type representing a homogeneous strip of blue oak east of the Central Valley, and a Central Valley savanna type with blue oak and a grass understory.

Bolsinger (1988) described only two general blue oak types: blue oak with the presence of shrubs and generally one or more other species of tree, and pure blue oak and grass. He suggested that blue oak woodlands with shrubs were usually higher elevation sites, or moister, lower elevation sites. Bolsinger (1988) suggested that pure blue oak, with a grass understory, occupied the lower elevation, arid end of the moisture range of blue oak in California.

Unlike these general systems, this classification provides detailed information on the diversity of blue oak communities such that managers can generalize experimental results to similar sites. Analysis of 1000 blue oak plots not previously used in Allen et al. (1989) supports the idea that the subseries, as described, are repeatable, recognizable units on the ground.

Four of the 12 blue oak subseries have substantial cover (>5 and <20 percent) and high constancy (>80 percent) of shrub species, although five additional subseries contain some shrub species. The four subseries include QUDO/CECU2/GR, QUDO-PISA2/CECU2-CEBE2, and QUDO/HALI the highest elevation subseries in the blue oak woodland (Table 3), and QUDO-PISA2/ARVI3/GR characterized by the presence of whiteleaf manzanita which occupies sites at elevations higher than the pure blue oak types. These four blue oak subseries also contain foothill pine and/or other tree species.

On the driest sites, QUDO/GR and QUDO-UQUDO/GR contain only grass species in the understory. The QUDO-UQUDO/GR subseries is unique because of the high constancy of blue oak less than 10 cm dbh. Both blue oak/grass types occupy similar sites in the Sierra Nevada and Coast Range (Table 3), yet further research will have to explain the occurrence of small diameter blue oak trees on particular sites.

Analysis of similarity coefficients suggest potential successional or management caused relationships between subseries. For example, we suggest that the QUDO/CECU2/GR subseries is closely related to a number of other subseries (Tables 2 and 3). It occurs in the Sierra Nevada, with blue oak, interior live oak, and foothill pine in moderately dense stands (Table 4), though up to five other tree species may rarely occur in the type depending on the site. QUDO/CECU2/GR may be an early seral stage of QUWI-QUDO-PISA2 which has significantly more ($p < 0.05$) basal area of the dominant trees (Table 3), and less cover and constancy of buck brush. QUWI-QUDO-PISA2 is the densest of any of the blue oak subseries, containing an average of 380 TPH (154 TPA) (Table 4). This relationship is consistent with the expectation that buck brush would drop out of older stands, and that older stands would have more basal area and possibly higher densities of large trees. Other environmental characteristics between the two subseries are very similar.

QUDO/CECU2/GR is also closely related to QUDO-QUWI/GR, and distinguished from it by containing a significantly ($p < 0.05$) greater basal area of foothill pine and a higher cover of buck brush. These differences may be related to fire frequency and/or intensity since buck brush is a prolific sprouter after fire (Sampson and Jesperson 1963) and foothill pine cones are adapted to fire. Again, other environmental characteristics between the two subseries are very similar (Table 3), which supports the suggestion that disturbance

TABLE 5. TABULAR ARRANGEMENT OF SUBSERIES AND SPECIES OCCURRING WITH GREATER THAN 15 PERCENT CONSTANCY. Arrangement of species and subseries indicates similarity between blue oak subseries and reflects geographic distribution of those types occurring in both the Sierra Nevada and Coast Range, the Sierra Nevada, or the Coast Range respectively.

Vegcode	Common name	QUDO/GR	QUDO-UQUDO/GR	QUDO-PISA2/GR	QUDO-PISA2/ARVI3/GR	QUDO-QUWI/GR	QUDO/CECU2/GR	QUWI-QUDO-PISA2	QUDO-QULO/GR	QUDO-QULO-QUAG/GR	QUDO-QUAG/GR	QUDO/HALI	QUDO-PISA2/CECU2-CEBE2
QUDO	Blue oak	1	1	1	1	1	1	1	1	1	1	1	1
UQUDO	Understory blue oak		1		1	1	1	1			1	1	1
PISA-2	Foothill pine			1	1	1	1	1				1	1
CECU-2	Wedgeleaf ceanothus				1	1	1	1	1				1
RHCR	Redberry			1		1	1				1		1
LOSU-3	Southern honeysuckle			1									1
RHDI	Poison-oak				1	1	1	1		1			
QUWI	Interior live oak					1	1	1	1				
UQUWI	Understory interior oak					1	1						
ARVI-3	Whiteleaf manzanita				1		1	1					
ARMA-3	Common manzanita				1	1							
HEAR-2	Toyon, christmas berry					1							
UAECA-2	Understory California buckeye						1						
RICA-1	Hillside gooseberry					1							
QULO	Valley oak						1	1	1				
QUAG	Coast live oak								1	1			
ARCA-7	Coast sagebrush										1		1
UJUCA-3	Understory juniper											1	1
ERFA	California buckwheat											1	1
HALI	Narrowleaf goldenbush											1	1
ARGL-5	Bigberry manzanita												1
CEBE-2	Birchleaf mountain-mahogany												1
ADFA	Chamise												1

(fire) may be the major variable affecting whether the subseries is identified as QUDO/CECU2/GR or QUDO-QUWI/GR.

Two other closely related subseries are QUDO-PISA2/GR and QUDO-PISA2/CECU2-CEBE2 (Table 2). In the Coast Range, QUDO-PISA2/CECU2-CEBE2 occurs at a significantly higher ($p < 0.05$) elevation on north to northeast aspects, and contains a higher shrub component, probably reflecting moister conditions than

QUDO-PISA2/GR. Although the QUDO-PISA2/GR subseries is the more dense of the two (Table 4), the differences are not statistically significant.

We suggest that QUDO-QULO-QUAG/GR may be a late seral subseries in the Coast Range blue oak woodland containing coast live oak and/or valley oak. The three coastal subseries are only distinguished from each other based on oak species dominance. QUDO-QULO-QUAG/GR contains significantly more basal area (Table 3) and is significantly denser than QUDO-QULO/GR or QUDO-QUAG/GR (Table 4). It also has significantly more large diameter class trees than any of the other blue oak subseries (Table 4), though as McClaran and Bartolome (1990) found, age and diameter are only weakly correlated in blue oak.

Table 5 displays all species that occur in one or more subseries at greater than 15 percent constancy. Species and subseries are arranged in the table to qualitatively show species similarity among subseries. This complements the Jaccard's coefficients, and visually displays the pattern in species among subseries.

Several general relationships can be noted among blue oak subseries. For example, there are no significant differences in total mean trees per hectare or mean trees per hectare by diameter class within subseries that occur in both the Sierra and Coast Range. However, coastal variants tend to occur at higher elevations, have denser stands and more large trees (Tables 1 and 4). In general, blue oak woodland subseries do not have large diameter class (89+ cm) trees (Table 4). In fact, trees of the five studied species are rare in the 60–89 cm DBH class, which supports studies completed by Bolsinger (1988) and Standiford and Howitt (1988). Similarly, mean basal area of the dominant trees for 10 of the 12 subseries is about 12 m^2/ha (50 ft^2/acre), while only QUDO-QULO-QUAG/GR and QUWI-QUDO-PISA2 have more than 23 m^2/ha (100 ft^2/acre) on average.

We suggest that subseries descriptions presented in this paper are the appropriate level of detail for linking research in blue oak woodlands to management practices. As research continues, relationships among subseries will be further sorted and capabilities for predicting type response to management inputs will improve.

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EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA

TONY L. BURGESS, JANICE E. BOWERS, and RAYMOND M. TURNER
U.S. Geological Survey, Research Project Office,
1675 West Anklam Road, Tucson, AZ 85705

ABSTRACT

A census and mapping of the exotic flora of the Desert Laboratory grounds, Tucson, Arizona, is described. Most of the 52 exotic species are restricted to disturbed habitats. Five annuals (*Bromus rubens, Erodium cicutarium, Hordeum murinum, Sisymbrium irio,* and *Schismus* sp.) and one perennial grass (*Pennisetum ciliare*) have invaded extensive areas of undisturbed Sonoran Desert vegetation. Shared features of these six species are discussed with respect to climates of origin, evolution with pastoralism, grazing history of southern Arizona, integration into native food webs, and reproductive biology. The invasions appear to be irreversible, and other exotic species show signs of becoming increasingly invasive. What has occurred on the Desert Laboratory grounds may represent the future pattern for much of the eastern Sonoran Desert. The present status and history of introduction of each exotic species are presented in an appendix.

In 1903 the Carnegie Institute of Washington established the Desert Laboratory at Tucson, Arizona, to investigate desert plant ecology (Coville et al. 1903). Soon afterwards, Spalding (1909) mapped the distribution of two exotic plant species, *Erodium cicutarium* and *Hordeum murinum,* on the Desert Laboratory grounds. *Cynodon dactylon* was the only other exotic in the Desert Laboratory flora (Spalding 1909). Since then, exotic species have proliferated, and the total is now 52 (Bowers and Turner 1985; Turner and Bowers 1988).

Much research on exotic plants in the North American deserts has concentrated on disturbed habitats. In the Great Basin, Eurasian annuals such as *Salsola australis, Bromus tectorum* L., *Sisymbrium altissimum* L., and *Descurainia sophia* (L.) Webb. naturalized in sagebrush scrub following intensive burning and grazing (Piemeisel 1951; Young et al. 1972; Yensen 1981; Mack 1981, 1986). In the Sonoran Desert, *Salsola australis, Schismus* spp., *Sisymbrium irio, Bromus rubens* and *Erodium cicutarium* colonized abandoned farmland (Karpiscak 1980). *Erodium cicutarium* and *Bromus rubens* established on land that had been denuded of vegetation but not plowed in the Mojave Desert (Piemeisel 1932) as well as on other disturbed sites (Rickard and Sauer 1982). Less attention has been paid to establishment of exotics in undisturbed desert communities. Beatley's (1966) study of *Bromus* species in the Mojave Desert is a notable exception. The goal of the present study was to document the status

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and history of exotic plants at the Desert Laboratory, particularly those naturalized in undisturbed habitats.

STUDY AREA

The Desert Laboratory grounds include Tumamoc Hill and the level to gently rolling plain to the west, 352 ha in all (Fig. 1). A rocky outlier of the Tucson Mountains, the hill rises 245 m above the surrounding plain to an elevation of 948 m and is composed of Tertiary volcanics. Adjacent lower areas contain alluvial deposits of varying ages and outcrops of Cretaceous clay.

The climate features mild winters, hot summers and biseasonal precipitation. Afternoon temperatures from June through September often exceed 38°C. Minimum temperatures on the hill may remain above freezing in a mild winter or drop as low as −8.9°C in the coldest ones. In the rather severe winter of 1931–1932, there were 18 freezing nights on the hill (Turnage and Hinckley 1938). Yearly rainfall from 1904 to 1980 averaged about 250 mm/year. About half of the yearly total comes during July, August and September. Most of the remainder falls between October and April.

Study-area vegetation is typical of the Arizona Upland Subdivision of the Sonoran Desert (Shreve 1951). Dominants include *Cercidium microphyllum* (Torr.) Rose & I. M. Johnst., *Larrea tridentata* (DC.) Cov., *Opuntia versicolor* Engelm., *O. phaeacantha* Engelm., *Fouquieria splendens* Engelm., *Lycium berlandieri* Dun., *Encelia farinosa* Gray, and *Ambrosia deltoidea* (Torr.) Payne. Along the washes *Cercidium floridum* Benth., *Prosopis velutina* Woot., *Acacia constricta* Benth., and *A. greggii* Gray are common. Spalding (1909) and Goldberg and Turner (1986) provide more detailed descriptions.

Grazing on the Desert Laboratory grounds ceased when the property was fenced in 1907. Before then, cattle and goats fed "in considerable numbers" on Tumamoc Hill (Bowers 1989). Grazing was severe enough that after four years of protection, Thornber detected "a marked increase in the perennial grasses," notably *Hilaria mutica* (Buckl.) Benth., *Hilaria belangeri* (Steud.) Nash, *Bouteloua curtipendula* (Michx.) Torr., and *Muhlenbergia porteri* Scribn. (Thornber 1910, p. 292). After fencing, the grounds were little disturbed until the 1950's, when easements were granted for three gas pipelines and three electric powerlines. Other localized disturbances in the past three decades have included a sanitary landfill and a clay quarry (both now abandoned) and several roads.

Despite these local alterations, the Desert Laboratory grounds, situated 5 km west of downtown Tucson, have been stable relative to their environs. In 1910 Tucson's population was 13,913 and its urban area was 3.1 km^2 (Bufkin 1981). North and east of the Desert Laboratory were cultivated fields; south and west lay undeveloped

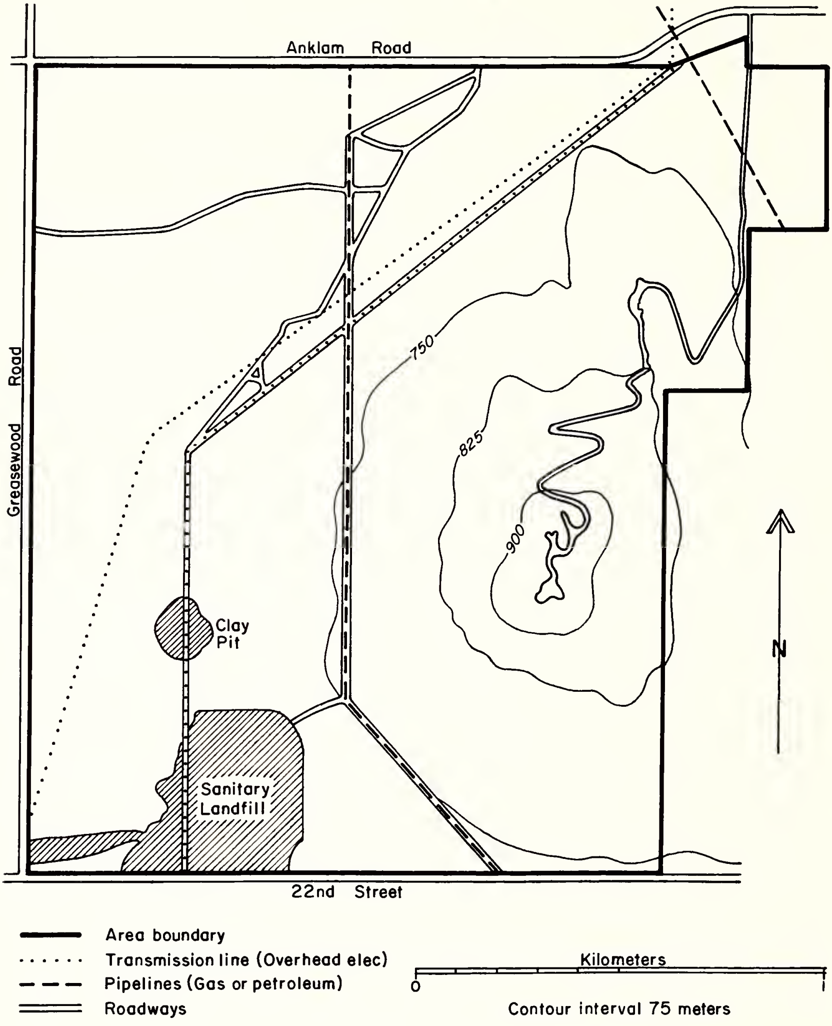

FIG. 1. Map of Desert Laboratory showing boundaries, paved road, outline of landfill and washes.

desert. By 1980 Tucson's urbanized area held approximately 500,000 people in 324 km^2, and the Desert Laboratory grounds were almost surrounded by suburban developments.

SURVEY FOR EXOTIC PLANTS

We surveyed the Desert Laboratory grounds for exotic plants from February to June of 1983. We marked gridlines on aerial photographs (scale 1:2256) of the property, then, using the photographs as a guide, we walked each gridline, remaining on it insofar as possible. The gridlines were 226 m apart and had a total length of about 40 km. We recorded the Cartesian coordinates and relative abundance of all exotic plants encountered within about 2 m of the lines. We also surveyed the paved road (Fig. 1) and all other disturbed or artificial habitats not intersected by the grid. Using the coordinates, we generated a distribution map for each species encountered. In the course of this survey we found 33 of the 52 exotics in the flora (Appendix 1). The remainder are so infrequent that our survey grid did not intersect them.

RESULTS AND DISCUSSION

Localized exotics. A few of the exotics recorded during our survey are restricted to particular, usually artificial, habitats. These include such species as *Phalaris minor* and *Polypogon monspeliensis,* known from ephemeral ponds at the landfill, and *Salsola australis,* abundant on dry, disturbed landfill substrates. *Salsola* seeds cannot germinate once the soil has formed a crust; thus the species is most characteristic of recently disturbed sites (Karpiscak 1980).

Many more exotics, while local in distribution, can be identified with no particular habitat. Some apparently require soil disturbance. *Matthiola longipetala* is occasional on the landfill and nearby roadsides, whence it is spreading to disturbed habitats nearby. Others seem not to need disturbed seedbeds and may eventually spread extensively. In the 30 years since *Brassica tournefortii* first appeared near Yuma, Arizona (Mason 1960), it has established along roads and in undisturbed desert in western Arizona. On the Desert Laboratory grounds, this species is especially abundant along the western boundary fenceline whence it is colonizing the grounds using washes as corridors. *Dimorphotheca sinuata,* an ornamental annual commonly cultivated in Tucson, is invading from the southwest edge of the property, where it has doubtless escaped from cultivation in a nearby housing development. Like *Brassica, Dimorphotheca* spreads along washes.

The process of introduction continues. Two exotics appeared on the grounds after the 1983 survey—*Caesalpinia gilliesii* and *Opuntia microdasys.* Both are common ornamentals in nearby yards and gardens.

Naturalized exotics. Five exotic annuals and one exotic perennial have naturalized on our study area; that is, they self-seed in undisturbed habitats and occur as frequently as common native species. *Erodium cicutarium* and *Hordeum murinum* occupied scattered patches on the northwest side of the Tumamoc Hill property in 1906 (Saplding 1909). Both have since naturalized throughout the grounds

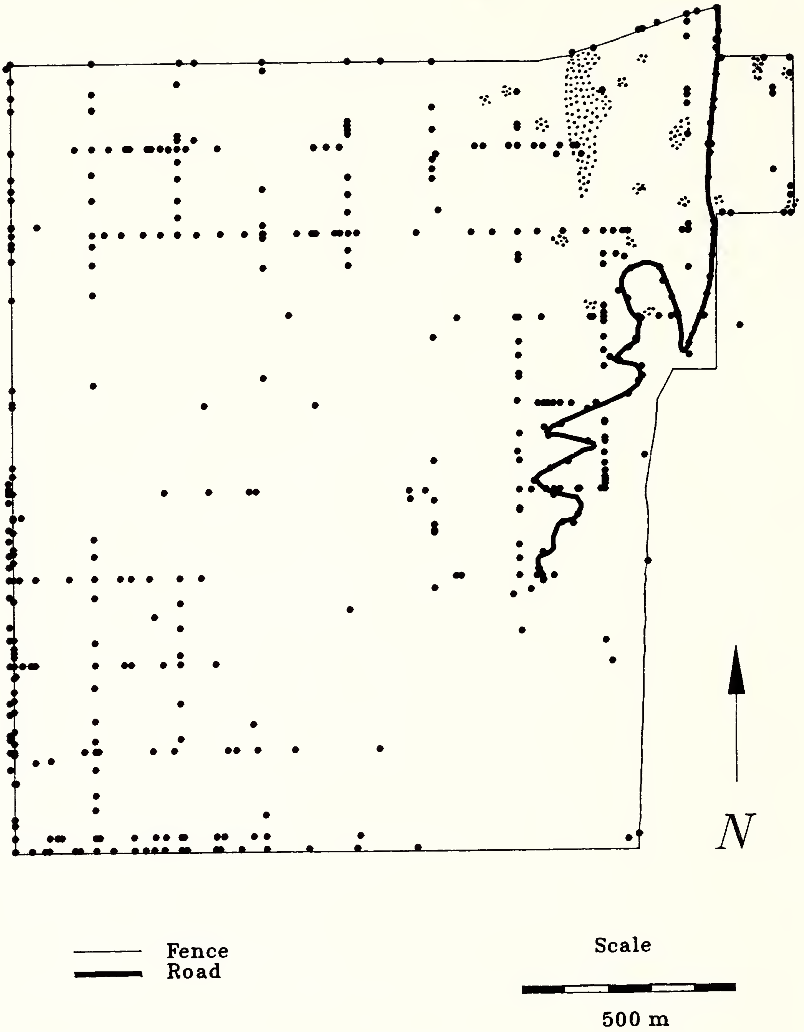

FIG. 2. Distribution of *Erodium cicutarium* at Desert Laboratory in 1906 (stippled areas) and 1983 (dots). From Turner and Bowers (1988).

(Figs. 2, 3). *Sisymbrium irio, Bromus rubens,* and *Schismus* spp. have also naturalized on our study area, apparently within the last 50 to 76 years (Appendix 1). *Pennisetum ciliare,* a perennial grass, forms colonies up to 20 m across on rocky slopes of Tumamoc Hill and is also common along some washes. It has spread steadily since our 1983 survey and, like the six exotic annuals, establishes well in undisturbed habitats.

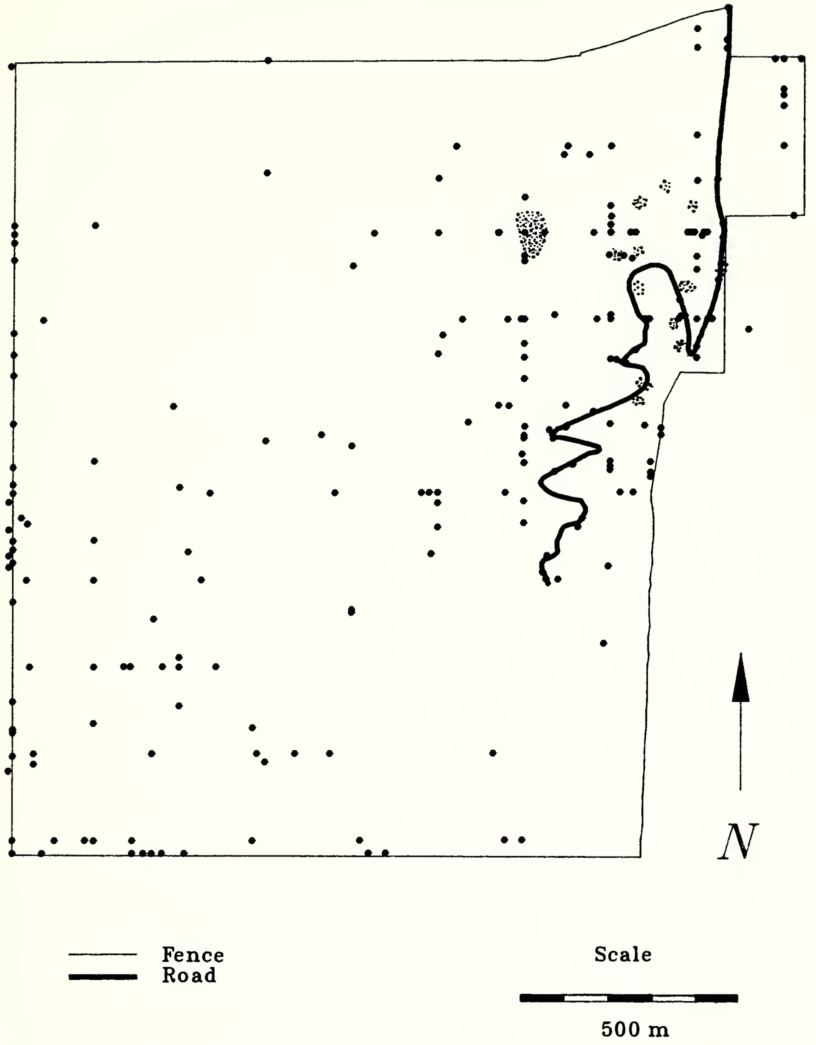

FIG. 3. Distribution of *Hordeum murinum* at Desert Laboratory in 1906 (stippled areas) and 1983 (dots). From Turner and Bowers (1988).

Why have these seven exotics been able to invade habitats that have undergone no appreciable disturbance for decades? We offer several mutually dependent explanations: favorable climate, prior evolution in regions with intensive pastoralism, the grazing history of southern Arizona, minimal integration into native food webs, and reproductive biology.

Climate. Exotics typically naturalize where climate and vegetation are similar to those of their source areas (Baker 1986). Biseasonal rainfall and subtropical temperatures make the northeastern Sonoran Desert vulnerable to two separate legacies of human landscape alteration: the "Mediterraneanization" of California (Heady 1977; Le Houerou in press) and the "Africanization" of the Neotropics (Baker 1978; Parsons 1970).

The six naturalized annuals on our grounds are native to the Mediterranean region and the Near East, where they grow in winter-rainy climates. *Bromus rubens* ranges from Asia Minor through the Mediterranean region (Tsvelev 1983), where it occurs in natural steppe vegetation and cultivated fields (Feinbrun-Dothan 1986; Hubl and Holzner 1982; Ayyad and Ammar 1974). Since its introduction in the mid-1880's, the species has spread from California to Texas and south into Baja California (Correll and Johnston 1970; Gould and Moran 1981). Its virtual absence from the Great Basin is probably related to sensitivity to frost (Hulbert 1955). *Schismus barbatus* and *S. arabicus,* both highly successful invaders in the Mojave and Sonoran deserts, grow in a variety of arid and semi-arid vegetation types as well as in disturbed sites from the Mediterranean through the Near East (Conert and Turpe 1974; Feinbrun-Dothan 1986). *Hordeum murinum* typically grows in disturbed, ruderal sites (Davison 1971; Frenkel 1977; Zohary 1973) or cultivated fields (Tadros and Atta 1959; Zohary 1950). It does not often dominate in stands of perennial vegetation in its native Eurasia, but it can be a common component of annual pastures elsewhere, as in Australia (Rossiter 1966) and California (Heady 1977; Jackson 1985). *Erodium cicutarium* can be found in disturbed or open habitats over most of Eurasia (Webb and Chater 1968; Vvedenskii 1974; Zohary 1972). It was among the earlier invaders in California (Heady 1977; Wester 1981). Various forms in the *Sisymbrium irio* complex can be found from Europe to India (Khoshoo 1955, Titz 1969). The species spread from southern to northern Europe during the seventeenth through nineteenth centuries (Ball 1964; Ellenberg 1988; Salisbury 1964), more or less concurrently with its colonization of North America.

The Africanization of our study site is evident in the establishment of the introduced perennial grass *Pennisetum ciliare,* which is native from northwestern India through the Middle East to southern Africa (DeLisle 1963). Coming from an area where climates are subhumid to arid with predominantly warm-season rainfall, *P. ciliare* is well adapted to exploit soil-moisture regimes typical of the summer and fall in southern Arizona (Cox et al. 1988). Although present on our study area since at least 1968, this species did not become extensively naturalized until the 1980's, after two periods of unusually wet summers. During the first of these, from 1970 to 1972, warm-season (October–May) rainfall exceeded the average (186 mm) by 103, 128 and 119 mm, respectively. During the second, from 1982 to 1984, warm-season totals were 134, 200 and 116 mm, respectively, above the average. Undoubtedly the more recent wet interlude and perhaps also the earlier one contributed to the increase of *P. ciliare.* Climatic fluctuations may also promote invasions by causing mortality of established natives, thereby creating openings for establishment (Tisdale et al. 1965). On slopes where *P. ciliare* has been invading, there has been considerable mortality of *Encelia farinosa,* apparently caused by freezing.

Evolution with pastoralism. The pattern of invasions between arid habitats in the Old and New worlds is not symmetrical. New World annuals and grasses have not become widely established outside of ruderal sites in either North Africa (Le Floc'h et al. 1990, Le Houerou in press) or southern Africa (Brown and Gubb 1986). Highly disturbed ruderal and segetal conditions developed earlier and more extensively in the Old World (Diamond 1988). While the emerging symbiosis among humans, large domestic animals and crops subjected Old World floras to selection under increasing disturbance (Jackson 1985; Naveh 1967; Young et al. 1972), Holocene vegetation in North America developed with a significantly reduced megafauna (Martin and Klein 1984) and no pastoralist societies. These contrasting histories resulted in the Sonoran Desert having relatively few species adapted to intensive grazing in comparison with floras from similar climates in the Old World.

Grazing history. There are strong connections between invasions of exotic plants and the advent of widespread pastoralism in the Sonoran Desert. The pattern of overgrazing on Arizona rangelands around the turn of the century has been well-documented (Wagoner 1952; Bahere and Bradbury 1978). The drought of 1890–1892, one of the worst on record for Arizona, aggravated the effects of overgrazing (Bahre and Bradbury 1978). By 1910, the desert grassland had been denuded of perennial grasses, and native annuals such as *Aristida adscensionis* and *Bouteloua aristidoides* had replaced them (Griffiths 1910).

Exotic annuals also increased as perennial grasses declined. *Erodium cicutarium* appeared in the San Pedro Valley east of Tucson by 1880 (Arizona Daily Star, February 10, 1880) and in the Sulphur Springs Valley by 1866 (Thornber 1906). By 1903 this species was locally naturalized on overgrazed ranges south of Tucson (Thornber 1903), and by 1910, *Hordeum murinum* was also becoming established on ranges in the vicinity (Thornber 1910). Range managers deliberately introduced certain exotic species. *Bromus rubens* was one of 24 annual forage species sown on the Santa Rita Experimental Range south of Tucson in the winters of 1906–1907 and 1907–1908 (Thornber 1910). *Eordium cicutarium* was also sown by at least one rancher (Arizona Daily Star, June 13, 1880).

The timing of these events strongly suggests that overgrazing fostered establishment of exotic annuals on southern Arizona ranges. A similar process has been implicated in California, where decades of overgrazing removed the native cover, leaving the land vulnerable to colonization of exotics (Biswell 1956; Naveh 1967; Frenkel 1977; Wester 1981). Although we have no quantitative evidence regarding the history of livestock on the Desert Laboratory grounds, it is likely that grazing before 1907 favored the establishment of exotics in the vicinity.

This is not to say that disturbance by pastoralism is the sole cause of invasions. McKell et al. (1962) suggested that communities of annual plants—such as those in the deserts of California—are "extraordinarily open." In 1986, after a drier than normal winter, we first detected *Schismus* sp. and *Brassica tournefortii* on the floor of MacDougal Crater in northwestern Sonora, Mexico. The crater is inaccessible to domestic livestock, and anthropogenic disturbance has been limited to occasional visits by botanists and others. This and similar examples suggest that Sonoran Desert communities are relatively open to invasion by Old World exotics. Such "openness" may result from a combination of factors, among them an initial lack of integration into food webs, the reproductive biology of invading species and competitive effects.

Integration into food webs. An invading species, particularly one from another continent, is unlikely to meet resident pathogens or predators adapted to exploit it intensively. Exotic plant species may profit from a period free of such biotic checks as diseases and insects, as noted by McKell et al. (1962) for the grass *Taeniatherum asperum* (Simonaki) Nevskii. Even highly palatable invaders may be 'hidden' when outnumbered by other species (Risch and Carroll 1986). Once an invading plant increases, evolutionary and behavioral responses of consumers and pathogens begin to integrate it into the food web, and its initial advantage declines. Seeds of *Erodium cicutarium,* for example, are heavily used by native granivores (Inouye et al. 1980; Soholt 1973; Stamp and Ohmart 1978; De Vita 1979). Herbivore effects are not always negative, however; in many cases, native consumers are effective dispersal agents (Knight 1986; Rissing 1986).

Reproductive biology. With the possible exception of *Sisymbrium irio,* the naturalized exotics on our study site are apparently self-compatible or apomictic (Booth and Richards 1976; DeGroote and Sherwood 1984; Faruqi and Quraish 1979; Martin and Harding 1982; Wu and Jain 1978), conforming with Baker's (1955) observations on successful weeds.

Most native annuals studied to date show relatively precise requirements for germination (Went 1948, 1949; Went and Westergaard 1949; Juhren et al. 1956; Tevis 1958), so that in a given year there are seldom enough temperature-moisture combinations to germinate all the species in the seed bank (Juhren et al. 1956). Many require a rainfall event of more than 25 mm to germinate (Beatley 1974). Germination requirements of the naturalized exotics appear to be less precise. Thus, in years unfavorable for germination of native annuals, such exotic species as *Bromus rubens, Sisymbrium irio* and *Schismus barbatus* still establish and reproduce in favorable microsites.

Some native annuals may have density-dependent germination (Inouye 1980) whereby the presence of established plants on a site prevents others from germinating. *Bromus rubens, Hordeum murinum* and *Schismus barbatus* do not suppress germination at high densities (Wu and Jain 1979; Szarek et al. 1982; Borchert and Jain 1978; Davison 1971). After good rains, mass germination in these species produces dense stands that suppress other ephemerals.

Seeds of *Erodium* and *Sisymbrium* can have extended dormancy (Roberts 1986; Wilson and Duff 1984). In contrast, *Schismus, Hordeum* and *Bromus* do not normally form long-lasting seed banks (Loria and Noy-Meir 1980; Popay 1981; Roberts 1981; Wu and Jain 1979). Populations build up rapidly during a series of good years, but a bad season can cause catastrophic losses. Following a poor year, seeds are dispersed into depleted areas from individuals that reproduced in more mesic sites.

In short, the lack of specificity in germination requirements, the ability to reproduce under intense crowding and marginal conditions, and effective seed dispersal are critical factors in the successful naturalization of certain exotics at the Desert Laboratory.

Competitive effects. Whether naturalized annuals are crowding native species out of the habitat is unknown. The native *Erodium texanum* is a common associate of *E. cicutarium* at the Desert Laboratory. Inouye et al. (1980) indicate possible competition between the two.

It appears that *Pennisetum ciliare* is displacing *Encelia farinosa* from some rocky slopes. The root systems of both exploit the upper soil horizons (Cannon 1911; Christie 1975), but some temporal partitioning of soil moisture should exist. *Pennisetum* is most active during the warm season whereas *Encelia* grows in late winter and spring. *Encelia* has not reestablished within larger stands of *Pennisetum.* Apparently a temporary competitive release can start a *P. ciliare* invasion (Danin 1976) which may be consolidated by allelopathic effects (Cheam 1984; Hussain et al. 1982).

Because *Pennisetum ciliare* tolerates burning better than most long-lived Sonoran Desert perennials (Mayeux and Hamilton 1983; Mott 1982; 't Mannetje et al. 1983), occasional fires may promote its increase at the expense of native species. *Bromus rubens* can produce substantial biomass, particularly during wet winters (Beatley 1969; Bowers 1987). The resulting dry litter seems to promote the spread of fires that restructure the perennial vegetation without adversely affecting *B. rubens* (Beatley 1966; Brown and Minnich 1986; Rogers and Steele 1980).

CONCLUSIONS

Though much of the Desert Laboratory grounds has been protected for decades, certain exotic plant species occur throughout the property on disturbed and undisturbed sites alike. Winter annuals from the Mediterranean and Near East predominate in the exotic flora, whereas introduced summer annuals play a minor role. The changes that have occurred over the last 50 to 75 years appear irreversible. Grazing before 1907 could have created conditions that favored the initial invasion by exotic annuals. Exotic perennial grasses were introduced later (Cox et al. 1988), and their invasion appears to be accelerating. The most successful exotics, whether annual or perennial, share features that indicate evolution in ruderal habitats in climates similar to that of the Sonoran Desert.

The character and rate of change in the Desert Laboratory flora have undoubtedly been influenced by its proximity to the rapidly growing city of Tucson, which has often served as a source of propagules. Parts of the Sonoran Desert remote from urban centers have not undergone the rapid proliferation of exotics seen at the Desert Laboratory; nevertheless, the invasion of relatively undisturbed habitats within the grounds indicates a possible future of Sonoran Desert vegetation.

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APPENDIX I.

STATUS AND HISTORY OF SELECTED EXOTICS AT THE DESERT LABORATORY, TUCSON, ARIZONA

The vouchers cited below are deposited at ARIZ. It is difficult to determine when most of these introductions occurred. An exotic species may have been established on our study area many years before its initial documentation.

Avena fatua L. Scattered and rare; distrubed sites along roads and in washes. Established in California by 1824 (Frenkel 1977); present in Arizona by 1902 (*Thornber s.n.*); first Desert Laboratory collection made in 1983 (*Bowers and Turner 2222*).

Brassica tournefortii Gouan. Scattered and rare; fence lines and washes. Introduced into Arizona ca. 1960 (Mason 1960); first Desert Laboratory collection made in 1978 (*Turner 78-1*).

Bromus rubens L. Widespread and common. Established in California by 1848 (Frenkel 1977), though not naturalizing to any appreciable extent for another 45 years (Davidson 1907); present in Tucson by 1909 (Thornber 1909) and beginning to spread to nearby "mesas" by 1910 (Thornber 1910); first Desert Laboratory collection made in 1968 (*Mason and Turner 68-130*). Perhaps introduced into Tucson area when sown as potential annual forage plant on Santa Rita Experimental Range in winter of 1906–1907 and 1907–1908 (Thornber 1910).

Bromus catharticus Vahl. Scattered and occasional; disturbed sites, often in low-lying areas. Present in Arizona by 1894 (Britton and Kearney 1894); first Desert Laboratory collection made in 1968 (*Mason and Turner 68-131*).

Caesalpinia gilliesii (Hook.) Wall. Local and rare. Wash borders near the west boundary and riparian thickets where floodwaters pond. First Desert Laboratory collection made in 1989 (*Burgess 7611*).

Centaurea melitensis L. Confined to landfill, where occasional. Established in California by 1824 (Frenkel 1977); present in Arizona by 1897 (Toumey 1897); first noted at Desert Laboratory in 1983.

Chenopodium murale L. Scattered and occasional; disturbed sites, often along fence lines. Established in California by 1824 (Frenkel 1977); present in Arizona by 1901 (*Thornber 4433*); not known from Desert Laboratory until 1983 (*Bowers 2587*).

Cynodon dactylon L. Scattered and locally abundant; disturbed, low-lying areas. Established in California by 1860 (Frenkel 1977); growing without cultivation in Arizona by 1891 (*Toumey s.n.*); known from Desert Laboratory Hill since 1909 (Spalding 1909).

Dimorphotheca sinuata DC. Scattered and rare; usually along washes. Cultivated in Arizona since the 1940's, naturalized in various locations by the 1970's (Earle 1973); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-8*).

Eragrostis lehmanniana Nees. Local and common; usually on disturbed sites but occasionally elsewhere. Introduced at Tucson in 1934 by the Soil Conservation Service (Flory and Marshall 1942); well established along roadsides in Tucson by 1946 (Gould 1946); first Desert Laboratory collection made in 1983 (*Bowers 2703*).

Erodium cicutarium (L.) L'Her. Widespread and common. Established in California by 1824 (Frenkel 1977); present in Arizona by 1866, no doubt introduced into the state by sheep from California (Thornber 1906) and also sown deliberately by at least one rancher (Arizona Daily Star, June 13, 1880); known from the San Pedro Valley since 1880 (Arizona Daily Star, February 10, 1880), the Tucson area since 1903 (Thornber 1903) and from Desert Laboratory since 1906 (Spalding 1909).

Hordeum murinum L. subsp. *glaucum* (Steud.) Tzvelev. Widespread and occasional. Established in California by 1824 (Frenkel 1977); present in Arizona by 1894 (Britton and Kearney 1894); established in the Salt River valley by 1897 (Toumey 1897) and a noxious weed there by 1901 (McClatchie 1901); known from Desert Laboratory since 1906 (Spalding 1909); uncommon in the Tucson area until at least 1910 (Thornber 1910). Three major taxa have been defined in the *Hordeum murinum* group. On the basis of anther length, both *H. murinum* subsp. *leporinum* and *H. murinum* subsp. *glaucum* have been collected on the Desert Laboratory grounds. Lodicules are considered a more reliable diagnostic character (Baum and Bailey 1984a, b), and in this feature our collections conform to *H. murinum* subsp. *glaucum.*

Lactuca serriola L. Scattered and rare; disturbed sites, most often in washes. Established in California by 1860 (Frenkel 1977); present in Arizona by 1905 (*Thornber 5572*); first noted on Desert Laboratory grounds in 1983.

Lantana horrida H.B.K. Scattered and rare. An ornamental commonly cultivated in and around Tucson; first Desert Laboratory collection made in 1983 (*Bowers 2704*).

Lepidium oblongum Small. Local, occasional to common. Introduced into Arizona by 1902 (*Thornber s.n.*); first Desert Laboratory collection made in 1983 (*Bowers and Turner 2225*).

Malva parviflora L. Scattered and rare; low-lying disturbed sites. Established in California by 1824 (Frenkel 1977); present in Tucson by 1891 (*Toumey s.n.*); first Desert Laboratory collection made in 1978 (*Turner 78-5*).

Matthiola longipetala (Vent.) DC. ssp. *bicornis* Sibth. & Sm. Scattered and rare; on landfill and fence lines. Introduced into Tucson ca. 1905 and escaping from cultivation (Thornber 1909); first Desert Laboratory collection made in 1983 (*Turner and Goldberg 78-13*).

Melia azederach L. Local and rare on landfill. Common ornamental in and around Tucson; first Desert Laboratory collection made in 1983 (*Turner 83-4*).

Melilotus indicus (L.) All. Local and rare; moist sites near ponds. Established in California by 1848 (Frenkel 1977); present in Arizona by 1891 (*Toumey s.n.*); common weed in southern Arizona by 1900 (McClatchie 1900); first Desert Laboratory collection made in 1983 (*Bowers and Turner 2210*).

Molucella laevis L. Scattered and rare; usually in moist sites. An ornamental commonly cultivated in and around Tucson; first Desert Laboratory collection made in 1979 (*Turner and VanHylckama 79-64*).

Nicotiana glauca Grah. Scattered and rare; usually in moist sites, but also on steep slopes with southerly aspects. Established in California by 1848 (Frenkel 1977); cultivated in Tucson by 1891 and escaping from cultivation by 1904 (*Thornber 480*); first Desert Laboratory collection made in 1983 (*Turner 83-11*).

Opuntia microdasys (Lehm.) Pfeiffer. Local and rare; gravelly flats near the west boundary; first noted on Desert Laboratory grounds in 1984.

Parkinsonia aculeata L. Scattered and rare; most common on sanitary landfill. Cultivated in and around Tucson; first Desert Laboratory collection made in 1968 (*Warren and Turner 68-155*).

Pennisetum ciliare (L.) Link. Scattered, rare to abundant. Introduced to Arizona by Soil Conservation Service ca. 1938, spreading from plantings by 1954 (Kearney 1954); first Desert Laboratory collection made in 1968 (*Warren and Turner 68-11*).

Pennisetum setaceum (Forsk.) Chiov. Local and occasional. Usually in disturbed sites where runoff collects, also in crevices of some basalt outcrops; first Desert Laboratory collection made in 1983 (*Bowers 2754*).

Phacelia campanularia Gray. Local and rare; not established. A California native, doubtless spreading to our area from nearby plantings; first Desert Laboratory collection made in 1983 (*Bowers and Turner 2226*).

Phalaris minor Retz. Local and occasional; moist sites. Introduced into California by 1882 (Robbins 1940); present in Arizona by 1913 (*Thornber s.n.*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-18*).

Polypogon monspeliensis (L.) Desf. Local and occasional; moist sites. Established in California by 1848 (Frenkel 1977); present in Arizona by 1891 (*Toumey s.n.*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-20*).

Rhus lancea L. Local and rare; moist areas along washes. Introduced into California in 1919; first planted in Tucson in 1928 (Schmidt 1969); first Desert Laboratory collection made in 1984 (*Bowers 2970*).

Salsola australis R. Brown. Scattered and common; abundant on landfill. Introduced into U.S. in 1886 in flax seed sown in South Dakota and established in California by 1895 (Robbins 1940); first collected in Tucson in 1892 (*Toumey s.n.*). Oddly, in 1897 Toumey wrote, "There is no direct evidence that this weed had yet found its way into Arizona," and in 1904, Griffiths described *Salsola* as common along railway lines in northern Arizona but added, "so far as known it does not occur in the southern part of Arizona at all." In any case by 1913, *Salsola* was apparently well established in Tucson (*Thornber 7305, Thornber s.n.*). The first Desert Laboratory collection was made in 1968 (*Warren and Turner 68-160*).

Schismus arabicus Nees. Widespread, common to abundant. Present in Arizona by 1933 (*Peebles 9098*); first Desert Laboratory collection made in 1968 (*Mason and Turner 68-128*).

Schismus barbatus (L.) Thell. Widespread, common to abundant. First collected in Arizona in 1926, naturalized in central part of state by 1931 (Kearney 1931) and in southern part by 1949 (Gould 1949); first Desert laboratory collection made in 1983 (*Bowers 2455*). Apparently not introduced into California until 1935 (Robbins 1940). It is unclear whether *S. arabicus* and *S. barbatus* both occur in our study area. Faruqi and Quaraish (1979) and Faruqi (1981) found that in Libya, intermediate forms apparently derived from hybridization and backcrossing between the two taxa have been stabilized by high rates of autogamy. They concluded that there is no justification for regarding *S. barbatus* and *S. arabicus* as separate species. Specimens from the Desert Laboratory fit *S. barbatus* as defined by Conert and Turpe (1974). A review of the North American material seems in order.

Sisymbrium irio L. Widespread and occasional. Present in Arizona by 1909 (*Thornber s.n.*), in California by 1918 (Robbins 1940); abundant in the Phoenix area by 1933 (Hamilton 1933); first Desert Laboratory collection made in 1968 (*Warren and Turner 68-47*).

Sisymbrium orientale L. Scattered and occasional; along washes. Present in Arizona by 1931 (*Harrison et al. 7554*); first Desert Laboratory collection made in 1978 (*Turner and Goldberg 78-11*).

Sonchus oleraceus L. Scattered and rare; often along washes. Established in California by 1824 (Frenkel 1977); present in Tucson by 1897 (Toumey 1897); first Desert Laboratory collection made in 1983 (*Bowers 2502*).

Tamarix ramosissima Ledeb. Occasional at ponds in clay quarries. First collected in Arizona in 1901 (Horton 1964); first Desert Laboratory collection made in 1968 (*Warren and Turner 68-120*). A cultivated species that has become widely naturalized in the Southwest.

NATURAL HYBRIDIZATION IN WESTERN GOOSEBERRIES (*RIBES* SUBGENUS *GROSSULARIA*: GROSSULARIACEAE)

Michael R. Mesler, R. Jane Cole, and Paul Wilson[1]
Department of Biological Sciences, Humboldt State University,
Arcata, CA 95521

Abstract

We describe three cases of hybridization between species of *Ribes* in the Klamath Mountains of northern California and southern Oregon. Based on their intermediacy and reduced pollen viability, we identified putative hybrids between *R. lobbii* and *R. roezlii* var. *cruentum, R. binominatum* and *R. marshallii,* and *R. binominatum* and *R. lobbii.* The hybrids live in recently cleared forests, where logging created extensive areas suitable for seedling establishment. Even though they are partially fertile, backcrossing and interbreeding have not generated an extensive array of recombinant types. Judging from field observations and surveys of herbarium specimens, hybridization between these species of *Ribes* appears to be uncommon, and there is little evidence that introgression is blurring the distinctions between them.

Like members of many other woody genera, closely related species of *Ribes* are interfertile (Keep 1962) and presumably capable of hybridizing where sympatric. Numerous reports of spontaneous garden hybrids attest to this potential (Janczweski 1907, 1909, 1911, 1916). Not surprisingly, many botanists assume that hybridization is common in *Ribes,* as it is in other genera with comparable patterns of interspecific fertility (e.g., Grant 1981, p. 312). However, as yet there is little field evidence to support this view. We know of only three papers that describe wild *Ribes* hybrids. Two of these (Henry 1919, *R. lobbii* × *R. divaricatum*; Anderson, 1943, *R. bracteosum* × *R. laxiflorum*) are very brief accounts, based on the discovery of a single specimen. Sinnott (1985) discussed several possible cases of hybridization in his revision of section *Grossularia,* but he did not present detailed supporting evidence. At least some of the patterns he observed could be the result of divergent evolution. Clearly, the importance of natural hybridization in *Ribes* is not yet known.

In this paper we document three cases of natural hybridization between species of *Ribes* in the Klamath Mountains of northern California and southern Oregon. Based on their morphological intermediacy and reduced pollen fertility, we have identified hybrids between *R. lobbii* A. Gray and *R. roezlii* Regel var. *cruentum* (E. Greene) Rehder, *R. binominatum* Heller and *R. marshallii* E. Greene, and *R. binominatum* and *R. lobbii.*

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[1] Present address: Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794.

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METHODS

The species. The four parental species are compared in Table 1 and Figures 1 and 2. All are members of subgenus *Grossularia* (P. Miller) Pers., and all have glabrous styles, unlike the species that comprise section *Grossularia* (Sinnott 1985). Otherwise, the relationships of the four species inter se are uncertain. *R. roezlii* is more closely related to other species with connivent, lanceolate anthers (like *R. menziesii* Pursh) than it is to *R. binominatum, R. lobbii,* or *R. marshallii* (Berger, 1924). Likewise, *R. binominatum* appears to be more closely allied to *R. watsonianum* Koehne and *R. tularense* (Coville) Fedde. Janczewski (1907) and Berger (1924) both regarded *R. lobbii* and *R. marshallii* as close relatives, although the two species differ in many respects, especially petal shape and fruit vestiture. In fact, *R. lobbii* strongly resembles *R. roezlii* in petal shape and flower color, and it is similar to *R. sericeum* Eastwood in other respects. The relationships of *R. marshallii* are least apparent; its distinctive deeply concave petals, and complete lack of glandular hairs, set it off sharply from other gooseberries. Keep (1962) did not attempt garden crosses involving the four parental species, so we do not know to what degree they are interfertile.

Study sites. We made our observations at five sites in northern California and southern Oregon (Appendix I). We chose three sites where *R. lobbii, R. roezlii,* and suspected hybrids occurred together. Morphometric data are presented for only one of these (Horse Mountain) because the patterns at all sites were similar. We studied hybridization between *R. binominatum* and *R. marshallii* and between *R. binominatum* and *R. lobbii* at a site in southern Oregon (Bigelow Lake). Additional hybrids between *R. binominatum* and *R. marshallii* were collected about 1 km away (Mt. Elijah) and included in the analysis. Voucher specimens are filed at HSC.

With the exception of Mt. Elijah, the sites were large disturbed areas in forests that had been completely logged 15 or more years ago. At Mt. Elijah, the suspected hybrids grew along a disturbed roadside adjacent to a relatively undisturbed forest. At all sites, the suspected hybrids were less common than the parental species. Hybrids and parents grew intermixed except at Bigelow Lake, where *R. marshallii* appeared to be restricted to shady sites in the understory of the forest adjacent to the cleared area.

Sampling and morphological analysis. At each site we collected several flowering branches from a sample of parental species and suspected hybrids. At all sites except Big Flat, the samples consisted of more than 90% of the flowering individuals present at the locality. At Big Flat, a random sample of plants was collected along three 50 m transects. Plants at Horse Mountain were marked so that mature

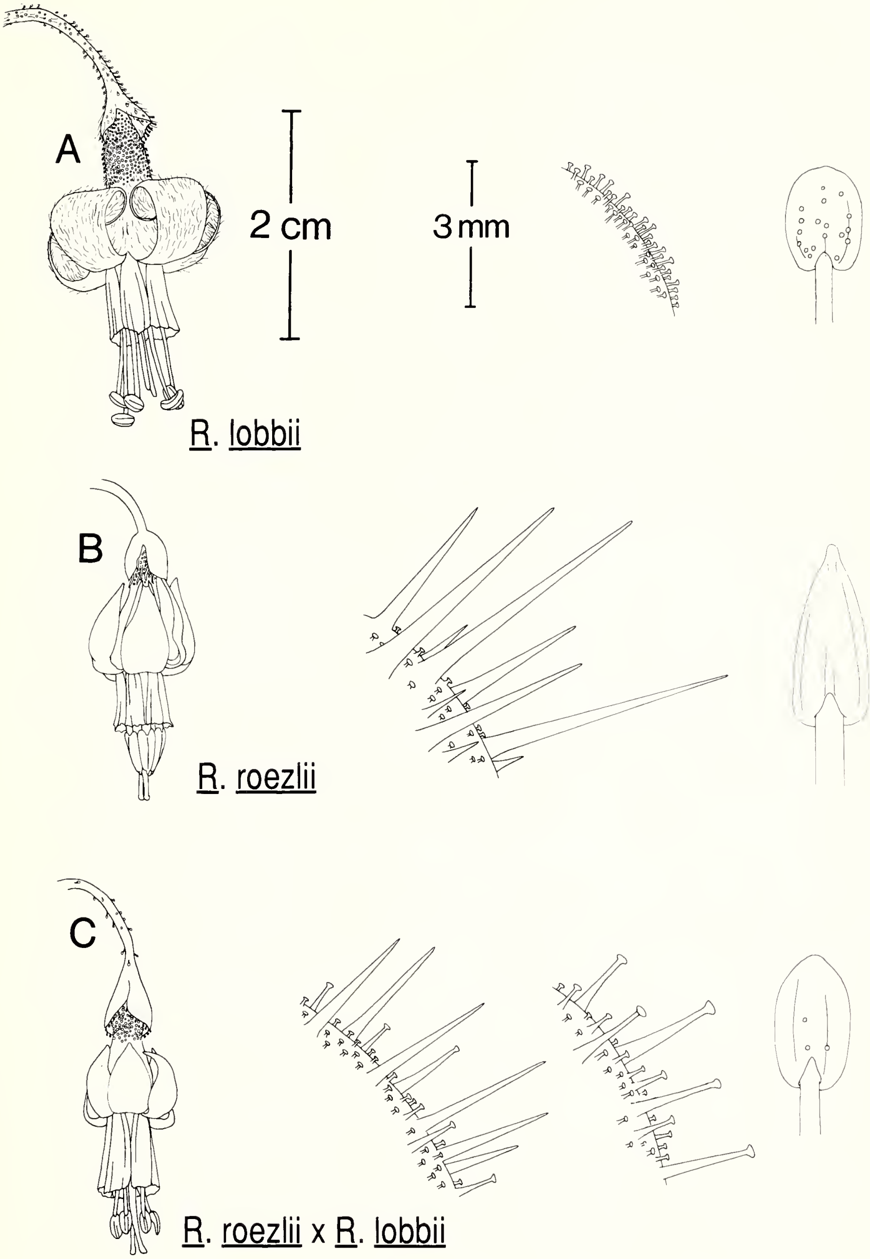

FIG. 1. Flowers, fruit surfaces, and anthers of *Ribes lobbii, R. roezlii* var. *cruentum,* and hybrid from the Horse Mountain population. A. *R. lobbii.* B. *R. roezlii* var. *cruentum.* C. Putative F_1 hybrid. Fruits of two individuals are shown.

TABLE 1. DIAGNOSTIC FEATURES AND DISTRIBUTIONS OF THE FOUR PARENTAL SPECIES.

Character	*R. roezlii* var. *cruentum*	*R. lobbii*	*R. binominatum*	*R. marshallii*
Habit	upright shrub, >1 m, with rigid, divergent branches	upright shrub, >1 m, with rigid, divergent branches	low, trailing shrub, mostly <1 m, rooting along horizontal branches	low, ± upright shrub, to about 1 m, spreading by arching shoots that root at tip
Glands on lower surface of short shoot leaves	absent	present	present	absent
Number of flowers/inflorescence	1 [2]	1–2 [3]	2–3 [1, 4]	1 [2]
Sepal color	crimson	crimson	green [red margin]	dark maroon
Petal				
Color	white [pink]	white [pink]	white [pink]	bright yellow
Shape	tubular (margins involute)	tubular (margins involute)	shallowly concave, rounded at apex	deeply concave, hooded at apex
Stamen exsertion	just beyond petals, filaments barely visible	well beyond petals, filaments clearly visible	just beyond petals, filaments barely visible	well beyond petals, filaments clearly visible
Anther				
Color	purple	purple	white	yellow
Shape (after dehiscence)	lanceolate, with an apiculate apex	oblong, with a blunt or round apex	oblong, with rounded apex	oblong, with rounded apex
Position	connivent about the style	widely separated	widely separated	widely separated
Orientation (after dehiscence)	vertical, parallel to filaments	reflexed, perpendicular to filaments	vertical, parallel to filaments	vertical, parallel to filaments
Glands	absent	present	absent	absent
Fruit surface	non-glandular spines + short glandular hairs	even length glandular bristles	non-glandular spines + glandular hairs + non-glandular hairs	non-glandular spines + appressed non-glandular hairs
Elevational range	170–2000 m	1000–2300 m	900–2500 m	1500–2400 m

TABLE 1. CONTINUED.

Character	*R. roezlii* var. *cruentum*	*R. lobbii*	*R. binominatum*	*R. marshallii*
Distribution	Klamath, North Coast, and Cascade ranges, from Napa Co., CA to southern OR	Klamath, North Coast, and Cascade ranges, from northern CA to British Columbia	Klamath, North Coast, and Cascade ranges, from Lake Co. to southern OR	Klamath Mountains, northwest CA and southern OR

fruits could be collected later in the season. The fruits of the other groups could not be studied.

We used a series of univariate comparisons to test for overall intermediacy of the suspected hybrids and Anderson-style pictorialized scattergrams to look for evidence of hybridization beyond the F_1 generation. The characters used to study the three hybrid combinations are described below. In the case of *R. lobbii, R. roezlii,* and their hybrids, we made a single measurement or count per character per individual, except where noted, because preliminary studies showed relatively little within-plant variation (Cole, 1978). Otherwise, values are averages of three or more measurements per individual.

R. lobbii × *R. roezlii.* We scored 11 quantitative and two qualitative characters. Number of blade glands was indexed by counting the number of glands in a 5 mm × 5 mm area on the lower surface of the blade of a leaf taken from a short shoot. Degree of ovary exposure was calculated as the difference between bract length and the distance between the base of the pedicel and the top of the ovary. Number of bract margin glands was indexed by counting the glands along a 1 mm increment at the midpoint of the bract margin. Hypanthium length was measured from the top of the ovary to the insertion of petals and filaments. Petal length was measured from the hypanthium to the tip of the petal. Filament length is the length of the longest filament. Filament length difference is the difference between the length of the longest and shortest filament. Filament exsertion is the difference between filament length and petal length. Anther length was measured from the tip of a dehisced anther to the base of the lobes, if present. Number of anther glands is the average number of glands present on the abaxial surface of 10 anthers. Anther shape after dehiscence was scored as *R. roezlii*-like

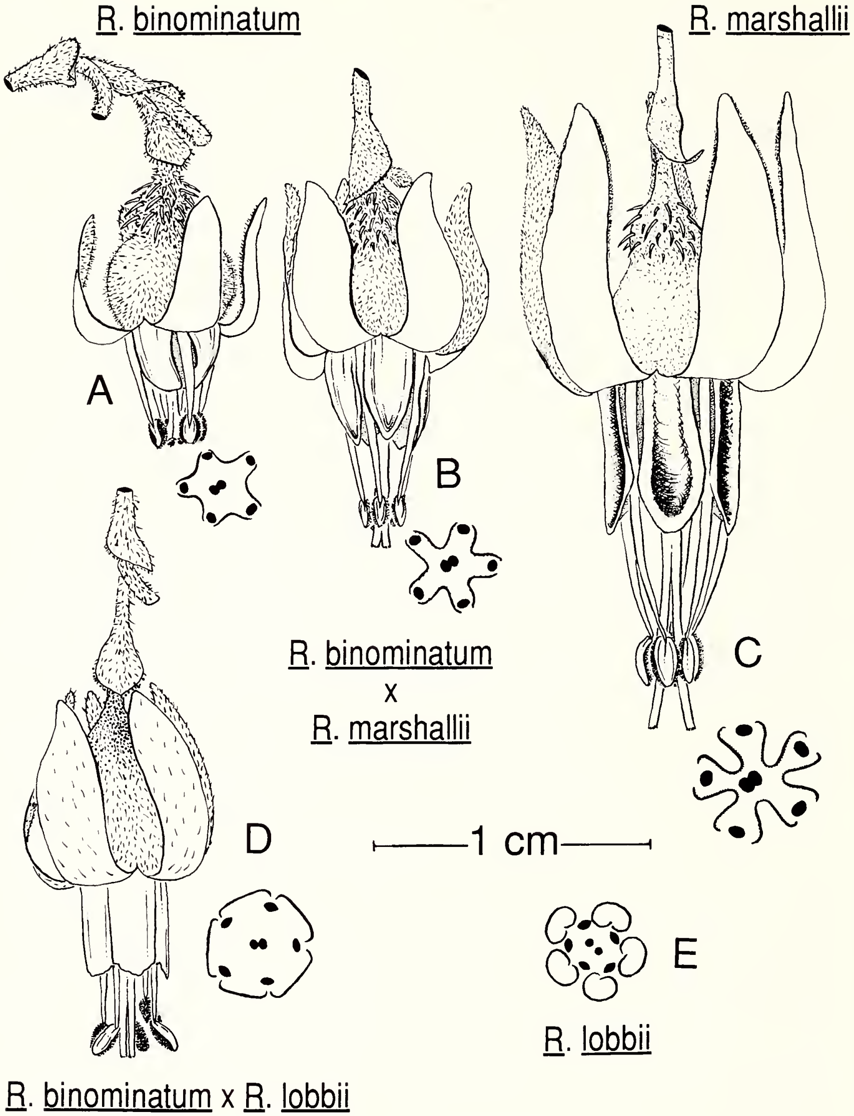

FIG. 2. Flowers and flower cross-sections of *Ribes* from the Bigelow Lake population. Cross-sections show petals, styles, and filaments. A. *R. binominatum.* B. Putative F_1 hybrid between *R. binominatum* and *R. marshallii.* C. *R. marshallii.* D. Putative F_1 between *R. lobbii* and *R. binominatum.* E. *R. lobbii* (cross-section only).

(lanceolate, with a narrow apiculum), *R. lobbii*-like (oblong, with a rounded or truncate apex), or intermediate. Degree of style fusion is the ratio of the fused increment of the style to total style length. Fruit surface was scored subjectively as *R. roezlii*-like (long eglandular spines of varying length plus short glandular hairs), *R. lobbii*-like (glandular bristles of the same length), or intermediate. A synthetic character, degree of overall glandularity, was calculated for use in the scattergram analysis. This measure is the sum of the number of blade, bract margin, and anther glands. Plants with no glands were scored as *R. roezlii*-like, with >20 glands as *R. lobbii*-like, and with 1–20 glands as intermediate.

R. binominatum × *R. marshallii and R. binominatum* × *R. lobbii.* Petal length, filament length, filament exsertion, and number of anther glands were scored as described above. Number of flowers per inflorescence is an average based on counts of 10 inflorescences per plant. In the scattergram analysis, plants with an average of ≤ 1.1 flowers per inflorescence were scored as *R. marshallii*-like, with >2 flowers as *R. binominatum*-like, and with 1.2–2 as intermediate. Degree of blade pubescence was scored as glabrous, densely pubescent, or intermediate. Sepal length was measured from the hypanthium to the tip of the sepal. Sepal color, petal color, and petal shape were scored subjectively as either a parental or intermediate state.

Pollen fertility. We estimated the relative fertility of the parental species and the suspected hybrids by comparing the percentage of pollen grains that stained in lactophenol blue. We scored 200 grains per plant from 10 plants in each of the three groups at Big Flat, and from five plants in each group at Bigelow Lake, except for *R. binominatum* × *R. lobbii* ($n = 2$). Pairwise tests of significance (hybrid vs. parental species) were made using the non-parametric STP procedure (Sokal and Rohlf 1969) for the comparisons at Big Flat (see Cole 1978) and Mann-Whitney tests for the comparisons at Bigelow Lake, except for *R. binominatum* × *R. lobbii,* where the sample size precluded testing.

RESULTS

Morphology. R. lobbii × *R. roezlii.* The plants we identified as putative hybrids proved to be more-or-less intermediate between *R. lobbii* and *R. roezlii* in most respects. Mean values for all 11 quantitative variables lay between those of the two parental species, although in most cases their ranges overlapped substantially. Figure 3 shows comparisons for 10 of the 11 characters. With one exception (hypanthium length), all differences between the means of hybrids and parents were significant ($p < 0.05$, Dunn's nonparametric multiple comparison test, Zar 1984).

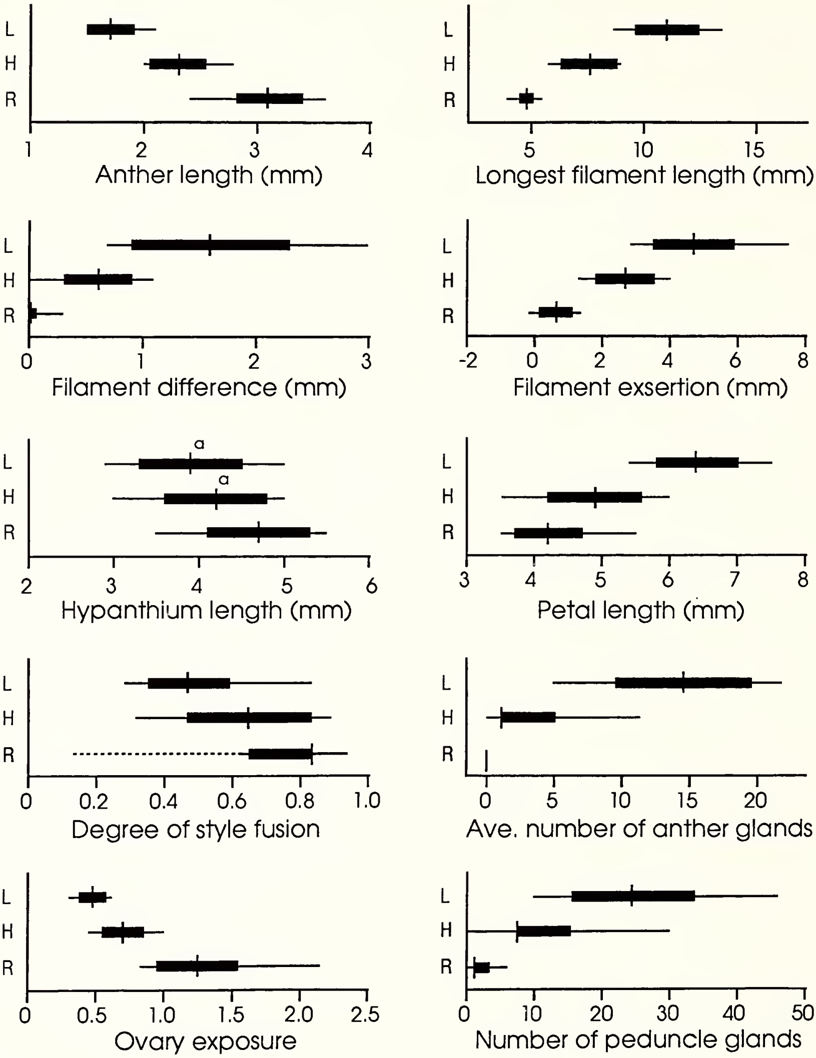

FIG. 3. Comparison of *R. lobbii* (L), *R. roezlii* (R), and putative hybrids (H) at the Horse Mountain population. Mean, SD, and range are shown for 10 reproductive characters. An extreme outlier for style fusion is shown with a dotted line. n = 18 for L, 25 for R, and 14 for L × R. All pairwise comparisons of means are significant at the 0.05 level, except for the one indicated by the same lowercase letter.

Individuals are plotted as a function of anther and filament length on the scattergram shown in Figure 4. The symbols depict variation in fruit morphology, anther shape, and degree of overall glandularity. The scattergram shows a loose cluster of points between the two

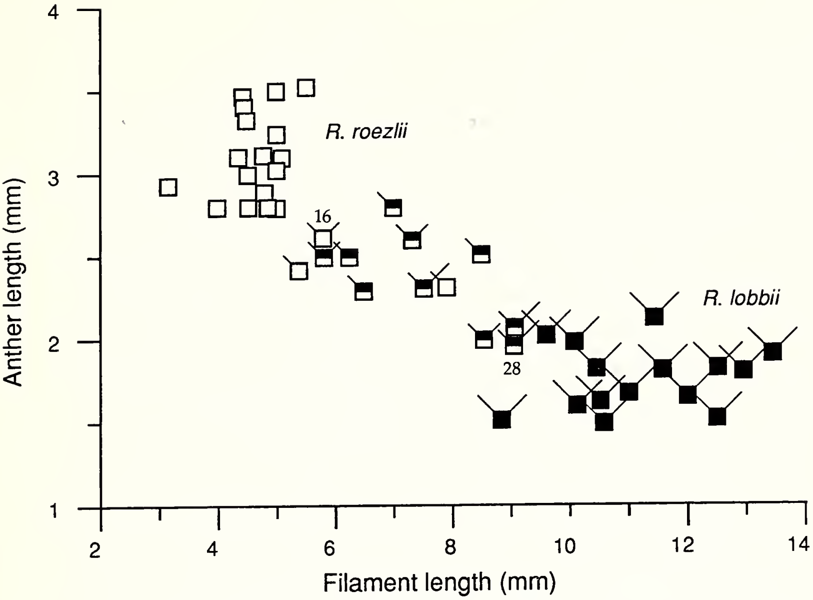

FIG. 4. Scattergram of plants at Horse Mountain. Box shading indicates anther shape (unshaded = *R. roezlii*-like, shaded = *R. lobbii*-like, half-shaded = intermediate). Arms represent degree of overall glandularity (right corner) and fruit surface (left corner). No arm = *R. roezlii*-like, full arm = *R. lobbii*-like, half-arm = intermediate. Numbered plants are discussed in the text.

species that corresponds to the putative hybrids. Most of the central plants are probably F_1 hybrids, although several are much less glandular than expected. A few plants resemble one or the other parent in some respects but have other characters that are intermediate. These may be the products of backcrossing. For example, plant 16 approaches *R. roezlii* in anther length, anther shape, and filament length but has intermediate fruits and glandularity. Plant 28 resembles *R. lobbii* in having long filaments, short anthers, and numerous glands, but is intermediate in anther shape and fruit morphology.

Hybrids can be distinguished from *R. roezlii* by their well-exserted filaments, the presence of at least a few glands on blades, bract margins, and/or anthers, anthers that do not form a tight cone around the style, and fruits with short spines, some or all of which are gland-tipped, depending on the individual (Fig. 1). They can be distinguished from *R. lobbii* by their subequal filaments, relatively long, narrow anthers that are not reflexed after dehiscence, and fruits with short spines in addition to shorter glandular bristles and hairs.

R. binominatum × *R. marshallii.* The putative hybrids combine parental traits in an obviously intermediate fashion. Hybrids are not

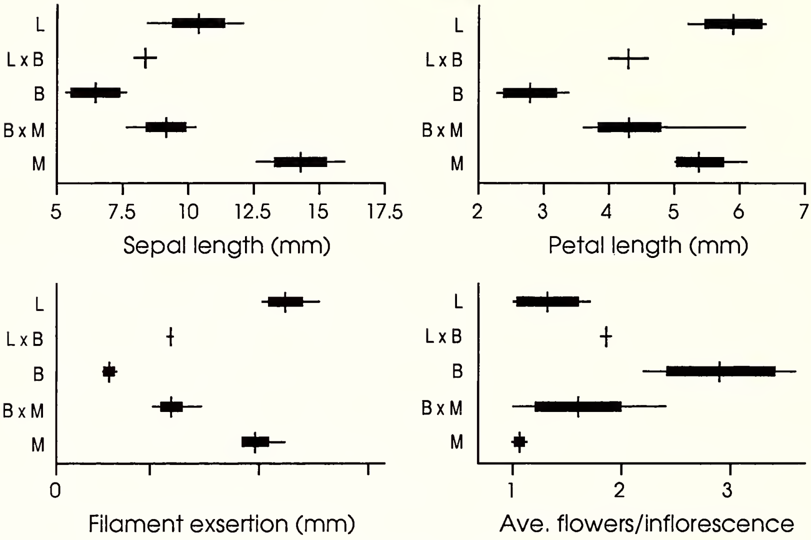

FIG. 5. Comparison of *R. binominatum* (B), *R. lobbii* (L), *R. marshallii* (M), and putative hybrids (H) at the Bigelow Lake and Mt. Elijah populations. Mean, SD, and range are shown for 4 floral traits. n = 10 for B, 10 for L, 9 for M, 21 for B × M, and 2 for B × L. All pairwise comparisons of means involving B, M, and B × M are significant at the 0.05 level.

as low-growing as *R. binominatum,* but they have a scrambling habit, with more-or-less horizontal branches that root at the tip. Individuals can form tangled low brambles several meters in diameter that clamber over downed logs and stumps. Hybrids have moderately pubescent blades with a few glands on the lower surface. Their sepals and petals are pale maroon and pale yellow, respectively, the expected result of combining the light colors of the *R. binominatum* perianth with the intense colors of *R. marshallii.* The petals of hybrids are more strongly concave than those of *R. binominatum* but lack the hooded apex characteristic of *R. marshallii* (Fig. 2). Hybrid intermediacy in four additional characters is shown in Figure 5.

The scattergram (Fig. 6) confirms the intermediate character of the putative hybrids, which appear tightly grouped in the center of the graph. Three apparent hybrids resemble *R. binominatum* in sepal length and filament exsertion, but otherwise the central plants have a uniform set of intermediate traits, consistent with the idea that they are F_1's.

R. binominatum × *R. lobbii.* We found two individuals at the Bigelow Lake site that appear to be F_1 hybrids between *R. binominatum* and *R. lobbii.* Both are upright shrubs less than 1 m tall. Their

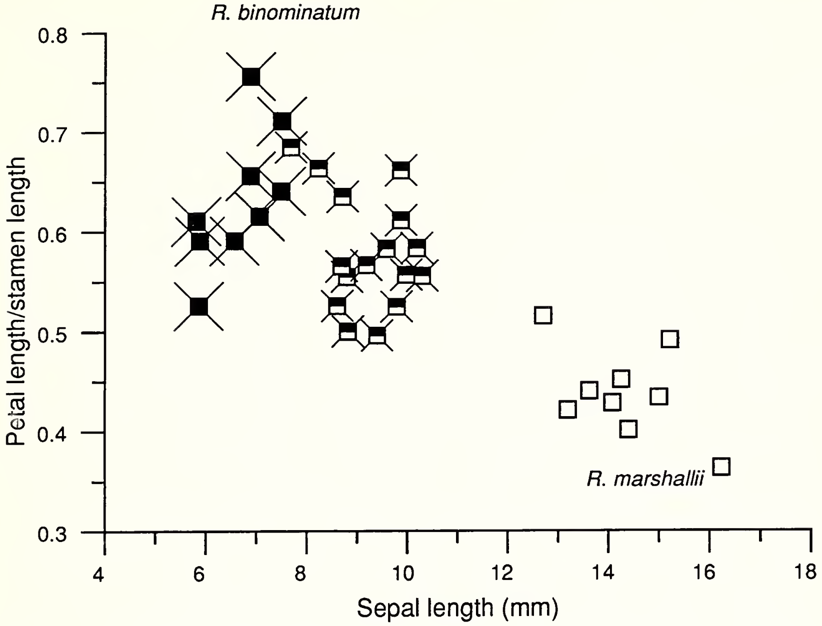

FIG. 6. Scattergram of plants of *R. binominatum, R. marshallii,* and putative hybrids from Bigelow Lake and Mt. Elijah. Box shading indicates degree of blade pubescence, and the arms show variation in petal color, petal shape, sepal color, and the average number of flowers/inflorescence. No arm = *R. marshallii*-like, full arm = *R. binominatum*-like, half-arm = intermediate.

flowers resemble those of *R. lobbii* but are smaller and have pale red (versus crimson) sepals and flat petals with the margins only involute. Anthers are tan, with a few glands on the abaxial surface, and are held at approximately a 45° angle to the filament. The two plants are also intermediate in sepal and petal length, degree of filament exsertion, and in the number of flowers per inflorescence (Fig. 5).

Not surprisingly, these hybrids resemble those between *R. binominatum* and *R. marshallii* (Fig. 2) but can be recognized easily by their sepal color (pale red versus pale maroon), petal color (white to pink versus pale yellow), petal morphology (flat with involute margins versus concave), anther color (tan versus pale yellow), and the presence of a few anther glands.

Pollen fertility. In all three cases, hybrids had a lower percentage of stained and presumably viable grains than the parental species. At Big Flat, average values were: *R. lobbii* (95%), *R. lobbii* × *R. roezlii* (85%), *R. roezlii* (97%). At Bigelow Lake, averages were: *R. marshallii* (93%), *R. binominatum* × *R. marshallii* (68%), *R. bi-*

nominatum (91%), *R. binominatum* × *R. lobbii* (51%), *R. lobbii* (82%). The small sample size precluded testing the difference between *R. binominatum* × *R. lobbii* and its parents, but the differences between the other two hybrids and their parents were significant ($p < 0.05$).

Discussion

Morphological intermediacy and reduced pollen stainability support the idea that *R. lobbii* and *R. roezlii, R. binominatum* and *R. marshallii,* and *R. binominatum* and *R. lobbii* hybridize in the Klamath Mountains. Other evidence, however, suggests that hybridization between these species is infrequent and localized, and that it has had little impact on the integrity of the species.

Our surveys of herbarium collections from northern California and southern Oregon, together with several years of field observation, indicate that hybridization involving the four species of gooseberries is uncommon. To date, the only hybrids between *R. binominatum* and *R. lobbii* we have found are the two plants at our Bigelow Lake study site. Hybrids between *R. binominatum* and *R. marshallii* are common at the same site, but currently we know of only two other places where they occur. Hybridization between *R. lobbii* and *R. roezlii* appears to be more common, which is not surprising considering the relatively greater zone of contact between the two species. Nevertheless, even though the species are commonly sympatric, we know of fewer than 10 localities where hybrids occur, although additional ones are likely to be discovered in the future.

More important than frequency of occurrence to an understanding of the evolutionary significance of hybridization is the issue of whether interbreeding goes beyond the F_1 generation. We believe that it seldom does in this group of gooseberries. With few exceptions, plants in the field were readily identifiable as one of the parental taxa or as putative F_1 hybrids. Our scattergrams confirm this initial impression that mixed populations consisted of distinct groups, with little or no intergradation between them. The graphs show little evidence of the kind of recombination of parental traits that would be expected as the result of backcrossing or interbreeding among hybrids. A few hybrid-type individuals at Horse Mountain appear to vary in the direction of either *R. lobbii* or *R. roezlii,* but these are in the minority. In most cases, hybridization between these species appears to stop at the F_1 stage.

Even with limited backcrossing, genes from one species may be incorporated into another via introgression. Our preliminary analyses of allopatric populations of the four parental species reveal little, if any, gene transfer between the species. The only possible exceptions are a few populations of *R. roezlii* that appear to vary in the direction of *R. lobbii* in one or another respect. For example, in some populations of *R. roezlii*, the filaments are exserted more strongly than is usual for the species, suggesting the influence of *R. lobbii*, which has strongly exserted filaments. In other cases, glands are present on the peduncles (normally glabrous) or the bracts cover the ovary less completely than the norm for the species. However, since only a single trait is involved in these cases, we believe that coincidental within-species variation is a more parsimonious explanation than introgressive transfer of genes from *R. lobbii*.

Several factors may limit hybridization in this group of *Ribes*. The relatively high pollen fertility of the suspected F_1 hybrids suggests that the species are interfertile, but since garden crosses have not been made, there is a possibility that some form of internal reproductive barrier (e.g., partial hybrid inviability, hybrid breakdown) limits hybridization. Several external mechanisms may also operate. Even though their ranges overlap in the Klamath Mountains, habitat specialization partially isolates the four species. For example, *R. roezlii* typically occurs at lower elevations than the other three species, in somewhat drier sites. In contrast, *R. marshallii* is restricted to mesic forests and meadows above 1500 m. Peak flowering is earlier for *R. roezlii* than for *R. lobbii* (Cole 1978), but the flowering periods of all four species overlap substantially, which should provide ample opportunity for hybridization where they are sympatric. The flowers of *R. lobbii* and *R. roezlii* are very similar, and not surprisingly, they are visited by the same set of pollinators (Cole 1978). By contrast, the flowers of *R. binominatum* and *R. marshallii* differ in many respects, suggesting that interspecific pollen transfer might be limited by mechanical or ethological factors (sensu Grant 1981). However, the abundance of F_1 hybrids between these two divergent species at Bigelow Lake indicates that floral isolation may be relatively unimportant in *Ribes* in general. Finally, the availability of suitable sites for establishment of hybrid seedlings may play an important role in determining the frequency and extent of hybridization. Hybrids are abundant only at localities where logging has created extensive open areas (Cole 1978). Large scale disturbance presumably provides ample room for establishment of parental species and enough time for recruitment of F_1 hybrid progeny before conditions become less favorable for seedling growth because of regeneration. At sites like Horse Mountain and Bigelow Lake, where plants of the parental species and F_1 hybrids are common, a dense herb layer probably prevents seedling establishment, which may help explain why backcrossing has not generated hybrid swarms.

Hybridization between interfertile species can result in the production of true-breeding homoploid derivatives that combine the traits of the species in "kaleidoscopic fashion" (Raven 1976, p. 295). This mode of evolution, termed hybrid speciation (Grant 1981), has been a dominant factor in the diversification of several groups of woody and herbaceous perennials in California (Raven and Axelrod 1978). Has hybridization played a comparable role in the evolution of *Ribes,* a genus with nearly one-fourth of its species native to the state? Sinnott (1985, p. 218), believed that "hybridization and reticulate evolution dominate the genus." Raven and Axelrod (1978, p. 79) included *Ribes* in a list of genera having "patterns suggestive of reticulate evolution." In contrast, our view is that the importance of hybridization in the genus is still poorly understood. Compared to other groups of woody plants with the "*Ceanothus* pattern" of species interfertility (Grant 1981; e.g., *Arctostaphylos, Ceanothus, Quercus,* and *Pinus*), the number of published records of hybridization in *Ribes* is surprisingly meagre. This apparent difference is intriguing, but at present our knowledge is too limited to determine whether it is simply an artifact of poor field sampling or is a real distinction requiring an explanation. Additional garden work is needed to determine the degree of interfertility of related species. Field studies are needed to establish how often interfertile species occur together and how often (and to what degree) they hybridize.

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APPENDIX I.

Study Sites

R. lobbii, R. roezlii, R. lobbii × *R. roezlii*

BIG FLAT. California: Trinity Co., Shasta-Trinity National Forest, T38N, R9W, S31, on steep slope above Coffee Creek Rd, in logged white fir forest, 1570 m.
BUCK PEAK. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S3, below weather station, near the end of Rd 067, 0.9 mi from Rd 4613, logged white fir forest, 1700 m.
HORSE MOUNTAIN. California: Humboldt Co., Six Rivers National Forest, T6N, R4E, S29, on both sides of Titlow Rd, logged white fir forest, 1300 m.

R. binominatum, R. lobbii, R. marshallii, R. binominatum × *R. marshallii, R. binominatum* × *R. lobbii*

BIGELOW LAKE. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S11, SE of intersection of Rds 070 and 079, approximately 1 mi NE of Oregon Natl. Monument, logged white fir forest, 1700 m.

R. binominatum × *R. marshallii*

MT. ELIJAH. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S22, north side of Rd 048, approximately 0.75 mi S of Oregon Caves Natl. Monument, disturbed roadside through unlogged white fir forest, 1730 m.

THE GENERIC DISTINCTNESS OF *SCHOENOLIRION* and *HASTINGSIA*

Harry L. Sherman
Division of Science and Mathematics,
Mississippi University of Women,
Columbus, MS 39701

Rudolf W. Becking
College of Natural Resources, Humboldt State University,
Arcata, CA 95521

Abstract

Schoenolirion Torrey and *Hastingsia* S. Watson are both representatives of a distinctly North American subtribe of lilies, the Chlorogalinae. The two species groups have been considered to be congeneric in a number of previous publications, but a comparison of morphological traits provides strong support for their generic separation. Comprehensive descriptions of the two genera are provided, along with a synopsis of species included in each.

Historically, the name *Schoenolirion* has been applied to a small group of lilies occurring in several southeastern states and in northern California and southwestern Oregon. Watson (1879) transferred the one western species known at the time (*S. album*) to his new genus *Hastingsia*, but some more recent floras of California and Oregon (Abrams 1923; Jepson 1925, 1936; Munz 1959; Peck 1961; Ferlatte, 1974) continued to use the older generic name.

A comprehensive study of the southeastern species of *Schoenolirion* (Sherman 1969), including a comparison with the western plants (Table 1), provided compelling evidence in support of the generic separation of the two geographically-isolated species groups. Studies of the California/Oregon species by Becking (1986, 1989) have further defined the diversity within *Hastingsia.*

History of the Nomenclature

The nomenclatural history of *Schoenolirion* was reviewed by Sherman (1964) in a proposal (later withdrawn) to conserve *S. album* Durand as the type species of the genus. The name was published originally by Durand (1855) with the description of *S. album,* a plant restricted to northern California and southwestern Oregon. However, *Schoenolirion* was first used by J. Torrey in a manuscript combination, *S. michauxii,* applied to a southeastern species.

Watson (1879) recognized the morphological distinctness of the

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southeastern and western species that previous authors had grouped together as *Schoenolirion.* He considered *Schoenolirion* to be the correct name for the southeastern plants and proposed the new genus *Hastingsia* to include the western species, *H. album,* originally described by Durand.

Schoenolirion was one of the original 405 generic names conserved by the Vienna Congress, 1905, with Rafinesque's *Amblostima* and *Oxytria* listed as nomina rejicienda. Following the adoption of the type method by the Vienna Congress, 1935, *S. album* Durand was proposed as the type species for the genus and was listed as such until Rickett and Stafleu (1959) revised the list of *Nomina Generica Conservanda et Rejicienda.* They proposed *S. michauxii* Torrey as the type species, and its official designation as the type in the Edinburgh Code (1966) fixes the application of the name *Schoenolirion* to the southeastern species.

RELATIONSHIPS

Schoenolirion, Hastingsia and *Chlorogalum* seem to represent a distinct North American group of lilies, a taxonomic alliance first suggested by Watson (1879) when he placed the three genera in the subtribe Clorogalinae. This treatment also was followed by Bentham and Hooker (1883), Krause (1930), and Hutchinson (1959). All three genera may be characterized as being scapose with racemose or paniculate inflorescences and having distinct perianth segments that persist in fruit and anthers that are dorsifixed, versatile and introrsely dehiscent. The fruit in all three genera is a loculicidally dehiscent capsule with two seeds per locule.

Both *Hastingsia* and *Chlorogalum* possess distinct bulbs enclosed by fibrous tunics. *Schoenolirion* is basically bulbous with membranous scales, but is unique in possessing a prominent fleshy rootstock that may best be described as a "vertical rhizome." The rootstock increases in length from year to year (up to 12 cm) because the stem axis persists after the bulb scales or leaf bases are lost. In *S. albiflorum,* the leaf bases are not fleshy and there is some development of a fibrous tunic. In addition to the vertical rootstock, *Schoenolirion* differs from *Hastingsia* in having significantly longer pedicels (6–15 mm), a sessile ovary, an entire or only slightly lobed stigma, and globose seeds with a smooth, glossy coat. In *Hastingsia,* the pedicels are generally much shorter (2–3 mm), the ovary is short-stipitate, the stigma is distinctly 3-lobed, and the seeds are elongated with a rough, reticulated coat. The leaves of *S. croceum* and *S. wrightii* tend to be flat and only slightly keeled, if at all. The leaves of *S. albiflorum* are much more variable, ranging from flattened to almost terete in cross-section and persist as dead foliage at the top of the vertical rootstock. In *Hastingsia,* the leaves are flattened and prominently keeled, and the dead foliage usually is persistent as fibrous tunic around the bulb.

Schoenolirion croceum exhibits a degree of aneuploidy with chromosome numbers $n=12$, $n=15$, $n=16$ usually distinguishing different populations. *S. wrightii* appears to have a constant number of $n=12$, while *S. albiflorum* is a tetraploid with $n=24$. In all cases, the chromosomes of *Schoenolirion* show considerable morphological diversity.

Cave (1970) reported chromosome numbers for *Hastingsia alba* to be $n=26$ or $n=27$ (with query). She also reported $n=15$, $n=17$, $n=18$, and $n=30$ for various species of *Chlorogalum*.

Considering the fact that *Chlorogalum, Hastingsia,* and *Schoenolirion* are all basically bulbous, the subtribe Chlorogalinae should be placed in tribe Scilleae, rather than tribe Asphodeleae. This arrangement would not be without precedent, since Small (1903, 1933) placed *Schoenolirion* (as *Oxytria*) in Scilleae, while Hoover (1940) considered *Chlorogalum* to be a typical member of the Scilleae as defined by Krause.

Dahlgren et al. (1985) included *Schoenolirion, Hastingsia* (as *Schoenolirion*) and *Chlorogalum* in the Family Hyacinthaceae (a taxonomic segregate of the Liliaceae), along with many of the genera traditionally placed in the Scilleae. However, the authors suggested that the three North American genera are peripheral in the Hyacinthaceae and may merit familial rank of their own.

Any discussion of the generic affinities of *Schoenolirion* and *Hastingsia* should include some consideration of *Camassia,* usually placed among the Scillas because of its bulbous habit. The primary distinction between *Camassia* and the three genera of Chlorogalinae is a difference in the number of ovules per locule. *Camassia* has several to many ovules per locule rather than the two that are typical of *Schoenolirion, Hastingsia* and *Chlorogalum.*

Camassia scilloides (Raf.) Cory shares a chromosome number, $n=15$, with some species of *Schoenolirion* and *Chlorogalum,* and it is the only species in any of the four genera (including *Hastingsia*) that exhibits any suggestion of a trans-continental distribution. It occurs sympatrically with *Schoenolirion croceum* in parts of its southeastern range, and the two plants are occasionally found growing together in the same habitat.

TAXONOMIC TREATMENT

Schoenolirion Torrey in Durand. J. Acad. Sci. Philadelphia 3:103. 1885. *Nomen conservandum.*—TYPE: *Schoenolirion michauxii* Torrey—*Amblostima* Raf. Fl. Tellur. 2:26. 1837.—*Oxytria* Raf. Fl. Tellur. 2:26. 1837.

Herbaceous, glabrous perennial with thick, fleshy, vertical rootstock, grass-like leaves, and a simple or branched racemose inflorescence. Vertical rootstock 1–12 cm long, with or without prominent fleshy apical bulb, the rootstock being the persistent stem portion of the bulb that is exposed when the bulb scales wither. Bulb, when present, ovoid or elongated, scales lunate; principal roots from top of vertical rootstock, contractile, persistent 1–2 years. Leaves arising directly from top of rootstock or from bulb, flat or elliptical in transverse section, striate-fibrous. Inflorescence simple or with 1–3 (sometimes more) branches, usually loosely flowered. Bracts short, ¼ to ⅓ of the length of the pedicel. Pedicels slender, jointed at the apex. Flowers yellow or white, often with some red on the abaxial surface, unfertilized ones soon deciduous. Perianth segments 6, distinct, 3–7 nerved, with minute distal tuft of hairs on the adaxial surface, ovate to ovate-oblong, (4.0–)4.5–6.5(–7.5) mm long, (1.5–) 2.0–3.5(–4.0) mm wide, withering separately to base, persistent. Stamens 6, of equal length, shorter than the perianth segments, antipetalous ones nectariferous at base; anthers versatile, extrorsely dehiscent, 1–2 mm long. Ovary sessile, globulose, 3-lobed, with axile placentation; ovules 2 per locule, anatropous; style conical, short, about equalling the stamens; stigma minute, entire or very slightly 3-lobed. Capsules globulose, flattened and indented at top, prominently 3-lobed, loculicidally dehiscent, 4.0–6.5 mm broad. Seeds 1–2 per locule, globose, usually flattened on one side, smooth, glossy black, 2–3 mm broad.

KEY TO *SCHOENOLIRION* SPECIES

a. Leaves without fleshy bases, arising directly from top of vertical rootstock, flat or terete in cross-section, sometimes slightly keeled, withering to persistent fibers; scape robust, much longer than the leaves; inflorescence usually 1–3 branched; perianth segments white or greenish-white. .... *S. albiflorum*

a′. Leaves arising from a prominent fleshy bulb at top of vertical rootstock, flat to distinctly keeled, bases withering to persistent scales; scape usually simple, with unbranched inflorescence; perianth segments white or yellow.

  b. Perianth segments yellow, with green or reddish stripe on abaxial surface, 3–5 nerved; pistils yellow or green; leaves mostly longer than the inflorescence. .... *S. croceum*

  b′. Perianth segments white with green stripe on abaxial surface, mostly 3-nerved; pistils green; leaves mostly shorter than the inflorescence. ... . *S. wrightii*

1. *Schoenolirion albiflorum* (Raf.) Gates, J. Linn. Soc., Bot. 44:167. 1918.—*Amblostima albiflora* Raf., Fl. Tellur. 2:26. 1837.—*Oxytria albiflora* (Raf.) Pollard, Bull. Torrey Bot. Club 24:406. 1897.—NEOTYPE (here designated): Florida, boggy pine barrens near Seville, 7 Jun 1901, *Curtis 6804* (neotype, US!).

Ornithogalum croceum sensu Elliott, Sketch Bot. S. Carolina, 399–

400. 1823. non *Phalangium croceum* Michx., 1803. Rafinesque based the protologue of *Amblostima albiflora* upon Elliott's description of *O. croceum*, plus ". . . a specimen from Elliott himself." Since none of the type material has been found, there is some question concerning the identity of the plant described by Elliott and Rafinesque.

Schoenolirion michauxii Torrey, Bot. Mex. Bound. 220. 1859.—LECTOTYPE (here designated): Buckley, s.n. "East Florida," ex John J. Torrey Herb., with plate of penciled sketches labeled "Phalangium croceum" (lectotype, NY!). Torrey apparently used elements of three species in his description, the Buckley and Chapman specimens mentioned by him being representative of *S. albiflorum*.

Schoenolirion elliottii A. Gray, Amer. Naturalist 10:427. 1876.—LECTOTYPE (here designated): *Chapman s.n.*, "Marshes, Fla." with note: "Don't believe this to be Michaux's plant" (lectotype, GH!).

A tetraploid species differing from *S. croceum* and *S. wrightii* in its much coarser habit, usually branched inflorescence, and lack of fleshy bulb at top of vertical rootstock; occurring in marshy pinelands, cypress bogs, and wet savannahs of southeastern Georgia and throughout most of peninsular Florida; flowering in May in southern part of range, in late May to early June in northern part.

2. *Schoenolirion croceum* (Michaux) Alph. Wood, Am. Bot. & Flor. 344–345. 1870.—*Phalangium croceum* Michaux, Fl. Bor.-Amer. 196. 1803.—*Phalangium croceum* Nutt., Gen. No. Amer. Pl. I: 219–220. 1818.—*Oxytria crocea* Raf., Fl. Tellur. 2:26. 1837.—*Amblostima crocea* Raf., Fl. Tellur. 2:26. 1837.—*Schoenolirion croceum* (Michaux) A. Gray, Amer. Naturalist 10:427. 1876.—TYPE: Georgia, in herbosis humidus sylvarum, *Michaux s.n.* (holotype, P, photo!).

Schoenolirion michauxii Torrey, pro parte, Bot. Mex. Bound. 220. 1859. (Torrey apparently used elements of three species in his description, the Hale collection mentioned by him being representative of *S. croceum*.)

A yellow-flowered species with a prominent bulb at the top of a thick, fleshy rootstock; occurring in organic, acid soil on limestone outcrops in central Tennessee and northern Alabama, sandstone outcrops of the Alabama plateau region, outcrops of Selma chalk in west-central Alabama, granite outcrops of the Georgia Piedmont, moist pinelands and boggy areas of southern Georgia, northern Florida, western Louisiana, and eastern Texas; flowering from mid-March through mid-April in southern and western portion of range, April through mid-May in northern portion, becoming dormant by late June.

3. *Schoenolirion wrightii* Sherman, Southw. Naturalist 24:123–126, 1979.—TYPE: "wet places on the Colorado of Texas," *Wright, Mexican Boundary Survey 1470* (holotype, NY!).

Schoenolirion michauxii Torrey, pro parte, Bot. Mex. Bound. 220. 1859. (Torrey apparently used elements of three species in his description, the Wright specimen cited by him being representative of *S. wrightii.*)

Schoenolirion texanum A. Gray, Amer. Naturalist 10:426–427. 1876. [This name was based upon *Ornithogalum texanum* Scheele, representative of *Camassia scilloides* (Raf.) Cory, not *Schoenolirion.*]—*Oxytria texana* Pollard, Bull. Torrey Bot. Club 24: 405–406. 1887.

An endangered species very similar to *Schoenolirion croceum,* except for white flowers; highly localized on sandstone outcrops of the Alabama plateau region (Cullman, DeKalb, Cherokee, and Etowah counties) and in wet pinelands and boggy areas of southern Arkansas (Ashley, Bradley, Calhoun, and Drew counties) and eastern Texas (Austin, Brazos, Houston, Walker and Waller counties); flowering from late March to mid-April in Texas and Arkansas, mid-April to early May in Alabama, becoming dormant in mid-June.

Hastingsia (Durand) S. Watson. Proc. Amer. Acad. Arts 14:213–288. 1855.—TYPE: *Hastingsia alba* (Durand) S. Watson.

Schoenolirion Torrey in Durand, pro parte. J. Acad. Nat. Sci. Philadelphia 3:103. 1855.

Herbaceous, glabrous perennial with a fleshy bulb. Bulb ovoid to elongate, densely packed with lunate scales. Leaves grass-like, prominently keeled. Bulb scales and leaf bases shriveling to form fibrous tunica enclosing the bulb. Inflorescence simple to 1–3(–7)-branched with shorter ascending branches, densley flowered. Pedicels 2–3 mm long; perianth segments 6, 3-nerved, white, creamy-white or dark purple, ovate to linear, 5–12 mm long and 1–2 mm wide, tips often triangular, with minute distal glandular hairs on the adaxial surface; tepals withering separately to the base, persistent; stamens 6, with 3 longer and 3 shorter in freshly opened flowers, later being of about equal length. Style with a distinctly 3-parted stigma; ovary globulose, 3-lobed, with axial placentation; ovules 2 per locule, anatropous. Capsule broadly oblong, 6–10 mm long, 5–7.5 mm wide, short-stalked. Seed elongate with shiny black, roughened reticulate coat, usually adaxially flattened.

TABLE 1. SUMMARY OF GENERIC CHARACTER DIFFERENCES BETWEEN *SCHOENOLIRION* AND *HASTINGSIA*.

Schoenolirion	*Hastingsia*
Rootstock a thick, fleshy "vertical rhizome," with or without terminal bulb.	Rootstock ("vertical rhizome") absent.
Bulb, when present, with lunate scales drying to persistent scales around bulb.	Bulb scales densely packed, shriveling to form black, fibrous tunica enclosing the bulb.
Leaves flat or elliptical in cross-section, sometimes slightly keeled, persistent as dead foliage only in *S. albiflorum*.	Leaves prominently keeled or almost terete, often persistent as dead foliage.
Inflorescence (5)12–45(75) flowered raceme.	Inflorescence (15)24–65(110) flowered raceme.
Pedicels of flowers 6–15(30) mm long.	Pedicels of flowers 2–3 mm long.
Perianth segments white or yellow with central green or reddish stripe on abaxial surface.	Perianth segments white, creamy white, or dark purple with central green, yellowish or purplish stripe.
Perianth segments 3–7-nerved 3–5(6) mm long, with distal non-glandular hairs.	Perianth segments 3-nerved, 5–12 mm long, with minute glandular hairs.
Stamens 6, with equal length filaments (1–2 mm long).	Stamens 6, with 3 longer and 3 shorter filaments (4.6–6.6 mm long).
Style with entire or slightly 3-lobed stigma.	Style with distinctly 3-lobed stigma.
Capsule globose, indented at the top, 4–6.5 mm long, 4–6.5 mm wide.	Capsule broadly oblong, 6–10 mm long, 5–7.5 mm wide.
Seeds globose with glossy black, smooth coat.	Seeds elongate with shiny black, rough, reticulate coat.
Chromosome numbers ($n = 12$, $n = 15$, $n = 16$, $n = 24$)—Sherman 1969.	Chromosome numbers ($n = 26$)—Cave 1970.

KEY TO *HASTINGSIA* SPECIES

a. Perianth segments 5–7 mm long and 1–2 mm wide, narrow-lanceolate, white or yellowish tinged with green or pink, usually spreading or sharply reflexed, exposing the stamens.

b. Scape 28.6–51.4 cm long; bulb small without black fibrous tunic; leaves 21–27 cm long, 2–6 mm wide; perianth lobes 5–6 mm long, sharply reflexed about ⅔ of their length, fully exposing the stamens; raceme mostly unbranched, 3.8–12 cm long, 24–35 flowers per 10 cm of raceme. .... *H. serpentinicola*

b′. Scape 40–85 cm long; bulb large, often with black, fibrous tunic; leaves 35–41 cm long, 7–13 mm wide; perianth lobes 5–7.5 mm long, partly closed with tips reflexed outward, exposing only the upper parts of the stamens; racemes mostly 1–4 branched, 14.2–26.9 cm long, 44–51 flowers per 10 cm of raceme. .... *H. alba*

a′. Perianth segments 8–10 mm long and 2 mm wide, oblong-lanceolate, acuminate, yellowish-white or dark purple-black, fully enclosing the stamens.

c. Perianth segments dark purple-black with pale green central vein; ovary dark purple; leaves 37.3–44 cm long, 8.4–9.8 mm wide, glaucous green; 30–36 flowers per 10 cm of raceme. .... *H. atropurpurea* c′. Perianth segments yellowish-white with a slightly more yellow central vein; ovary dark gray-green; leaves 31.4–38.2 cm long, 5.8–6.7 mm wide, yellowish-green; 25–30 flowers per 10 cm of raceme. .... *H. bracteosa*

1. *Hastingsia alba* (Durand) S. Watson, Proc. Amer. Acad. Arts 14: 242. 1879.—*Schoenolirion album* Durand, J. Acad. Nat. Sci. Philadelphia 2(3):103. 1855.—TYPE: California, Nevada Co., Deer Creek, *H. Pratten* (lectotype, PH!).

A species of the Klamath Mountains and Cascades–Northern Sierra geological provinces, occurring from southern Oregon (Curry and Josephine counties) through the Northern Coast Range in California (Del Norte, Siskiyou, Trinity, Humboldt, Lake, and Glenn counties) and the northern Cascades and Sierra Nevada Ranges (Shasta, Tehama, Plumas, and Nevada counties); usually found in open, rocky habitats with a good permanent water supply or in bogs or wet meadows, especially at high elevations; flowering May to June, capsules maturing July to August, becoming dormant September to October.

2. *Hastingsia atropurpurea* Becking, Madroño 33(3):175–181. 1986.—TYPE: Oregon, Josephine Co., O'Brien, Woodcock Mt., *Darlingtonia* bog, 4 Jul 1984 (holotype, CAS).

A species restricted to Woodcock Mtn., Tennessee Mtn., and middle and upper parts of the Josephine Creek watershed in Josephine County, OR.; found almost exclusively in permanently wet *Darlingtonia* bogs (sometimes with *H. bracteosa*), occasionally in permanently wet sites on river bars; flowering in May and June, capsules maturing in June and July, becoming dormant at the end of August.

3. *Hastingsia bracteosa* S. Watson, Proc. Amer. Acad. Arts 20:377. 1885. TYPE: Oregon, Curry Co. (=Josephine Co.), Eight Dollar Mt., *Thomas Howell s.n.* (holotype, GH!).

Common but almost totally limited to Eight Dollar Mtn. near Selma, Oregon; occurring on all sides along the base of the mountain, at the mouth of Josephine Creek, the lower parts of Mike's Gulch, Day's Gulch, and Fiddler Gulch; restricted to *Darlingtonia* bogs that remain permanently wet; listed as a candidate endangered species (Federal Register 45:82480–82569, 15 Dec 1980).

4. *Hastingsia serpentinicola* Becking, Madroño 36:208–216. 1989.—TYPE: Oregon, Josephine Co., Cave Junction, Eight Dollar Mt., *Darlingtonia* bog, 28 May, 1985 *R. Becking 850500* (holotype, CAS).

A species occurring almost exclusively on ultramafic or serpentine rock outcrops of the Klamath Mountains and North Coast Range where it occupies open sites that are moist in the spring and dry out rapidly in early summer. It has recently been segregated from *H. alba* because of its significantly less robust habit, usually unbranched raceme, and sharply reflexed perianth segments.

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NOTES

ADDITIONS TO THE PEATLAND FLORA OF THE SOUTHERN ROCKY MOUNTAINS: HABITAT DESCRIPTIONS AND WATER CHEMISTRY.—David J. Cooper, Department of Environmental Sciences and Engineering Ecology, Colorado School of Mines, Golden, CO 80401.

Investigations of the flora and ecology of three minerotrophic peatlands (fens) in the area of South Park, Park County, central Colorado, during 1989 resulted in the addition of a number of important new vascular plant species records, rediscoveries and range extensions for the southern Rocky Mountains. Peatlands are wetlands with organic soils. They usually are waterlogged for much of the growing season. The two main classes of peatlands are bog and fen. Bogs are ombrotrophic and ombrogenous while fens are minerotrophic. Bogs are restricted to humid regions and do not occur in the southern Rocky Mountains. Fens can occur wherever a constant water supply is available. The mineral nutrients in the water supply also determine the nutrients available to the plants living in the fen. Where the water has been in contact only with hard crystalline rocks, relatively nutrient poor conditions may occur and a poor fen develops. Where water has been in contact with calcareous substrates relatively nutrient rich water occurs and rich or extremely rich fen conditions occur. Intermediate fens have conditions intermediate between poor and rich fens. The rich to poor fen gradient is based solely on nutrients not species richness, but many plant species with exacting nutrient requirements are restricted to intermediate or rich fens and some to extreme rich fens. The chemical characteristics of the different types of fens has been carefully defined for Minnesota (Glaser, USDI Fish and Wildlife Service, Biological Report 85(7.14), 1987), but not for the Rocky Mountains. Plant nomenclature follows Weber (Colorado Flora: Eastern Slope, 1990).

Fens are fairly common in many portions of the southern Rocky Mountains at elevations above 2600 meters. Poor to intermediate fens are the most common type because the crystalline bedrock of most mountain ranges releases few nutrients and a large flush of nutrient poor snowmelt water dominates their hydrologic regime early in the summer.

The three fens investigated in the present study are ecologically distinct. The High Creek fen is an extremely rich fen, fed by springs whose water supply has been in contact with calcareous bedrock, till and outwash from the Mosquito Range on the western side of South Park (Fig. 1). It occurs at an elevation of 2950 m. The fen covers an area of approximately 485 hectares. The water chemistry is shown in Table 1.

The East Lost Park fen is a intermediate fen in the Tarryall Mountains on the northeastern side of South Park. It occurs at an elevation of 2743 m. The Tarryall Mountains are a range of unglaciated granitic domes. The large floating mats of these spring-fed peatlands indicate the later stages of hydroseres, with very little open water remaining. The water chemistry is shown in Table 1.

TABLE 1. WATER CHEMISTRY. pH measured with Corning model 101 pH millivolt meter. Conductance measured with YSI C–S–T meter, in mmhos/cm^2. Calcium, sodium and magnesium cations measured directly from filtered and acidified water samples with a Perkin-Elmer atomic absorption spectophotometer.

	pH	Conductance	Ca^{++}	Na^{+}	Mg^{++}
High Creek	7.4–8.6	270–640	43–94	7–32	21–68
E. Lost Park	6.3–6.9	24–59	2.4–4.1	2.3–3.3	0.4–0.8
Guanella Pass	6.9–7.3	90–98	19–57	2.3–3.2	4.0–4.2

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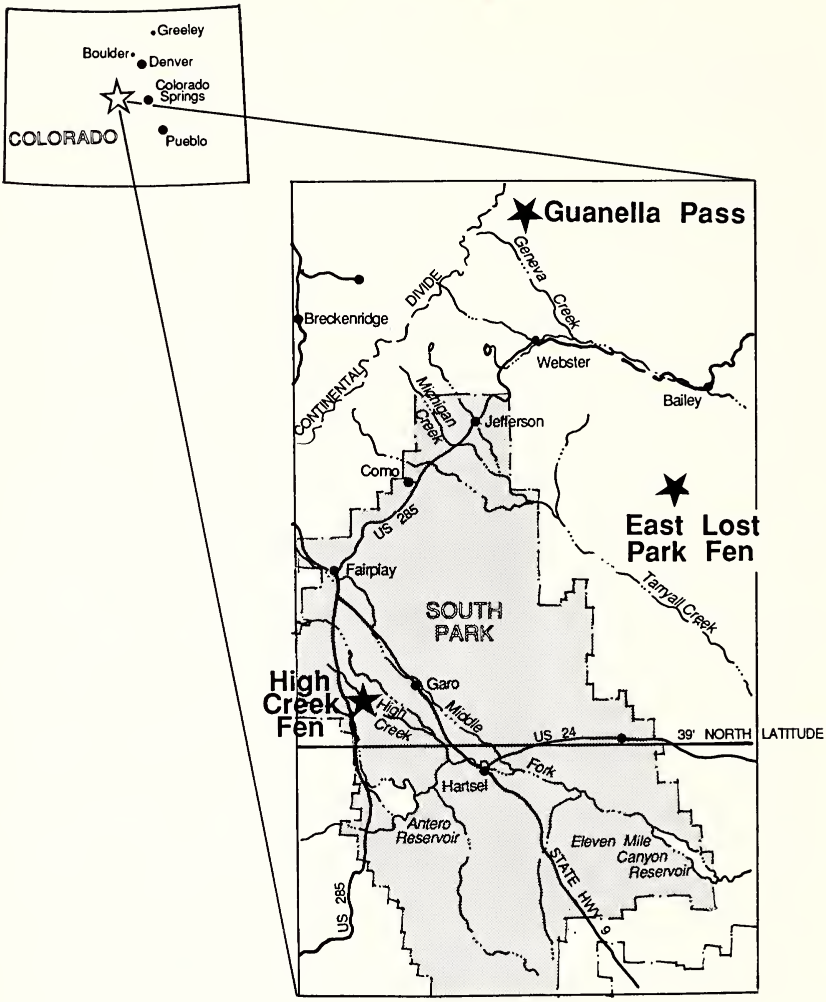

FIG. 1. Central Colorado peatland study sites.

The Guanella Pass fens occur just below the summit of Guanella Pass on the north side of South Park at an elevation of 3540 m. The peatlands are spring-fed rich fens. Peat accumulation occurs around pools which have abundant moss cover. The water chemistry is shown in Table 1.

The High Creek fen contains a number of communities which are dominated by *Carex aquatilis* Wahlenberg, *Eleocharis quinqueflora* (Hartman) Schwartz, *Kobresia simpliciuscula* (Wahlenberg) Mackenzie, *Triglochin maritima* L. and *Juncus alpino-articulatus* Chaix. The following rare species were also collected. *Salix myrtillifolia* Andersson sensu Argus (*Cooper 1678,* COLO, CAN) is a calciphile at its southern range limit. It is a North American species that is widespread in the boreal regions of the continent. The South Park population is apparently the first reported in the western United States. This species has been reported from Wyoming (Dorn Vascular Plants of Wyoming, Mountain West, 1987), however, according to Argus (personal communication to W. A. Weber), the Wyoming plants are glaucous and do not represent the typical form of the species. The species occupies peat hummocks throughout the wetter portion of the fen. *Salix candida* Fluegge (*Cooper 1677,* COLO), also present, is otherwise known in Colorado only from the Laramie River drainage, 160 km to the north, and occurs on hummocks with *S. myrtillifolia. Packera* (*Senecio*) *pauciflora* (Pursh) A. Löve & D. Löve grows on peat hummocks throughout the fen (*Weber and Cooper 18016,* COLO). It is a North American species that has been reported previously in the Rocky Mountains as far south as northern Wyoming. *Carex scirpoidea* Michx. was rediscovered here (*Weber and Cooper 18027,* COLO). It was known previously from an historic specimen collected in South Park by John Wolf. It is very common at this site, dominating the more seasonally dry fen margins. It is noted also in the Lost Park fen and in peatlands along Sacramento Creek west of Fairplay, also in South Park. *Carex viridula* Michx. occurs scattered on hummocks throughout the fen (*Weber and Cooper 18021,* COLO). It is known previously in Colorado only from the San Juan Mountains. *Trichophorum pumilum* (Vahl) Schinz & Thellung (*Scirpus pumilus*) another very rare species is common on peat hummocks with *Kobresia simpliciuscula.*

The floating peat mats in East Lost Park are dominated by *Carex limosa* L. and *Eleocharis quinqueflora.* Growing in the mats is *Carex livida* (Wahlenberg) Willd., a boreal circumpolar species that has been reported previously in the Rocky Mountain region as far south as northern Montana and Idaho (*Weber and Cooper 18034,* COLO). This species has been found also in the Boston Peak wetland in the Laramie River drainage (*Cooper 1680,* COLO) and in the High Creek fen (*Cooper 1685,* COLO). Scattered populations of *Carex tenuiflora* Wahlenb. also occur in the floating mats at East Lost Park (*Weber and Cooper 18036,* COLO). This is a boreal circumpolar species that is new to the contiguous western U.S. and represents a range extension westward from Minnesota. *Eriophorum gracile* K. Koch forms large reddish colored lawns on the floating mats in East Lost Park (*Weber and Cooper 18035,* COLO). It was also found in the Sacramento Creek drainage (*Weber and Cooper 18040,* COLO) and in the Guanella Pass fen (*Cooper 1691,* COLO).

The occurrence of these taxa in Colorado underscores the long-term stability and importance of peatlands as critical habitat for small disjunct populations of plant species whose present distribution is largely boreal.

I appreciate the companionship and help of Dr. W. A. Weber in the collection and identification of the species discussed. Appreciation is expressed to G. Argus for verification of *S. myrtillifolia.* This work was funded by Park Co., CO.

(Received 25 Jan 1990; revision accepted 30 Nov 1990.)

STATUS AND DISTRIBUTION OF *CASTILLEJA MOLLIS* (SCROPHULARIACEAE).

—Lawrence R. Heckard, Jepson Herbarium, University of California, Berkeley, CA 94720, Stephen W. Ingram, Herbarium, University of California, Santa Barbara, CA 93106; Tsan-Iang Chuang, Dept. of Biological Sciences, Illinois State University, Normal, IL 61761.

Castilleja mollis Pennell (Proceedings of the Academy of Natural Sciences, Philadelphia 99:185, 1947), a federal C2 candidate for listing under the Endangered Species Act, was described on the basis of a single collection from Santa Rosa Island of the Channel Islands of California. The epithet reflects the indument of branched hairs. The distribution of this species, considered by Pennell (in Abrams, Illustrated Flora of the Pacific States 3:836, 1951) to be a Santa Rosa Island endemic, was expanded by Munz (A California Flora, 1959, p. 669) and Bacigalupi (Leaflets in Western Botany

10:286–287, 1966) to include plants of coastal sand dunes of San Luis Obispo County with copious branched hairs. Heckard (Brittonia 20:212–226, 1968) presented chromosome data showing that the sand-dune plants presumed to be *C. mollis* were hexaploids (n=36) and that this number as well as n=48 was found in *C. affinis* var. *contentiosa* (J. F. Macbr.) Bacigalupi (Leaflets in Western Botany 10:286–287, 1966), a variety Bacigalupi interpreted as accommodating the coastal plants of *C. affinis* in San Luis Obispo and Santa Barbara counties with branched hairs. Bacigalupi suggested that the branched hairs were the result of hybridization with *C. mollis.* Questions have arisen subsequently as to the distinctness of *C. mollis* from *C. affinis* both on the mainland and on Santa Rosa Island. Unpublished studies by Chuang and Heckard confirm that all the coastal bluff and dune plants of *Castilleja* in San Luis Obispo and Santa Barbara counties are polyploid (n=36, 48) and fit within the variation pattern of *C. affinis,* although they possess branched hairs in varying degrees. We consider them to be too variable to be considered a formal variety (*C. affinis* var. *contentiosa*).

Recent observations and collections of *Castilleja mollis* and *C. affinis* on Santa Rosa Island by Stephen W. Ingram supply new evidence on the differences between the two species and support the conclusion that *C. mollis* is endemic to Santa Rosa Island (and possibly San Miguel Island: Point Bennett, *F. H. Elmore 341* in 1938, RSA, SBBG). Past introduction(s) of *C. mollis* to the mainland remains a likely source of the branched hairs and occasional features reminiscent of *C. mollis* in coastal *C. affinis.* Chromosome number differences of the two species on Santa Rosa Island indicate that a polyploid barrier is acting to limit gene exchange between the two species on the island. T. I. and F. M. Chuang (unpublished data) found *C. mollis* to be a diploid with n=12 (Carrington Point in stabilized dunes, *Ingram & Danielson 445,* JEPS, UCSB) and *C. affinis* to be hexaploid with n=36 (Verde Canyon, *Ingram & Danielson 442,* JEPS, UCSB; Windmill Canyon, *Danielson* cytological collection only—an earlier collection is available as a voucher from this locality: *Blakely 3173,* SBBG). The diploid count for *C. mollis* adds evidence that this species is not on the mainland at present, although its genes may well be incorporated into the polyploid makeup of coastal *C. affinis.* Occasional hybrids were observed (*Ingram & Danielson 446,* JEPS, UCSB). Branched hairs, which are found in most specimens of *C. affinis* on Santa Rosa Island, indicate that polyploid barriers to hybridization are incomplete as is usual in *Castilleja.* There is some evidence that habitat preferences may also be operating within the species to keep them apart; *C. mollis* is found only on sand-dunes while *C. affinis* is generally found in more rocky habitats although it also may grow in sandy areas.

The principal features that distinguish *C. mollis* from *C. affinis* besides its dense indument of branched hairs are: semi-prostrate habit; bracts and upper leaves that are grayish, fleshy, broad and rounded (obovate to ovate), and crowded at the apex; bract and calyx yellow to yellowish green above. These features are rare in *C. affinis,* and when present in coastal San Luis Obispo and Santa Barbara counties may be the result of introgression from *C. mollis.* The closest relative of *C. mollis* appears to be *C. latifolia* Benth., an endemic of coastal bluffs and dunes of the Monterey Peninsula and adjacent coast that is without branched hairs.

The only extant populations of *C. mollis* known on Santa Rosa Island are at Carrington Point and an unverified report at Jaw Gulch. Field study is needed of the plants cited above from San Miguel Island to ascertain their relationship to *C. mollis.* Protection of the species is critical and recommendations are proposed by Ingram in a study done through the Herbarium, University of California, Santa Barbara (A Report to The Nature Conservancy—Nipomo Dunes Preserve/Central Coast and Valley Office, San Luis Obispo, CA, 1990).

(Received 9 Oct 1990; revision accepted 23 Dec 1990.)

ON THE USE OF THE TERM "BAJA CALIFORNIA NORTE."—Lee W. Lenz and Dulce Arias, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

In referring to the northern state of the Baja California peninsula many authors incorrectly apply the term "Baja California Norte." In April 1849, the peninsula was divided administratively into "Norte" and "Sur" and in 1930 the two sections were designated as territories. On 16 Feb. 1952, the northern territory became the State of Baja California, and on 24 Oct. 1974, the southern territory became the State of Baja California Sur. If it is deemed necessary to further identify the northern state, the terms, "State of Baja California," "Estado de Baja California," or Edo. B.C. may be used.

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ANNOUNCEMENT

REPRINT COVERS

In light of increasing concern over limiting resources, **MADROÑO** considers it environmentally sound policy to discontinue offering covers with reprints. It is hoped that authors will view this step in a positive light.

NOTEWORTHY COLLECTIONS

California

Chrysothamnus nauseosus (Pallas) Britton ssp. *bernardinus* (H. M. Hall) H. M. Hall & Clements (Asteraceae).—San Diego Co., rocky gabbro outcrops in mixed coniferous forest, N side of Cherry Flat near Conejos Hiking Trail, ca. 0.5 mi below summit of Cuyamaca Peak, Cuyamaca Mts., 32°57′34″N, 116°36′35″W, ca. 1800 m, 28 Jul 1987, *Hirshberg s.n.* (SD); same location, 28 Aug 1989, *Hirshberg 97* (ARIZ, KANU, LSU, RSA, SD, TEX, UC, UCR).

Significance. A range extension of ca. 90 km S from the San Jacinto Mts., Riverside Co., CA. Previously known from the San Gabriel, San Bernardino, and San Jacinto mts.

Epilobium minutum Lindley ex Hooker (Onagraceae).—San Diego Co., gabbro outcrop on N slope of Cuyamaca Peak, W of Conejos Trail ca. 0.25–0.5 mi SW of small meadow, 32°57′30″N, 116°36′20″W, 1750 m, 15 May 1988, *Hirshberg s.n.* (SD); same location, 12 Jun 1988, *Hirshberg s.n.* (SD).

Significance. A range extension of ca. 300 km SE from Ventura Co., CA. Known previously from BC, Canada, S to Ventura and Madera cos., CA, and E to MT and NV.

Polygonum parryi E. Green (Polygonaceae).—San Diego Co., Cuyamaca Mts., rare in open chaparral E of small meadow on N side of CA hwy 79, ca. ¼ mi E of Chambers Park, 32°59′32″N, 116°34′26″W, 1425 m, 16 May 1988, *Hirshberg s.n.* (SD); rare in pebbly areas in open chaparral on N side of CA hwy 79, across from Chambers Park, 32°59′29″N, 116°34′33″W, 1425 m, 21 May 1988, *Levin and Hirshberg 2020* (SD); rare in gravelly soil, grassland at edge of chaparral, ca. 300 m WNW of jct. of CA hwy 79 and road to Camp Hual-Cu-Cuish, 32°58′40″N, 116°35′W, 1450 m, 21 May 1988, *Levin and Hirshberg 2024* (SD); rare in gravelly areas, N-facing gabbro meadow S of Wolahi Rd, 32°59′20″N, 116°35′20″W, 1400 m, 13 Jun 1988, *Hirshberg s.n.* (SD); about 100–200 plants scattered along edge of Lake Trail N of Cuyamaca Store, 32°59′N, 116°35′W, 1420 m, 13 Jun 1988, *Hirshberg s.n.* (SD). (The determinations of both Levin and Hirshberg specimens and the May Hirshberg specimen were confirmed by J. C. Hickman, 1988).

Significance. Reported from the Cuyamaca Mts. by Jepson (Manual of Flowering Plants of California, 1923, p. 290) and several subsequent authors, but prior to these collections no specimens of this species were known from the Peninsular Ranges (J. C. Hickman, personal communication). This inconspicuous annual, otherwise found from the Sierra Nevada N to WA, appears to be uncommon to rare in gravelly soil around the Cuyamaca Lake Basin.

—Geoffrey A. Levin (see below) and Jerilynn Hirshberg, P.O. Box 2, Julian, CA 92036.

Ribes viburnifolium A. Gray (Grossulariaceae).—San Diego Co., small side canyon off Goat Canyon at W end of Spooner's Mesa, steep N-facing slope with *Rhus integrifolia, Heteromeles arbutifolia, Polypodium californicum,* T19S, R2W, NW¼ of NW¼ of NW¼, sect. 9, 32°32′21″N, 117°05′54″W, 75 m, 14 Mar 1989, *V. Scheidt s.n.* (SD); same location, 9 April 1990, *Levin and M. Howe 2053* (RSA, SD, UC).

Significance. First native record for mainland USA (cf. Moran, Madroño 26:49, 1979), a range extension of ca. 6 km N from La Joya, Baja California, México. Previously known from northern coastal Baja California and Isla de Cedros, México, and Santa Catalina Island, CA.

—Geoffrey A. Levin, Botany Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

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IDAHO

BUTOMUS UMBELLATUS L. (BUTOMACEAE).—Bingham Co., flowering emergent and sterile submersed forms along water's edge on both sides of the main Aberdeen–Springfield Canal, 6 km W of Springfield, N of American Falls Reservoir, T4S, R32E, SE¼ sect. 7, 1357 m, 14 Jul 1990, *T. C. Fuller, K. W. Fuller, and G. D. Barbe 4387, 4388* (CDA).

Previous knowledge. Flowering rush was first collected along the banks of the Snake River at Idaho Falls, Bonneville Co., 9 Aug 1956, *Anderson 643* (CAS). It was reported to have been there for at least 10 years prior, making its introduction sometime before 1946. Flowering rush also was collected from a small pond on the west fork of Felton Creek 5 miles northeast of Moscow, Latah Co., *Francq s.n.* (ID) (Leaflets in Western Botany 10:109, 1964), but Anderson (Bulletin of the Torrey Botanical Club 101:292–296, 1974) was unable to locate the voucher for that collection and unable to relocate the population from which it came. This Eurasian species is presently widespread in the St. Lawrence River Basin, south central Canada, and the northern prairie states. It is a frequent weed of rice cultivation in southern Europe.

Significance. This aggressive aquatic weed presents a serious threat to irrigated agriculture in ID and other western states, and to rice cultivation in CA, by impeding water flow, causing heavy sedimentation, and reducing the carrying capacity of water delivery systems. The species has severely infested a 19 km segment of the main Aberdeen–Springfield Canal. This westernmost collection is approximately 80 km downstream and SW of the original occurrence at Idaho Falls. Efforts to control the weed in ID have not been successful; mechanical removal has only caused it to propagate and spread.

—KEN FULLER, Bureau or Land Management, 200 South Oakley Highway, Burley, ID 83318; THOMAS C. FULLER, and G. D. BARBE, California Department of Food and Agriculture, 1220 N Street, Sacramento, CA 95814.

OREGON

CYTISUS STRIATUS (Hill.) Rothm. (LEGUMINOSAE).—Lane Co., on sand dunes along South Jetty Road, ca. 2 km SW of Florence, frequent, with *C. scoparius,* T18S R12W S33, SW¼, 24 Aug 1982, *Wagner 2901* (ORE, OSC, UC).

Significance. First record for OR and the western states. Introduced from Europe.

TILLAEA MUSCOSA L. (CRASSULACEAE).—Josephine Co. along Interstate 5 freeway at Manzanita Rest Area (W side of freeway, off S-bound lanes), ca. 8 km NNW of Grants Pass, drying flats wet in winter, with grasses and other annual weeds, T35S R06W S24, 28 April 1984, *Wagner 3252* (ORE, OSC).

Significance. First record for OR; previously known from CA (Munz, A California Flora with Supplement, 1968).

EQUISETUM TELMATEIA Ehrh. (EQUISETACEAE).—Umatilla Co. along South Fork Umatilla River ca. 100 m above confluence with Thomas Creek, T02N R37E S5, 820 m, 30 Jun 1990, *Wagner 4369* (ORE, OSC, WTU, UC, NY).

Significance. Previously unknown E of the Cascade Mts. in OR; growing with *Alnus rubra, A. incana* and *Alnus rubra* × *incana* hybrids, indicating a refugium of coastal disjuncts parallel to those found in central ID (Northwest Science 52:205–211, 1978).

EBUROPHYTON AUSTINIAE (A. Gray) Heller (ORCHIDACEAE).—Umatilla Co., along North Fork Umatilla River ca. 1 km up from confluence with South Fork, T03N R37E S22, 732 m, 30 Jun 1990, observed and positively identified by D. Wagner, but not collected because only a single individual seen.

Significance. Previously unknown east of the Cascade Mtns. in OR, a coastal disjunct as the *Equisetum,* above, and like it also found in west central ID (Hitchcock and Cronquist, A Flora of the Pacific Northwest, 1973).

LYCOPODIUM COMPLANATUM L. (LYCOPODIACEAE).—Union Co., 32 km SW of LaGrande, along a small tributary of the Grande Ronde near the junction of Forest Service Roads 4305-960 and 4305-980, T05S R36E S18 SE¼ SW¼, 1370 m, 13 Jul 1990, *Paula J. Brooks s.n.* (ORE).

Significance. First record for eastern OR, all the other OR sites being on Mt. Hood (personal communication, Oregon Natural Heritage Data Base). Unlike the above two coastal disjuncts, this is a southward range extension of a circumboreal species.

TIARELLA TRIFOLIATA L. var. *LACINIATA* (Hook.) Wheelock (SAXIFRAGACEAE).—Lane Co., Battle Crk. ca. 5 km SSE of Crow, in wetland created by beaver dams along crk., under *Acer macrophyllum* and *Alnus rubra,* T19S R05W S5 SW¼ NW¼, 183 m, 15 May 1990, *Steve Acker s.n.* (ORE); Lane Co., 1.6 km W of Noti, in a steep draw under *Acer macrophyllum* and *Alnus rubra,* T17S R06W S42 NW¼ NW¼, 244 m, 13 May 1990, *Danna Lytjen s.n.* (ORE).

Significance. A considerable range extension from "Vancouver Island and adjacent Puget Sound islands, Washington" (Hitchcock and Cronquist, A Flora of the Pacific Northwest, 1973). Peck (A Manual of the Higher Plants of Oregon, 1961) reports it from "Northwestern Oregon" but there are no supporting specimens in the Peck herbarium (WILLU).

—DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403.

ANNOUNCEMENT

SOUTHWEST BOTANICAL SYSTEMATICS SYMPOSIUM

The Seventh Annual Southwestern Botanical Systematics Symposium will be held May 24–25. This year's topic is "Modes of Speciation." Invited speakers include Jerrold Davis, Cornell University; Leslie Gottlieb, University of California, Davis; R. C. Jackson, Texas Tech University; Donald Levin, University of Texas; Loren Rieseberg, Rancho Santa Ana Botanic Garden; and Robert Wyatt, University of Georgia. The evening address "Reflections on Speciation" will be given by Harlen Lewis, University of California, Los Angeles. The cost is $45.00 ($35.00 for students), which includes Friday evening social, box lunch, and Saturday banquet. To register, send your name, address, and telephone or Fax number, with a check payable to: Rancho Santa Ana Botanic Garden, Systematics Symposium, 1500 N. College Avenue, Claremont, CA 91711. For more information, call (714) 625-8767, ext. 51.

OBITUARY

Fritz W. Went, botanist and plant physiologist died in Reno, Nevada, on 15 May 1990 at the age of 86. Went is perhaps best known as the discoverer of the plant hormone auxin. He was a faculty member at Cal Tech in Pasadena (1933–1958), Director of the Missouri Botanical Garden and later Director of the Desert Research Institute at Reno, Nevada. During his tenure at Cal Tech, Went's interest in controlled plant growth studies led him to design a very complex plant growth facility for the purpose of controlling environmental conditions. According to Bonner (1991) this structure was named a "phytotron" by Went's irreverent collegues (from "phyton" for plant and "tron" for big, expensive, complex machine). Today, the term phytotron is part of the botanical lexicon.

Fritz West was a scientist with diverse interests who also contributed to the fields of ecology and evolution. He had a keen interest in desert plants and germination (Went 1948, 1949). In the 1940's, in association with Philip Munz, he initiated a study of seed longevity and germination behavior of California plants (Went and Munz 1949; Went 1969). He published papers on postfire chaparral regeneration (Went et al. 1952) and the allelopathic effect of desert shrubs on the herbaceous understory. It is of interest that his early study on the putative allelopathic effect of *Encelia farinosa* (Went 1942) attracted another scientist, Cornelius Muller, to studies of allelopathy. Curiously, Muller, who later made his reputation in studies of allelopathy began the study of allelopathy (Muller 1953) by re-examining Went's purported case and concluded that the pattern Went observed was not due to allelopathy.

Fritz Went was a creative scientist and not afraid to speculate about new ideas. In 1971 he published an article on the phenomenon of convergent or parallel evolution in which he proposed a novel explanation for the evolution of parallel structures in a common environment; such as the abundance of red, tubular hummingbird pollinated flowers in the California flora. The accepted paradigm is that these structures are the result of natural selection working on gradual genetic changes that arise by mutation and recombination. Went (1971) made the provocative suggestion that these could arise by the non-sexual transfer of chromosomal fragments, perhaps through viral vectors. Although not a widely accepted view (e.g., Tucker 1974), it does illustrate the creative side of this colorful and important contributor to our discipline.

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—Jon E. Keeley, editor.

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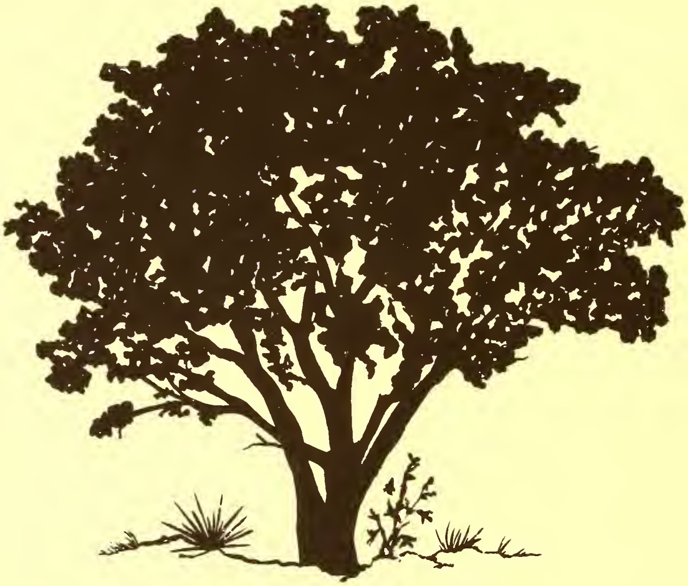

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INFLUENCE OF SHADE AND HERBACEOUS COMPETITION ON THE SEEDLING GROWTH OF TWO WOODY SPECIES

O. W. Van Auken and J. K. Bush
Division of Life Sciences,
The University of Texas at San Antonio,
San Antonio, TX 78249

Abstract

The effects of shade and herbaceous competition on the growth of *Acacia smallii* and *Celtis laevigata* seedlings were studied using a factorial field experiment. *Acacia smallii* grew best in full sunlight when there were no competitors. Growth was intermediate in shade alone or in full sunlight with herbaceous competitors and least in shade with competitors. There was a significant interaction between light level and competition for *A. smallii,* with growth being greater than expected in full sun when competitors were absent. *Celtis laevigata* seedling growth was not significantly reduced by shade, but was lower in the presence of herbaceous competition. Combined negative effects of shade and herbaceous competition suggest that *A. smallii* is an early successional species requiring disturbances or vegetation gaps for establishment. *Celtis laevigata* is a late successional species that is little affected by low light levels, but its growth would be promoted by vegetation gaps in nutrient rich grasslands or below a woody plant overstory.

Increased density of many woody species has been reported in grasslands of the southwestern United States and many other parts of the world (Buffington and Herbel 1965; Hastings and Turner 1965; Harris 1966; Harrington et al. 1984; Smith and Goodman 1987). Changes in species composition and density could be caused by lower fire frequency, reduced competitive ability of the grasses mediated by heavy grazing, climatic changes or a combination of these factors (Neilson 1986; Van Auken and Bush 1989). To establish in grasslands, woody plants must avoid or overcome negative effects of established plants. Factors that may be critical to establishing plants include light levels, the concentration of soil nutrients, and moisture availability.

Acacia smallii Isley (huisache, syn: *Acacia farnesiana* [L.] Willd., Clarke et al. 1989), a woody legume, occurs from northern Florida to California (Correll and Johnston 1970) and has a high density on over 1.1 million ha in Texas (Smith and Rechenthin 1964). *Acacia smallii* is more commonly found in old fields or grasslands that have been heavily grazed than in native grasslands (Van Auken and Bush 1985). It appears to establish in vegetational gaps or areas that have low cover or density of grasses. Areas of low or reduced soil nitrogen are prone to colonization by *A. smallii* because of its low soil nitrogen

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requirement (Bush and Van Auken 1986b). It does not occur below its own or other woody species canopies because of its intolerance to shade (Bush and Van Auken 1986a; Lohstroh and Van Auken 1987). It does not seem to occur with high densities of grass because of negative effects of the grass, which have been demonstrated in greenhouse studies (Cohn et al. 1989; Van Auken and Bush 1990). Another reason why it is absent from some grasslands could be because of low light below the grass canopy. However, field testing of negative effects of grasses on *A. smallii* has not been conducted and its absence from some grasslands is not well understood.

Celtis laevigata Willd. (Texas sugarberry) is often associated with *A. smallii,* especially in the central and eastern part of the range of *A. smallii* (Correll and Johnston 1970). *Celtis laevigata* is tolerant of shade (Bush and Van Auken 1986a) and requires higher levels of soil nitrogen (Van Auken et al. 1985), characteristics of late successional species (Bazzaz 1979; Van Auken et al. 1985; Bush and Van Auken 1986b). *Celtis laevigata* grows below its own canopy and probably in low density grasslands; however, field studies examining its response to competing grasses are lacking.

Growth of seedlings of *A. smallii* and *C. laevigata* has been measured below an *A. smallii* canopy and in open areas between the *A. smallii* trees. *Acacia smallii* grew best in the open, whereas *C. laevigata* grew better below the canopy (Lohstroh and Van Auken 1987; Van Auken and Lohstroh 1990). However, partitioning the cause of reduced plant growth between reduced light levels and competition for soil resources under tree canopies is difficult. Light levels are altered below the canopy, but so are soil temperature, soil nutrient level, and soil water content (Tiedemann and Klemmedson 1973, 1977, 1986; Bush and Van Auken 1986b). Effects of light levels and herbaceous competition can however, be better evaluated by using a single phase community (a grassland), with a relatively uniform distribution of soil resources and light levels, although soil moisture is difficult to control. Plant density can be modified with herbicide and light level with shade cloth.

The purpose of this field study was to evaluate the impact of shading and herbaceous competition on the growth of seedlings of *A. smallii* and *C. laevigata,* by manipulating grassland density and light levels. Both species are important components of riparian and upland communities in central and south Texas (Van Auken and Bush 1985) and have been suggested as invaders of grasslands. Although many studies have been conducted using these species, field experiments in native grasslands have not been completed.

METHODS

The study was carried out in the grassland phase of a savanna in northern Bexar County, TX, USA (98°36′W and 29°37′N). Vegetation of the study site includes clumps of *Prosopis glandulosa* Torrey (honey mesquite), *Diospyros texana* Scheele (Texas persimmon), *Quercus fusiformis* Small (live oak), *Juniperus ashei* Buchholz (mountain cedar), *Aloysia gratissima* Gillies & Hook. (white brush), and at lower densities *Acacia smallii* and *Celtis laevigata.* Interspersed with the trees are open areas dominated by *Stipa leucotricha* Trinius & Ruprecht (Texas winter-grass), with *Panicum obtusum* Kunth (vine-mesquite) and *Sorghum halepense* (L.) Persoon (Johnson grass) present at low density. The study site is within the range of both *A. smallii* and *C. laevigata,* and individuals of both are found within 50 m of the field site.

Fruits of *A. smallii* and *C. laevigata* were collected in Bexar County, TX, in late summer and fall of 1986. Seeds of *A. smallii* were mechanically separated from fruit tissue, placed in plastic bags and stored at 4°C. Fruits of *C. laevigata* were placed in plastic bags and stored the same way. Prior to planting, *A. smallii* seeds were soaked in concentrated H_2SO_4 for twenty min (with agitation), then rinsed thoroughly with tap water. *Celtis laevigata* seeds were soaked in 5 mM gibberellic acid for three hr and rinsed in tap water (Kahn 1968). Seeds of both species were then sown in plastic trays filled with a sandy-loam of the Patrick series (Taylor et al. 1966). Four weeks later, the seedlings were transplanted into the field.

A 2 × 2 factorial experiment was designed to test the main effects of shade and herbaceous competition on the growth of seedlings of *A. smallii* and *C. laevigata.* The four treatments in the experiment included: 1, full sunlight and no competition; 2, full sunlight with competition; 3, shade and no competition; and 4, shade with competition.

Forty plots (1 m^2 each) were established in the grassland phase of the savanna. Half meter buffers separated each treatment plot. Treatments and species were assigned to each plot randomly. Half the plots were sprayed with 2.7 g/m^2 of a glyphosphate herbicide (isopropylamine salt of N-[phosphonomethyl] glycine, Round-up®) to kill all herbaceous vegetation. Two weeks after treatment, the sprayed plots were raked to remove standing dead plant material. All newly emerged plants were hand removed from the herbicided plots weekly for the duration of the experiment. On 15 July 1987, 25 seedlings of each species were selected for uniformity of size. One seedling was planted in the center of each plot (5 plots/treatment). Five seedlings of each species were used to determine initial dry weight, the remaining 20 were planted. All seedlings were watered daily with one liter for two weeks and dusted once per week for two weeks with 5% Sevin®.

Two layers of a commercial shade fabric were draped on a frame, 50 cm above the ground over five herbicide and five non-herbicide plots of each species to approximate light levels observed under adult tree canopies. Photosynthetically active photon flux density

(PPFD, 400–700 nm) was measured on a clear spring day at solar noon with an integrating quantum sensor (Li-Cor® Li-188). Two measurements were made near the center of each plot at the soil surface.

Experimental plants of both species were harvested on 13 November 1988, 16 months after transplanting into the field. Seedlings were clipped at the cotyledon scars, number of basal stems were counted, stem length and basal diameter were measured. Vernier calipers were used to measure basal diameter just above the cotyledon scars. Stem length was the distance from the cotyledon scars to the apical meristem plus the distance from the main stem to the apical meristems of all of the secondary stems. Leaves and stems were dried at 100°C to a constant weight. Live and standing dead biomass of the herbaceous competitors was determined by clipping one, 20 × 20 cm quadrat from each competition plot. The herbaceous biomass was separated into *Stipa leucotricha,* forbs, and dead (the only grass present was *S. leucotricha*), and then dried at 100°C.

Homogeneity of variance among treatments was tested by the F-max test and none showed significant heterogeneity (Tietjen and Beckman 1972). Factorial ANOVA's were performed using light condition and competition as main effects, and the interaction between these terms (Steel and Torrie 1980; SAS 1982).

RESULTS

Shading alone reduced surface light 83%, but if herbaceous plants were present, surface light levels were reduced 91% (Table 1). Herbaceous vegetation by itself reduced surface light by 40%. Shade treatments approximated light levels below a mature *Acacia smallii* canopy (72–369 $\mu M \cdot m^{-2} \cdot sec^{-1}$, Bush and Van Auken 1986a).

Initial measurements of *A. smallii* and *Celtis laevigata* aboveground dry weights were 0.08 ± 0.02 ($\bar{x} \pm SD$) and 0.05 ± 0.02 g respectively. At the end of the experiment, effects of both light level and herbaceous competition were significant for all variables measured for *A. smallii* (Table 2). In addition, the light × competition interaction was also significant for all variables. That is, the effect of light level on *A. smallii* growth was significantly greater than expected when there were no competitors present. Dry weight of *A. smallii* was greater than expected in light without competition or less than expected in shade without competition (parallel lines indicate no significant interaction, Fig. 1).

For *C. laevigata,* only competition was significant (Table 2). Neither of the main factors had a significant effect on number of *C. laevigata* stems. There was no significant interaction between these factors for *C. laevigata* (Fig. 1).

TABLE 1. LIGHT LEVELS AND PERCENT FULL SUNLIGHT IN FOUR EXPERIMENTAL TREATMENTS. Measurements are mean photosynthetically active photon flux densities (PPFD, $\mu mol \cdot m^{-2} \cdot sec^{-1} \pm 1$ SD) and were made at solar noon on a clear spring day (March 11, 1988). Ten measurements were made for each treatment.

Treatment	PPFD	Percent
Light without competition	1805 ± 217	100
Light with competition	1083 ± 531	60
Shade without competition	306 ± 126	17
Shade with competition	159 ± 114	9

For *A. smallii,* the greatest values for number of stems, stem length, basal diameter and above-ground dry weight occurred in the full light no competition treatment (Fig. 2A, C). Treatments with one adverse factor (light plus competition or shade without competition) were essentially equal and significantly lower than the light treatment without competition. The smallest plants were in the shade plus competition treatment. These plants had increased in dry weight five times during the experiment, but were 20 times smaller than the plants in the light without competition, which had increased in dry weight 114 times.

Number of *C. laevigata* stems did not change with treatment (Fig. 2B). *Celtis laevigata* seedlings without competition had slightly greater stem length, basal diameter and 3.45 times more dry weight than those plants grown with herbaceous competitors (Fig. 2B, D). *Celtis laevigata* plants with competition and regardless of light treatment increased in dry weight 24.8 times over the course of the experiment, but, those plants without competition and regardless of light treatment increased 85.6 times.

In the light treatment, 96% of the live biomass consisted of *Stipa leucotricha* with the remainder being unidentified forbs (Table 3).

TABLE 2. ANOVA TABLE OF *F* VALUES AND LEVELS OF SIGNIFICANCE FOR *ACACIA SMALLII* (AS) AND *CELTIS LAEVIGATA* (CL) IN AN ARTIFICIAL SHADE—COMPETITION EXPERIMENT. Error degrees of freedom = 16, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

Species	Source	df	No. stems	Stem length	Basal diameter	Above-ground dry weight
AS	Light	1	22.9***	9.7**	55.8****	22.7***
	Competition	1	22.9***	17.8***	39.5****	19.6***
	Light × Competition	1	22.9***	13.5**	30.5****	17.0***
CL	Light	1	1.0	3.7	2.2	2.2
	Competition	1	1.0	5.2*	5.8*	5.3*
	Light × Competition	1	1.0	0.6	1.6	3.3

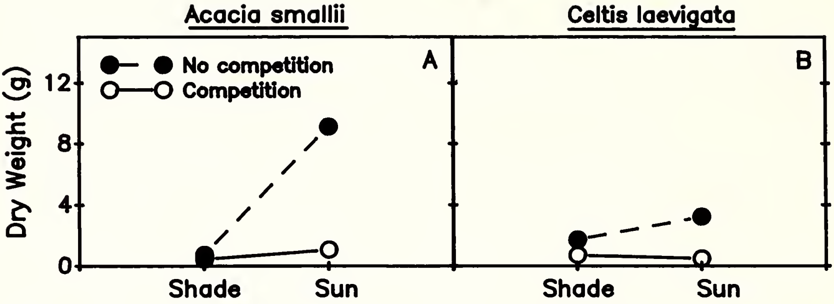

FIG. 1. Plot of the dry weight of *Acacia smallii* (A) and *Celtis laevigata* (B) showing the interaction of light levels and competition. The interaction is significant for *A. smallii* ($P < 0.05$), but not for *C. laevigata*. When lines are parallel there is no significant interaction ($P \geq 0.05$).

Live biomass was 26% of the total standing biomass. In the shade treatment, *S. leucotricha* was 83% less than unshaded plots while the forbs were seven times more than the unshaded plots. Total live biomass in the shade treatment decreased 56% and total standing biomass decreased 40% compared to unshaded plots.

DISCUSSION

A number of investigators have shown that shading reduces aboveground dry weight and that there are differences between sun and shade plants (Grime 1965; Bazzaz 1979; Bush and Van Auken 1986a; Lohstroh and Van Auken 1987; Van Auken and Lohstroh 1990). In addition, grasses have been shown to have negative effects on seedlings of various woody species (Glendening and Paulsen 1955; Felker et al. 1984; Van Auken and Bush 1987, 1988, 1989, 1990). What has not been shown in most other studies is the combined negative effects of reduced light levels and competition. Light level and competition do not act independently. Negative effects of shade and competition on *A. smallii* are greater than would be expected. The same response was not found for *C. laevigata*; it was stimulated very

TABLE 3. STANDING BIOMASS FOR THE FULL SUNLIGHT WITH COMPETITION AND ARTIFICIAL SHADE WITH COMPETITION TREATMENTS. Measurements are mean g/m² ± SD collected at the end of the experiment (n = 5 per treatment).

Unit measured	Light	Shade
Stipa leucotricha	192 ± 62	33 ± 32
Forbs	8 ± 7	56 ± 83
Total live biomass	199 ± 71	88 ± 96
Standing dead biomass	555 ± 201	367 ± 286
Total biomass	754 ± 573	455 ± 354

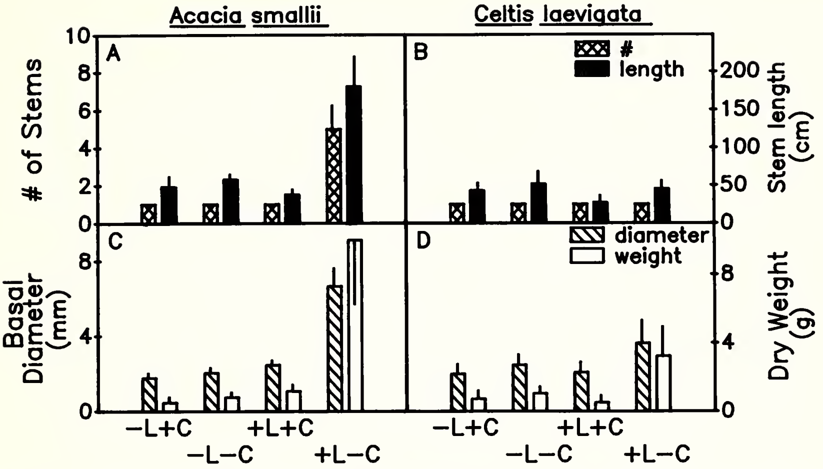

FIG. 2. Mean number of stems, stem length, basal diameter and dry weight for seedlings of *Acacia smallii* (A, C) and *Celtis laevigata* (B, D) grown in shade with herbaceous competition (−L+C), shade without competition (−L−C), full sunlight with competition (+L+C) and in full sunlight without competition (+L−C). Lines at the top of each bar represent one standard error of the mean for that treatment.

little by higher levels of light. The presence of other plants had the greatest negative effect on the growth of *C. laevigata.* In addition, there was no significant interaction of factors and *C. laevigata* is not an invasive species (Smith and Rechenthin 1965).

Numerous studies have shown that light levels, competition, herbivory, fire, nutrients or water can reduce woody plant growth, but woody plants are not usually completely suppressed in native communities (Bartholomew 1970; Wright et al. 1976; Harper 1977; Bazzaz 1979; McAuliffe 1986). It seems that negative effects from several factors may be required to prevent a plant from becoming established in a given habitat. Drastic changes in the grasslands, such as the concomitant reduction in grass competitive ability for soil resources and increased soil surface light intensity as a result of heavy grazing may allow establishment by certain woody plants. The seeds of woody plants or small seedlings may already be present, but growing very slowly. Plants may be released from competitive suppression as a result of lower grass biomass, and as surface light levels are increased by grass removal, woody plant growth may then be unrestricted.

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SHRUB FACILITATION OF COAST LIVE OAK ESTABLISHMENT IN CENTRAL CALIFORNIA

Ragan M. Callaway and Carla M. D'Antonio[1]
Department of Biological Sciences, University of California,
Santa Barbara, CA 93106

Abstract

Seedlings of *Quercus agrifolia* were found to be strongly associated with shrubs at two sites in central California. Although shrub cover occupied only 30% of the total cover, over 80% of all *Q. agrifolia* seedlings were found under shrub canopies. Although one site was grazed by livestock and the other was not, in both sites seedlings under shrubs were less browsed than seedlings in the open grassland. In field experiments where seedlings were grown with and without shrub cover, survivorship after two years in the open was 0, whereas 31% of seedlings survived under shrubs (18% of the experimental shrubs had living seedlings under their canopies). Seedling survival was not the same under all shrub species. Shoot mortality in these experiments attributed to water or temperature stress was 17% under shrubs and 63% in the open. These results indicate that *Q. agrifolia* may have a "nurse plant" interaction with some species of shrubs.

Recruitment of young *Quercus agrifolia* Nee (coastal live oak), is too low to maintain the existing adult populations in much of its range (Muick and Bartolome 1987) and the preservation of this woodland has become a major conservation issue in California, USA. Although the factors that limit regeneration of other oak species in the state are complex, they include drought stress and seedling predation from deer, gophers and livestock (Griffin 1971, 1976; Borchert et al. 1989). The causes of low regeneration of *Q. agrifolia* have not been studied, but they are likely to be similar to those reported for other species.

Quercus agrifolia is an evergreen tree, 10 to 20 m tall, and is endemic to California, USA and northern Baja California, Mexico (Munz 1959). It is widely distributed throughout the central and southern coastal ranges of California and is often adjacent to shrub vegetation or intermixed with shrubs (Sawyer et al. 1977). Acorns mature and drop to the ground and/or are dispersed by vertebrates in autumn and germination occurs in late autumn or early winter. The climate in which the species occurs is mediterranean, with precipitation occurring primarily between September and April.

Muick and Bartolome (1987) reported that seedlings and saplings of *Q. agrifolia* were uncommon in many of their study sites. In

[1] Present address: Department of Integrative Biology, University of California, Berkeley, CA 94720

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preliminary surveys we also found that young *Q. agrifolia* were uncommon, but that seedlings and saplings appeared to be associated with shrub cover. This observation is consistent with the following hypotheses: 1) acorns are not randomly dispersed between open grassland and shrub cover; 2) germination rates are not the same in these microhabitats; and/or 3) seedling survival is restricted to certain microhabitats. The latter two hypotheses have been investigated in other plant associations and have been included in the general phenomenon of "nurse plant" interactions in which established plants ameliorate climatic extremes and /or provide refuge from predators for seedlings of other plant species. Such associations have been previously reported for a wide range of desert taxa and habitats (Steenbergh and Lowe 1977; Everett et al. 1986; Franco and Nobel 1989; McAuliffe 1988), but not for oaks or other species in California woodlands.

To test the hypothesis that oak tree seedling recruitment is dependent upon a nurse plant association with established shrubs, we documented the natural distribution and condition of *Q. agrifolia* seedlings and saplings relative to shrub cover in two sites, each with approximately equal cover of mixed oak savanna and chaparral. We then followed the survivorship of seedlings planted from acorns both in the open and under shrubs at a third site, and documented the probable causes of mortality of these seedlings over two years.

STUDY SITES

Natural distributions of seedlings in the field were measured at two sites in the Santa Ynez Valley in northern Santa Barbara County. The first site was a mixed oak woodland at Cachuma State Park (200 m elevation, 34°35′N, 119°59′W) where stands of *Q. agrifolia* and *Q. lobata* Nee (valley oak) were scattered throughout annual grassland and adjacent to coastal scrub dominated by *Salvia leucophylla* E. Greene (purple sage) and *Artemisia californica* Less. (California sagebrush). The site had been free from livestock grazing for over 10 years, but native herbivores such as mule deer (*Odocoileus hemionus*) and pocket gophers (*Thomomys bottae*) were common. The second site was located at Sedgwick Ranch, in the Santa Ynez Mountains (350 m elevation, 34°41′N, 120°2′W). Here *Q. agrifolia* was mixed with *Q. lobata* and *Q. douglasii* Hook. & Arn. (blue oak) and occured adjacent to coastal scrub dominated by *S. leucophylla* and *A. californica.* This site was grazed by livestock as well as native herbivores.

An experiment to test the hypothesis that shrubs facilitate establishment of oak seedlings was set up at a third site in northern Santa Barbara County in conjunction with a revegetation project. This site was located approximately 8 km W of the other two sites at the base of the Purisima Hills (200 m elevation, 34°32′N, 120°27′W). The experiment was established in a oil pipeline right-of-way that formerly had supported both *Q. agrifolia* and a variety of shrub species. Shrubs, primarily *A. californica, Ericameria ericoides* Jepson, *Mimulus aurantiacus* Curtis, and *Lupinus chamissonis* Eschsch., had reestablished on the right-of-way by both artificial and natural seeding during the two years between the completion of the pipeline and the beginning of the experiment. Soil at this site was uniformly medium sand (Davis et al. 1988) underlain by marine sedimentary rocks and gravels which are covered with Orcutt sandstone (Dibblee 1950). The section of right-of-way that we used followed gently rolling topography with slope steepness ranging from 0 to 3%, and slope aspects facing either E or W. Rainfall averaged 36 cm annually. Livestock were excluded from this site but natural predators including mule deer and pocket gophers were abundant.

METHODS

Natural seedling distribution. We searched for naturally occurring seedlings in ten 20 × 20 m plots at Cachuma and eight 20 × 20 m plots at Sedgwick Ranch that had been randomly located in the woodland-shrubland ecotone. We recorded the number of oak seedlings, vegetative cover type with which seedlings were associated (seedlings under shrub and tree canopies were recorded as associated with the cover type of the shrub species), average diameter of each shrub canopy associated with an oak seedling, the percentage of leaves that were brown on each seedling, and the percentage of leaves that had been browsed in each plot. All field distribution patterns were sampled in the fall of 1987, before the current crop of acorns had germinated. Thus, only seedlings that had germinated in 1986 or before were recorded. We use the term "seedling" for continuity, however, many were several years old.

Experimental seedling establishment. In November 1987, viable acorns that had been collected at the Purisima Hills site were planted in 100 plots in the following experimental design. Each plot was centered on a randomly chosen shrub, regardless of species, which was permanently tagged. The species of shrubs that were used were *A. californica* (23 shrubs), *E. ericoides* (49 shrubs), *M. aurantiacus* (19 shrubs), and *L. chamissonis* (9 shrubs). These shrubs had regenerated after the completion of construction, two years prior to our experiment. Shrubs were from 30 to 55 cm tall, and 35 to 50 cm in diameter. Four acorns were buried 2 cm deep under each central shrub, approximately 20 cm apart, one at each cardinal compass point under the shrubs. Four acorns were also planted in the open, one at each cardinal compass point 1 m from the edge of the

TABLE 1. DISTRIBUTION OF *QUERCUS AGRIFOLIA* SEEDLINGS WITH RESPECT TO VEGETATION COVER TYPE. Chi-square statistics are for goodness-of-fit tests for numbers of seedlings associated with a given cover type.

Study area	Cover type	Relative frequency	Number of associated *Quercus agrifolia* seedlings Obs.	Exp.
Cachuma	Open grassland	0.605	6	126
	Quercus agrifolia	0.038	35	8
	Artemisia californica	0.193	73	40
	Salvia leucophylla	0.162	94	34
		n = 208 seedlings $\chi^2 = 338.5$, df = 3, $p < 0.001$		
Sedgwick	Open grassland	0.581	0	28
	Quercus agrifolia	0.118	7	6
	Artemisia californica	0.107	11	6
	Salvia leucophylla	0.165	31	8
		n = 49 seedlings $\chi^2 = 98.5$, df = 3, $p < 0.001$		

shrub canopies. Thus, the total number of acorns planted was 400 under shrubs (100 shrubs) and 400 in the open.

Shoot emergence was first recorded in March 1988 and survivorship of shoots was recorded in July and September 1988, January 1989, and February 1990. We recorded the presence of dead, desiccated shoots and missing shoots in order to estimate mortality due environmental stress and that due to herbivory. Survivorship was analyzed by plot to avoid psuedoreplicaton, and also by individual seedlings. Statistics were conducted with Systat (Wilkinson 1988).

RESULTS

Natural seedling distributions. Numbers of naturally established oak seedlings were much higher under shrubs than in the open grassland in both of the surveyed study sites. At the Cachuma site, the most common shrubs, *S. leucophylla* and *A. californica,* covered 36% of the total study area but 80% of all *Q. agrifolia* seedlings were found under these two species (Table 1). Only 3% of the seedlings were found in the open grassland, yet this was the predominant cover class at the site. At Sedgwick, the site with livestock, the same shrub species occupied 27% of the total study area but 86% of all oak seedlings were found under them, and no seedlings were found in the open grassland (Table 1). In both of the study sites approximately 15% of the seedlings were located under adult *Q. agrifolia* trees and with no shrub cover, but at the Cachuma site the number of oak seedlings found under adult oak canopies was four times that

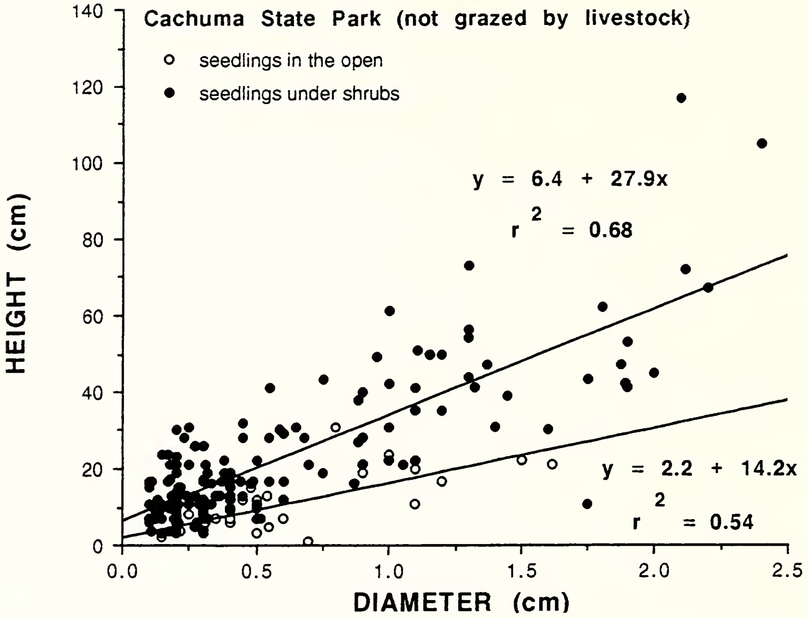

FIG. 1. Regression of *Quercus agrifolia* seedling diameter (2 cm above soil surface) and seedling height at Cachuma State Park.

expected on the basis of the relative frequency of this cover type (Table 1). At the Cachuma site the total density of oak seedlings was 5.2 ± 6.0 (SD) per 100 m^2, whereas at the Sedgwick site total seedling density was 1.5 ± 1.8 per 100 m^2. Seedling distributions were highly clumped, as indicated by variance to mean ratios of 49.4 and 7.0 for the Cachuma and Sedgwick Sites respectively (see Whittaker 1975). There was no difference in the percent of seedling foliage that was brown between seedlings under shrubs and seedlings in the open in either site, but browsing intensity was substantially higher in the open grassland and under adult *Q. agrifolia* canopies than under shrubs (Table 2). Regression equations between the height and diameter of seedlings (2 cm above the soil surface) showed that seedlings under shrubs tended to be taller than seedlings of similar diameters in the open grassland (Fig. 1), and in many cases the seedlings had overtopped the shrubs in which they grew.

Experimental seedling establishment. Although acorn germination occurs shortly after the first heavy rains, shoots are often not visible until the late winter. In March 1988, five months after planting, we located 117 seedlings under experimental shrubs (29% of the planted acorns) and 69 seedlings in the open near the shrubs (17% of the

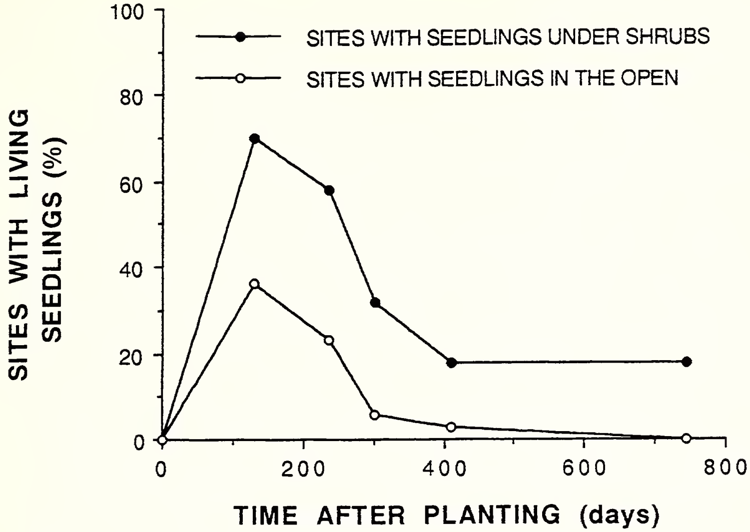

FIG. 2. Percentage of plots with surviving *Quercus agrifolia* seedlings under shrubs, and percentage of plots with surviving *Q. agrifolia* seedlings in the open in the Purisima Hills. Acorns were planted in November 1987.

planted acorns). Within two years all seedlings in the open had died or disappeared, whereas 18% of the plots had living seedlings under shrubs (Fig. 2) and 36/117 (31%) of the seedlings under shrubs were still alive (Fig. 3). Some resprouting of "dead" seedlings occurred during the experiment as can be noted in the slight increase in survivorship under shrubs between January 1989 and February 1990.

TABLE 2. CHARACTERISTICS OF NATURALLY ESTABLISHED *QUERCUS AGRIFOLIA* SEEDLINGS UNDER SHRUBS AND IN THE OPEN AT CACHUMA STATE PARK. Diameter was recorded 2 cm above the soil surface. x̄ ± SD = mean plus or minus one standard deviation. Shared letters indicate means that are not statistically different (Tukey HSD, $p < 0.05$).

Cover type	Diameter (cm) x̄ ± SD		Height (cm) x̄ ± SD		Browsed (%) x̄ ± SD		Brown (%) x̄ ± SD	
A. californica (n = 71)	0.59^{a}	0.51	21.3^{a}	14.2	7.7^{a}	14.0	14.1^{a}	20.9
S. leucophylla (n = 93)	0.51^{a}	0.50	20.4^{a}	19.4	8.7^{a}	14.7	12.6^{a}	15.3
Quercus agrifolia (n = 34)	0.46^{a}	0.25	8.7^{b}	5.2	52.9^{b}	32.2	15.6^{a}	18.0
Open grassland (n = 6)	0.90^{a}	0.61	13.8^{b}	8.2	50.0^{b}	35.9	20.0^{a}	12.6

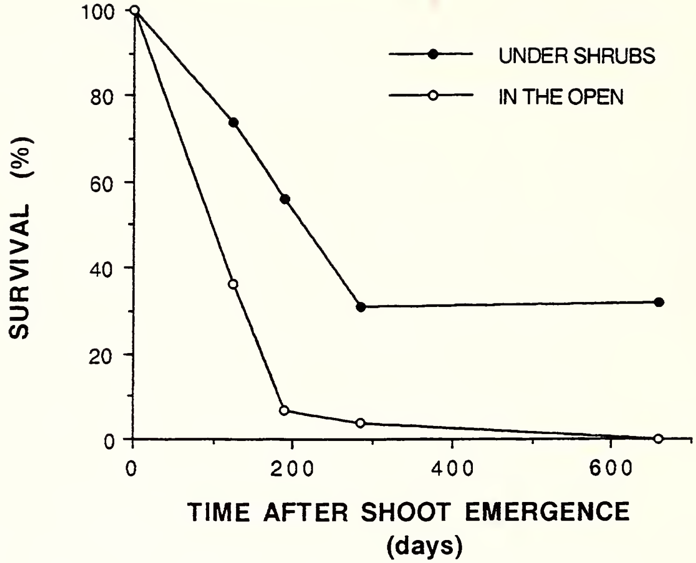

FIG. 3. Survivorship of *Quercus agrifolia* seedlings under shrubs and in the open in the Purisima Hills. Survival is presented as the percent of the original cohort remaining at each date. Shoots were first counted in March 1988.

During the first six months after emergence the rate of mortality was 64/69 (93%) of the seedlings in the open in comparison to 50/117 (43% under shrubs (Fig. 3). Of the 81 seedlings that died under shrubs, 14 (17%) dried in place and 67 (83%) disappeared (shoots were missing). Of the 69 seedlings that died in the open, 43 (62%) dried in place and 26 (38%) disappeared. Herbivore species may have differed under shrubs and in the open. In the open, most shoots disappeared with no evidence of soil disturbance and were probably eaten by deer, based on the abundance of scat and tracks. Shoot disappearance under shrubs was usually associated with conspicuous gopher tunneling.

Not all species of shrubs facilitated oak establishment. In plots with *E. ericoides* as the central shrub, 14/49 (29%) plots had living seedlings under shrub cover after two years. In comparison, 4/23 (17%) sites with *A. californica,* 1/19 (5%) sites with *M. aurantiacus* and 0/9 sites with *L. chamissonis* as central shrubs had living oak seedlings under the shrub canopies after two years. Total seedling survival was 24/56 (43%) under *E. ericoides,* 11/32 (34%) under *A. californica,* 1/22 (5%) sites under *M. aurantiacus,* and 0/7 under *L. chamissonis.* Oak seedling survival did not differ significantly between *E. ericoides* and *A. californica* whether analyzed by plot (χ^2

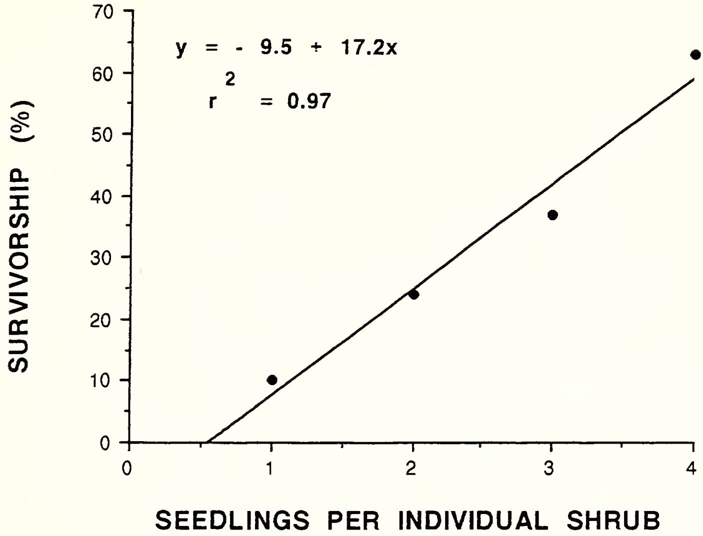

FIG. 4. Regression of the number of shoots emerging under individual shrubs in March 1988 and survivorship in these categories in February 1990 at Purisima Hills.

= 0.98, $p > 0.5$) or by total number of seedlings ($\chi^2 = 0.42$, $p > 0.4$).

Survivorship was inversely correlated with the number of seedlings that emerged under an individual shrub (Fig. 4). Of the seedlings that emerged in groups of four, 63% survived for the entire experiment, whereas only 10% of the seedlings that emerged alone under shrubs survived.

DISCUSSION

Our data strongly indicate that some shrubs may act as nurse plants for *Q. agrifolia* seedlings. Distributions of naturally established seedlings were highly associated with shrubs, and seedlings under shrubs were less browsed than seedlings in the open. Our field experiments showed that oak seedling survivorship under shrubs was significantly higher than survivorship in the open only 1 m from the shrubs. At the time of our first sampling more seedlings were present under shrubs than in the open, which suggests that either germination conditions were more favorable under shrubs, acorn predation was lower under shrubs, or that our first sampling date missed high rates of predation in the open soon after emergence.

The number of seedlings under adult *Q. agrifolia* canopies site was higher than expected on the basis of cover frequency at the Cachuma site and as high as expected at the Sedgwick site (Table

1). This suggests that *Quercus agrifolia* seedlings may recruit in the shade of conspecific adults, but long-term recruitment under adults would have to occur without protection from herbivory, and without eventual release from shade.

The heavy browsing of seedlings in the open at Cachuma and Sedgwick Ranch and evidence that environmental stress (i.e., dried, brown foliage on seedlings) did not differ between seedlings in the open and seedlings under shrubs (Table 2) suggests that protection from herbivory may be the primary nurse plant effect there. Mortality estimates of the experimental seedlings, however, indicate that although herbivory was reduced by nurse shrubs, protection from environmental stress by shrubs was even more important in reducing mortality: more shoots dried in place than disappeared. It is possible that the relative importance of mortality due to herbivory versus environmental stress varied between the year when we measured natural seedling distributions and the years when we conducted the field experiment. Or it may have differed between the sites where we measured natural patterns of seedling distribution and the site where we conducted the experiment. Additionally, we may have overestimated mortality due to environmental stress because of undetected root herbivory and subsequent drying of shoots.

The fact that survivorship was inversely correlated (Fig. 4) with the number of seedlings that emerged under an individual shrub suggests that microhabitat differences were more important than seedling densities for determining seedling survival, at least in the early stages of development. This also emphasizes the importance of analyzing seedling survival by plots as well as by total seedlings. Microsite differences were not obvious in the field, but they were likely to include slight changes in elevation, slope aspect, soil characteristics or gopher densities. Bullock (1981) also reported similar patterns of high seedling survival in aggregated conditions for *Prunus ilicifolia* Walpers.

Reasons for different rates of oak seedling survival under different shrub species were not obvious either. High seedling survival may have been associated with species-specific characteristics of the nurse plants such as the amount of shade provided, root interactions, susceptibility to herbivory, or differences in throughfall chemistry. Differences in "nurse plant" quality among species have also been reported in desert communities (McAuliffe 1988).

Rainfall in central California was below average during each of the years of this study and it is unclear how facilitative effects might change in years with normal or above average rainfall. Although in wet years survivorship of seedlings may increase in open, unsheltered habitats, the fact that any seedlings at all survived two years of drought emphasizes the significance of the facilitative effects of nurse shrubs.

Natural oak/shrub nurse plant associations may be initiated by bird dispersal of acorns. Scrub Jays (*Aphelocoma coerulescens*) are potential dispersers of acorns into shrub protected sites (Griffin 1976). These birds have been observed burying acorns under shrubs in other California oak woodlands (Griffin pers. obs.). Individuals of this same species cache over 6000 acorns per bird per autumn in oak woodlands in Florida and recover only one-third of the these acorns (DeGange et al. 1989). Bird caching may also explain the clumped spatial distribution of naturally established seedlings.

Although nurse plant interactions have not been reported in oak woodlands, they are common in other semiarid and arid environments. Phillips (1909) and Everett et al. (1986) reported that *Pinus monophylla* Torrey & Fremont (single-leaved pinyon) required nurse plants to survive in parts of the Great Basin Desert. Nurse plant effects have also been reported for desert cacti (Steenbergh and Lowe 1969; Yeaton 1978; Nobel 1980; Franco and Nobel 1989), desert agave (Franco and Nobel 1988), desert shrubs (McAuliffe 1988), and desert trees (McAuliffe 1986). In these studies the effects of nurse plants on understory microclimate and herbivory were considered to be primary factors that improved the survivorship of seedlings.

Young plants may eventually compete with and kill, or outlive their nurse plants (McAuliffe 1984, 1988). This also may occur in *Q. agrifolia*-shrub interactions. We found young oaks that had grown through the tops of their nurse shrubs, and older oaks that had established in the shrubland which did not have living shrubs under their canopies, although shrubs surrounded the canopies of these same trees. It is conceivable that *Q. agrifolia* may eventually create an environment too low in light, moisture or nutrients for the survival or recruitment of shrubs. Thus a cycle of nurse plant facilitation and eventual tree-shrub competition may affect overall patterns and boundaries of shrubland, grassland, and woodland. In other areas that are similar to our study sites, *Q. agrifolia* appears to be successional to shrubs when fires are infrequent (Wells 1962; Griffin 1978; Davis et al. 1988).

Although our data indicate that shrubs significantly improve the survivorship of *Q. agrifolia* seedlings, two important questions remain. First, what proportion of this effect can be attributed to microsite differences? It is possible that oak seedlings and shrubs survive better in the same microsite and that the nurse plant phenomenon is simply an artifact. Second, what facilitative mechanisms are operating that improve seedling survival (e.g., seed deposition patterns, germination cues, shade, or herbivore refuge).

In conclusion, we have presented evidence that native shrubs can function as nurse plants for young *Q. agrifolia,* including associations between naturally occurring oak seedlings and chaparral shrubs and higher survival of planted seedlings under shrubs at a site where natural vegetation was being restored. The role of native shrubs as nurse plants may be important for the improvement of regeneration of *Q. agrifolia* as well as other oak species.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

CALL FOR SLIDES OF CALIFORNIA'S THREATENED AND ENDANGERED PLANTS

The California Department of Fish and Game and the California Native Plant Society are publishing a book about California's endangered plants. The goal is to provide a readable and informative reference to help the general public understand the plight of endangered plants and their endangered habitats. The book will complete the two-volume set on California's threatened and endangered species. To date, the enthusiasm generated by "California's Wild Heritage, Threatened and Endangered Animals in the Golden State" has been tremendous and the public is interested in another volume. The companion volume on plants will be 150 pages and feature the over 200 California state-listed rare, threatened and endangered plants with excellent color photographs and illustrations. **We are searching for the best possible photographs of these species and their habitats.** A list of state-listed plants can be found in Smith and Berg's (1988) "CNPS's Inventory of Rare and Endangered Vascular Plants of California" or can be obtained from the Department of Fish and Game. Please send a list of color slides that you have of state-listed plants to: Diane Ikeda, Natural Heritage Division, California Department of Fish and Game, 1416 Ninth Street, Sacramento, CA 95814. For further inquiries, call (916) 327-5957.

SOME ASPECTS OF THE NITROGEN CYCLE IN A CALIFORNIAN STRAND ECOSYSTEM[1]

BOOKER HOLTON, JR., MICHAEL G. BARBOUR,
and SCOTT N. MARTENS
Department of Botany, University of California,
Davis, CA 95616-8537

ABSTRACT

Nitrogen inputs and storage pools were quantified for 20 months on a perennial grass dominated beach-foredune area at Pt. Reyes National Seashore, CA. Atmospheric input of ammonium and nitrate by bulk precipitation (rain + dry fallout) was 1.6 kg N ha^{-1} yr^{-1} and by summer fog condensation was 4.2 kg N ha^{-1} yr^{-1}. Non-symbiotic nitrogen fixation was not detected and fixation by a nodulated legume species is negligible relative to atmospheric inputs. The total ecosystem nitrogen pool was only 390 kg ha^{-1}, 78% of which was soil organic nitrogen, 18% was in vegetation, and 4% was inorganic soil nitrogen. Living vascular plant tissue contained 1.7% nitrogen—a value typical of crop plants on fertile soil—despite soil nitrogen content $<0.006\%$.

Dune sands are often deficient in many plant nutrients, particularly nitrogen. Nitrogen levels of 0.006–0.02% have been measured in dune sands dominated by the dune grass *Ammophila arenaria* (Willis et al. 1959; Hassouna and Wareing 1964; Barbour 1970), whereas typical soil nitrogen values for cultivated soils fall within the 0.06–0.5% range (Bremner 1965). Low soil nitrogen is intensified in dune sands by low organic matter accumulation and excessive leaching, but the losses may be offset by nitrogen inputs from sources unique to the beach-dune environment, such as wave-deposited organic debris, nitrogen fixation, sea spray, and fog (Wilson 1959; Wagner 1964; Berenyi 1966; Ranwell 1972; van der Valk 1974a, b). In general, quantitative data for such inputs along the California coast have not been published.

An objective of this study was to quantify some of the storage pools and transfer processes thought to be important in a conceptual, first approximation model of a nitrogen cycle in a northern California strand. The storage pools to be identified and quantified were: 1) nitrogen bound in the vegetation, 2) nitrogen bound in the organic soil fraction, and 3) nitrogen in the inorganic soil fraction. Nitrogen inputs to be identified and quantified were: 1) precipitation, 2) fog and sea spray, and 3) biological nitrogen fixation.

[1] Correspondence should be sent to Michael G. Barbour.

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STUDY AREA

A study site on the ocean-facing beach at Point Reyes National Seashore (38°N and 123°W) was selected with the cooperation of the National Park Service. The study extended from April 1975 through January 1977. The beach extends in a N–S direction 18 km between Point Reyes in the south and the Tomales Point headland at Kehoe Creek. The biota and physical environment of the area have been described by Elliott and Wehausen (1974), Grams et al. (1977), Holton and Johnson (1979), Barbour (1978), Holton (1980), and Barbour et al. (1982). Along this beach, stabilized dunes form narrow ridges parallel to the prevailing wind direction, extending 0.5–2.0 km inland onto coastal grassland. These dunes are perched on cliffs composed chiefly of Monterey Shale and are therefore cut off from invasion by beach sands except at points where the cliff is low or absent. Inland sand movement has, within the past 50 yr, been additionally slowed by a foredune formed by the sand-stilling qualities of the introduced European beachgrass, *Ammophila arenaria.*

The climate at Point Reyes falls under the Koppen class of Csb (Durrenberger 1974): a temperate, mediterranean climate with mild, rainy winters and cool, dry summers. During the summer months, the Pacific Subtropical High lies over the ocean to the west, and air descending from this high produces moderate northwest to west winds which cross the coast. Oceanic upwelling cools the air offshore, causing frequent fog during the night and early morning hours. During the fall, the westerlies shift southward and frontal passages produce showers and rain. Generally, about 90% of the 610 mm annual precipitation falls from November through April. Mean annual temperature is 11.4°C, and the range between the means of the hottest and coldest months is moderated by proximity to the ocean to only 3.7°C (U.S. Weather Bureau, Climatological Data, California Section, 1913–1974; Howell 1970).

A representative 0.5 km long portion of the beach was subjectively chosen for field work. The beach consisted of a lower portion devoid of vegetation, an upper portion which exhibited scattered cover by about seven species, and a foredune more densely covered by perennial grasses.

The lower beach extended approximately 40 m from mean tide line inland to the leading edge of vegetation. Elevation rise was approximately 2 m. This region included a berm and rows of detritus deposited at the most recent highest tide marks. The upper beach exhibited 10% cover by scattered clumps of *Atriplex leucophylla, Abronia latifolia, Ammophila arenaria, Cakile maritima, Leymus mollis* (Trin) Pilger, *Ambrosia chamissonis, Lathyrus littoralis,* and several less common species. This portion of the beach was approximately 25 m wide and included an additional 2 m increase in elevation above mean tidal datum. The foredune was densely covered with *Ammophila arenaria* and *Leymus mollis,* reaching 100% cover but averaging 60% cover. Foredune height averaged 3 m above the upper beach. Plant nomenclature follows Munz (1968) except for *Leymus mollis.*

METHODS

Nitrogen input in bulk precipitation and fog condensation. Bulk precipitation was collected biweekly from June 1975 through March 1976, in three devices similar to those described by Carlisle et al. (1966) and as modified by Reiners (1972). The collectors were placed at equal intervals along the 0.5 km of beach front, positioned at the top of the foredune but away from vegetation. These collectors consisted of 4 liter Nalgene bottles, fitted with Nalgene funnels (17 cm outside diameter). The funnels were plugged with nylon wool and covered with nylon mesh to keep out wind-blown debris. The bottles were painted with aluminum paint to retard algal growth, and a few crystals of phenol were placed into each bottle prior to each sampling period to inhibit bacterial growth. These bottles were buried to within 30 cm of the top of the funnels. Rainfall was measured with a portable rain gauge placed near the bottles.

Fog condensation was collected biweekly during the summer of 1975, using three collection screens similar to those of Azevedo and Morgan (1974). An aluminum screen (18 × 16 mm mesh) rolled into a tube, 76 cm long and 8 cm in diameter, was placed on top of each of the three funnel-bottle assemblies described earlier. This fog collection assembly extended about 1 m above ground. Summer fog along the coast condenses on plants during the cool morning hours, and dune grasses reach up to 1 m above the ground surface; therefore, collection screens 1 m high simulated this vegetation.

The three fog traps were placed near the bulk precipitation collectors on or near the top of the foredune, away from obstructing vegetation. Precautions against algal and bacterial growth were as earlier described.

All bulk precipitation and condensed fog samples were refrigerated (4°C) for later chemical analyses. Nitrate in all water samples was determined by the phenoldisulfonic acid method (Chapman and Pratt 1961). The water samples were pretreated with silver sulfate to remove interfering chloride ions. Ammonium in the water was determined with an Orion specific ion electrode. Salinity level was estimated from conductivity measurements using a Lectro Mhometer (Lab-Line, Inc.).

Nitrogen in soil. Soils were sampled at eight locations along the

0.5 km of beach front. Root-free samples were taken at the surface and at depths of 20 cm and 40 cm. At each of the eight locations, samples were taken at four topographic positions: tide-mark, seaward foredune face, foredune top, and landward foredune face. All samples were kept in sealed plastic bags, stored at 4°C, and chemically analyzed within 2 wk. Nitrate and ammonium were determined as for water samples and organic nitrogen was determined by macro-Kjeldahl analysis. Soils were sampled in June 1975 and September 1976.

Nitrogen in plant tissue. Standing above-ground biomass was sampled in September 1976 from a series of clippings within quadrats of varying sizes. Since the two grasses *Leymus mollis* and *Ammophila arenaria* dominate the dune plant cover, sampling was limited to only these species.

Optimum sampling area for each species was determined using the nested quadrat method of Wiegert (1962). This method enables an optimal choice of quadrat size to be made, based on cost in time and labor and on sampling precision. On the basis of minimal cost and reduced within-plot sample variance, a quadrat size of 0.15 m^2 was selected for *Ammophila* stands and one of 1.0 m^2 for *Leymus*-dominated stands. (*Leymus* stands are much less dense than *Ammophila* stands, 30–60% cover, as opposed to 80–100% cover.)

In the field, a grid of contiguous plots was laid out within subjectively chosen foredune stands of each grass type. The stands were selected as representative of foredune vegetation within the 0.5 km length of beach. The size of the *Ammophila* grid was 6 × 3 m and that for the *Leymus* grid was 6 × 6 m. Each grid was replicated three times. The size of the cells composing each grid was the same as the respective quadrat sizes mentioned above.

Within each grid, 12 randomly selected quadrats were clipped to ground level. Clippings were separated into living and dead components, oven-dried at 70°C for 72 hr, and weighed. Samples used for chemical analysis were milled in a Wiley mill to 40-mesh and stored at room temperature in screw-capped jars. Nitrogen was determined by macro-Kjeldahl analysis.

Other plant species of lesser cover were not sampled for biomass estimation, but above-ground tissue was collected in the upper beach at several times through the late summer and winter of 1976 and analyzed for nitrogen.

Below-ground biomass was estimated from 12 quadrats subjectively placed on representative foredune vegetation along the 0.5 km of beach. Six 1.0 m^2 quadrats were placed in *Leymus*-dominated stands, and six 0.15 m^2 quadrats were placed in *Ammophila*-dominated stands. Cover was 30–100%, as for above-ground samples. Sand was excavated beneath each quadrat to a depth of 40 cm and later sieved to separate root material from sand. Roots were oven-dried at 70°C for 72 hr and weighed. No nitrogen analyses of root tissue were made.

Estimates of nitrogen-fixation in the soil. Selected dune plants were assayed for the ability to fix nitrogen by the acetylene reduction technique (Stewart et al. 1967; Hardy et al. 1968; Waugham 1971, 1972). This method measures the reduction of acetylene to ethylene by the nitrogenase enzyme system common to all nitrogen-fixing organisms.

Rhizosphere soil, roots, and (where present) nodules were collected randomly along the 0.5 km length of upper beach at various soil depths and at several times between August 1976 and January 1977. Soil and roots of the dominant grasses and excised nodules of legumes were incubated in a 10% acetylene–air mixture in rubber-stoppered 25 ml serum tubes. The same material incubated in air alone served as controls.

Gas samples were subsequently withdrawn and subjected to analysis with a gas chromatograph (Perkin-Elmer model 3920B) equipped with a hydrogen flame ionization detector. Acetylene and ethylene were separated on a column (0.3 × 122 cm) filled with Poropak-R (100–200 mesh). Nitrogen gas served as a carrier at a flow rate of 30 ml $\min^{-1}$ and a temperature of 45°C.

RESULTS AND DISCUSSION

Nitrogen in bulk precipitation and fog condensation. The seasonal precipitation total of 254 mm (Fig. 1) was considerably below the normal yearly average of 610 mm, because 1975–1976 was the first of a 2-yr drought period. Rainfall measurements made with portable rain gauges correlated well with volume of precipitation in the collection bottles ($r = 0.99$).

Ammonium-N and nitrate-N concentrations in bulk precipitation varied with collection period (Fig. 2). The concentration of ammonium-N ranged from trace amounts to about 7 ppm, averaging 1.10 ppm. Nitrate-N concentrations were extremely low, ranging from trace amounts to 1.0 ppm, with an average concentration of 0.15 ppm.

Ammonium-N concentration was positively correlated with the salinity of the precipitation, a relationship which may indicate an oceanic source of this form of nitrogen. Such a relationship did not exist for nitrate. The concentration of both salt and ammonium-N decreased with increased rainfall above a threshold value of 0.2 liter of collected rainwater, which is equivalent to 7 mm of precipitation. Thus, during periods of little or no precipitation, dry fallout of dust and particulate material from sea spray would be relatively more concentrated in salts and ammonium.

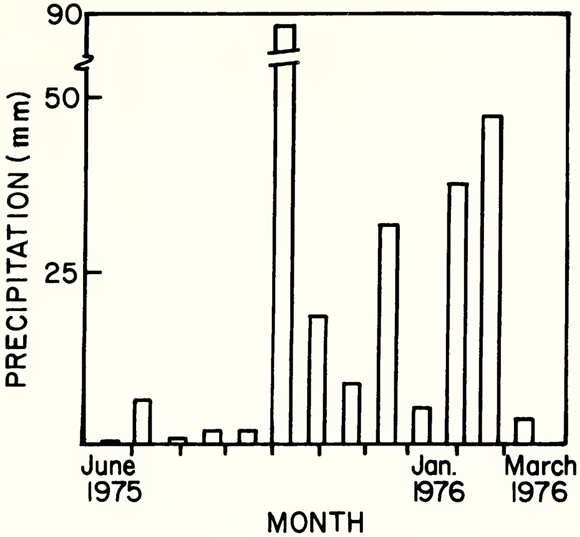

FIG. 1. Bulk precipitation, collected biweekly, June 1975–March 1976 at Pt. Reyes National Seashore, CA.

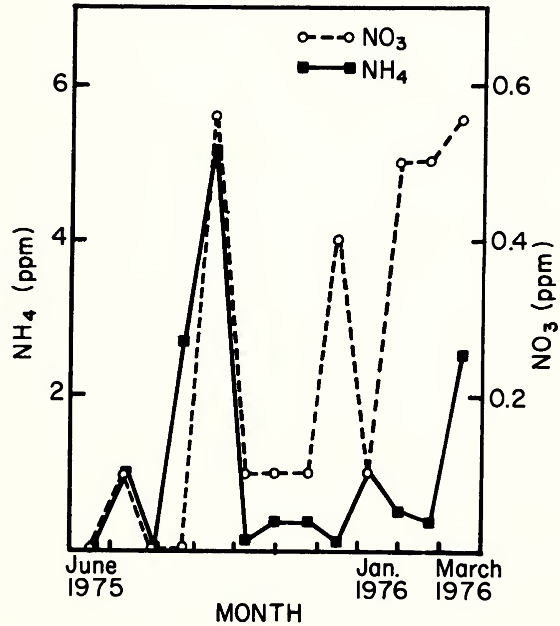

FIG. 2. Nitrate-N and ammonium-N content of bulk precipitation samples collected between June 1975 and March 1976 at Pt. Reyes National Seashore, CA.

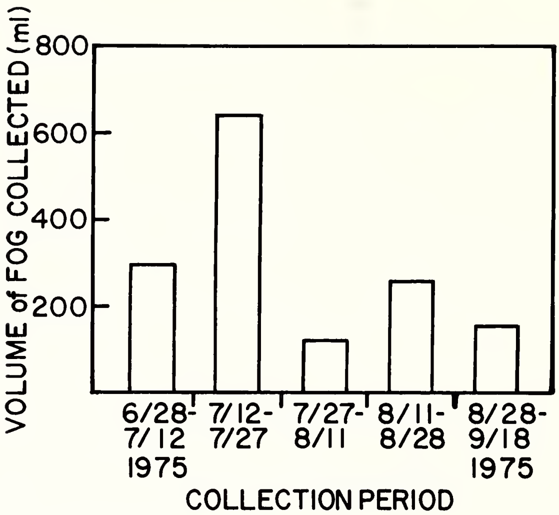

FIG. 3. Fog condensation collected biweekly, June–September 1975 at Pt. Reyes National Seashore, CA.

The annual nitrogen input in bulk precipitation can be calculated from data on precipitation volume per unit collection surface area, and from the concentrations of both ammonium-N and nitrate-N per collection period, summed over the rainfall season. This annual input is estimated to be 1.6 kg ha^{-1}. Of this total, 0.9 kg is ammonium-N, and 0.7 kg is nitrate-N.

The annual nitrate-N (0.7 kg ha^{-1}) and ammonium-N (0.9 kg ha^{-1}) inputs in bulk precipitation measured at Point Reyes compare well with similar measurements at other California sites. At Berkeley, California, about 60 km to the southeast, McColl and Bush (1978) estimated the annual inputs of nitrate-N and ammonium-N; during the precipitation year 1974–1975 they were 1.02 and <0.98 kg ha^{-1}, respectively. For eight northern California sites, McColl et al. (1982) measured an average of 2.5 kg N ha^{-1} in wet and dry ionic fallout during the wet season (November 1978–March 1979). Schlesinger and Hasey (1980) measured 1.0 kg N ha^{-1} yr^{-1} deposition in bulk precipitation at a site 10 km from the coast in the Santa Ynez Mountains of southern California during 1977–1978. A mean of 2.0 kg N ha^{-1} yr^{-1} deposition, mostly in dry fallout, was measured by Schlesinger et al. (1982) in 1978–1980 in the same mountains. Ellis et al. (1983) measured 1.5 kg N ha^{-1} yr^{-1} in bulk precipitation at a site 75 km inland in San Diego County. These N input values are relatively low compared to measurements in eastern regions of the U.S. (Boring et al. 1988), although high N deposition

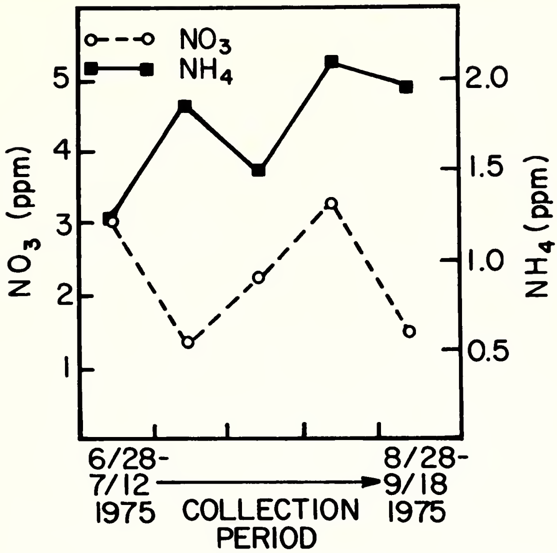

FIG. 4. Nitrate-N and ammonium-N content of fog condensation collected June–September 1975 at Pt. Reyes National Seashore, CA.

(8.2 kg ha^{-1} yr^{-1}) has been reported for the urbanized Los Angeles basin of California (Riggan et al. 1985).

Judging from data collected by Barbour et al. (1973) for nearby Bodega Head, about 60% of all foggy days in a typical year occur in our sampled period between June and September (Fig. 3). Salt concentration of condensed fog decreased with collection volume. The concentration of ammonium-N and nitrate-N varied with collection period (Fig. 4). Ammonium-N ranged from 1.2 to 2.5 ppm, averaging 1.72 ppm. Nitrate-N ranged from 1.0 to 6.0 ppm, with an average of 2.45 ppm. Nitrogen input by summer fog condensation can be calculated from data on screen surface area, condensation volume, and concentrations of ammonium-N and nitrate-N per collection period. This nitrogen contribution was approximately 2.5 kg ha^{-1} during the sampling period, with 1.4 kg from nitrate and 1.1 kg from ammonium sources.

Extrapolation from collection screens to a ground-level surface area or to a vegetation canopy may overestimate total nitrogen input. A rigid, vertical screen extending 1 m above the ground may be a more efficient sea spray or fog collector than a horizontal surface near the ground or a leaf surface in a vegetation canopy. Barbour (1978) found this to be the case for salt spray deposition on the beach at Point Reyes.

Fog condensation is likely to be a significant N source for the

TABLE 1. TOTAL NITROGEN, NITRATE, AND AMMONIUM IN SAND COLLECTED AT SEVERAL DEPTHS IN THE FOREDUNE AT PT. REYES NATIONAL SEASHORE, CA. Values expressed as mean (±SE). n = 24 for total nitrogen, 17 for nitrate and ammonium. Soil collected in summers of 1975 and 1976.

Soil depth (cm)	% nitrogen	ppm NO_3^--N	ppm NH_4^+-N
Surface	0.003 (0.001)	0	0
20	0.004 (0.001)	1.88 (0.37)	1.52 (0.10)
40	0.006 (0.001)	0.65 (0.11)	0.74 (0.18)

coastal strand ecosystem. Azevedo and Morgan (1974) showed the importance of fog drip in two coastal forests of northern California. Fog water collected in these forests averaged 1.7 and 4.1 ppm ammonium-N, which is similar to the 1.7 ppm ammonium-N we measured at Point Reyes. Schlesinger and Hasey (1980) found significant fog drip in collectors mounted with artificial foliage. They attributed the increased nitrogen deposition in these collectors to more efficient interception of dry aerosols. Jacob et al. (1985) measured 0.6–4.6 ppm ammonium-N and 0.08–7.4 ppm nitrate-N in fogwater collected in August 1982 at Pt. Reyes. When an offshore wind prevailed, fogwater had less sea salt and more soil dust and automobile exhaust than when onshore winds prevailed.

Nitrogen in soil. No significant differences could be detected in soil nitrogen between the seaward foredune face, landward face, and the top. Values were very low, 0.003–0.006%, depending on depth (Table 1). In comparison, higher soil nitrogen values were associated with the tide-mark (0.006–0.01%) and the stabilized dune (0.04–0.2%), again depending on depth. The available inorganic nitrogen pool in the foredune was low, <2 ppm of nitrate-N or ammonium-N (Table 1).

Using an average bulk density = 1.51 g cm^{-3}, organic N percentage by weight = 0.005%, average concentrations of nitrate-N = 1.3 ppm, and ammonium-N = 1.2 ppm, we estimated the organically bound soil nitrogen pool to be approximately 302 kg ha^{-1} to a depth of 40 cm, and the available soil nitrogen pool, to the same depth, to be 15 kg ha^{-1}.

TABLE 2. MEAN (±SE) ABOVE-GROUND BIOMASS (G M^{-2}) IN REPRESENTATIVE FOREDUNE PATCHES OF *LEYMUS* AND *AMMOPHILA* AT PT. REYES NATIONAL SEASHORE, CA. Material collected in September, 1976. n = 36.

Species	Living	Dead	Total
Leymus mollis	129.4 (23.7)	82.6 (12.0)	211.9 (33.5)
Ammophila arenaria	445.7 (58.0)	188.4 (23.7)	632.1 (76.3)

TABLE 3. NITROGEN IN ABOVE-GROUND LIVING TISSUE OF UPPER BEACH SPECIES COLLECTED IN FALL AND WINTER, 1976 AT PT. REYES NATIONAL SEASHORE, CA.

Species	n (%)
Abronia latifolia	1.52
Ammophila arenaria	1.40
Atriplex leucophylla	2.00
Cakile maritima	2.74
Leymus mollis	2.80
Ambrosia chamissonis	2.54

Nitrogen in plant tissue. Californian upper beaches and foredunes have a very low standing crop biomass, estimated to be 20–400 g m^{-2}, corresponding to that of desert or arid steppe communities (Barbour and Robichaux 1976). The estimated above-ground biomass from our field clippings of *Leymus mollis* and *Ammophila arenaria* falls near the upper part of this range (Table 2).

The average tissue nitrogen concentration of the most common beach and dune plant species at Point Reyes is 1.5–3.0% (Table 3). Dead matter averaged 0.6% N. Stout (1961) and Epstein (1965) considered a tissue nitrogen concentration of 1.5% to be adequate for most plant growth, and to be typical of N content of mesic crop plants. Thus, these strand species have a relatively high nitrogen content, despite a soil substrate which is very low in nitrogen.

Assuming an average tissue nitrogen concentration of 1.7% in the living material and 0.6% in the dead material, bound nitrogen in the above-ground living biomass of the foredune is estimated to be 49.4 kg ha^{-1}, and that bound in the dead material to be 8.2 kg ha^{-1}.

Belowground, our limited number of quadrat excavations to a depth of 40 cm indicated that 70–190 g m^{-2} of live roots, exclusive of the many fine roots, could be expected. Although we did not measure nitrogen content in our root samples, Pavlik (1983a, b) provides data for these same species from Point Reyes. Root nitrogen concentration of greenhouse-grown plants was 0.6%; therefore, the estimated below-ground N content of roots in the foredune is 4.2–11.4 kg ha^{-1}.

The well-developed rhizome systems of *Ammophila* and *Leymus* also contribute significantly to the below-ground nitrogen pool. We did not measure rhizome mass or N content but pertinent data on greenhouse-grown plants are available from Pavlik (1983b). Rhizome nitrogen concentration was 1.0% and rhizome biomass was 27–30% of root biomass. From these data and our measured root biomass data we estimate the minimum below-ground nitrogen pool in rhizomes to be 2.0–5.4 kg ha^{-1}.

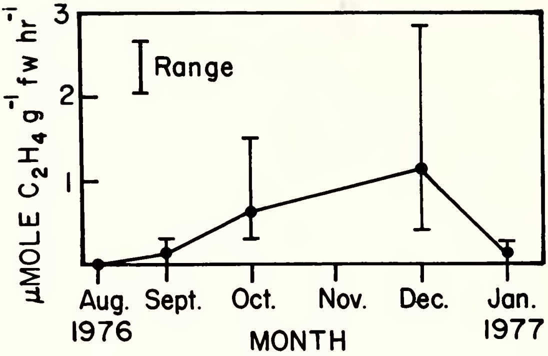

FIG. 5. Seasonal variation in ethylene production from acetylene by nodules of *Lathyrus littoralis* on the upper beach at Pt. Reyes National Seashore, CA.

Nitrogen fixation. Sand cores with associated grass root material, which were routinely assayed using the acetylene reduction technique, failed to show detectable levels of nitrogen fixation under ambient field conditions. Attempts to isolate nitrogen fixing bacteria on artificial N-free media inoculated with dune sand also were negative. These results contrast with those of others (Abdel Wahab 1975; Abdel Wahab and Wareing 1980; Hassouna and Wareing 1964) who have found significant rhizosphere nitrogen fixation in *Ammophila arenaria* in Welsh dunes.

Three leguminous species were found to be nodulated and to have the ability to reduce acetylene to ethylene. Two of these species, *Lupinus arboreus* and *L. chamissonis,* are dominants on the more stabilized, perched dunes, and showed rates of 0.05–0.6 µmol ethylene g^{-1} fresh weight hr^{-1}. Nodules of both species were deep (1–1.5 m) and ranged from 0.1 g to 0.55 g fresh weight.

Lathyrus littoralis is found on the upper beach in a few restricted localities and it is not a dominant. *Lathyrus* had the highest nitrogenase activity of the three, a range of 0.01–2.83 µmol ethylene g^{-1} fresh weight hr^{-1} (Fig. 5). The lower late summer rates were associated with dark-colored, fibrous nodules; higher winter rates were associated with light-colored, fleshy nodules. Most *Lathyrus* nodules were at 30–70 cm depth, and nodule size was 6–60 mg fresh weight.

As we did not estimate nodule biomass per unit of surface area, an extrapolation of our nitrogen-fixation rates to an areal basis is not possible. Considering the low cover by *Lathyrus,* however, the contribution of nitrogen fixation is negligible relative to the atmospheric inputs of nitrogen measured for the strand ecosystem.

Synthesis. Despite the obvious need for additional information to describe the complete nitrogen cycle, a summary of the major pools

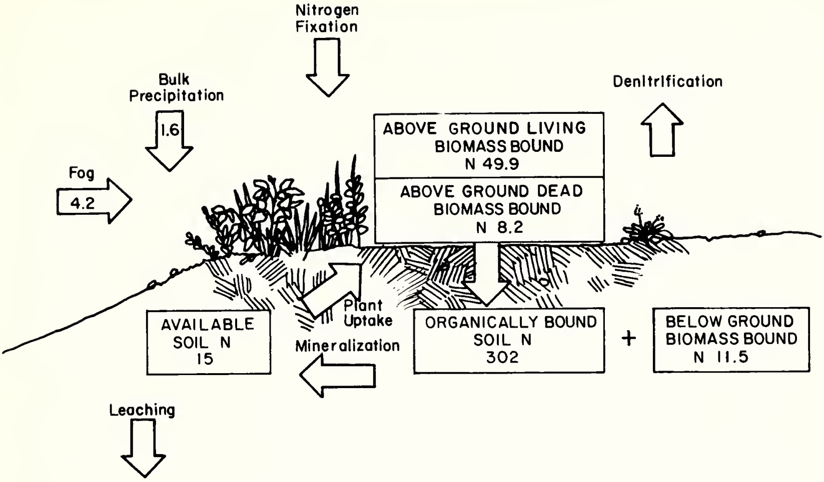

FIG. 6. Annual nitrogen inputs (kg ha^{-1} yr^{-1}) and pools (kg ha^{-1}) examined in this paper.

examined in this paper appears in Figure 6. The total ecosystem nitrogen pool of ~390 kg ha^{-1} is quite low; approximately 78% is soil organic nitrogen, about 4% exists as available soil inorganic nitrogen, and 18% is bound in the biomass.

Nitrogen input in bulk precipitation was 1.6 kg N ha^{-1} yr^{-1} and is similar to other bulk precipitation measurements made in California (McColl and Bush 1978; Schlesinger and Hasey 1980; Schlesinger et al. 1982; Ellis et al. 1983). However, bulk precipitation measurements may underestimate total atmospheric nitrogen deposition by 30–40% because they do not include all forms of wet and dry deposition (Boring et al. 1988).

Fog condensation provided a larger nitrogen input, 4.2 kg N ha^{-1} yr^{-1}, than bulk precipitation. It is difficult to assess the accuracy of this value because we don't know how comparable fog condensation on screens is, to that on natural vegetation. Certainly the same physical processes operate in both cases and fog or cloud condensation has been shown to be an important source of nutrients in other systems (Schlesinger and Hasey 1980; Lovett et al. 1982).

Our preliminary survey of nitrogen fixation, determined by acetylene reduction, did not detect microbial and algal fixation of nitrogen in the free-living or associative forms within the Point Reyes dunes. The nodulated legumes *Lupinus arboreus, L. chamissonis,* and *Lathyrus littoralis* are only locally important on stabilized dunes and on the upper beach and so account for little nitrogen input. In other dune sand systems non-symbiotic (Hassouna and Wareing

1964; Abdel Wahab and Wareing 1980) and symbiotic nitrogen fixation (Gadgil 1971; Sprent 1973) have been shown to provide important nitrogen inputs.

Other possible sources of nitrogen for the coastal strand system include seaweed wrack and seafoam. Wave-deposited and wind-transported seaweed could be an important nitrogen source at the tidemark and upper beach. Holton (1980) showed that the seaweeds *Egregia* and *Macrocystis* decomposed more rapidly and released more nitrogen than the marine angiosperm *Phyllospadix.* Seafoam, a largely algal product with a nitrogen concentration close to that of seaweed, is wind transported and intercepted by vegetation on the foredune and could also be a nitrogen source for the strand ecosystem (S. Wing, personal communication).

The available soil nitrogen pool is small despite measured annual atmospheric inputs which are nearly 40% of its size. The largest output from this pool is probably from leaching. Inorganic nitrogen is easily leached from the coarse sands due to their lack of clay or organic matter for cation retention. Nitrogen loss by denitrification is likely to be low in well-drained sands with low nitrate and organic matter concentrations (Focht and Verstraete 1977).

Development of an extensive root architecture may be one means whereby dune plants are able to maintain adequate tissue nitrogen (1.4–2.8%) despite the low nitrogen status of these dunes. The root length densities under *Ammophila* and *Leymus* at Point Reyes have been reported to be 15–40 m root length per liter of soil (Holton 1980). These densities compare with those reported for more dense stands of grasses (66–548 m liter^{-1}) and sugar-cane (18 m liter^{-1}) reported by Dittmer (1938) and Evans (1938).

ACKNOWLEDGMENTS

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VEGETATION OF TWO SOUTHEASTERN ARIZONA DESERT MARSHES

ANNE FERNALD CROSS
Department of Botany, Duke University,
Durham, NC 27706

ABSTRACT

Detrended Canonical Correspondence Analysis (DCCA) was used to identify and classify groups of vascular plants in two desert marshes, the Babocomari Ciénega and the Canelo Hills Ciénega, in southeastern Arizona. Species composition and the effect of several environmental factors on species distributions were identified by direct gradient analysis using DCCA. The species distributions were best correlated with environmental factors related to the moisture regime (Babocomari Ciénega) and to the amount of canopy cover (Canelo Hills Ciénega). They were least correlated with disturbance and bare ground at both the Babocomari Ciénega and the Canelo Hills Ciénega. Based on the selected environmental factors, three main species groups were identified at the Babocomari Ciénega and at the Canelo Hills Ciénega. *Rorippa nasturtium-aquaticum* and *Berula erecta* dominate the stream area where water is deepest and flowing and canopy cover is the greatest. *Eleocharis macrostachya* and *Muhlenbergia asperifolia* dominate the ciénega area where water is shallow and standing. *Muhlenbergia rigens* and *Ambrosia trifida* dominate the periphery where there is no standing water and soils are dry. Differences in species composition within these areas between ciénegas may reflect differences due to land use history.

RESUMEN

Para identificar y clasificar grupos de plantas vasculares en dos ciénegas desérticas del sureste del Arizona, la Babocomari Ciénega y la Canelo Hills Ciénega, se usó la técnica de ordenación "Detrended Canonical Correspondence Analysis" (DCCA). La composición florística y el efecto de varios factores ambientales en la distribución de las especies se identificaron con un análisis directo de gradiente usando DCCA. La distribución de las especies estuvo mejor correlacionada con factores ambientales asociados con el régimen de humedad (Babocomari Ciénega) y con la coberatura vegetal (Canelo Hills Ciénega); pero menos correlacionada con las perturbaciones y la proporción de suelo desnudo. Con base en los factores ambientales selectos, se identificaron tres grupos principales de especies en la Babocomari Ciénega y la Canelo Hills Ciénega. *Rorippa nasturtium-aquaticum* y *Berula erecta* dominaron en la zona de corriente, donde el agua fluye y es más profunda. *Eleocharis macrostachya* y *Muhlenbergia asperifolia* dominaron en la zona ciénega, donde el agua es somera y quieta. *Muhlenbergia rigens* y *Ambrosia trifida* dominaron en la periferia donde no hay agua y el suelo está seco. Las diferencias en composición florística de las ciénegas dentro de estas zonas puede reflejar diferencias históricas en el uso de la tierra.

Ciénegas are unique freshwater wetlands found in semiarid grasslands of the southwestern United States and northern Mexico. Located along streams or near freshwater springs, wetland conditions are maintained by a permanent water supply, and soil chemistry is

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controlled by permanently saturated conditions (Hendrickson and Minckley 1985). Although riparian woody species, such as *Populus fremontii* and *Salix gooddingii,* identify the location of ciénegas in grasslands, much of the surface area in ciénegas is comprised of herbaceous and graminoid species.

This vegetation often appears to be zoned in linear bands parallel to the stream channel. Several descriptions of ciénega vegetation suggest that the local moisture conditions may influence species composition and distribution, but plant species composition may also be determined by other biotic and abiotic factors (Hendrickson and Minckley 1985; Marrs-Smith 1983; Yatskievych and Jenkins 1981). In addition, vegetation patterns may also reflect the disturbance and land use history of the ciénega.

Most ciénegas have been used by humans for at least the last 500 years (Bahre 1977). Beginning with the Native Americans, ciénegas have been used for agriculture since the 1400's (Di Peso 1953) and for cattle ranching since the arrival of the Spanish colonists in the 1500's (Bahre 1977). Today, of 15 extant ciénegas in southwestern New Mexico and southeastern Arizona, only five are protected from cattle grazing and farming (Hendrickson and Minckley 1985). Natural disturbances that affect the local hydrological regime, such as periodic droughts or floods (Sellers et al. 1985) and prolonged freezing temperatures (Bowers 1981) may also influence species distribution patterns. Most ciénegas are located near stream headwaters, and dams that are built downstream to check erosion do little to control flooding (Hendrickson and Minckley 1985).

The purpose of my research was to describe the plant species composition of two ciénegas with differing land use histories, and to relate the species distribution patterns to several environmental factors. Understanding ciénega vegetation is essential for the successful management and preservation of this rare ecosystem.

Study Site and Methods

Site location. Both the Babocomari Ciénega and the Canelo Hills Ciénega are located in the high desert grasslands of the San Pedro River Basin, Arizona. The ciénegas share a semiarid climate with a bimodal pattern of precipitation averaging 41 cm annually, falling as winter and summer rain. Temperatures recorded within two kilometers of each site show that the highest average temperature (24°C) occurs in June and the lowest average temperature (6°C) occurs in December (Sellers et al. 1985).

Five desert mountain ranges encircle the basin: Santa Rita Mountains, Canelo Hills, Huachuca Mountains, Patagonia Mountains, and Mustang Mountains (Vice 1974; Feth 1947). Runoff from these mountains, in addition to precipitation, provides water to the ciénegas.

At an elevation of 1365 m, the Babocomari Ciénega is part of the San Ignacio del Babocomari Land Grant in Santa Cruz and Cochise Counties, Arizona. The Babocomari Ciénega covers 62.5 ha of the 13,600-ha Babocomari Ranch in the Babocomari River basin at the base of the Mustang Mountains. Many small stream channels dissect the basin and converge into one stream channel near a dam built in the 1930's.

The Canelo Hills Ciénega, formerly called Knipe Ciénega, is located at 1485 m on O'Donnell Creek, a tributary of the Babocomari River. It is included in the Nature Conservancy Canelo Hills Ciénega Preserve in Santa Cruz County, Arizona. The Canelo Hills Ciénega covers 12.5 ha on the preserve and approximately 25 ha of adjacent property. The water regime differs slightly from that at the Babocomari Ciénega, as it also includes inputs from two nearby springs. There are fewer stream channels than at the Babocomari Ciénega, and these converge at a dam built in 1969.

Except for the last 20 years, the land use history has been similar at the Babocomari Ciénega and the Canelo Hills Ciénega. Both have been used either for farming or ranching by Native Americans, Spanish colonists and missionaries, army troops, homesteaders, and cattle ranchers. Both experienced drought in the 1890's and in the 1950's and prolonged freezing temperatures in 1975. Flood records are unavailable for the Babocomari Ciénega, but the Nature Conservancy records indicate that the last major flood at the Canelo Hills Ciénega occurred in 1969 before the dam was installed. Aside from major flood events, there is undoubtedly annual variation and fluctuation in the water level depending on precipitation and runoff input. The Babocomari Ciénega has been an operating cattle ranch since the 1930's and remains so, whereas the Canelo Hills Ciénega was grazed prior to its purchase by the Nature Conservancy in 1969. Preserve managers have burned the Canelo Hills Ciénega several times since 1969 in order to simulate a natural fire cycle.

Vegetation sampling. In June and July 1985, the vegetation at the Babocomari Ciénega was identified and recorded along 16, 350-m north–south, line transects (Greig-Smith 1983) 100 m apart. Supplementing these preliminary measurements with aerial photographs (taken in 1985) and visual reconnaissance, four main vegetation zones were observed along a moisture gradient and were classified as: (1) grassland, (2) high ciénega, (3) low ciénega, and (4) stream.

The vegetation was sampled at the Babocomari Ciénega and the Canelo Hills Ciénega using this classification in June and July 1986. By randomly sampling the vegetation within these areas, a large data set that was representative of ciénega vegetation was obtained. In each ciénega, 79 quadrats were sampled: 20 quadrats were placed randomly in each of the high ciénega, low ciénega, and grassland areas and 19 quadrats were randomly placed in the stream area. Species abundance was estimated within 1-m^2 quadrat frames that were divided into 100 10-cm^2 squares. The number of squares in which a species occurred was used as an estimate of abundance. Voucher specimens were verified by Dr. William A. Weber and were deposited at the University of Colorado Herbarium (COLO). A complete list of the 135 species collected is in Fernald (1987). Nomenclature follows Lehr (1978) with verifications by Dr. Weber.

Environment sampling. In 1986, ranked values for 12 environmental factors thought to influence vegetation patterns were recorded for each 1-m^2 quadrat in both ciénegas. The 12 factors were: (1) disturbance, (2) stability, (3) site moisture, (4) soil moisture, (5) water depth, (6) water flow velocity, (7) water clarity, (8) slope, (9) canopy cover, (10) percentage bare ground, (11) percentage litter cover, (12) percentage grass and herbaceous plant cover (for a complete explanation of descriptors see Fernald 1987). Elevation was determined from United States Geological Survey 7.5″ topographical maps for the O'Donnell Canyon and Mustang Mountains quadrangles.

Data analysis. Analyses of 1985 transect data considered only species cover at the Babocomari Ciénega. Analyses of 1986 data used only species that occurred in 10 or more quadrats at the Babocomari Ciénega and the Canelo Hills Ciénega. Detrended Canonical Correspondence (DCCA) or direct gradient analysis (ter Braak 1987; Jongman et al. 1987) was used to ordinate vegetation with the environmental variables. Analysis with Detrended Correspondence Analysis (DCA), an indirect gradient analysis, was also performed to examine species composition without the constraints imposed by the environmental factors. DCA results were similar to DCCA and will not be discussed here. In addition, when environmental factors have been measured, DCCA is thought to be more effective than the traditional indirect method of DCA (ter Braak and Prentice 1988). The DCCA analyses were performed with the Canonical Community Ordination program (CANOCO) (ter Braak 1987). Detrending-by-polynomials was used, because it is considered to be a stable means of reducing polynomial distortion of the first DCCA axis onto subsequent axes (ter Braak 1987). However, due to the lack of an arch effect (Gauch 1982) with respect to the second DCCA axis no detrending was performed on this axis for either ciénega.

RESULTS

Generally, the vegetation at the Babocomari Ciénega and at the Canelo Hills Ciénega was distributed along an elevation-moisture gradient. In both ciénegas, the stream channel could be readily identified by the tall-statured cottonwood and willow riparian species. Immediately adjacent to the stream channel was an expansive, flat ciénega area that was dominated by various rush and sedge species. A mix of invasive herbaceous species was gradually replaced by native grass species in the drier areas above the ciénega. The mesic vegetation of the ciénegas was easily distinguished from the surrounding oak-savanna vegetation that defines the semiarid grasslands of southeastern Arizona.

The transect data showed that two species, *Eleocharis macrostachya* and *Carex praegracilis,* covered about 29% at the Babocomari Ciénega. Other monocotyledonous species, primarily grasses, sedges, and rushes, covered 57%, and herbaceous dicotyledonous species covered 14%. These data were not collected at the Canelo Hills Ciénega.

Of the 30 species analyzed, 27 occurred at the Babocomari Ciénega and 28 occurred at the Canelo Hills Ciénega. *Anemopsis californica* and *Muhlenbergia asperifolia* were restricted to the Babocomari Ciénega and *Scirpus americana* and *Apocynum suksdorfii* were restricted to the Canelo Hills Ciénega, but all other species used in the analyses were found in both locations.

DCCA results showed that for the Babocomari Ciénega primary environmental factors that may have explained the first axis (eigenvalue [e] = 0.72) and the second axis (e = 0.42) were related to the moisture gradient. Canonical correlation coefficients (c) for site moisture and soil moisture with the first axis were 0.9140 and 0.8876 respectively. The first axis separated species in group I (dry, peripheral sites) from species in groups II and III (wet sites, stream and ciénega) (Fig. 1). Although these variables appeared to be related, the inflation factor, a descriptor that estimates the relationship between the environmental variables, was low (<50 [ter Braak 1987]), and both of these variables were used to interpret the first axis. The second axis was explained primarily by water clarity (c = 0.4040), which roughly estimated the amount of turbidity. This axis separated species in group II (high turbidity) from groups I and III (low or no turbidity) (Fig. 1). The third axis (e = 0.24) and fourth axis (e = 0.19) were not strong enough to explain much of the variation, but are illustrated in Fernald (1987).

DCCA results showed that for the Canelo Hills Ciénega the primary environmental factors that were used to explain the first axis (e = 0.67) were percentage slope and percentage litter cover and for the second axis (e = 0.57) percentage canopy cover. Canonical correlation coefficients for the first axis with slope and litter were 0.4869 and 0.6213 respectively. The first axis separated species where the topography was essentially level in the ciénega (group I) and the stream (group II) from grass species along the slope of the periphery (group III) (Fig. 2). The second axis may be explained primarily by

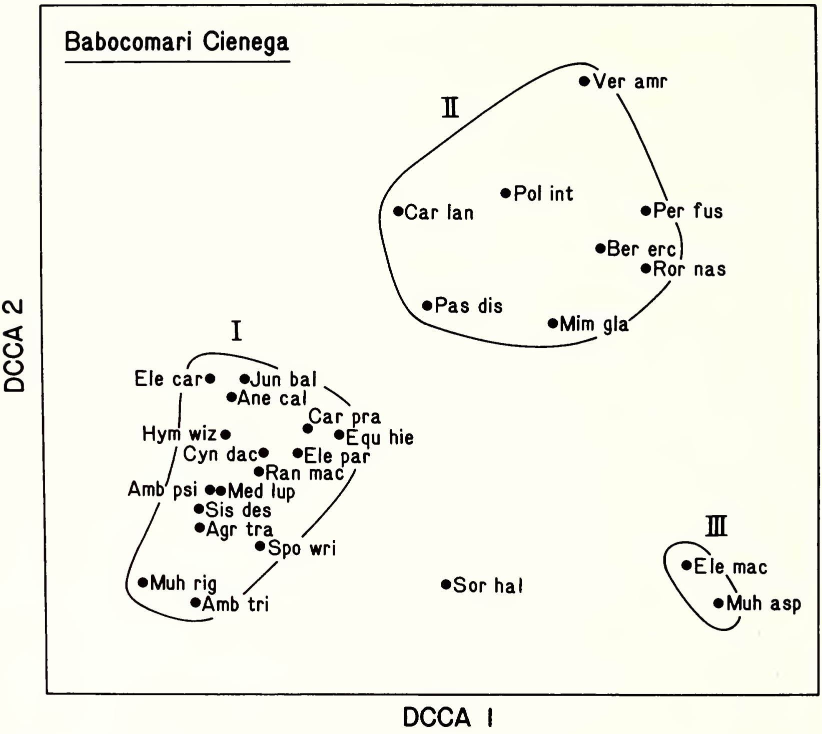

FIG. 1. Detrended canonical correspondence analysis (DCCA) ordination of species-by-environment variables for the Babocomari Ciénega (summer 1986). Species groups generally represent the following locations along the moisture gradient: I = dry, peripheral sites, II = wet, stream sites, and III = wet, ciénega sites. Names for species' abbreviations are listed in Table 1.

canopy cover (c = −0.7938) which differentiates between plots under trees and in the open. This axis separated species in group II (100% canopy) from species in group I (50% canopy) and from species in group III (0% canopy) (Fig. 2). The third axis (e = 0.32) and the fourth axis (e = 0.30) were not strong enough to explain much of the variation, but are illustrated in Fernald (1987).

Generally, several plant species may be used to identify the vegetation-by-environment groups that were separated by DCCA. *Rorippa nasturtium-aquaticum* and *Berula erecta* dominated the stream area that was characterized by deep, flowing water, saturated soils, and nearly complete canopy cover. *Eleocharis macrostachya* and *Muhlenbergia asperifolia* dominated the ciénega area that was characterized by shallow, standing water, intermittently saturated soils, and sparse, patchy canopy cover. *Muhlenbergia rigens* and *Ambrosia*

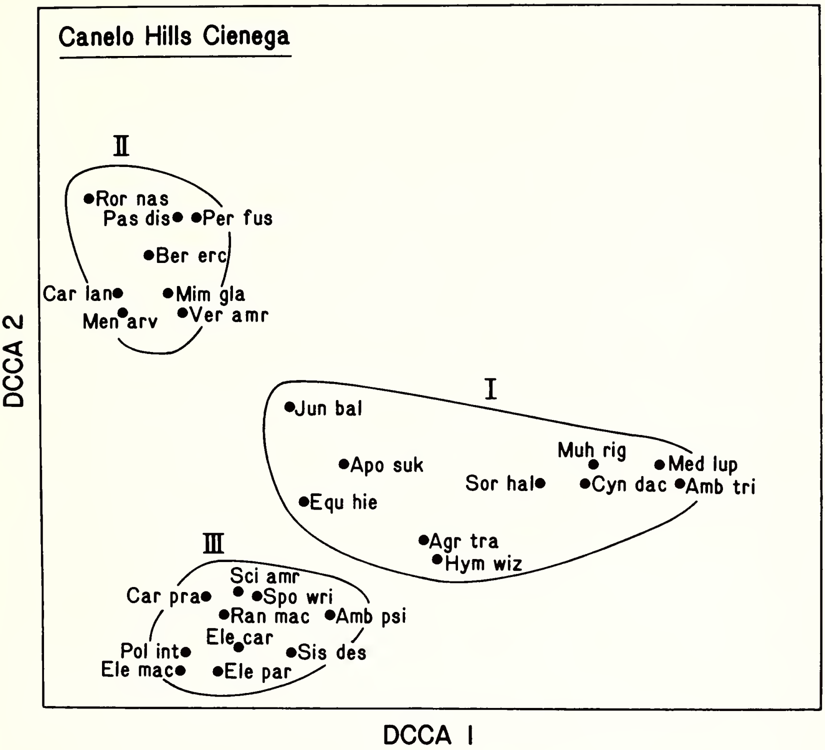

FIG. 2. Detrended canonical correspondence analysis (DCCA) ordination of species-by-environment variables for the Canelo Hills Ciénega (summer 1986). Species groups generally represent the following locations along the moisture gradient: I = dry, peripheral sites, II = wet, stream sites, and III = wet, ciénega sites. Names for species abbreviations are listed in Table 1.

trifida dominated the periphery that was characterized by a lack of standing water, dry soils, and no canopy cover.

Species used in all DCCA and DCA analyses for both ciénegas are listed in Table 1.

DISCUSSION

The floristic composition of graminoid and herbaceous species at the Babocomari Ciénega and the Canelo Hills Ciénega is similar to that found in other ciénegas in southeastern Arizona (Marrs-Smith 1980; Yatskievych and Jenkins 1981). Of the 135 species collected in 1985 at Babocomari Ciénega and the Canelo Hills Ciénega, many have been introduced from Eurasia or from range extensions north from Mexico (Correll and Correll 1975). Because no pristine ciénegas

TABLE 1. HERBACEOUS AND GRAMINOID PLANT SPECIES USED IN DETRENDED CANONICAL CORRESPONDENCE ANALYSIS AND DETRENDED CORRESPONDENCE ANALYSIS FROM THE BABOCOMARI CIÉNEGA AND THE CANELO HILLS CIÉNEGA.

Species	Abbreviations used in Figures 1 and 2
Agropyron trachycalum (Link.) Malte.	Agr tra
Ambrosia psilostachya DC.	Amb psi
Ambrosia trifida L.	Amb tri
Anemopsis californica (Nutt.) H. & A.	Ane cal
Apocynum suksdorfii Greene.	Apo suk
Berula erecta (Huds.) Coville.	Ber erc
Carex lanuginosa Michx.	Car lan
Carex praegracilis W. Boott.	Car pra
Cynodon dactylon (L.) Pers.	Cyn dac
Eleocharis caribaea (Rottb.) Blake.	Ele car
Eleocharis macrostachya Britt.	Ele mac
Eleocharis parishii Britt.	Ele par
Equisetum hiemale L.	Equ hie
Hymenothrix wislizenii Gray.	Hym wiz
Juncus balticus Willd.	Jun bal
Persicaria fusiforme Greene.	Per fus
Polypogon interruptus H.B.K.	Pol int
Medicago lupulina L.	Med lup
Mentha arvensis L.	Men arv
Mimulus glabratus H.B.K.	Mim gla
Muhlenbergia asperifolia (Nees & Mey) Parodi.	Muh asp
Muhlenbergia rigens Torr.	Muh rig
Paspalum distichum L.	Pas dis
Ranunculus macranthus Scheele.	Ran mac
Rorippa nasturtium-aquaticum (L.) Schinz & Thell.	Ror nas
Scirpus americanus Pers.	Sci amr
Sisyrinchium demissum Greene.	Sis des
Sorghum halpense (L.) Pers.	Sor hal
Sporobolus wrightii Munro ex Scribn.	Spo wri
Veronica americana (Raf.) Schwein.	Ver amr

exist, most extant ciénega vegetation reflects the local disturbance history.

The Babocomari Ciénega and the Canelo Hills Ciénega have a similar floristic composition because they have similar climatic regimes, environmental conditions, and disturbance histories. However, of the 30 species included in the analysis, four were not shared by both sites. Because of the large sample size, most species present were likely found; the discrepancy may be due to unidentified site-specific biotic and abiotic factors, such as interspecific competition or variation in soil nutrient concentrations.

Differences may also be attributed to subtleties in the local watershed hydrology; the Canelo Hills Ciénega is located in a much smaller, narrower basin with steeper slopes than the Babocomari Ciénega. In addition, soil erosion was probably greater at the Canelo

Hills Ciénega than at the Babocomari Ciénega because the dam was installed 30 years later. It has been shown that ciénegas without manmade dams have either been lost entirely due to soil erosion or have a limited flora that is typically associated with grasslands, not ciénegas (Hendrickson and Minckley 1985; Marrs-Smith 1980).

The high eigenvalues ($e > 0.50$) for the first and second axes at the Babocomari Ciénega and the Canelo Hills Ciénega suggest that the chosen environmental variables are sufficient to explain most of the variation in species composition and distribution (Jongman et al. 1987). However, the eigenvalues at the Canelo Hills Ciénega are lower than for Babocomari Ciénega and this may reflect the fact that the sampling scheme was chosen based on a reconnaissance of Babocomari Ciénega. Also, inclusion of variables that more accurately reflect the grazing or flooding disturbance regime, such as clipped grasses or soil erosion, might increase the amount of variation explained by the environmental variables.

Finally, differences between the Babocomari Ciénega and the Canelo Hills Ciénega plant distributions and species composition may be due to recent changes in land use practices, specifically grazing by domestic cattle. A rare orchid, *Spiranthes graminea* Lindl., that is flourishing at Babocomari Ciénega, has gradually been replaced by invading grasses at the Canelo Hills Ciénega. Managers at the Nature Conservancy Preserve surmise that the removal of domestic cattle from the Canelo Hills Ciénega may be indirectly responsible for the demise of *S. graminea* (Campbell and Wiley pers. comm.). It is likely that cattle grazing reduces the competition for space or nutrients. While the Canelo Hills Ciénega has not been grazed for 20 years, in the early 1960's it was grazed until nothing remained but cracked, dry soil (Mr. Bud Ewing pers. comm.). On the other hand, the Babocomari Ciénega has been continuously grazed since at least the early 1930's. Because the Babocomari Ciénega is grazed, the invasion of *Juniperus deppeana* Steud. is restricted to areas unaccessible to cattle, whereas at the Canelo Hills Ciénega its presence may be due to a recent invasion following the removal of grazing pressures (Gawith 1987).

In conclusion, three similar species groups, including a stream group, a ciénega group and a grassland peripheral group, have been identified at the Babocomari Ciénega and the Canelo Hills Ciénega. These results establish a baseline for future studies that could focus on the abiotic and biotic interactions that influence the dynamic ecology of plant species that are unique to ciénega ecosystems of the southwestern United States.

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PECTIS PIMANA (ASTERACEAE: TAGETEAE): A NEW SPECIES FROM NORTHWESTERN MEXICO

JOSEPH E. LAFERRIÈRE
Department of Ecology and Evolutionary Biology,
University of Arizona, Tucson, AZ 85721

DAVID J. KEIL
Biological Sciences Department,
California Polytechnic State University,
San Luis Obispo, CA 93407

ABSTRACT

Pectis pimana is a new species of west-central Chihuahua, Mexico. It is most closely related to *P. filipes* of sect. *Pectothrix* from which it differs most conspicuously by its 8-rayed instead of 5-rayed heads and more numerous pappus awns.

RESUMEN

Pectis pimana se describe como nueva especie del parte oeste-central de Chihuahua, México. Está emparentada lo más cercana con *P. filipes* de la Sección *Pectothrix,* de cual se distingue por sus cabezuellas con 8 rayas en vez de 5, y por sus aristas del vilano más numerosas.

During recent ethnobotanical investigations among the Mountain Pima Indians of Chihuahua, Mexico, a native Pima consultant brought to Laferrière a specimen of *Pectis* that could not be assigned to any known taxon. It is herein described as a new species.

Pectis pimana Laferrière & Keil, sp. nov. (Fig. 1).—TYPE: MEXICO: Chihuahua, Mpio. Temósachi, Nabogame, 28°30′N, 108°30′W, growing in pasture, 1800 m, Sep 1988, *Laferrière and Alvarez 2013* (holotype, ARIZ; isotypes: MEXU, OBI).

Pectidi filipedi affinis a qua imprimis differt phyllariis radiisque capitulorum 8 et pappo pluriaristato.

Strongly scented, tap-rooted annuals. Stems 1–several from the base, 10–20 cm long, erect, cymosely branched above, sparingly and minutely scaberulous at the nodes, otherwise glabrous. Leaves linear, 10–25 mm long, 1–2.8 mm wide, often revolute, proximally ciliate with 3–7 pairs of reddish-brown bristles 2–4 mm long, puberulent on margins and on abaxial surface of midrib, submarginally punctate with conspicuous elliptic to rounded glands 0.2–0.5 mm diameter. Heads solitary and terminal or in diffuse cymes, 6–8 mm tall, 5–10 mm diameter; peduncles 1.5–5 cm long, glabrous, bearing 3–5 scat-

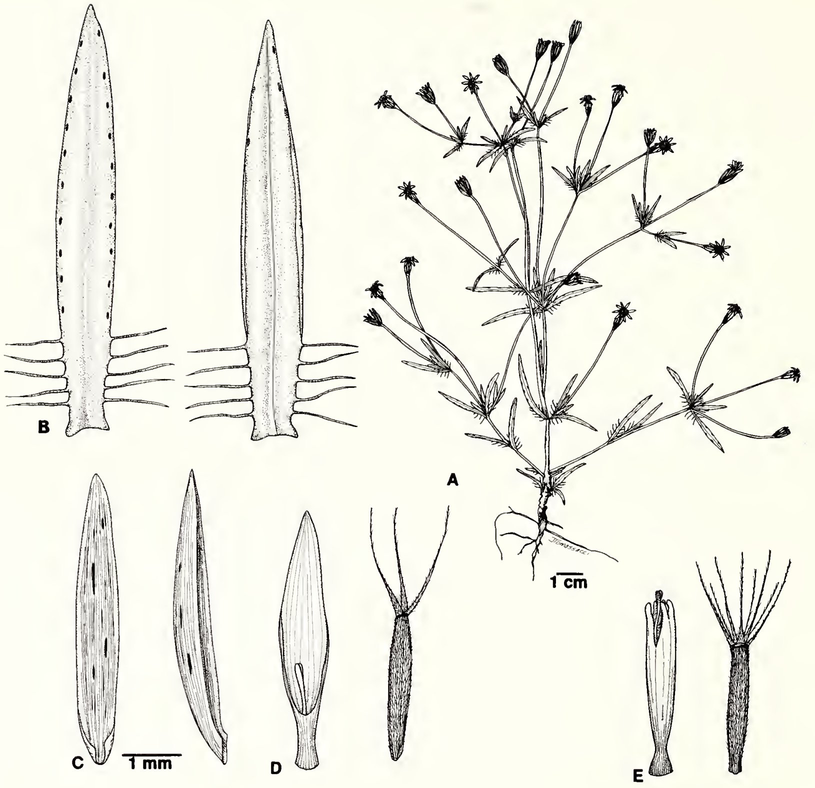

FIG. 1. *Pectis pimana* Laferrière & Keil. A. Habit. B. Leaves (adaxial and abaxial surfaces). C. Phyllaries (abaxial surface and lateral view). D. Ray corolla and achene. E. Disk corolla and achene. C–E, same scale. Drawn from isotype at OBI.

tered reddish-brown, lanceolate bractlets 1–2 mm long. Involucres cylindric or narrowly campanulate; phyllaries 8, linear, 5–7 mm long, 0.5–0.7 mm broad, not or scarcely overlapping, obtuse, abaxially rounded with a basally gibbous midrib, inconspicuously punctate with elongated submarginal glands, the margin narrowly hyaline, distally villous-ciliolate. Ray florets 8; corollas bright yellow, 3–4.5 mm long, glabrous, tube 1–1.5 mm long, ligules 2–2.5 mm long. Disk florets 10–15; corollas 3–3.5 mm long, the tube and throat not well differentiated externally, together 2.2–2.7 mm long, the limb 0.8 mm long, weakly bilateral with the anterior lip ca. 2× the length of the 4 lobes of the posterior lip. Achenes 3–4 mm long, strigillose with straight bicellular hairs 0.1–0.2 mm long. Pappus of 3 (ray) or 4–5 (disk) slender subequal awns 3–3.5 mm long, sometimes with

1–5 additional, shorter, more slender awns. Chromosome number unknown.

The new species is named for the Mountain Pima inhabitants of the region where it occurs. The plant is called "hierba de la hormiga" because it is said to smell like ants. A tea made from the leaves is used to treat fever.

Distribution. Pectis pimana is known only from the type collection from extreme west-central Chihuahua, ca. 18 km NW of Yepachi and 10 km E of the Sonoran border. The plant was found growing in grassy fields where it is apparently uncommon. Vegetation of surrounding areas is a pine-oak forest dominated by *Quercus chihuahuaensis* Trel., *Q. viminea* Trel., and *Pinus engelmannii* Carrière.

Relationships. Pectis pimana is a member of sect. *Pectothrix* A. Gray and is most similar and closely related to *P. filipes* Harv. & A. Gray, differing by its 8-rayed rather than 5-rayed heads and 3–5(–8) rather than 0–3 principal pappus awns. *Pectis filipes* var. *subnuda* Fern. occurs in similar habitats and at similar elevations in the Sierra Madre Occidental of Chihuahua (Keil 1977) but has not been found in the vicinity of Nabogame.

Because of its 8-rayed heads and aristate pappus, the new species would key to either *P. pringlei* Fern. or *P. stenophylla* A. Gray var. *rosei* (Fern.) Keil in Keil's (1977) revision of sect. *Pectothrix. Pectis pringlei,* a Chihuahuan Desert species, differs from the new species in having broader phyllaries with prominent subterminal glands, larger, more conspicuous ray corollas, radially symmetric disk corollas, and fewer, stouter pappus awns. *Pectis stenophylla* var. *rosei,* known only from its type collection in southeastern Sonora, has much smaller heads and fewer pappus awns than does *P. pimana.*

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YERMO XANTHOCEPHALUS (ASTERACEAE: SENECIONEAE): A NEW GENUS AND SPECIES FROM WYOMING

ROBERT D. DORN
Box 1471, Cheyenne, WY 82003

ABSTRACT

Yermo xanthocephalus, a new genus and species from Wyoming, is described and illustrated. It appears most closely related to species of *Cacalia* Section *Conophora* (*Mesadenia, Arnoglossum*) that occur in eastern and midwestern North America. It is unique in the entire cacalioid group and nearly unique in the family Asteraceae in having yellow involucral bracts. It also has yellow corollas, which are very rare in the cacalioid group.

I recently encountered a very unusual plant in the central Wyoming desert that was readily assigned to the Tribe Senecioneae in Asteraceae, but it did not closely resemble any genus in the region. Further study indicated that it was apparently most closely related to species of *Cacalia* Section *Conophora* (*Mesadenia, Arnoglossum*), particularly *Cacalia plantaginea* (Raf.) Shinners (use of *Cacalia* in this paper is for reference only and should not imply that I agree with that use). Plants of this section occur in eastern and midwestern North America, over 1000 km to the E.

The newly discovered plant is unique in the cacalioid group in having yellow involucral bracts, a thick, elongate taproot, and in its distribution in a desert habitat. It also has yellow corollas, which are very rare in the group. The most closely related species (*Cacalia* Section *Conophora*) have green involucral bracts, fibrous or fleshy-fibrous roots sometimes crowned with a short tuber, white or whitish corollas, and they grow in moist or wet places. The yellow involucral bracts are very rare in the family, as I could not find reference to any North American species with yellow involucral bracts. The new species grows on the Split Rock Formation, which is of Miocene age (Van Houten 1964; Lohman and Andrews 1968). It is notable that in the Miocene, the temperate deciduous forest was being pushed eastward from Wyoming due to drying conditions (Dorn 1977). Species of *Cacalia* Section *Conophora* are found today in the eastern deciduous forest. The new species is likely derived from an extinct common ancestor. It appears to be quite old and perhaps on its way to extinction; there are ca. 500 plants on about 1 hectare. Similar habitats nearby were unoccupied by the species. The yellow involucre likely evolved to enhance pollination in a dry environment

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where insects are less common than in moist locations. Ironically, this may prove to be the species' demise. Seed set in 1990 was almost nil due to insect destruction of the achenes and drought. Individuals came into flower at different times so that flowering occurred nearly throughout the summer. This is rather unusual for a desert plant in this area.

There has been considerable disagreement on generic classification in the cacalioid group of the tribe. It is doubtful if all of the genera recognized by Robinson and Brettell (1973a, b, c) and Nordenstam (1977) will be maintained. On the other hand, the broader concept of *Cacalia* of Pippen (1978) will likely require refinement once the evolutionary history of the group is better understood. The problems are reminiscent of those in the Tribe Astereae.

At the supraspecific level, one has two choices for classifying this new species: describe a new subgenus or section under the genus that includes *Cacalia plantaginea,* or describe a new genus. The best one can do is anticipate the probable outcome of a more stable classification by considering the evolving classification in other tribes where much more work has been done. Practical considerations for the present should not be ignored, however. When considering the evolving generic classification in the Tribe Astereae and differences between genera like *Aster, Erigeron, Conyza, Machaeranthera, Xylorhiza, Haplopappus,* and others, and practical matters, it seems most appropriate to erect a new genus to accommodate the newly discovered species. Perhaps it is justifiable on the basis of the yellow involucre alone.

Yermo xanthocephalus Dorn, gen. et sp. nov. (Fig. 1)—TYPE: USA, Wyoming, Fremont Co., T31N R95W section line of SW¼ of Sect. 27 and NW¼ of Sect. 34, ca. 10 km N of Sweetwater Station, barren outcrop of white silty clay, 2040 m, 28 June 1990, *Dorn 5093* (holotype, RM; isotypes, to be distributed).

Herba perennis ad 3 dm alta; radice crassa elongata; foliis basali et alterno, coriaceis, lanceolatis ad ovatis vel obovatis, integris vel dentatis, 4–25 cm longis, 1–6 cm latis, sursum gradatim reductis; capitulis multis (25–180); involucro cylindrico 8–15 mm longo, tegulis 5(4–6) carinatus luteis cucullatis; receptaculo nudo; radiis nullis; floribus discis 5(4–6) luteis, tubo ca. 3 mm longo, fauce ca. 2 mm longa, lobis linearibus patentibus ca. 2 mm longis; pappo capilliformi deciduo; acheniis brunneis 6–7 mm longis ellipticus vel oblanceolatis.

Perennial herb, glabrous except sometimes the achenes; stems hollow, to 3 dm high, 1 to several from a thick, elongate taproot; leaves basal and alternate, petioled, coriaceous, lanceolate to ovate

FIG. 1. *Yermo xanthocephalus.* A. Habit. B. Individual head at left, top view of individual head in bud at right. C. Mature achene. D. Disk floret with pappus removed. E. Disk floret with pappus intact. F. Stigmas. G. Anther.

or obovate, entire to variously toothed, 4–25 cm long, 1–6 cm wide, gradually reduced upward, generally with a rounded fold lengthwise, the main 3 veins somewhat parallel; heads numerous (25–180), in a crowded corymbiform cyme; involucre cylindrical, 8–15 mm long, the bracts in a single series, usually 5, occasionally 4, rarely 6, strongly keeled, the keel greenish-yellow, the rest bright yellow but drying pale, generally cucullate at tip, usually with a few much reduced bractlets at base; receptacle naked, flat or sometimes with a sharp projection from center; rays none; disk florets usually as many as involucral bracts (4–6) except sometimes fewer by abortion, barely exserted from involucre, yellow, the tube about 3 mm long, the throat about 2 mm long, the lobes linear, widely spreading and about 2 mm long; anthers with a pair of minute lobes at base; style branches obtuse-truncate and pubescent at tip, stigmatic surface covering entire inner face; pappus copious, of capillary bristles, subequal to corolla tube and throat, borne on an expanded disk at top of achene, deciduous in fruit; achenes often short-pubescent, usually about 10 nerved, brown, 6–7 mm long, slightly flattened, elliptic to oblanceolate in outline.

The bright yellow involucres, mostly 5 involucral bracts and 5 disk florets, lack of ray florets, yellow corollas with linear lobes, and the thick elongate taproot easily separate this genus from all the other genera in the Tribe Senecioneae. The yellow involucre alone will separate it from all genera of the Asteraceae in the region and most of the world.

The generic name is a Spanish word meaning uninhabited land or desert, descriptive of the location where the plant grows. The word is masculine. The translated Latin name provides a common name, desert yellowhead.

ACKNOWLEDGMENTS

I thank Ronald Hartman, curator of RM, for use of those facilities.

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(Received 8 Feb 1991; revision accepted 28 Mar 1991.)

NOTES

NEW LOCALITIES FOR *ASTER CURTUS* IN WESTERN OREGON.—Edward R. Alverson, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

Aster curtus Cronq. (Asteraceae) is a strongly clonal, rhizomatous perennial herb of low elevation grasslands west of the Cascade Mountains. Its geographic range extends from southwestern British Columbia, S through western Washington, to the Willamette Valley, Oregon (Clampitt, American Journal of Botany 74:941–946, 1987). *Aster curtus* is a candidate for federal listing as a threatened or endangered species and is currently included on the list of species thought to be threatened in Oregon (*Rare, threatened, and endangered plants and animals of Oregon,* Oregon Natural Heritage Data Base, 1989).

Known extant populations of *A. curtus* are concentrated primarily on southwestern Vancouver Island, the gravelly glacial outwash prairies of Pierce and Thurston Cos., Washington, and in wet *Deschampsia cespitosa* grasslands in the southern Willamette Valley near Eugene, Lane Co., Oregon. In Washington and British Columbia, gaps in the distribution of the species are largely due to lack of suitable grassland habitats. In the Willamette Valley, grasslands dominated the presettlement landscape, though their extent has been reduced dramatically since Euroamerican settlement (Johannessen et al., Annals of the Association of American Geographers 61:286–302, 1971). Other than the Lane Co. populations, the only historical collections are from near Salem, Marion Co., and from Portland, Multnomah Co.

Several additional populations of *A. curtus* have recently been located in remnant fragments of Willamette Valley prairie and oak savannah habitats. Two are in Marion Co., where the species was last collected in 1918. Both populations are small, and are associated with upland grassland and oak savannah remnants in the foothills east of Salem (Alverson, New York State Museum Bulletin 471:107–112, 1990). The localities are E of Waldo Hills Drive, elev. 195 m, 7 km NE of Aumsville, 2 Aug 1987, *Alverson 1255* (OSC), and E of Edison Rd., elev. 240 m, 4 km S of Silverton, 8 Aug 1987, *Alverson 1271* (OSC). The Waldo Hills Dr. population consisted of four discrete clones, with about 50 ramets each, and a single colony with 250 ramets was observed at the Edison Rd. site.

A population in Linn Co., E of Kingston-Lyons Rd., elev. 235 m, 5 km SE of Stayton, 22 July 1990, *Alverson 1565* (OSC), was found in a native grassland remnant that also harbors three other threatened or endangered plant species endemic to Willamette Valley grasslands. Four patches with approximately 100 ramets total were observed along a road right-of-way, where they may have been protected from the effects of grazing livestock.

The Polk Co. site, 23 Aug 1989, *Thiel s.n.* (OSC) is not in the Willamette Valley proper, but at an elevation of 760 m in the eastern part of the Coast Range. The site is a Bureau of Land Management Area of Critical Environmental Concern located on Rickreal Ridge, about 17 km W of Dallas. The *A. curtus* population is quite small and grows on an open rocky ridgetop.

Aster curtus has been relocated in the Portland metropolitan area in the Nature Conservancy's Camassia Natural Area, above the Willamette River at an elevation of 85 m in West Linn, Clackamas Co. One colony with about 170 ramets was observed in this area of oak thickets and grassy openings, 4 Aug 1990, *Alverson 1576* (OSC). *Aster curtus* had not previously been reported from Clackamas Co.

These newly discovered populations bring to six the number of Oregon counties in which *A. curtus* has been collected. They also document that this species occurs

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in Oregon in well-drained upland grasslands, as it does in Washington and British Columbia. Only in Lane Co., at the southern distributional limit, is *A. curtus* known to occur in the wet *Deschampsia cespitosa* grassland community.

These five populations of *A. curtus* are all relatively small and isolated, so their discovery does little to improve the status of the species in Oregon. Because *A. curtus* appears to be relatively rare and occurs in habitats that are greatly threatened by agriculture and development, it still should be considered a threatened species in Oregon.

I thank K. Chambers, J. Thiel, and D. Wagner for helpful comments.

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NOTEWORTHY COLLECTIONS

OREGON

CAREX PLURIFLORA Hulten (CYPERACEAE).—Clatsop Co., Gearhart Bog, 4 km NE of Gearhart. T7N, R10W, SE¼ sect. 27. On hummocks of *Sphagnum henryense* in *Pinus contorta/Ledum groenlandicum/Sphagnum* mire, with *Drosera rotundifolia, Eriophorum chamissonis, Trientalis arctica, Menyanthes trifoliata* and *Sphagnum capillifolium,* elev. 6 m, 19 Sep 1989, *J. A. Christy 7289* (ORE).

Previous knowledge. North circum-Pacific, from Clallam and Whatcom counties, Washington, mostly along the coast, through the Aleutian Islands to coastal Siberia and the Kurile Islands (Hitchcock, Cronquist, Ownby and Thompson, Vascular Plants of the Pacific Northwest, 1969; Taylor, The Sedge Family (Cyperaceae), British Columbia Provincial Museum Handbook 43, 1983; Hulten, Flora of Alaska and Neighboring Territories, 1968; Washington Department of Natural Resources, Natural Heritage Program Information System).

Significance. New to flora of Oregon. Extends range 215 km S of previously known southernmost occurrence at Mink Lake, Olympic National Park, Clallam Co., Washington.

—JOHN A. CHRISTY, Oregon Natural Heritage Program, 1205 NW 25th Ave., Portland, OR 97210.

COPTIS TRIFOLIA (L.) Salisb. (RANUNCULACEAE).—Clackamas Co., Mt. Hood National Forest, in swampy area along Crater Creek, ca. 1.9 km N of Little Crater Lake, T5S R8.5E sect. 2, elev. 1000 m, 2 June 1990, *Helliwell 894* (OSC). (Verified by K. Chambers, OSC.)

Significance. First record for OR and an extension of ca. 450 km from Vancouver Is. and southern British Columbia. A second, smaller population was located ca. 6 km to the east in Wasco Co., Warm Springs Indian Reservation, T5S R9E sect. 9.

—RICHARD HELLIWELL, Mt. Hood National Forest, Bear Springs Ranger District, Route 1 Box 222, Maupin, OR 97037.

JUNCUS MARGINATUS Rostk. var. *SETOSUS* Coville (JUNCACEAE).—Lane Co., Coast Fork Willamette River drainage, 0.2 km E of Papenfus Creek, junction of Enterprise and Morningstar Roads, ca. 9 air km ENE of Creswell, T19S R2W S3 SE¼ of NW¼, ca. 100 plants in flooded roadside ditches, mapped as McAlpin silty clay loam (W. R. Patching, Soil Survey of Lane County Area, Oregon, USDA Soil Conservation Service, 1987), with *Juncus bolanderi* Engelm., *J. bufonius* L., *J. effusus* L., *J. ensifolius* Wiks., *J. patens* E. Meyer and *J. tenuis* Willd. and weedy taxa such as *Bidens frondosa* L., *Centaurium umbellatum* Gilib., *Festuca arundinacea* Schreb., *Holcus lanatus* L., *Hypochaeris radicata* L. and *Mentha pulegium* L., elev. ca. 185 m, 13 Jan 1991, *Zika, Brainerd & Newhouse 11050* (NY, ORE, OSC).

Significance. The first record for Oregon and a range extension of ca. 550 km N from California (P. A. Munz, A Supplement to the California Flora, University of

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California Press, 1968). Absent in regional manuals, and apparently the first record for the Pacific Northwest. The species habit is illustrated in Clemants (Juncaceae of New York State, New York State Museum Bulletin 475:26, 1990) and the native SW variety is detailed in Hermann (Manual of the Rushes of the Rocky Mountains and Colorado Basin, USDA Forest Service General Technical Report RM-18:57, 1975). The Lane Co. population matches eastern collections of the nominate variety of the species but has the long inner tepals with acuminate to subulate apices characteristic of *J. marginatus* var. *setosus.* Doubtfully native in Oregon, as it appears to be highly localized in a human-created habitat along a road near other locally rare wide-ranging adventives, e.g., *Cyperus eragrostis* Lam., *Cynodon dactylon* (L.) Pers., and *Panicum dichotomiflorum* Michx.

—PETER F. ZIKA, Oregon Natural Heritage Data Base, 1205 NW 25th, Portland, OR 97210.

REVIEWS

Packrat Middens: The Last 40,000 Years of Biotic Change. Edited by J. L. Betancourt, T. R. Van Devender, and P. S. Martin. 1990. University of Arizona Press, Tucson. vii +467 pp. Hardcover: $55.00, ISBN 0-8165-1115-2.

The analysis of remains from packrat (*Neotoma* sp.) middens has accelerated the study of paleoecology in the arid regions of North America. Packrat middens are discrete deposits of fossil materials (primarily plant debris, but including also vertebrate remains, arthropods and pollen) that have been cemented together and preserved by the urine and feces of the packrat itself. In an area where traditional sedimentary deposits (such as lakes and bogs) with well-preserved organic remains are rare, midden analysis has been particularly helpful in our interpretation of biotic and biogeographic change over the last 40,000 years. Over 1100 middens have been analyzed from eleven states in the U.S. as well as five in Mexico, providing a large amount of data on biotic change through time and in space.

This book contains 21 chapters written by 26 authors. It is divided into four sections, with an introduction and a summary. The introduction serves as a history of the subject, from the initial reports of the deposits in 1849 to the first publication involving midden analysis in 1964. Part I contains papers pertaining to the ecology of the packrat as well as methodology of the subject and interpretation of the data. It becomes clear from these discussions that a tremendous database exists, but standardization of methods and quantitative interpretation of vegetation has not yet been accomplished. This is often the case in a young, developing field of research.

For individuals interested in regional vegetation and climate reconstructions, Part II is the heart of the volume. Regional summaries are provided for the Chihuahuan, Sonoran, Mojave and Great Basin deserts, as well as the Grand Canyon and Colorado Plateau. Most summaries include a synopsis of major vegetational change, with sections on biogeographic and paleoclimatic implications. The authors have done an admirable job in summarizing the available data for each region.

Part III includes five chapters that detail specialized studies. These studies include comparison of midden deposits with contemporaneous sediments from nearby lakes, implications for the occurrence of grass species in middens from the Sonoran Desert, mammalian and arthropod remains from Chihuahuan and Sonoran Desert middens, respectively, and climatic implications of deuterium concentrations in plant cellulose. The chapters are representative of a range of special investigations possible from middens. Additional subjects could have been included, such as the pollen, herpetological and archeological records from middens.

Part IV, entitled "Middens Abroad", presents three chapters that explore similar deposits from other regions of the world. These include the potential for analysis of hyrax (Procaviidae) and dassie rat (Petromuridae) in the Middle East and Africa, as well as the stick-nest rat (Muridae) from Australia. For several of these animals, the chapters here represent the only publications on the subject. The potential for the Middle East is particularly exciting, as little is known about the characteristics of native vegetation prior to the advent of agriculture, and the subsequent human impact on the remnants of natural vegetation.

The book is technically well-crafted and well-edited—typographic and lay-out errors are few. All considered, this book provides an excellent reference for midden analysis. However, those persons interested in the fossil record from other types of sedimentary deposits (e.g., lake sediments, alluvial sections, etc.) will need to look elsewhere. I recommend this book to all individuals interested in perspectives on

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changing environments through time, and on the biogeography of the western U.S. and Mexico. This would include individuals as diverse as botanists, ecologists, zoologists, Quaternary scientists and resource managers. The volume is particularly timely in light of current interest in global climate change. Arid regions may be among the most severely impacted regions of the world.

—R. SCOTT ANDERSON, Bilby Research Center, Northern Arizona University, Flagstaff, AZ 86011.

Vernal Pool Plants: their Habitat and Biology. Edited by D. H. IKEDA and R. A. SCHLISING. 1990. Studies from the Herbarium, California State University, Chico, Number 8. xi + 178 pp. Softcover: $11.00. (Available from Herbarium, CSU, Chico, CA 95929.)

This attractive and inexpensive book includes the eight papers delivered at a symposium of the same name at the Pacific Division meetings of the American Association for the Advancement of Science at California State University, Chico, in June 1989. Remarkably, the publication appeared exactly one year after the symposium, doubtless possible because of desktop publishing methods; the manuscripts were read by outside reviewers. According to the editors, the symposium was "designed to emphasize biological and environmental information on the plants of vernal pools—information which may be of interest and of importance in wetlands research and conservation."

Jokerst's contribution is concerned with volcanic mudflow vernal pools, mostly in the Sacramento Valley. Species richness of vernal pools appears to be weakly associated with the area of a pool; Jokerst suggests that it is also weakly correlated with pool depth. The uniqueness of the individual florulas of pools in close proximity that has been noted by others is confirmed, and Jokerst determined that often, but not always, pools near each other have greater floristic similarity than to those more distant. The methods he uses in his analyses will be of interest to those concerned with characterization and comparison of vernal pool floras elsewhere. Holland and Dains emphasize the fact that substrate characteristics have a strong influence on vegetation patterns in vernal pools, and that these substrate variations are often so local that they do not appear on standard soil survey maps. These authors conclude that mitigation efforts by developers will ultimately fail because the subtleties of edaphic influences are not taken into consideration in such efforts and probably could not be accommodated if they were. Hanes, Hecht, and Stromberg conclude that direct precipitation rather than watershed inflow is the primary source of the water that fills vernal pools in the Sacramento region, although subsurface inflows may help maintain water volume once the local soil becomes charged with water. Keeley, working with southern California pools, notes the sequential leaf heteromorphism that is so common in vernal pool plants during a given growing season, and contrasts the types of photosynthesis carried on by aerial versus submerged leaves. Despite the gross morphological convergences that may exist among many unrelated vernal pool denizens, each may display a characteristic and different spectrum of physiological attributes. He also concludes that differences in numbers of individual species in a pool in dry versus wet years is attributable to interspecific differences in photosynthetic rates in dry versus wet conditions. Stone suggests that the majority of vernal pool endemics are of recent evolutionary origin, this speciation often associated with aneuploid decrease in chromosome number or changes in breeding systems. Patterns of distribution of individual species are described; of particular interest to me are the several species that are widely distributed, but generally occur at very low frequencies throughout their range and often with more abundant congeners. One wonders what the explanation is for this pattern. He errs in considering *Lasthenia conjugens* a Great Valley endemic, since this species once grew at the south end of San Francisco Bay, coastal Mendocino County, and near Santa Barbara. He points out, quite correctly, that while much attention has been directed toward threatened vernal pool taxa, the common ones limited to this habitat may soon be in trouble as well due to loss of pools. Thorp presents a very interesting description of the close synchronization of flowering patterns of vernal pool angiosperms and the life cycles of their oligolectic andrenid bee pollinators, pointing out that conservation efforts for vernal pools must also consider conservation of the nesting sites of the associated specialized pollinators. Zedler, working with vernal pools in San Diego County, characterizes their angiosperm inhabitants as predominantly annuals, likely to be autogamous, and with apparently poor seed dispersibility. He explores the possible explanations for each of these features; a comparison with inhabitants of permanent bodies of fresh water might have been illuminating, since I believe these are predominantly xenogamous perennials with high dispersal potentials. Is the difference related to permanent vs. ephemeral water, to spatial relationships of the two kinds of aquatic habitats, or to other causes? In the final paper in the volume, Ferren and Gevirtz describe and discuss various kinds of manipulation aimed at restoration or creation of vernal pools. They point out the lack of established criteria that can be used in assessing the success of such restoration and creation. They believe there is no conclusive evidence that either restoration or creation has been successful in producing anything that closely resembles the real thing, and are not optimistic that true restoration or replication is possible. Certainly, our experience with what is probably the first artificial offsite vernal pool to be constructed, one still at the University of California Botanical Garden, indicates that even after three decades this pool requires annual maintenance, largely to prevent the invasion by exotics such as *Juncus bufonius* and to recharge the seed bank of natives.

The papers in this volume and Schlising's fine color photographs of still intact vernal pools in the Sacramento Valley strengthen my conviction that these unique and marvelous features of our vegetational landscape are best preserved by concentrating our efforts on in situ habitat conservation. To give in to alternatives seems, with our present state of knowledge, to invite failure.

—ROBERT ORNDUFF, Department of Integrative Biology, University of California, Berkeley, CA 94720.

ANNOUNCEMENT

RECENT PUBLICATIONS

GOLDBLATT, P. AND D. E. JOHNSON. 1990. *Index to plant chromosome numbers 1986–1987.* Monographs in Systematic Botany, Missouri Botanical Garden, Volume 30. ix + 243 pp. Softcover, ISBN 0161-1542.

W. W. WEBER. 1990. *Colorado flora: eastern slope.* University Press of Colorado, Niwot, CO 80544. xxxvi + 396 pp. Hardcover: $32.50, ISBN 087081-213-0. Softcover: $19.95, ISBN 087081-213-9.

TODD KEELER-WOLF. 1990. *Ecological surveys of Forest Service Research Natural Areas in California,* USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-125. 177 pp.

This report, produced by the Pacific Southwest Regional Research Natural Areas Program of the USDA Forest Service, summarizes each of the 68 ecological surveys conducted from 1975 through 1988 on Forest Service candidate and established Research Natural Areas in California. The original surveys represent an important but largely unknown contribution to the ecological literature of California. For each summary, information on location, target elements, distinctive features, physical characteristics, association types, plant diversity, and conflicting impacts is provided. Comparisons are made between similar vegetation types at different sites. Tables and appendices summarize the plant communities, target elements, rare species, and tree species occurring on all areas. Maps of all areas and photographs of most areas are included.

Todd Keeler-Wolf specializes in California terrestrial ecology and has written over 30 of the original ecological surveys for Research Natural Areas in California.

Single copies of this publication are available free from: PSW Publication Distribution, USDA Forest Service, Box 245, Berkeley, CA 97401.

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ANNOUNCEMENT

Endangered Habitats League

As conservationists, we recognize that the Federal Endangered Species Act, despite its value as one of the "crown jewels" of environmental legislation, is not a perfect way to deal with the problems of declining or threatened populations. Rather than focusing on ecosystems, the Act instead addresses the individual components of a community. The Endangered Habitats League is an alliance of individuals and conservation organizations sharing a common commitment to the preservation of California's rare and endangered natural habitats. At the present time the League's focus is on the Coastal Sage Scrub community; in the future, other conservation efforts dealing with different ecosystems may be enhanced through the communication and cooperation developed among the League's membership. Specifically, our present objectives are as follows:

1) Create a strong and effective coalition to represent southern California's environmental community.
2) Seek immediate protection and recovery of the California Gnatcatcher under Federal and State endangered species acts.
3) Protect coastal sage scrub and other endangered southern California habitats through monitoring activities and education. We are not a lobbying organization, but will serve to disseminate information among League members, the public, the media, and the scientific community.
4) Work proactively with both public and private groups to develop ecosystem-scale, multispecies habitat conservation plans and wildlife corridors.
5) Conduct needed scientific research and provide expert testimony.

Membership is open to individuals and organizations. Contact Dr. Dan Silver, 1422 N. Sweetzer Ave., #401, Los Angeles, CA 90069.

ANNOUNCEMENT

REPRINT COVERS

In light of increasing concern over limiting resources, *Madroño* considers it environmentally sound policy to discontinue offering covers with reprints. It is hoped that authors will view this step in a positive light.

ANNOUNCEMENT

THE PENINSULAR RANGES OF ALTA AND BAJA CALIFORNIA

On *Saturday, October 26, 1991,* Southern California Botanists will hold their 17th annual symposium on the topic of The Peninsular Ranges of Alta and Baja California. This topic is a timely one because of renewed interest in these ranges as a major biogeographic region of relict endemism. It is also important for the study of fire ecology because of different philosophies about fire suppression on each side of the international boundary. The program will include the following topics and speakers:

A COMPARATIVE OVERVIEW OF THE PLANT COMMUNITIES AND UNIQUE PLANTS OF THE PENINSULAR RANGES
Robert Thorne—Rancho Santa Ana Botanic Garden, Claremont

FIRE ECOLOGY OF MIXED CONIFEROUS FOREST IN BAJA AND ALTA CALIFORNIA
Jack Burk—California State University, Fullerton

INTERESTING CONIFERS IN BAJA AND ALTA CALIFORNIA: A STORY OF RELICT ENDEMISM
Allan Schoenherr—Fullerton College, Fullerton

BIOGEOGRAPHY AND HOST PLANTS OF MONTANE BUTTERFLIES IN THE PENINSULAR RANGES
John Brown and David Faulkner—San Diego Natural History Museum

UNIQUE SOILS AND PLANTS OF LIMITED DISTRIBUTION IN THE PENINSULAR RANGES
Tom Oberbauer—San Diego County Planning Department

This program is cosponsored by the Department of Biology at Cal State Fullerton and will be held in the Ruby Gerontology Center on the Cal State Fullerton campus. Registration begins at 8:00 AM. Coffee and donuts will be served. Registration fee is $10.00 for non-members of SCB, $8.00 for students, and $15.00 for members of Southern California Botanists (including renewal of the $8.00 annual membership). For more information contact Terry Daubert at the Fullerton Arboretum (714) 773-3579.

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SUBSCRIPTIONS—MEMBERSHIP

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A BIOSYSTEMATIC STUDY OF *ERIOPHYLLUM CONGDONII* AND *E. NUBIGENUM* (COMPOSITAE, HELENIEAE)

JOHN S. MOORING
Biology Department, Santa Clara University,
Santa Clara, CA 95053

ABSTRACT

Eriophyllum congdonii and *E. nubigenum*, rare taxa, have also been treated as *E. nubigenum* and *E. nubigenum* var. *congdonii*. Study of F_1, F_2, and F_3 plants shows that experimentally the taxa are interfertile but the morphological differences that separate them in nature are maintained in the greenhouse. They should be treated as species.

Eriophyllum nubigenum Greene and *E. congdonii* Brandegee are annuals known from about 10 sites in a 900 km^2 area of Mariposa Co., California (Fig. 1). The California Native Plant Society inventory of rare and endangered species lists them as R-E-D: 2-1-3. Their state/federal status is CR/C3c (Smith and Berg 1988). *Eriophyllum nubigenum* is based on a Curran collection from Cloud's Rest (A. Gray 1883) and until 1980 was known only from collections there and at three other montane sites in Yosemite National Park. Brandegee (1899) named a similar but lower elevation taxon *E. congdonii*. He based it on material given him by Congdon, who called it *E. nubigenum*. Until 1981 *E. congdonii* appeared to be restricted to a Merced River locale near El Portal. The taxa closely resemble each other, but seemed to occur at different elevations.

Taxonomic treatments differ: Jepson (1925) treated *E. congdonii* without mentioning *E. nubigenum* (one assumes an oversight). Constance (1937) listed *E. congdonii* as a variety of *E. nubigenum*. Abrams and Ferris (1960) followed Brandegee, whereas Munz (1959) followed Constance. Constance commented that the taxa "present an interesting problem in determination of specific delimitations" (p. 115), and suggested that habitat differences associated with elevation might account for differences in pubescence and in size and number of some structures. He interpreted them as extremes, ascribing the gap to inadequate collecting. The "variety is the normal state of the plant, while the type of the species is a dwarfed alpine representative of it" (p. 116). According to him, inadequacy of material allowed *E. congdonii* to be retained as a variety, and additional collections might permit eliminating it as a variety. This was a reasonable treatment when *E. nubigenum* had not been collected

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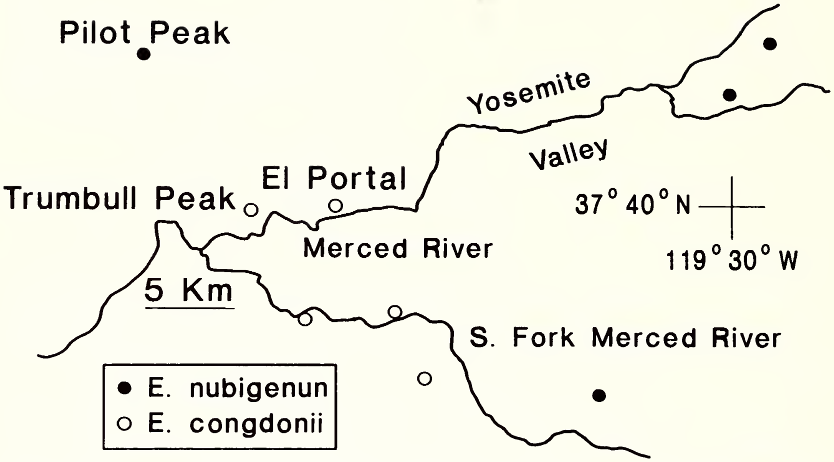

FIG. 1. Distribution of *Eriophyllum congdonii* and *E. nubigenum,* Mariposa Co., California.

since 1897, and might be extinct (Botti 1982a), and when *E. congdonii* seemed to be a low elevation taxon restricted to a Merced River site. Moreover, rarity of the taxa discouraged further study. Rediscovery of the four Yosemite populations of *E. nubigenum* (Botti 1982a), and of additional low elevation populations and a montane population of *E. congdonii* (Botti 1982b) made study of the latter taxon feasible. The Yosemite populations of *E. nubigenum,* however, were so small that no seeds were collected. Dean Taylor's discovery of a large population outside the Park made an experimental study of the relationship between the taxa feasible. In this paper I describe the results of that study.

MATERIALS AND METHODS

The USDA Forest Service and the USDI Park Service permitted me to collect achenes. The *E. congdonii* achenes came from two sites near El Portal (elev 550 m) and from Trumbull Peak (1524 m), the *E. nubigenum* achenes from Pilot Peak (1828 m), about 11 km from Trumbull Peak (Fig. 1). The two El Portal progenies each came from several plants, and each of the seven Trumbull Peak ones came from a different plant. The 13 *E. nubigenum* progenies came from different plants. All achenes (7–14) in each head were sown. Most were stiff and black and were assumed to have an embryo. Such achenes are referred to below as "fair to good," and "apparently viable." In the later generations only "apparently viable" achenes were sown.

Achenes were germinated in vermiculite in an unheated greenhouse. Seedlings were transplanted to 4-inch pots filled with "UC Mix" soil, and grown to senescence in a pollinator-free greenhouse. Two plants were grown in each pot to have the maximum number and to minimize pot-to-pot environmental differences. Pollen viability was estimated by examining fresh grains stained overnight in cotton blue-lactophenol. Except as noted below, each estimate rests on a minimum of 300 grains per sample, and each plant was sampled twice, on different days. Pollen from all *E. congdonii* plants and from most hybrids was obtained by tapping a head over a slide, then adding a drop of cotton blue-lactophenol and a cover slip. *Eriophyllum nubigenum* treated this way mostly did not furnish enough pollen, nor did some F_1 plants closely resembling it. Here, anthers were dissected and squashed in the stain. Extensive tests showed no significant difference between the results obtained by the two techniques.

Hybridizations were made by rubbing together the flowering heads of isolated plants once a day for a period of from 3 to 5 days. Isolation consisted of separating plants so that heads were at least 15 cm apart. Caging involved placing a muslin cage around an isolated plant. Bagging is simpler but may cause hybridizations to fail (Briggs and Walters 1984, p. 190). Chromosome counts and analysis of meiosis in hybrids were obtained from microsporocytes squashed in acetocarmine and examined at diakinesis or Metaphase I with a phase microscope, following fixation of young heads in 1:3 acetic alcohol. Observation of at least 15 clear cells per plant was accompanied by sketches or camera lucida drawings of configurations. Voucher specimens were deposited in SACL. Color slides supplemented herbarium specimens. The hybrid index used Anderson's (1949) method of scoring a character as 0, 2, or 1, depending on whether it was most similar to, respectively, *E. nubigenum, E. congdonii,* or was intermediate.

RESULTS

Parental generation. Nine lots of *E. congdonii* achenes and 13 of *E. nubigenum* were sown 11 Nov 1984. Percentage germination and flowering time were similar, but pollen production and stainability varied greatly (Table 1). Germination occurred in every lot, averaging 37 to 52% in *E. congdonii* lots and 10 to 75% in *E. nubigenum* ones. The quickest germination was six days in *E. congdonii* and seven in *E. nubigenum.* The two were morphologically indistinguishable in the seedling stage, but 30 days after germination *E. congdonii* plants averaged about twice as tall and were more vigorous and resistant to wilt fungi. Distinguishing characteristics began to appear as the plants approached flowering. *Eriophyllum congdonii* tended to flower slightly earlier. The greenhouse plants of both taxa

TABLE 1. COMPARISONS OF GERMINATION, FLOWERING, AND POLLEN STAINABILITY IN ARTIFICIAL HYBRIDIZATIONS BETWEEN *ERIOPHYLLUM CONGDONII* AND *E. NUBIGENUM*.

	Percentage germination		Days, sowing to				Percentage stainable pollen		Pollen production
			First germination per lot	First flower per plant					
	X̄ ± SD	N	X̄ ± SD	Median	Range	N	X̄ ± SD	N	
Parental generation									
E. congdonii	40 ± 6	482	7 ± 1	158	32	94	98 ± 5	61	Copious
E. nubigenum	45 ± 15	63	9 ± 1	166	46	53	44 ± 19	4	Scanty
First generation									
Seed parent *E. c.*	62 ± 25		9 ± 1	162	58	66			
hybrid index values	13–16						95 ± 9	47	Copious
hybrid index values	2–12						96 ± 4	19	Copious
Seed parent *E. n.*	54 ± 32		10 ± 3	167	67	87			
hybrid index values	0–3						78 ± 17	50	Mostly copious
hybrid index values	4–14						95 ± 8	37	Copious
Second generation	59 ± 21		9 ± 2	146	79	40	90 ± 6	34	Mostly copious
Third generation	23 ± 14		—	—	—	—	—	—	

TABLE 2. COMPATIBILITY IN GREENHOUSE-GROWN *ERIOPHYLLUM CONGDONII* AND *E. NUBIGENUM*.

	Number of fruits examined per plant	Achenes black and stiff	
		N	Percentage
Isolated plants			
E. nubigenum	114	90	78.9
E. congdonii	302	18	0.6
	381	11	2.9
	629	337	53.6
	195	6	3.1
Caged plants			
E. nubigenum	20	7	35.0
	8	4	50.0
E. congdonii	12	2	16.7
	27	5	18.5
	15	0	
	7	1	14.2

were greener and more succulent than wild ones, and the *E. congdonii* ones mostly were taller and more spindly. The greenhouse plants varied, but the morphological hiatus was as wide in the greenhouse as in nature—no plants were intermediate. The onset of warm nights in late April increased the wilt (*Botrytis*?) and whitefly problems; nevertheless 93% of the *E. congdonii* and 91% of the *E. nubigenum* plants that were potted survived to flower. *Eriophyllum congdonii* produced masses of pollen whose stainability was more than double that of *E. nubigenum*. In contrast, only four *E. nubigenum* individuals released more than 100 grains. The other 50 released none or fewer than 10 (Table 1).

Self-compatibility, present in both taxa, is better developed in *E. nubigenum* (Table 2). Artificial self-pollination of caged or isolated plants was not done. Some of the viable achenes of *E. congdonii* may have resulted from pollen transfer within heads or falling from upper to lower heads of the same plant.

Estimating crossability was achieved by artificial hybridization involving 62 plants in 79 different combinations. Each cross produced viable-looking fruit. With *E. nubigenum* as the seed parent (46 crosses involving 26 *E. nubigenum* plants), 80.3% of the 5863 achenes examined were "fair to good." With *E. congdonii* as the seed parent (56 crosses involving 34 *E. congdonii* plants), only 20.4% of 6903 achenes were "fair to good."

First generation. This generation includes some plants resulting from self-pollination, because both taxa exhibit some self-compatibility. The use of the term "F_1" is consistent with P. Gray's (1967) definition, and will be used in that sense.

TABLE 3. HYBRID INDEX CHARACTERS IN *ERIOPHYLLUM NUBIGENUM* AND *E. CONGDONII.*

Characters	*E. nubigenum*	*E. congdonii*
Length of peduncle in fruit (mm)	9–23	48–152
Number of achenes per head	7–20	40–100
Involucre width (mm)	3–4	6–8
Involucre height (mm)	5–6	8–10
Number of ray flowers per head	5	7–9
Diameter of fresh head at anthesis (mm)	3–5	14–23
Number of phyllaries per head	5	8
Leaf margin	unlobed	lobed

The F_1 generation came from the most viable-looking achenes, 10 per cross, from 45 crosses, with *E. nubigenum* being the seed parent in 25 of these. Only seven were reciprocal crosses. Different *E. nubigenum* plants were used in each of the 25 crosses for which it was the seed parent, and in these crosses 22 different *E. congdonii* plants were used. Eighteen different plants of each taxon were used with *E. congdonii* as the seed parent.

The achenes were sown 16 Nov 1985. Percentage germination, onset of flowering, and pollen production and stainability varied. The fastest germination was eight days with *E. congdonii* as the seed parent, and nine days with *E. nubigenum.* Germination occurred in every lot with *E. congdonii* as the seed parent, and in 22 of the 25 lots with *E. nubigenum* as the seed parent. These three "failed" crosses involved six different plants. Replanting with the most viable-looking achenes in these "failed" crosses resulted in germination rates of 10, 36, and 71%. The germination rate per lot with *E. congdonii* as the seed parent was 10 to 100%. The germination percentage with *E. nubigenum* as the seed parent was 10 to 100 ($\bar{X}$ = 61) for the 22 lots in which germination occurred initially, compared to 0 to 100 ($\bar{X}$ = 54) for all 25 lots (Table 1). The mean for 25 lots after replanting was 59%. F_1's with *E. congdonii* as seed parent tended to flower slightly earlier (Table 1).

The morphological differences distinguishing the taxa did not appear until the F_1's began forming buds. Then some progeny began to resemble *E. congdonii,* some *E. nubigenum,* and others were intermediate. Warm nights and hotter days in April and May were associated with a higher mortality rate (mostly fungal wilt) for this generation compared to the parental one. Which taxon served as seed parent made little difference here—79% of those having *E. congdonii* as seed parent survived to flower versus 77% for those having *E. nubigenum.*

The approximately 200 adult F_1's (selfs and hybrids) comprised a spectrum that completely bridged the morphological gap between the taxa. More than half, however, strongly resembled their seed

TABLE 4. HYBRID INDEX VALUES FOR F_1'S FROM *ERIOPHYLLUM NUBIGENUM* SEED PARENTS, CROSSES 1–25.

	Hybrid index scores																	
Cross	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	N
1	3	1						1	2									7
2	2							1		1			1					5
3	4			1	1													6
4	3							1		1			1					6
5	5											1						6
6	no data																	—
7						1				1								2
8					1				1									2
9				1							1							2
10	1	1								1								3
11												1	2	1	1			5
12	1																	1
13	1													1				2
14	1	2												1				4
15	1																	1
16		2	1								1			1				5
17				1														1
18			2							1	1			1	1			6
19		4										1						5
20		2	2															4
21	1				1			1		1								4
22		1					1											2
23		2	1	1					1									5
24	2	2		1					1									6
25		1																1
Totals	25	18	6	5	3	1	1	4	5	6	3	3	4	5	2	0	0	91

parent. The 160 that survived to senescence were assigned a hybrid index number based on the characters in Table 3, "pure" *E. nubigenum* being scored 0 and "pure" *E. congdonii* 16. Table 4 details the distribution of hybrid index values in the 25 progenies with *E. nubigenum* as seed parent. No plants survived to produce complete data in cross #6, but in the others values were 0 to 14. Almost all the crosses produced dissimilar values within progenies. The most different offspring were in crosses 13 and 14 with values of 0 and 13. In several instances the widely unlike individuals were in the same pot, as in cross #13. Of the 91 individuals, 47% were scored 0 or 1, similar to or strongly resembling *E. nubigenum.* Table 5 shows the distribution of hybrid index values in the 20 crosses with *E. congdonii* as the seed parent. The spread of values within these progenies is much less than in the reciprocal kind of cross, with 8 and 16 (cross #43) being the most extreme. Again, strong within-pot differences (e.g., 8 and 15 in cross #43), indicate the effect of genetic rather than microenvironmental differences. Considering all

Table 5. Hybrid Index Values for F_1's from *Eriophyllum congdonii* Seed Parents, Crosses 26–45.

	Hybrid index scores																	
Cross	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	N
26										1	1	1	2	1	1			7
27													1	1				2
28													1	2	1	2		6
29								1						2	1			4
30	no data																	—
31									1			1	1	1				4
32											1			2		1		4
33												1	1	1				3
34										1		1	2			1	1	6
35			1															1
36	no data																	—
37	no data																	—
38												1			1	1	1	4
39														1	1			2
40													1			1	4	6
41																2		2
42															1	1	4	6
43									1					1	1	2	3	8
44																	2	2
45															1	1		2
Totals			1					1	2	2	2	5	9	12	8	12	15	69

the crosses, however, the spread of hybrid index values is as wide as in the reciprocal sort of cross, 2 to 16. These crosses also were like the reciprocals in that many of the individuals resembled the seed parent: 39% of the 69 individuals were scored 15 or 16.

Metaphase I and diakinesis studies of F_1's with hybrid index values of 8 to 14 revealed that all but one regularly formed seven bivalents, and it occasionally formed seven bivalents (Table 6). Meiosis appeared to be as regular as that in the parental taxa (Mooring 1986). Analysis at pachytene might have detected structural differences. Jackson (1984) has lamented the loss of information that comes from restricting meiotic studies to post-pachytene stages.

Mean pollen stainability was 18% lower and more variable in the

Table 6. Diakinesis and M_1 Associations in F_1 Hybrids Between *Eriophyllum congdonii* and *E. nubigenum*. The latter was the seed parent of all individuals except 26-2A.

Individual	8-1	24-3A	16-1	5-3A	19-4A	2-2B	11-1	26-2A
Association	7II	7II	7II	7II	7II	7II	7II	6II 2I
Index value	8	8	10	11	11	12	14	14
Voucher	3574	3578	—	3573	3577	3572	3575	3579

F_1's with hybrid index values of 0–3 than in the other F_1 groups shown in Table 1. All but one of the 0–3 group had *E. nubigenum* as seed parent. The stainability range was 20 to 100%, compared to 70 to 100% for plants grouped by other hybrid index values. Pollen production in the 0–3 group was low in 27 of the 50 plants. But stainability and pollen production were much higher than in *E. nubigenum* parents (Table 1).

The F_1's produced varying proportions of viable-looking (black and stiff) achenes. Pollinators were absent, but cross-pollination could occur by contact of heads, although the plants were spaced and treated to minimize that possibility. (Years of growing *E. lanatum* under similar conditions show that accidental self-pollination almost never occurs.) The high percentages (63–77) of viable-looking achenes in plants of hybrid index values (HIV) of 0–4 contrasted sharply with those (12–42) of other HIV levels. Only 14% of the HIV 0–4 individuals produced less than 50% viable-looking fruit. Viable-looking achenes generally germinated; samples taken from each of 19 F_1 plants with a HIV of 0 had germination percentages of 18 to 98 ($\bar{X} = 50$). Clearly, self-compatibility is much higher in the HIV 0–4 group.

Second generation. The F_2 generation was obtained by making 11 crosses of 16 F_1 individuals. The percentage of viable-looking achenes produced by these F_1's was 43 to 83 ($\bar{X} = 60$). The F_2 generation came from 10 of these crosses, and each cross differed in hybrid index values (Table 7). Each F_2 progeny started from 10 viable-looking achenes, which were sown 13 Dec 1986. The quickest germination was 8 days, every lot had germination, and percentage germination was 30 to 100. They flowered sooner than the preceding generations (Table 1). Most were considerably smaller and had fewer heads than the F_1's. The percentage of stainable pollen ($\bar{X} = 90$) varied only over a 17-point range. The progeny that produced no pollen numbered just four plants, and only one survived to flower. The F_2's, neither isolated nor purposely pollinated, exhibited self-compatibility. The percentage of viable-looking fruits was 19 to 68 ($\bar{X} = 43 \pm 14$).

Third generation. To test the viability of the achenes produced by the F_2 generation, all the achenes derived from four of the crosses were planted on 12 Dec 1987. Germination occurred in each lot and was 10 to 40% ($\bar{X} = 23 \pm 14$). The F_3 plants, like the F_2's, were smaller and had fewer heads than the F_1's. Pollen fertility and achene viability were not studied.

Artificial hybridizations with E. lanatum. Eriophyllum congdonii resembles *E. lanatum,* particularly vars. *achillaeoides* and *grandiflorum.* Diploid (N=8) representatives of nearby populations of both

TABLE 7. PERCENTAGE POLLEN STAINABILITY AND ACHENE VIABILITY IN UNISOLATED F_2 PLANTS.

Hybrid index values of parents		Percentage pollen grain stainability	Achenes black and stiff		
			Plants	Achenes	Percentage
	N	$\bar{X}$ ± SD	N	N	$\bar{X}$ ± SD
7 × 7	1	No pollen	1	4	75
5 × 8	1	97 ± 1	0		—
13 × 13	3	80 ± 24	1	5	40
13 × 16	6	89 ± 14	4	73	46 ± 23
7 × 15	7	93 ± 11	6	113	42 ± 17
7 × 8	4	84 ± 21	3	48	41 ± 27
7 × 12	1	98 ± 1	1	28	68
7 × 16	4	93 ± 12	4	69	42 ± 29
8 × 16	4	85 ± 3	3	49	51 ± 30
12 × 12	4	87 ± 16	5	81	19 ± 15

varieties were crossed to *E. congdonii.* The var. *achillaeoides* plant came from a Groveland population, the two var. *grandiflorum* ones from Pilot Peak. All but one of the *E. congdonii* plants came from the Trumbull Peak population. I have not found mixed stands of *E. congdonii* and *E. lanatum,* but many plants of the latter were within 100 m of *E. nubigenum* at Pilot Peak. Crosses involving var. *grandiflorum* (pollen stainabilities % 95 ± 3, 94 ± 4) were more successful than those with var. *achillaeoides* (pollen stainability % 49 ± 3). The hybrids were vigorous and morphologically more like the *E. lanatum* parent. Pollen production varied from 0 to copious, but the grains were morphologically abnormal or non-stainable, or both. The one hybrid analyzed had 15 univalents at diakinesis and M I. Attempts to cross *E. nubigenum* with var. *grandiflorum* yielded only selfs.

DISCUSSION

A caveat: Although pollen stainability is routinely used as an indicator of pollen viability (fertility), stainable grains may not germinate (Briggs and Walters 1984, p. 190; Stace 1980, p. 144). Assuming that stainability = viability, pollen of *E. congdonii* was more than twice as viable as that of *E. nubigenum* (Table 1). The greater viability and production of *E. congdonii* pollen, together with the higher degree of self-compatibility in *E. nubigenum* (Table 2), may explain the sharply different distributions of hybrid index values in Tables 4 and 5. Masses of highly viable *E. congdonii* pollen can cover the stigmas of *E. nubigenum,* whereas the scanty and lower-viability pollen of *E. nubigenum* cannot easily effect pollination on *E. congdonii* stigmas. Consequently, Table 4 shows a much greater frequency of intermediate phenotypes, with continuous hybrid index values from 0 to 14. In contrast, values in Table 5 are discontinuous and skewed toward the *E. congdonii* side. Both taxa can produce selfs, but *E. nubigenum* does so more readily, accounting for some of the 27% of the F_1's that had 0 as a hybrid index value.

Because both species are self-compatible, and the lower-viability pollen of *E. nubigenum* is scanty, what proportion of the F_1's were selfs rather than hybrids? Only 11% of the F_1's were narrowly intermediate (hybrid index values of 7–9), and hybrid intermediacy is often believed to be the norm. Hybrids, in fact, may closely resemble one of the parents (e.g., Ornduff 1969; Raven 1976; Stace 1980, p. 140). In crosses with *E. nubigenum* as the seed parent, higher pollen production and percentage stainability in the F_1's with hybrid index values of 0 support the possibility that some are hybrids rather than selfs. These F_1's usually produced much more pollen than the *E. nubigenum* plants that were tested. Pollen production and stainability in F_1's with *E. nubigenum* as seed parent were higher in those with hybrid index values of 1, 2, and 3 than in those with 0.

The crossing program revealed no barriers to interbreeding. The number and variety of the crosses should have adequately sampled the genetic diversity in the Pilot Peak population. Over 60% of the crosses (Tables 4, 5) show representatives in the 4–12 columns that portray clearly intermediate phenotypes. Moreover, although 63% of the F_1's showed parental resemblances (hybrid index values of 0–3 or 13–16), many of those in the 0–3 category may have been hybrids rather than selfs, as discussed above. Percentage germination of the most viable-looking achenes in the F_1 and the F_2 generations exceeded the germination of unselected achenes in the parental generation. Pollen stainability was high (Table 1). Vigor in the F_1's equalled or exceeded that of the parents, although survival to flowering was 85% of that in the parental generation. Most of the F_2's, however, were less vigorous, and 68% survived to flower, versus 92% and 78% for, respectively, the parental and F_1 generations. I attribute the reduced vigor to the fact that this generation was planted 27 days later in the growing season than the F_1 generation. A hot period in early April probably resulted in higher mortality and earlier maturation (Table 1). Hybrid weakness, however, cannot be eliminated as a possible cause of reduced vigor. Percentage germination in the F_3 generation was 39% of that in the F_2, and the F_3's had reduced vigor comparable to the F_2's. If "hybrid weakness" was present, it was much less than that described in *Layia* and *Zauschneria* (Clausen 1951, pp. 108–111).

Artificial hybridizations of *E. congdonii* to *E. nubigenum* derived from the Yosemite National Park populations might show barriers to gene exchange. The Park populations are on granitic rather than metamorphic rock, and are separated from the Pilot Peak population by about 30 km (Fig. 1). Autogamous annuals whose population size may vary erratically from year to year probably are more genetically variable than their morphology suggests. Strid (1972) found semi-sterility in 36% of the F_1 combinations among populations of *Nigella doerfleri,* an autogamous annual of the Aegean Islands. The populations of *E. nubigenum* likewise have an "island" distribution (Fig. 1). Instances of intersterility or reduced fertility between populations of the same taxonomic species are known, e.g., *Clarkia rhomboidea* (Mosquin 1964) and *Lasthenia californica* (as *L. chrysostoma*) (Ornduff 1966).

The morphological differences that distinguish *E. nubigenum* from *E. congdonii* in nature also exist in the greenhouse, and the gap between the taxa there is equally wide. The closest approaches to an intermediate condition were a few dwarfed *E. congdonii* individuals with smaller ligules and reduced leaf lobing. The characters that distinguish *E. nubigenum* from *E. congdonii* are thus genetic and are not environmental modifications. These results do not support Constance's (1937, p. 116) hypothesis that they are one species, with *E. congdonii* being the low-elevation and normal phase and *E. nubigenum* its "dwarfed alpine representative." On the other hand, the experimental demonstration of the vigor and fertility of the F_1 generation and the fertility of the F_2 generation show that the taxa are interfertile.

The taxa could be treated as species or subspecies, depending on the relative importance given to interfertility. Species status seems more practical. They are morphologically clearly distinct, and distance, flowering period, and the inbreeding system of *E. nubigenum* suggest that natural hybridization would be unlikely. The closest approach to sympatry seems to be the 11 km distance between the Trumbull Peak and Pilot Peak populations of *E. congdonii* and *E. nubigenum,* respectively. Trumbull Peak is about 300 m lower. Environmental conditions seem similar, although soil pH (colorimetric test) was about 5 rather than the 6 obtained for Pilot Peak. On 25 Jun 1984, the numerous *E. congdonii* plants were all dead but had not shed their fruit. In contrast, the far fewer *E. nubigenum* individuals were in late flower and early fruit. In the greenhouse *E. congdonii* flowered a few days earlier, but the flowering period overlapped by a month. A species of beetle visited the El Portal plants of *E. congdonii,* but no potential pollinators were seen at Pilot Peak. Meager observations of greenhouse plants of both taxa that were placed in a garden showed that bees and syrphid flies visited *E. congdonii* but not *E. nubigenum.* The paucity and lower viability of its pollen, and the seeming lack of pollinators suggest that *E. nubigenum* would be unlikely to serve as the pollen parent in nature. Interfertility under garden conditions could not be tested because greenhouse plants died before they could be moved to the garden.

Those wedded to one of the biological species concepts (BSC) (Templeton 1989) may prefer subspecific rather than specific rank. After all, the taxa are interfertile, but so are many taxonomically "good" species. Baker (1970), Raven (1976, 1980), Jonsell (1984), Barrett (1989) and Stuessy (1990), among others, have discussed the utility of the BSC. Grant (1981, p. 145) tabulated crossability and hybrid sterility by life form. Interfertility in annuals, in contrast to woody and herbaceous perennials, is uncommon. I believe that the BSC should not be a shibboleth that obscures recognition of two distinct, allopatric, rare taxa. The survival of *E. nubigenum* may depend on its not being confused with the more abundant *E. congdonii.*

Constance (1937, p. 72) suggested that among eriophyllums the variable *E. lanatum,* a biennial or herbaceous perennial, had the largest number of characters believed to be primitive, and that either var. *achillaeoides* or var. *grandiflorum* was "basal" in that species. He hypothesized (p. 73) that *E. nubigenum* originated from *E. lanatum,* and *E. congdonii* from *E. nubigenum.* Autogamy probably is more frequently a derived condition, so an *E. lanatum–E. congdonii–E. nubigenum* phylogeny seems more likely. Possibly *E. congdonii* has originated from *E. lanatum* relatively recently by quantum speciation (Grant 1981, pp. 155–160) involving chromosome repatterning and a loss of a pair of centromeres. Population structure and environmental conditions here favor rapid speciation. The origin of *Clarkia lingulata* from *C. biloba* (Lewis and Roberts 1956), a classic example of quantum speciation (Grant 1981, pp. 155–160) by chromosome repatterning, occurred nearby in the Merced River canyon. *Eriophyllum nubigenum* probably has been derived from *E. congdonii* through decrease in ligule size and a shift to autogamy. Ligules are absent in the annual *E. pringlei,* and frequently absent in some individuals or populations of the perennials *E. confertiflorum* and *E. tanacetiflorum,* as well as in vars. *achillaeoides, grandiflorum,* and *leucophyllum* of the *E. lanatum* complex.

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PERCENTAGE SEED SET, SPROUTING HABIT AND PLOIDY LEVEL IN *ARCTOSTAPHYLOS* (ERICACEAE)

VICTORIA R. KELLY[1] and V. THOMAS PARKER
Department of Biology, San Francisco State University,
San Francisco, CA 94132

ABSTRACT

Comparisons of sprouting and nonsprouting, diploid ($2n$) and tetraploid ($4n$) *Arctostaphylos* species revealed that reduced seed set was associated with tetraploidy in addition to the sprouting habit. When sprouting and nonsprouting species were combined, percentage seed set values, measured as seed to ovule ratios, were significantly higher for $2n$ species than for $4n$ species ($P < 0.01$), but when $2n$ and $4n$ species were combined, comparisons between sprouting and nonsprouting species were not significantly different. Sprouting $4n$ species consistently had the lowest seed set values. These results have important implications for interpretation of comparative life history studies among sprouting and nonsprouting *Arctostaphylos* species.

Comparative seed bank studies of post-fire sprouting and nonsprouting *Arctostaphylos* species have reported lower seed viability, and consequently lower viable seed bank densities among sprouters (Keeley 1977, 1987; Kelly 1986; Kelly and Parker 1990). All sprouters examined in the above studies, however, were tetraploid whereas the nonsprouters were diploid (Wells 1968). (Most *Arctostaphylos* sprouters are tetraploid.) Thus, lower number of viable seeds seems to be associated with two characteristics, ploidy level and life history (sprouting and nonsprouting).

Differences among sprouters and nonsprouters in several papers have favored nonsprouters, and have often been interpreted as being the result of differential life history selection (Carpenter and Recher 1979; Fulton and Carpenter 1979; Parker 1984). However, the conclusions reached in the studies favoring nonsprouters have not always been consistent with regard to differences between sprouters and nonsprouters in seed production or persistent seed bank sizes in other studies (e.g., Keeley 1977; Lamont 1985; Kelly and Parker 1990; Cowling et al. 1987). These inconsistencies may result from factors not taken into account, such as reduced seed set. We propose that for *Arctostaphylos* species, lower seed numbers among sprouters is associated with ploidy rather than the sprouting character. The purpose of this study, therefore, was to test the null hypothesis that tetraploid and diploid *Arctostaphylos* species set the same percentage of seeds regardless of their ability to sprout.

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[1] Present address: Institute of Ecosystem Studies, The New York Botanical Garden, Mary Flagler Cary Arboretum, Millbrook, NY 12545.

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METHODS

Seed to ovule ratios were used to estimate seed set for fourteen (1986) and seven (1987) sprouting and nonsprouting *Arctostaphylos* species from widely separated locations in California. Ratios were determined by dividing the mean number of seeds per fruit by the mean number of ovules per ovary. The ovaries and fruit used were only those not damaged by insects or any other outside forces. Seeds were counted only if they were plump and white, which indicates a viable seed. Sample sizes were determined by availability and varied from 10 to 100 for ovaries, and 10 to 50 for fruit. Flowers and fruit were collected at the peak of flowering or fruiting season, from all sides of the plants, and from at least 10 different plants at each location or as many plants as were bearing flowers or fruit.

To avoid differences due to environmental limitations, we examined species from widely separated locations, and as much as possible, we chose sites that contained more than one species, preferably, species that differed in ploidy. The species examined, their ploidy level (Wells 1968) ($2n$ = diploid, $4n$ = tetraploid), mode of reproduction (S = sprouting, NS = nonsprouting), locations and respective elevations were: *A. patula* E. Greene ($2n$, S) and *A. mewukka* Merriam ($4n$, S) from Peavine Ridge, El Dorado County (1600 m); *A. stanfordiana* Parry ($2n$, NS), *A. glandulosa* Eastw. ($4n$, S) (900 m) and *A. manzanita* C. Parry ($4n$, NS) (700 m), from Hopland Research Station, Mendocino County; *A. pungens* Kunth var. *montana* (Eastw.) Munz ($4n$, NS) (350 m), *A. glandulosa* ($4n$, S) (400 m) from Carson Ridge, Marin County; *A. canescens* Eastw. ($2n$, NS) and *A. glandulosa* ($4n$, S) from Mt. Tamalpais, Marin County (600 m); *A. andersonii* A. Gray var. *imbricata* (Eastw.) J. Adams ex McMinn ($2n$, NS) and *A. tomentosa* (Pursh) Lindl. ($4n$, S) from San Pedro Valley Park, Pacifica, San Mateo County (60 m); *A. glauca* Lindl. ($2n$, NS) from Henry Coe State Park, Santa Clara County (750 m); *A. morroensis* Wiesl. Schreib. ($2n$, NS) from Montaña de Oro State Park, San Luis Obispo County (60 m); *A. rudis* Jeps. & Wiesl. ($2n$, S) from Burton Mesa, Santa Barbara County (85 m); and *A. pugens* Kunth ($2n$, NS) from Hwy. 79, San Diego County (1100 m). Nomenclature follows Munz (1959).

The 1986 percentage seed set values of all diploid and tetraploid species (regardless of habit) were combined and compared using Wilcoxon's rank-sum test (SAS 1987). Likewise, 1986 percentage seed set values for all sprouting and nonsprouting species (regardless of ploidy) were combined and compared using the same test. The 1987 data were not tested for significance because they do not differ substantially from 1986 data and because there are too few data to warrant statistical analysis.

TABLE 1. MEAN NUMBER OF OVULES PER OVARY, SEEDS PER FRUIT AND PERCENTAGE SEED SET FOR 1986 AND 1987 FOR SPROUTING AND NONSPROUTING 2N AND 4N *ARCTOSTAPHYLOS* SPECIES. Sample sizes are 100 ovaries and 50 fruit for 1986, and 50 ovaries and fruit for 1987 except where noted in parentheses.

	1986			1987		
Species	Ovules (N)	Seeds (N)	% Seed set	Ovules (N)	Seeds (N)	% Seed set
2*n*, NS						
A. stanfordiana	6.10	4.20	68.8			
A. canescens	8.07	5.76	71.4			
A. andersonii var. *imbricata*	7.27	4.52	62.2	7.46	5.53 (15)	74.1
A. glauca	6.20	3.70	59.7	6.16	3.65 (17)	59.3
A. morroensis	7.29	5.32	73.0			
A. pungens				6.12	4.90	80.1
			$\bar{X}$ = 69%			$\bar{X}$ = 71%
2*n*, S						
A. patula	6.84	4.25 (12)	62.1			
A. rudis	5.86	4.62	78.8	6.12	4.24	69.3
			$\bar{X}$ = 70%			$\bar{X}$ = 69%
4*n*, NS						
A. manzanita	6.52	3.30	50.6	6.58	4.17 (12)	63.4
A. pungens var. *montana*	7.06	4.90	69.4	7.02	4.20 (10)	59.8
			$\bar{X}$ = 60%			$\bar{X}$ = 62%
4*n*, S						
A. mewukka	7.60	3.94 (17)	51.8			
A. glandulosa (Hopland)	7.40 (50)	3.70	50.0			
A. glandulosa (Carson Ridge)	7.56 (50)	3.84	50.8			
A. glandulosa (Mt. Tamalpais)	7.58	4.70	62.0			
A. tomentosa	7.89	4.50 (15)	57.0	7.70 (10)	2.50 (10)	32.5
			$\bar{X}$ = 54%			$\bar{X}$ = 32%
		2*n*	$\bar{X}$ = 68%* (SD = 7.0, N = 7)			
		4*n*	$\bar{X}$ = 56%* (SD = 7.4, N = 7)			
		NS	$\bar{X}$ = 65% (SD = 8.0, N = 7)			
		S	$\bar{X}$ = 59% (SD = 10.1, N = 7)			

* Differences between 2*n* and 4*n* species significant at $P < 0.01$.
Differences between NS and S species not significant.

RESULTS

Mean number of ovules per ovary, seeds per fruit and percentage seed set values for 1986 and 1987 are summarized in Table 1. The values for mean number of ovules per ovary in 1987 were all within 96% of 1986 values, but the mean number of seeds per fruit varied between years from 56% to 99%. The variation between years may be due to environmental variability during seed set within a site between years.

Overall, in each year the average percentage seed set values were higher for $2n$ species than for $4n$ species ($P < 0.01$ for 1986) and $4n$ sprouters had the lowest average seed set. Differences between sprouting and nonsprouting species in percentage seed set in 1986 were not significantly different. The four types of species for 1986 ranged from high to low in this order: $2n$, *S* > $2n$, NS > $4n$, NS > $4n$, S; and for 1987 in this order: $2n$, NS > $2n$, S > $4n$, NS > $4n$, S. Within sites, the lowest percentage seed set values consistently belonged to $4n$ sprouters. For example, at Hopland, where a $4n$ nonsprouter occurred with a $2n$ nonsprouter and a $4n$ sprouter, percentage seed set ranged accordingly: $2n$, NS > $4n$, NS > $4n$, S.

DISCUSSION

Comparisons among several sets of sprouting and nonsprouting tetraploid ($4n$) and diploid ($2n$) *Arctostaphylos* species revealed that tetraploids showed significantly reduced percentage seed set, and that seed set was lowest among sprouting $4n$ species (Table 1). Sterility and polyploidy were discussed by Stebbins (1947, 1950, 1980) and evidenced in the work of Birari (1980). Polyploid species often show reduced fertility (deWet 1980), usually due to meiotic chromosomal irregularities and cytologically unbalanced gametes (Stebbins 1971). The absence of sterility in old, established polyploids is probably due to selection in the past for genetic changes that led to progressive "diploidization" so that meiotic pairing resembles that of diploids (Stebbins 1947, 1950). Alternatively, reduced seed fertility may be overcome by asexual reproduction, which may be the case for $4n$ sprouting *Arctostaphylos* species. Reduced fertility also has been found in some polyploid species where regular meiosis was observed; the lower fertility was attributed to physiological disturbances (Tal 1980).

In this study, we found consistently higher percentage seed set in $4n$ nonsprouting species than in $4n$ sprouters. These results seem contrary to what we expected, which was equal seed set between $4n$ sprouters and nonsprouters. However, nonsprouters suffer the risk of becoming eliminated upon disturbance unless they reproduce by seed. It may be, then, that selection for "diploidization" is stronger in 4*n* nonsprouting species than in sprouting species. Sprouting species are usually well-established in their habitats because they have retained or developed the ability to continuously resprout after fires. Therefore, selection for increased ability to set seed among 4*n* sprouting species may not be as strong as for 4*n* nonsprouting species.

The high incidence of reduced seed set among 4*n* species and especially in 4*n* sprouting species suggests that the number of seeds produced and seen in the seed banks of *Arctostaphylos* species is largely associated with the genetics of these organisms rather than their ecological mode of regeneration. It would be erroneous to interpret these patterns simply in terms of life history selection. The evolution of ecological differences between sprouting 4*n* and nonsprouting 2*n* species is probably largely a result of their ploidal history as well as ecological conditions.

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NOTES

NOMENCLATURAL CHANGE IN *SISYRINCHIUM DOUGLASII*.—Anita F. Cholewa, Department of Plant Biology, University of Minnesota, St. Paul, MN 55108 and Douglass M. Henderson, Department of Biological Sciences, University of Idaho, Moscow, ID 83843.

Recent phylogenetic work in *Sisyrinchium* and its relatives by Goldblatt et al. (1990, Systematic Botany 15:497–510) has revived the genus *Olsynium.* The latter name was first used by Rafinesque (1836, New flora and botany of North America 1:72) and generally included those species with terete stems, non-equitant leaves, pink to purple flowers, and a filament tube somewhat inflated at the base. The only North American species is *Olsynium douglasii* (A. Diet.) Bickn., found in the Pacific Northwest, the northern Intermountain Region, and California. The resurrection of the genus, with which we fully agree, requires that the following new combination be made.

OLSYNIUM DOUGLASII (A. Dietr.) Bickn. var. INFLATUM (Suksd.) Cholewa & Henderson, comb. nov.—TYPE: USA, Washington, Spangle, 24 April 1916, *Suksdorf 8507* (lectotype designated in Cholewa & Henderson [1985, Brittonia 37:163–164]: WS!)—*Olsynium inflatum* Suksd., Werdenda 1:8. 1923.—*Sisyrinchium inflatum* (Suksd.) St. John, Report of the Provincial Museum of Natural History B.C. 1930:12. 1931.—*Sisyrinchium douglasii* A. Dietr. var. *inflatum* (Suksd.) P. Holmgren, Intermountain Flora, Vol. 6:540. 1977.

SISYRINCHIUM INFLATUM (Sudsd.) St. John f. ALBA St. John, Rep. Prov. Mus. Nat. Hist. B.C. 1930:12. 1931.—TYPE: USA, Washington, Yakima Co., Glade Creek, 3 km N of Bluelight. 12 Apr 1929, *St. John et al. 9785* (holotype: WS!).

SISYRINCHIUM INALATUM A. Nelson, Bot. Gaz. 54:136. 1912.—TYPE: USA, Idaho, Owyhee Co., Silver City, 17 Jun 1911, *Macbride 909* (holotype: RM).

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RECOGNITION OF THE TETRAPLOID, *POLYPODIUM CALIRHIZA* (POLYPODIACEAE), IN WESTERN NORTH AMERICA

SHERRY A. WHITMORE
Department of Biological Sciences, University of California,
Santa Barbara, CA 93106

ALAN R. SMITH
University Herbarium, University of California,
Berkeley, CA 94720

ABSTRACT

Taxonomic study of the *Polypodium californicum/glycyrrhiza* complex in California reveals four taxa: a tetraploid, a triploid, and two diploids, *P. californicum* and *P. glycyrrhiza.* The tetraploid, here named *Polypodium calirhiza,* mimics some forms of *P. californicum* in southern California but is readily distinct in northern and central parts of the state. It is probably of allopolyploid origin involving the two diploids, as judged by its morphological intermediacy and chromosome pairing in triploid hybrids with *P. glycyrrhiza.* A principal components analysis also demonstrates this intermediacy. *Polypodium calirhiza* shows a wider tolerance for different habitats and greater range than either of its putative parents.

RESUMEN

El estudio taxonómico del complejo *Polypodium californicum/glycyrrhiza* en California revela cuatro taxa: un tetraploide, un triploide, y dos diploides, *P. californicum* y *P. glycyrrhiza.* El tetraploide, aquí nombrado *Polypodium calirhiza,* mimetiza algunas formas de *P. californicum* en el sur de California pero es fácilmente distinguible de los áreas de norte y centro del estado. Probablemente esta nueva especie sea de origen alopoliploide implicando los dos diploides a juzgar por su forma intermedia morfológicomente y su sinapsis cromosómico en híbridos triploides con *P. glycyrrhiza.* Un análisis de los componentes principales también demuestra esta naturaleza intermedia. *Polypodium calirhiza* demuestra una mejor tolerancia a más diversos hábitates y una área de distribución más amplia que cualquiera de sus dos teóricos progenitores.

The *Polypodium vulgare* L. group, comprising perhaps 15 mostly north-temperate species worldwide, is represented in California by six species and several hybrids. Recent cytological and electrophoretic data have provided solid evidence for the relationships among western North American species, and have allowed circumscription of biologically discrete taxa. Such studies also have allowed an assessment of kinship to species from outside western North America.

Perhaps the most difficult problem taxonomically in California has involved *P. californicum* Kaulf. sensu lato (Lloyd 1962; Lloyd and Lang 1964). Hooker and Arnott (1840) distinguished *P. inter-*

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medium and implied that their new species was intermediate between *P. californicum* and *P. vulgare* L., the latter based on a European type. The original circumscriptions of *P. californicum* and *P. intermedium,* even though somewhat vague, represented a separation of diploid and tetraploid cytotypes respectively; however, chromosome information would not be forthcoming for more than 100 years. It is now known that the type of *P. californicum* is very likely diploid, whereas the type of *P. intermedium* appears to be tetraploid.

Several authors (Eaton 1877–1879; Fernald 1922; Farwell 1931) subsequently made new combinations with these epithets. Unfortunately, they included both diploids and tetraploids for each taxon in their lists of representative specimens and used these specimens to expand descriptions of the taxa. Munz and Johnston (1922) added to the confusion by recognizing var. *kaulfussii* D. Eaton, a name homotypically synonymous with *P. californicum,* as a distinct entity. More recent treatments in regional and local floras (e.g., Howell et al. 1958; Munz 1973) have followed Abrams (1923) in the recognition of *P. californicum,* the placement of *P. intermedium* in synonymy, and the acceptance of var. *kaulfussii* as a distinct variety.

The first chromosome counts for *P. californicum* s.l. (Manton 1951) were tetraploid, $n = 74$. Lloyd (1962, 1963) discovered that *P. californicum* included both diploid and tetraploid entities. Lloyd and Lang (1964) retained both cytotypes under *P. californicum,* but they hypothesized that the tetraploid was possibly an alloploid arising from hybridization between diploids *P. californicum* and *P. glycyrrhiza* (Lloyd 1962; Lloyd and Lang 1964). Lovis (1977), using morphology alone, and Ranker (1982) and Ranker and Mesler (1982), using also guard cell and spore length, suggested both autoploid and alloploid origins for the tetraploids. By measuring guard cells of plants of known ploidy and using calculations to predict expected guard cell size in diploid parents and polyploid offspring, Barrington et al. (1986) refuted the autoploid hypothesis and supported the alloploid origin for the tetraploid.

Previous studies using morphological, cytological, karyotypic, chemical (flavonoid), and electrophoretic evidence have revealed that several other tetraploids in *Polypodium* are of allopolyploid origin. These include *P. vulgare* (Manton 1947, 1951, 1958; Shivas 1961a, b) and *P. interjectum* Shivas (Manton 1950; Shivas 1961a, b; Murray 1985) in Europe and *P. hesperium* Maxon (Lang 1965, 1971; Windham 1985) and *P. virginianum* (Manton 1957, 1958; Shivas 1961a; Evans 1970; Bryan and Soltis 1987) in North America. Even though autoploid origins have been suggested for several taxa, no autoploids have been verified in any of these species. The predominance of allopolyploidy as a speciation mechanism in this group has recently been reemphasized by Haufler and Windham (1991), who implicate a boreal diploid, *P. sibericum* Siplivinskij, in the formation of two tetraploids, *P. saximontanum* Windham and *P. virginianum.*

It has become clear to us that the most widespread polypody in California is tetraploid. It shows generally additive morphology between two diploids, *P. glycyrrhiza* and *P. californicum.* Although the tetraploid, here named *P. calirhiza,* is of probable hybrid origin, it behaves as a distinct species. It shows no apparent reduction in fertility and has a widespread distribution with distinct habitat and community preferences, indicating a well-established species. Generally it is allopatric with respect to *P. californicum*; in the San Francisco Bay area and the Monterey/Pt. Lobos area the ranges of the two overlap, but field work has shown different habitat preferences. We have not seen the two growing together in the same population.

The decision to recognize the allotetraploid as a distinct species made it necessary to ascertain whether the name *P. californicum* had originally been applied to the diploid or the tetraploid. The original description of *P. californicum* is inconclusive, but probable type material at LE is clearly conspecific with specimens we regard as diploid (Whitmore, ms.). Because there exists no available name at species rank for the tetraploid, we describe it as new and base it on a specimen of known ploidy.

Polypodium calirhiza S. Whitm. & A. R. Smith, sp. nov. (Fig. 1)—Type: USA, California, Contra Costa Co., Mount Diablo, arroyo on S slopes, 1.2 miles N of south gate entry to Mount Diablo State Park along South Gate Road, 1 Jan 1982, $2n = 74$ II, *Whitmore 1388* (holotype, UCSB; isotypes, UC, US, RSA, from same rhizome as holotype).

Polypodium intermedium Hook. & Arn. (non Colla, 1836), Bot. Beechey Voy. 405. 1840, a later homonym and hence illegitimate.—*Polypodium californicum* Kaulf. var. *intermedium* D. Eaton, Ferns N. Amer. 1:244, pl. 31. 1878.—*Polypodium vulgare* L. var. *intermedium* (D. Eaton) Fernald, Rhodora 24:139. 1922.—*Goniophlebium cambricum* (L.) Farwell var. *intermedium* (D. Eaton) Farwell, Amer. Midl. Naturalist 12:295. 1931.—Type: [USA], California, [San Francisco Co.], San Francisco, *Sinclair s.n.* (holotype, K!, frond on left side of sheet; photo, UC!).

Polypodium vulgare L. var. *intermedium* (D. Eaton) Fernald forma *projectum* Fernald, Rhodora 24:140. 1922.—Type: [USA], California, Butte Co., Chico Canyon, *Copeland 2749* (holotype, GH; isotype, POM!).

Polypodium californicum Kaulf. forma *parsonsiae* C. Morton, Amer. Fern J. 51:75. 1961.—Type: greenhouse specimen originally

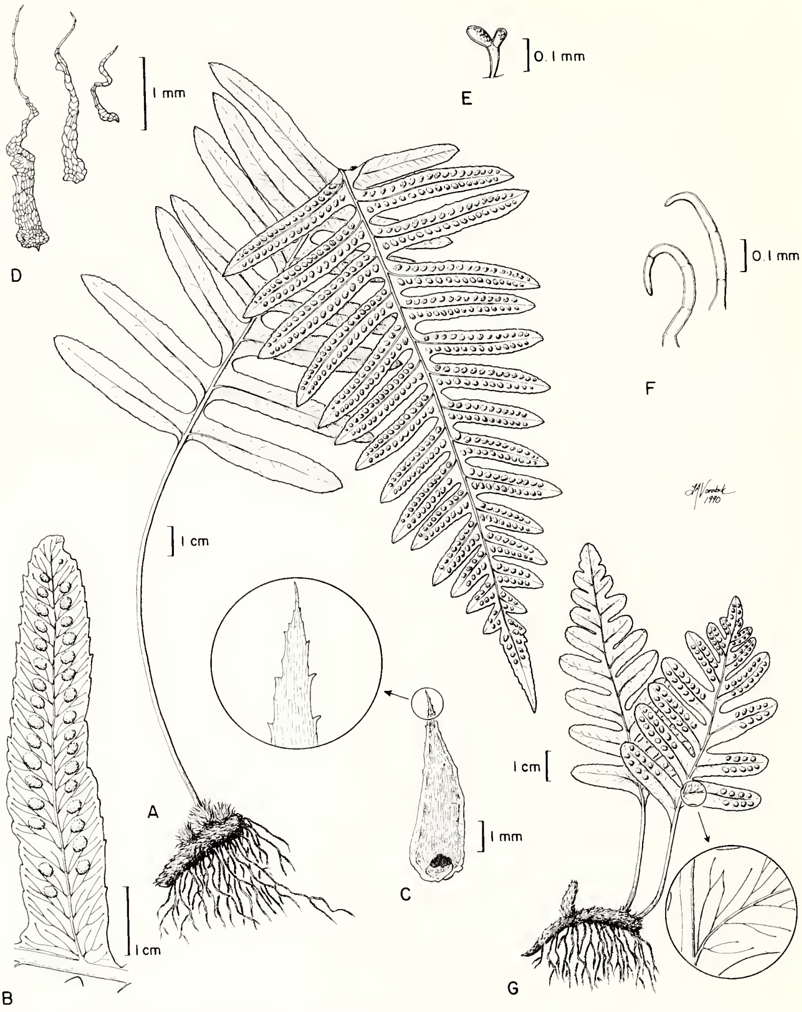

FIG. 1. *Polypodium calirhiza.* A, habit (A–C drawn from *Whitmore 1391,* UC, a topotype). B, pinna. C, rhizome scale. D, stipe and rachis scales (*Whitmore et al. 786,* UCSB). E, glandular trichome from abaxial epidermal surface (*Whitmore 948,* UCSB). F, arcuate, non-glandular trichome from adaxial rachis, typically found on specimens of *P. calirhiza.* G, habit (*Constance 494,* UC).

from USA, California, Marin Co., near Kentfield, 14 Sep 1903, *Parsons s.n.* (holotype, US!).

A *Polypodio californico* et *P. glycyrrhiza* combinatione characterum sequentium differt: rhizomatibus parum dulcibus et acerbis; frondibus demissis; paleis stipitum et rhachidum lanceolato-ovatis, 4–8(–12) cellulis in latitudine; laminis oblongo-ovatis, leviter glaucis abaxialiter; pinnis acutis vel obtusis ad apicem; venis irregularibus, perparce vel plerumque anastomosantibus usque ad 33(–56)%; soris ovalibus, (1.5–)2–4 mm diametro; sporis verrucatis vel tuberculatis, ut videtur normalibus; chromosomatum numero $2n = 74$ II.

Rhizome creeping, 5–10 mm diam., pale brown with an acrid plus slightly sweet taste, covered with acuminate, light brown scales; stipe green to greenish brown; abaxial surface of distal part of stipe and proximal part of rachis and costae sparsely covered with light brown, very narrowly acuminate, caducous scales with slightly erose margins; abaxial surface of the lamina with short, 2–3(–8)-celled, branched or unbranched, glandular trichomes; adaxial surface of the rachis and costae densely to moderately pubescent with arcuate, multicellular (4–8–celled), uniseriate, non-glandular trichomes and with occasional, short, 2–3(–8)-celled, branched or unbranched, glandular trichomes; blade oblong-ovate, normally pinnatifid although occasionally with secondary pinnatification of proximal pinnae, herbaceous to chartaceous, stiff, slightly thickened, 10–20(5–40) × 4–9(3–15) cm; 8–12(6–25) pinna-pairs per frond; pinnae narrowly oblong, proximal 1–3 pairs distinctly shorter than middle pinnae, tips acute to somewhat obtuse with conspicuous serrations, margins serrate to dentate, with the teeth spreading; veins mostly free, anastomosing irregularly and only occasionally near rachis, to anastomosing more frequently between the rachis and the proximal ⅓–½ of pinna, number of anastomosing pairs per pinna 0–several, occasionally many, varying from pinna to pinna on each blade; vein pathways commonly slightly uneven and forming an irregular pattern; sori oval, orange-brown to brown, (1.5–)2–4 × 1–2 mm, distinctly raised, often increasing in size closer to rachis, sometimes becoming confluent near rachis, lacking soral sporangiasters or paraphyses with sporangial-length stalks; capsule of sporangium without trichomes and with 11–14(8–17) indurated annulus cells; spores bilateral, yellow at maturity with coarsely verrucate to tuberculate surface, 57–86 μm long (mean = 68 μm; measurements include tubercles); chromosome number $2n = 74$ II.

The epithet *calirhiza* is derived by combining parts of the names of the putative parents, *P. californicum* and *P. glycyrrhiza.*

Representative specimens.—MEXICO: MEXICO: Munic. Tezcoco, 14 km SE of Tezcoco, 9 km SE of Tequesquinahuac, on Cerro Tlaloc, 22 Feb 1978, *Koch 789* [*7809*?] (NY). OAXACA: Dist. Ixtlán, S edge of Cuajimoloyas, 23 km N of Dias Ordaz, 2 Oct 1973, *Mickel 7426* (NY, UCSB).

UNITED STATES: CALIFORNIA: Alameda Co., Redwood Ridge, 23 Mar 1932, *Constance 494* (UC); Amador Co., Ione, Dec 1904, *Braunton 1265* (NY, UC); Amador Co., Ione, Dec 1904, *Braunton s.n.* (POM); Butte Co., Feather River, near Yankee Hill, 29 Mar 1919, *Heller 13090* (CAS); Contra Costa Co., Mount Diablo State Park, ridge above Devil's Elbow Trail, 19 Nov 1981, *Smith & Lemieux 828* (UC); Humboldt Co., Ocean Beach at Samoa, opposite Eureka, 27 Jan 1901, *Tracy 985* (UC); Kern Co., Tehachapi Mountains, El Paso Canyon, Tejon Ranch, 23 May 1961, *Twisselmann 6162* (CAS); Lake Co., Mount Konocti, 7 Mar 1923, *Blankinship s.n.* (CAS); Marin Co., Mt. Tamalpais, Jun 1874, *McLean s.n.* (UC); Marin Co., near Stinson Beach School, 3 Mar 1962, *Penalosa 2244* (CAS); Marin Co., Point Reyes National Seashore, along Sky Trail, 31 Dec 1981, *Smith 835* (UC); Mariposa Co., Yosemite National Park, above Tunnel View on Fresno Road, 20 Dec 1981, *Parris & Croxall 9654* (K); Mendocino Co., Russian Gulch State Park, 29 Jul 1961, *Lloyd 502* (RSA); Napa Co., St. Helena Creek, near Patten's, 21 Mar 1926, *Howell 1729* (CAS); Nevada Co., Sierra Nevada Mountains, South Yuba River, Excelsior Ditch, Feb 1966, *Mott s.n.* (CAS); Plumas Co., canyon of the North Fork of the Feather River, granite near mouth of Chambers Creek, 22 Jun 1967, *Howell 42658* (CAS); San Benito Co., Pinnacles National Monument, along Bear Gulch Trail, Dec 1981, *Smith 831* (UC); San Francisco Co., San Francisco, gully S of Stanley Drive, E of Lake Merced, 4 Nov 1956, *Rubtzoff 3054* (CAS, RSA); San Mateo Co., San Bruno Mountain, 9 Mar 1963, *Penalosa 2700* (CAS); Santa Clara Co., foothills W of Los Gatos, 5 Mar 1904, *Heller 7255* (NY, UC); Sierra Co., Sierra Nevada, Sierra Valley, E of Downieville and Sierra City, NE of Yuba Pass, along Highway 49, 1880, *Lemmon s.n.* (POM); Siskiyou Co., Klamath National Forest, Indian Creek, 4 ml N of Happy Camp, 13 Aug 1934, *Lee 1056* (UC); Solano Co., Vaca Mountains, N of Fairfield, 16 Jan 1954, *Raven 6376* (CAS); Sonoma Co., Adobe Canyon, Mar 1892, *Michener & Bioletti s.n.* (UC); Sutter Co., S part of Marysville Buttes [Sutter Buttes], 7 Apr 1928, *Vortriede s.n.* (CAS); Tulare Co., southern Sierra Nevada, Tule River Canyon, Soda Creek, 27 Jul 1963, *Kiefer 647* (LA); Tuolumne Co., Italian Bar, 5 Jun 1915, *Jepson 6365* (JEPS, UC). OREGON: Lincoln Co., near ocean shore S of Newport, 18 May 1918, *Lawrence 1484* (UC).

Distribution (Fig. 2).—*Polypodium calirhiza* occurs throughout the coast ranges of northern and central California to Anastasia Canyon, Monterey Co., through the interior foothills of the Sierra Nevada from the Feather River, Plumas Co., south to the Tehachapi Mountains in Kern Co. It is slightly disjunct in the coast ranges at Newport, Oregon, and greatly disjunct in the states of Mexico and Oaxaca (Mickel and Beitel 1988) in southern Mexico.

Habitat.—The distribution of *P. calirhiza* includes a wide diversity of habitats and vegetation types ranging from coastal headlands to the drier interior foothill regions. In the central California coast ranges it is found in mixed evergreen forest, oak savanna, riparian

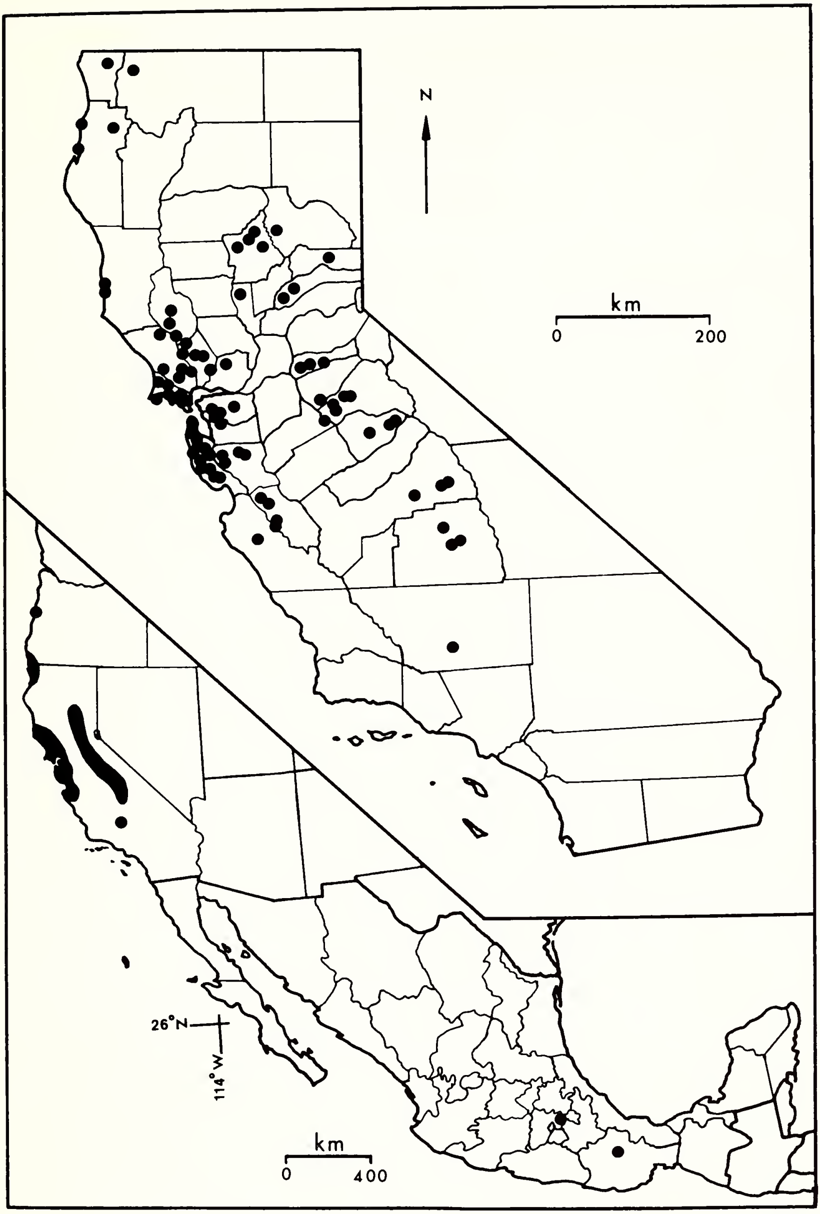

FIG. 2. Distribution of *Polypodium calirhiza*. Each dot represents one or more collections at single site, or two or more at adjacent sites.

TABLE 1. CHROMOSOME COUNT VOUCHERS FOR *POLYPODIUM CALIRHIZA*. ALL COUNTS ARE $2N = 74$ II OR CA. 74 II. VOUCHERS ARE IN UCSB UNLESS OTHERWISE INDICATED.

USA: California: Alameda Co.: Redwood Regional Park, 14 Mar 1981, *Smith 811* (UC). Contra Costa Co.: Mt. Diablo St. Park, N slope of Mt. Diablo, 19 Nov 1981, *Smith (& Lemieux) 826* (UC), above Devil's Elbow Trail, *Smith (& Lemieux) 828* (UC); Mt. Diablo, S slopes, along South Gate Road, 1 Jan 1982, *Whitmore 1388*. Marin Co.: Pt. Reyes Nat. Seashore, Pt. Reyes, 6 Feb 1979, *Whitmore et al. 433*; San Anselmo, Sir Francis Drake Blvd., 16 Nov 1979, *Whitmore 692*; San Anselmo, Sir Francis Drake Blvd., 6 Feb 1980, *Whitmore (& Smith) 786*; Lucas Valley Road, 15 Dec 1980, *Whitmore (& Smith) 948*; Panoramic Hwy., E of Stinson Beach, 16 Dec 1980, *Whitmore 975*; Hwy. 1, near Marshall, 17 Dec 1980, *Whitmore 1006*; Pt. Reyes Nat. Seashore, along Bear Valley Trail, 10 Dec 1981, *Whitmore (& Smith) 1311*; Pt. Reyes Nat. Seashore, along Sky Trail, 31 Dec 1981, *Smith 836* (UC); Pt. Reyes Nat. Seashore, along Bear Valley Trail, 31 Dec 1981, *Smith (& Whitmore) 838* (UC); end of Lagunitas Rd., trail to Phoenix Lake, 15 Dec 1978, *Smith 714* (UC). Mendocino Co.: 1 mi N of Ten Mile River along Hwy 1, *Lemieux s.n.* (UC). Plumas Co.: Feather River, collected from greenhouse plant (SBBG 76-128), 14 Dec 1979, *Whitmore 762*. San Benito Co.: Pinnacles Nat. Monument, along loop of Juniper Canyon Trail, 28 Dec 1981, *Smith 830* (UC), along Bear Gulch Trail, *Smith 831* (UC), along Old Pinnacles Trail, *Smith 832* (UC). San Mateo Co.: Skyline Blvd., N of jct. with Hwy 84, 10 Feb 1980, *Whitmore 883*; King's Mt. Rd., E of Skyline Blvd., 8 Jan 1981, *Whitmore 1051*. Santa Cruz Co.: Ben Lomond, along San Lorenzo River, 2 Apr 1978, *Whitmore 291*. Sonoma Co.: Bodega, base of E cliffs, 7 Feb 1980, *Whitmore 894*.

woodland, and sometimes coastal redwood forest up to 1220 m; in the Sierra Nevada it occurs in oak savanna and foothill chaparral up to 1370 m; in the Tehachapis it occurs in oak savanna/riparian woodland. *Polypodium calirhiza* most commonly grows in disturbed habitats such as roadcuts and landslide areas, rocky cliffs with unstable surfaces, and rocky outcrops in grazed pastures. It also may be found in relatively undisturbed habitats: crevices of rocks, rocky cliffs, rocks or rocky outcrops in grasslands, and creek banks. Proliferation around rocky outcrops is particularly common in the warmer or drier habitats. *Polypodium calirhiza* can occur in shady or sunny situations in all of the above habitats. It also grows on old stumps, or at the bases of trees, or even high on tree trunks of *Acer macrophyllum* or *Umbellularia californica* in particular.

Cytology.—*Polypodium calirhiza* usually has 74 bivalents at meiosis (base number 37); occasionally ca. 72 bivalents and 2–4 significantly smaller chromosome configurations have been seen (see Table 1 for localities). The triploid hybrid frequently growing in association with this tetraploid has ca. 37 II + 37 I during meiosis. The occurrence of regular bivalent formation in the tetraploid and a genomic number of bivalents and univalents in the triploid hybrid suggest allosyndetic pairing of chromosomes in both the tetraploid and triploid hybrid. As indicated by Lovis (1977), further evidence for the alloploid origin of *P. calirhiza* might obtain from the discovery of equal numbers of bivalents and univalents in the other (as yet unknown) backcross triploid.

We have found no diploid hybrids between *P. californicum* and *P. glycyrrhiza* in their area of sympatry or in the range of *P. calirhiza.* Cytological examination of plants that are morphologically intermediate between *P. californicum* and *P. glycyrrhiza* has not revealed any of the following kinds of evidence of hybridity: univalents and bivalents in meiosis I; lagging chromosomes at the metaphase plate; or a significant percentage of malformed spores. All such plants have proven to be assignable to either *P. calirhiza* or to variant forms of *P. californicum* or *P. glycyrrhiza.* This absence of diploid hybrids is typical of *Polypodium* in North America and Europe (Lang 1965, 1971).

Morphology.—Table 2 summarizes selected morphological characters of *P. calirhiza,* its putative diploid parents, and the triploid hybrid. Numerical data are means or ranges of measurements of specimens that have been determined by chromosome count, or in some cases by spore length measurements. Spore surface terminology follows Tryon and Tryon (1982).

Polypodium calirhiza displays morphological characteristics of both putative diploid parents, *P. californicum* and *P. glycyrrhiza,* supporting the hypothesis that it is of allopolyploid origin. It also has characters found exclusively in only one parent: the epiphytic habit of *P. glycyrrhiza* and the tuberculate verrucae of the spores and anastomosing venation of typical *P. californicum.* The triploid, *P. calirhiza* × *glycyrrhiza,* is morphologically intermediate between *P. calirhiza* and *P. glycyrrhiza* but perhaps generally closer to *P. glycyrrhiza,* suggesting that it is a hybrid between those two taxa rather than between *P. californicum* and *P. calirhiza.*

Polypodium calirhiza differs from *P. glycyrrhiza* by the venation pattern: *P. glycyrrhiza* has veins that are free with vein pathways even and regular, whereas *P. calirhiza* has at least one set of vein endings anastomosing per frond and more commonly, 1–2 (up to about half) of the vein sets anastomosing per pinna. Separating *P. calirhiza* from type material of *P. californicum* and from specimens of *P. californicum* from the central coast of California is relatively straightforward using the following characters of *P. californicum*: a bland, or very slightly sweet rhizome, pinnae having mostly anastomosing veins forming a row of oblique areoles with the anastomosing points usually several mm from the margin, a rachis that is almost glabrous adaxially or sometimes with scattered to moderate pubescence, and a succulent blade. Spore or guard cell measurements or chromosome number are more definitive but usually unnecessary.

It can be quite difficult to distinguish *P. calirhiza* from some specimens of *P. californicum* from southern California. The most

Table 2. Comparison of Taxa in the *Polypodium californicum/glycyrrhiza* Complex with Selected Characters.

Character	*Polypodium californicum*	*Polypodium calirhiza*	*Polypodium calirhiza × glycyrrhiza*	*Polypodium glycyrrhiza*
Chromosome number	$2n = 37$ II	$2n = 74$ II	$2n = 37$ II + 37 I, or variable: $2n =$ ca. 35–37 II + 35–37 I + multivalents	$2n = 37$ II; rarely $2n = 36$ II + 2 I
Rhizome taste	Acrid or bland	Sweet plus acrid	Sweet plus ± acrid	Intensely sweet, and ± bitter aftertaste
Blade shape	Deltate to ovate	Oblong-ovate	Oblong-ovate	Lanceolate-ovate
Frond aspect	Upright	± drooping	Drooping	Drooping, arching
Stipe/rachis scales and number of cells wide	Deltate-ovate, 12–18(–20)	Lanceolate-ovate, 4–8(–12)	Lanceolate, 3–6(–8)	Lanceolate, 3–6(–8)
Abaxial surface of blade	Not noticeably glaucous	Slightly glaucous	Glaucous	Glaucous
Pinna tip shape	Widely obtuse to acute	Acute to obtuse	Acute to ± obtuse	Attenuate to acute
Percent of veins anastomosing/pinna	100–5.0%	0–33(–53.6)%	0–12.5%	0%
Venation pattern	Highly irregular	Irregular	Irreg to ± regular	Regular, even
Sorus shape and size	Elongate-oval–round; (1.5–)2–3(–3.5) mm	Oval, raised; (1.5–)2–4 mm	Round to ± oval; 1.3–2.5(–3) mm	Round, rarely ± oval; raised; 1.0–2.5 mm
Number of indurated annulus cells	(10–)11–17(–27!)	(8–)11–14(–17)	(9–)11–13(–17)	(9–)12–13(–16)
Spore surface	Tuberculate	Verrucate to tuberculate	Rugose to ± verrucate	Rugose to ± verrucate
Spores % malformed	Mostly normal; <10% malformed	Mostly normal; <10% malformed	Mostly malformed; >40% malformed	Mostly normal; <10% malformed
Habitat	Epipetric, terrestrial	Epipetric, epiphytic	Epipetric, epiphytic	Epipetric, epiphytic
Geographic range	Ore. to Baja California	C. Ore. to C. Calif. and S. Mexico	S. Ore. to C. Calif.	Alaska to C. Calif.

reliable method is to count chromosomes or measure spore lengths or guard cells. More subtle characters that can be useful are the regular blade outline, the commonly ovate blade shape, and the more evergreen fronds (with frequent summer rain or watering) of *P. calirhiza* relative to the "sloppy", slightly irregular blade and pinna outline, the frequently deltate blade, and the summer-deciduous fronds of *P. californicum.*

Thicker textured forms of both *P. calirhiza* and *P. californicum* in coastal California are sometimes confused with *P. scouleri,* which is restricted to the fog-belt from Baja California to British Columbia. *Polypodium calirhiza* can be distinguished from *P. scouleri* Hook. & Grev. by its abundant arcuate trichomes along the adaxial rachis, thinner lamina, and verrucate spores (vs. nearly smooth under the light microscope in *P. scouleri*). The spore differences alone strongly suggest to us that *P. scouleri* is not involved in the parentage of *P. calirhiza.* From species of the *P. vulgare* complex in Europe, *P. virginianum* in eastern North America, and the *P. amorphum* Suksdorf/*P. hesperium* group in central and western North America, *P. calirhiza* differs by its abundant pubescence of arcuate, non-glandular trichomes along the adaxial rachis and lack of sporangiasters. Production of mostly normal spores (less than 10% malformed) separates *P. calirhiza* from triploid *Polypodium* hybrids in western North America.

Polypodium calirhiza is exceedingly variable possibly as a result of several factors: an increase in heterozygosity because of genome contributions from two parents differing in phenotypic expression and habitat preference; and increased abnormality and variability in morphology because of reduced genetic control (Wagner 1962). It may also be polyphyletic as a result of more than one hybridization event between the diploid progenitors, as has been documented in allopolyploid species of *Asplenium* (Werth et al. 1985). A result of this morphological diversity is the more extensive distribution of the tetraploid vis-à-vis the two diploids.

Statistical analysis.—A principal components analysis (PCA) was performed using a program by Kovach (M.V.S.P.: A multivariate statistical package for the IBM PC and compatibles, 1986) to evaluate the distances of specimens within and between taxa. Specimens collected from natural populations were primarily used; some specimens were greenhouse- or lathhouse-grown. Ploidy of most specimens was determined by chromosome count or occasionally by spore length, which is generally correlated with ploidy in *Polypodium* (Evans 1970; Kott and Britton 1982) and in other pteridophytes (Barrington et al. 1986). Characters used in the PCA were selected from those more useful or reliable in identification. An effort was made to choose characters that are more variable among taxa than within a taxon.

TABLE 3. CHARACTERS AND CHARACTER STATES SCORED FOR THE PRINCIPAL COMPONENTS ANALYSIS OF THE TAXA IN THE *POLYPODIUM CALIFORNICUM/GLYCYRRHIZA* COMPLEX. Factor loadings for the first two principal components.

Character/character states	PC I	PC II
1. Ratio of pinna length (mm) to pinna width (mm)	−0.22	−0.61
2. Regularity of vein patterns (1 = regular, 2 = slightly irregular, 3 = very irregular)	0.33	−0.28
3. Pinna thickness (mm)	0.07	−0.00
4. Shape of pinna tip (1 = attenuate, 2 = acute, 3 = broadly acute, 4 = obtuse, 5 = broadly obtuse, 6 = rounded)	0.52	0.49
5. Number of anastomosing points per vein pair per pinna	0.42	−0.52
6. Location of anastomosing points relative to pinna margin (qualitative: 1–4)	0.08	−0.13
7. Distance (mm) from pinna margin to anastomosing point	0.15	−0.13
8. Ratio of distance (mm) from pinna margin to anastomosing point to distance (mm) from pinna margin to costal vein	−0.00	−0.02
9. Sorus length (mm)	0.18	−0.06
10. Sorus shape (1 = round, 2 = slightly oval, 3 = oval, 4 = elongate-oval)	0.57	−0.05
11. Number of indurated annulus cells in sporangium	0.03	−0.05
Eigenvalue	3.688	1.050
Percent of total variance	57.94	16.49

From the original 20 characters or ratios, 11 were selected for use in the PCA; seven are quantitative and four are qualitative (Table 3). Generally four or five measurements were made per specimen for each character, except that 20–25 sporangia were used to count the indurated annulus cells. Cytological or related data (spore or guard cell length) were not used in the PCA, to avoid overpowering the morphological data with the very distinct ploidal-level categories. Data were log-transformed, and a centered correlation matrix was used (Neff and Marcus 1980).

The first and second principal components of the resulting analysis (Table 3) have similar character loadings. Characters that load heavily on both the first and second principal components are: shape of pinna tip, number of anastomosing points per pinna, and vein patterns, with two other characters, pinna length/width ratio and sorus size, contributing to a lesser degree. Two exceptions here are sorus shape, which contributes heavily to the first component and very little to the second, and pinna length/width ratio, which loads heavily

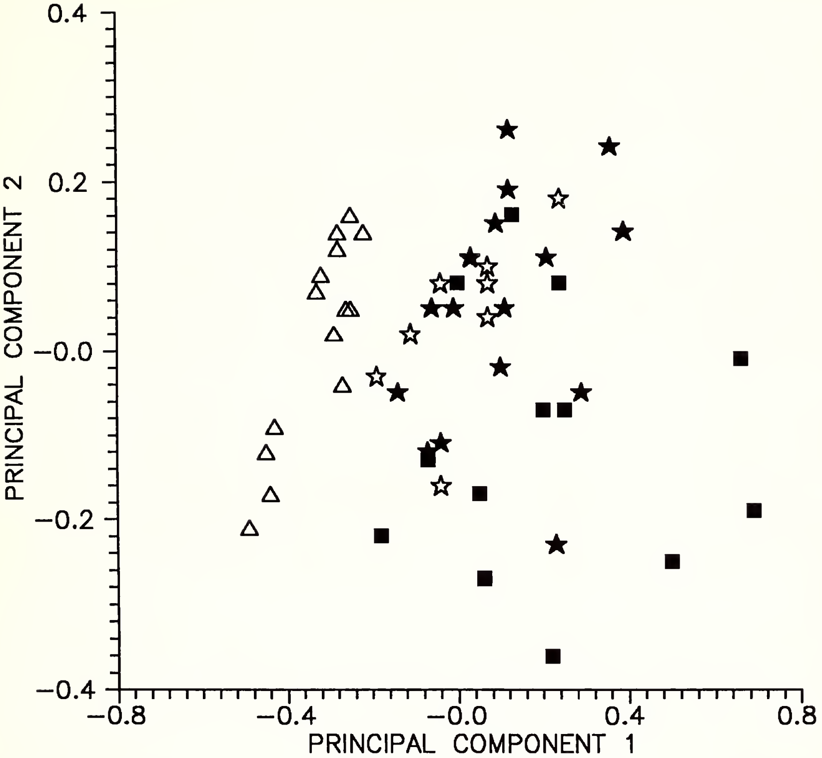

FIG. 3. Ordination of scores of the first and second principal components from a PCA using 11 morphological characters or ratios. The first and second principal components account for 57.9% and 16.5% of the variance respectively (total for the two equals 74.4% of the variance). Ploidal level of most specimens was determined by chromosome count, that of some specimens was determined by measurement of spore length. Taxa include: *Polypodium calirhiza* (solid stars); *P. glycyrrhiza* (triangles); *P. calirhiza* × *glycyrrhiza* (open stars); and *P. californicum* (squares).

on the second component and only moderately on the first. Although the first component is usually a linear combination of size characters (Reyment et al. 1984), three of the five size or dimension characters load only moderately on the first component and the remaining two size characters do not contribute much at all.

A plot of the first two principal components from the PCA (Fig. 3) shows a clear separation of the two putative parents, *P. glycyrrhiza* and *P. californicum,* with *P. calirhiza* generally intermediate between them. The triploid hybrid appears to be similarly intermediate with a somewhat closer affinity to *P. glycyrrhiza.* These point distributions reflect the morphological variability of natural populations of *Polypodium* and emphasize the difficulty frequently encountered in distinguishing the taxa. The conspicuous variability in the distribution of graph points for *P. californicum* correlates to some extent with the extremes seen in that species: the five points at the central- and lower right represent specimens similar to type material for *P. californicum,* while many of the *P. californicum* data points in the central region of the graph represent southern California specimens closer to the other end of the gradient.

Ecology.—The ecological behavior of these taxa correlates somewhat with the morphological differences. All four taxa are generally sympatric in the central coastal California region, yet they have distinct habitat preferences. *Polypodium californicum* grows on coastal bluffs and wind-swept grassy headlands while *P. calirhiza* grows in more protected ravines or further inland. *Polypodium calirhiza* is frequently found on roadcuts associated with the triploid hybrid, *P. calirhiza* × *glycyrrhiza.* If the habitat has enough moisture and shade, and has not been disturbed too much, then *P. glycyrrhiza* may also occur with them.

KEY TO TAXA

The following key will separate most specimens of the complex in California. *Polypodium scouleri* is also included because of occasional confusion and sympatry with the other species. Specimens with 50% or more shriveled or malformed spores are most likely hybrids, the commonest being *P. calirhiza* × *glycyrrhiza.* Such hybrids may key to any of the taxa marked with an asterisk.

a. Veins all free, usually pellucid, vein pathways regular; lamina thin; sori usually round, sometimes oval, conspicuously raised, usually 1–2(–3) mm diam. .... *P. glycyrrhiza**

a′. Veins sparingly (1–2 pairs per frond, rarely 0) to commonly anastomosing, not pellucid, vein pathways uneven, irregular, or if regular, lamina coriaceous to leathery; sori oval to round, flat to conspicuously raised.

  b. Rhizome pruinose; fronds leathery and stiff, or chartaceous and brittle (living fronds and pinnae snapping easily when bent); pinnae with crenate, cartilaginous margins; sori 2–5 (usually over 3) mm long. . *P. scouleri* and hybrids

  b′. Rhizome dull or sometimes slightly glaucous; fronds membranaceous to chartaceous but not leathery, usually not brittle when living; pinnae with serrate margins; sori 1.5–3(–4) mm long.

    c. Lamina oblong-ovate, regular in outline, proximal 1–3 pinna pairs shorter than those above; sori oval, prominent, frequently becoming confluent near rachis; spores 57–86 μm long (mean: 68 μm, including tubercles). . ... *P. calirhiza**

    c′. Lamina deltate to oblong to ovate, often somewhat irregular in outline; proximal 1–3 pinna pairs as long as or longer than those above; sori round to oval, relatively flat to raised; spores 42–67 μm long (mean: 52 μm, including tubercles). .... *P. californicum**

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ENVIRONMENTAL RELATIONSHIPS OF HERBS IN BLUE OAK (*QUERCUS DOUGLASII*) WOODLANDS OF CENTRAL COASTAL CALIFORNIA

MARK BORCHERT
Los Padres National Forest, Goleta, CA 93117

FRANK W. DAVIS
Geography Department, University of California,
Santa Barbara, CA 93106

BARBARA ALLEN-DIAZ
Department of Forestry and Resource Management,
University of California, Berkeley, CA 94720

ABSTRACT

Compositional patterns of herbaceous vegetation and its relationship to environmental factors were investigated in blue oak woodlands and forests in southern San Luis Obispo and northern Santa Barbara counties, California, Based on ordination and classification analyses, herbaceous cover data from 208 0.04-ha plots clustered into three distinct geographic regions. Herbaceous vegetation was strongly associated with overstory crown cover, slope, potential solar insolation and elevation. A-horizon coarse fragment was a significant variable in two regions and available water capacity was important in one region.

Blue oak (*Quercus douglasii* H. & A.) woodland is the dominant hardwood type in California covering over one million hectares. Although blue oak co-occurs with other tree species, it typically covers extensive areas in monospecific stands. The blue oak series is composed of at least twelve different subseries, four of which have a relatively high cover of understory shrubs (Allen et al. 1990). For the most prevalent subseries, however, the shrub component is insignificant compared to the ubiquitous herbaceous understory dominated by annual forbs and grasses.

Because blue oak woodland provides 65% of the state's livestock forage (Bartolome 1987), research on understory herbaceous vegetation has focused on the effects of overstory removal on forage production (Murphy and Crampton 1964; Murphy and Berry 1973; Kay 1987), differences in forage production and species composition between oak canopies and adjacent open grassland (Holland 1980; Frost and McDougald 1989; McClaran and Bartolome 1989), and responses of a relatively limited number of species, e.g., *Avena* spp., *Bromus* spp., *Vulpia* spp. and *Erodium* spp. to different grazing regimes (Rosiere 1987). Holland (1973) and Callaway (1990) have studied the influence of the canopy on ungrazed herbaceous cover.

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We know of no studies, however, that have examined variation in blue oak understory vegetation on a regional scale in relation to environmental factors. In this paper we describe quantitative relationships between herbaceous composition and environmental factors for blue oak woodlands and forests in the southern end of its range. Classification and management of these ecosystems will be presented in a subsequent paper.

SITES AND METHODS

Study area. The study area included 8 7.5′-topographic quadrangles and was a patchwork of blue oak woodland and forest in southern San Luis Obispo and northern Santa Barbara counties at the juncture of three mountain ranges: the La Panza Range, Garcia Mountain, and the Sierra Madre Mountains (Fig. 1). The center of the study area (35°10′N, 122°10′W) was located approximately 52 km ESE of San Luis Obispo. Climate is mediterranean with cool wet winters and warm dry summers. Most precipitation falls between November and March. Average annual precipitation declines rapidly from west to east. For the relatively more coastal stations of Pozo and Pine Canyon average annual precipitation is 526 mm and 450 mm, respectively. In contrast, average annual precipitation at La Panza Ranch east of the La Panza Range is 223 mm and at Cuyama east of the Sierra Madre Mountains it is 163 mm. We sampled the vegetation over a four year period from 1986–1989. Precipitation at Pozo was 713 mm in 1986, higher than the average, but below average in the remaining years: 269, 453, and 328 mm in 1987, 1988, and 1989, respectively.

Basement rock of the area is granite and Franciscan sandstone overlain by early Tertiary sedimentary rocks composed of marine sandstone, shale, and conglomerates (Dibblee 1976). Soils in the area are variable but most are mollisols, primarily argixerolls and haploxerolls.

The ten allotments within the study area have been grazed almost continuously by cattle since 1900. Grazing regimes of the allotments have been highly variable historically. Currently four allotments are grazed year around and the others are grazed from one to five months. None of the plots had burned within a period of 5 years before the study.

Sampling methods. Plot data were collected from the study area over a period of four years from late March to late May. In 1986 and 1987, 77 plots were sampled in the area from Pozo to Cuyama River west of Branch Mountain (Fig. 1). Five of these, representing a spectrum of environments, were revisited in 1987. In 1987, 53 plots were sampled in the area from Cuyama River to Miranda Pine

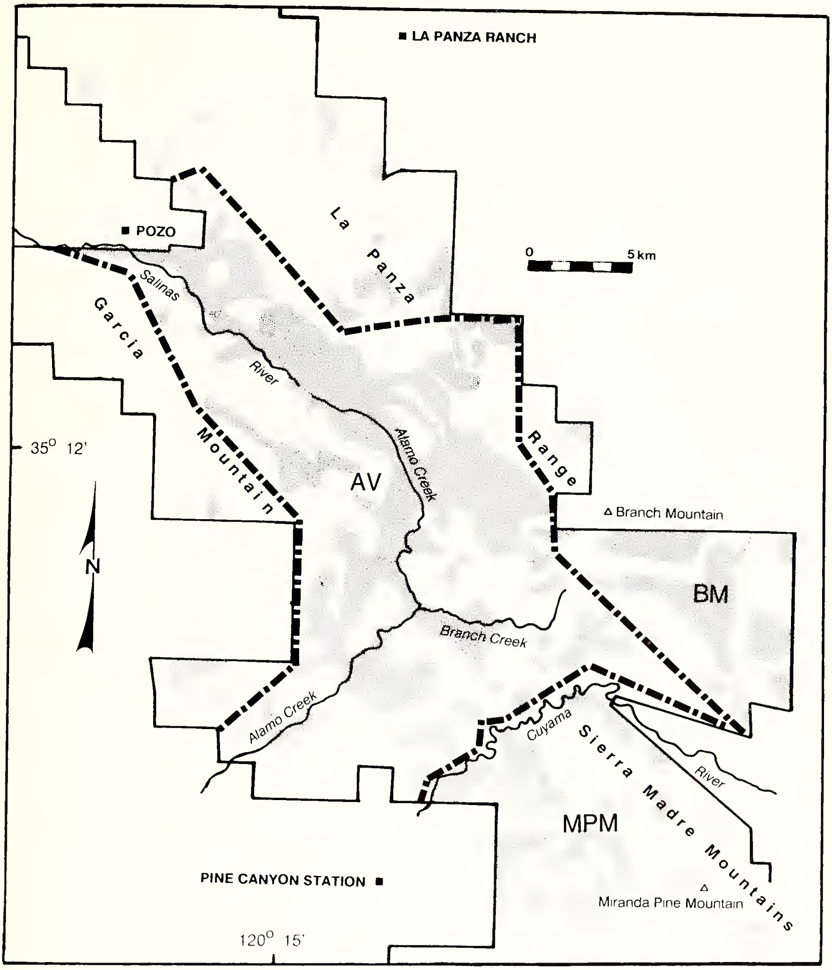

FIG. 1. Map of the study area. Shaded areas are oak woodland and forest. Herbaceous vegetation regions indicated by the dot-dashed lines are: Avenales (AV), Miranda Pine Mountain (MPM) and Branch Mountain (BM). Solid line is the boundary of Los Padres National Forest.

Mountain, four of which were revisited in 1989. In 1988, 78 plots were sampled in the area east of Branch Mountain, six of which had been sampled in 1987.

Plots of four hundred square meters were subjectively located in stands where blue oak overstory crown cover attained at least 20 percent and understory herbaceous cover exceeded 60 percent. A stand was sampled if oaks were relatively evenly distributed over the plot on the same slope and aspect.

Slope angle, aspect, elevation, landform, slope position, and within-plot vertical and horizontal microrelief were recorded for each plot. Slope and aspect were used to obtain an estimate of potential annual solar insolation (solar insolation) using the tables of Frank and Lee (1966).

Percentage foliar cover of all plant species was estimated visually and recorded into a modified Braun-Blanquet cover scale: 0–1%, 2–5%, 6–25%, 26–50%, 51–75%, and 76–100%. Midpoints of each of these cover classes were used in data analysis. The cover of overstory trees was measured with a spherical densiometer (Lemmon 1956) by averaging five values taken in the plot: one at plot center and the others 7.5 m parallel and perpendicular to the slope contour from plot center. Trees larger than 5 cm dbh were counted and their diameters measured at 1.4 m.

A soil pit was excavated in each plot to a depth of 100 cm or bedrock, whichever was encountered first. Thickness of the A horizon was measured and its color, texture, and pH noted. The same parameters also were taken for the subsoil. In addition, percentage coarse fragment content was estimated for each layer. Soil drainage, rootability, and lithology were recorded. Available water capacity (AWC) was calculated for the top 50 cm of soil where most herbaceous species were rooted.

Data analysis. We analyzed herbaceous species cover data using two-way indicator species analysis (TWINSPAN) (Hill 1979), detrended correspondence analysis (DCA) (Hill and Gauch 1980), and canonical correspondence analysis (CCA) (Ter Braak 1986). Only herbaceous species were analyzed because they are most similar in their ecological requirements. TWINSPAN, a polythetic divisive classification technique, was used to elucidate regional variation in understory vegetation. Detrended correspondence analysis (DCA) was then utilized to examine compositional variation and overlap of the TWINSPAN groups; it is ordination method that portrays the relative similarity of samples along a few principal axes of variation. Also, DCA was used to compare changes in the positions of the 15 resampled plots in the ordination space. Canonical correspondence analysis (CCA) was used to examine species–environment relationships for each of the regions identified using two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DCA). Canonical correspondence analysis (CCA) is designed to detect unimodal relationships between species and external variables by performing a constrained correspondence analysis ordination; that is, the ordination axes extracted by this method are required to be a linear combination of environmental variables. Axes appear in order of the variance explained.

Continuous variables used in the CCA analysis included elevation, aspect, slope, solar insolation, tree density, overstory crown cover, A-horizon coarse fragment content, subsoil coarse fragment content, and available water capacity of the soil. Soil pH showed little variability and was not used. If necessary, continuous variables first were normalized and then standardized to a mean of 0 and standard deviation of 1. Categorical variables used in the analysis included slope position, within-plot horizontal and vertical microrelief, and A-horizon surface texture.

Rare species were downweighted by reducing species abundance values in proportion to their frequencies of occurrence, for species with frequencies less than 20% of the most frequent species. Nomenclature follows Hoover (1970).

RESULTS

Based on TWINSPAN and DCA results we recognized three vegetation groups associated with three distinct geographic regions, referred to as Avenales, Miranda Pine Mountain and Branch Mountain (Figs. 1 and 2). The Cuyama River separates the Avenales and Miranda Pine Mountain regions and the boundary between the Branch Mountain and Avenales regions follows the north–south trending chaparral-covered ridge west of Branch Mountain. Compositional differences among the regions were both the result of differences in species composition (Table 1) and changes in species cover. The first DCA axis was correlated with overstory crown cover ($r = 0.40$, $P < 0.001$) and the second axis was correlated with solar insolation ($r = -0.69$, $P < 0.001$) and slope ($r = 0.44$, $P < 0.001$).

Plot ordination scores were not very sensitive to sampling year; that is, resampled plots remained within the same region in the DCA ordination space (Fig. 2). Moreover, when the 15 resampled plots were combined with the 208 plots in a TWINSPAN analysis, they remained in the same regions of the ordination (Fig. 2). Interannual differences in plot ordination scores were influenced primarily by the presence or absence of species with less than 1% cover rather than by marked fluctuations in the cover of dominant species.

In the analysis of Avenales 163 species entered the CCA. For Avenales samples, slope, overstory crown cover and solar insolation are correlated with the first canonical axis (Table 2). A-horizon coarse fragment is correlated with the second axis and elevation is correlated with the third axis. Inspection of bivariate scattergrams of canonical scores vs. environmental variables revealed that seven plots with overstory crown cover of less than 50% strongly influenced the CCA results and produced the strong relationship of CCA with overstory crown cover (Fig. 3). After removing these plots, overstory crown cover was not related to CCA axes. The contributions of slope and solar insolation remained the same. The coefficients for eleva-

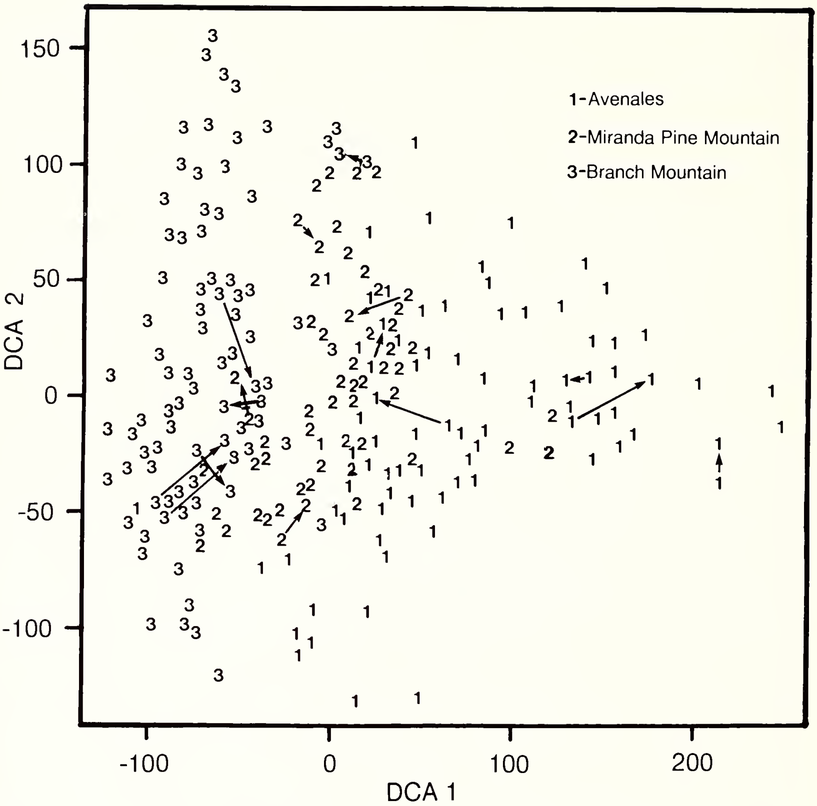

FIG. 2. Detrended correspondence analysis (DCA) ordination of the 208 plots. Arrows show the trajectories of compositional change for the 15 plots visited for two years. Axis 1 is correlated with overstory crown cover (r = 0.40) and axis 2 is correlated with solar insolation (r = −0.69) and slope (r = 0.44).

tion and A-horizon coarse fragment changed in magnitude but not direction (Table 3).

Arrow length in the canonical correspondence analysis (CCA) ordination diagram (Fig. 4) is proportional to the strength of the correlation between environmental variable and ordination axes. Arrow direction indicates whether a variable is positively or negatively related to the axis. A species point projected perpendicularly onto each environmental axis corresponds approximately to the ranking of the weighted average of the species with respect to that environmental variable. The weighted averages are approximated in the diagram as deviations from the grand mean of each variable. The origin of the plot represents the grand mean. Table 4 presents the means of variables shown in the CCA ordination diagrams. The

TABLE 1. SPECIES CONCENTRATED IN A PARTICULAR REGION. Values are percentage of plots in a region in which a species is present.

	Avenales	Miranda Pine Mountain	Branch Mountain
Agoseris grandiflora	28	1	7
Avena fatua	66	22	9
Bromus carinatus	20	3	1
Euphorbia spathulata	43	6	1
Lotus micranthus	12	—	—
Lotus purshianus	11	—	—
Lotus strigosus	4	—	—
Lupinus nannus	8	—	—
Medicago polymorpha	65	23	1
Microseris elegans	4	—	—
Nemophila pedunculata	19	—	—
Ranunculus californicus	34	—	—
Sisyrinchium bellum	25	—	—
Sonchus oleraceus	8	—	—
Torilis nodosa	15	—	—
Trifolium bifidum	29	—	—
Vicia americana	6	—	—
Vicia exigua	14	—	—
Vicia sativa	8	—	—
Athysanus pusillus	—	30	54
Calochortus venustus	—	13	—
Gilia achilleaefolia	—	4	—
Monardella villosa	—	5	—
Phacelia imbricata	—	6	—
Sitanion hystrix	—	4	—
Stellaria nitens	—	11	—
Stipa cernua	—	13	—
Alchemilla occidentalis	5	—	36
Androsace acuta	—	3	33
Arenaria douglasii	—	—	14
Astragalus antisellii	—	—	9
Bromus rubens	16	39	77
Capsella bursa-pastoris	3	11	26
Filago gallica	—	—	8
Lactuca serriola	5	3	27
Lagophylla ramosissima	—	12	47
Lasthenia chrysostoma	2	1	33
Linanthus androsaceus	—	—	13
Lithophragma affine	—	—	9
Lupinus subvexus	—	—	58
Navarretia mitracarpa	—	—	28
Plagiobothrys tenellus	—	—	10
Polypogon monspeliensis	—	—	10
Rigiopappus leptocladus	—	—	37
Tropidocarpum gracile	—	—	12

TABLE 2. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE AVENALES REGION, N = 77. The first three axes explain 89% of the variance in the weighted average of the species with respect to the environmental variables. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. Canonical correspondence analysis canonical coefficients are the regression coefficients used to derive axes from a linear combination of the standardized environmental variables. Intraset correlations are the correlations among the standardized environmental variables and the canonical correspondence analysis axes.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.27	0.28	0.05	−0.71	0.36	0.07
Overstory cover	0.15	−0.02	−0.09	0.62	0.05	−0.16
Slope	0.18	0.02	0.19	0.58	0.31	0.32
A-horizon coarse fragment	−0.10	−0.24	0.11	−0.35	−0.41	0.43
Elevation	0.05	0.02	0.22	0.06	−0.14	0.60

pattern of species points in Figure 4 indicates that they are fairly equally distributed between environments on steep slopes with low solar insolation (upper right quadrant) and gentle slopes with high solar insolation (upper left quadrant). Furthermore, species tend to be more prevalent on soils with lower A-horizon coarse fragments, e.g., *Bromus arenarius. Trifolium tridentatum,* in contrast, occurs on soils with high coarse fragment content.

Because of the large number of species in the analysis, we selected 12 species (6 native and 6 introduced) that were present in all the regions to make the diagrams more readily interpretable. To demonstrate the relationship between the ranking of a species on an environmental variable in the CCA ordination diagrams and the actual values of a species for a variable, we present median solar insolation values for 8 species and the median solar insolation value

TABLE 3. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE AVENALES REGION AFTER REMOVING PLOTS WITH LESS THAN 50% OVERSTORY CROWN COVER, N = 70. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 78% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	0.25	0.21	0.14	0.66	0.30	0.19
Solar insolation	−0.23	0.21	0.20	−0.64	0.29	0.36
A-horizon coarse fragment	−0.02	−0.27	0.06	−0.00	−0.57	0.36
Elevation	0.08	−0.03	−0.19	0.24	−0.28	0.54

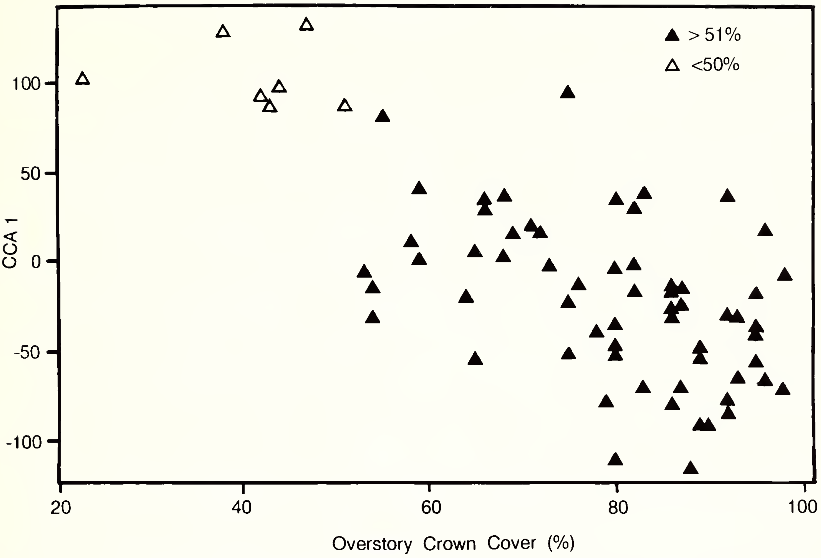

FIG. 3. Canonical correspondence analysis (CCA) first-axis scores plotted against overstory crown cover for the 77 Avenales plots. Plots with cover of less than 50% are indicated by open triangles.

for all the plots in a region (Fig. 5). Median solar insolation values were calculated for plots in which the species cover was at least 5%. We did not include plots with less than 5% cover because chance occurrences are more likely in this cover interval. Such occurrences could distort median values and the overall pattern.

In Avenales (Fig. 5a) median values for *Sanicula bipinnata, Claytonia perfoliata* and *Bromus madratensis* are below the median value for all the plots, *Bromus diandrus* and *Avena barbata* near the all-

TABLE 4. MEANS OF ENVIRONMENTAL VARIABLES SHOWN IN THE CANONICAL CORRESPONDENCE ANALYSIS ORDINATION DIAGRAMS. A one-way analysis of variance indicated only available water capacity was significantly different ($P < 0.05$) among the regions.

Variable	Avenales	Miranda Pine Mountain	Branch Mountain
Elevation (m)	746	723	728
Slope (degrees)	21	18	18
Potential annual solar insolation (kg calories cm^{-2} yr^{-1})	232	232	252
A-horizon coarse fragment (%)	7	8	12
Available water capacity (cm^3 of water 50–cm^{-3} soil)	0.97	0.84	0.68

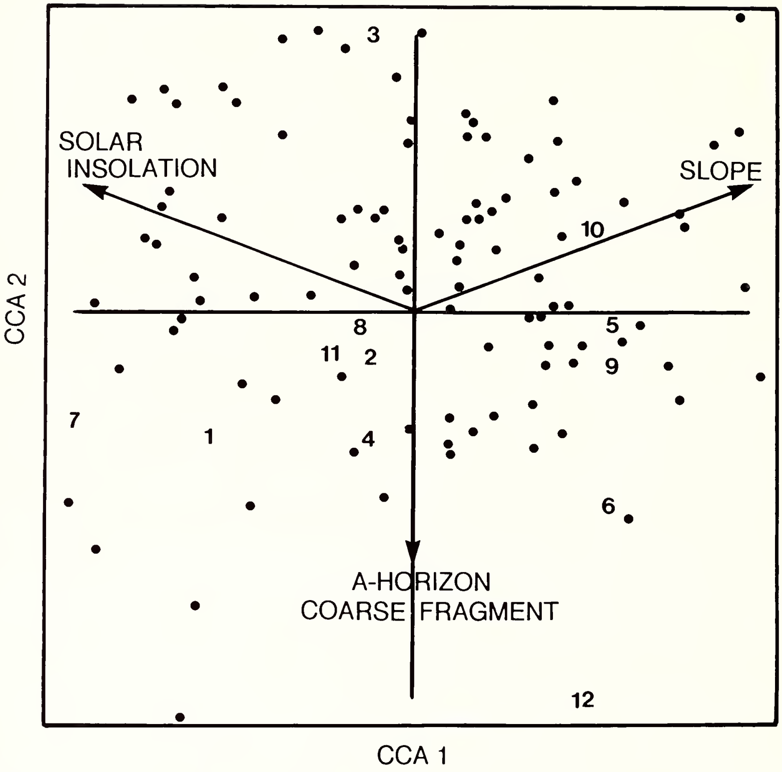

FIG. 4. Canonical correspondence analysis (CCA) ordination diagram with species and environmental variables (arrows) for the 70 Avenales plots. Dots indicate positions of species with at least 20% frequency in the plots. Species are as follows: 1 *Amsinkia intermedia,* 2 *Avena barbata,* 3 *Bromus arenarius,* 4 *Bromus diandrus,* 5 *Bromus madritensis,* 6 *Claytonia perfoliata,* 7 *Erodium moschatum,* 8 *Lupinus bicolor,* 9 *Madia gracilis,* 10 *Sanicula bipinnata,* 11 *Stellaria media,* and 12 *Trifolium tridentatum.*

plot median and *Bromus arenarius, Lupinus bicolor,* and *Amsinkia intermedia* above the all-plot median. Because CCA scores are based on all plots, species ranking on the solar insolation variable in the diagram (Fig. 4) does not correspond exactly to the ordering of the median values (Fig. 5a). However, the species are correctly located in Figure 4 relative to the origin (grand mean of the variable), indicating that, although the variability in solar insolation is high (Fig. 5a) for each species, CCA accurately retrieves the species–environmental gradient.

Results of the canonical correspondence analysis (CCA) for the 53 Miranda Pine Mountain plots are presented in Table 5. In this region there were 165 species. Slope, overstory cover and solar in-

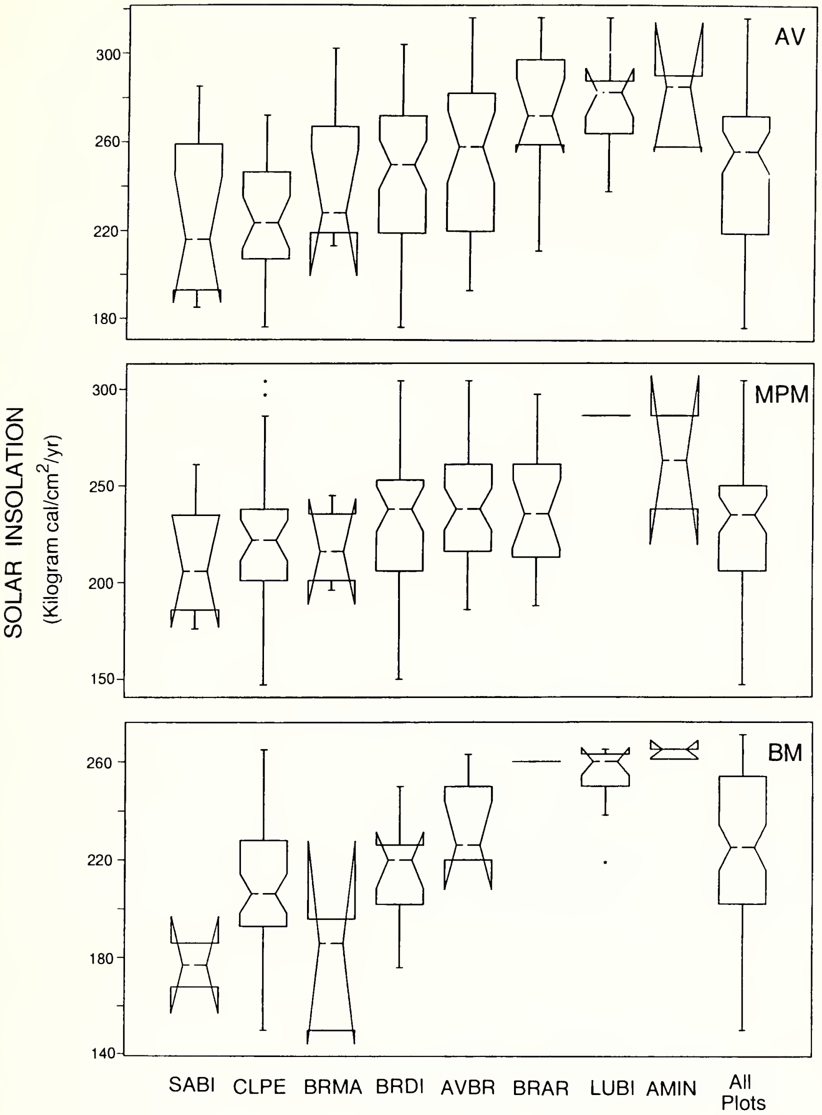

FIG. 5. Solar insolation values for *Sanicula bipinnata* (SABI), *Claytonia perfoliata* (CLPE), *Bromus madritensis* (BRMA), *Bromus diandrus* (BRDI), *Avena barbata* (AVBR), *Bromus arenarius* (BRAR), *Lupinus bicolor* (LUBI), *Amsinkia intermedia* (AMIN) and all the plots in (a) Avenales (AV), (b) Miranda Pine Mountain (MPM) and (c) Branch Mountain (BM). Fifty percent of the observations are within the upper and lower horizontal lines. Vertical lines show the range of values; asterisks are outliers, Non-overlapping of notches among boxes indicates significant differences between distributions at roughly 95% significance level. Reversals occur where the confidence interval exceeds the quartiles.

TABLE 5. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE MIRANDA PINE MOUNTAIN REGION, N = 53. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes explain 78% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	−0.36	−0.04	−0.24	−0.77	−0.02	−0.31
Solar insolation	0.12	−0.05	−0.20	0.64	−0.28	−0.27
Overstory cover	−0.08	0.00	0.04	−0.41	0.35	0.27
Elevation	−0.11	−0.28	0.15	−0.21	−0.81	0.23
Tree density	−0.10	0.13	0.16	−0.38	0.53	0.35

solation are correlated with the first canonical axis while the second axis is correlated with elevation and density. After the removal of 11 plots with overstory crown cover of less than 50% and one sample with an unusually high A-horizon coarse fragment content, three variables remained: elevation, slope, and solar insolation (Table 6). Nevertheless, correlation coefficients for these variables changed little from the analysis with 53 plots. The CCA ordination diagram for variables in Table 6 is shown in Figure 6. Most species are concentrated at lower elevations, on steeper slopes with low solar insolation values. A comparison of solar insolation values for species in Figure 5b with their ranking and position relative to the origin in the CCA ordination diagram (Fig. 6) indicates a poorer fit. For example, species with high median solar insolation values like *Amsinkia intermedia* and *Lupinus bicolor* are placed near the mean and in the low solar insolation portion of the diagram, respectively. In addition, *Bromus arenarius* should be closer to the origin based on its median value.

TABLE 6. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE MIRANDA PINE MOUNTAIN REGION AFTER REMOVING PLOTS WITH LESS THAN 50% OVERSTORY CROWN COVER, N = 42. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 74% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	0.38	−0.09	0.17	0.76	−0.08	0.23
Solar insolation	−0.12	−0.06	0.26	−0.63	−0.08	0.47
Elevation	0.02	−0.32	−0.02	−0.10	−0.84	−0.11

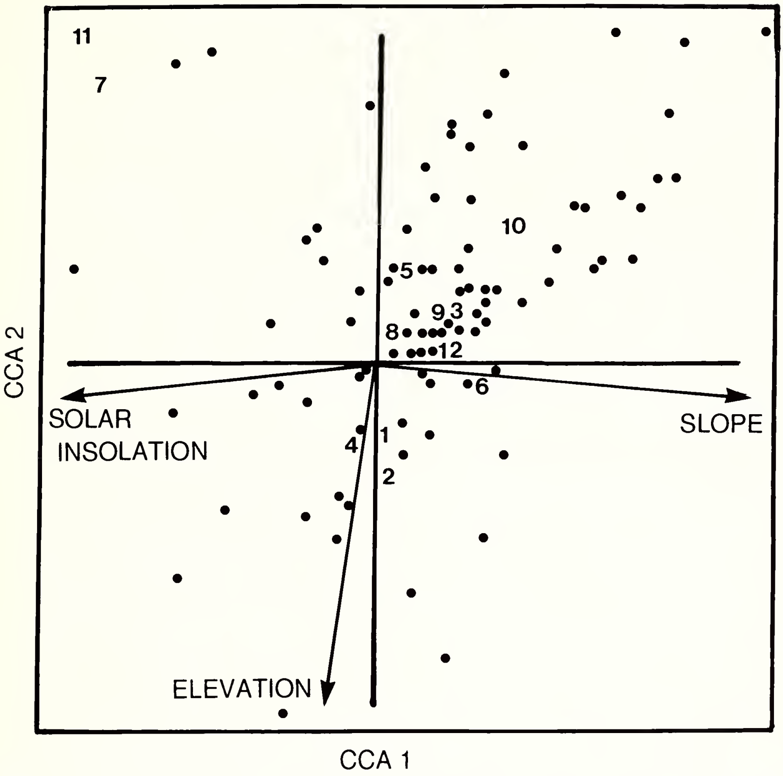

FIG. 6. Canonical correspondence analysis (CCA) ordination diagram with species (O) and environmental variables (arrows) for the 42 Miranda Pine Mountain plots. Species are as follows: 1 *Amsinkia intermedia,* 2 *Avena barbata,* 3 *Bromus arenarius,* 4 *Bromus diandrus,* 5 *Bromus madritensis,* 6 *Claytonia perfoliata,* 7 *Erodium moschatum,* 8 *Lupinus bicolor,* 9 *Madia gracilis,* 10 *Sanicula bipinnata,* 11 *Stellaria media,* and 12, *Trifolium tridentatum.*

One hundred and sixty-one species were analyzed for Branch Mountain. Results of the canonical correspondence analysis (CCA) for the 78 Branch Mountain plots are presented in Table 7. Overstory crown cover, elevation and solar insolation are correlated with the first axis. Available water capacity and elevation are correlated with the second axis. Slope is correlated with the third axis. After 10 plots with overstory crown cover of less than 40% were deleted, the number of variables remained the same but overstory crown cover (Table 7) was replaced by A-horizon coarse fragment which is correlated with the first axis (Table 8). Slope changed from a negative correlation with the third axis to a positive correlation with the first axis. Axis correlations for elevation and solar insolation were little changed by plot deletions.

TABLE 7. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE BRANCH MOUNTAIN REGION, N = 78. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes explain 86% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.42	−0.23	−0.15	−0.75	0.33	−0.19
Elevation	0.15	−0.40	−0.08	0.52	−0.59	0.01
Overstory cover	0.13	0.11	0.19	0.43	0.10	0.35
Available water capacity	−0.06	0.09	0.00	−0.19	0.41	−0.18
Slope	−0.04	−0.06	−0.32	0.38	0.30	−0.55

The CCA ordination diagram for the results of Table 8 are shown in Figure 7. A greater number of species occur at lower elevations, but otherwise they are equally distributed between the environments with gentle slopes and high solar insolation and steeper, lower solar insolation slopes. In general, the species median solar insolation values (Fig. 5c) correspond well to their placement on the solar insolation gradient in Figure 7.

DISCUSSION

Within this small portion of the range of blue oak there is considerable variability in herbaceous vegetation. When all plots for each region were analyzed, compositional patterns are clearly influenced by overstory crown cover, solar insolation and slope but significant vegetation changes also coincide with major geographic fea-

TABLE 8. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE BRANCH MOUNTAIN REGION AFTER REMOVING PLOTS WITH LESS THAN 40% OVERSTORY CROWN COVER, N = 68. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 83% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.38	−0.24	0.20	−0.72	−0.42	−0.10
Elevation	0.19	−0.37	0.10	0.59	−0.55	0.11
Slope	−0.01	−0.02	0.28	0.46	0.41	0.37
A-horizon coarse fragment	0.10	0.20	−0.08	0.42	−0.12	−0.15
Available water capacity	−0.08	0.07	−0.00	−0.18	0.45	0.04

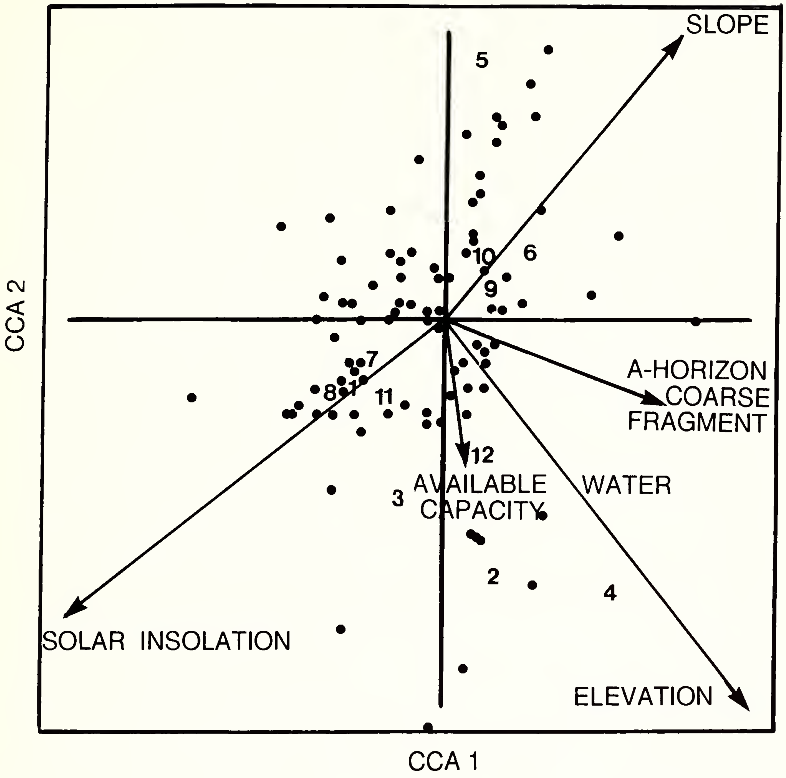

FIG. 7. Canonical correspondence analysis (CCA) ordination diagram with species (O) and environmental variables (arrows) for the 68 Branch Mountain plots. Species are as follows: 1 *Amsinkia intermedia,* 2 *Avena barbata,* 3 *Bromus arenarius,* 4 *Bromus diandrus,* 5 *Bromus madritensis,* 6 *Claytonia perfoliata,* 7 *Erodium moschatum,* 8 *Lupinus bicolor,* 9 *Madia gracilis,* 10 *Sanicula bipinnata,* 11 *Stellaria media,* and 12 *Trifolium tridentatum.*

tures of the study area. Factors responsible for these discontinuities appear complex. Although the first axis of the detrended correspondence analysis (DCA) for the 208 plots is broadly related to overstory crown cover, the ordering of the regions on this axis also suggests the influence of the steep coastal to inland precipitation and temperature gradient. Precipitation stations suggest that Avenales has relatively higher annual precipitation than the other two regions. Additionally, Avenales experiences an ameliorating maritime fog influence during much of the year. Fog is less frequent in the more arid inland regions. Drier inland conditions may explain the importance of elevation as a variable for Miranda Pine Mountain and Branch Mountain since precipitation is correlated with elevation. Livestock grazing also can have a marked effect on regional oak herbaceous vegetation as demonstrated for *Quercus garrayana* woodland (Smith 1985). Unfortunately, grazing regimes in the study area and within each region are highly variable and historic use records are too incomplete to evaluate directly the impact of grazing on the vegetation. Nevertheless, grazing may reinforce climatically-determined vegetation patterns.

Overstory crown cover was consistently an important variable in each region, an expected finding since numerous studies have demonstrated the effect of individual oaks on the composition of herbaceous vegetation. The results, however, show a nonlinear relationship between canopy cover and vegetation change. Composition showed a threshold change when canopy cover increased to 40–50% (Fig. 3) but for higher canopy cover the change was much less pronounced.

Slope and solar insolation also assumed a prominent role in controlling herbaceous vegetation. In temperate latitudes aspect differences in the duration and intensity of solar beam radiation have a dramatic effect on air and soil temperatures and atmospheric and soil moisture (Holland and Steyn 1975; Evans and Young 1989) which in turn influence the vegetation. McNaughton (1968) observed consistent changes in composition and biomass in relation to aspect in ungrazed California annual grasslands on sandstone and serpentine. Similarly, Borchert et al. (1989) noted a solar insolation-related influence on herbaceous composition within a several hectare blue oak forest. The relationship of the vegetation to solar insolation is likely even stronger than reported here because potential annual solar insolation is a relatively crude measure of solar insolation. Potential annual solar insolation does not take into account topographic influences such as horizon shading nor does it weight radiation on east and west aspects differentially even though east-facing aspects have a higher daily heat load than western exposures (Dargie 1987). Solar insolation in this ecosystem is probably best measured in late winter and early spring when its effect on vegetation growth is greatest (Chiariello 1989) rather than the yearly average employed here. Furthermore, because blue oak grows more abundantly on north-facing aspects in the southern part of its range (Menke 1989), tree density likely reinforces solar insolation-related effects.

Slope is important in the three regions because it probably reflects the influence of livestock grazing on the vegetation since livestock grazing generally decreases with increasing slope (Mueggler 1965; Cook 1966; White 1966) and may accentuate vegetation patterns created by solar insolation, elevation and soil factors (Milchunas et al. 1989).

An unexpected result of this study is the emergence of A-horizon coarse fragment content as a factor affecting vegetation patterns in Avenales and Branch Mountain. A-horizon coarse fragment influences soil properties in very complex ways and we can only speculate on its potential significance. Coarse fragment may indirectly create a soil productivity gradient. According to this hypothesis, as coarse fragment content increases, soil productivity decreases because there is relatively less volume of soil and therefore relatively less mineral nutrients and organic matter available for plant growth. Hildebaugh (1984), however, found no consistent effect of A-horizon rock fragments on yields of crops, pasture or woodlands but, as he points out, there has been little research on the effects of rock fragments on soil productivity. A-horizon coarse fragment also may reflect a moisture gradient that available water capacity is not measuring. Again, the effects of coarse fragments on soil water are complex. For example, in some soils coarse fragments can increase rather than decrease water available to plants if the rock fragments are porous (Hanson and Blevins 1979). Vegetation gradients in this study, however, suggest that coarse fragments are decreasing soil water. Another unknown factor is the distribution of oak roots in the A-horizon and how they may be directly influencing the water available to the herbs especially when coarse fragment content is high.

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COMMENTS ON *SIDALCEA* (MALVACEAE) OF THE KLAMATH MOUNTAINS OF OREGON AND CALIFORNIA

JENNIFER DIMLING
Department of Biology, University of Oregon,
Eugene, OR 97403

ABSTRACT

Analysis of the taxonomic status of *Sidalcea setosa* and related taxa from the Klamath Mountains of southwest Oregon and northwest California resulted in the following conclusions: (1) *Sidalcea setosa* should be treated as a synonym of *S. oregana* var. *spicata,* (2) *Sidalcea virgata* should be treated as *S. malvaeflora* ssp. *asprella* var. *virgata* and, (3) the relationship between *S. malvaeflora* ssp. *asprella* and *S. malvaeflora* ssp. *nana* should be investigated further to determine whether ssp. *nana* might not be submerged into ssp. *asprella.*

Botanists have recently expressed concern over the rarity of *Sidalcea setosa* C. L. Hitchc. ssp. *setosa,* placed in the Oregon Natural Heritage Data Base's List 1, "taxa threatened throughout range," in 1989 (Kagan et al. 1989). *Sidalcea setosa* is a Candidate 2 species for proposed listing as a threatened or endangered species by the U.S. Fish and Wildlife Service. Since state and federal agencies must manage sensitive plant species and their habitats, there is a need for practical classifications that permit as clear a separation of taxa as is taxonomically defensible.

In the first monograph on *Sidalcea,* Roush (1931) did not separate *Sidalcea setosa* from *S. spicata* (Regel) Greene. She felt that *S. spicata* exhibits highly plastic morphology. Her explanation for variability hinged on ecology: "a slight difference in the amount of available moisture (both soil and atmospheric) may make a great difference in the degree and kind of pubescence in this species" (Roush 1931, p. 166). She also noted that inflorescence, leaf form, and carpel architecture are variable. She did not address stem bases. Six of the specimens Roush examined were later annotated by Hitchcock as *Sidalcea invisa,* a herbarium name later published as *Sidalcea setosa* (Hitchcock 1957).

Sidalcea setosa was removed from the *oregana* complex by Hitchcock in his monograph on the perennial species of *Sidalcea* (1957). He perceived *S. setosa* to be intermediate between *S. oregana* (Nutt.) A. Gray ssp. *spicata* (Regel) C. L. Hitchc. and *S. malvaeflora* (DC.) Gray ex Benth. ssp. *asprella* (Greene) Jepson. *Sidalcea setosa* was described as sharing only range and stellate stem pubescence with *S. malvaeflora* ssp. *asprella.* In all other characters it was most closely related to *S. oregana* ssp. *spicata.*

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Hitchcock (1957, p. 53) states "there seems good reason to maintain the taxon *setosa* as distinct from the *oregana-spicata* complex, on the basis of its distinctive range, more nearly rhizomatous habit, more prominently reticulated carpels, and different pubescence".

Roush (1931) recognized only one of the many members of the *malvaeflora* group in the Klamath Mountain region, *S. asprella* Greene. The characters that distinguished *S. asprella* are its stellate pubescence, similar basal and cauline leaves, and erect stature. She considered *S. elegans* Greene to be conspecific with *S. asprella.* Roush considered *S. virgata* T. J. Howell to be a Willamette Valley (Oregon) endemic. Although "the leaves and pubescence (of *S. virgata*) are much like those of *S. asprella*" she wrote, "the inflorescence is entirely distinct" (Roush 1931, p. 179). In Roush's opinion, *S. asprella* and *S. virgata* are related through *S. malvaeflora,* a coastal species, with which they share similar leaf form and pubescence.

Hitchcock (1957) divided Roush's *S. asprella* in the Klamath Mountains into 3 subspecies of *S. malvaeflora* (DC.) Gray ex Benth.: *asprella* (E. Greene) C. L. Hitchc., *elegans* (E. Greene) C. L. Hitchc., and *nana* (Jeps.) C. L. Hitchc. He also reduced *S. virgata* to *S. malvaeflora* ssp. *virgata* (T. J. Howell) C. L. Hitchc. and noted that the subspecies *virgata* and *asprella* "are maintainable only on very inconsistent morphological characters, and since it is known that they interbreed freely, they may more properly be treated as fairly well-defined geographical or ecological races . . ." (Hitchcock 1957, p. 13). More recently (Hitchcock and Cronquist 1973) he reinstated *S. virgata* to the rank of species.

Hitchcock's treatment of *S. malvaeflora* ssp. *asprella* and ssp. *virgata* centers around stem and calyx pubescence. "In general 'typical' *virgata* can be distinguished from 'typical' *asprella* because of the finer, uniform stellae of the calyx and longer, softer hairs of the lower stem, but at the s(outhern) limit of its range, in s(outhern) Douglas and Josephine cos(.), it intergrades with ssp. *asprella* . . ." (Hitchcock 1957, p. 25).

Sidalcea malvaeflora ssp. *nana* is also similar to ssp. *asprella.* Hitchcock (1957, p. 29) pointed out, "Jepson referred the plant [ssp. *nana*] to *S. reptans,* largely (it would seem) on the basis of its creeping habit, since otherwise it has little resemblance to *reptans,* the leaves, inflorescence, calyx, and carpels being similar to those of ssp. *asprella.*" According to Hitchcock (1957, p. 29), *S. malvaeflora* ssp. *nana* is "distinguished chiefly by its very fine stellae."

Sidalcea malvaeflora ssp. *elegans* is also closely related to and sympatric with ssp. *asprella,* but may be easily distinguished by its large, few-flowered, often glabrous, slender inflorescences, trailing slender rhizomatous habit, dissected cauline leaves, and possible serpentine endemism. Since this subspecies is so clearly distinct from *S. malvaeflora* ssp. *asprella,* its taxonomic identity will not be discussed further.

METHODS

Seventy-four *Sidalcea* sites in Josephine and Jackson counties of Oregon and Del Norte, Siskiyou, and Trinity counties of California (Fig. 1) were visited between June and August, 1989. Data such as soil type and moisture content, associated species, growth form, and population size were recorded for each population. I collected one to three specimens from each population. Eight hundred and fifty-two specimens from eight regional herbaria were borrowed for morphological analysis.

I examined the morphological characters used by Hitchcock to separate *S. setosa* and *S. oregana* ssp. *spicata* (Table 1) using specimens collected in the field, all herbarium specimens annotated as *S. invisa* and *S. setosa* by Hitchcock, and one herbarium specimen of *S. oregana* ssp. *spicata* from each county in which it was collected. Due to the lack of stem bases in some of the specimens examined, this character was not used for comparison.

Morphological characters used by Hitchcock to separate *S. malvaeflora* ssp. *asprella* and ssp. *virgata* (Table 2) were examined in specimens collected in the field, one herbarium specimen of *S. malvaeflora* ssp. *asprella* and 2 herbarium specimens of *S. malvaeflora* ssp. *virgata* from each county in which they were collected.

RESULTS

The historical range of plants recognized as *S. setosa* encompasses Douglas, Josephine, Jackson, and Curry counties in Oregon and Siskiyou County in California. The populations occur in valleys (Rogue River watershed, Umpqua Valley, Roseburg, Glendale, Grant's Pass, and Edgewood) as well as in mountains (Mt. Ashland, High Cascades). This range seems to be within the central part of the range of *S. oregana* var. *spicata,* which extends north to the middle Cascades of Oregon and south to the middle of California, barely entering western Nevada (Hitchcock, 1957 Map 3). The ranges are not mutually exclusive.

Results of comparison of morphological characters show that there is variability in some characters that should be, according to Hitchcock's treatment, unique to *S. setosa* (Table 3). Both carpel ornamentation and stem pubescence seem to be consistent; *spicata* has smooth carpels and hirsute stem pubescence and *setosa* has slightly reticulate carpels and stellate stem pubescence. Bristly calyx pubescence, on the other hand, is not unique to *S. setosa*; roughly half of the *spicata* specimens examined had bristly stellae.

One may understand why botanists have been confused over the identity of these two groups in the study area; the high predominance of hirsute stem pubescence (*spicata* character) combined with bristly calyces (*setosa* character) in specimens collected in 1989 is perplexing. A further analysis of specimen characters from the study area

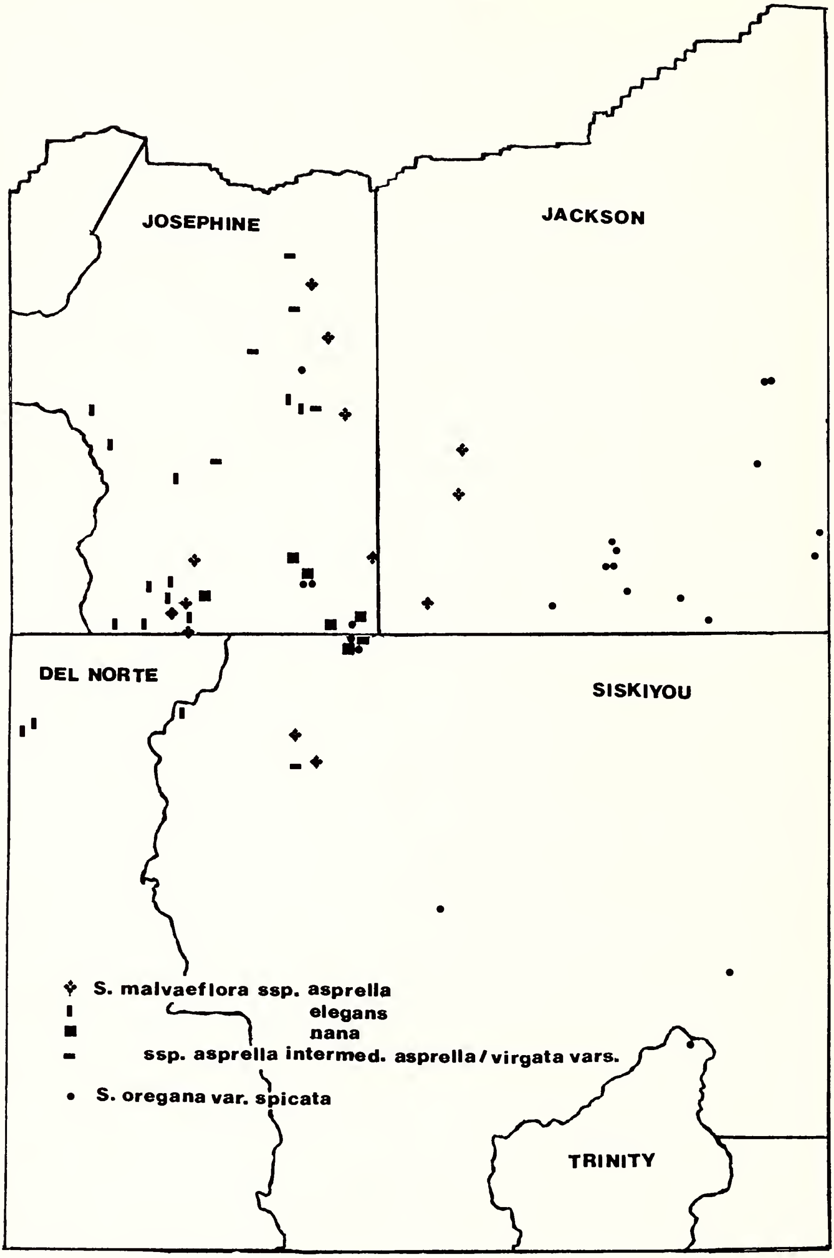

FIG. 1. Distribution of *Sidalcea* species in the Klamath Mountains of Oregon from sites visited in 1989.

TABLE 1. MORPHOLOGICAL CHARACTERS OF *SIDALCEA SETOSA* AND *SIDALCEA OREGANA* VAR. *SPICATA* USED BY HITCHCOCK TO SEPARATE THE TAXA.

	setosa	*spicata*
Stem	short rootstocks	no rootstocks
Carpels	reticulate	smooth to lightly reticulate
Stem pubescence	stellate w/longer simple or forked hairs (hirsute or stellate)	soft-hirsute, some w/ forked to 4-rayed hairs, occasionally stellate (glabrous)
Calyx pubescence	bristly stellate	uniformly short stellate to conspicuously hirsute

indicates that 26% of specimens had hirsute stem pubescence and bristly calyces, 48% had *spicata*-like characters, and 26% had *setosa* characters. One specimen from Baker County, Oregon has both hirsute stem pubescence and a bristly calyx.

The variability in morphology in the study area combined with duplication of characters outside of the study area leads me to conclude, like Roush, that *S. setosa* is part of a highly variable *S. oregana* var. *spicata* whose pubescence varies with ecological factors and whose carpel characters are also variable.

Comparison of morphological characters in *S. malvaeflora* ssp. *asprella* and ssp. *virgata* (Table 2) leads to the conclusion that the separation of the "typical" phases of *S. malvaeflora* ssp. *asprella* and ssp. *virgata* are possible only at the limits of their ranges. All of the following characters overlap: lower stem pubescence, rhizomatous habit, calyx length and shape, flower number, petal length, pedicel length, and carpel characters. Both subspecies have stellae of uniform lengths and stellae of mixed lengths on their calyces (Table 4). They both have predominantly stellate stem pubescence. The one character that separates the two in herbarium specimens is

TABLE 2. MORPHOLOGICAL CHARACTERS OF *SIDALCEA MALVAEFLORA* SSP. *VIRGATA*, SSP. *ASPRELLA* AND SSP. *NANA* USED BY HITCHCOCK TO SEPARATE THE TAXA.

	virgata	*asprella*	*nana*
Calyx pubescence	uniformly, densely, finely stellate	densely, finely stellate with a scattering of longer stellae	uniformly, densely, finely stellate
Stem pubescence	long, soft several-rayed hairs (hirsute, glabrous)	rough-pubescent stellate and simple hairs (stellate)	very finely stellate
Inflorescence structure	often closely many-flowered	open, loosely-flowered	open, loosely-flowered

TABLE 3. COMPARISON OF CHARACTERS USED IN HITCHCOCK'S TREATMENT OF *SIDALCEA SETOSA* AND *OREGANA* VAR. *SPICATA* IN HERBARIUM SPECIMENS AND SPECIMENS COLLECTED IN 1989.

	spicata (herb.)*	*setosa* (herb.)	field (1989)
Carpel architecture			
reticulate	1	9	2
smooth	11	1	8
Stem pubescence			
stellate	2	20	6
hirsute	19	0	17
mixed	2	1	1
glabrous	4	0	3
Calyx pubescence			
hirsute	4	0	8
bristly	12	20	14
short stellate	11	0	7

* N = 27 *spicata* from the herbarium; N = 22 *setosa* from the herbarium; N = 27 field specimens collected in 1989. See list.

inflorescence structure. Specimens annotated as intermediate between *asprella* and *virgata* have congested racemes, but are not spicate. In specimens collected in 1989, I initially used Greene's type description of *S. asprella,* a plant with basal and cauline leaves essentially alike, to make determinations. Examination of specimens from throughout *S. asprella*'s range showed that only small localized areas (Butte and Yuba counties in California and Jackson county in Oregon) harbor plants with the cauline leaf type described by Greene, demonstrating that this character is not taxonomically useful. Because inflorescence structure seems to be the only differentiating character, I propose these taxa be combined into one variable group, *Sidalcea malvaeflora* ssp. *asprella,* whose varieties intergrade, as Hitchcock pointed out, in the study area.

Because of its usually distinct inflorescence and more northerly range, I think *S. virgata* warrants varietal status under ssp. *asprella.* Table 5 compares attributes of the two varieties of ssp. *asprella,* var. *asprella* and var. *virgata* (Howell) Dimling.

The one character used, short stellate pubescence of calyx and stem, to separate ssp. *nana* from ssp. *asprella* has not proven useful. Based on collections from the study area, ssp. *nana* has stem pubescence composed of stellae of mixed lengths and short stellate calyx pubescence. Approximately 25% of the ssp. *asprella* specimens examined had similar calyx pubescence and most had similar stem pubescence. Further investigation into the relationship between these two subspecies is needed using specimens from throughout their reported ranges. If the pattern observed in this study area holds true

TABLE 4. COMPARISON OF CHARACTERS USED IN HITCHCOCK'S CLASSIFICATION OF *SIDALCEA MALVAEFLORA* SSP. *VIRGATA* AND *ASPRELLA* FROM HERBARIUM SPECIMENS AND SPECIMENS COLLECTED IN 1989.

	virgata (herb.)*	*asprella* (herb.)	field (1989)
Calyx pubescence			
uniform	4	6	4
stellae of mixed lengths	6	13	14
Stem pubescence			
stellate	7	13	7
hirsute	0	1	6
mixed	2	2	4
glabrous	1	3	1
Inflorescence structure			
loose	0	19	12
spicate	10	0	0
congested	0	0	6
Cauline leaf shape			
similar to basal	0	5	4
dissected	10	14	14

* N = 10 *virgata* and N = 19 *asprella* specimens from the herbarium; N = 18 specimens from the study area. See list.

throughout its distribution, this subspecies will probably not warrant taxonomic recognition.

KEY TO *SIDLACEA* SPECIES OF THE KLAMATH MOUNTAINS

a. Plants with loosely arranged inflorescences (spicate in var. *virgata*); petals 10–25 mm; calyces 5–12 mm, short stellate often with slightly longer stellate hairs; pedicels 3–10 mm; carpels reticulate; inhabiting dry woodlands, clearcuts and low elevation meadows; flowers May to July. .... *Sidalcea malvaeflora*

  b. Plants with a spicate inflorescence, 122–366 m; mixed woodlands, roadsides; May–June. .... ssp. *asprella* var. *virgata*

  b′. Plants with open, loosely arranged inflorescences; 183–1829 m; habitats various; May–July.

TABLE 5. COMPARISON OF CHARACTERS DISTINGUISHING *SIDALCEA MALVAEFLORA* SSP. *ASPRELLA* VAR. *ASPRELLA* FROM VAR. *VIRGATA*.

	var. *asprella*	var. *virgata*
Geographical distribution	Fresno Co., CA–Douglas Co., OR	Siskiyou Co., CA–Yamhill Co., OR
Inflorescence	loosely-flowered	spicate
Stem pubescence	usually stellate, some simple hirsute or glabrous	stellate
Habitat	valley to mountains	valley

c. Plants mat-forming; slender rhizomes, infrequently with a taproot; upright stems slender and glabrous above; inflorescence usually simple; mixed woodlands, oak flats, manzanita/pine parks, often in serpentine soil; 122–805 m; May–June. .... ssp. *elegans*

c′. Plants of larger stature, clump-forming; woody rhizomatous; stems usually stout, rarely glabrous; inflorescence with axillary racemes; mixed or coniferous woodlands, clearcuts, low elevation meadows; 183–1829 m; June–July.

  d. Calyx pubescence uniformly short stellate; stem pubescence long/short stellate mixture; open coniferous woodlands, clearcuts; 914–1829 m; July. .... ssp. *nana*

  d′. Calyx pubescence short stellate, most with a mix of longer stellae on the midveins and margins; stem pubescence stellate, sometimes hirsute or glabrous; openings in mixed woodlands, meadows; 183–1036 m; June–July. .... ssp. *asprella* var. *asprella*

a′. Plants with spicate raceme; petals 5–15 mm; calyces 4–8 mm, pubescence varying from short stellate to bristly stellate to long simple hairs; pedicels 1–3(5) mm; carpels usually smooth, sometimes lightly reticulate; meadows; 914–1829 m; July–August. .... *S. oregana* var. *spicata*

TAXONOMIC TREATMENT

1. *Sidalcea oregana* (Nutt. in T.& G.) Gray var. *spicata* (Regel) Jeps., Fl. Calif. 2:492. 1836.—*Callirhoe spicata* Regel, Gartenfl. 21: 291. pl. 737. 1952.—*S. spicata* Greene, Bull. Calif. Acad. Sci. 1:76. 1885.—*S. oregana* ssp. *spicata* (Regel) C. L. Hitchc., Univ. Washington Publ. Biol. 18:64. 1957.—TYPE: Plate in Gartenflora, drawn from seeds supposedly collected in the Sierra Nevada of California.

Sidalcea spicata var. *tonsa* Peck, Madrono 6:14. 1941.—TYPE: USA, Oregon, Crook Co., Big Summit Prairie, 1941, *Peck 17224* (WILLU!).

Sidalcea setosa C. L. Hitchc., Univ. Wash. Publ. Biol. 18:53. 1957.—*Sidalcea invisa* C. L. Hitchc., nom. nud. in herb.—TYPE: USA, Oregon, Josephine Co., Grant's Pass, June 15, 1915, *Cusick 4796* (WS!).

Representative specimens. USA, California, Alpine Co.: N of Red L., *Alexander* and *Kellogg 3541* (UC). Butte Co.: Jonesville, *Copeland 659* (CAS). El Dorado Co.: Camp Sacramento, July–August, 1931, *Vortrilde s.n.* (CAS). Humboldt Co.: Box Camp Meadow, *Tracy 17822* (CAS). Lassen Co.: Dixie Valley, 3 July, *Baker s.n.* (UC). Modoc Co.: Eight Mile Cr., *Alexander* and *Kellogg 4976* (CAS). Mono Co.: Between Mammouth and Lake George, 21 June 1925, *Larson s.n.* (CAS). Nevada Co.: Donner L., 10 July 1903, *Heller s.n.* (CAS). Placer Co.: Summit Valley, *Howell 18570* (UC). Plumas Co.: Prattville, 20 July 1882, *Austin s.n.* (UC). Shasta Co.: Lassen National Park near Summit L., *Ferris* and *Lorraine 10468* (CAS). Sierra Co.: Webber L., 6–12 August 1927, *Haley s.n.* (CAS). Siskiyou Co.: Taylor L., *Alexander* and *Kellogg 5609* (CAS); Azalea L., *Rolle*

279 (OSC, ORE); N of Buck Pk., *Rolle 270* (OSC); Shakleford Cr. Trail, *Dimling 155* (OSC); Deadfall Meadow, *Dimling 154* (OSC, ORE, NY); Edgewood, *Dimling 154* (OSC). Tehama Co.: Government Flat, *Baker 9800* (CAS). Trinity Co.: Deer Cr. on trail to Red Mtn., *Kruckeberg 3749* (WTU). Nevada, Douglas Co.: L. Tahoe, *Kruckeberg 3655* (WTU). Ormsby Co.: Marlette L., *Allen 536* (CAS). Washoe Co.: Jones Canyon, 22 July 1907, *Brown s.n.* (CAS). Oregon, Baker Co.: 5 km W of Whitney, *Peck 10351* (CAS). Clackamas Co.: Mt. Hood, summer 1929, *Van Dyke s.n.* (UC). Deschutes Co.: island in Deschutes R. at Tumalo, *Whited 252* (CAS). Douglas Co.: *Roseburg, *Howell 472* (ORE); *Umpqua Valley, June 1887, *Howell s.n.* (ORE). Harney Co.: 42 km N of Burns, *Thompson 13305* (WTU). Jackson Co.: *Ashland Pk., *Thompson 12341* (WTU, OSC); *High Cascades, June 1927, *Heckner s.n.* (WTU, OSC); *near Woodville, *Peck 6870* (OSC); *Mt. Ashland, 19 July 1938, *Rossbach* and *Rossbach s.n.* (UW); 42 km E of Ashland, *Dimling 130* (OSC); Johnson Creek, *Dimling 131* (OSC); Deadwood Cr., *Dimling 146* (OSC, ORE); Pilot Rock Rd., *Dimling 147* (OSC, ORE); Wagner Butte, *Dimling/Rolle 150, 151* (OSC, ORE); Wagner Butte Tr., *Dimling/Rolle 152* (OSC, ORE), 153 (OSC, ORE, NY); Mt. Ashland, *Dimling 156* (OSC, ORE, NY); Wrangle Camp, *Dimling 157* (OSC); Fish L. *Rolle 281, 282* (OSC). Jefferson Co.: Camp Sherman, 8 August 1853, *Constance* (UC). Josephine Co.: Grant's Pass, *Dimling 117* (OSC); Bigelow Trailhead, *Dimling 144* (OSC, ORE); Bigelow L., *Dimling 145* (OSC, ORE, NY); *Grant's Pass, 20 May 1886, *Henderson s.n.* (CAS); *Grant's Pass, 26 June 1886, *Henderson s.n.* (CAS); *Grant's Pass, *Cusick 4796* (WS); *Grant's Pass, *Cusick 4787* (WS); *Grant's Pass, 20 June 1886, *Henderson s.n.* (ORE); *Glendale and Grant's Pass, *Henderson 151* (ORE); *Grant's Pass, *Peck 6871* (OSC); *Grant's Pass, *Peck 6864* (OSC); *near Glendale, 12 July 1887, *Henderson s.n.* (ORE); *Grant's Pass, 20 June 1889, *Henderson* (UW); *Grant's Pass, *Canby 89* (OSC); *Grant's Pass, *Hitchcock 19601* (WTU); *Grant's Pass, *Peck 6863* (OSC); *Grant's Pass, *Peck 6865* (OSC). Klamath Co.: S of Klamath Falls, *Mott 6765* (CAS). Lake Co.: Whitworth Cr., *Applegate 7851* (CAS). Umatilla Co.: meadow, *Peck 6869* (OSC). Wallows Co.: Buckhorn Springs, 29 June 1934, *Peck 18334* (UC). Unknown: *Southern Oregon, 12 July 1887, *Henderson s.n.* (CAS, ORE).

* Denotes specimens annotated as *S. invisa* by C. L. Hitchcock.

One population cited as a possible *setosa/asprella* intermediate (Hitchcock 1957), *Keck 4815,* was seen in 1989 and was determined as *S. malvaeflora* (DC.) Gray ex Benth. ssp. *asprella* (Greene) Jepson var. *virgata* Dimling because of stellate pubescence, congested inflorescence and location.

2. *Sidalcea malvaeflora* (DC.) Gray ex Benth. ssp. *nana* (Jeps.) C. L. Hitchc., Univ. Washington Publ. Biol. 18:29. 1957.—*S. reptans* Greene var. *nana* Jeps., Fl. Calif. 2:489. 1936.—TYPE: USA, California, Trinity Co., Yollo Bolly Mts., Soldier's Ridge, *Jepson 14601* (JEPS? not seen).

Representative specimens. USA, Oregon, Jackson Co.: USFS Road 1030/400, *Dimling 139* (OSC); Arnold Mine, *Dimling 140* (OSC). Josephine Co.: USFS Rd. 4613, *Dimling 143* (OSC); Elder Cr., *Dimling 134* (OSC); Bigelow Salvage, July 1989, Wolf/*Seda/Sisko s.n.* (OSC). California, Siskiyou Co.: NE of Buck Pk., *Rolle 271* (OSC); NW of Azalea L., *Rolle 278* (OSC).

3. *Sidalcea malvaeflora* (DC.) Gray ex Benth. ssp. *asprella* (Greene) C.L. Hitchc. var. *asprella,* Univ. Washington Publ. Biol. 18:25. 1957.—*S. asprella* Greene., Bull. Calif. Acad. Sci. 1:78. 1885.—*S. malvaeflora* var. *asprella* Jeps., Man. Fl. Pl. Calif. 630. 1925.—TYPE: USA, California, Yuba Co., near Camptonville, 1 July 1884, *Greene s.n.* (ND? not seen).

Representative specimens. USA, California, Amador Co.: SE of Plymouth, *Nordstrom 795* (UC). Butte Co.: Oroville–Forbestown Rd., *Hitchcock 19536* (ORE). Calaveras Co.: W of Avery, *Tracy 5713* (UC). El Dorado Co.: N of Placerville, *Wiggins 11209* (WS). Fresno Co.: Shaver L., 18 May 1940, *Winblad s.n.* (CAS). Humboldt Co.: Bridgeville, 15 June 1893, *Blankinship s.n.* (UC). Lassen Co.: Big Valley Mtns., *Eastwood* and *Howell 7982* (CAS). Mariposa Co.: Wawona, *Howell 171* (CAS). Modoc Co.: Lakeshore, July 1898, *Austin s.n.* (CAS). Nevada Co.: Nevada City, 21–22 June 1912, *Eastwood s.n.* (CAS). Placer Co.: W of Baxter, *Hitchcock 6338* (WTU). Plumas Co.: Jamison Cr., *Howell 27620* (CAS). Shasta Co.: E of Redding, *Hitchcock 6448* (WS). Siskiyou Co.: near Dunsmuir, April 1925, *Reinvehl s.n.* (CAS). Tuolumne Co.: Coulterville, *Wolf 4877* (UC). Trinity Co.: N of Covelo, *Hitchcock 20025* (WTU). Yuba Co.: SE of Challenge, *Hitchcock 19539* (WS). Oregon, Curry Co.: N of Agness, *Hitchcock 19923* (WTU). Douglas Co.: W of Elkton, *Sundberg 84* (ORE). Jackson Co.: Cantrell-Buckley Campground, *Dimling 106*; Applegate L., *Dimling 107* (OSC); Forest Cr. Rd., *Dimling 108* (OSC). Josephine Co.: E of Murphy, *Dimling 126* (OSC); *Elk Cr., *Dimling 135* (OSC); *Manzanita Wayside, *Dimling 86* (OSC); *Walker Mtn., *Dimling 90* (OSC); *Waldo Hill, *Dimling 135*; *Longwood Fire, July 1989, *Wolf/Seda s.n.* (OSC); *Poker Cr., *Dimling 122* (OSC, ORE). Lane Co.: near Coburg, 4 May 1887, *Howell s.n.* (CAS). *Specimens originally annotated by Dimling as ssp. *asprella* var. *virgata* because of cauline leaves (see text).

4. *Sidalcea malvaeflora* (DC.) Gray ex Benth. ssp. *asprella* (Greene) C. L. Hitchc. var. *virgata* (T. J. Howell) Dimling comb. et stat.

nov.—*S. virgata* T. J. Howell, Fl. N. W. Am. 101. 1897.—*S. malvaeflora* ssp. *virgata* (T. J. Howell) C. L. Hitchc., Univ. Washington. Publ. Biol. 18:24. 1957.—LECTOTYPE: USA, Oregon, Marion Co., Silverton, June 1882, *T. J. Howell s.n.* (ORE!).

Representative specimens. USA, Oregon, Benton Co.: Corvallis, *Craig 53* (ORE); Sulfur Springs, *Wagner 72* (ORE). Douglas Co.: Glendale, *Howell 733* (ORE); Sutherlin, *Henderson 12622* (ORE); Yoncalla, *Henderson 12623* (ORE). Lane Co.: Hills Cr., *Detling 2814* (ORE); near Jasper, *Henderson 13501* (ORE); Cottage Grove, 14 June 1935, *Leach s.n.* (ORE). Polk Co.: W of Pedee, *Hitchcock 19317* (ORE); Yamhill Co.: Willamena, *Leach 3571* (ORE).

Intermediate between ssp. *asprella* and ssp. *virgata*: USA, California, Siskiyou Co.: E of Happy Camp, *Dimling 109* (OSC). Oregon, Josephine Co.: E of Merlin, *Dimling 89* (OSC); Robertson Br., *Dimling 92* (OSC); Leland, *Dimling 91* (OSC); Triller Ln., *Dimling 96* (OSC); L. Selmac, *Dimling 125* (OSC).

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A REVISION OF *ACANTHOMINTHA OBOVATA* (LAMIACEAE) AND A KEY TO THE TAXA OF *ACANTHOMINTHA*

James D. Jokerst
California Academy of Science, Golden Gate Park,
San Francisco, CA 94118

Abstract

A reevaluation of *Acanthomintha obovata* indicates that subspecies *duttonii* is more appropriately recognized as a species, and that material previously referred to as subspecies *obovata* is comprised of two geographically and morphologically distinct subspecies. Nomenclatural innovations are published with a key to the species and subspecies of *Acanthomintha.*

The distinctive Lamiaceae genus *Acanthomintha* A. Gray ex Benth. & Hook. consists of four species endemic to central and southern California, USA, and northern Baja California, Mexico (Fig. 1). The genus has not been monographed or the subject of published taxonomic or ecologic inquiry.

Herbarium studies for the Jepson Manual project indicate the need to revise the taxonomy of *A. obovata* Jepson. Traditionally, *A. obovata* has been treated as consisting of subsp. *obovata* and *duttonii* Abrams (Abrams 1951; Munz 1959, 1974). Morphologic characteristics and geographic distributions indicate that subsp. *duttonii* should be elevated to full species status and *A. obovata* sensu stricto is divisible into two subspecies. These changes are presented below with supporting observations and other notes. The article concludes with a key to currently recognized taxa of *Acanthomintha.*

1. **Acanthomintha duttonii** (Abrams) Jokerst stat. et comb. nov. *A. obovata* Jepson subsp. *duttonii* Abrams. Illustrated Flora of the Pacific States. Vol. III: 635. 1951.—Type: USA, California, San Mateo Co., "Woodside serpentine", 17 April 1900, *H. A. Dutton 63392* (holotype, CAS!).

Stem 0.4–2 dm tall; typically unbranched but most populations with some plants branched at base; upright or decumbent at the base; glabrous or sparsely hispidulous. Leaves 8–12 mm long (excluding petiole), lance-oblong to obovate, entire or serrate, teeth not armed with acicular spine. Inflorescence generally capitate, 1 per stem, occasionally the uppermost leaf axils will also produce small flower clusters; bracts 5–11 mm long (excluding spines), 4–11 mm wide, ovate but slightly longer than wide, green or less commonly

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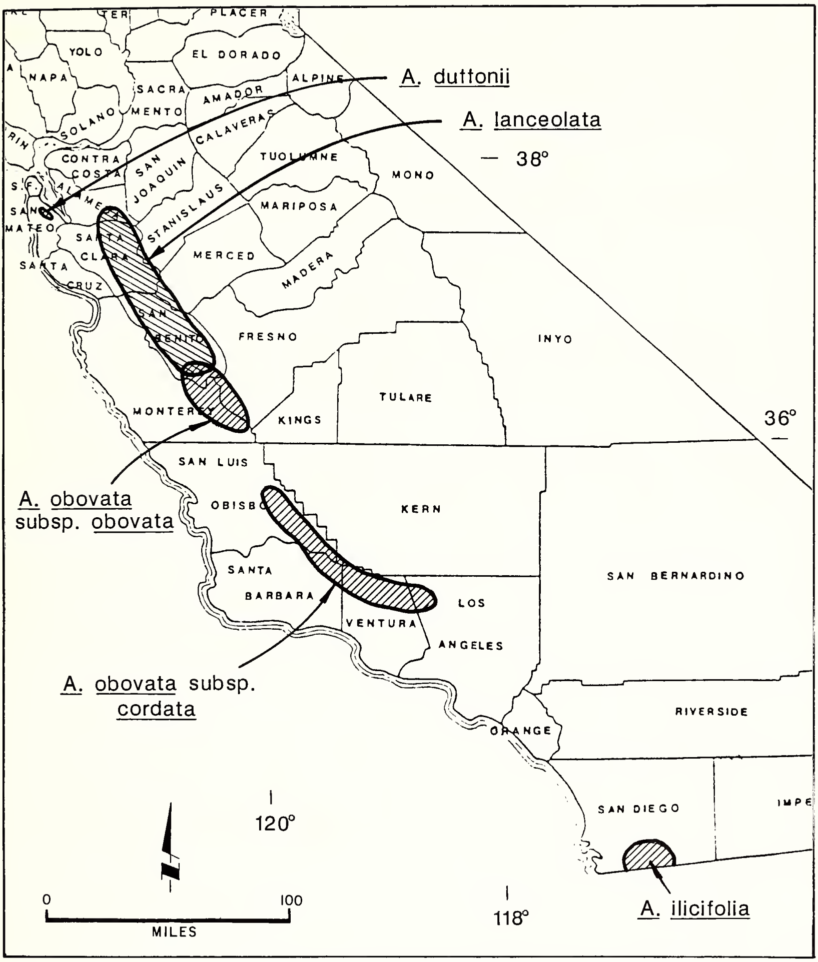

FIG. 1. Generalized distribution of *Acanthomintha* taxa in California.

straw-colored during anthesis, armed with 5, 7, or 9 marginal spines. Calyx 5–8 mm long, outer surface glabrous or microscopically hispidulous, inner surface of calyx teeth sparsely hirsute; acicular teeth of lobes 0.5–1.5 mm long. Corolla 12–16 mm long, white, lower lateral lobes occasionally lavender and the central lobe rose-lavender; upper lip erect, slightly hooded over stamens, entire; lower lip reflexed at 90-degree angle to the tube, three-lobed. Stamens glabrous, upper 11–15 mm long, lower 9–14 mm long; anthers glabrous, pink–red; pollen cream. Style 11–16 mm long, glabrous.

Geographic range. Endemic to San Mateo County (Smith and Berg 1988); never collected beyond a narrow, 6-mile-long strip from Lower Crystal Springs Reservoir south to Woodside (Fig. 1). Reported extant at two sites separated by ca. 1 km in and adjacent to Edgewood Park (Bittman, personal communication). Disjunct ca. 185 km from the nearest *A. obovata* in San Benito and Monterey counties east of King City. *Acanthomintha lanceolata* occupies the south Coast Range foothill region separating *A. duttonii* and *A. obovata.*

Habitat. Slopes and flats with deep, heavy-clay soil inclusions surrounded by the more typical rocky serpentine soil. Reported from slopes, depressional areas, and vernal pools. The heavy-clay soil inclusion at the Edgewood Park site supports a species-rich forb association that distinguishes the site from the surrounding serpentine grasslands and supports *Agoseris heterophylla, Calochortus albus, Delphinium variegatum, Holocarpha virgata, Lotus micranthus, L. subpinnatus, Lolium multiflorum, Orthocarpus lithospermoides, O. purpurescens, Sidalcea malvaeflora, Stipa pulchra,* and *Trifolium fucatum* (taxonomy according to Munz 1959).

Relationships. Acanthomintha duttonii is most closely related to *A. obovata* and *A. ilicifolia* A. Gray. The three species have the same habit and corolla shape and each has a glabrous style. Important characteristics shared by *A. duttonii* and *A. obovata* include four stamens with hairy or woolly anthers and growth habit. Other characteristics that *A. duttonii* and *A. ilicifolia* share include cordate or truncate bract base; glabrous or sparsely hispidulous stems, leaves, and calyces; calyces less than 8 mm long; and sparse, villous-hispid anthers. *Acanthomintha ilicifolia,* with 2 stamens and glabrous anthers, is disjunct ca. 250 km miles south of the nearest *A. obovata* station in Los Angeles County.

Acanthomintha duttonii differs from *A. obovata* and other congeners in the absence of acicular marginal spines on the upper leaves; pink–red anthers; and generally unbranched habit with a solitary capitate flower cluster per stem. These morphological differences and the wholly discrete geographic range of the populations support their status as a species.

Legal status. Acanthomintha duttonii is listed as endangered under both the California and federal Endangered Species Acts (ESAs). The larger occurrence in Edgewood Park is threatened by urban development.

Exsiccatae. USA, CA, San Mateo Co.: Woodside serpentine, 17 April 1900, *H. A. Dutton 63392* (holotype, CAS!); Crystal Springs Reservoir, May 1903, *A. D. E. Elmer 4538* (CAS!, UC!); near Menlo Golf Club, small area in sandy soil on hillside sloping to the S, 26 and 29 May 1915, *H. A. Dutton 3819* (CAS!, UC!); serpentine back of Redwood City, 2 June 1920, *H. R. Davis 182* (CAS!); serpentine back of Redwood City, 1 July 1920, *L. R. Abrams 7500* (CAS!); open grassy hill above upper Emerald Lake, 24 May 1929, *C. B. Wolf 3723* (CAS!, UC!); Emerald Lake area, 21 April 1930, *D. K. Gillesfice 9220* (CAS!); Redwood Hills, 17 May 1933, *L. S. Rose 331171* (CAS!, UC!); Emerald Lake, 100 m, dry rain pool, 28 May 1936, *L. S. Rose 36303* (CAS!); Emerald Lake west of Redwood City, 15 May 1940, *D. D. Keck 5034* (CAS!, UC!); Redwood City Hills, 20 May 1941, *R. F. Hoover 5110* (UC!); near Crystal Springs Reservoir near Hwy 92, 16 April 1972, *J. H. Thomas 16065A* (CAS!); serpentinized slope east side of Upper Crystal Springs Reservoir, below and west of state hwy interchange, 16 April 1972, *L. Heckard 2903* (JEPS!).

2. ACANTHOMINTHA OBOVATA Jepson, Man. Fl. Pl. Calif. 873. 1925. See subspecies headings for typification.

Stem 0.4–3 dm tall; branched at base or simple; glabrous, or sparsely to conspicuously hispidulous, with or without conspicuous villous glandular and eglandular hairs. Leaves 8–12 mm long (excluding petiole), lance-oblong, ovate, or obovate, hispidulous or villous with glandular and eglandular hairs; margin of the lower entire or serrate, those subtending flowering bracts with acicular spines on teeth. Inflorescence capitate and axillary; bracts 7–15 mm long, shiny, straw-colored at anthesis, glabrous or hispidulous, armed with 7, 9, or 11 marginal spines, 5–8 mm long. Calyx 7–13 mm long, hispidulous or villous with glandular and eglandular hairs, teeth conspicuously hirsute within, armed with acicular spines 1.5–3.5 mm long. Corolla 12–27 mm long, glabrous or finely pubescent, white, occasionally tinged lavender; upper lip erect, slightly hooded over stamens, entire; lower lip reflexed at 90-degree angle to the tube, three-lobed. Stamen filaments glabrous, upper 14–27 mm long, lower 15–23 mm long; anthers moderately to densely woolly, yellow; pollen cream. Style glabrous.

2a. ACANTHOMINTHA OBOVATA Jepson subsp. CORDATA Jokerst subsp. nov.—TYPE: USA, California, Ventura Co., Wagon Canyon Rd., 14 June 1956, E. C. Twisselmann, 2986 (holotype, CAS!; isotypes, CAS! [2 sheets]).

Caulis glaber hispidulusve. Folia supra spinis acicularibus in marginibus. Inflorescentia in fasciculis capitatis et axillis. Bracteae late-ovatae, cordatae-amplecteus ad basim. Calyx glaber hispidulusve, dentes hirsuti interius. Anthera lanatae.

Stem 0.4–2.5 dm tall; generally branched at base, occasionally unbranched; glabrous or sparsely hispidulous, sometimes visible only under magnification. Bracts of inflorescence 7–15 mm long, 6–16 mm wide, broadly ovate, generally slightly wider than long, base cordate-clasping, glabrous or hispidulous. Calyx 9–13 mm long, glabrous or sparsely hispidulous. Anthers moderately to densely woolly.

Geographic range. Western Transverse Ranges in northwest Los Angeles, southeast San Luis Obispo, northern Ventura, and eastern Santa Barbara counties (Fig. 1). *Acanthomintha ilicifolia* occurs 250 km south of subsp. *cordata.* Subspecies *cordata* is (Fig. 1) disjunct ca. 115 km south of the nearest reported subsp. *obovata* population near Parkfield, Monterey County. Judging from the uniformity of vegetation and climate, additional populations of either *A. obovata* subspecies could be located in the area separating them, unless their distributions are limited by edaphic or geologic factors.

Habitat. Heavy adobe-clay soil (probably a Vertisol) of hillside slopes, saddles, and ridges, which desiccates by early June, cracking into large polygonal blocks. Grassy openings in woodlands of *Quercus douglasii* Benth., *Pinus sabiniana* Dougl., *Juniperus californica* Carr., and *Pinus monophylla* Torr. & Frem., also reported from chaparral openings (Smith 1976).

Relationships. Subspecies *cordata* closely resembles subsp. *obovata* in all morphological features except bract shape and stem, calyx, and anther vestiture. Subspecies *cordata* lacks gland-tipped hairs, and has glabrous or sparsely hispidulous stems and calyces, moderately to densely woolly anthers, and broadly ovate bracts that are generally as wide as they are long with cordate-clasping bases. Subspecies *obovata,* in contrast, always has some gland-tipped hairs, densely hispidulous stems and calyces that may or may not also have villous hairs, sparsely to moderately woolly anthers, and narrowly ovate bracts that are wider than long with truncate or obtuse bases. Although the vestiture traits are consistent among the specimens examined and have a strong geographic component, they are not substantial enough to warrant recognition of these clusters of populations above the subspecies level.

A Karen Brandegee collection from western Fresno County (s.n., 11 May 1916, west of summit between Coalinga and Parkfield, UC!) is the only specimen that had intermediate traits between the two *obovata* subspecies. Only one plant of the collection has villous hairs; the remainder have sparsely hispidulous stems and calyces that resemble subsp. *cordata.* This collection is assigned to subsp. *obovata* because of its bract shape, the presence of some plants with villous hairs, and its location at the south end of the range of subsp. *obovata.* A collection from a dry hillside west of Coalinga (Condit s.n., 13 June 1910, UC!) presumably from the vicinity of the Brandegee collection, is typical of subsp. *obovata.* Field studies may reveal that the ranges of the two subspecies overlap in the region.

Legal status. Neither subsp. *obovata* nor *cordata* have legal status under state or federal ESAs. Subspecies *obovata* is considered a plant of limited distribution by Smith and Berg (1988). At a minimum, subsp. *cordata* warrants the same status. Both subspecies are poorly represented in herbaria. The relatively narrow range of subsp. *cordata* and small number of populations indicates it should be considered for inclusion on the California Native Plant Society's list of rare or endangered species (List 1b in Smith and Berg 1988). Threats to the species have not been evaluated. Possible threats include grazing and off-road vehicles. Both subspecies should be evaluated and periodically monitored to determine threats and need for legal protection.

Exsiccatae. USA, CA, Los Angeles Co.: Tejon Pass on route toward Castaic off Hwy 99 S and above Oso Canyon, 13 June 1962, *S. M. Kaune 385* (CAS!). Ventura Co.: 24 km W of Frazier Park, *A. M. Vollmer 11* (CAS!); Wagon Canyon Rd, 14 June 1956, *E. C. Twisselmann 2986* (CAS!); branch of Ballinger Canyon near its summit, 7 June 1955, *E. C. Twisselmann 2127* (CAS!); Wagon Canyon Rd approaching Lockwood Valley, 22 June 1949, *H. M. Pollard s.n.* (CAS!); near S base of Mt Pinos 16 km W of Lockwood Valley along Ozena–Lebec Rd, 19 June 1935, *R. Bacigalupi 2353* (CAS!, UC!); 1.6 km S of Lockwood Valley on road to Thorn Meadows, San Emigdio Range, 12 May 1962, *D. E. Breedlove 2734* (CAS!); upper Lockwood Valley, 25 June 1896, *W. R. Dudley 4679* (CAS!, UC!); Lockwood Valley, 18 July, 1905, *H. M. Hall 6698* (UC!). San Luis Obispo Co.: La Panza District, 30 April 1950, *R. F. Hoover 7862* (CAS!, UC!); T32S, R19E, S14, 4.2 km W of Painted Rock, 31 May 1957, *P. L. Johannsen 1179* (UC!), E slope of Caliente Mtn, 820 m, 3 May 1957, *E. C. Twisselmann 3468* (CAS!).

2b. ACANTHOMINTHA OBOVATA Jepson subsp. OBOVATA.—TYPE: USA, California, San Benito Co., "Lorenzo Creek", 12 Jun 1922, *Bettys s.n.,* (holotype, JEPS! isotypes, JEPS! [2 sheets]).

Stem 0.4–3 dm tall, generally branched at base; hispidulous, with or without glandular and eglandular villous hairs. Infloresence bracts 8–13 mm long, 4–11 mm wide (excluding spine), generally longer than wide, base truncate or obtuse, hispidulous, with or without villous glandular and eglandular hairs. Calyx 7–12 mm long, hispidulous, with or without glandular and eglandular hairs. Anthers moderately woolly.

Geographic range. South Coast Ranges in southern San Benito, western Fresno, and southwestern Monterey counties (Fig. 1). Southern station in Parkfield, Monterey County, ca. 115 km north of the nearest recorded subsp. *cordata*.

Habitat. Based on herbarium specimen label data, *A. obovata* subsp. *obovata* is roughly similar to subsp. *cordata,* that is grasslands with adobe-clay soil, including openings in oak woodland and chaparral.

Relationships. Refer to above discussion for relationship with subsp. *cordata.* Subspecies *obovata* has two notable forms distinguished by the presence or absence of conspicuous villous hairs on the stems, leaves, bracts, and calyces, some of which are glandular. Based on herbarium specimens, the villous form appears to be less prevalent than the hispidulous form. The holotype of subsp. *obovata* is hispidulous while one of the isotypes is villous. The villous isotype is annotated by Jepson's hand as "*A. vilosa* n. sp."; the name was never published.

Legal status. See discussion above under subsp. *cordata.*

Exsiccatae. USA, CA, Fresno Co.: W of Coalinga, 13 Jun 1910, *Condit s.n.* (UC!); W of summit between Coalinga to Parkfield (UC!, JEPS!); 11 May 1916, *K. Brandege s.n.*; divide at head of Los Gatos Creek, 7 Jun 1927, *W. L. Jepson 12185* (JEPS!); W of Alcalde, 12 Jun 1915, *H. M. Hall 10029* (UC!). Monterey Co.: Priest Valley, 11 May 1936, *L. S. Rose 36290* (CAS!); summit of Mustang Ridge between Priest Valley and Long Valley, May 1952, *G. L. Stebbins 5048* (CAS!); E of Mustang Grade near Priest Valley, 11 May 1936, *J. T. Howell 2466* (CAS!). San Benito Co.: Bettys Ranch, 18 May 1919, *H. A. Walker 5094* (CAS!); 14.7 km from junction, N of Bitterwater on road to New Idria, 11 May 1957, *P. Raven et al. 10815* (CAS!); near Harrison's, Hernandez, 1 Jun 1899, *W. R. Dudley s.n.* (CAS!); near Hernandez, 17 Aug 1933, *J. T. Howell 11547* (CAS!); summit between Hernandez (Laguna) and Hernandez Valley, 1 May 1933, *D. D. Keck 2046* (CAS!); NE of San Antonio Mission, E of Pine Canyon Rd, 28 May 1962, *C. B. Hardham 10372* (CAS!); 18.3 km from Hernandez on road to San Benito, 29 Mar 1931, *J. T. Howell 6020A* (CAS!); near Hernandez, 17 Aug, 1931, *J. T. Howell 11547* (CAS!); Lorenzo Canyon along Hernandez Valley ca. 13.3 km W of Bitterwater, 13 May 1925, *J. A. Bettys s.n.* (CAS!); Lorenzo Canyon along Hernandez Valley ca. 13.3 km W of Bitterwater, May 1919, *J. A. Bettys s.n.* (UC!, JEPS!); Lorenzo Creek, 12 Jun 1922, *J. A. Bettys s.n.* (holotype, two isotypes, CAS!).

NOTES ON *ACANTHOMINTHA*

The genus *Acanthomintha* is ideally suited for evolutionary and ecological studies because the morphologically distinct species each have narrow geographic ranges and occur in small, isolated populations. The isolated nature of populations likely relates to the affinity of *Acanthomintha* species for edaphically peculiar habitats.

Acanthomintha lanceolata Curran, the most distinctive *Acanthomintha* species, occurs on arid, rocky slopes, most often on serpentine and less frequently on shale, basalt, and other bedrock types. In contrast, the closely related triad of *A. ilicifolia* A. Gray, *A. duttonii* (Abrams) Jokerst, and *A. obovata* Jepson are reported from heavy, clay-rich soils on various geologic formations and soil series.

Acanthomintha ilicifolia of coastal mesas in San Diego County and northern Baja California is primarily associated with vernal pools. Open grasslands on serpentine formations in San Mateo County support *A. duttonii,* although a collection by L. S. Rose (36063 CAS!) is from a "dry winter pool". A couple *Acanthomintha obovata* herbarium collections are reported from vernal pools, but most labels indicate a strict preference for heavy-clay soil.

The nomenclatural changes proposed above are summarized and contrasted with other taxa in the following key to *Acanthomintha.*

KEY TO THE GENUS *ACANTHOMINTHA*

a. Stem conspicuously and densely villous, most hairs gland-tipped; aristate calyx teeth 5–7 mm long; style hairy; corolla lips more or less equal, upper lip 2-lobed, deeply hooded over stamens; anthers glabrous or sparse-hirsute. .... *A. lanceolata* Curran

a′. Stem glabrous, hispidulous, or villous, gland-tipped hairs only present in *A. obovata* subsp. *obovata,* and these uncommon; aristate calyx teeth 1–3.5 mm long; style glabrous; lower corolla lip > than upper, upper lip entire, shallowly-hooded over stamens; anthers glabrous or woolly.

  b. Fertile stamens 2, anthers glabrous; San Diego Co. and Baja California. .... *A. ilicifolia* (A. Gray) A. Gray

  b′. Fertile stamens 4, anthers hairy to woolly; South Coast and Transverse ranges.

    c. Anthers pink-red with cream-yellow pollen, sparsely hispidulous; leaves subtending bracts lacking acicular spines on teeth; stem generally unbranched and erect at base with a solitary, capitate head of flowers, San Mateo Co. .... *A. duttonii* (Abrams) Jokerst

    c′. Anthers cream-yellow with cream-yellow pollen, woolly; leaves subtending bracts with acicular spines on teeth; stem generally branched at base with flowers in capitate and axillary clusters; South Coast and Transverse ranges from southern Monterey and San Benito counties to Los Angeles Co. .... *A. obovata* Jepson

      d. Stem and calyx with some gland-tipped hairs, densely hispidulous, with or without villous hairs; anthers sparsely to moderately woolly; bracts slightly longer than wide, obtuse or truncate at the base; western Fresno, eastern Monterey, and San Benito counties. .... subsp. *obovata* Jepson

      d′. Stem and calyx lacking gland-tipped hairs, glabrous or sparsely hispidulous; anthers moderately to densely woolly; bracts circular or wider than long, cordate clasping at base; northwest Los Angeles, southeast San Luis Obispo, and northern Ventura counties. .... subsp. *cordata* Jokerst

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HOLOCENE BIOGEOGRAPHY OF SPRUCE–FIR FORESTS IN SOUTHEASTERN ARIZONA—IMPLICATIONS FOR THE ENDANGERED MT. GRAHAM RED SQUIRREL

R. Scott Anderson
Quaternary Studies and Environmental Sciences Programs,
Bilby Research Center, Northern Arizona University,
Flagstaff, AZ 86011

David S. Shafer[1]
Department of Geosciences, University of Arizona,
Tucson, AZ 85721

Abstract

Pollen, plant macrofossils, and radiocarbon dates on sediments from a small cienega on Mt. Graham in southeastern Arizona suggest that the occurrence of the present Engelmann spruce–subalpine fir forest on the mountaintop extends back to at least 8000 years ago. This is important biogeographically, since the forest type reaches its southernmost limit on Mt. Graham, and ecologically, as it is the primary habitat of the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*).

Studies of Holocene biogeography and vegetation change in southern Arizona and New Mexico have been largely limited to the study of packrat (*Neotoma*) middens (see compilation in Van Devender 1990a, b), or from cores of sediment deposited in playa lakes such as Willcox Playa (Martin 1963; Martin and Mehringer 1965), Lake Estancia (Bachhuber and McClellan 1977) or the San Agustin Plains (Clisby and Sears 1956; Markgraf et al. 1984). Midden and playa lake records have been most useful for vegetation reconstructions at low- to mid-elevations within the region. In contrast, the Holocene vegetation history of higher elevation forest types, such as the modern Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*) association, presently confined to elevations above ca. 2700 m on isolated mountain ranges within the region (Moir and Ludwig 1979), is largely unknown. Characteristics of this vegetation type are not recorded by analysis of either playa or packrat midden deposits.

However, cienegas, small sedimentary basins occurring on several of the higher mountains within the region, serve as sites for the accumulation of plant materials through time. To better understand the vegetation history of the spruce–fir forest type, sediment cores were obtained from the High Water (Emerald Springs) Cienega on Mt. Graham in the Pinaleño (or Graham) Mountains, Graham

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[1] Present address: U.S. Department of Energy, Richland Operations Office, P.O. Box 550, Richland, WA 99352.

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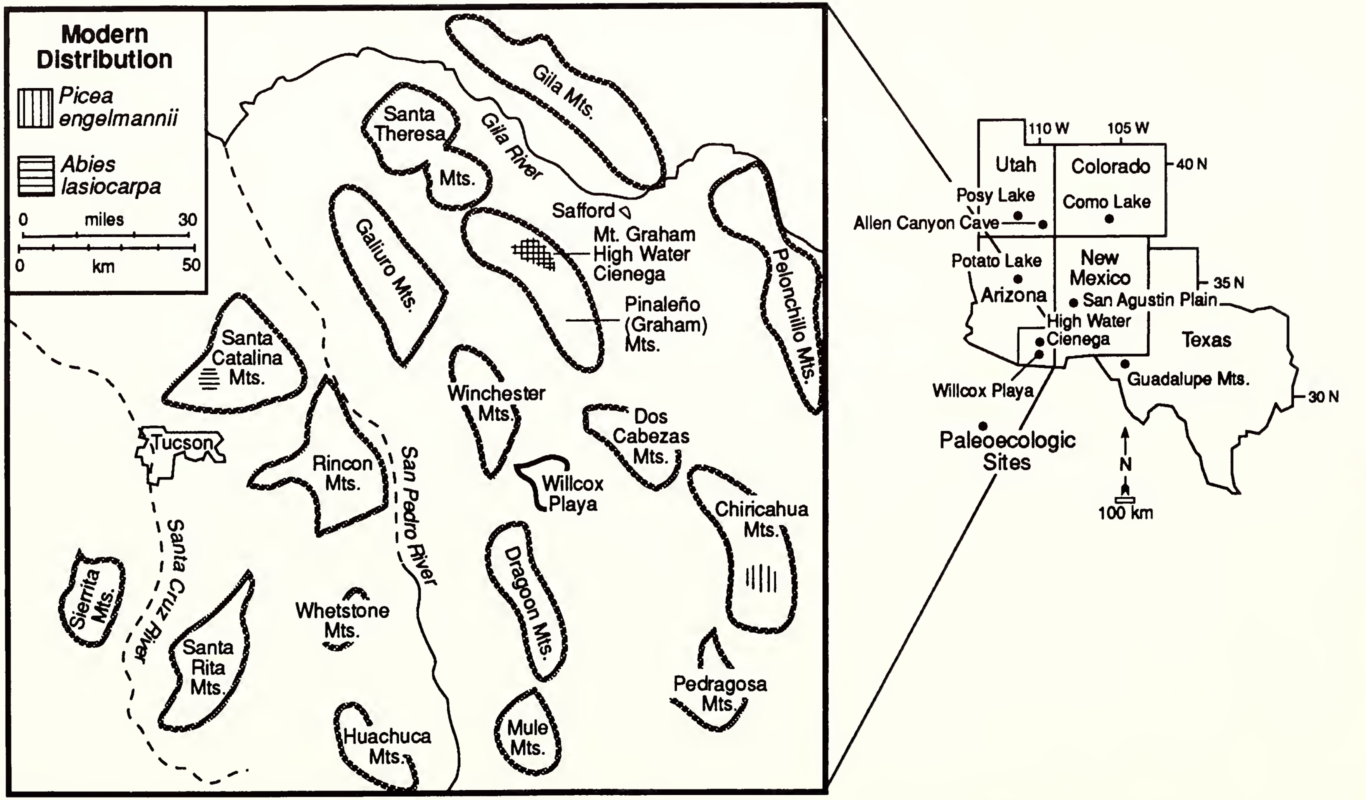

FIG. 1. Location of High Water (Emerald Springs) Cienega, Mt. Graham, Pinaleno Mountains, Arizona, in relation to other sites mentioned in the text.

County, Arizona (Fig. 1). The cienega, in actuality a wet meadow, is located in a small nivation hollow at 3143 m (32°42′00″N, 109°53′30″W; Webb Peak 7.5′ USGS Quadrangle). The site is ca. 20 km southwest of Safford and 120 km northeast of Tucson, Arizona.

A study of the Engelmann spruce–subalpine fir vegetation type through time in southeastern Arizona is important in understanding the factors determining its southern range limit, which occurs in the Pinaleño Mountains (Pase and Brown 1982). The old growth Engelmann spruce–subalpine fir forest type is the preferred habitat of the endemic, endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) (Brown 1984), found today only on Mt. Graham, the highest peak in the range.

Vegetation surrounding the cienega today consists predominantly of Engelmann spruce with a few individuals of subalpine fir. Understory growth is sparse, consisting of currant (*Ribes wolfii*), orange gooseberry (*R. pinetorum*), cranesbill (*Geranium richardsonii*) and blueberry (*Vaccinium myrtillus*) (nomenclature follows Johnson 1988). Grasses (Poaceae) and sedges (Cyperaceae) cover the cienega proper. At the lower border of the subalpine forest (ca. 2920 m), Engelmann spruce and subalpine fir mix with Douglas-fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis*), ponderosa pine (*P. ponderosa*), quaking aspen (*Populus tremuloides*) and willow (*Salix scouleriana*) (Whittaker and Niering 1965). A complete list of plants occurring in the range is found in Johnson (1988).

METHODS

A 134-cm core (#1) was extracted with a modified Dachnowsky corer outfitted with a 50-cm core barrel on 5 October 1986. An additional 119-cm core (#2) was obtained on 15 October 1987. Sediment is mostly sandy peat or peaty sand, with sand increasing toward the base. Sparse oxidized granitic granules occur below 100 cm depth.

Pollen was concentrated from the raw sediment of core #1 by standard chemical techniques (Faegri and Iversen 1975), including treatments with dilute KOH, HCl, HF, and acetolysis solution, with final suspension in silicone oil. *Lycopodium* tracer spores were added for calculation of pollen concentration. Because of poor pollen recovery from core #1, the procedure was slightly modified for core #2, eliminating the KOH treatment and limiting the time for acetolysis digestion to 30 seconds. For plant macrofossil and charcoal analysis, five-cm long, half-core sections of core were allowed to disaggregate overnight in water, and the macrofossils were extracted by gentle water washing of the sediment over U.S. Standard Soil

TABLE 1. RADIOCARBON DATES FOR THE HIGH WATER (EMERALD SPRINGS) CIENEGA SEDIMENT CORES, PINALEÑO MOUNTAINS, ARIZONA.

Laboratory #	Core	Depth (cm)	Date (yr BP)
Beta-18365	1	121–129	8250 ± 160
Beta-32263	2	107–112	6010 ± 150

Sieves (mesh 20 and 80). The laboratory analyses were performed both at the Palynology Laboratory, Department of Geosciences, University of Arizona, and at the Laboratory of Paleoecology, Bilby Research Center, Northern Arizona University.

RESULTS

Basal radiocarbon dates (core #1, 8250 ± 160 yr BP; core #2, 6010 ± 150 yr BP) suggest the record from High Water Cienega extends back into the early middle Holocene (Table 1). Pollen assemblages were analyzed from 13 samples of core #1. A minimum of 29 pollen and spore types were found in these samples. Pollen preservation was excellent and pollen concentration was high (to 130,000 grains cc^{-1} of raw sediment) for the top 10 cm of the core, but declined rapidly with depth (Table 2). This was true for individual major pollen types encountered in the analyses including spruce (*Picea*), fir (*Abies*), pine (*Pinus*), oak (*Quercus*), composite and goosefoot families (Compositae and Chenopodiaceae, respectively). The exception to this was pollen of the grass family (Gramineae) that remained relatively abundant throughout the core (median value = 16,000 grains cc^{-1}). Pollen concentration declined with depth, probably reflecting decreased preservation. Pollen recovery from core #2 was similar to core #1.

Identifiable plant macrofossil remains were also recovered from both cores. Charcoal particles were very abundant within the stratigraphic column. The dominant identifiable macroremains were Engelmann spruce needle fragments, found in the three levels analyzed in core #1, and at 11 of the 12 levels analyzed for core #2. Needle fragments of subalpine fir as well as achenes of sedge (*Carex*) were also found, although at fewer levels (Table 3). All fragments were carbonized and their preservation was probably enhanced due to burning during ancient forest fires.

DISCUSSION

The co-occurrence of Englemann spruce with subalpine fir remains in fossil deposits of late Wisconsin age is rare; subalpine fir has only been recorded from Allen Canyon Cave, Utah (Betancourt 1984, 1990). However, Engelmann spruce has been identified from several

TABLE 2. POLLEN CONCENTRATION (GRAINS/CC) FOR SELECTED POLLEN TYPES, CORE #1, HIGH WATER (EMERALD SPRINGS) CIENEGA, PINALEÑO MOUNTAINS, ARIZONA.

Depth (cm	Estimated Age (yr BP)	*Picea*	*Abies*	*Pinus*	*Quercus*	Other Compositae	Cheno-*Ams*	Gramineae	Total
0	0	69210	2375	11535	1360	5770	6785	24430	133,000
10	660	9630	4740	2220	590	2075	4300	19705	49,500
25	1650	13615	0	1300	0	2600	4540	14910	45,375
30	1980	2240	450	900	300	2540	3000	31520	48,250
40	2640	4070	0	510	0	4070	7120	26440	33,250
50	3300	1860	0	2320	1395	1625	2670	10090	30,850
60	3960	1400	0	280	560	1120	1955	10330	20,400
75	4950	1325	95	380	0	95	1140	33415	38,200
80	5280	500	0	500	0	0	500	8430	7150
95	6270	4565	210	1450	1040	1450	4770	165735	191,250
105	6930	500	0	0	750	1490	250	15910	20,200
110	7260	1630	0	130	485	840	575	19030	27,150
120	7920	0	0	0	430	1720	860	13750	17,850

TABLE 3. MACROFOSSILS EXTRACTED FROM CORE #2, HIGH WATER (EMERALD SPRINGS) CIENEGA, PINALEÑO MOUNTAINS, ARIZONA.

Depth (cm)	Estimated Age (yr BP)	*Picea engelmannii*	*Abies lasiocarpa*	Macro-charcoal	*Carex*
0–5	0–274	N, O, S, T	N, S	X	Nt
7.5–12.5	412–686	N, T		X	Nt
17.5–22.5	960–1235			X	Nt
27.5–32.5	1510–1784	N		X	
37.5–42.5	2058–2333	N		X	
47.5–52.5	2608–2882	N		X	
57.5–62.5	3156–3430	N		X	
67.5–72.5	3705–3980	N		X	
77.5–82.5	4254–4528	N	N	X	
87.5–92.5	4803–5077	N		X	
97.5–102.5	5351–5626	N		X	
110.5–115	6037–6312	N		X	

N = needle fragment; Nt = nutlet; O = other; S = seed or seed wing; T = twig; X = charcoal present.

locations below its modern elevational limit during the late Wisconsin, including Allen Canyon Cave, Utah (2200 m; Betancourt 1984), Potato Lake, Arizona (2222 m; Anderson 1989) and the Guadalupe Mountains, Texas (2000 m; Van Devender et al. 1979). Spruce pollen (Clisby and Sears 1956) as well as spruce needles (Markgraf et al. 1984; no specific identification) were found in sediments of San Agustin Lake, New Mexico (2065 m), dating ca. 15–18,000 years ago. Spruce pollen was also recovered from Pluvial Lake Cochise sediments at 1260 m elevation near Willcox, Arizona (Martin 1963; Martin and Mehringer 1965). Occurrence of spruce at these locations suggests that either Engelmann or blue spruce was more abundant within the drainages of those lakes during the late Wisconsin. Of the two, Engelmann spruce is the most likely; today the tree grows as low as 2800 m in the Chiricahua Mountains (Moir and Ludwig 1979) and 2700 m in the Pinaleños (Whittaker and Niering 1965). This represents a minimum lowering of 700 m elevation during the late Wisconsin.

Climatic conditions causing elevational depressions of 700 m may have been insufficient to establish a corridor allowing subalpine species to span gaps between mountain ranges of the region. Based upon fossil pollen evidence, Jacobs (1985) suggested Wisconsin-age spruce occurrence in the White Mountains of Arizona, the closest known locality to Mt. Graham. From the White Mountains, spruce could have expanded southwest into the Gila Mountains. Even so, spanning the Gila River valley, with a floor of ca. 800–1050 m, would have been unlikely. Similarly, spruce potentially could have grown in the Santa Teresa and Pinal mountains to the northwest of the Pinaleños. However, significant gaps of low elevation would have impeded movement between those ranges and Mt. Graham also. To the southwest, gaps of 20–30 km would have existed between the Dos Cabezas and Chiricahua mountain ranges. Although spruce is absent from them today, several other ranges to the southwest of Mt. Graham (Santa Catalina, Huachucha and Santa Rita) could have had viable populations of spruce during the Pleistocene, but are even further away from those discussed above.

These data suggest that the subalpine forest on Mt. Graham has been isolated from other populations since a glacial episode prior to the late Wisconsin. If true, isolation of the Mt. Graham red squirrel may have paralleled that of spruce there. Location and analysis of packrat middens from elevations within the potential Pleistocene range of spruce should provide answers to the late Wisconsin distribution of the subalpine forest.

By the early Holocene, however, Engelmann spruce, retreating upslope in response to warmer summer temperatures, had became established within its modern elevational range in southern Colorado (by ca. 10,500 yr BP at Como Lake, 3523 m; Shafer 1989; Jodry et al. 1989), southern Utah (by ca. 9000 yr BP at Posy Lake, 2653 m; Shafer 1989) and in southern Arizona at High Water Cienega. With the High Water Cienega data it cannot be determined when spruce was established on Mt. Graham, but it was present by at least 8000 years ago. The occurrence of spruce at high elevations in southern Arizona by this time coincides with the demise of the lowland juniper woodlands and the change from a single season (winter) to a bi-seasonal (winter and summer) precipitation regime, as discussed by Van Devender (1990a, b) and earlier publications.

Deposits containing identifiable organic remains are very rare at the highest elevations of mountain ranges within the desert regions of southern Arizona and New Mexico. This is probably due to a lack of suitable deposition sites in ranges that did not experience Pleistocene glaciation, such as the Pinaleño Mountains. Small Wisconsin-age nivation hollows, such as those on Mt. Graham, hold the potential for accumulation of organic remains during the Holocene. However, problems in preservation of pollen and plant macrofossils may exist. Even though limited, the records from High Water Cienega provide initial information on the antiquity of the spruce–fir forest at high elevations within the region.

CONCLUSIONS

Three tentative conclusions are deduced from these preliminary data. First, High Water Cienega is at least 8250 radiocarbon years old. The lack of clear sediment hiatuses suggests this rare, high-elevation wetland, an important source of moisture for wildlife in the mountain range, has existed over the last 8000 years. Second, remains of Engelmann spruce are found in virtually all macrofossil samples analyzed so far from the Mt. Graham cores, suggesting it has persisted continuously near the site for at least the last 8000 years, and provides a minimum age for the establishment of the forest type. Although the record for subalpine fir is less definitive, the trace amounts of *Abies* pollen at nearly all sediment levels (Fig. 1) suggests fir was probably present around the cienega. Consequently, what is today the preferred habitat of the Mt. Graham red squirrel has been present at the site for at least 8000 years. In addition, the forests of Mt. Graham probably have been isolated since before the last glaciation. Third, since macroscopic charcoal is abundant in all core samples and virtually all recovered macrofossils are carbonized, fires have regularly burned the cienega and surrounding upland areas during the Holocene. Additional analyses are needed from similar locations within the desert southwest to provide a more specific picture of vegetation changes at high elevations during the Holocene.

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NOTES

CRUPINA VULGARIS CASS. (ASTERACEAE: CYNAREAE), ESTABLISHED IN SONOMA COUNTY, CALIORNIA AT ANNADEL STATE PARK.—Liam H. Davis and Robert J. Sherman, Biology Department, Sonoma State University, Rohnert Park, CA 94928.

Crupina vulgaris Cass. is native to the eastern Mediterranean region of Europe and is an economic pest to rangeland in southern Russia. In 1969 this weedy species became established in North America in Idaho. By 1989 *C. vulgaris* had invaded 9300 ha of rangeland in northcentral Idaho and 405 ha of rangeland in northeastern Oregon. It is now listed as a federal noxious weed.

In 1975 a California infestation scattered over approximately 1 ha was eradicated from an abandoned field southeast of Bennett Valley Golf Course in the city of Santa Rosa, Sonoma County. This site is approximately 1 km from a present infestation of 6 ha of Annadel State Park and 4 ha of bordering cattle pasture. This infestation is in predominantly south-facing oak grassland with dry, steep, well drained soils.

Two European references (Tutin et al., Flora Europeae. 1976; Davis, Flora of Turkey and the east Aegean Islands. 1975) provide descriptions of *C. vulgaris.* We have drawn upon these and the Annadel material to develop the following description:

CRUPINA VULGARIS Cass., Dist. Sci. Nat. 12:68 (1817). Syn. *Centaurea crupina* L., Sp. Pl. 909 (1753). Ic. Sibth. & Sm., Fl. Graeca 9: t. 900 (1837), as *Centaurea crupina.*

Annual herb with one or more slender erect stems from taproot. Stems 10–70 cm, unbranched except for inflorescence. Basal leaves ovate to oblong, dentate to entire, petiolate to sessile, scabrid; soon decaying. Cauline leaves pinnatisect, scabrid and sessile with lobes 0.5–1.5 mm wide, linear and denticulate, upper leaves decreasing in size; branches of corymb leafless. Involucre fusiform when young, expanding to obconical, 8–15 × 3–5 mm at anthesis, bracts imbricate, unequal, oblong-lanceolate, acute, light green, becoming purple distally with age. Capitula heterogamous, with 3–5 florets, inner hermaphrodite, outer sterile. Corolla regularly 5-lobed, purple to pinkish, exceeding involucre. Achenes 3–4 × 2–2.5 mm, puberulent at dark brown base, villous towards apex, subcylindrical, with orbicular median basal hilum. Pappus of several concentric series, outer rows grading from short, flattened bristles to blackish-brown barbellate bristles, 5–7 mm, the inner single series of 5–10 triangular-lanceolate, acute scales. Chromosome number $2n=30$.

We are investigating the invaded areas and comparing these habitats with those of the eastern Mediterranean, where *C. vulgaris* is native, to evaluate the species potential in Sonoma County. A study of the effects of grazing, non-grazing, fire, and fire exclusion, as well as a survey for additional infestations is anticipated. The Sonoma County Department of Agriculture, United States Department of Agriculture, California Department of Food and Agriculture, and California Department of Parks and Recreation are coordinating efforts to develop an effective eradication strategy. We express appreciation for the criticism and help from Dr. Charles F. Quibell, Biology Department, Sonoma State University.

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NOTEWORTHY COLLECTIONS

MONTANA

ANDROPOGON SCOPARIUS Michx. [=*Schizachyrium scoparium* (Michx.) Nash] (POACEAE).—Sanders Co., Flathead Indian Reservation, large island in Flathead River ca. 11 km downstream from Dixon, locally common in gravelly soil with *Poa pratensis* and *Aristida longiseta,* T18N R22W S17, 780 m, 10 July 1988, *P. Lesica 4642* (MONTU, NY).

Significance. A range extension of 140 km W from Lewis & Clark Co. Hitchcock and Cronquist (1973, *Flora of the Pacific Northwest*) mention a "questionable" report of this species from near Flathead Lake; however, this is the first confirmed record of this Great Plains species W of the Continental Divide in MT.

CARDAMINE OLIGOSPERMA Nutt. var. *KAMTSCHATICA* (Regel) Det. (BRASSICACEAE).—Flathead Co., Glacier National Park, N side of Gyrfalcon Lake ca. 22 km E of Polebridge, uncommon in moist, open soil along a small stream, 2225 m, 31 August 1988, *P. Lesica 4743* (MONTU, GH). Verified by R. C. Rollins (GH).

Significance. First record for MT and the Northern Rocky Mtns.; a range extension ca. 250 km S from Alta.

ERIGERON LEIOMERUS Gray (ASTERACEAE).—Beaverhead Co.; Beaverhead Mtns., just W of Nicholia–Deadman Pass 24 km SW of Lima, locally common in coarse, partially stabilized limestone talus with *Hulsea algida* and *Stellaria longipes,* T10S R16W S8, 2925 m, 12 August 1989, *P. Lesica & S. Cooper 5010* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First record for MT.

GNAPHALIUM ULIGINOSUM L. (ASTERACEAE).—Lake Co., Swan Valley ca. 3 km S of Swan Lake, locally common along the edge of a logging road with *Trifolium agrarium* and *Filago arvense,* T25N R18W S25, 980 m, 23 August 1989, *P. Lesica 5026* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First report of this European species for MT.

HIERACIUM PILOSELLOIDES Vill. [=*H. FLORENTINUM* All.] (ASTERACEAE).—Lake Co., Swan Valley ca. 3 km S of Ferndale, a few small colonies in the middle of an abandoned logging road, T31N R22W S6, 915 m, 17 June 1989, *P. Lesica 4842* (MONTU, MRC); upper end of the road to Mission Lookout Tower ca. 3 km S of Swan Lake with *Poa pratensis* and *Achillea millefolium,* T25N R18W S27, 1125 m, 24 June 1989, *P. Lesica 4850* (MONTU, NY). *P. Lesica 4850* determined by A. Cronquist (NY).

Significance. First report of this Eurasian species for MT and the Northern Rocky Mtns.

LAGOPHYLLA RAMOSISSIMA Nutt. (ASTERACEAE).—Sanders Co., 4 km E of Plains along Deemer Creek ca. 0.8 km above confluence with Boyer Creek, along the road in overgrazed pasture with *Poa pratensis* and *Hypericum perforatum,* T20N R25W S30, 1005 m, 21 September 1975, *G. L. Moore 328* (MRC); 6 km E of Plains near Henry Creek, uncommon with *Poa secunda* and *P. pratensis,* T20N R25W S33 NW¼, 915 m, 10 August 1968, *G. Halvorson 217* (MRC, RM); Camas Prairie Basin, N end of Giant Ripple Marks ca. 10 km S of Hot Springs, local in open soil around ground squirrel diggings in arid grasslands with *Poa secunda* and *Agropyron cristatum,* T21N

R23W S1 NW¼, 915 m, 4 September 1988, *P. Lesica 4757* (MONTU, NY). *P. Lesica 4757* verified by A. Cronquist (NY).

Significance. First report for MT and a range extension eastward of 175 km from Nez Perce Co., ID.

Mollugo verticillata L. (Aizoaceae).—Yellowstone Co., south shore of Government Island in the Yellowstone River near the confluence with the Big Horn River, common in sandy and gravelly soil with *Eragrostis hypnoides* and *E. pectinacea,* T5N R34E S28, 825 m, 19 August 1990, *P. Lesica & S. Miles 5244* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First report of this widespread Eurasian weed for MT.

Petasites frigidus (L.) Fries var. *nivalis* (Greene) Cronq. (Asteraceae).—Flathead Co., Glacier National Park ca. 5 km NE of Polebridge, common in wet soil in an open spruce swamp with *Senecio pseudaureus* and *Petasites sagittatus,* T35N R21W S12, 1220 m, 23 May 1990, *P. Lesica & R. Yanishevsky 5050* (MONTU, NY). Verified by A. Cronquist (NY).

Significance. First report for MT and the Northern Rocky Mtns.; a range extension SW of ca. 100 km from Alta. Although *P. frigidus* occurs at this site with *P. sagittatus,* I observed no apparent intermediates.

Scirpus pumilus Vahl. [=*S. rollandii* Fern.] (Cyperaceae).—Teton Co., Pine Butte Swamp Preserve, MacDonald Fen ca. 1 km N of Pine Butte ca. 32 km W of Choteau, locally common in a calcareous mire with *Carex livida* and *Juncus balticus,* T24N R7W S6, 1400 m, 27 July 1990, *P. Lesica 5193* (MONTU, PH); Glacier Co., Blackfeet Indian Reservation, head of Flatiron Creek ca. 11 km W of Browning, common in a fen with *Carex livida* and *Juncus balticus,* T32N R12W S16 NE¼, 1465 m, 5 September 1990, *P. Lesica 5275* (MONTU, PH, NY). *P. Lesica 5275* verified by A. E. Schuyler (PH) and A. Cronquist (NY).

Significance. First report for MT and a range extension southward of 250 km from Alta.

I am grateful to Ronald Hartman (RM), Douglass Henderson (ID), Matt Lavin (MONTU) and Peter Stickney (MRC) for providing collection data from their herbaria.

—Peter Lesica, Herbarium, Division of Biological Sciences, University of Montana, Missoula, MT 59812.

New Mexico

Apacheria chiricahuensis C. T. Mason (Crossomataceae).—Sierra Co., White Sands Missile Range, W edge of San Andres Mts. in Chalk Hills, ca. 47 air km E of Truth or Consequences, on vertical E- to NE-facing limestone cliffs immediately S of Big Gap, *Spellenberg & Hoban 10656* (ID, NMC, NY, RM).

Previous knowledge. The range of this comparatively recently described genus (Mason, Madroño 23:105–108, 1975) has been expanded steadily eastward by work of NM botanists (N.M. Native Plant Advisory Committee, A Handbook of Rare and Endemic Plants of New Mexico, 1983). Until the collection reported here, the easternmost record for the species was in west central NM in Socorro Co. All previous collections are from rhyolitic rock.

Significance. An eastward range extension of ca. 60 km from the San Mateo Mts. in Socorro Co., the first record east of the Rio Grande, and the only population known from limestone.

Calyptocarpus vialis Less. (Asteraceae).—Doña Ana Co., Las Cruces, 1675 Cole Village on New Mexico State University campus, 1160 m, 7 Oct 1988, *Klingensmith 503* (NMC).

Significance. First record for New Mexico for a "troublesome lawn weed" (Correll and Johnston, Manual of the Vascular Plants of Texas, 1972). The species is widespread in southern North America.

CERASTIUM GLOMERATUM Thuill. (CARYOPHYLLACEAE).—Doña Ana Co., NE side of Organ Mts., White Sands Missile Range, ca. 23 air km ENE of Las Cruces, middle reaches of Texas Canyon above old stamp mill, canyon bottom, wet, mossy soil at spring, uncommon, T22S, R4E, ec sect. 35, 20 Apr 1990, Spellenberg & Mahrt 10129 (Escuela Superior de Agricultura "Hermanos Escobar" [Juarez], ID, MO, NMC, RM, NY).

Significance. First record for NM for a species reported in several regional floras as naturalized from Europe and now widely distributed in North America. Martin and Hutchins (A flora of New Mexico, vol. 1, 1980) note that this species is to be expected in NM.

COOPERIA DRUMMONDII Herb. (LILIACEAE).—Doña Ana Co., White Sands Missile Range, 25 air km NE of Las Cruces, San Augustin Mts., 1.4 mi N of San Augustin Pass on US Hwy. 70, steep E-facing slope ca. ¼ mi. N of San Augustin Peak, T21S, R4E, ne corner sect. 31, 1980 m, 16 Aug 1990, *Spellenberg & Mahrt 10502* (NMC).

Significance. The species is reported for the state in the Flora of the Great Plains (Great Plains Flora Association 1986) and in the Manual of the Vascular Plants of Texas (Correll and Johnston 1972). Martin and Hutchins (A Flora of New Mexico, vol. 1, 1980), however, indicate no certain records for NM, and map the species as "to be expected" in the southeastern portion of the state. This record confirms the presence of the species in NM, and extends its range westward by about 200 km beyond that predicted by Martin and Hutchins.

CROTON LINDHEIMERIANUS Scheele (EUPHORBIACEAE).—Doña Ana Co., White Sands Missile Range, 36 air km NNE of Las Cruces in southern end of San Andres Mts., near head of Bear Canyon, T20S, R4E, SE¼ sect. 26, 1555 m, 27 Aug 1990, *Spellenberg & Brozka 10540* (NMC).

Significance. A species common on the Great Plains (Great Plains Flora Assoc., Flora of the Great Plains, 1986), but reported uncertainly from New Mexico only from a single record in Socorro Co. (Martin and Hutchins, A Flora of New Mexico, vol. 1, 1980). This record, one of two plants seen in the arroyo, confirms the presence of the species in NM.

CRYPTANTHA PTEROCARYA (Torr.) Greene var. PTEROCARYA (BORAGINACEAE).—Doña Ana Co., NE base of Organ Mts., White Sands Missile Range, SW edge of headquarters area, ca. 25 air km ENE of Las Cruces, SE of Texas Canyon arroyo, T22S, R4E, wc sect. 25, 1340 m, 20 Apr 1990, *Spellenberg & Mahrt 10110* (NMC); San Juan Co., hills E of Farmington, T30N, R12E, SW¼ sect. 34, 5700 ft, 10 May 1982, *Fletcher 5941* (UNM); ca. 3 mi E of Waterflow, T30N, R15W, SW corner sect. 28, 2 June 1982, *Spellenberg, Soreng, & Diswood 6505* (NMC).

Previous knowledge. A variety of the Intermountain Region (Cronquist et al., Intermountain Flora, vol. 4, 1984), previously known to extend southward to W AZ and UT. The variety *cycloptera* (Greene) Macbr. is common southward.

Significance. First reports for NM. The two collections from San Juan Co., confirm Martin and Hutchin's (A Flora of New Mexico, vol. 2, 1981) prediction that the variety *pterocarya* can be expected in the northwestern part of the state; our Doña Ana Co. record extends the known range of the variety 500 km southward, where it might have been introduced by early ranching activities.

GALIUM FRANKLINIENSE Correll (RUBIACEAE).—Doña Ana Co., San Augustin Mts., Black Prince Arroyo, ca. 27 air km NE of Las Cruces, 1.5 km N of US Hwy 70 and 2 km E of San Augustin Pass, T21S, R4E, SW corner sect. 28, 1660 m, 16 Aug 1990, *Spellenberg & Mahrt 10490* (NMC).

Significance. First record for New Mexico, a northward range extension of ca. 60

km from the Franklin Mts. of extreme western Texas, where the species was previously considered to be endemic (Correll and Johnston, Manual of Vascular Plants of Texas, p. 1484, 1972).

Houstonia rupicola Greenm. (Rubiaceae).—Guadalupe Co., ca. 1 km N of Vaughn, on karst limestone bluffs, 1830 m, 3 Jul 1981, *Spellenberg, Soreng, & Ward 6076* (NMC, NY); Eddy Co., a few meters N of Texas border, ca. 1/2 mi SE of U.S. Hwy 62-180, on gypsum, 1190 m, 1 Sep 1985, *Spellenberg & Spurrier 8257* (NMC, NY).

Significance. First report for NM. Both these collections were identified as the very similar *Hedyotis nigricans* (Lam.) Fosb. var. *rigidiscula* (Gray) Shinners; the presence of *Houstonia rupicola* in NM was called to our attention by Guy Nesom (TEX). *Hedyotis nigricans* var. *parviflora* (Gray) W. H. Lewis, of which *Houstonia rupicola* is considered a synonym (Correll and Johnston, A Manual of the Vascular Plants of Texas, 1972), is reported by Correll and Johnston to be "infrequent in rocky crevices and hillsides in w. Tex."

Lomatium foeniculaceum Coult. & Rose subsp. *macdougalii* (Coult. & Rose) Theobald (Apiaceae).—Hidalgo Co., 5 mi NE of Virden, north end of Black Mountain, T18S, R20W, wc sect. 22, 4600 ft, NW slope of basaltic rock cobble, *Spellenberg, Zucker, & Zimmerman 8410* (NMC, UC).

Significance. First record for NM for a primarily Great Basin species that previously was known to extend southward to central Arizona (Theobald, Brittonia 18:1–18, 1966). Lincoln Constance (UC) confirmed the identification of our collection. *Astragalus eremiticus* Sheld. (*Spellenberg et al. 8401*) and *Allium acuminatum* Hook. (Spellenberg et al., Sida 11:455–470, 1986) were also collected in the same area, all an indication of a hitherto unrecognized extension of a more western flora into this portion of NM.

Quercus chrysolepis Liebm. (Fagaceae).—Grant Co., Apache Box, steep narrow canyon with sheer cliff faces, talus slopes at the base leading to a boulder creek bottom, rhyolite, T16S, R21E, SW¼ NW¼ sect. 10, 5100–5400 ft 22 Jun 1987, *Muldavin 100* (CAS, NMC, NY), *Muldavin 101* (BH, CAS, NMC, NY, UNM).

Significance. First records for New Mexico, extending range slightly eastward from eastern Arizona. Closest previously known populations to New Mexico are from a few kilometers south of the U.S.–Mexico boundary in Chihuahua (Tucker and Haskell, Brittonia 12:196–219, 1960).

Quercus palmeri Engelm. (Fagaceae).—At site of *Q. chrysolepis,* above. *Muldavin 102* (CAS, NMC), and with an apparent intergrade to *Q. chrysolepis, Muldavin 103* (CAS, NMC).

Significance. Apparently first certain record for New Mexico. Little (Atlas of United States Trees, Vol. 3, Minor Western Hardwoods, 1976) maps the species for southwestern New Mexico, but no documented specimens have been seen in the preparation of this note. Landrum (unpub. mss., Fagaceae for Flora of Arizona) and Tucker and Haskell (cited above) do not note species to occur in NM. Martin and Hutchins (Flora of New Mexico, vol. 1, p. 522, 1980) note that plants reported as *Q. wilcoxii* Rydb. for New Mexico (Wooton and Standley, Contributions of the US National Herbarium, 19:169, 1915) are relegated to other species. Wooton and Standley's cited distribution matches that plotted by Little, and may have been the source of information for those maps.

Plantago virginica L. (Plantaginaceae).—Doña Ana Co., NE side of Organ Mts., White Sands Missile Range, ca. 23 air km ENE of Las Cruces, middle reaches of Texas Canyon above old stamp mill, canyon bottom, wet mossy soil at spring, common, T22S, R4E, ec sect. 35, 1680 m, 20 Apr 1990, *Spellenberg & Mahrt 10131* (Escuela Superior de Agricultura "Hermanos Escobar" [Juarez], ID, NMC, NY).

Significance. Apparently the first record for NM for this species of the eastern United States, reported as introduced westward in several regional floras. Martin and Hutchins (A Flora of New Mexico, vol. 2, 1981) indicate that the species is "occasional" in NM, but map it only as "expected" in two western counties.

STELLARIA NITENS Nutt. in Torr. & Gray (CARYOPHYLLACEAE).—Correction. This was reported erroneously as a record for the state (Soreng and Spellenberg, Madroño 28:87–88, 1981). The collection (NMC, NY) remained bothersome to us, and was finally sent to Ron Hartman (RM) for examination. Hartman corrected the identification to *Drymaria leptophylla* (Cham. & Schlecht.) Rohrb. var. *leptophylla,* a taxon commonly treated as *D. tenella* A. Gray in treatments of southwestern U.S. plants.

VULPIA MICROSTACHYS (Nutt.) Benth. var. *MICROSTACHYS* (POACEAE).—Doña Ana Co., White Sands Missile Range, ca. 15 air mi. ENE of Las Cruces, E. side of Organ Mts., N-facing side of mouth of Texas Canyon, T22S, R4E, sect. 35, 1635 m, in moss and sand at base of rock, *Spellenberg & Mahrt 10410 (NMC).*

Significance. First record of the species for NM, and an eastward range extension for the variety from southern California or western Nevada (Cronquist et al., Intermountain Flora, vol. 6, 1977). R. Lonard (PAUH) confirmed our identification. The canyon from which this collection and several others reported herein had mining activity in the past. Plants may have been introduced by the activities surrounding mining and processing of ore.

—RICHARD SPELLENBERG and MATTHEW MAHRT, Department of Biology, New Mexico State University, Las Cruces, NM 88003, and Robert Brozka, Construction Engineering Research Laboratory, Army Corps of Engineers, P.O. Box 9005, Champaign, IL 61826–9005.

ANNOUNCEMENT

NEW PUBLICATIONS

SIMPSON, G. M. 1990. *Seed dormancy in grasses.* ix + 297 p. ISBN 0-521-37288-7. Cambridge University Press, Cambridge.

PAKES, A. G. 1990. *Mathematical ecology of plant species competition: a class of deterministic models for binary mixtures of plant genotypes.* ISBN 0-521-37388-3 Cambridge University Press, Cambridge.

REVIEW

In Our Own Hands: A Strategy For Conserving Biological Diversity in California. By Deborah B. Jensen, Margaret Torn and John Hart. 1990. California Policy Seminar, University of California, Berkeley. xx + 184 pages, appendices. (no ISBN no.).

This book reports on the present status of biodiversity in California, and reads like a casualty list from a disaster. With excruciating and painful detail, the extent of damage to California's rich natural history is outlined. If for no other reason, this text is important because of the excellent documentation of threats to the existing tattered fabric of biodiversity in California. However, there is more to *In Our Hands* than a collection of descriptive statistics.

The book begins by listing reasons for the preservation of biodiversity. The preservation of biodiversity is justified both on economic (e.g., ecological services, recreation opportunities) and aesthetic grounds. This discussion does a good job of the difficult task of enumerating the monetary benefits of conservation. Following sections explain how biodiversity is lost, how much is left (chapter three alluded to above), and the factors responsible for putting our remaining biodiversity at risk. One notable highlight in the first half of the book is the excellent discussion of water, water rights, and the impact on aquatic habitats. These first four chapters are a wealth of documented and undocumented information for the biologist writing significant impacts sections in EIR's as well as the concerned citizen.

The remainder of *In Our Hands* is devoted to explaining why the present system of agencies is unable to enforce adequately the preservation of biodiversity and proposing an alternative strategy. The alternative calls for, among other things, a habitat protection act and a California Biodiversity Research Institute. The explanation of the shortcomings of CEQA and reasons behind the failure of the lead agencies' enforcement of CEQA is enlightening, especially for those doing impact or mitigation work who are more comfortable identifying fungi than struggling with bureaucracy. This book is one of the few sources I've encountered which pointed out that the subjective nature of defining impacts and cumulative impacts poses a problem for the advancement of conservation, particularly at the level of the habitat.

There were two negative aspects of the book. First, the majority of the examples were drawn from northern and central California. This is to be expected given that the book was written in Berkeley. However, relying heavily on policy examples from the San Francisco Bay area doesn't further the cause of statewide biodiversity. Second and more important, the assumption that rural or suburban land conversion does not eliminate all native wildlife is misleading. (The definition of rural is fewer than six structures per ten acres.) True, mockingbirds, scrub jays and certain migrating sparrows will always be happy to rest or forage in a suburban setting, but where are the thrashers, grosbeaks, and wren tits? Native wildlife willing to share a golf course with people or a back yard with domestic animals are generally not species of concern, and the notion that low density is better than high density is misguided in light of shrinking areas of open space.

I applaud the strategies outlined in the final chapter of the book, but will voter support needed for implementation of a biodiversity research institute be available given the advertising dollars of special interest groups who have much to lose from increased vigilance over the environment? Land speculation has been part of California's economy since the gold rush, if not before. Suburban sprawl, fueled by white flight motivated by the social and environmental problems present in cities, is a critical link between land speculation and the incremental loss of open space, a leading cause of declining biodiversity.

The policy discussion ignores the relationship between the environment, the economy, and the social fabric, a relationship central to viable public policy for the

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preservation of biodiversity. Much attention was given to the possible consequences of global change on the diversity of California, but unless suburban sprawl is checked, not only will the impact of global change on biodiversity be insignificant, California will be doing more than its fair share to further the cause of global warming as a result of fossil fuel consumption.

In spite of these shortcomings, the authors have taken care to produce a scientifically correct text unintimidating to the non-scientist. *In Our Hands* belongs on the bookshelf of every environmental specialist and planner, both in the public and private sector.

—CHERYL C. SWIFT, Impact Sciences, Inc., Thousand Oaks, CA and Whittier College, Whittier, CA.

ANNOUNCEMENT

"INTERFACE BETWEEN ECOLOGY AND LAND DEVELOPMENT IN CALIFORNIA"

This will be the title of a symposium to be held at the annual meeting of the Southern California Academy of Sciences, 1–2 May 1992 at Occidental College in Los Angeles. The meeting will begin Friday morning with a plenary address by Dr. Peter Raven, followed by morning and afternoon sessions on both Friday and Saturday. It is anticipated that the symposium will consist of four sessions on: Biodiversity and Habitat Loss, Mitigation of Development, Restoration of Damaged Communities, and Wildlife Corridors. The focus of the meeting is to bring together persons involved in basic research, applied environmental consulting and governmental policy. Persons interested in participating or suggestions for related sessions should contact: Dr. Jon Keeley, Department of Biology, Occidental College, Los Angeles, CA 90041; 213-259-2958(fax).

ANNOUNCEMENT

REPRINT COVERS

In light of increasing concern over limiting resources, MADROÑO considers it environmentally sound policy to discontinue offering covers with reprints. It is hoped that authors will view this step in a positive light.

ANNOUNCEMENT

California Botanical Society

JOINT PROCEEDINGS
GRADUATE STUDENT MEETING AND ANNUAL BANQUET

February 22, 1992
San Francisco State University

This year's Graduate Student Meeting and the Annual Banquet will be held on the same day, Saturday, February 22, 1992, on the campus of San Francisco State University. Further details will follow concerning the Graduate Student Meeting. The Annual Banquet will be held at the Seven Hills Conference Center and will feature a keynote address by Dr. Daniel Crawford of Ohio State University. Dr. Crawford is a renowned plant systematist and author of *Plant Molecular Systematics: Macromolecular Approaches* (1990). The title of his talk is "Molecules in service to organismal biology (or taking advantage of your local molecualr biologist): some comments and predictions". Lodging is available on campus. For further information, write Michael Vasey at the Department of Biology, San Francisco State University, 1600 Halloway Avenue, San Francisco, CA 94132 or call him at (415) 338-1957.

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California Botanical Society

SCHEDULE OF SPEAKERS
1991–1992

8:00 PM UNIVERSITY OF CALIFORNIA, BERKELEY,
RM 159, MULFORD HALL

Theme: Recent Advances in Plant Evolution

DATE	**SPEAKER & TOPIC**
OCT 17	Michael Vasey, San Francisco State University "Origin by quantum speciation: The case of *Lasthenia maritima,* an endemic of seabird-breeding habitats"
NOV 21	Robert Ornduff, Univ. California, Berkeley "My days with dimorphism"
JAN 16	G. Ledyard Stebbins, Univ. California, Davis "The impact of molecular and genetical research on understanding plant development: bryophytes, gametophytes and angiosperm flowers"
FEB 22*	**Daniel Crawford, Ohio State University** "Molecules in service to organismal biology (or taking advantage of your local molecular biologist): some comments and predictions"
MAR 19	Kenton L. Chambers, University of Oregon "*Microseris*: An evolutionary model for genetic and developmental studies"
APR 16	Dieter Wilken, Univ. California, Berkeley "Demographic studies of population structure in *Ipomopsis*"
MAY 21	Barbara Ertter, Univ. California, Berkeley "Islands in the western desert: the distribution and evolution of *Ivesia*"

***Annual Banquet** — Seven Hills Conference Center, San Francisco State University

EDITOR'S REPORT FOR VOLUME 38

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on the journal. Between 1 July 1990 and 30 June 1991, 50 manuscripts were received. These comprised 27 articles (10 published, 8 in press, 4 in revision and 5 rejected), 11 notes (4 published, 5 in press and 2 in review) and 12 noteworthy collections (9 published, 1 in press and 2 in review). Volume 38 was composed of 25 articles (11 ecological, 12 systematic, 2 paleoecological), 8 notes, 9 noteworthy collections, 4 book reviews, 1 obituary and several announcements. A number of format changes beginning with volume 38 include printing the journal's name, issue no., etc., on the spine, reduction in use of abbreviations in both text and Literature Cited and increasing visibility of authors' names in notes and noteworthy collections. Also, in light of increasing global concern over limiting resources, covers for reprints are no longer offered.

I thank all of the Board of Editors for editorial assistance and Steven Timbrook for his continuing contribution of the annual Index and Table of Contents. I thank Peter Raven for assistance with the dedication and appreciate the help of David Keil in making my first year as editor relatively painless.

I am encouraged by the generally high quality of manuscripts I have dealt with during my first year. Also, I am pleased with the thorough, tactful and helpful comments by reviewers and, although high levels of community service normally set the research sciences apart from other professions, I believe the members of the botanical community I have dealt with this year have been particularly generous with their time.—J.E.K. 1 Oct 1991.

REVIEWERS OF MANUSCRIPTS

As Editor, I thank all reviewers for their contribution to the continued excellence of the journal. Special thanks are extended to those who reviewed more than one manuscript published in 1991 (indicated with *). The California Botanical Society appreciates the generosity of time and ideas of the following reviewers for volume 38:

David Adam
Geraldine Allen
P. W. Ball
Theodore Barkeley
James Bartolome
Randall Bayer
*Mitch Beauchamp
Jane Bock
Gregory Brenner
Steven Bullock
Charles Burandt
Henrietta Chambers
*Kenton Chambers
Anita Cholewa
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Dirk Walters
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Dieter Wilken
George Yatsckievych
Joy Zedler
Paul Zedler

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Number 2, pages 63–147, published 6 June 1991
Number 3, pages 149–212, published 13 August 1991
Number 4, pages 213–311, published 27 November 1991

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Although his studies have extended to a number of other genera, the name of Harlan Lewis will permanently be associated with his perceptive and original investigations of the genus *Clarkia* (Onagraceae). As a result of the attention that he and his students and associates have given the group, the dozens of species of godetias and clarkias, which bid farewell to spring with their attractive masses of rose-purple flowers each year as the hills of California return to a rich golden-brown hue, have yielded abundant insight into chromosomal evolution and the mechanisms by which new species are formed in plants.

Through his friendly and enthusiastic personality, Harlan Lewis has encouraged two generations of biosystematists to treat their problems critically, thus contributing fundamentally to our understanding of plant evolution. The members of the California Botanical Society take great pleasure in joining his many students and others who have benefited from knowing him and his wife and coauthor Margaret Ensign Lewis in sincerely wishing them continued good health and many more happy and productive years.

In this spirit, the 1991 volume of *Madroño* is dedicated to Harlan Lewis.

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THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

AN ELECTROPHORETIC TEST OF THE GENETIC INDEPENDENCE OF A NEWLY DISCOVERED POPULATION OF *CLARKIA FRANCISCANA*

L. D. Gottlieb
Department of Genetics, University of California,
Davis, CA 95616

S. W. Edwards
Regional Parks Botanic Garden, 11500 Skyline Blvd.,
Oakland, CA 94619

Abstract

Clarkia franciscana, originally known from a single population in San Francisco, is a California State-listed rare and endangered species that has figured importantly in our understanding of plant speciation. A second population was recently discovered in the Oakland Hills. To determine whether the Oakland Hills population was genetically distinct from the San Francisco one, we carried out an electrophoretic analysis of isozymes. The two populations are fixed for different alleles at five of the 31 genes examined. This result strongly suggests that the Oakland Hills population did not originate by seed transfer from San Francisco, and that it must be regarded as indigenous to its present locality. We discuss certain implications of this finding for plant conservation policy.

Many plant species designated rare and endangered by federal or state agencies are known from only single populations. The discovery of a second population is important because it will likely influence conservation and recovery programs. However, since range extensions of listed plants are unexpected, it is critical to determine if the second population is indigenous to its site.

Such a concern is relevant to *Clarkia franciscana* (Onagraceae), a slender annual herb originally known and described from a single serpentine outcrop just south of the Golden Gate in the Presidio of San Francisco, California (Lewis and Raven 1958a, b). *Clarkia franciscana* is listed as rare and endangered by the State of California and, as a consequence, its protection is mandated.

A second population has recently been discovered on a serpentine site across the Bay in the hills above Oakland. The possibility that *C. franciscana* seeds had been taken from the Presidio and sown in the Oakland Hills has to be considered because the site is located in the East Bay Regional Park District and the former director of the District's Botanic Garden had grown the species for a number of years at the garden from seeds collected in the Presidio (Roof 1972).

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Clarkia franciscana is important to biologists interested in mechanisms of speciation and genetic divergence. Along with *C. lingulata,* it provided the model that led Professor Harlan Lewis and his colleagues to propose an elegant theory of speciation, termed catastrophic selection, that suggested that plant species often originate in geographically peripheral populations that are subject to severe reductions in population size (Lewis 1962, 1966, 1973).

Clarkia franciscana with its derived self-pollinating breeding system was thought to have originated, perhaps recently, from the survivors of a drought-stricken population of *C. rubicunda,* a morphologically similar species that grows nearby (Lewis and Raven 1958a). The extensive difference between the species in chromosome structural arrangement was considered an indirect consequence of forced inbreeding among the surviving individuals.

However, electrophoretic analysis of isozymes revealed that *C. franciscana* was fixed for a large number of genes that were not present in *C. rubicunda* (Gottlieb 1973). It was later shown that *C. franciscana* also had a duplicated gene for alcohol dehydrogenase that further distinguished the two species (Gottlieb 1974). Such marked genetic divergence suggested that their phylogenetic separation occurred much longer ago than presumed and made the proposed direct mode of origin of *C. franciscana* from *C. rubicunda* unlikely because, if it had originated recently, most of its genes would still be present in its parent (Gottlieb 1973).

The electrophoretic study revealed that the Presidio population of *C. franciscana* was monomorphic at all but one gene, consistent with its predominant self-pollination. This genetic homogeneity simplifies an electrophoretic comparison of the Presidio population with the newly discovered Oakland Hills population since it is sufficient to test, for each sampled gene, whether both populations have the same allele or not. If the Presidio population had been outcrossing and highly polymorphic it might have been difficult to interpret likely differences in allelic frequencies.

Here we test the similarity of the two populations by an electrophoretic analysis of isozymes. If the Oakland Hills population has different alleles than the Presidio population at many genes, it probably is indigenous and represents a significant range extension. However, if the two populations are indistinguishable, it will not be possible to reject the contention that the Oakland Hills population was merely transplanted from the Presidio.

Materials and Methods

The Presidio population of *C. franciscana* is located on a serpentine slope at the east end of the Presidio, San Francisco (Lewis and Raven 1958b). The Oakland Hills population is located on the Skyline Serpentinite Prairie, Redwood Regional Park, E of Skyline Boulevard, Alameda Co., California. A cultivated population has been grown for many years in the Regional Parks Botanic Garden in Tilden Park from seeds originally collected at the Presidio site.

We studied the Oakland Hills population, the Botanic Garden population, and two lines, 8–13 and 37–1, that were originally collected as seeds from the Presidio population on 7 August 1971. These two lines had been included in the previous electrophoretic study (Gottlieb 1973), and had since been maintained by occasional self-pollination in a greenhouse at UC–Davis.

We did not sample the population of *C. franciscana* now growing at the Presidio because all genes possibly present there must be a subset of those now in the Botanic Garden selection or in LDG's lines. We have evidence that Roof collected seeds at the Presidio in 1964 (Roof 1972; and letter to LDG dated 13 January 1973), subsequently grew out plants yearly at the Botanic Garden, and then returned seeds to the Presidio location in 1972. (Note that the return of seeds was after LDG's collection in August 1971.)

The Oakland Hills population was estimated by a field count on 2 June 1990 to contain about 5000 plants. Since they were distributed in a large number of patches, sampling was done by collecting seeds from each of ten plants growing in each of ten widely spaced sites throughout the population. In addition, seeds were collected from 25 plants growing in the Botanic Garden.

Sixteen enzyme systems were studied by horizontal starch gel electrophoresis: acid phosphatase (APH; EC 3.1.3.2); alcohol dehydrogenase (ADH; EC 1.1.1.1); catalase (CAT; EC 1.11.1.6); glutamate dehydrogenase (GDH; EC 1.4.1.2); glutamate oxaloacetate transaminase (GOT; EC 2.6.1.1); leucine aminopeptidase (LAP; EC 3.4.11.1); malate dehydrogenase (MDH; EC 1.1.1.37); phosphoglucose isomerase (PGI; EC 5.3.1.9); esterase (EST; EC 3.1.1.–); isocitric dehydrogenase (IDH; EC 1.1.1.41); malic enzyme (ME; EC 1.1.1.40); mannose-6-phosphate isomerase (MPI; EC 5.3.1.8); phosphoglucomutase (PGM; EC 5.4.2.2); 6-phosphogluconate dehydrogenase (6PGD; EC 1.1.1.44); skikimic dehydrogenase (SKD; EC 1.1.1.25); and triose phosphate isomerase (TPI; EC 5.3.1.1).

The first eight of these systems were previously examined (Gottlieb 1973). Three gel electrode buffer combinations were utilized: 6PGD was examined in a pH 6.5 morpholine system (Odryzkoski and Gottlieb 1984), IDH, ME, MDH and SKD in a pH 7.0 histidine–HCl system (System IV, Gottlieb 1981), and all the others in a pH 8.3 tris-citric system (System I, Gottlieb 1981). The enzymes were extracted from leaves of 3–5 week old seedlings in a cold extraction buffer as previously described (Gottlieb 1981). Standard assays of enzyme activity were used (Wendel and Weeden 1989).

Twenty extracts were run on each gel. To facilitate direct visual comparison of the electrophoretic mobility of each isozyme, extracts from individuals of the two populations were run side by side in different combinations on each gel.

RESULTS

The present study of *C. franciscana* included all eight enzymes previously reported (Gottlieb 1973) and eight additional ones. The improved assay for catalase made it possible to detect two isozymes whereas only a single one had previously been found. Two additional isozymes of acid phosphatase were also detected in the present study.

The 16 enzymes examined appear to be encoded by 31 genes. Depending on the enzyme, 34 to 66 families were analyzed from the Oakland Hills population and 17 to 20 families from the cultivated Botanic Garden population. We also studied two additional lines from the Presidio that had been previously examined (Gottlieb 1973). A family is defined as individuals, usually one or two, grown from seeds collected on different plants in nature.

All plants from the Oakland Hills population proved to have identical electrophoretic mobility for each isozyme; there was no observed polymorphism. Likewise, all plants from the Presidio (the Botanic Garden collection and LDG's lines) also exhibited identical electrophoretic mobility for each isozyme. Thus, for this data set, each population is represented by any single individual.

The Oakland Hills population differed from the Presidio population at five genes or 16% of those sampled. These included *Aphl, Est, Lap, 6Pgd4* and *Tpi2* (Table 1). In addition, at *Got2,* the Oakland Hills population exhibited the "slow" allele and the Presidio population the "fast" allele. Both *Got2* alleles had previously been detected in the Presidio population and this gene was the only one shown to be polymorphic in the species (Gottlieb 1973). Thus, for *Got2,* the Oakland Hills population appears to be monomorphic for one of the two alleles segregating in the Presidio population.

DISCUSSION

The finding that the Oakland Hills population of *Clarkia franciscana* contains at least five genes encoding enzymes that are absent from the Presidio population strongly suggests that it did not originate by seed transfer from the Presidio. Consequently, it must be regarded as indigenous to its present serpentine locality.

This conclusion is further strengthened by the finding that the plants grown in the Botanic Garden are identical to two lines collected at the Presidio about 20 years ago. These lines were fully representative at that time (with the exception that they possessed only one of the two *Got2* alleles).

The Oakland Hills population may be as much as five times larger than the Presidio population and because it is located in a regional

Table 1. Relative Electrophoretic Mobilities of Isozymes Extracted from Plants from the Presidio and Oakland Hills Populations. The mobilities are calculated relative to the migration of the bromphenol blue front at 100 mm. [1] Multiple activity bands for ADH reflect duplication of coding gene. [2] Multiple activity bands present; number coding genes uncertain.

	Relative electrophoretic mobilities of isozymes		
Enzyme	Presidio (Botanic Garden)	Presidio (lines 8–13 and 37–1)	Oakland Hills
ADH	50/48/46[1]	50/48/46[1]	50/48/46[1]
APH–1	74	74	71
APH–2	66	66	66
APH–3	41	41	41
CAT–1	41	41	41
CAT–2	28	28	28
EST	80	80	90/78[2]
GDH	31/28/25[2]	31/28/25[2]	31/28/25[2]
GOT–1	56	56	56
GOT–2	51	51	44
IDH	35/29[2]	35/29[2]	35/29[2]
LAP	58	58	60
MDH–1	31	31	31
MDH–2	28	28	28
MDH–3	9	9	9
ME–1	35	35	35
ME–2	22	22	22
MPI	62	62	62
6PGD–1	30	30	30
6PGD–2	27	27	27
6PGD–3	26	26	26
6PGD–4	15	15	12
PGI–1	63	63	63
PGI–2	45	45	45
PGM–1	56	56	56
PGM–2	49	49	49
PGM-3	45	45	45
SKD	35	35	35
TPI-1	76	76	76
TPI-2	68	68	60
TPI-3	46	46	46

park it will be easier and less expensive to protect and conserve. The Skyline site is noteworthy in that as many as 15 species of native perennial grasses as well as a remarkable diversity of wildflowers are also found there, making it one of the richest such areas in the San Francisco Bay Region.

Although neither the Oakland Hills or Presidio populations have much, if any, genetic variability, at least judging from the electrophoretic evidence, the substantial differences between them indicate that *C. franciscana* has a reasonable level of variability and this may prove useful for future management decisions. Although we now know the species is less rare than previously thought, it still requires protection. Its prospects for persistence are much enhanced by the new discovery.

In addition to the Regional Park site, a small number of plants of the species was discovered on a serpentine outcrop next to the Oakland Hills Tennis Club. The owner of the club was required by the local Planning Commission to hire a botanist to protect them during construction work on his property (Oakland Tribune, 3 November 1989). These plants are almost certainly an historical part of the main population now in the Regional Park, which is uphill and less than a mile away.

It is worth noting that if our study had failed to show that the Oakland Hills population was distinct from the one in the Presidio, leaving the impression that it had originated by human agency, such a transfer would not necessarily have been misguided or the new site unworthy of protection. Plant conservation will almost certainly require deliberate movement of plants and/or propagules to new sites and the problem will be to identify appropriate ones. Obviously this is a difficult task because short term success in a new site does not necessarily predict long term establishment.

Finally, we point out that Roof's replacement of *C. franciscana* seeds in the Presidio in 1972 was done because he could not find the species there in 1969 and 1970 and believed it extinct (letter to LDG previously cited). This was in fact not the case because LDG collected seeds from numerous plants there in 1971. Roof's action almost certainly had little or no genetic consequence because *C. franciscana* is nearly monomorphic and probably has been for some time. However, more generally, seed augmentation of outcrossing plants has the potential to change allelic frequencies. Roof's concern for conservation should probably be viewed favorably. It may be that the botanical community and our native plant societies should debate such practical measures to conserve the California plant heritage.

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ANNOUNCEMENT

The 1991 Jesse M. Greenman Award

The 1991 Jesse M. Greenman Award has been won by Scott Zona for his publication "A monograph of *Sabal* (Arecaceae: Coryphoideae)", published in Aliso 12:583–666, 1990. This monographic study is part of a Ph.D. dissertation from Claremont Graduate School, Claremont, California, under the direction of Dr. Sherwin Carlquist.

The Greenman Award, a certificate and a cash prize of $500, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1991 are now being accepted for the 24th annual award, which will be presented in the summer of 1992. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1992 award, reprints must be received by 1 June 1992.

A REVISION OF *CHABOISSAEA* (POACEAE: ERAGROSTIDEAE)

PAUL M. PETERSON and CAROL R. ANNABLE
Department of Botany, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560

ABSTRACT

Chaboissaea is a New World genus of open, marshy meadows that includes four species, three ranging from northwestern Chihuahua to Distrito Federal, Mexico, and one endemic to Jujuy and Salta, Argentina. It is characterized by gray to grayish-yellow spikelets with one, two, or occasionally three florets per spikelet, the lower floret perfect and the upper pedicelled floret often staminate or sterile; and a base chromosome number of $x = 8$. The revision includes a key, descriptions of morphology and anatomy, a hypothesized phylogeny, distribution maps, and illustrations for each species. *Chaboissaea atacamensis* represents a transfer from *Muhlenbergia.* A key distinguishing *Bealia, Blepharoneuron, Chaboissaea, Muhlenbergia,* and *Sporobolus* is presented.

RESUMEN

Chaboissaea es un género del Nuevo Mundo, de praderas cenagosas, con especies, de las cuales tres se encuentran en México, en la región del nordeste de Chihuahua hasta el Distrito Federal y una es endémica de Jujuy y Salta, Argentina. El género se caracteriza por la presencia de espiguillas grisáceas o amarillo cenizo, con uno, dos y ocasionalmente tres flósculos por espiguilla; los flósculos basales son perfectos y los distales generalmente estaminados o estériles; el género tiene un número cromosómico básico $x = 8$. Esta revisión incluye una clave, descripciones morfológicas y anatómicas, mapas de distribución, ilustra cada una de las especies y postula una hipótesis filogenética. *Chaboissaea atacamensis* es transferida del género *Muhlenbergia.* El presente artículo provee una clave para los géneros *Bealia, Blepharoneuron, Chaboissaea, Muhlenbergia* y *Sporobolus.*

Historically, *Chaboissaea* Fourn., s. str., contained a single species, *C. ligulata* Fourn., that ranged from northern Chihuahua to Distrito Federal, Mexico. It differs from other eragrostoid genera in having gray to grayish-yellow spikelets with one, two, or occasionally three florets per spikelet, the lowermost perfect and the upper pedicelled florets usually staminate or reduced and sterile; and a base chromosome number of $x = 8$. *Chaboissaea ligulata* is rather scantily distributed in Mexico and is restricted to blackish clay soil in meadows, drainage ditches, and irrigation canals.

Based on specimens collected in San Luis Potosi by Virlet d'Aoust, the genus *Chaboissaea* was first recognized by Fournier (1886) as containing a single perennial species, *C. ligulata.* In his generic description, Fournier stressed that *Chaboissaea* has 2-flowered spikelets containing a lower fertile floret and a pedicelled, upper sterile

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floret, and an entire or toothless palea. Lamson-Scribner and Merrill (1901) legitimately transferred *C. ligulata* to *Muhlenbergia* Schreb. but did not see the type, basing their decision on two collections from Durango (*Palmer 731 & 948*) which they incorrectly assumed were the same species. Hitchcock (1935) later recognized the Durango collections as belonging to a separate annual species, *M. subbiflora,* and designated *Palmer 948* as the type. Even before these specimens from Durango were appropriately named, Lamson-Scribner and Merrill thought these collections were conspecific with *C. ligulata.*

Although the transfer of *C. ligulata* to *Muhlenbergia* was based on *M. subbiflora* its use as *M. ligulata* was accepted by Hitchcock (1913), Bews (1929), Conzatti (1946), and more recently Watson et al. (1985) and Clayton and Renvoize (1986). Conzatti (1946) placed *Chaboissaea* in the unnatural and no longer recognized tribe, Agrostideae, and Sohns (1953) placed it in the Festuceae (=Pooideae).

In the southern hemisphere, Parodi (1948) described an annual species, *M. atacamensis,* from Jujuy, Argentina, designating one of his own collections as the type (*Parodi 9656*). In his observations he notes, "La especie [*M. atacamensis*] mas emparentada es *M. ligulata* [=*C. ligulata*] de Mexico." Therefore, he viewed the closest relative to be *C. ligulata,* which he included in *Muhlenbergia.*

Based on collections from Chihuahua by Hernandez X. and Tapia J., Swallen (1958) described another annual species, *M. decumbens,* which he stated was "closely related to *Muhlenbergia subbiflora* Hitchc." More recently Reeder and Reeder (1988) transferred *M. decumbens* and *M. subbiflora* to *Chaboissaea.*

In the Eragrostideae (sensu Clayton and Renvoize 1986) the base chromosome number is generally 10 and only *Bealia* Scribner in Hackel, *Blepharoneuron* Nash, *Chaboissaea, Dasyochloa* Willdenow ex Rydberg, *Erioneuron* Nash, and *Munroa* Torrey have a base number of 8 (Gould 1958; Peterson 1988b, 1989; Peterson and Annable 1990; Reeder 1967, 1968, 1971, 1977; Reeder and Reeder 1988; Tateoka 1961). Reported chromosome counts for *C. ligulata* and *C. subbiflora* indicate these species are diploid ($2n=16$), although the latter possesses an aneuploid series of $2n=14$, 16, 18 (Reeder 1967, 1968; Reeder and Reeder 1988). *Chaboissaea decumbens* is a tetraploid ($2n=32$) with all counts being made from individuals of a single population in two successive years (Reeder and Reeder 1988).

While working on a revision of the annual species of *Muhlenbergia* Schreb. (Peterson and Annable 1991) and collecting throughout Mexico in 1985 and 1986, we recognized the morphological similarities among *M. decumbens* Swallen, *M. subbiflora* Hitchc., and *C. ligulata.* Reeder and Reeder (1975) suggested that *M. decumbens* and *M. subbiflora* should be placed in *Chaboissaea.* Subsequently, Peterson (June, 1988a) stated in an abstract that he would be transferring these two annual species into *Chaboissaea.* Later that year, Reeder and Reeder (June, 1988) published the new combinations of *C. decumbens* (Swallen) J. & C. Reeder and *C. subbiflora* (Hitchc.) J. & C. Reeder. Even though *C. decumbens* and *C. subbiflora* are allopatric, they occur in similar habitats, i.e., cienagas or marshy meadows in clayish soils, and are sometimes associated with *C. ligulata.*

After reviewing type specimens of *Muhlenbergia* at United States National Herbarium (US) we became aware that *M. atacamensis* Parodi, a regional endemic from Jujuy and Salta, Argentina, also belonged in *Chaboissaea.* Parodi (1948) suggested this affinity but did not place this species in *Chaboissaea* because he treated this genus as a synonym of *Muhlenbergia.* This species occurs in cienagas, muddy sumps, ephemeral pools along roadside ditches in clayish soil, and sandy margins surrounding lagoons.

The need for a revision of this genus is apparent, since it was treated as monotypic from its inception and more recently by Sohns (1953), McVaugh (1983), and Beetle (1987). There is no treatment of *Chaboissaea* containing keys to the species, adequate descriptions comparing the four species, and citations of recent collections. Nor has there been a thorough anatomical examination comparing the four species (Schwabe 1948; Decker 1964; Peterson et al. 1989). The present revision is based on field work, combined with laboratory and herbarium studies of morphology, anatomy, and chromosome numbers. In the present study we examine the phylogenetic relationships of the four species within *Chaboissaea* through cladistic analyses of morphological attributes.

METHODS

The external morphology of the study group was examined by observing living plants in the field and in culture, and by examining herbarium specimens. A complete set of vouchers has been deposited in the US and duplicates have been distributed to various herbaria (see specimen citations).

For the anatomical studies field-collected leaf blades from the mid-culm region were fixed in FAA. In *C. atacamensis,* the leaf blades from an herbarium specimen were soaked for 24 hours in a solution of water and tween 20 before dehydration in alcohol. After dehydration in an increasing ethanol series, the leaves were embedded in paraffin, sectioned at 8–10 μm thickness, and stained with safranin/fast green (Berlyn and Miksche 1976). Leaf scrapes were prepared in alcohol and stained with safranin and celestine blue B. Samples were examined and photographed on an Olympus BH–2 photomicroscope using Kodak Technical Pan film. Anatomical de-

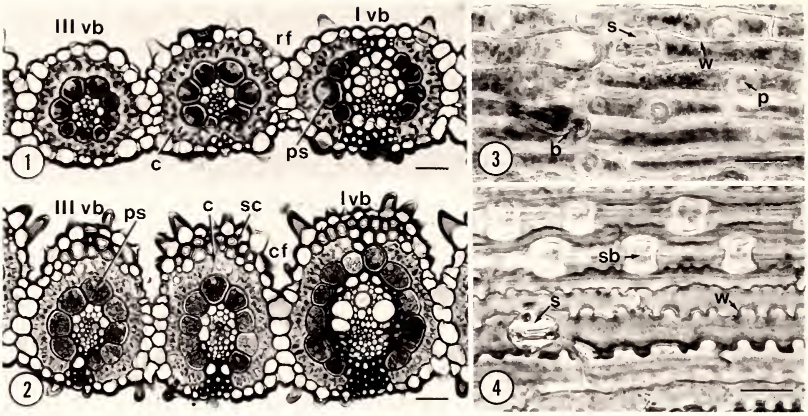
TABLE 1. DATA SET AND CHARACTERS USED IN THE CLADISTIC ANALYSES OF *CHABOISSAEA*. 1—duration: annual (1), perennial (2); 2—number of florets: one (1), two to three (2); 3—ligule length: less than 3.5 mm (1), 6–10 mm long (2); 4—palea awns: present (1), absent (2); 5—awn-tipped glumes: absent (1), present (2); 6—rooting at lower nodes: present (1), absent (2); 7—lemma length: less than 3 mm (1), more than 3 mm (2); 8—anther length: less than 1.2 mm (1), more than 1.2 mm (2); 9—anther color: olivaceous or greenish (1), purplish (2); 10—chromosome base (*x*): eight (1), ten (2); 11—adaxial furrow of leaf blade: rounded (1), cleft (2); 12—walls of intercostal long cell: sinuous (1), straight (2); 13—walls of costal short cells: straight (1), sinuous (2).

C. atacamensis	1	2	1	1	2	2	1	1	1	1	1	1	2
C. decumbens	1	2	1	1	2	1	2	1	1	1	1	1	2
C. ligulata	2	2	2	2	2	2	2	2	2	1	2	1	1
C. subbiflora	1	2	1	1	2	2	1	2	2	1	1	2	1
Bealia mexicana	1	1	1	2	1	2	2	2	2	1	1	2	1
Muhlenbergia richardsonis	2	1	1	2	1	2	1	2	2	2	1	1	2

scriptions were completed following the procedure for standardizing comparative leaf anatomy as outlined by Ellis (1976, 1979). For purposes of comparison and standardization, primary, I° vascular bundles (first order) are defined as those containing large metaxylem vessels on either side of the protoxylem elements and usually associated with sclerenchyma girders or strands (Ellis 1976). All other vascular bundles are considered as tertiary, III° (third order), and contain indistinguishable xylem and phloem elements.

Floral buds were field collected and fixed in ethanol-acetic acid (3:1, V:V) prior to storage under refrigeration in 70% ethanol. Meiotic chromosome counts were obtained from aceto-carmine squashes of pollen mother cells. Representative cells were photographed using Kodak Technical Pan film and interpretations were based on 20 or more cells.

Cladistics. A total of thirteen morphological attributes were scored for each species and used in the cladistic analyses (Table 1). Phylogenetic analyses were conducted on an IBM-model 80 computer using version 2.4 of phylogenetic analysis using parsimony (PAUP) written by Swofford (1985). In addition to the four species of *Chaboissaea, Bealia mexicana* Scribn. in Beal, a closely allied annual with a similar base chromosome number, and *Muhlenbergia richardsonis* (Trin.) Rydb., a low, mat-forming, rhizomatous perennial of similar habitats and spikelet characteristics, were used as outgroups to determine character polarities. For all analyses, the ALLTREES option, was employed and all character transformations were unordered. With *Bealia mexicana* as the designated outgroup, character 10 was invariant and therefore deleted from the cladistic analysis.



FIGS. 1–4. Leaf anatomy of *Chaboissaea,* adaxial surface uppermost in Figs. 1 and 2. 1. *C. decumbens* with rounded adaxial furrows. 2. *C. ligulata* with cleft adaxial furrows and well developed sclerenchyma just below the adaxial epidermis of each vascular bundle. 3. *C. subbiflora* in abaxial view with straight intercostal long cell walls and prominent papillae. 4. *C. ligulata* in abaxial view with sinuous intercostal long cell walls and saddle shaped silica bodies. Scales = 25 μm. b = bicellular microhair; c = chlorenchyma; cf = cleft furrows; p = papillae; ps = parenchyma bundle sheath; rf = rounded furrow; s = stomata; sb = silica body; sc = sclerenchyma; w = intercostal long cell wall; I vb = primary vascular bundle; III vb = tertiary vascular bundle.

LEAF ANATOMY

Chaboissaea is a typical c_4 chloridoid that exhibits kranz leaf anatomy, particularly the P.S., XyMS+ subtype where the perivascular sheath is composed of an inner mestome sheath and an outer parenchymatous bundle sheath (Brown 1977; Hattersley and Watson 1976). A cursory survey of the leaf anatomy reported that *C. ligulata* exhibits eragrostoid structure, oval-shaped stomata, bulbous bicellular microhairs, and saddle-shaped siliceous cells (Decker 1964). An excellent illustration of the transection of *C. atacamensis* is given in the treatment of the leaf anatomy of some Agrostideae (Schwabe 1948). The following descriptions refer to all four species unless otherwise noted.

Leaf blade in transverse section (Figs. 1 and 2). The lamina is flat to outwardly bowed near the margins with shallow (less than ¼ blade thickness) to medium (⅓ to ½ blade thickness), rounded adaxial furrows whereas the adaxial furrows in *C. ligulata* are cleft shaped. The abaxial ribs are much smaller than the adaxial ribs. The abaxial projection of the midrib or keel is comprised of a single vascular bundle that is very inconspicuous and flat with a small girder of sclerenchyma one to six cell layers thick. There are two tertiary (III°) vascular bundles between each primary (I°) vascular bundle. Primary

(I°) and tertiary (III°) vascular bundles are circular and the phloem without sclerenchyma tissue adjoins the mestome sheath. The parenchyma sheath of each primary (I°) vascular bundle is interrupted on the abaxial surface and sometimes the adaxial surface by a narrow to broad, often triangular girder (less than four fibers deep) of sclerenchyma. The parenchyma sheath of the tertiary (III°) vascular bundle is complete on the abaxial and adaxial surface and interrupted on the abaxial surface by a narrow girder of sclerenchyma in *C. ligulata.* A small strand (2–4 fibers wide) to a well developed (wider than deep) band of adaxial sclerenchyma is located between the chlorenchyma and the epidermis just above the vascular bundle. It is always a well developed band in *C. ligulata.* A sclerenchyma cap varying from a few fibers deep to wider than the tertiary (III°) vascular bundle is present at the margin of the leaf. The chlorenchyma tissue is composed of a single radiate layer of tightly packed tabular cells that surround each vascular bundle, commonly interrupted on the abaxial surface and occasionally interrupted on the adaxial surface. Each vascular bundle is separated by a group of colorless cells interspersed with larger, more inflated bulliform cells. These bulliform cells and colorless cells form a 1, 2, or occasionally 3 cell wide column that extends from the abaxial to the adaxial epidermis. Macrohairs have a sunken, nonconstricted base and are embedded between bulliform/colorless cells.

Leaf epidermis in abaxial view (Figs. 3 and 4). The intercostal long cells are three times or more longer than wide with moderately thickened walls. The walls are sinuous except in *C. subbiflora* where they are straight to slightly undulating. The intercostal short cells are tall and narrow with smooth to slightly undulating walls. These cells are more numerous in *C. ligulata* than the other species. Dome-shaped stomata are common and occur in two bands, one band on each side of the costal zone, each band with one, occasionally two rows of stomata. One distally positioned, dome-shaped papilla with unthickened walls per epidermal long cell. In *C. subbiflora* the papillae are large and conspicuous. Chloridoid-type (clavate) bicellular microhairs are attached to short cells in a single row in the middle of furrow. Prickle hairs are restricted to the leaf margins and macrohairs are absent. One or two rows of silica cells are located in the costal zone. The silica bodies are saddle-shaped to cuboid, sometimes elongate. Silica cells alternate with rectangular short cells that are less than three times longer than wide. In *C. atacamensis* and *C. decumbens,* the walls of the short cells are sinuous whereas in *C. ligulata* and *C. subbiflora* the walls are straight or only slightly undulate.

Leaf epidermis in adaxial view. Unicellular macrohairs and prickle hairs occur sporadically on the costal zone and papillae are prominent and generally larger than on the abaxial surface. Other characters are similar to the abaxial surface.

PHYLOGENY

A recent classification places *Chaboissaea* as a synonym of *Muhlenbergia* in the subtribe Sporobolinae which includes *Crypsis* Aiton, *Lycurus* Kunth, *Muhlenbergia,* and *Sporobolus* R. Brown (Clayton and Renvoize 1986). On the basis of cork and silica cell distribution on the surface of the lemma, Valdes-Reyna and Hatch (in manuscript) suggested that *Blepharoneuron* is also closely related to *Chaboissaea.* Additional data from restriction site variation of chloroplast genomes and gross morphology may help in discerning the relationship of this genus within the Eragrostideae (Duvall and Peterson in preparation).

At two locations (*Peterson & Annable 10319, 10323*) individuals of *C. atacamensis* were found be diploid at $2n=16$ (Fig. 5). This lends karological evidence that the morphological similarity of *C. atacamensis* with other members of the genus is a consequence of common ancestry. At present morphological traits are the only suitable characters available for evaluating the relationship among the four species of *Chaboissaea.*

Cladistics. Using *Muhlenbergia richardsonis* as the designated outgroup produced a single tree of 15 steps with a consistency index of 0.87 (Fig. 6). *Chaboissaea ligulata* is the most basal member of the group suggesting that the annual species of *Chaboissaea* were probably derived from perennial ancestors very similar to *C. ligulata.* Two synapomorphies, the annual habit (1) and the possession of awned paleas (4), support the clade of *C. atacamensis, C. decumbens,* and *C. subbiflora. Chaboissaea atacamensis* and *C. decumbens* form a closely related couplet supported by two synapomorphies, small, greenish or olivaceous anthers (8, 9) and a reversal involving the walls of the costal short cells (13), also shared by *M. richardsonis.* Three synapomorphies support the monophylesis of the ingroup: possession of two or three florets (2), awn-tipped glumes (5), and a base chromosome number of $x = 8$. While none of these characters are unique in the Eragrostideae, in combination they strongly suggest that these four species are monophyletic.

When *Bealia mexicana* is used as the designated outgroup two equally parsimonious trees are produced, each with 14 steps and a consistency index of 0.86. One tree has the same topography as the tree derived from using *M. richardsonis* as the outgroup (Fig. 6) and will not be discussed further. In the second tree, *C. subbiflora* is the most basal member of the group, supported by the parallel derivation of a short lemma (7), a very plastic character (Fig. 7). Since *Bealia mexicana* is an annual, an additional autapomorphy (1) is added to

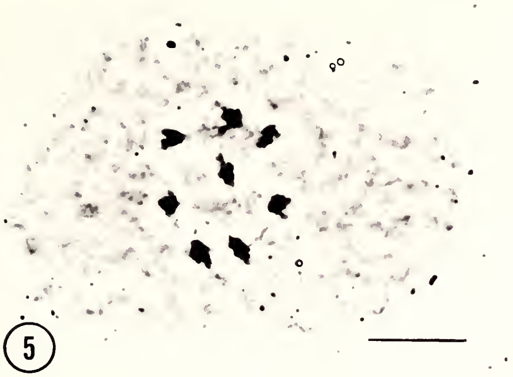


FIG. 5. Photomicrograph of meiotic chromosomes of *Chaboissaea atacamensis* in diakinesis, $n = 8$, *Peterson & Annable 10319.* Line scale = 5 μm.

the *C. ligulata* branch, thereby inverting the position of the latter taxon with *C. subbiflora.* The possession of awned paleas (4) in relation to *Bealia mexicana* is reversed and lost in *C. ligulata* but still found in the other three species of *Chaboissaea.*

The first cladogram (Fig. 6) seems to represent a more parsimonious explanation of the phylogenetic history of the genus and can perhaps be used to postulate the geographic origin. There are many cases of North/South American amphitropical disjunctions occurring within the same species of Eragrostideae, i.e., *Eragrostis lugens* Nees, *Erioneuron avenaceum* (Kunth) Tateoka, *E. pilosum* (Buckl.)

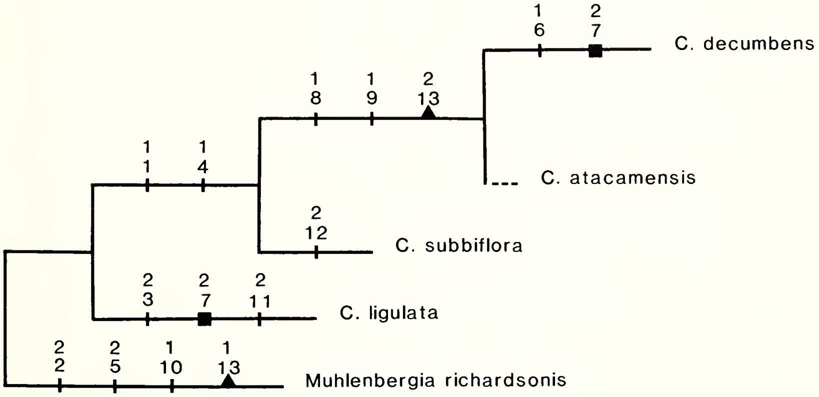


FIG. 6. Cladogram of the four species of *Chaboissaea* rooted with *Muhlenbergia richardsonis* (cf. Table 1). Lower numbers along branches refer to characters, upper numbers refer to character states, squares indicate parallelisms, and triangles indicate reversals. Length = 15, consistency index = 0.87.

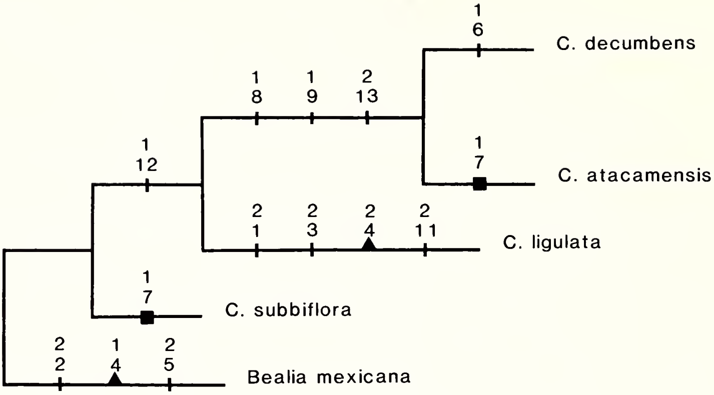


FIG. 7. Cladogram of the four species of *Chaboissaea* rooted with *Bealia mexicana* (cf. Table 1). Lower numbers along branches refer to characters, upper numbers refer to character states, squares indicate parallelisms, and triangles indicate reversals. Length = 14, consistency index = 0.86.

Nash, *Leptochloa dubia* (Kunth) Nees, *L. filiformis* (Lam.) Beauv., *L. uninervia* (Presl) Hitchc., *L. virgata* (L.) Beauv., *Lycurus setosus* (Nutt.) C. Reeder, *Muhlenbergia asperifolia* (Nees & Meyen) Parodi, *M. ramulosa* (Kunth) Kunth, *M. peruviana* (Beauv.) Steud., *M. tenuifolia* (Kunth) Kunth, *M. torreyi* (Kunth) Hitchc. ex Bush, *Scleropogon brevifolius* Philippi, and *Tripogon spicatus* (Nees) E. Ekman. Our evidence from morphology and biogeography suggests that the genus arose in northcentral Mexico where three species still exist (Fig. 8) and migrated to Argentina via long distance dispersal by a chance event or more probably by jumping from "islands" of similar habitats (Raven 1963; Thorne 1972). There is very little morphological divergence among all three annual species of *Chaboissaea* which suggests the migration event could be very recent. Preliminary data from enzyme electrophoresis of the North American species indicate that *C. decumbens* and *C. subbiflora* are more similar in their allozymic phenotypes than either is to *C. ligulata* (Peterson and Duvall unpublished data). It appears that the widespread perennial, *C. ligulata,* gave rise to the rather narrowly distributed annual endemics by sympatric speciation, followed by subsequent radiation.

The unusual morphological characters in *Chaboissaea* of spikelets with one, two, or occasionally three florets per spikelet, the lower floret perfect and the upper pedicelled floret often staminate; and a base chromosome number of $x = 8$ support the hypothesized monophyly of these four species. The following key is provided to distinguish among *Bealia, Blepharoneuron, Chaboissaea, Muhlenbergia,* and *Sporobolus* using gross morphological features.

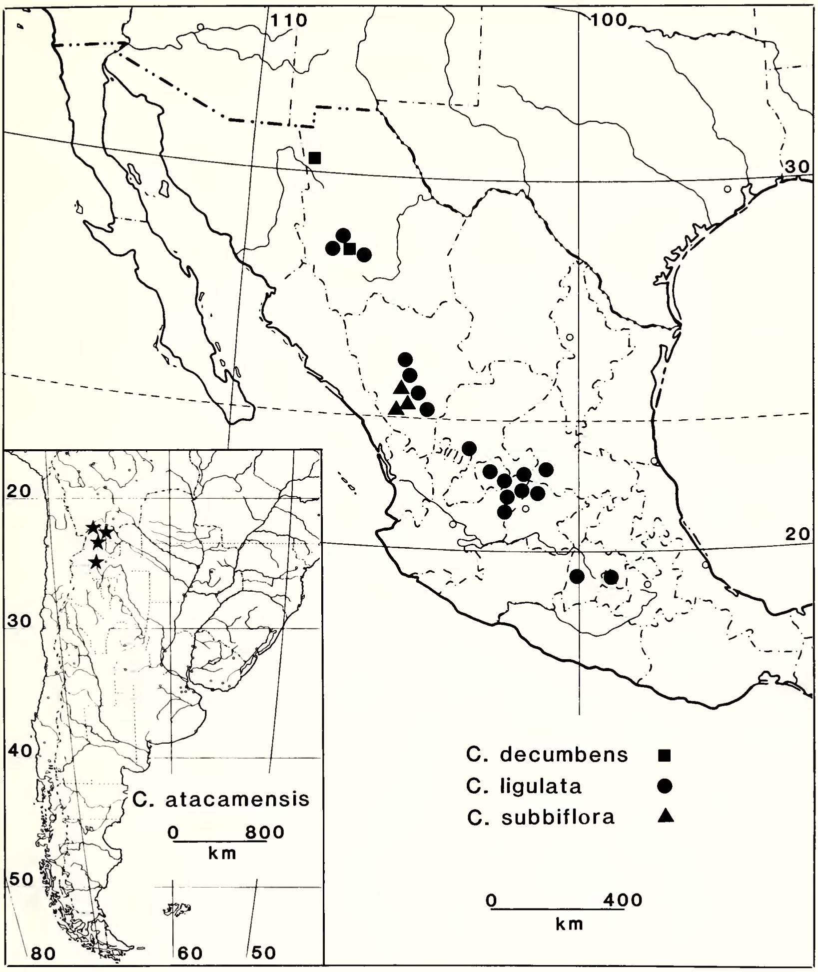


FIG. 8. Distribution of *Chaboissaea atacamensis, C. decumbens, C. ligulata,* and *C. subbiflora.*

KEY TO RELATED GENERA

a. Lemma 1–nerved; ligule a short fringe of hairs or ciliate membrane; fruit with a seed coat remaining separate from the pericarp (a true achene), the seed usually falling free from the lemma and the palea at maturity .... *Sporobolus*

a′. Lemma 3–nerved; ligule usually membranous, occasionally ciliate, but never hairy; fruit a caryopsis with an attached, hardened pericarp, the seed usually tightly enclosed by the lemma and palea at maturity.

  b. Lemma with densely appressed to spreading, silky, whitish hairs on the midnerve and margins, these hairs often appearing as ridges on the surface at 20×; paleas densely silky-villous between the two nerves. .... *Blepharoneuron*

  b.′ Lemma glabrous or with appressed to spreading hairs on the midnerve and margins, but without silky, whitish hairs that appear as ridges on the surface at 20×; palea glabrous, occasionally with appressed to spreading hairs between the two nerves.

- c. Spikelet with one, two, or occasionally three florets, the lowermost perfect, the upper pedicelled florets usually staminate, reduced, and/or sterile. .... *Chaboissaea*
- c′. Spikelet with one floret, or when occasionally two-flowered the upper floret usually fertile.
  - d. Lemma deeply bilobed, the lobes 1–1.4 mm long, rounded to obtuse; awn crisped-curled to flexuous, borne between the lobes; a single annual species in Chihuahua and Durango, Mexico. .... *Bealia*
  - d′. Lemma not deeply bilobed (except in the perennial, *M. argentea* Vasey), sometimes minutely bifid, then the teeth less than 1 mm long, usually acuminate to aristate; awn straight to flexuous; wide ranging in North and South America to SE Asia. .... *Muhlenbergia*

SYSTEMATIC TREATMENT

CHABOISSAEA Fournier, Mex. Pl. 2:112. 1886.—TYPE: *Chaboissaea ligulata* Fournier.

Tufted perennials with slender upright stems or decumbent annuals sometimes rooting at the lower nodes. Culms glabrous, hollow. Sheaths open, glabrous, usually shorter than the internodes. Ligules hyaline often scarious, truncate to acute-acuminate. Blades flat to loosely involute, scaberulous above and along margins, glabrous to scaberulous below. Inflorescence a terminal narrow panicle, with distant, alternate, subdivided, strongly appressed branches. Spikelets mostly appressed along secondary branches, dark gray or plumbeous to grayish-yellow, 1- or 2-flowered, occasionally 3-flowered, when 2-flowered the lower floret perfect and the upper usually staminate or neuter, articulation above the glumes. Glumes subequal, mostly shorter than the florets, acute or acuminate, often awn-tipped, 1-nerved, sometimes obscurely so. Lemmas chartaceous, obscurely 3-nerved, lanceolate, mottled, somewhat compressed keeled, awned or unawned, minute appressed hairs along the margins and midnerve below; apex long acuminate to acute. Paleas lanceolate, usually shorter than the lemmas, glabrous, strongly 2-nerved, often extending into short awns. Lodicules two, short, fleshy, truncate, lateral margins thin. Ovary glabrous; styles not all united at the base, the two stigmas plumose, dark gray. Anthers three. Caryopses fusiform, brownish, usually not falling free from the lemma and the palea. Embryo large, with an epiblast, scutellar tail, and elongated mesocotyl internode; embryonic leaf margins meeting, endosperm hard. $x = 8$.

Four species, three in Mexico and one in northern Argentina.

KEY TO THE SPECIES OF *CHABOISSAEA*

a. Tufted perennials; ligules 6–10 m long; nerves of palea not extending into awns. .... 3. *C. ligulata*

a′. Erect or decumbent annuals; ligules 1.6–3.2 mm long; nerves of palea usually extending into awns 0.3–1.2 mm long.
  b. Lemmas 3.0–3.8 mm long; plants commonly rooting at the lower nodes; north-central Chihuahua, Mexico. .... 2. *C. decumbens*
  b′. Lemmas 1.8–2.9 mm long; plants not rooting at the lower nodes; Durango, Mexico or Jujuy and Salta, Argentina.
    c. Plants (3)5–10(15) cm tall; anthers 0.9–1.1 mm long, olivaceous; inflorescence 1–5.4 cm long; northern Argentina. .... 1. *C. atacamensis*
    c′. Plants 20–50 cm tall; anthers 1.4–2.0 mm long, purplish to grayish; inflorescence 7–12 cm long; southwestern Durango, Mexico. 4. *C. subbiflora*

1. **Chaboissaea atacamensis** (Parodi) Peterson & Annable, comb. nov.—(Fig. 9). *Muhlenbergia atacamensis* Parodi, Rev. Argentina Agron. 15:248. 1948.—TYPE: Argentina, Provincia de Jujuy, La Quiaca, 15 Feb 1931, *Parodi 9656* (holotype: BAA!; isotype: BAA! US!).

Muhlenbergia atacamensis Parodi var. *brachyanthera* Parodi, Rev. Argentina Agron. 15:250. 1948.—TYPE: Argentina, Provincia de Jujuy, Departamento de Cochinoca, Puesto del Marques, 30 Jan 1943, *Cabrera 7785* (holotype: BAA!)

Slender, weak annuals. Culms (3)5–10(15) cm tall, upright, sometimes spreading and sprawling, freely branching below, glabrous below the nodes, 0.3–0.4 mm diam. just below the inflorescence. Sheaths 1.0–2.4 mm long, glabrous, sometimes keeled, shorter than the internodes, margins hyaline. Ligule 1.5–3.2 mm long, hyaline, the apex acuminate, entire, the margins entire, decurrent. Blades 1.2–7.0 cm long, 0.7–3.0 mm wide, flat, lax, scaberulous, the margins scabrous especially towards apex. Inflorescence 1.0–5.4 cm long, 0.4–2.4 cm wide, a narrow panicle with ascending primary branches appressed or spreading 0–80° from the culm axis, the secondary branches appressed; the pedicels 1–3 mm long, stiff, scabrous; nodes per inflorescence 6–10; usually one inflorescence branch per node, 0.3–1.8 cm long. Spikelets erect, 1- or 2-flowered, grayish-yellow to grayish-green. Glumes 1–2.0 mm long, subequal, yellowish to greenish with gray mottles, glabrous and scabrous along the midnerve, acute to obtuse, the first 1–1.7 mm long, the second 1.3–2.0 mm long. Lemmas 1.8–2.9 mm long, lanceolate, unawned or awned, compressed-keeled towards the apex, with appressed hairs on the midnerve and margins on the proximal ⅔, the hairs up to 0.2 mm long, scabrous along the midnerve and up the awn; yellow to greenish with gray mottles, and sometimes purplish near the apex; apex acuminate to acute, the awn up to 2 mm long. Paleas 1.7–2.8 mm long, narrowly lanceolate to lanceolate, the scabrous nerves usually extending into short awns; yellow to greenish with gray mottles; apex acute, the awns 0–0.3 mm long. Anthers 0.9–1.1 mm long, olivaceous. Caryopsis 1.3–1.5 mm long, fusiform, brownish. Chromosome number, $n = 8$.

Phenology and distribution (Fig. 8). Flowering January and February. Seasonally wet marshes, meadows, moist clay flats, gravelly roadside pools, margins of ephemeral pools, and sandy margins of lagoons in the Atacama Puna, associated with *Bouteloua simplex* Lag., *Poa annua* L., *Muhlenbergia fastigiata* (Presl) Henr., *Distichlis, Festuca, Eleocharis, Polypogon, Cynodon, Eragrostis,* and *Marsilea*; known from the Provincias de Jujuy and Salta, Argentina, but suspected to occur just north of La Quiaca in Potosi, Bolivia; 2900–3700 m.

Specimens examined. ARGENTINA. Jujuy: Santa Catalina, 5 km de Santa Catalina camino a oratorio, 8 Feb 1978, *Okada, Montes & Clausen 6707 1/2* (SI); Cochinoca, campos algo huinedos, 1959, *Cabezas 23168* (SI); 2 km W of Abra Pampa on road to Cochinoca at the Rio Miraflores Puente, 14 Feb 1991, *Peterson & Annable 10294* (US); 34 km S of La Quiaca on Ruta Nacional 9 towards Abra Pampa, at "Demostrativo La Intermedia," 15 Feb 1991, *Peterson & Annable 10300* (US); 29 km W of La Quiaca and 7.5 km E of Cieneguillas on Hwy 5, at Toquero, 16 Feb 1991, *Peterson & Annable 10319* (US), $n = 8$; 2.4 km NW of Cieneguillas at Junction of road to Santa Catalina and Casira/Piscuno, 16 Feb 1991, *Peterson & Annable 10323* (US), $n = 8$; 14 km S of Cieneguillas on road to Abra Pampa, just E of Lago Pozuelos, 16 Feb 1991, *Peterson & Annable 10327* (US); 36 km S of Cieneguillas and 57 km NW of Abra Pampa, just E of Lago Pozuelos, 17 Feb 1991, *Peterson & Annable 10337* (US). Salta: Depto. Cachi, Las Pailas, 24 Feb 1987, *Nicora et al. 9125* (SI); Nevado de Cachi, 15 km NW of Cachi just below the Ruinas Las Pailas, 10 Feb 1991, *Peterson et al. 10183* (US).

2. CHABOISSAEA DECUMBENS (Swallen) J. & C. Reeder, Phytologia 65:156. 1988.—(Fig. 10). *Muhlenbergia decumbens* Swallen, Bol. Soc. Bot. Mexico 23:30. 1958.—TYPE: Mexico, Chihuahua, road between Cuauhtémoc and V. Guerrero, 27 Oct 1954, *Hernandez X. & Tania J. N-359* (holotype: US!).

Slender, weak annuals. Culms 12–30 cm tall, decumbent spreading below freely branching, rooting at the lower nodes, glabrous below the nodes, 0.4–0.7 mm diam. just below the inflorescence. Sheaths 1.2–4.6 cm long, glabrous, usually about half as long as the internodes, margins hyaline. Ligules 1.6–2.5 mm long, hyaline, the apex truncate to broadly rounded, entire, the margins entire, decurrent. Blades, 2.5–8.0 cm long, 0.8–1.4 mm wide, flat, scaberulous, the margins scabrous especially towards apex. Inflorescence (4.5)8–11 cm long, 1.5–4.5 cm wide, a narrow panicle with ascending primary branches appressed or spreading 0–80° from the culm axis, the secondary branches appressed; the pedicels 1–3 mm long, stiff, scabrous;

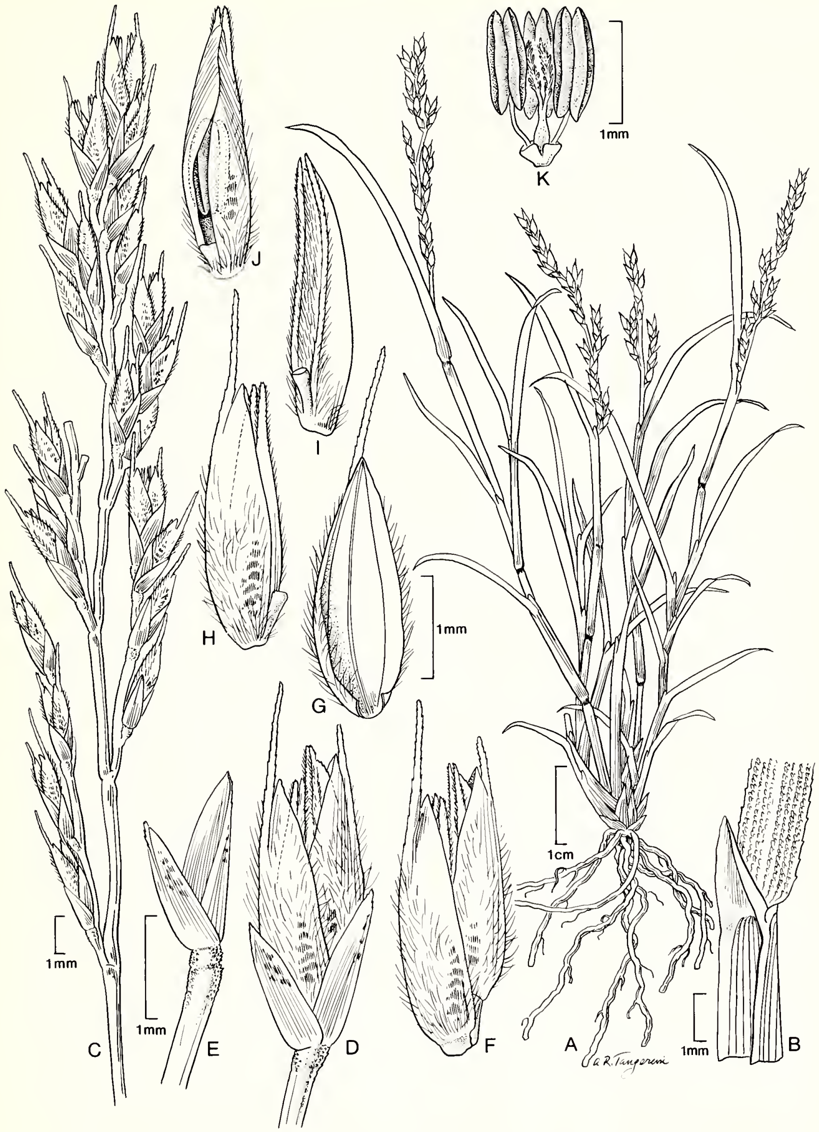


FIG. 9. *Chaboissaea atacamensis,* Jujuy, Argentina (*Parodi 9656*). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Two florets. G. Upper floret. H. Lower floret. I. Upper palea, ventral view. J. Lower palea, ventral view. K. Stamens, pistil, and lodicules.

FIG. 10. *Chaboissaea decumbens,* Chihuahua, Mexico (*Peterson & Annable 4533*). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Two florets. G. Lower floret. H. Upper floret. I. Lemma. J. Lower palea, dorsal view. K. Lower palea, ventral view. L. Lower palea, side view. M. Stamens, pistil, and lodicules.

nodes per inflorescence 6–10; usually a single primary inflorescence branch per node, 2.5–4.8 cm long. Spikelets erect, 1- or 2-flowered, plumbeous. Glumes 1.8–3.2 mm long, subequal, grayish, glabrous and scabrous along the midnerve, the apex acuminate sometimes awn-tipped, the awn up to 0.6 mm long, the first 1.8–2.5 cm long, the second 2.4–3.2 mm long, broader than the first. Lemmas 3.0–3.8 mm long, lanceolate, compressed-keeled towards apex, awned or unawned, with appressed hairs on the margins and lower third, the hairs up to 0.2 mm long, scabrous along the midnerve continuing up the awn; dark-green to gray with lighter greenish-white areas; apex long acuminate to acuminate, the awn 0.2–3 mm long. Paleas 3.0–3.7 mm long, narrowly lanceolate, glabrous, the scabrous nerves extending into short awns; dark green to gray with lighter greenish-white areas; apex acute, the awns 0.3–0.6 mm long. Anthers 0.9–1.1 mm long, greenish. Caryopsis 2–2.3 mm long, fusiform brownish. Chromosome number $n = 16$.

Phenology and distribution (Fig. 8). Flowering September and October. Sandy clay loam to dark clay soil along slough and wet sticky depressions in black soil in pine–oak–juniper woodlands; known only from two or three locations in northwestern Chihuahua, Mexico; 2200 m.

Specimens examined. MEXICO. Chihuahua: W of Casas Grandes, 5 mi S of Hernandez, 18 Sep 1960, *Reeder et al. 3510* (US); about 11 mi W of Cuauhtémoc, 5 Oct 1966, *Reeder & Reeder 4593* (ARIZ, MICH, US), *Reeder & Reeder 4601* (ARIZ, MICH, UC, US); 4 Sep 1967, *Reeder & Reeder 4848* (ARIZ, US); 13 mi W of Cuauhtémoc on Hwy 16, 21 Sep 1986, *Peterson & Annable 4533* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 23 Sep 1988, *Peterson & Annable 5820* (US); 9 Sep 1989, *Peterson & Annable 7983* (US); 23 Aug 1990, *Peterson 9587* (US).

3. CHABOISSAEA LIGULATA Fournier, Mex. Pl. 2:112. 1886.—(Fig. 11). *Muhlenbergia ligulata* (Fournier) Scribner & Merrill, U.S.D.A. Div. Agrostol. Bull. 24:19. 1901.—TYPE: Mexico, San Luis Potosi, 1851, *Virlet d'Aoust s.n.* (holotype: P, fragment US!).

Tufted perennials. Culms (10)20–70(90) cm tall, upright, leafy below, glabrous and sometimes purplish below the nodes, 0.5–1.1 mm diam. just below the inflorescence. Sheaths (0.8)2.5–11(13) cm long, glabrous, keeled, usually shorter than the internodes, margins hyaline. Ligule 6–10 mm long, hyaline, the apex acuminate, lacerate, the margins entire, decurrent. Blades (3)5–15(20) cm long, 1–2.5 mm wide, flat to conduplicate or involute, glabrous above and scaberulous below, the margins scabrous especially towards apex. Inflorescence 6–28 cm long, 1–10 cm wide, a somewhat narrow panicle with ascending primary branches 10–70° from the culm axis, the secondary branches appressed or narrowly spreading; the pedicels 0.2–3 mm long, stiff, scabrous; nodes per inflorescence 9–12; usually one inflorescence branch per node, 0.5–10 cm long. Spikelets erect, 1-, 2-, or occasionally 3-flowered plumbeous. Glumes 1.0–4.0 mm long, subequal in length, grayish, glabrous and scabrous along the midnerve, the apex acute to acuminate, sometimes awn-tipped, the awn up to 0.5 mm long, the first 1.0–3.2 mm long, the second 1.2–4.0 mm long. Lemmas (2.0)2.4–3.5(4.0) mm long, lanceolate, unawned or awned, compressed-keeled towards the apex, with appressed hairs on the midnerve and margins of the proximal ½, the hairs up to 0.2 mm long, scabrous along the midnerve and up the awn; greenish-yellow with dark-gray mottles, sometimes purplish near apex; apex acuminate to acute, the awn up to 2 mm long. Palea (1.9)2.4–3.3(3.8) mm long, lanceolate, unawned; greenish-yellow with dark gray mottles; apex acute or obtuse. Anthers 1.4–1.8 mm long, yellowish to purplish. Caryopsis 1.1–1.3 mm long, fusiform, brownish. Chromosome number $n = 8$.

Phenology and distribution (Fig. 8). Flowering mid August to mid November. Drainage ditches, irrigation canals, and meadows in blackish clay soil often in muddy water, associated *Acacia* and *Prosopis* grasslands with *Cyperus, Juncus, Leptochloa,* and occasionally *Chaboissaea subbiflora* and *C. decumbens*; Chihuahua, Durango, Zacatecas, Aguascalientes, San Luis Potosi, Jalisco, Guanajuato, Mexico, and Distrito Federal, Mexico; 1900–2500 m.

Specimens examined. MEXICO. Aguascalientes: La Congoja, municipio de San José de Gracia, 17 Oct 1973, *McVaugh 850* (MICH), *McVaugh 851* (MICH, MO). Chihuahua: Sanchez, 12 Oct 1910, *Hitchcock 7693* (US); 13 mi W of Cuauhtémoc on Hwy 16, 21 Sep 1986, *Peterson & Annable 4532* (GH, MO, NY, RSA, US, WS); 11.5 mi W of Cuauhtémoc on Hwy 16, 23 Sep 1988, *Peterson & Annable 5819* (US); 54.4 mi N of Parral on MEX 24 to Chihuahua, 14 Sep 1989, *Peterson & Annable 8111* (US). Distrito Federal: 3.5 km SE of Ixtapalapa, on road to Los Reyes, 17 Aug 1960, *Iltis & Koeppen 1302* (US). Durango: 36 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4638* (MEXU, RSA, US); 29 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4641* (US); about 41 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6480* (US); about 34 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6486* (RSA, US); ca. 8 km E of Durango, 6 Sep 1984, *Herrera 427* (ANSM, MEXU); Rancho El Tamascal, municipio de Suchil, 25 Oct 1984, Acevedo 147 (GUADA, MEXU); 66 km N of Durango on Hwy 45, 27 Sep 1988, *Peterson & Annable 5989* (US); 55 km N of Durango on Mex 45, S of turnoff to Canatlan (Hwy 26), 26 Aug 1990, *Peterson 9635* (US); 6 mi E of Durango on Mex 45 to Zacatecas, 27 Aug 1990, *Peterson*

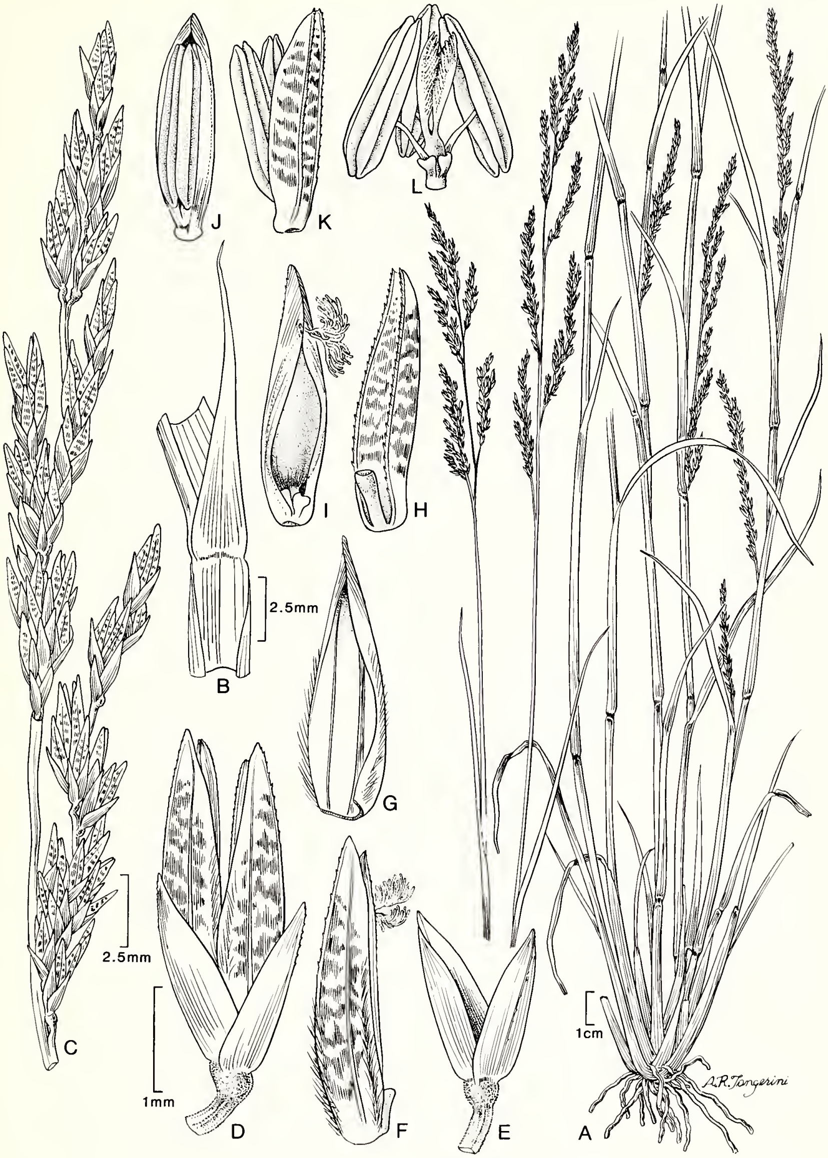


FIG. 11. *Chaboissaea ligulata,* Zacatecas, Mexico (*Peterson & Annable 6198*). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Lower floret. G. Lemma, ventral view. H. Lower palea, dorsal view. I. Lower palea, ventral view. J. Upper palea. K. Upper palea, ventral view. L. Stamens, pistil, and lodicules.

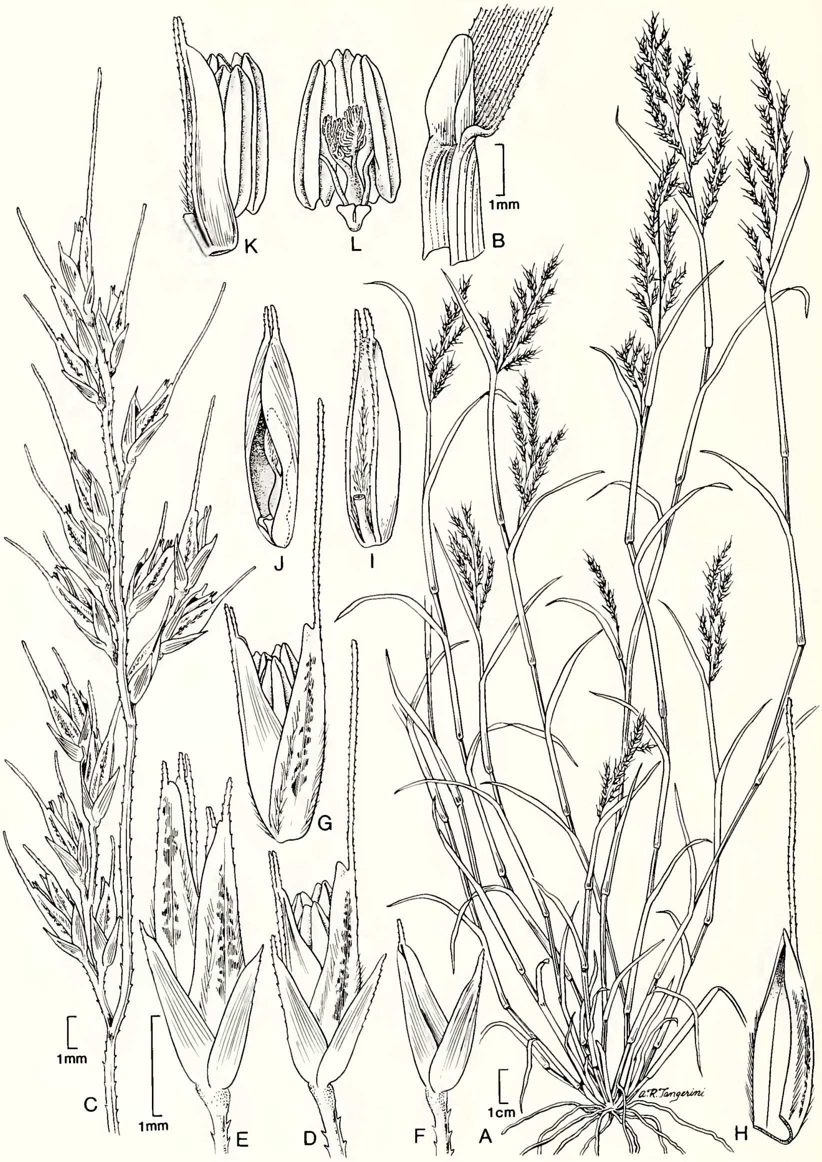


FIG. 12. *Chaboissaea subbiflora,* Durango, Mexico (*Reeder & Reeder 6481*). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Spikelet from *Reeder & Reeder 6488a.* F. Glumes. G. Lower spikelet. H. Lemma, ventral view. I. Lower palea, dorsal view. J. Lower palea, ventral view. K. Lower palea, side view. L. Stamens, pistil, and lodicules.

9650 (US). Jalisco: along the Ojuelos-Aguascalientes highway, about 1.5 km E of state line, 17 Aug 1958, *McVaugh 17058* (MICH, TAES, US); 14–15 km E of Arandas, 14 Nov 1970, *McVaugh 24376* (MICH); Presa El Cuarenta, entre Lagos de moreno y ojuelos, municipio de Lagos de Moreno, 30 Jul 1985, *Santana Michel 1596* (GUADA); 14.5 mi E of Aguascalientes on Hwy 70 towards San Luis Potosi, 7 Oct 1988, *Peterson & Annable 6185* (US); 29 Aug 1990, *Peterson 9680* (US). Guanajuato: about 6 km E of San Felipe, 24 Oct 1952, *Sohns 398, 411* (US); 26 Oct 1952, *Sohns 446* (MICH, MO, US); 10 mi SE of Ojuelos de Jalisco on Hwy 51 towards Ocampo, 29 Aug 1990, *Peterson 9682* (US); 1.4 mi SE of San Felipe on Mex 37 to Leon, 30 Aug 1990, *Peterson 9685* (US); 24.1 mi SE of San Felipe and 28.5 mi NE of Leon on Mex 37, 30 Aug 1990, *Peterson 9697* (US). Mexico: Villa de Allende, 5 Oct 1952, *Matuda et al. 27664* (MEXU, US). Zacatecas: about 1 mi E of Ojuelos, Jalisco, 18 Nov 1964, *Reeder & Reeder 4183* (RSA, US); about 13 mi W of Huejucar, 3 Oct 1974, *Reeder & Reeder 6459* (RSA, US); 3 mi E of Ojuelos de Jalisco on Hwy 70 to San Luis Potosi, 7 Oct 1988, *Peterson & Annable 6198* (US); 2.5 mi E of Ojuelos de Jalisco on Hwy 80 towards San Luis Potosi, 29 Aug 1990, *Peterson 9681* (US).

4. CHABOISSAEA SUBBIFLORA (Hitchcock) J. & C. Reeder, Phytologia 65:156. 1988.—(Fig. 12). *Muhlenbergia subbiflora* Hitchcock, North Amer. Flora 17:437. 1935.—TYPE: Mexico, Durango, City of Durango and vicinity, Nov 1896, *Palmer 948* (holotype: US!; isotypes: MEXU! MO! US!).

Slender, weak annuals. Culms 20–50 cm tall, upright, sometimes spreading and sprawling, freely branching below, glabrous below the nodes, 0.4–0.6 mm diameter just below the inflorescence. Sheaths 1.5–4.5 cm long, glabrous, usually about half as long as the internodes, the margins hyaline. Ligules 2.0–3.0 mm long, membranous to hyaline, the apex acute to obtuse, entire, the margins decurrent. Blades 2–8 cm long, 0.8–1.4 mm wide, flat, scaberulous above and along margins, glabrous below. Inflorescence 7–12 cm long, 1.8–5.5 cm wide, a narrow panicle sometimes included in the sheath below and appearing axillary with ascending primary branches appressed or spreading 0–70° from the culm axis, the secondary branches appressed or narrowly spreading; the pedicels 1–3 mm long, stiff, scabrous; nodes per inflorescence 8–15; usually a single primary inflorescence branch per node, 2.0–5.5 cm long. Spikelets erect on stout pedicels, 1- or 2-flowered, grayish. Glumes 1.0–2.2 mm long, subequal, grayish, glabrous and scabrous along the midnerve, the apex acute to acuminate, occasionally obtuse, sometimes awn-tipped, the awn up to 0.3 mm long, the first 1.0–2.0 mm long, the second 1.2–2.2 mm long, broader than the first. Lemmas 2.2–2.9 mm long, lanceolate, awned, occasionally unawned, somewhat compressed-keeled towards apex, with appressed hairs along the midnerve and margins on the proximal ⅔, the hairs up to 0.2 mm long; greenish-yellow with dark greenish-gray mottles, sometimes purplish near apex; apex acuminate or acute, sometimes minutely bifid, the awn 1–6 mm long, straight or flexuous. Paleas 2.1–2.9 mm long, lanceolate, awned, occasionally unawned, the nerves extending into short awns; greenish-yellow, occasionally with greenish-gray mottles; apex obtuse to rounded, the awns 0.3–1.2 mm long. Anthers 1.4–2.0 mm long, purplish to grayish. Caryopsis 1.0–2.5 mm long, fusiform, brownish. Chromosome number n = 7, 8, 9.

Phenology and distribution (Fig. 8). Flowering September through November. Gravelly, alkaline flats and open bottomlands with clay loam soils often growing in standing water in gramma (*Bouteloua*) grasslands with *Prosopis* and *Acacia*; known only from in and around the city of Durango, Mexico; 1900–2000 m.

Specimens examined. MEXICO: Durango: city of Durango and vicinity, Sep 1896, *Palmer 731* (GH, MEXU, MO, NY, US); 6 mi SE of Ciudad Durango near Rio Mesquital, 1 Oct 1948, *Gentry 8436* (GH, MICH, MO, US); 40 mi N of Ciudad Durango, 3 Oct 1948, *Gentry 8589* (GH, MEXU, MICH, US); 10.4 mi NE of Durango, 30 Sep 1959, *Soderstrom 804* (US); 27 Aug 1990, *Peterson 9651* (US); 4 mi E of Cd. Durango, 26 Sep 1963, *Reeder & Reeder 3828* (ARIZ); 40 mi N of Cd. Durango, 1 Sep 1965, *Reeder & Reeder 4485* (ARIZ); 39 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4636* (ARIZ, US); 29 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4640* (ARIZ, US); 22 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4642,* (ARIZ, US); 4 mi E of Durango, 9 Oct 1966, *Reeder & Reeder 4643* (ARIZ, US); 41 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6479, 6481* (ARIZ, US); 34 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6485* (ARIZ, US); 26 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6487* (ARIZ, US); 4 mi E of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6488, 6488a* (ARIZ, US); 10 mi NE of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6491* (ARIZ, US); 66 km N of Durango on Hwy 45, 8 Sep 1985, *Peterson & Annable 4086* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 27 Sep 1988, *Peterson & Annable 5988* (US); 3 Oct 1989, *Peterson & King 8266* (US); 25 Aug 1990, *Peterson 9619* (US); 26 Aug 1990, *Peterson 9630* (US); 64 km N of Durango on Hwy 45, 8 Sep 1985, *Peterson & Annable 4087* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 27 Sep 1986, *Peterson & Annable 4580* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 55 km N of Durango on Mex 45, just S of the turnoff to Canatlan (Hwy

26), 26 Aug 1990, *Peterson 9637* (US); 2.5 mi S of Durango on road to Ferreria, just before crossing rio, 27 Aug 1990, *Peterson 9652* (US).

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A NEW SUBSPECIES OF *ROSA STELLATA* (ROSACEAE) FROM NORTHWESTERN ARIZONA

Arthur M. Phillips, III
P.O. Box 201, Flagstaff, AZ 86002

Abstract

Rosa stellata subspecies **abyssa,** a new taxon from the rims of the Grand Canyon and Kanab Canyon in northwestern AZ, is described and illustrated. It differs from related taxa in having densely bristly hypanthia and densely stipitate-glandular stems.

Although *Rosa stellata* Wooton has been known from Coconino and Mohave counties, Arizona, since since it was first collected in the Grand Canyon region in 1908 (Kearney and Peebles 1960), Arizona specimens were not included in the most recent monograph of *Rosa* subgenus *Hesperhodos* (Lewis 1965). New population found by several investigators on the rims of the Grand Canyon and Kanab Canyon on the Arizona Strip in Mohave Co., Arizona, during the course of floristic surveys for the Bureau of Land Management, US Fish and Wildlife Service, Lake Mead National Recreation Area, and Grand Canyon National Park, have increased our understanding of its distribution and habitat requirements. The Arizona populations represent a distinct taxon, and a disjunction of at least 750 km from the nearest localities in New Mexico.

Rosa stellata Wooton subspecies **abyssa** A. Phillips, subsp. nov. (Fig. 1).—Type: USA, Arizona, Mohave Co.: SW edge of Shivwits Plateau, along W rim of Twin Point, 18 km S of Oak Grove, T30N R12W NW¼ sect. 7, 36°01′N, 113°37′W, 1823 m, in sandy to gravelly soils with limestone chips, derived from Kaibab limestone, in first 100 m from edge of plateau, open Great Basin conifer woodland, 15 Jun 1980, *A. M. Phillips, III, 80-103* (holotype, ARIZ; isotypes, ASC, ASU, DES, MNA, MO, NY, UNLV, UNM, US, Lake Mead National Recreation Area herbarium).

Frutex clonibus caulibus plurimus rigidis erectis, 0.25–1.5 m longis armatus spinis plurimis longis rectis. Caules dense stipitati glandulosi. Folia foliosis tribus usque ad quinque obovatis, grosse serratis insuper medium. Flores 5 cm diametro, solitari, terminales; hypanthium et sepala dense hispida aculeis longis crassis. Fructu sphaeroideum. Semina fusca laevia 4 mm longa.

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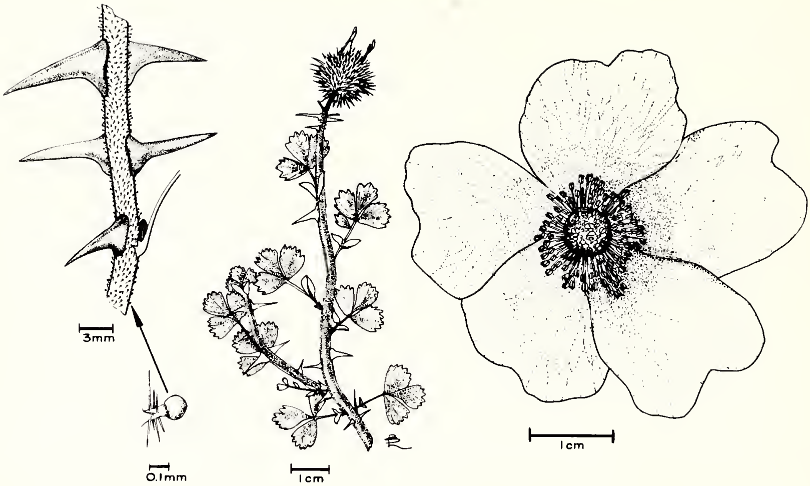

FIG. 1. *Rosa stellata* subsp. *abyssa*. Stem and stipitate gland, fertile stem with fruit, and flower. Drawn from the holotype (*A. M. Phillips, III 80-103*) and paratype (*A. Phillips and B. Phillips 79-742*) by Pamela S. Lungé. Used with permission of US Fish & Wildlife Service.

Clonal shrub with numerous stiff upright stems, 0.25–1.5 m long and armed with numerous long straight white to straw-colored paired infrastipular spines and with or without scattered internodal bristles and prickles. Stems brown, densely pubescent with short stipitate glands, these often encircled by stiff, white, stellately-arranged basal pubescence. Leaves with 3–5 obovate leaflets 5–12 mm long and 3–9 mm wide, cuneate at base, with 4–8 crenate or dentate coarse serrations above the widest part, occasionally minutely doubly serrate, bearing minute white sericeous pubescence on the margins, upper surface, and rachis, and few to numerous glands on leaflets immediately below the inflorescence; stipules adnate to the petiole, foliaceous above. Flowers solitary, terminal, about 5 cm across, sepals ovate-lanceolate, stiff, to 25 mm long, the free tips caudate-acuminate and slightly spatulate, often linear lobed, densely long-bristly below the tip, persistent and erect in fruit; petals obovate, dark pink, 15–20 mm wide, 17–25 mm long; hypanthium densely covered with long, stout, straight prickles, some gland-tipped. Fruit spheroid, 10–18 mm in diameter; seeds brown, smooth, about 4 mm long. Flowering May–June, fruiting September.

Paratypes. USA, AZ, Mohave Co.: type locality, 23 Sep 1979, in fruit, *A. Phillips and B. Phillips 79-742* (ARIZ, ASC, ASU, DES, MNA, MO, NY, UNLV, UNM, US, Lake Mead National Recreation Area herbarium); 27 Jul 1975, *Holland 690* (UNLV); W rim of Kanab Canyon, gravelly soil, T38N R3W sect. 30, 1585 m, 2 Aug 1977, *Gierisch 3978* (ASC, ASU); 8 Jun 1978, *Gierisch 4388* (ARIZ, ASU, USDA Forest Service Herb., Albuquerque, NM); W rim of Kanab Canyon in small drainage 30 m from edge, restricted to Kaibab limestone conglomerate, T38N R3W NW¼ sect. 29, 1550 m, 13 Jun 1979, *A. Phillips and B. Phillips 79-624* (MNA); W rim of Kanab Canyon S of Water Canyon, in depression caused by breccia pipe collapse, T38N R3W NW¼ SW¼ sect. 8, 1525 m, 22 May 1980, *A. Phillips 80-91* (ARIZ, ASC, ASU, MNA, UNLV, UNM, BLM Arizona Strip District herbarium); Grand Canyon National Monument (Park), head of SB Trail, 1372 m, 24 May 1958, *Riffey s.n.* (UNLV, COLO); between SB Point and Hades Knoll, side canyon, 1675 m, 30 May 1978, *Reichhardt 123* (MNA). Coconino Co.: Mesa Eremita, S rim of Grand Canyon, 1980 m, 12 Jun 1935, *Hawbecker s.n.* (Grand Canyon National Park Study Collection); Dutton Point, N rim of Grand Canyon, dry ledge overlooking canyon, 2285 m, 17 Jul 1947, *Bryant and Cooper s.n.* (Grand Canyon National Park Study Collection, 2 specimens).

Specimen not examined. AZ: Coconino Co., Powell Plateau, N rim of Grand Canyon, in a dry, rocky situation, *Ferriss s.n. in 1908,* cited in Kearney and Peebles (1960), location of specimen unknown.

Habitat and distribution. Rosa stellata subsp. *abyssa* is known from Mesa Eremita on the South Rim of the Grand Canyon, and from Twin Point, Dutton Point, between Hades Knoll and SB Point, and W rim of Kanab Canyon, N of the Grand Canyon. All known populations are on or near canyon rims or the tops of cliffs at the edges of mesas or plateaus, suggesting the subspecific epithet.

The Twin Point population is the largest known, consisting of 1000–2000 stems in 10,000 m^2 when studied in 1979 (Phillips and Phillips 1982). They were growing in thin sandy-gravelly soils with limestone pebbles, overlying the Kaibab limestone bedrock, in an open Great Basin conifer woodland (Brown and Lowe 1980) with *Juniperus osteosperma* (Torrey) Little, *Purshia stansburiana* (Torrey) J. Henrickson, *Ephedra nevadensis* Watson, and *Yucca baccata* Torrey. Although the edge of the population was abrupt, there was no apparent corresponding change in habitat. No additional populations were found on Twin Point or on nearby Kelley Point in similar areas.

In contrast, three small localities in a 3 km long area along the W rim of Kanab Canyon, approximately 120 km E of Twin Point, are confined to areas that are geologically distinctive, shallow depressions at the upper ends of collapsed breccia pipes. A thin deposit of the Timpoweap Member of the Moenkopi Formation in the depressions represents ancient stream deposition at the contact with the upper member of the Kaibab Formation (G. Billingsley, USGS, Flagstaff, AZ, personal communication). The rarity of the taxon at Kanab Canyon is apparently due to its restriction to this specific, limited substrate. Associated species within the Great Basin Desertscrub (Brown 1982) include *Purshia stansburiana, Berberis fremontii* Torrey, *Fallugia paradoxa* (D. Don) Endlicher, and *Yucca baccata.* BLM personnel in 1986 reported the loss of all plants in the two southern localities, T38N R3W sect. 29 and 30, without stating the cause, while the larger locality about 4 km N in sect. 8 remained vigorous. Uranium mining, often focusing on breccia pipes near canyon rims, was identified in the status report by Phillips and Phillips (1982) as a major potential threat. Although the Kaibab North Mine has subsequently been developed 1.5 km south of the sect. 8 site, no plants are known to have been lost due to uranium mining or associated activities.

Relationships. In his systematic treatment of *Rosa* subgenus *Hesperhodos* Cockerell ex Rehder, Lewis (1965) recognized two subspecies of *R. stellata*: *R. s.* subsp. *stellata* of the Organ and San Andres mts., Doña Ana County, New Mexico; and *R. s.* subsp. *mirifica* (Greene) W. H. Lewis of the Sacramento and White mts., Otero county, New Mexico, Guadalupe Mts., Culberson County, Texas, and Eagle Mts., Hudspeth County, Texas. The most apparent morphological difference between *R. s.* subsp. *abyssa* and all other taxa of *R. stellata* is the consistent presence of very robust, dense prickles on the hypanthium of the Arizona specimens. Although the hypanthium prickles are somewhat variable in the specimens from New Mexico and Texas, they are not as dense as in Arizona specimens.

The Arizona taxon appears to be most closely related to *R. s.* subsp. *stellata* based on the presence of stellately-arranged stiff hairs and gland-tipped projections on the young stems of most specimens of both taxa. The "stellate hairs" on the stems of *R. s.* subsp. *stellata*

TABLE 1. COMPARISON OF STEM AND HYPANTHIUM INDUMENTUM FOR THE THREE SUBSPECIES OF *ROSA STELLATA*.

	R. s. ssp. *abyssa*	*R. s.* ssp. *stellata*	*R. s.* ssp. *mirifica*
Stems			
Stalked glands with basal hairs	Present or absent	Present	Rare
Stellate hairs without stalked glands	Absent	Abundant	Absent
Prickles without apical glands	Absent	Rare	Abundant
Prickles with apical glands	Rare	Rare	Abundant
Hypanthium prickles			
Avg. no./5 mm	9.4	3.9	4.6
Range	4–17	2–5	3–8
Avg. length (mm)	4.0	1.6	2.8
Range (mm)	2.0–6.0	1.0–2.5	1.7–5.0

appear to have originated as a ring of minute, stiff, white hairs around the base of a gland-tipped projection. After many of the projections were reduced and lost, the stiff basal hairs remained on the stem in a stellate pattern. In *R. s.* subsp. *abyssa* the projections have not been lost or reduced, and the stiff, white hairs, when present, form a ring around the base of a prominent stipitate gland. The projections range from abundant soft-stalked glands to stiff gland-tipped prickles, which are usually rare.

Stellately-arranged pubescence and soft stipitate glands are both generally absent in *R. s.* subsp. *mirifica,* which has abundant small, stiff internodal bristles and prickles, with or without terminal glands. Comparisons of stem indumentum and hypanthium prickle characteristics for three subspecies of *R. stellata* are shown in Table 1.

Stipitate glands are a consistently prominent and abundant feature on Arizona specimens from all localities. Plants from Kanab Creek and Mesa Eremita populations generally have fewer stiff hairs at the base of the gland-tipped projections, and somewhat shorter, less robust prickles on the hypanthia than plants from the Shivwits Plateau. There are usually a few hairs on some stipitate glands on the upper parts of fertile stems, however, and the gland-tipped projections themselves seem to be otherwise identical to those of the Shivwits Plateau plants. As some of the latter also lack pubescence on the stipitate glands, and since characteristics of the pubescence are so variable in New Mexico and Texas populations and taxa, I recognize but a single taxon in northwestern Arizona.

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THE IMPACT OF EUROPEAN SETTLEMENT ON BLUE OAK (*QUERCUS DOUGLASII*) REGENERATION AND RECRUITMENT IN THE TEHACHAPI MOUNTAINS, CALIFORNIA

SCOTT A. MENSING
Department of Geography, University of California,
Berkeley, CA 94720

ABSTRACT

Absence of blue oak (*Quercus douglasii* Hook. & Arn.) saplings and seedlings has been noted throughout much of the species range. Our ability to assess whether the present poor regeneration is a natural pattern or a response to human induced environmental change is limited by lack of data on the history of blue oak recruitment. In this study, stand age analysis is used to reconstruct former patterns of blue oak regeneration and recruitment in three blue oak woodlands on the Tejon Ranch, Kern County, California. Analysis of 279 cross-sections showed that 56% of all stems sampled were recruited in 1856. Prior to 1856, recruitment was relatively continuous. Only 3% of all stems stems aged date to the period from 1864 to the present. Analysis of fire scars found an increase in fire frequency during the 1850's and 60's, followed by a distinct decrease in fires for a 70 year period. Differing patterns of regeneration were found to coincide with changes in local land use. During Indian occupation of the area, the woodland appears to have been less dense, with a slow but steady process of replacement, adequate to maintain the woodland. Changes in fire frequency and browsing patterns, associated with European settlement in the mid-19th century, resulted in unusually high rates of regeneration and recruitment. Since the 1860's, commercial livestock grazing, reduction of fire frequency, and an increase in density have resulted in virtually complete suppression of regeneration.

Recent assessments of blue oak (*Quercus douglasii* Hook. & Arn.) regeneration in California have found that recruitment of saplings to trees appears insufficient at the present time to replace many existing stands (Muick and Bartolome 1987; Bolsinger 1988). Stand age analyses have identified several periods of successful regeneration and recruitment since the mid-1800's. Evidence of blue oak recruitment during the period from 1860–1900 has been found in Monterey County (White 1966), Sequoia National Park (Vankat and Major 1978), Yuba County and Tulare County (McClaran 1986). McClaran (1986) also found a period of successful regeneration on grazed sites in Tulare county between 1890–1940. At each site, a lack of regeneration has been noticed since the early 1900's, except the grazed sites in Tulare county where recruitment declined after 1940.

White (1966) noted that European settlement during the late 1800's produced a period of dynamic land use, but felt that the changes

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were too varied to identify which factors may have affected regeneration. Vankat and Major (1978) suggested that successful regeneration occurred at a time when the Indian presence was diminishing and livestock grazing was increasing. They hypothesized that successful regeneration was initiated by livestock grazing, which both removed competing herbaceous species and decreased fuel levels, resulting in less intense fires. McClaran (1986) found no clear relationship between livestock grazing and regeneration; however, fire had a positive effect, with 70–85% of the trees becoming established within one year after a fire.

Because of insufficient data on the long term regeneration history of blue oak, it is unclear whether the present pattern represents a natural cycle, or a response to environmental change associated with European settlement (Bartolome et al. 1987). The record of tree establishment prior to 1860 is poorly documented, because of both natural tree mortality and because study sites have been located in areas of extensive settlement where clearing has occurred. Recognition of natural patterns of regeneration and recruitment are also complicated by the ability of blue oak to resprout following cutting. In this study an area of woodland is examined that has been undisturbed by cutting throughout the period of European settlement. The presence of many very large trees at the site also provided the potential for obtaining a long temporal record. Evidence is presented that suggests regeneration was relatively continuous prior to European settlement in the mid-1800's, but has been generally absent since the late part of that century. Local land use and fire history are examined to explain the effect of land use on blue oak regeneration and recruitment.

STUDY SITE AND METHODS

Location and physical description. Tejon Ranch is located east of Lebec in the Tehachapi Mountains in southern Kern County (Fig. 1). The ranch has been held as a single property since the 1860's, and includes some of the largest undisturbed oak woodlands in the state. The study area is at the southern edge of the range of blue oak. Three sites were chosen which had been selectively cut for firewood between 1982 and 1987. Tree cover was pure blue oak with an herbaceous understory. The sites were between 975–1150 m elevation, on Anaverde gravelly loam and Walong sandy loam (USDA Soil Conservation Service 1981). Slope averaged from 20–25% with aspects of 45, 210, and 320 degrees. Sites each covered approximately 2.5 hectares, with a tree density of 224, 173, and 163 trees per hectare before cutting.

Collection of cross-sections. Cross-sections were collected from a total of 279 stumps. To test whether a subsample of stumps rep-

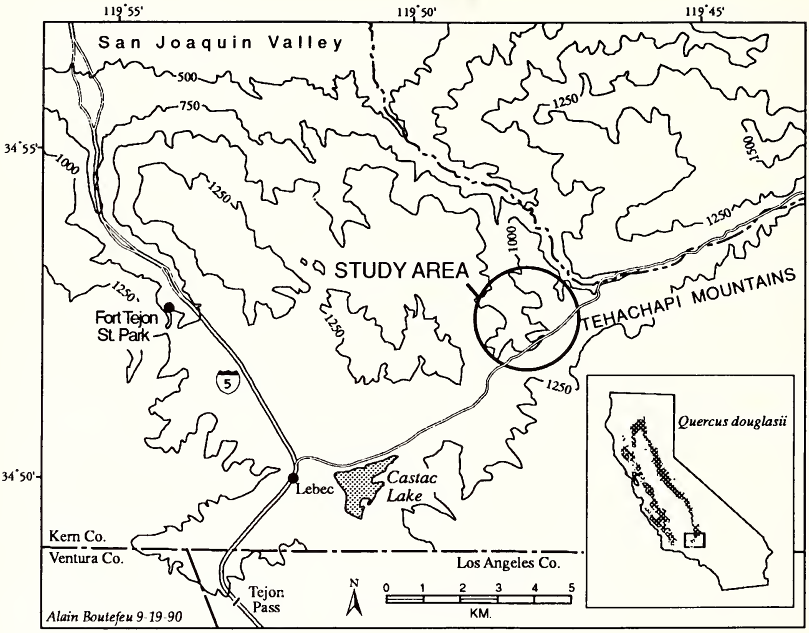

FIG. 1. Study area at the Tejon Ranch, near Lebec, Kern County, California. Contours are in meters. Inset map of the distribution of *Quercus douglasii* is after Griffin and Critchfield (1972).

resented the stand as a whole, sites were randomly sampled using the point-quarter method (Cottam and Curtis 1956), including standing and cut trees. Tree basal diameter was measured, and four broad size classes were identified: <20 cm; 20–<45 cm; 45–<70 cm; and 70 cm and over. The percentage frequency distribution for each size class in the stand was determined, and compared with the available stumps on each site. Adequate numbers of stumps were available in all size classes to cut one hundred cross-sections from each stand; however, only stumps that appeared solid to the center were collected. On site "B" only 90 cross-sections were collected because heart-rot in the largest size class (70 cm and over) reduced the number of usable stumps. For the same reason, only 89 cross-sections were collected from site "C". On site "A", there were not enough stumps available in the smallest size class (<20 cm) because the woodcutters had avoided smaller trees. This shortage was supplemented by collecting cores from ten randomly selected trees.

Stumps were cut at or below ground level in order to obtain the oldest possible age count, since it has been shown that samples taken from higher up the stem give younger dates (McClaran 1986; Harvey

1989). To achieve this, the surrounding soil was excavated to ground level on the downhill side before cutting.

Tree ring analysis. Cross-sections and cores were prepared and analyzed at the University of California, Berkeley, Department of Forestry laboratory. Samples were planed, sanded with 400 grit, wetted with water and counted under a 10–30× binocular dissecting microscope. Marker rings of narrow and wide growth patterns were identified as a cross-check for counting annual rings (Fritts 1976). Tree rings were counted along two separate axes. In a few cases where ring growth was wide and marker rings were easily identified, a single count was assumed to be sufficient. In cases where two counts produced different ages, these were averaged to provide a single date for analysis. The greatest error rate for differing counts was 2 years per 100 years. Where multiple centers were present in an individual cross-section, the number of centers was counted.

Fire history. Fire scars were identified and ages determined. Scars were cross-dated by comparing clearly identifiable ring sequences between cross-sections as suggested by McBride (1983). Following McBride and Jacobs (1980), mean fire interval (Romme 1980) was calculated by site, for three different land use periods. The earliest period (pre-1842), predates European settlement and reflects aboriginal burning. Period two (1843–1865) represents a settlement transition period during which European activity dramatically increased in the area, but the Mexican land grants were not occupied and utilized by the owners. The final period, (1866 to the present) is characterized by a commercial interest in the property, continuous livestock grazing, and fire control efforts.

RESULTS

Tree recruitment. The ability of blue oak to sprout after the stem has died (Griffin 1971) makes it impossible to determine the original

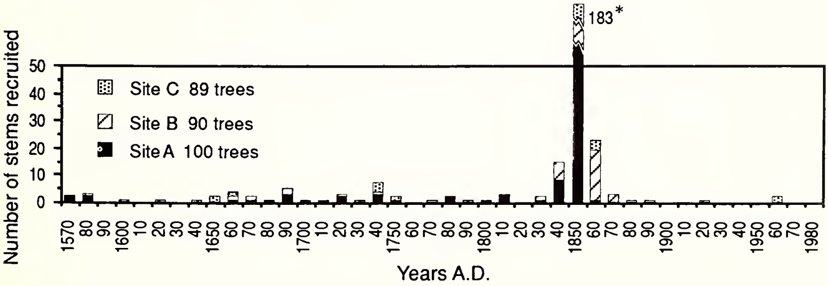

FIG. 2. Number of blue oaks recruited per decade for three sites on Tejon Ranch, Kern County, California. *Of the 183 trees recruited in the 1850's, 65 are from site "A", 50 from site "B", and 68 from site "C". More specifically, 156 trees date to the year 1856, including 61 from site "A", 44 from site "B", and 51 from site "C".

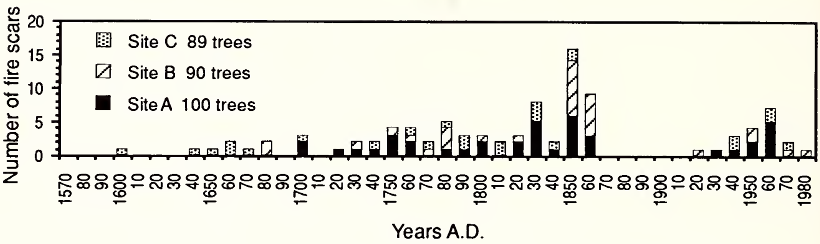

FIG. 3. Number of fire scars on blue oaks, per decade, for three sites on Tejon Ranch, Kern County, California.

date of acorn germination and seedling establishment. Ages assigned to trees in this study represent stem age and do not necessarily reflect the actual date of seedling establishment. As will be explained in the discussion, many of the existing trees probably represent sprouts from an existing root structure following the death of the former stem.

The pattern of tree recruitment is fairly continuous from 1570 to 1850, punctuated by a dramatic regeneration peak in the 1850's, and followed by an almost complete absence of recruitment since the 1860's (Fig. 2). Fifty-six percent (156) of the stems aged date to 1856. Only three percent (9) of the stems date to the period from 1864 to the present, and several of these were shrubby saplings less than three feet tall. Though the woodland included many small trees with basal diameters less than 20 cm, most of these were found to be over 100 years old. Five trees were over 400 years in age, with the oldest being 412 years.

Fire history analysis. Fire scars were found on sixty-nine trees. Sixteen trees had multiple scars, with one having seven. A chronolog-

TABLE 1. MEAN FIRE-FREE INTERVAL FOR THREE DIFFERENT LAND USE PERIODS AT THREE SITES ON THE TEJON RANCH, KERN COUNTY, CALIFORNIA, BASED ON FIRE SCARS IN BLUE OAKS. Land use periods are described as follows: 1680–1842 = California Indian period, 1843–1865 = Settlement transition period with a transient population at Fort Tejon, 1866–1987 = Tejon Ranch period with commercial livestock grazing and controlled access to the land.

Period	Site "A"	Site "B" Interval in years	Site "C"
1680 A.D.–1842 A.D.	9.6	13.6	12.5
1843 A.D.–1865 A.D.	3.3	3.8	5.8
1866 A.D.–1987 A.D.	13.5	20.3	18.0

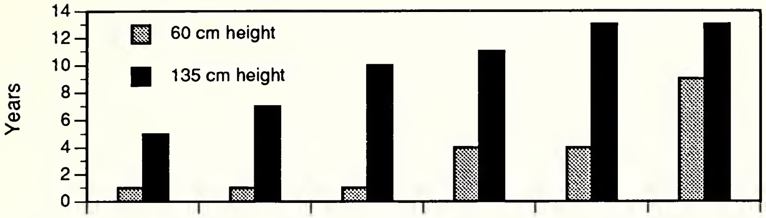

FIG. 4. Vertical growth rate for six blue oaks established in 1856, from Tejon Ranch, Kern County, California. Tree age was measured at the 60 and 135 cm heights.

ical graph of fire scars shows that fires occurred on a regular basis prior to the 1860's, with periodic peaks of increased frequency and a mean fire interval of approximately ten years or less, accounting for the probable absence of some fires from the scar record (Fig. 3). Fires were most common during the 1850's. After 1864, there was a complete absence of fire scars until the late 1920's, a span of more than 60 years. Mean fire interval during the period from 1843–1865 averaged four to five years (Table 1). Fires occurred every year from 1853 through 1856.

Vertical growth rates. In order to obtain an estimate of the vertical growth rates of trees established in 1856, several standing trees were cored at the base to determine their age. Six of these trees had become established in 1856. These six trees were then cored again at the 60 and 135 cm heights (McClaran 1986). The latter height is considered the browseline for cattle and deer, and is considered a critical point for sapling survival. All of the trees cored reached 135 cm within thirteen years (Fig. 4) with one growing to this height in only five years, a fairly rapid rate for blue oak.

Multiple centers. One third of all trees sampled had multiple centers. In the 1856 cohort, almost 40% had multiple centers. In all cases, each stem produced the same ring count, providing a single age for each tree.

DISCUSSION

Land use changes and oak regeneration. The results seem to suggest three distinct patterns of regeneration and recruitment that coincide with different periods of local land use. During the period of California Indian occupation, prior to European settlement, recruitment of new trees into the canopy was low but relatively continuous. The current mortality rate for California hardwoods has been estimated to be 0.3% (Bolsinger 1988). At this rate, recruitment of only five trees per hectare per decade would be sufficient to maintain these woodlands. Given the inevitable gaps in the record from mortality and heart rot, the data suggest that during the Indian period there was no regeneration and recruitment problem. Furthermore, recruitment appears to have been a continual process, rather than an episodic event.

During the mid 1800's, regeneration and recruitment were unusually successful, with a dramatic regeneration peak in 1856. This coincides with the initial phase of European settlement in the region. Four Mexican land grants were established in the 1840's; however, active European settlement did not begin until 1853 with the formation of Sebastian Indian Reservation, followed by the construction of Fort Tejon in 1854 (Giffen 1942; Crowe 1957). Fort Tejon housed up to 200 dragoons at any one time, and had a small population of merchants in the vicinity. The increase in human activity coincided with a dry period, as shown by narrow growth ring patterns and Sacramento precipitation records (McAdie 1903; Martin 1930). The increase in fire frequency during the 1850's–60's, with fires every year from 1853–56, is probably a result of increased ignitions by a transient population during a period of dry conditions.

Successful regeneration in the 1850's and 1860's is most likely the result of sprout growth rather than seedling establishment from acorns. In dry years, blue oak acorn germination is generally poor and few seedlings appear (Griffin 1971, 1980; McCreary 1989); however, under favorable conditions blue oak acorns readily germinate and establish seedlings. Subsequent drought, fire or predation often cause seedlings to die back, but they are capable of resprouting in the following growing season (Griffin 1971). The dry conditions present during this time period suggest that the regeneration peak was not due to the abundant establishment of seedlings, but more likely resprouting of seedlings and saplings burned by frequent fires.

Although mature blue oaks are fairly fire resistant, fire removes the above ground stem and foliage of saplings and seedlings (Lawrence 1966). Based on the relatively continuous recruitment of new trees into the woodland during the Indian period, it seems likely that seedlings, saplings, and small trees were present, and possibly abundant, when European settlement began. A series of fires would have removed the above ground portions of these small plants, initiating sprouting from the base. McClaran (1986) demonstrated that 70–85% of the blue oak in a stand may originate as sprouts within one year of a fire. By this process, fire temporally concentrates postfire sprouts (McClaran and Bartolome 1989). The 1856 regeneration peak provides clear evidence of this process.

Additional evidence for postfire sprouting is the high percentage of forked, or multiple-centered trees. In a previously cut blue oak stand, White (1966) found that 54% of the trees were forked below breast height, and suggested a high percentage of forking would be expected in a stand of sprouts. Almost 40% of the trees in the 1856 cohort were multiple-centered. Cutting as the mechanism stimulating sprouting is unlikely in this case since the site is remote, fuelwood is common, and there is no historical record of woodcutting in the area.

Successful recruitment. Successful sprouting does not necessarily result in recruitment of saplings and trees into the stand. Deer and livestock are capable of suppressing vertical growth for long periods by browsing young shoots and trampling seedlings. Repeated deer browsing has been shown to maintain blue oaks as small shrubs for as long as thirty years (Griffin oral communication). In the 1856 regeneration cohort, the six trees sampled for vertical growth rate all reached the browseline within thirteen years, with one surpassing this point in only five years. Clearly, vertical shoot growth does not appear to have been suppressed by browsing.

Historical evidence suggests that deer populations and browsing pressure were probably reduced during Fort Tejon's occupational period, from 1854–1864. The soldiers were known to have held hunting parties on a regular basis (Giffen 1942). The increase in hunting may have been enough to reduce the local deer population through mortality and migration.

McClaran and Bartolome (1989) have suggested that even under heavier livestock browsing pressure, plants that surpass the browseline (135 cm) in approximately 10–13 years will be recruited into the canopy. Postfire sprouts have been shown to grow almost twice as fast as other trees (McClaran 1986). A decade of reduced browsing pressure and rapid vertical growth were probably key factors contributing to the high rate of survival of the 1856 cohort.

A new period of land use began in the 1860's when General Edward Beale purchased all four Mexican land grants, consolidating the property under the control of one individual. Beale introduced commercial grazing in 1864, moving 14,000 head of sheep onto the property (Giffen 1942; Crowe 1957). Sheep were exchanged for cattle in the 1880's, and commercial grazing has continued to the present. Following the introduction of livestock, there was a sixty year period with a very low fire frequency. This decrease in fires was probably due to a reduction of ground fuels consumed by grazing livestock, combined with new efforts to control ignitions. While on a collecting trip, Grinnell (1905) noted, ". . . the whole of the country is fenced, and hunters and campers kept out for fear of starting fires or disturbing the stock." Cessation of fire further contributed to survival of stems recruited during the 1850's–60's, and resulted in an increase in tree density and canopy cover, similar to changes documented for oak woodlands on the prairie-forest border of the American Midwest after European settlers suppressed Indian fires (Cottam 1949). By 1930 when fire frequency increased, the trees were large enough to survive most ground fires.

Current lack of regeneration. Since the 1860's, almost no new trees have been recruited. A number of potential factors, or most likely, a combination of factors may be responsible for this. The introduction of commercial livestock grazing in the 1860's has probably had a negative effect on seedling establishment and sapling growth. Although McClaran (1986) did not find a clear relationship between presence of livestock and successful blue oak regeneration, in other studies cattle have been clearly identified with acorn and seedling mortality (Borchert et al. 1989; Rossi 1979), and reductions in recruitment (Harvey 1989).

The replacement of a perennial grass understory with introduced annual grasses may increase competition with oak seedlings for soil moisture, potentially reducing the available seedling bank (Gordon et al. 1989).

Intraspecific competition may contribute to lack of recruitment of saplings to trees. The flush of regeneration in the mid-19th century would have created a denser woodland than was present under Indian occupation, with an increase in canopy cover. Muick and Bartolome (1987) found that although 60% of blue oak seedlings grew under the canopy, 84% of all saplings were on the canopy edge or in the open. A reduction in openings may contribute to lack of sapling growth by decreasing suitable sites.

In summary, land use has changed significantly during the last two centuries; most important here are changes in fire frequency and the introduction of livestock and competitive annuals. This study has shown that the present stand structure is different from what existed during the pre-European period. The existing woodland is therefore not the result of an ongoing process of natural regeneration and recruitment, but of changes in land use practices, associated with European settlement. Vankat and Major (1978) reported a similar situation in Sequoia National Park, where an increase in blue oak density followed the demise of the Indians and the beginning of livestock grazing in the 1860's and 1870's. In this respect, lack of regeneration is perhaps a more complicated consequence of European settlement than has generally been recognized. It is not simply that grazing, changes in fire frequency, and competition from annuals have prevented regeneration, but furthermore that the density of stands themselves is an artifact of European impacts.

Acknowledgments

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SURVIVAL OF *QUERCUS DOUGLASII* (FAGACEAE) SEEDLINGS UNDER THE INFLUENCE OF FIRE AND GRAZING

Barbara H. Allen-Diaz and James W. Bartolome
Department of Forestry and Resource Management,
University of California, Berkeley, CA 94720

Abstract

Recent burning and sheep grazing did not affect recruitment, survival, or growth of seedling *Quercus douglasii* Hooker & Arnott over four years at the Hopland Field Station, California. Recruitment did vary considerably among years. Once a seedling's shoot emerged, the probability of surviving to the next year remained constant, at about 0.5, unaffected by year, seedling size or age, past fire, or present sheep grazing. Established seedlings did not increase in size, and showed no indication of growing out of the seedling class into the sapling class. Successful natural regeneration appears to depend on factors controlling growth, not on factors associated with mortality during the seedling stage.

In many areas of California, *Quercus douglasii* (blue oak) regenerates poorly (Muick and Bartolome 1987). The age-structure of stands reveals abundant recruitment in the latter 19th and early 20th centuries (Griffin 1977) but little since. Often stands of a few large trees (diameter at breast height (dbh) >40 cm), many smaller trees (dbh >10 cm but <40 cm), and no saplings (dbh <10 cm), contain seedlings of less than 10 cm height (Muick and Bartolome 1987). A bottleneck in recruitment appears at the sapling stage because seedlings either do not establish or survive into the sapling class.

The causes for failure to recruit have been the subject of considerable speculation and include most environmental and managerial influences (Bartolome et al. 1987). Two factors of considerable importance, because they changed dramatically at the same time of the last period of significant blue oak recruitment, are livestock grazing and fire (McClaran and Bartolome 1989).

Experimental studies of the factors affecting seedling recruitment have used planted acorns (Griffin 1971; Adams et al. 1987; Borchert et al. 1989; Gordon et al. 1989; Matsuda et al. 1989). No study has combined naturally regenerating seedlings with an experimental treatment, although Swiecki et al. 1990 recently reported observations of marked naturally regenerating blue oaks at several northern California sites. Our experiment examines the effects of prescribed fire and sheep grazing on naturally regenerating blue oak seedlings.

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METHODS

The study was conducted at the University of California's Hopland Field Station, located in Mendocino County, California. The 2168 ha station supports vegetation typical of the inner Coast Ranges: a mixture of open annual grasslands, oak woodlands of varying canopy coverage, and shrublands (Murphy and Heady 1983). Annual precipitation, concentrated in winter, averages about 95 cm, but during the four years of this study ranged from 60 to 72 cm. The two study pastures, each approximately 30 ha, have been grazed by sheep since before the establishment of the Station in 1951.

Vegetation in the experimental pastures is 76 percent blue oak woodland between 10 and 75 percent tree canopy cover and 18 percent open grassland with <10 percent overstory cover. The remaining 6 percent consists of dense oak stands with >75 percent canopy cover, usually with interior liveoaks (*Quercus wislizenii* A. de Candolle). The herbaceous understory is dominated by introduced annual grasses averaging 65 percent cover and 1500 kg ha^{-1} annual production (Bartolome 1986).

In fall 1986, three 0.5 ha experimental blocks were selected, having an overstory of blue oak (>10 cm dbh) and local canopy coverage of 50 percent. Each block had four treatments randomly applied to experimental units: 1) burning and sheep grazing, 2) burning and no sheep grazing, 3) no burning and sheep grazing, and 4) no burning and no sheep grazing.

Sheep, generally dry ewes, grazed the two study pastures each year from 15 May until 15 October, the dormant season in the annual grassland. Stocking rates were adjusted to produce residue levels in October close to the 600 kg ha^{-1} recommended for understory in mixed annual grassland and woodland (Clawson et al. 1982). On 15 October of each year the sheep were removed, to return 15 December. On 15 February animals were again removed until 15 May. Sheep grazed each pasture in the same seasons beginning in 1986. The grazing part of the experimental treatment compares sheep exclusion to the normal repeated seasonal grazing system in the pastures.

The prescribed burning was conducted in October 1986, after the first fall rains. Conditions were good for a fall burn, with temperatures at the time of the fire (1200 hr) 18°C and relative humidity at 40 percent. Wind speed was between 5 and 10 kph. Fuel consisted of a mix of dry grass, oak litter, and a small amount (50 kg ha^{-1}) of new grass totalling 750 kg ha^{-1}. Grass and oak litter at the soil surface were not completely consumed by the fire, but all herbaceous plants and all oak seedlings were top-killed.

We located two permanent 2 m × 10 m belt transects within each treatment combination (total $n = 24$) in which all blue oaks were

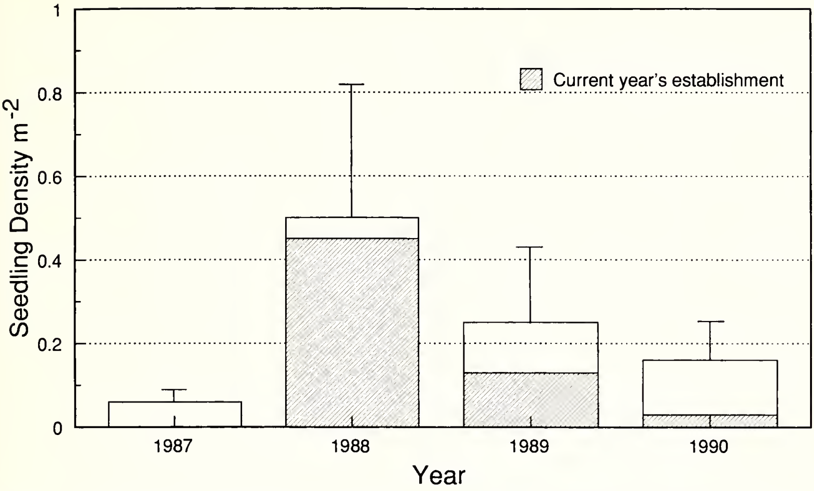

FIG. 1. Mean *Quercus douglasii* seedling densities by year on 24 2 × 10 m transects. Error bars represent 95% C.I. for means from t-values. Current year's establishment is not known for 1987.

counted yearly beginning in spring 1987. Beginning in May 1988 and continuing through May 1990 individuals were also permanently marked, mapped, and measured. Initially, only half of the individuals present were marked and mapped in 1988 on five of the transects; in 1989 and 1990 all individuals were marked and mapped. Measurements included number of seedlings, number of new seedlings, numbers and characteristics of seedlings surviving or dying. For each plant we measured height to top meristem, number of leaves, number of resprouts, and number of stems. Number of new seedlings was evaluated with analysis of variance using a randomized block split for time (Cook and Stubbendieck 1986). Other variables, which did not meet assumptions needed for analysis of variance, were analyzed by comparing means with t-tests or with simple regression.

RESULTS AND DISCUSSION

Average blue oak seedling density changed considerably among years on the experimental plots (Fig. 1). Seedling density was low in 1987, increased greatly in 1988, then declined towards 1987 levels in 1989 and 1990.

Dynamics within the seedling population are best examined by individually marking and following each new seedling as it appears and dies. Not surprisingly seedling appearance varied significantly by year from 1988 through 1990 (Table 1). Analysis of variance for

TABLE 1. RESULTS FOR ANALYSIS OF VARIANCE USING NEW BLUE OAK SEEDLINGS PER 40 M^2 AS DEPENDENT VARIABLE IN A RANDOMIZED BLOCK SPLIT FOR YEAR. Treatments: 1) grazed, burned; 2) ungrazed, burned; 3) grazed, unburned; and 4) ungrazed, unburned. Of the three possible F-ratios for this design, only the one marked * is significant for $F_{2,4}$ $P < 0.10$, others are not significant.

Source of variation	df	Sum of squares	MSE	F-ratio
Total	35	11,575	330.7	
Main plots	8	3292	411.5	
Blocks	2	638	319.0	
Year	2	1853	927.0	4.60*
Error	4	800.7	200.2	
Treatments	3	990.3	330.1	0.96
Year × treatments	6	1100.8	183.5	0.53
Subplots	18	6192	344.0	

new seedlings showed that only the year factor approached significance ($F = 4.60$, $P < 0.10$). However, even in the years of declining average density, 1989 and 1990 (Fig. 1), new seedlings continued to establish. Experimental treatments had no significant effect on number of new seedlings.

We were surprised to find that marked blue oak seedlings suffered similar mortality rates between years of about 50 percent (Table 2). Our results for mortality rates fall within the range of 5 to 65 percent per year found in the survey by Sweicki et al. (1990).

Plant size was unrelated to age (Table 3). Although the plants present in spring 1988, the oldest cohort followed, changed in size between years, averaging a taller stature in 1989, then shorter in 1990, this change is not related to age of the seedlings as the same pattern shows up each year for seedlings originating in the 1989 and 1990 cohorts. The 1990 season was simply poor for shoot growth in seedlings of all ages.

Mortality of seedlings was not significantly associated (t-test for mean differences between survivors and dead) with any measured characteristic of the plants the year prior to death, including age,

TABLE 2. TRANSITION PROBABILITIES AND SAMPLE SIZES FOR MARKED AND MAPPED *QUERCUS DOUGLASII* SEEDLINGS ON 24 2 × 20 M TRANSECTS. n = number of marked and mapped plants at beginning of period. P = proportion of plants alive and therefore surviving into the next sample period.

Years			
1988–1989		1989–1990	
n	P	n	P
110	0.51	56	0.57
		63	0.52

TABLE 3. NUMBER OF RESPROUTS, NUMBER OF LEAVES, AND HEIGHT OF *QUERCUS DOUGLASII* SEEDLINGS MEASURED EACH MAY. Numbers in parentheses are standard deviations. n is number of seedlings in each category. True seedling age is known for 1988 and 1989 cohorts, but not for the first year seedlings were marked, 1987 cohort.

Fall 1987 cohort

Year	Age (yr)	Resprouts (no.)	Leaves (no.)	Height (cm)	n
1988	1+	1.74 (0.96)	5.99 (2.78)	4.33 (1.74)	110
1989	2+	2.84 (1.10)	5.66 (2.24)	5.08 (1.70)	56
1990	3+	2.94 (1.03)	5.09 (1.91)	3.73 (1.16)	32

Fall 1988 cohort

Year	Age (yr)	Resprouts (no.)	Leaves (no.)	Height (cm)	n
1989	1	2.63 (0.91)	5.33 (2.71)	4.75 (1.93)	63
1990	2	2.76 (0.82)	4.51 (1.86)	3.65 (1.67)	33

Fall 1989 cohort

Year	Age (yr)	Resprouts (no.)	Leaves (no.)	Height (cm)	n
1990	1	2.54 (0.65)	4.73 (1.76)	2.95 (1.18)	11

number of resprouts, or size of the seedling (Table 4). This result differs from the survey by Sweicki et al. (1990) who found a greater number of resprouts significantly associated with a higher likelihood of subsequent mortality. Our results have considerable importance for understanding natural regeneration and are contrary to the undocumented assumptions in the literature that blue oak seedlings are either ephemeral (Biswell 1956) or suffer increasing mortality as they age (White 1966).

These results have several important implications for understanding regeneration of blue oak. Seedling appearance varies considerably among years. Conditions in the fall of 1987 through spring 1988 were exceptionally good for seedling establishment, whereas the following years were not as good. However, even in the relatively poor years of 1989 and 1990 some new seedlings appeared.

Although often mentioned in the literature as factors influencing regeneration (Bartolome et al. 1987), sheep grazing and burning had no significant effect on seedling recruitment. Seedling establishment and initial survival did not differ due to burning or to sheep grazing. This result shows that seedling establishment is at least potentially compatible with fire and grazing. What it does not show is whether this result will hold for other sites. It also does not shed light on the role of fire and sheep browsing on the transition from seedling to sapling. Sapling blue oaks are not present in the study area and no

TABLE 4. NUMBER OF RESPROUTS, NUMBER OF LEAVES, AND HEIGHT OF *QUERCUS DOUGLASII* SEEDLINGS BY COHORT IN MAY OF YEAR PRIOR TO OBSERVED DEATH. Numbers in parentheses are standard deviations. n is number of seedlings in each category. True seedling age is known for 1988 and 1989 cohorts, but not for the first year seedlings were marked, 1987 cohort.

Fall 1987 cohort

Year	Age (yr)	Resprouts (no.)	Leaves (no.)	Height (cm)	n
1988	1+	1.76 (1.00)	6.12 (3.43)	4.56 (2.03)	54
1989	2+	2.58 (0.74)	5.04 (2.67)	4.69 (2.03)	26

Fall 1988 cohort

Year	Age (yr)	Resprouts (no.)	Leaves (no.)	Height (cm)	n
1989	1	2.59 (0.96)	5.00 (1.80)	5.09 (2.24)	29

seedling exceeded 12 cm height, thus the observations about seedlings do not suggest how sapling recruitment would be permitted.

The seedlings were present under a fairly dense canopy (50 percent) of blue oak. Most seedlings are found under and near the canopy (Muick and Bartolome 1987). Removal of the canopy may be needed for successful release but does not ensure release. The canopy may suppress seedling growth initially, then other factors may take over like browsing by wild and domestic animals, insect predation, fire, and competition with annuals. The constant mortality rate over time observed in this study suggests that none of these factors were important for seedling survival. This suggestion was also made recently by Sweicki et al. (1990).

Blue oak appears to possess a suitable strategy for the first stages of regeneration. Seedlings are always present in the understory, although numbers fluctuate, and spatial distribution is irregular. These seedlings suffered a constant mortality rate over time, awaiting conditions for release into the sapling stage. At Hopland those conditions did not appear on the study area.

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INVASION OF FENNEL (*FOENICULUM VULGARE*) INTO SHRUB COMMUNITIES ON SANTA CRUZ ISLAND, CALIFORNIA

S. W. Beatty and D. L. Licari
Department of Geography, University of Colorado,
Boulder, CO 80309-0260 USA

Abstract

Fennel (*Foeniculum vulgare* Mill.) was introduced to Santa Cruz Island in the 1850's, and is now present in 7.8% of the island grassland community. This study's goal was to determine the success of fennel invasion into chaparral and coastal sage communities bounding grassland infested by fennel, and whether fennel occurrence varied with physiognomic or disturbance parameters. Vegetation was sampled using line transects placed perpendicular to grassland/shrubland boundaries, in sites stratified by shrub community type, topographic position, and aspect. Results indicated that coastal sage was more susceptible than chaparral to invasion by fennel. Fennel cover in chaparral correlated positively with fennel cover in adjacent grassland, although fennel did not occur in chaparral past an average of 2–3 m. Where vegetation boundaries were most distinct, fennel was negatively correlated with shrub cover. Disturbance related to fennel occurrence only in grassland areas, and did not correspond to fennel invasion in shrub communities. With recent removal of grazers from the island, fennel expansion and natural vegetation recovery from grazing may be integrally related.

Baker (1965) listed fourteen attributes of the "ideal weed," but noted that probably no living plant has them all. The ideal weed is a competitive, self compatible, fast growing perennial adapted to growth in a wide range of environmental conditions. It may reproduce vegetatively or sexually, producing a large number of seeds with a wide range of dispersal, have long temporal viability, and no particular germination requirements. Newsome and Noble (1986) described fennel (*Foeniculum vulgare* Mill.; Apiaceae) as a mat-forming, shallow rooted, multistemmed perennial with "large leaves," and the ability to germinate in any season. Fennel is an introduced naturalized species from Old World Europe (Fernald 1950), and frequently occurs in roadside and waste places. Fennel populations commonly exhibit stem die-off after seed-set, with regeneration in the following year.

Typical of California grasslands, Santa Cruz Island's native grassland of perennial bunch grasses has been largely replaced by European annual grasses and their weedy associates, among them fennel which was introduced in the 1850's (Greene 1886; Dunkle 1950). Also introduced in the 1850's were sheep and pigs which formed substantial feral populations, and were the likely avenue of acci-

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dental point introduction of fennel around Prisoner's Harbor. A cattle ranching operation also affected a part of the island, within which the largest fennel populations exist today. Cattle, and the few dirt roads traversing the ranching areas, were the most likely avenues of fennel dispersal over the past 100 years. However, with the exception of areas with cattle, fennel has not expanded very far along roads leading out of grasslands containing large fennel populations. The Nature Conservancy currently owns and manages the island, and is concerned about future fennel expansion.

In recent surveys Beatty (1991) found fennel occurring on about 6.4% of the island, in contrast to the 83% (calculated by author) occupied by grasslands and habitats which should be suitable sites for fennel colonization. With the removal of the feral sheep in 1985 and the cattle ranching operation in 1988, the continued expansion of fennel on Santa Cruz Island will largely depend on its ability to invade through natural dispersal mechanisms. Previous research has suggested that fennel may be successfully competing with established perennials in coastal sage communities, but not in the chaparral (Hobbs 1983; Beatty 1988). Fennel is found mainly in the eastern central parts of the island (Fig. 1), covering much of the central valley, slopes of the northern range (east of Prisoner's Harbor to Chinese Harbor), and on the north slope of the southern range to

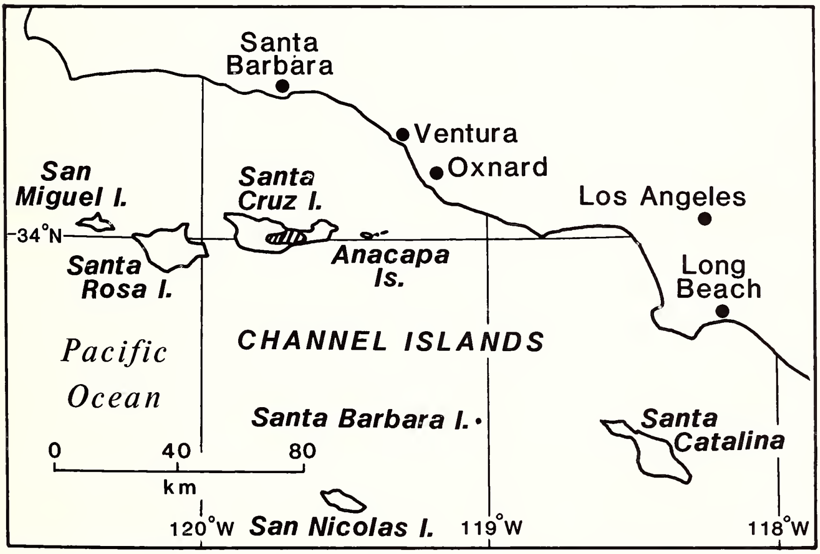


FIG. 1. Map showing location of Santa Cruz Island off the coast of southern California, USA. The shaded portion of the island indicates the area having the largest fennel populations, within which sample sites for the study were located.

the ridge. Throughout these areas, chaparral (mixed chamise, ceanothus, and manzanita) and coastal sage communities border grasslands such that fennel is located both upslope and downslope from shrub vegetation. The colonization potential of fennel could be related to whether dispersal was occurring upslope or downslope into the shrub communities because of variations in dispersal by overland flow, gravity, and/or wind associated with these topographic positions. Animal disturbances were of similar magnitude in all sites.

The hypotheses being tested in this study were: 1) chaparral and coastal shrub communities prevent fennel colonization and establishment, and 2) soil disturbance is associated with fennel colonization. If the first hypothesis is true, then such vegetation types may act as dispersal barriers for fennel. Potential for future fennel expansion could then be partially predicted in relation to vegetation patch sizes and distributions. Research on fennel seed dispersal dynamics and spatial components in dispersal is currently underway (Beatty 1991). The second hypothesis is relevant since feral pig disturbance is still widespread on the island, and such soil patches may serve to facilitate colonization, as has been found for other weedy aliens (Elton 1958; Platt 1975; Platt and Weis 1977; Grime 1979; Scorza 1983; Pickett and White 1985; Fox and Fox 1986).

Study Area

Santa Cruz Island is situated 39 km S of the Santa Barbara coastline and is the largest of the eight California Channel Islands (Fig. 1). The island has two east-west trending mountain ranges (ca. 410–595 m elevation) with an intervening central valley. The island has been under continuous occupation since the early 1850's, primarily for grazing of sheep and cattle. Considerable landscape and vegetation change has taken place since the introduction of sheep (Brumbaugh 1983), mainly due to overstocking and consequent overgrazing along with other human clearing and cultivation (Hobbs 1978, 1983; Van Vuren and Coblentz 1987). The extent of grazing is reflected to some degree by the abundance of exotic species present (Hochberg et al. 1980; Minnich 1980).

Plant communities of Santa Cruz Island, at the physiognomic and floristic levels, are generally comparable with the community equivalents found on the mainland (Minnich 1980; Brumbaugh 1983; Westman 1983). However a distinct characteristic of the floristics of the California island communities is that many species are not restricted to any particular community, and are wide ranging in habitat (Philbrick and Haller 1977; Hobbs 1978). Structurally, the island chaparral is different from that of the mainland. It tends to have a more open overstory (Hochberg 1980; Minnich 1980), and more varied growth form (Philbrick and Haller 1977; Minnich 1980).

These differences in species habitat and community structure may influence the ability of fennel to invade these vegetation types.

The most prominent communities are grassland, coastal sage, chaparral, oak woodland, riparian woodland, and closed-cone pine forest (Minnich 1980; Brumbaugh 1983). Coastal sage communities however, are often restricted to areas which had largely been free of feral sheep (Minnich 1980) owing to difficulty of access. Coastal sage dominants are *Artemisia californica* Less., *Eriogonum arborescens* E. Greene., *E. grande* (E. Greene) S. Stokes., *Rhus integrifolia* (Nutt.) Benth. & Hook., and *Lupinus* spp., but includes *Baccharis pilularis* DC. subsp. *consanguinea* (DC.) C. Wolf. *Opuntia littoralis* (Engelm.) Ckll., *O. oricola* Philbr. and hybrids of these two also occur (Philbrick and Haller 1977). *Quercus dumosa* Nutt., *Heteromeles arbutifolia* M. Roem. and *Rhus integrifolia* dominate the west end chaparral, with *Arctostaphylos subcordata* Eastw., *A. insularis* E. Greene., *A. tomentosa* (Pursh) Lindl. (manzanitas) dominating the upper areas of the southern ridge, grading into a more varied chaparral dominated by *Quercus dumosa* Nutt., *Q. macdonaldii* E. Greene., *Ceanothus megacarpus* Nutt. var. *insularis* Munz, *C. arboreus* E. Greene., *Cercocarpus betuloides* Nutt. ex Torrey & A. Gray, *Adenostoma fasciculatum* Hook. & Arn. (chamise), and *Rhus integrifolia* on the lower slopes of the central valley (Minnich 1980).

METHODS

Sample sites were chosen from aerial photographs and ground reconnaissance, using a stratified random design. Sites were stratified by shrub community (chaparral, coastal sage), aspect (north facing, south facing), and slope position of the vegetation boundary between grassland and shrub community (fennel upslope = upper sites, fennel downslope = lower sites). We had eight sample sites, with six replicate transects placed in each site.

Vegetation was sampled using 20 m line transects placed perpendicular to the grassland/shrub community boundary, and centered on the boundary (extending 10 m into each community). The location of the line transects were randomly determined on a 100 m baseline running parallel to the boundary. Each line transect was divided into 1 m contiguous samples, with the following observations made for each: 1) vegetative characteristics of percent intercept of previous year's fennel stems, the percent intercept of the current year's fennel growth (leaf fronds, flowering stems, and seedlings), the density of fennel canes intercepted (per meter and per plant on the transect), height of intercepted vegetation (fennel, woody vegetation), and the percent intercept of forb/herb, shrub (≤ 5 m), and "tree" (over 5 m) growth form categories; 2) physical characters of soil disturbance area and depth (including animal trails and pig

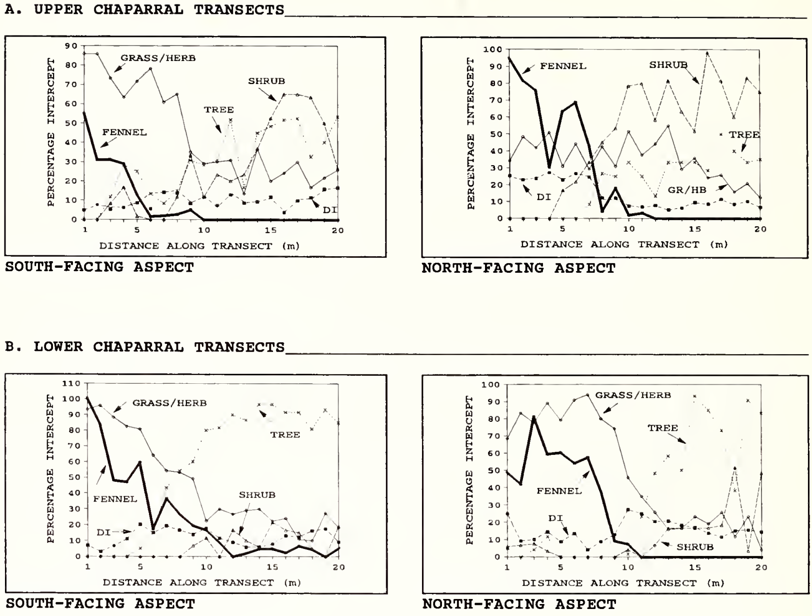


FIG. 2. Composite profile across (A) upper topographic positions (fennel/grassland upslope from shrub community) and (B) lower topographic positions (fennel/grassland downslope from shrub community) for boundaries between chaparral and grassland vegetation. Meter 1 was in grassland, meter 20 was in chaparral, and meter 10 was centered visually on the boundary. North-facing and south-facing aspects are shown for each topographic position, giving a total of 4 sites. Average (6 transects/site) percent intercept values per meter on 20 m line transects are given for fennel, grass/herb growth form, shrub growth form, and tree (>5 m tall) growth form. Disturbance index (DI) reflects the degree of bare and excavated soil per meter on the transects.

digging), litter depth, and rocks. Transect slope profiles were measured using an inclinometer and a telescopic surveying rod at subjectively identified breaks in slope.

Vegetation was sampled in growth form categories of forb/herb, shrub, and tree because characterization of community structure was considered an important factor in fennel colonization potential. Species composition among sites of like vegetation had previously been found to be similar in this study area (Sholes and Beatty 1987; Beatty 1988). Intercept values were averaged for corresponding meter length segments on the six transects, and a vegetation profile was constructed for each site (see also Hobbs 1986). The percent intercept of old-growth and new-growth fennel was combined to give a comprehensive view of fennel abundance and distribution. Separate analyses of fennel seedlings showed the same trends as those reported for total fennel abundance. Nomenclature of the plants follows Munz (1974).

A disturbance index (DI) was calculated as the square root of the product of the percent intercept of disturbance and the depth of disturbance in each meter segment. The purpose of the calculation was to provide an integrated index for the availability of open sites for fennel colonization, such that a site with very little bare ground or disturbance would have a very low DI, a site with much bare ground but no broken soil would be intermediate, and a site with disturbance would have a high DI. For the purposes of constructing the index, bare ground was designated to have a depth of 1 cm, so that only area cover contributed to the value for bare ground. The DI was averaged for each meter along the six transects in a site, and was included as part of the composite profiles.

RESULTS

Vegetation profiles. Chaparral-grassland boundaries were distinct, characterized by an abrupt increase in coverage of shrubs and "trees" (shrubs >5 m tall) and a decrease in grass-herb growth forms (Fig. 2). The latter persisted, however, throughout the entire length of the transects. In the upper transects where fennel could disperse into chaparral from upslope positions, fennel only penetrated an average of 1 m (Fig. 2A). Lower transects, where fennel dispersed from a downslope position into chaparral, showed fennel penetrating further into shrub canopies (Fig. 2B). There was a significant positive relationship between the average cover of fennel in the grassland portion of a transect, and the average cover of fennel established in the chaparral community (Fig. 3). Regressions of fennel cover on other vegetative cover for each chaparral site (Table 1), often showed

TABLE 1. LINEAR REGRESSION COEFFICIENTS (r^2) FOR ANALYSES PERFORMED ON AVERAGE FENNEL COVER m^{-1} TRANSECT (20 m LENGTH) (DEPENDENT VARIABLE) VERSUS AVERAGE COVER OF OTHER VEGETATION GROWTH FORM CATEGORIES (INDEPENDENT VARIABLE) IN THE FOUR CHAPARRAL SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, n = 20, df = 18. Significance is indicated by *P < 0.05, **P < 0.01. Trends are indicated as positive (+) or negative (−) even when relationships are not statistically significant.

Independent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Grass/herb cover	*0.48+	0.04+	**0.63+	**0.59+
Shrub cover	0.23−	**0.63−	0.25−	0.17−
Tree cover	0.42−	**0.63−	**0.56−	*0.48−
Shrub + tree cover	0.35−	**0.67−	*0.55−	*0.46−

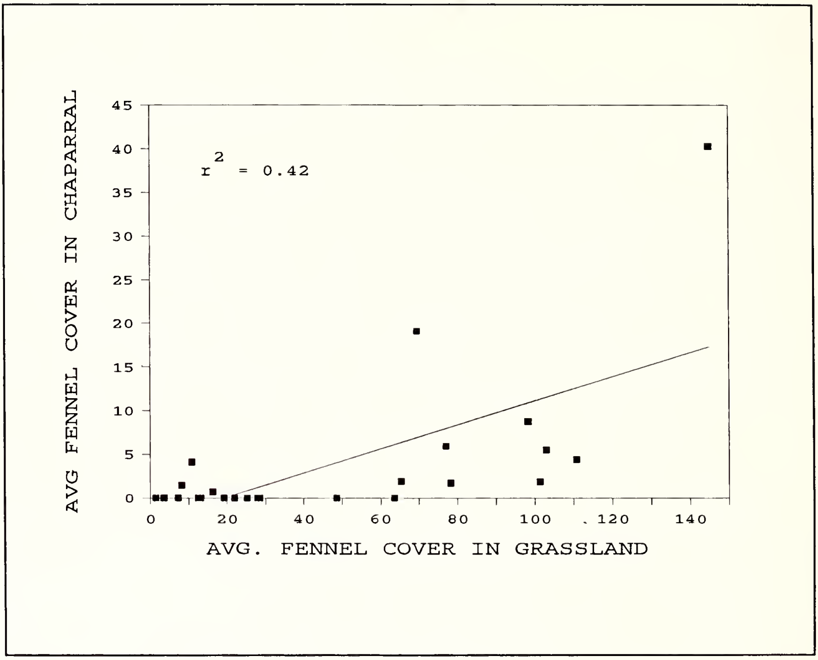


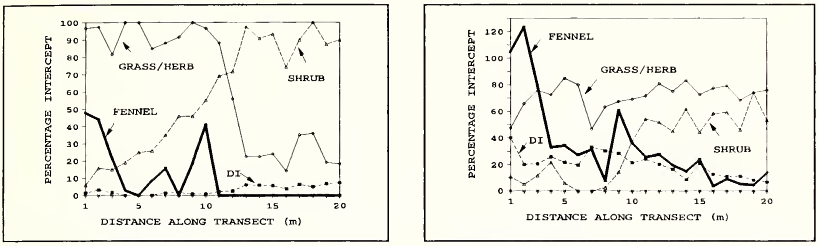
FIG. 3. Linear regression of average fennel cover/m on the grassland half of a transect versus average fennel cover/m on the chaparral half of a transect. Six transects per 4 chaparral sites = 24 replicates (df = 22); $r^2 = 0.42$; $P < 0.05$.

a significantly positive relationship between grass/herb and fennel cover, and a significantly negative relationship between shrub/tree and fennel cover. No aspect trends were apparent.

Grassland-coastal sage boundaries were less distinct (Fig. 4) than those for chaparral (Fig. 2). Shrub cover increased across the boundaries, but as is characteristic of coastal sage, the spacing between shrubs was greater than in chaparral communities. Grass-herb growth forms were present at all points along the transects; no tree growth forms existed. No differences were seen in fennel colonization ability between upper and lower sites; in all but one site fennel was present at all points along the transects. South-facing sites had more distinct shrub-grassland boundaries, and showed a sharper decline in fennel across the boundaries. In these sites, fennel cover was negatively correlated with shrub cover (Table 2).

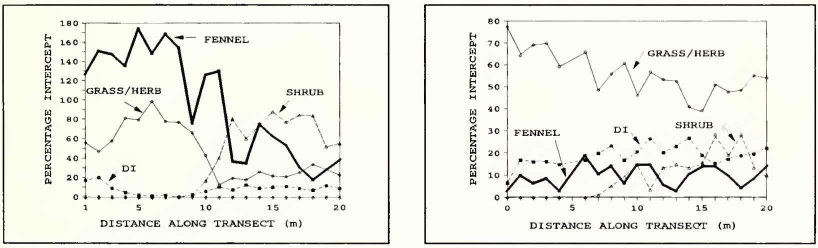
Disturbance effects. An examination of the profiles does not reveal a strong correspondence of fennel distribution and disturbance overall. In only one site (upper, north-facing chaparral) did fennel correlate significantly with disturbance index across the entire transect

A. UPPER COASTAL SAGE TRANSECTS



SOUTH-FACING ASPECT NORTH-FACING ASPECT

B. LOWER COASTAL SAGE TRANSECTS



SOUTH-FACING ASPECT NORTH-FACING ASPECT

FIG. 4. Composite profile across (A) upper topographic positions (fennel/grassland upslope from shrub community) and (B) lower topographic positions (fennel/grassland downslope from shrub community) for boundaries between coastal sage and grassland vegetation. Meter segment 1 was in grassland, meter segment 20 was in coastal sage shrubland, and meter 10 was centered visually on the boundary. North-facing and south-facing aspects are shown for each topographic position, giving a total of 4 sites. Average (6 transects/site) percent intercept values per meter on 20 m line transects are given for fennel, grass/herb growth form, and shrub growth form. Tree growth form was absent in coastal sage. Disturbance index (DI) reflects the degree of bare and excavated soil per meter on the transects.

length (Table 3). However, shrub/tree cover was negatively correlated with disturbance as well as with fennel in these sites. Other sites showed both positive and negative correlation trends between shrub/tree cover and disturbance (Table 3). In the two upper coastal sage sites, grass/herb cover was negatively related to disturbance, but both sites maintained substantial fennel populations (Fig. 4).

Disturbance may be associated with colonization by fennel in some grassland areas. The average cover of fennel was regressed against average disturbance index for grassland halves (10 m averages for six transects/site and four sites/community type; df = 22) and for shrubland halves of transects in chaparral and coastal sage communities. No significant correlations were found for coastal sage sites, either in grassland ($r^2 = 0.05$) or shrub ($r^2 = 0.00$) portions.

TABLE 2. LINEAR REGRESSION COEFFICIENTS (r^2) FOR ANALYSES PERFORMED ON AVERAGE FENNEL COVER m^{-1} TRANSECT (20 m LENGTH) (DEPENDENT VARIABLE) VERSUS AVERAGE COVER OF OTHER VEGETATION GROWTH FORM CATEGORIES (INDEPENDENT VARIABLE) IN THE FOUR COASTAL SAGE SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, n = 20, df = 18. Significance is indicated by *P < 0.05. Trends are indicated as positive (+) or negative (−) even when relationships are not statistically significant.

Independent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Grass/herb cover	0.39+	0.17−	0.29+	0.04−
Shrub cover	*0.48−	0.29−	*0.49−	0.00

However, fennel cover was significantly correlated with disturbance index in grassland portions of chaparral sites (Fig. 5), although not under chaparral shrub cover ($r^2 = 0.00$).

DISCUSSION AND CONCLUSIONS

Other studies have shown the success of alien species in displacing native species of communities they invade. A study of site susceptibility to invasion by *Melaleuca quinquenerva* in southern Florida (Meyers 1983) suggested that in this island-like peninsula the invader may displace the native vegetation in some sites. Weiss and Noble (1984) conducted a study on the invasion of *Chrysanthemoides monilifera* into coastal dune communities, and found that it was dis-

TABLE 3. LINEAR REGRESSION COEFFICIENTS (r^2) FOR SEPARATE ANALYSES PERFORMED ON AVERAGE COVER m^{-1} TRANSECT (20 m LENGTH) OF FENNEL AND OTHER GROWTH FORM CATEGORIES (DEPENDENT VARIABLES) VERSUS AVERAGE DISTURBANCE INDEX (DI = INDEPENDENT VARIABLE) IN THE EIGHT SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, n = 20, df = 18. Significance is indicated by *P < 0.05, **P < 0.01, and ***P < 0.005. Trends are indicated as positive (+) or negative (−) even when relationships are not statistically significant.

Dependent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Chaparral sites				
Fennel cover	0.16+	**0.64+	0.03+	0.23−
Shrub + tree cover	0.14+	***0.83−	0.00	0.02+
Grass/herb cover	0.14−	0.07+	0.03−	0.21−
Coastal sage sites				
Fennel cover	0.22−	0.23−	0.03−	0.04+
Shrub cover	**0.68+	*0.54−	0.06+	0.00
Grass/herb cover	***0.82−	*0.51−	0.32−	0.02−

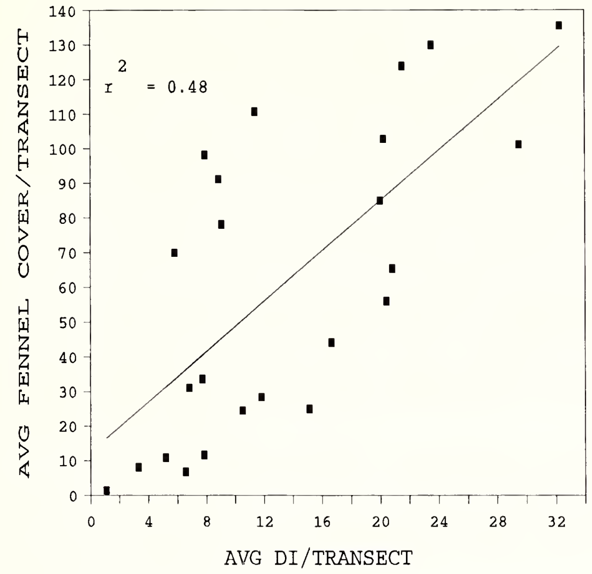


FIG. 5. Linear regression for average fennel cover against average disturbance index (DI), in grassland halves of the chaparral transects (4 sites, 6 replicate transects/site = 24 observations; df = 22). Averages are of values in the first 10 meter segments on each transect. The r^2 value is 0.48, with $P < 0.05$.

placing a structurally similar dominant native species *Acacia longifolia* Willd.. Fennel is not similar in structure (deep rooted herbaceous perennial), phenology (summer growth and flowering), or climatic origin to native species on Santa Cruz Island. It does not appear to be a true ruderal species, since it is abundant in areas with and without surface disturbance. The success of fennel in island communities may relate to its ability to exploit resources during the summer when most species are not active (see also Howard and Minnich 1989) in combination with both dispersal and maintenance by grazers. In a related study Beatty (1991) found species richness in fennel-infested grasslands to be lower, with mostly naturalized European annual grasses persisting in the densest fennel populations. Although there is no evidence that the presence of fennel has displaced native species to the point of local extinction, the potential for this will increase if fennel continues to expand in grassland and coastal sage communities.

Generally fennel is not successful in invading chaparral, but extends at least 10 m into coastal sage. Light limitations may be important in restricting fennel establishment. Lower chaparral boundaries had a higher proportion of trees and a lower proportion of shrubs than in the upper margins, resulting in a much more open understory. This may have contributed to the greater invasion of fennel into shrub canopies of lower topographic boundaries than upper boundaries, contrary to what we expected. A good predictor of fennel establishment under shrub canopies was the cover of fennel in the adjacent grassland communities (Fig. 3), although this relationship existed only for chaparral sites. In both chaparral and coastal sage sites fennel cover was often negatively correlated with shrub cover, but less notably for coastal sage which lacked tree (>5 m tall) growth forms. The south-facing coastal sage sites showed the greatest decline of fennel in the canopy (Fig. 4), and had significantly taller shrubs than north-facing coastal sage sites (0.84 m vs. 0.51 m; t-test, df = 22, $P < 0.001$).

There is no evidence that disturbance is associated with fennel invasion into shrub communities, but it may play a role in fennel occurrence in grassland. Although fennel was positively correlated with disturbance across the entire transect in one site (Table 3), the confounding effect of a negative correlation of shrub cover with disturbance and with fennel in that site (Table 1) appears to preclude the prospect that disturbance is associated with fennel establishment in the shrub community. Indeed, the coastal sage site with a significant increase in disturbance (upper, south-facing site) had a significant decrease in fennel cover under shrubs. Thus greater disturbance under shrubs did not correspond to greater fennel colonization there. Only in grassland portions of chaparral sites was fennel cover significantly related to disturbance (Fig. 5). Further work will be necessary before causal mechanisms can be firmly established.

Vegetation on Santa Cruz Island has been affected by the introduction of a variety of grazers, particularly seen in the reduction of the distribution of coastal sage (Brumbaugh 1980). Grazing by cattle has probably kept fennel populations at moderate levels in frequently grazed pasture, but grassland areas adjacent to such pastures show the greatest infestation by fennel (Beatty 1991). The removal of all grazers will encourage recovery in the natural vegetation (Hobbs 1983). Prior to this study sheep were removed from the island (1985), and we avoided areas of active cattle grazing in our sampling so that grazing was not a direct factor affecting establishment of fennel. Currently all grazers including cattle (1989) have been removed from the island, but feral pig populations are still present (although recently in decline). The future vegetation dynamics will not be shaped by grazing pressures or by as varied a soil disturbance regime as in the past (which included compaction and denudation). Since fennel successfully colonizes grassland and coastal sage communities but not chaparral, the future expansion of fennel may be affected by the distribution and degree of chaparral recovery. Conversely, the natural recovery of coastal sage and grassland communities may be adversely affected by continued occupation of these sites by fennel.

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INFLUENCE OF *AMMOPHILA ARENARIA* ON FOREDUNE PLANT MICRODISTRIBUTIONS AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

ROBERT S. BOYD
Department of Botany and Microbiology,
Alabama Agricultural Experiment Station,
Auburn University, AL 36849-5407

ABSTRACT

Association analysis was used to explore the microdistributions of foredune species. The introduced beachgrass, *Ammophila arenaria*, affected the microdistributions of some species. *Poa douglasii, Cakile maritima,* and *Abronia latifolia* were positively associated with *Elymus mollis.* These four were negatively associated with *Ammophila,* whereas *Mesembryanthemum chilense, Ambrosia chamissonis,* and *Camissonia cheiranthifolia* were not influenced by *Ammophila.* Positive associations between *Cakile/Agoseris apargioides* and *Mesembryanthemum/Ambrosia* were also detected. Examination of microdistributions relative to *Ammophila* patch borders indicated that only *Cakile* was significantly influenced by distant-dependent rodent foraging from *Ammophila* patches.

Marine beach communities have long attracted ecologists because of the pronounced zonation of plant species along the land/sea gradient. Many studies have examined the importance of physical factors (e.g., salt spray) which are primarily responsible for this zonation (Barbour 1978; Barbour and DeJong 1977; Doing 1985; Fink and Zedler 1990; Oosting 1945). Fewer attempts have been made to examine the microdistributional occurrences of beach plant species caused by other interactions which are not directly related to this gradient of physical factors (e.g., predation, allelopathy, or competition).

West Coast beach foredune vegetation from Canada through Central California is dominated by *Ammophila,* brought from Europe in the late 1800's to stabilize active sand dunes. It has replaced a native grass species (*Elymus mollis*) as the dominant member of the foredune community throughout the range of *Elymus.* A number of studies have pointed out some of the differences between the communities formed by these two grasses: *Ammophila* communities have fewer species of plants (Breckon and Barbour 1974) and burrowing insects (Slobodchikoff and Doyen 1977), a taller and more dense leaf canopy (Pavlik 1982), and the foredune itself is usually taller than in *Elymus* communities (Cooper 1967). The observed decrease in species richness of *Ammophila*-dominated areas has not

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been explained. It is intuitively obvious that the greater density of *Ammophila* culms and their taller canopy usurp aboveground space and therefore crowd out other species. Furthermore, the superior sand-stilling qualities of *Ammophila* may decrease the ability of other species to disperse (via the wind) into *Ammophila* areas. This latter factor may be partially offset by the protection from salt spray and sand-blast provided by a stand of *Ammophila,* as suggested by Breckon and Barbour (1974).

Herbivores also can have important effects on vegetation patterns. In cases where their activity varies spatially, as when foraging outward from a refuge from predation, they can cause zonation patterns by creating an herbivory gradient (Bartholemew 1970; Huntly 1987; Rood 1970). Pitts and Barbour (1979) showed that activities of the deer mouse, *Peromyscus maniculatus,* were concentrated in areas densely covered by *Ammophila.* They also showed that the rodents were omnivorous, consuming seeds and herbage of a number of plant species along with insects. Their observations suggest that higher levels of herbivore activity may be another factor which acts to decrease plant species richness in areas dominated by marram grass. In a recent paper, I showed that the microdistribution of *Cakile maritima* was strongly influenced by predation of seedlings and fruits (Boyd 1988). Because foraging by the main predator (*Peromyscus maniculatus*) was closely correlated with areas of high plant cover, borders of dense clumps of *Ammophila* had fewer *Cakile* plants. These results suggested that rodent predation might be a factor that contributes to decreasing species richness of plants and arthropods in areas dominated by *Ammophila.*

In this paper, data gathered during an earlier investigation of *Cakile* (Boyd 1988) were used to compare pairwise associations between foredune taxa, including the influence of *Ammophila* on these associations. Microdistributions of these taxa relative to *Ammophila* patches also were used as an indirect test of the significance of rodent herbivory in determining species richness in *Ammophila*-dominated areas.

METHODS

Study site. Point Reyes is located on the California coast 50 km north of San Francisco. The northern beach of Point Reyes National Seashore forms one of the longest unbroken stretches of beach in northern California, extending 18 km along the coast. As with most northern West Coast beaches (Barbour et al. 1976), the foredune is mostly dominated by *Ammophila arenaria.* One exception is a 1-km section of Kehoe Beach, where *Ammophila* patches are found interspersed with patches of the native grass, *Elymus mollis.* The *Ely-*

mus areas contain plant species which are relatively scarce in the *Ammophila* areas.

Microdistribution pattern. To document species microdistributions relative to the *Ammophila* patches, I selected a 0.5-km section of foredune which had both *Ammophila*-dominated and *Elymus*-dominated areas. *Ammophila* patches selected for sampling within this area were chosen so that transects would parallel the tideline. In this way, differences in abundance due to differences in species zonation would be avoided. At each of seven *Ammophila* patches, six contiguous 17 m-long transects were established running outward from patch borders into surrounding *Elymus* areas. For each transect, a 1-m^2 border plot was subjectively chosen. I chose border plots by determining where the amount of bare space approached that of non-*Ammophila* areas. Although the six transects at each *Ammophila* patch were contiguous, border plots may not have been contiguous, depending on the distribution of *Ammophila* within each transect.

Once the border plot was chosen, a 1-m^2 sampling frame was placed over the plot and the cover of each plant species present was recorded. Cover values were estimated for living plant parts only, except for the beachgrasses, where dead parts often formed a large fraction of the total cover. The area of bare sand present was calculated by subtracting total plant cover from 100%, except in rare cases where plant cover was high and significant canopy overlap occurred. In those cases, bare sand area was estimated directly in the field. From the border plot, two 1-m^2 plots were located farther into the *Ammophila* patch, and 14 1-m^2 plots were placed out into the surrounding *Elymus* area (Fig. 1). Altogether these formed a

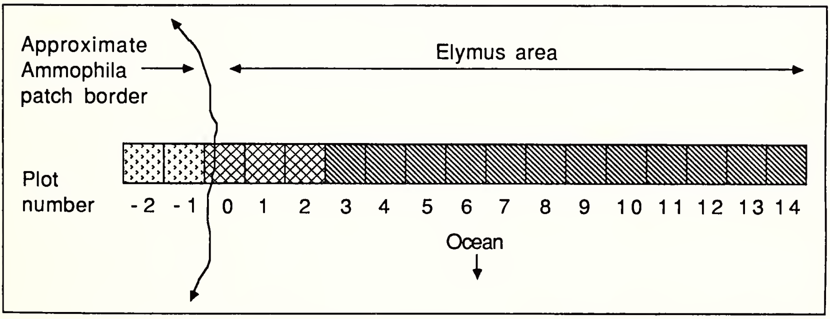

FIG. 1. Example sampling transect of 17 contiguous 1–m^2 plots established parallel to the beachfront. This transect is divided into within-*Ammophila* patch plots (plot numbers −2 and −1), border plots in the *Elymus* area (plot numbers 0–2), and more distant *Elymus* area plots (3–14). Not shown are the other five contiguous transects placed in each sampled area.

17-m long transect beginning 2 m inside an *Ammophila* patch. Sampling was done in November 1984, at the end of the reproductive season for *Cakile.*

The influence of herbivore activity on plant distribution was assessed indirectly by analyzing plant distribution patterns. If a species were negatively affected by amensalism with *Ammophila,* it would be scarce within the *Ammophila* patch, but its abundance in the border area should be similar to that farther outside the patch. As shown by Boyd (1988), a species affected by rodent herbivory would have decreased abundance beyond the patch border into quadrats 0–2 (Fig. 1). I compared the frequency of each species in the first 5 m (quadrats −2 to 3) with that in quadrats 4 to 14. I then compared frequency in the border 3 m (plots 0, 1, and 2) versus the remaining 12 m (plots 3–14) by the chi-square test (Zar 1984). Because of the relatively small numbers of quadrats used, I used the 0.01 probability level for this and the association analysis to decrease the chance of falsely concluding that pattern existed (Zar 1984). Species with overall frequency less than 5% were excluded from both analyses.

Association analysis. Association analysis between taxa may give clues to the existence of underlying ecological relationships (Mueller-Dombois and Ellenberg 1974). All pairs of species were examined for significant associations. The influence of *Ammophila* on these associations was assessed by testing for association on all data, and then excluding those quadrats containing *Ammophila* and testing for association again.

RESULTS

A total of 12 species was found along the transects (Table 1). Nine species were relatively abundant, being present in more than 5 percent of the quadrats. Three species (*Ammophila arenaria, Cakile maritima* and *Mesembryanthemum chilense*) were non-native. *Cakile* was the most short-lived species present, since most individuals do not survive more than two growing seasons (Boyd 1986). Those species with more than 5 percent frequency are, with the exception of *Agoseris apargioides,* widespread taxa characteristic of California beaches (Breckon and Barbour 1974).

Microdistribution pattern. Only 4 species showed significant microdistribution patterns relative to *Ammophila* patches (Table 2). Decreased frequency of *Ammophila* was not surprising because of the way patch boundaries and transects were delineated. This decrease was not influenced by inclusion of border plots (quadrats 0–2) in the analysis. The other two grasses in the study area (*Elymus* and *Poa*) were negatively affected by *Ammophila.* Both had significantly lower abundances within *Ammophila* patches but not in bor-

TABLE 1. FREQUENCY OF OCCURRENCE OF PLANT TAXA IN ALL SEVEN SAMPLING AREAS. Frequency is expressed as percentage of the 1-m^2 quadrats (n = 714) in which each species was present.

Species	Frequency
Elymus mollis Trin. ex Spreng.	87.1
Ammophila arenaria (L.) Link.	23.9
Cakile maritima Scop.	22.8
Mesembryanthemum chilense Mol.	20.0
Abronia latifolia Eschs.	16.9
Agoseris apargioides ssp. *maritima* (Sheld.) Q. Jones	8.7
Poa douglasii Nees.	8.1
Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann in Eng. & Prantl ssp. *cheiranthifolia*	7.7
Ambrosia chamissonis (Less.) Greene	7.6
Atriplex leucophylla (Moq.) D. Dietr.	2.1
Erigeron glaucus Ker.	0.7
Gnaphalium sp.	0.4

der areas, indicating that *Ammophila*'s negative influence did not extend beyond patch borders. *Cakile* showed a third pattern, decreasing in frequency both inside and in a zone bordering the *Ammophila* patches.

Association analysis. Several species (*Mesembryanthemum, Ambrosia,* and *Agoseris*) were not influenced by *Ammophila. Ammophila* had a large influence on other species associations, influencing them both directly and indirectly. *Elymus, Poa, Abronia,* and *Cakile* were all negatively associated with *Ammophila* (Table 3), indicating decreased frequency inside *Ammophila* patches. Positive associations between *Elymus* and *Cakile, Ambrosia,* and *Poa* were the indirect result of their negative associations with *Ammophila.* This was demonstrated by lack of significant associations when *Ammophila*-containing quadrats were excluded. Two other associations involving *Elymus* (with *Mesembryanthemum* and *Ambrosia*) seemed

TABLE 2. CHANGE IN FREQUENCY OF FOREDUNE SPECIES AS AFFECTED BY THE *AMMOPHILA* PATCH BORDER. Only those species for which a significant result ($P < 0.01$) was obtained are included. ns = not significant.

	Quadrats compared	
Species	−2 to +2 versus +3 to +14	0 to +2 versus +3 to +14
Ammophila arenaria	Decrease	Decrease
Elymus mollis	Increase	ns
Poa douglasii	Increase	ns
Cakile maritima	Increase	Increase

TABLE 3. STATISTICALLY SIGNIFICANT PAIR-WISE ASSOCIATIONS (POSITIVE OR NEGATIVE) BETWEEN SPECIES IN THE SAMPLED QUADRATS. Tests for association were made both for all quadrats and for those quadrats in which *Ammophila* was absent. Only those species pairs which showed a significant association in at least one case are listed. ns = no significant association (at $P < 0.01$).

Species pair	All quadrats	*Ammophila* quadrats excluded
Ammophila/Elymus	Negative	—
Ammophila/Poa	Negative	—
Ammophila/Cakile	Negative	—
Ammophila/Abronia	Negative	—
Elymus/Cakile	Positive	ns
Elymus/Abronia	Positive	ns
Elymus/Poa	Positive	ns
Elymus/Mesembryanthemum	ns	Positive
Elymus/Ambrosia	ns	Negative
Cakile/Agoseris	Positive	Positive
Mesembryanthemum/Ambrosia	Positive	Positive

to be influenced by *Ammophila,* being significant only when *Ammophila* quadrats were excluded from the analysis. These reflected an interaction between these species, one resulting in a positive and the other a negative association.

Only two interactions were detected which were not influenced by *Ammophila. Cakile* and *Agoseris* were positively associated and *Mesembryanthemum* and *Ambrosia* also were positively associated. I obtained this result both when *Ammophila*-containing plots were included in or excluded from the analysis.

DISCUSSION

Reports of lowered species richness of *Ammophila*-dominated beaches do not indicate which species may be most sensitive to *Ammophila.* Barbour et al. (1976) surveyed 34 Pacific Coast beaches from California to Washington. Half were classified as *Ammophila*-dominated and half as dominated by *Elymus, Cakile,* or other species. For comparative purposes I have summarized species presence on these beaches (% of beaches surveyed, presence on *Ammophila*-dominated vs. non-*Ammophila*-dominated beaches) as follows: *Ambrosia* (35 vs. 71), *Camissonia* (0 vs. 24), *Abronia* (59 vs. 82), *Poa* (18 vs. 6), *Cakile* (71 vs. 100). Based on this information, we might conclude that *Ambrosia, Camissonia, Abronia* and *Cakile* were all sensitive to the presence of *Ammophila* because they were found less frequently on *Ammophila*-dominated sites. The results of my study showed *Cakile, Abronia,* and *Poa* to be negatively associated with *Ammophila,* but *Camissonia* and *Ambrosia* were not affected by *Ammophila.* These contrasting results may be due in part to the confounding factor of non-overlapping species geographic distributions for some of these taxa (Breckon and Barbour 1974). The small scale at which I have examined associations also undoubtedly is a factor as it allows detection of fine-grained patterns.

Few other small scale examinations of Pacific Coast beach vegetation have been made. Bluestone (1981) reported no consistent patterns of association among species on the beach and foredune of Salinas River State Beach, California, but at that time little *Ammophila* was present on that site. Pitts (1976) reported a strong positive association of *Ambrosia* and *Cakile* in a large foredune quadrat at Point Reyes. I found these species to lack significant association in my study area.

The differential response of species to *Ammophila* may be due to a number of factors. Average cover inside an *Ammophila* patch was high, 50% for quadrat −2 (Boyd 1988). *Ammophila* and *Elymus* were by far the tallest of the species encountered. Therefore they would have shaded the other species encountered, but this shading effect may be positive or negative depending on the ecological circumstances. Payne (1980) reported that *Cakile edentula* plants growing under *Ammophila breviligulata* on Great Lakes beaches were often larger than unshaded plants when water was not limiting. She attributed this effect to *Ammophila* acting as a shelter for *Cakile* but pointed out that if water became limiting these sheltered plants usually died (presumably from competition with *Ammophila* for water). Barbour et al. (1976) mentioned a potential positive windscreen effect of *Ammophila* shoots, but this may be countered by greater sand accumulation in *Ammophila* areas (Barbour et al. 1985).

These results imply that the spread of *Ammophila* has been accompanied by decreases in abundance of some native species (*Elymus, Poa, Cakile,* and *Abronia*). I know of no historical data to verify this implication, but if true it may provide a partial explanation for decreased species diversity of arthropods in *Ammophila* areas (Slobodchikoff and Doyen 1977) as changes in the abundance of the plant species may have eliminated some dependent arthropod species. Another factor may be higher predation of insects by *Peromyscus* in *Ammophila* areas, as Pitts and Barbour (1979) demonstrated that they consume insects in addition to plant material.

The beach area studied has had both *Elymus* and *Ammophila* present for a long time (Cooper 1967), and they may have reached an equilibrium. If so, then the patterns observed in this study are not due to recent invasion by *Ammophila* but reflect the sorting of species across *Ammophila* patch borders over time. However, beach and dune systems are characterized by a rapidly changing habitat and differential patterns of colonization may be included in these results (Williams and Williams 1984).

Cakile was the only species for which evidence of a rodent-foraging effect was detected. The failure of other species to show distance effects similar to those of *Cakile* does not mean mice have no effect on them. It does imply that mice do not play as important a role in the microdistribution of these species as with *Cakile.* Their influence on *Cakile* may be greater because it is an annual or biennial (Maun et al. 1990) and hence more sensitive to seed and seedling predation. The other taxa are perennials and some reproduce asexually. Experiments conducted by Pitts and Barbour (1979) indicate *Cakile* may be a more important food source compared to the other species. They found *Cakile* leaves and fruits were preferred by *Peromyscus.* Fruits of *Poa* and *Ammophila* also were taken readily. The only other species encountered in my study and included in their tests was *Abronia,* which was not eaten. Rodent consumption of *Cakile* seeds has been noted on other California beaches (Johnson 1963), but not on Great Lakes (Payne and Maun 1984) or Atlantic Coast beaches (Keddy 1982), in spite of the ubiquitous distribution of *Peromyscus.* Rodent activity may be an important ecological factor for some beach plants only on the Pacific Coast, but it may simply have been overlooked in other studies.

The lack of a rodent-foraging effect for species other than *Cakile* implies that rodent herbivory is not a major factor in determining species microdistributions near *Ammophila* on the beach and foredune. In general, *Ammophila* is not an important food source for many herbivores. Huiskes (1979) noted that vegetative parts are disliked by rabbits, sheep, and cattle, and that *Ammophila* supports no monophagous insects. Pavlik (1982) noted that *Ammophila* was less desirable to herbivores than *Elymus.* Although it is tempting to suggest an herbivore-mediated mechanism for the replacement of *Elymus* by *Ammophila,* the lack of a zone of decreased *Elymus* frequency at *Ammophila* patch borders suggests a more direct mechanism of species exclusion. Herbivory is an important factor in the microdistribution of *Cakile,* but microdistributions of other species are apparently influenced by other types of ecological interactions.

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ANNOUNCEMENT

"Interface Between Ecology and Land Development in California"

This will be the title of a symposium to be held at the annual meeting of the Southern California Academy of Sciences, 1–2 May 1992 at Occidental College in Los Angeles. The meeting will begin Friday morning with a plenary address by Dr. Peter Raven, followed by morning and afternoon sessions on both Friday and Saturday. It is anticipated that the symposium will consist of four sessions on: Biodiversity and Habitat Loss, Mitigation of Development, restoration of Damaged Communities, and Wildlife Corridors. The focus of the meeting is to bring together persons involved in basic research, applied environmental consulting and governmental policy. For further information contact: Dr. Jon Keeley, Department of Biology, Occidental College, Los Angeles, CA 90041; 213-259-2958 (fax).

NOTES

LEDUM IN THE NEW JEPSON MANUAL AND A NEW COMBINATION FOR *LEDUM* IN *RHODODENDRON* (ERICACEAE).—Gary D. Wallace, Botany Section, Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007.

Kron and Judd (Systematic Botany 15:57–68, 1990) presented a cladistic analysis of the tribe Rhodoreae D. Don (Ericaceae). The Rhodoreae, Cladothamneae H. Copel., Epigaeae Britton & Brown and Phyllodoceae Drude in Engl. & Prantl comprise the bulk of the Rhododendroideae Endl. recognized by Stevens (Journal of the Linnean Society, Botany 64:1–53, 1971; Dissertation, Univ. of Edinburgh 1969) and Wallace (Botaniska Notiser 128:286–298, 1975). Kron and Judd (1990) found that by excluding *Therorhodion* (Maxim.) Small and including *Ledum* L., *Rhododendron* L. "is likely monophyletic". *Ledum* was reduced to a subsection of *Rhododendron* and two combinations were proposed, *Rhododendron palustre* (L.) Kron & Judd and *Rhododendron groenlandicum* (Oeder) Kron & Judd.

Harmaja (Annales Botanici Fennici 27:203–204, 1990) proposed *Rhododendron tomentosum* (Stokes) Harmaja to include *Ledum palustre* L. because the name *Rhododendron palustre* Turcz. ex DC. had already been used. Harmaja proposed the new name *Rhododendron neoglandulosum* Harmaja to accommodate *Ledum glandulosum* Nutt. The combination *Rhododendron glandulosum* (Standley) Millais made earlier, referred to another species.

For the new Jepson Manual of the Flowering Plants of California only one *Ledum* has been recognized. It seems best for clarity and so as not to perpetuate an older name to refer all of the material of this wide ranging species to *Rhododendron neoglandulosum* Harmaja.

Harmaja (1990) also proposed a new name, *Rhododendron subarcticum* Harmaja for the prostrate arctic plant previously known as *Ledum palustre* L. ssp. *decumbens* (Aiton) Hulten. This seems better accommodated, as in the past, as a subspecies. Therefore the following combination is proposed.

Rhododendron tomentosum (Stokes) Harmaja ssp. *subarcticum* (Harmaja) G. Wallace *comb. et stat. nov.*

Basionym: *Rhododendron subarcticum* Harmaja, Annales Botanici Fennici 27:203, 1990. Synonymy: *Ledum palustre* L. var. *decumbens* Aiton, Hortus Kewensis 2:65, 1789; *Ledum decumbens* (Aiton) Lodd. ex Steudel, Nomenclator botanicus (ed.2) 2: 20, 1840 (*non decumbens* D. Don ex G. Don, A General History of the Dichlamydeous Plants 3:846, 1834); *Ledum palustre* L. ssp. *decumbens* (Aiton) Hulten, Kongl. Svenska Vetenskapsakademiens Handlingar, Ser.3 8(2):8, 1930).

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A NOMENCLATURAL CHANGE IN *SYMPHORICARPOS* (CAPRIFOLIACEAE).—Lauramay T. Dempster, Jepson Herbarium, University of California, Berkeley, CA 94720.

In the course of revising Caprifoliaceae for the forthcoming revision of Jepson's Manual of the Flowering Plants of California, the following taxonomic problem was identified. Consequently a new name is proposed.

MADROÑO, Vol. 39, No. 1, pp. 77–78, 1992

Symphoricarpos rotundifolius A. Gray var. *parishii* (Rydberg) Dempster comb. nov. Based on *S. parishii* Rydberg, Bulletin of the Torrey Botanical Club 26:545, 1899. California: San Bernardino Co.: Mill Creek, San Bernardino Mts., Parish 2514, NY. Synonyms: *S. parvifolius* Eastwood, Bulletin of the Torrey Botanical Club 30:498, 1903. California: Tulare Co.: Hockett Meadows, Little Kern River, *Purpus 1792,* CAS. *S. oreophilus* A. Gray var. *parishii* (Rydberg) Cronquist, Intermountain Flora 4:539, 1984. This variety occurs in the mountains of Southern California from Riverside to Santa Barbara counties, and in the Sierra Nevada in Kern and western Inyo and Mono counties. It is a low trailing shrub, in contrast with var. *rotundifolius,* which is erect and divaricate. The two varieties differ also in hairiness of the corolla tubes. In var. *parishii* the upper two thirds of the corolla tube are pilose within, whereas in var. *rotundifolius* only the middle third is pilose, the upper third being glabrous. Variety *rotundifolius* occurs in the Sierra Nevada from Fresno and Inyo counties north to Modoc and central Siskiyou counties, California, northward to Washington, and east to Wyoming, Colorado, and western Texas. The two varieties are not precisely separable in western Inyo and Mono counties, where their ranges overlap. Plants from Nevada and Arizona, included by G. N. Jones (A monograph of the genus *Symphoricarpos.* Journal of the Arnold Arboretum 21:201–252, 1940) with *S. parishii* Rydberg differ a little from Californian plants, especially in their corollas, which are less hairy within, but they should probably be included in var. *parishii.*

The name *S. rotundifolius* var. *rotundifolius* is used here in a broad sense to include *S. vaccinioides* Rydberg, although G. N. Jones in his monograph (1940) stated that "*Symphoricarpos rotundifolius* is a rather local species confined to the mountainous areas of southwestern New Mexico, Arizona and adjacent Colorado", and that the northern plants (including those of eastern and northern California) are of another species, namely *S. vaccinioides.* There is, in fact, a great deal of variation within *S. rotundifolius* as here construed, but I have not found any significant correlation between different sets of characters, nor any discernible discontinuity, either morphological or geographic. Plants from California, Oregon, Washington and Nevada are consistently pubescent, whereas those from farther east are often glabrous, even usually so in Colorado and New Mexico. There is also a tendency toward narrower leaves in the western than in the eastern part of the range. Both pubescence and leaf shape show thus a definite east-west variational trend, but this trend is not associated with differences in floral characters. Corollas vary considerably in size and shape throughout the range, and the same can be said of stamens, ovaries and calyx-limb. None of these floral differences is correlated with pubescence, leaf-shape or locality. Jones based his narrow concept of *S. rotundifolius* primarily on the character of the pubescence on the young twigs, together with the shape of the corolla. The former seems trivial, and the latter is generally unreliable as a taxonomic character in this group.

S. oreophilus A. Gray (typus vidi) is an entirely glabrous form with extremely slender corollas and ovaries. The use of this name, whatever its merits elsewhere, is unjustified with reference to California plants.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

CUPRESSUS BAKERI Jeps. (CUPRESSACEAE).—Siskiyou Co., E.-facing slope of Mill Creek Canyon (123°05′48″W, 41°45′57″N) at 1450 m to 1360 m elevation, below ridge between Kuntze and Mill Creek drainages from Walker Creek Road (1.5 km from Seiad Valley on Highway 96), 6 Sept 1990. Cypresses on serpentine scree in association with *Pseudotsuga menziesii, Pinus jeffreyi, Calocedrus decurrens, Quercus vaccinifolia, Ceanothus cuneatus, Garrya fremontii* and *Ribes sanguineum.*

Significance. Baker cypress is restricted to a few disjunct locations in the Siskiyou Mountains of California and Oregon, the Cascade and Sierra Nevada Mountains of California. This report adds another locality in the Siskiyou Mountains. Morphologically, the trees resemble those from Seiad Creek in the Siskiyou Mountains and populations from the north-east side of Goosenest Mountain. These latter populations were attributed to subspp. *matthewsii* by Wolf and Wagener (Aliso 1:1–444, 1948), but our populational studies of morphological diversity (Proceedings International Symposium Population Genetics, p. 23, 1990) and chemical diversity (Biochemical Systematics and Ecology in press) do not support subspecies status in this species.

—RICHARD DODD, University of California at Berkeley, Forest Products Laboratory, 1301 South 46th Street, Richmond, CA 94804; Zara A. Rafii, Institut Méditerranéen d'Ecologie et Paléoécologie, Laboratoire de Botanique et Ecologie Méditerranéenne, Université d'Aix-Marseille III, 13397 Marseille Cedex 13, France.

CYTISUS STRIATUS (Hill) Rothm. (FABACEAE).—San Francisco Co., Diamond Heights, rocky slope off Diamond Street near Beacon Street, 18 Feb 1978, *Norris* 3738 (RSA). San Mateo Co., NE Ridge of San Bruno Mountain, near Guadelupe Valley Road, 23 May 1985, *Leen s.n.* (CAS). San Diego Co., N of Escondido off I 15 , 8 Apr 1987, *Leen s.n.* (CAS). Riverside Co., S of Temecula off I 15 , 8 Apr 1987, *Leen s.n.* (CAS). Los Angeles Co., Tujunga Canyon, 29 May 1987, *Leen s.n.* (CAS). Contra Costa Co., Alvarado Canyon, *Leen s.n.* (CAS). Marin Co., Marinchello Trail, Golden Gate National Recreation Area, 13 Oct 1987, *Leen s.n.* (CAS). Alameda Co., Caldecott Lane near Tunnel Road, 14 Oct 1987, *Leen s.n.* (CAS).

Significance. First report for CA.

—ROSEMARY LEEN, Division of Biological Control, University of California at Berkeley, 1050 San Pablo Avenue, Albany, CA 94706.

OPUNTIA BASILARIS var *TRELEASEI* (Coult.) Toumey (CACTACEAE).—Kern Co., base of N-facing bajada on coarse sandy soil containing many stones up to 30 cm long, non-native grassland disturbed by cattle grazing. Associated species: *Amsinkia tessellata, Asclepias californica, Astragalus lentiginosus* var *nigricalycis, Avena barbata, A. fatua, Brassica nigra, Bromus diandrus, B. rubens, Capsella bursa-pastoris, Datura meteloides, Erodium cicutarium, Eremocarpus setigerus, Euphorbia ocellata, Hemizonia pallida, H. pungens,* and *Lupinus bicolor.* Pleito Hills 32 km S of Bakersfield, NE1/4, section 26, T11N, R21W, 220 m, 18 April 1991, *Draper 931,932* (Bakersfield College).

Significance. This newly discovered population, covering approximately 12 ha, is one of the largest remaining stands of this federally endangered species.

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—MICHAEL D. ROURKE, Life Science Department, Bakersfield College, Bakersfield, CA 93305; Ray Draper and Paul E. Pruett, Pruett, Lawrence and Associates, 3616 View Street, Bakersfield, CA 93306.

OREGON

COTONEASTER FRANCHETII Bois. (ROSACEAE).—Curry Co., junction of US Rt. 101 and Itzen Drive, 1 km N of CA state border, roadside thickets, with *Rubus discolor* and *Alnus rubra,* ca. 30 m, 24 Oct 1990, *Zika 11026* OSC; US Rt. 101 between Gold Beach and Rogue River, roadside waste area, ca. 10 m, 24 Oct 1990, *Zika 11036* OSC; Lane Co., BLM Road 18–1E–26, 1.5 air km NE of Fall Creek Reservoir, roadside thicket, with *Salix sitchensis* and *Populus trichocarpa,* ca. 500 m, 27 Jun 1988, *Zika 10511* OSC; Lincoln Co., Waldport, Rt. 34, 1 km E. of US Rt. 101, thickets, with *Rubus spectabilis, R. parviflorus, R. discolor* and *Salix hookeriana,* 5 m, 18 Nov 1990, *Zika 11044* OSC; Tillamook Co., Cascade Head Preserve, 6 air km SSW of Neskowin, steep S. slope, grassland, with *Holcus lanatus,* 300 m, 13 Aug 1986, *Zika 9986* OSC.

Significance. First records of this Eurasian genus outside of cultivation in OR.

ILEX AQUIFOLIUM L. (AQUIFOLIACEAE).—Curry Co., junction of US Rt. 101 and Itzen Drive, 1 km N of CA state border, roadside thickets, with *Rubus discolor, Alnus rubra,* and *Lonicera involucrata,* ca. 30 m, 24 Oct 1990, *Zika 11023* OSC; Port Orford, US Rt. 101, roadside waste area, ca. 30 m, 24 Oct 1990, *Zika 11039* OSC; Lincoln Co., Roads End headland, Siuslaw National Forest, 2 air km S of Salmon River mouth, second-growth forest, with *Alnus rubra,* 120 m, 14 Aug 1986, *Zika 9988* OSC; Tillamook Co., Cascade Head Preserve, 6 air km SSW of Neskowin, second-growth forest, with *Alnus rubra* and *Picea sitchensis,* 245 m, 7 Aug 1986, *Zika 9974A* OSC.

Significance. First records of this family for OR outside of cultivation. This invasive European species, bird dispersed, is capable of invading shaded or sunny habitats west of the Cascades.

ORNITHOGALLUM NUTANS L. (LILIACEAE).—Linn Co., Blueberry Rd., 7 air km NE of Halsey, weed in seed crop of *Poa pratensis,* with *Dactylis glomerata,* ca. 80 m, 7 Apr 1991, *Zika 11068 & 11076* ORE, OSC.

Significance. First record for OR.

RANUNCULUS FICARIA L. (RANUNCULACEAE).—Multnomah Co., junction of Summit Ct. and Summit Ave, NW Portland, steep damp hillside, recently logged, with *Rubus discolor, Corylus cornuta, Polystichum munitum* and *Hedera helix,* ca. 70 m, 27 Mar 1991, *Zika 11064* OSC; Terwilliger Blvd. Ext., Tryon Creek State Park, SW Portland, roadside waste area, with *Rubus discolor, Alliaria officinalis* and *Rumex obtusifolius,* ca. 100 m, 4 Apr 1991, *Zika 11066* ORE, OSC.

Significance. First records of this European species outside of cultivation in OR.

—PETER F. ZIKA, Oregon Natural Heritage Program, 1205 NW 25, Portland, OR 97210.

WASHINGTON

CAREX ROSTRATA Stokes (CYPERACEAE).—Pend Oreille Co., Colville National Forest, headwaters of W Branch of LeClerc Cr., six miles W of Idaho state line and 22 miles S of Canada, T37N R44E S24, 4980 feet, 13 Aug 1990, Kovalchik 480. Bog complex where it dominates floating root mats.

Previous knowledge. Known from one site in Glacier National Park and five sites in Alberta; otherwise widely scattered in the Boreal Zone from Alaska to Newfoundland and common in Europe.

Significance. First record for WA and second for western United States. According to A. A. Reznicek, University of Michigan Herbarium, the name *C. rostrata* has been misapplied in North America. What has been called *C. rostrata* Stokes is *C. utricularia* Boott. The very rare *C. rostrata* described here has glaucous, involute leaves and stomata on the upper surface of the blades while *C. utricularia* blades are green on both sides with stomata below.

—BUD KOVALCHIK, Colville National Forest, 765 S. Main St., Colville, WA 99114.

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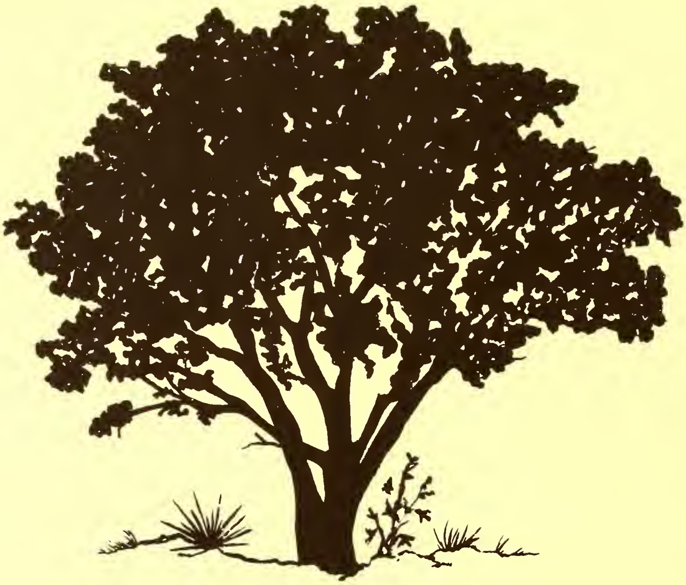

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A REAPPRAISAL OF *ALLIUM CRISTATUM* (ALLIACEAE) AND ITS ALLIES

DALE W. MCNEAL
Department of Biological Sciences, University of the Pacific,
Stockton, CA 95211

ABSTRACT

This investigation treats a group of *Allium* species from the Intermountain region of western North America characterized by a single, terete leaf per bulb and six prominent processes on the ovary, forming an ovarian crest. Cell shape and pattern on the inner epidermis of the leaf base indicate that previous authors have misunderstood the relationship between *A. nevadense* S. Watson, *A. cristatum* S. Watson and *A. atrorubens* S. Watson. A key to the two recognized species and one variety is presented. Typification of the names involved is given where necessary. A distribution map is included.

Allium cristatum S. Watson was described from specimens collected by Palmer "near St. George", Utah in 1877 (Watson 1879). It belongs to a very distinctive group of North American species characterized by having a single, terete leaf per bulb and two flattened processes near the summit of each ovary lobe forming an ovarian crest. Species with these characteristics were placed by Ownbey (Saghir et al. 1966) in the *Allium sanbornii* alliance. This alliance, with 22 taxa, is chiefly distributed in California; only five of the currently recognized taxa occur outside the state.

Watson specifically noted in his description that *A. cristatum* had some bulb coats "with very faint quadrangular reticulation". This contrasts with the otherwise somewhat similar appearing *A. nevadense,* which has distinct, elongate, contorted cellular reticulations on the bulb coat (Fig. 1), but is similar to *A. atrorubens* S. Wats., which lacks reticulations or has very obscure quadrate markings on the bulb coat. Both of these latter taxa are widespread in the Intermountain region. Jones (1902) also recognized *A. cristatum* and noted that the ovarian crest processes had margins that were somewhat glandularly toothed. Subsequently Ownbey (1947) reduced this taxon to a variety of *Allium nevadense* S. Watson (Munz 1959; Cronquist et al. 1977) and described the contorted reticulations characteristic of the outer bulb coats of that species as lacking or indistinct in the variety (Fig. 2). The bulb coat in question is derived from the adaxial epidermis of the foliage leaf (McNeal and Ownbey 1973). It seems clear that Ownbey assumed that the cells forming this layer were the same shape and formed the same pattern in both taxa, but

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that some other factor, possibly related to differential deposition of lignin, influenced the appearance of the reticulation pattern. Since bulb coat reticulation has proven to be an extremely valuable character in North American *Allium* systematics, this investigation was undertaken to analyze the available material for reticulation patterns and to look for other characters on which to base an interpretation of these taxa.

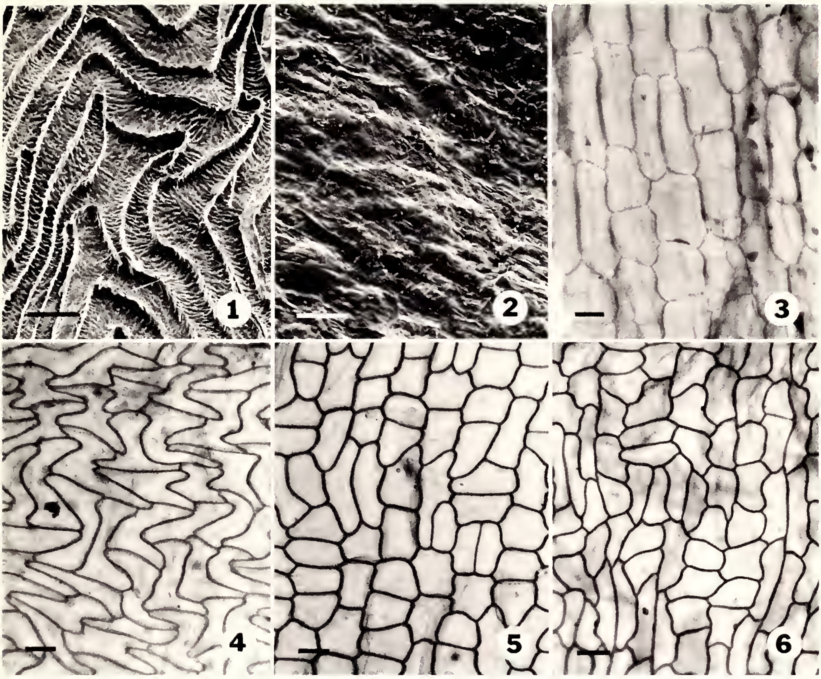
MATERIALS AND METHODS

As part of a revision of the *Allium sanbornii* alliance, specimens of *A. nevadense* and its allies, available from major American herbaria (CAS, CPH, DAV, DS, GH, JEPS, MO, NY, POM, RSA, UC, US, WS) were studied and extensive observations were made of living material of all putative taxa in the field and under cultivation in Stockton, CA. The chromosome number for the previously undetermined taxon was determined using aceto-orcein squashes of pollen mother cells from fresh buds. For investigation of bulb coat development the adaxial epidermis was peeled from the base of the foliage leaf of live specimens, stained with Fast Green and mounted to ascertain cell shape and arrangement. Mature bulb coats, developed from this layer, were removed, sputter coated with gold-palladium and examined by SEM.

RESULTS AND DISCUSSION

By using the presence, even if obscure, of contorted bulb coat reticulation to mark *A. nevadense,* it was possible to place most of the specimens studied in this taxon. However, a small residual group, lacking bulb coat reticulation, all from southwest Utah and northwest Arizona were considered to be separate entities. Included in this group was the type specimen of *A. cristatum.* In studying epidermal peels from specimens lacking obvious bulb coat reticulation it was possible to demonstrate that the shape and pattern of cells forming this layer (Fig. 3) are quite distinct from those seen on the mature bulb coat or epidermal peels (Fig. 4) of *A. nevadense.* It seems clear that specimens lacking cellular bulb-coat reticulation do so, in part at least, because they have different cell shapes and a different arrangement of these cells.

Perianth segments in the residual group are broadly lanceolate to ovate and erect at anthesis. This contrasts with lance-linear to lanceolate, widely spreading perianth segments in *A. nevadense.* Further, the ovarian crest processes in the residual group are narrow and either deeply notched at the apex or distinctly toothed on the outer margin, while the crests in *A. nevadense* tend to be broader and mostly entire or merely emarginate.



FIGS. 1–6. SEM (1–2) and light microscope micrographs (3–6) of adaxial epidermal cells of *Allium* bulbs. 1. *Allium nevadense* (*McNeal 1693*). 2. *Allium atrorubens* (*McNeal 1792*). 3. *Allium cristatum* (*McNeal 3422*). 4. *Allium nevadense* (*McNeal 3461*). 5. *Allium atrorubens* var. *inyonis* (*McNeal 3090*). 6. *Allium atrorubens* var. *atrorubens* (*McNeal et al. 1782*). Scale = 100 μm. (Voucher specimens deposited at CPH.)

Based on these characters I conclude that Watson was correct in separating the two taxa and that Ownbey erred in reducing *A. cristatum* to varietal status under *A. nevadense.* However, in surveying specimens of *A. atrorubens* S. Watson var. *inyonis* (M. E. Jones) F. Ownbey & Aase ex Cronq. & F. Ownbey, I noted a strong resemblance to *A. cristatum.* Epidermal peels revealed the same quadrate to rectangular cell shape (Fig. 5) seen in *A. cristatum.* In fact the only character used by Ownbey (Munz 1959) to distinguish between *A. cristatum* and *A. atrorubens* var. *inyonis* is the presence of obscurely reticulate bulb coats in some specimens of the former. A comparison of the Utah and Arizona material lacking cellular reticulations with specimens of *A. atrorubens* var. *inyonis* revealed no character or suite of characters that would satisfactorily separate the two groups. I suggest, therefore, that this material belongs to a single variety. This decision is based on the lack of bulb coat reticulation, similar cell pattern on the leaf base epidermis (Fig. 6), and erect perianth segments. The variety is, therefore, closely related to *A.*

atrorubens, from which it differs in having broader, acute to acuminate, pale pink or white tepals with darker midveins.

In combining these two varieties, article 57 of the International Code of Botanical Nomenclature (Greuter et al. 1988) requires retaining the oldest legitimate epithet for the rank. That epithet is *cristatum.*

Allium atrorubens S. Watson var. **cristatum** (S. Watson) McNeal, comb. nov.—TYPE: USA, Utah, Washington Co., St. George, Southern Utah. 1877, *Dr. E. Palmer* (holotype, GH!; isotypes, NY[4]!, MO[2]!, US!).

Allium cristatum S. Watson, Proc. Amer. Acad. Arts 14:232. 1879. *A. nevadense* var. *cristatum* (S. Watson) Ownbey, Res. Stud. State Coll. Wash. 15:228. 1947 [1949]. *A. n.* subsp. *cristatum* (S. Watson) Traub & F. Ownbey, Pl. Life 23:110. 1967.

Allium decipiens M. E. Jones, Contr. W. Bot. 10:16. 1902; not Fischer, 1812. *A. inyonis* M. E. Jones, Contr. W. Bot. 10:86. 1902. *A. atrorubens* subsp. *inyonis* Traub, Pl. Life 28:66. 1972. *A. atrorubens* var. *inyonis* F. Ownbey & Aase ex Cronq. & F. Ownbey, Intermountain Flora 6:515. 1977.—TYPE: USA, California, Inyo Co., Summit, Owens Valley, 22 May 1897, *M. E. Jones s.n.* (holotype, POM!).

Bulbs ovoid, 10–15 mm long, often proliferating by 1–2 stalked basal bulblets, the outer coat brown, lacking reticulations or with 2–3 vertical rows of cells just above the root pad, inner coats white or light pink to red. Scape (3–)5–15(–19) cm. Leaf 1, terete above the tubular sheath, to about 2× the scape, the terminal portion curling as it withers, but often broken off. Bracts 2–4, connate at base, lance-ovate to ovate, 4–7-nerved. Umbel loose, pedicels 10–50, equalling to twice the length of the perianth; tepals white or more commonly light pink with deep pink midveins, lance-ovate to ovate, acute to acuminate, ± erect, 8–12 mm long, the outer 2.5–4.5 mm wide, the inner narrower; stamens ½–⅘ as long; ovary conspicuously crested with 6 narrow, flattened processes that are deeply emarginate to toothed; stigma punctate, entire; seeds black, the coat cellular, the surface of the cells with 5–8 minute papillae; $n=7$ (California: Inyo Co.: Westgard Pass, White Mtns., 23 May 1985, *McNeal 3090.* Utah: Kane Co.: Bank of the Paria River ca. 300 m upstream from the abandoned townsite of Pahreah, 16 May 1989, *McNeal 3422*).

In sandy, rocky, or gravelly, or occasionally, clay soils in the White Mountains and Owens Valley of California east into central Nye Co., Nevada, and south into the desert mountains of eastern Inyo and northeastern San Bernardino cos., California. From there it

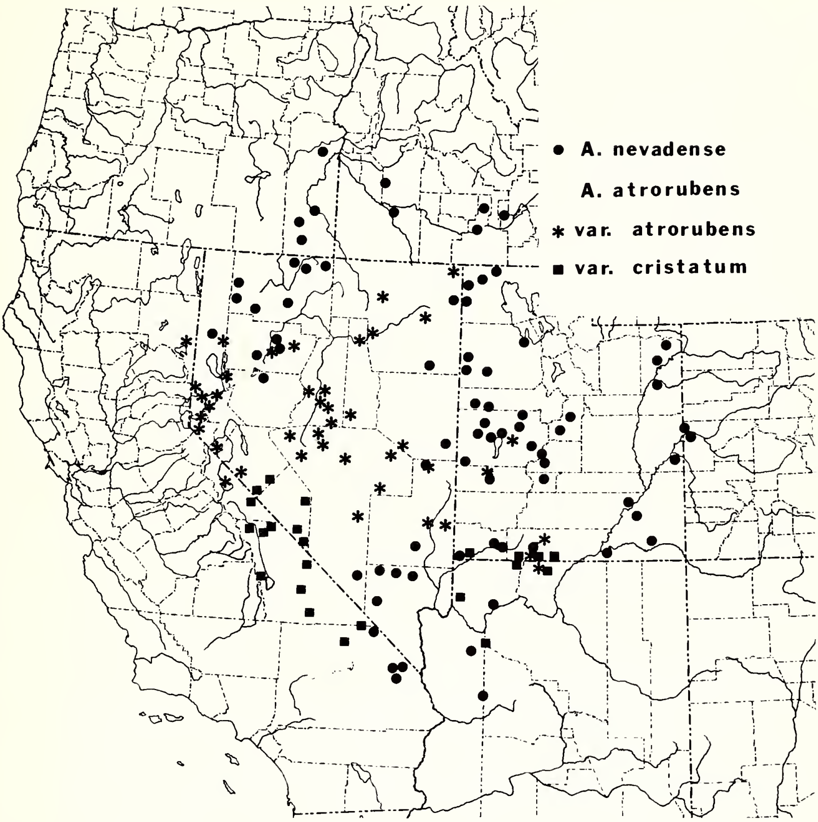


FIG. 7. Geographic distribution of *Allium atrorubens* var. *atrorubens, A. atrorubens* var. *cristatum,* and *A. nevadense.*

extends east into northwestern Arizona and southeastern Utah (Fig. 7).

It is noteworthy that *A. atrorubens* var. *cristatum* grows in the same area as *A. atrorubens* var. *atrorubens* and *A. nevadense* only in a small area near Kanab in southern Utah. In fact the latter two taxa are in close proximity to each other in only two other widely separated locations in Lincoln and Pershing counties, Nevada (Fig. 7).

Allium atrorubens var. *cristatum* bears a striking but superficial resemblance to *A. nevadense* in herbarium material. Bulb coat reticulation in *Allium* is often a difficult character to detect, and Ownbey might have been distracted by the specimens of *Allium nevadense* having the typical, if obscure, reticulation pattern and, therefore, missed the similarities between the few specimens from Utah and Arizona truly lacking reticulation and *A. atrorubens.* The material is clearly more closely related to this other widespread Great Basin species than to *A. nevadense* as he suggested.

This again points up the critical nature of the *Allium* bulb in classification and identification. Specimens lacking bulbs or with the "dirty" brown or gray bulb coats carefully removed are all too common in herbaria and are often virtually useless unless one is very familiar with the taxa involved and has a first hand appreciation of the variation within a particular taxon. Collectors should take care in removing dirt from bulbs not to dislodge the bulb coats and once the specimens are pressed and dried should recover any bulb coat material that has become detached in the process and include it in a fragment envelope. Alternatively, several bulbs should be collected in addition to those that are pressed for each collection and the bulb coats removed and placed into fragment envelopes to dry. Once the pressed specimens are dry, the fragment envelopes can be added to the specimens prior to distribution.

KEY DISTINGUISHING *ALLIUM ATRORUBENS* VAR. *CRISTATUM* FROM RELATED INTERMOUNTAIN TAXA

a. Outer bulb coats with ± transversely elongate, intricately contorted cellular reticulation. . . . . *Allium nevadense* S. Watson
a′. Outer bulb coat lacking cellular reticulation or with only 2–3 vertical rows of ± quadrate cells just above the rootpad.
  b. Tepals purple or rarely white, lance-linear to lance-ovate attenuate, the margins involute at tip, so appearing setaceous. . . . . *Allium atrorubens* S. Watson var. *atrorubens*
  b′. Tepals pale pink with darker midveins, lance-ovate to ovate, acute. . . . .*Allium atrorubens* S. Watson var. *cristatum* (S. Watson) McNeal

Several hundred herbarium specimens were examined during this investigation. Along with field observations, these form the basis for the morphological and distributional data presented. Lists of these specimens are available from the author.

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I thank the curators of the herbaria cited earlier who kindly loaned materials for this study. I also thank San Joaquin Delta College, Stockton, CA, for use of their scanning electron microscope in the course of this study. Support for this study from the Faculty Research Committee and the F. R. Hunter Memorial Fund of the University of the Pacific is gratefully acknowledged. I deeply appreciate the critical reviews of the manuscript and valuable suggestions by Dr. G. L. Smith, one anonymous reviewer and the Editor.

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MEETING

International Symposium on "BIODIVERSITY IN MANAGED LANDSCAPES: THEORY AND PRACTICE" to be held at the Capitol Plaza Holiday Inn, Sacramento, California, U.S.A., 13–17 July 1992. Sponsored by a host of U.S. Federal Agencies and International Conservation Organizations. The program's objectives are to provide the scientific basis for understanding biodiversity, document case examples of theory and concepts applied at differing scales, and examine policies that effect its conservation. A distinguished group of invited Speakers will address: genetic diversity; species diversity; community diversity; landscape diversity; setting objectives and priorities, inventory, monitoring, and assessment; management strategies; and policy and social considerations. For further information write or call: Dr. Robert C. Szaro, USDA Forest Service, Forest Environment Research, P.O. Box 96090, Washington, DC 20090-60090, Tel: (202) 205-1524 or FAX (202) 205-1551.

INNOVATIONS IN CALIFORNIA *TRIFOLIUM* AND *LATHYRUS*

Duane Isely
Department of Botany, Iowa State University,
Ames, IA 50011

Abstract

This report includes: **Trifolium buckwestiorum**, sp. nov., and taxonomic discussion about California *Lathyrus lanszwertii, L. nevadensis,* and *L. vestitus.* Nomenclatural transactions include the combinations: **L. lanszwertii** var. **tracyi**, and **L. vestitus** vars. **ochropetalus** and **alefeldii**.

Certain of the Leguminosae (Fabaceae) for the Jepson Manual Project require the following nomenclatural transactions.

Trifolium buckwestiorum Isely, sp. nov. (Fig. 1).—Type: USA, California, Santa Cruz Co., Scott Creek watershed, along old roadbed which goes from "Purdy Aluminum Barn" down into "Bettencourt Gulch," 1 Jun 1983, *West 107* (holotype, JEPS).

Est herba annua, involucrata, glabra; foliolis obovatis vel ellipticis; inflorescentiis inferioribus 2–5 flores cleistogamos a stipulis inclusis gerentibus, involucro carentibus; illis superioribus excertis 10–15+ flores chasmogamos ferentibus, involucro crateriformio subtentis; calycis lobis deltatis seta terminali 1–1.5 mm longa, etiam 2–3 apiculationibus lateralibus in quoque lato praeditis.

Annual herb, decumbent or ascending, glabrous. Stems usually abundantly branched at base, 0.5–4 cm long. Leaves cauline, the lower well-petioled, upper shortly petioled to subsessile; leaflets obovate or elliptic, 0.5–1.5 cm long, apically rounded or slightly notched, inconspicuously spinulose-dentate. Stipules shallowly lacerate, the divisions bristle-tipped. First-formed heads (from medial and lower stems) subsessile and enclosed by stipules, with 2–5 cleistogamous flowers, lacking involucre. Subsequent heads peduncled, capitate, 5–10 mm diam., involucrate, bearing 10–15 ascending flowers; involucre bowl-shaped, dissected ×0.2(–0.4) of height, the numerous divisions with short bristle-tips. Calyx 4–5 mm long, glabrous; lobes shorter than tube, deltate with 2–3 lateral apiculations on each side and a short terminal bristle tip, 1–1.5 mm long (Fig. 1). Corolla 6–

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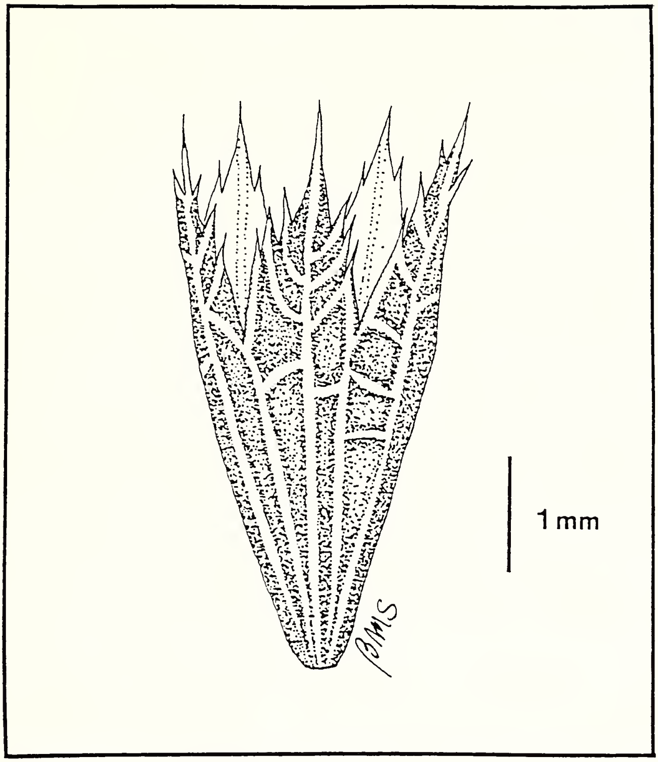

FIG. 1. Calyx from *Trifolium buckwestiorum.*

7 mm long, pale pink or white with darker keel. Legume shortly stipitate, included or slightly exserted. Seed 1.

Exsiccata. USA, California, Santa Cruz Co.: "Upper Pozzi Meadow," "Schoolhouse Ridge," hillside approx. 0.3 mi NE of Old Seaside School, Swanton, 20 May 1982, *Buck, West, Hawke, and Vigno 1* (CAN, JEPS). Scott Creek watershed, along old roadbed which goes from "Purdy Aluminum Barn" down into "Bettencourt Gulch," 6 May 1983, *West 73* (JEPS) (same population as type). Scott Creek watershed, lower "Schoolhouse Ridge," central portion of upper "Pozzi Meadow," 6 May 1983, *West 75* (JEPS) (same population as *Buck, West, Hawke, and Vigno 1*). H-H Ranch, SE of Greyhound Rock and W and NW of Old Seaside School, Swanton, on low ridge E of central "Old Road Gulch," on old roadbed, 13 May 1983, *Buck and West 272* (ISC, JEPS). H-H Ranch, SE of Greyhound Rock and W and NW of Old Seaside School, Swanton, S/SW-facing grassy slope comprising lower/central portion of "Old Road," 10 Jun 1983, *West 113* (JEPS, ISC) (same population as *Buck and West 272*).

Cusick meadow (NE corner), Nisene Marks State Park, near N end of Park, near summit of Santa Rosalia Mountain, ca. 2.8 km NW of Buzzard Lagoon, 11 air km NNE of Aptos, 25 May 1986, *Morgan and West 2* (JEPS).

This local, annual, involucrate clover resembles *Trifolium barbigerum* var. *barbigerum* in general aspect. It differs from that species most strikingly in its only shortly aristate, laterally toothed calyx lobes, the failure of post-anthesis inflation of the corolla, and in the production of cleistogamous flowers. Figure 1 illustrates the distinctive calyx.

Trifolium buckwestiorum is clearly distinctive in the United States. However, some annual, involucrate clovers of cismontane California are closely related to, or are seemingly identical with species found in western coastal Chile. A decision concerning the specific uniqueness of *T. buckwestiorum* is necessarily qualified by consideration of similar taxa from Chile.

Mélica Muñoz-Schick of the Museo Nacional de Historia Natural, Santiago, Chile (SGO), to whom I sent a fragment of the U.S. species, kindly sent me selected Chilean specimens for examination. She remarked, "The species that I am sending don't look very similar to the one you have sent." The Missouri Botanical Garden (MO) kindly loaned sheets selected by David Smith (ISC). Rupert Barneby, New York Botanical Garden (NY), compared a submitted specimen branch with their Chilean holdings. Nothing matches.

The closest resemblance in the literature to *T. buckwestiorum* is the Chilean *T. antucoensis* D. Heller, which, as illustrated by Zohary and Heller (1984, p. 536), has a similar calyx. But per description, it lacks the cleistogamous flowers. Also, the illustration shows a plant that has strongly emarginate leaflets, a conspicuously cut involucre, and a considerably longer corolla than *T. buckwestiorum*.

Trifolium buckwestiorum is named for its two initial collectors, Roy E. Buck and James A. West.

LATHYRUS LANSZWERTII Kellogg, Proc. Calif. Acad. Sci. 2:150. 1862.—TYPE: USA, Nevada, Washoe Co., Dismore Camp, Hunter Creek Canyon, 20–25 Jun 1907 (lectotype by Hitchcock 1952).

The California varieties of the wide ranging *L. lanszwertii* are compared as follows:

LATHYRUS LANSZWERTII var. LANSZWERTII

Plants usually trailing or climbing; leaflets commonly narrowly elliptic to oblong-lanceolate, to 1.2 cm wide; tendrils well developed and branched; corolla pale lavender to purple, 12–15 mm long. Northeast California (Modoc Co.); Sierra Nevada south to ca. Tuolumne Co.; Lake Tahoe vicinity.

Intergrading with var. *aridus* following:

LATHYRUS LANSZWERTII var. ARIDUS (Piper) Jepson, Fl. Calif. 2:389. 1936.

Plants short, erect; leaflets narrow, commonly linear, 1–5 mm wide; tendrils usually reduced to a short bristle, if longer not branched or prehensile; corolla lavender or nearly white, usually about 10 mm long. Klamath Ranges; Cascades and Sierra Nevada, south to ca. Tuolumne Co.

Lathyrus lanszwertii Kellogg var. **tracyi** (Bradshaw) Isely, comb. nov.—*L. tracyi* Bradshaw, Bot. Gaz. 80:245. 1925; *L. bolanderi* S. Watson var. *tracyi* (Bradshaw) Jepson, Fl. Calif. 2:391. 1936.—TYPE: USA, California, Humboldt Co., Grouse Mtn., near Janes Ranch, 6 May 1918, *Tracy 4943* (holotype, UC).

Plants climbing or erect; leaflets of diverse shape, elliptic to linear, to 1.2 cm wide; tendrils well developed or reduced to a bristle; corolla cream- or yellowish-white, often dark veined, 10–13 mm long. North cismontane California, primarily Klamath Ranges.

Broich (1983, p. 95) observed that "Most specimens of *L. tracyi* are barely distinguishable from *L. lanszwertii* ssp. *aridus,*" and (p. 96), "in all probability, *L. tracyi* is conspecific with *lanszwertii.*" I also see no substantive or consistent difference between *L. tracyi* of prior literature and *L. lanszwertii* in the Pacific states. Var. *tracyi* has a restricted range, peripheral to that of var. *aridus.*

LATHYRUS NEVADENSIS S. Watson, Proc. Amer. Acad. Arts Sci. 11: 133. 1876.—TYPE: USA, California, Calaveras Co., Mammoth Grove, *Bigelow s.n.* (lectotype by Hitchcock 1952).

Unlike prior authors (e.g., Hitchcock 1952), I recognize but two regional varieties of *L. nevadensis* as follows:

a. Plants of the Cascades and Sierra Nevada and west, Washington, south to Fresno Co., California; flowers usually pink to pink-purple or blue, 13–20(–22) mm long; leaflets 4–10, 1.5–4 times as long as wide; tendrils prehensile or reduced. .... var. *nevadensis*

a′. Plants of southeast Washington, northeast Oregon, and adjacent Idaho and Nevada (Elko Co.); flowers usually white, occasionally pink-tinged to blue, 20–25 mm long; leaflets 4–6(–8), 1.5–4 times as long as wide, or linear and more than 10 times longer than wide; tendrils lacking or scarcely prehensile... var. *parkeri*

LATHYRUS NEVADENSIS var. NEVADENSIS

Lathyrus nevadensis subsp. *nevadensis.*

Lathyrus nevadensis subsp. *lanceolatus* (T. Howell) C. Hitchc., Univ. Wash. Publ. Biol. 15:45. 1952.—*L. lanceolatus* T. Howell, Fl.

N.W. Amer. 1:158. 1898.—TYPE: USA, Oregon, at Glendale [Douglas Co.] (holotype, OSC).

Lathyrus nevadensis var. *nuttallii* (S. Watson) C. Hitchc., Univ. Wash. Publ. Biol. 15:45. 1952.—*L. nuttallii* S. Watson, Proc. Amer. Acad. Arts Sci. 21:450. 1886—TYPE: USA, "Upper California," *Nuttall s.n.* (holotype, UC).

Lathyrus nevadensis var. *puniceus* C. Hitchc., Univ. Wash. Publ. Biol. 15:46. 1952.—TYPE: USA, Washington, Chelan Co., 21 May 1949, *C. L. Hitchcock 18973* (holotype, WTU).

Lathyrus nevadensis var. *pilosellus* (Peck) C. Hitchc., Univ. Wash. Publ. Biol. 17(3):285. 1961.—*L. ridigus* var. *pilosellus* Peck, Torreya 28:55. 1928—TYPE: USA. Oregon, Lane Co., summit of Horse Mt., 11 mi SE of McKenzie, *Peck 7869* (holotype, WTU).

Hitchcock's subsp. *nevadensis* has reduced tendrils and large flowers, often to 20 mm, while subsp. *lanceolatus* ideally is characterized by evident tendrils and smaller flowers, less than 20 mm long. The two forms are sympatric in the Sierra Nevada and southern Cascades, the *lanceolatus* kind predominating northward in Oregon and the *nevadensis* type southward. However, they form a continuum. Even though Hitchcock (1952) gave them taxonomic status he remarked (p. 43), "Much of the material in herbaria is of an intermediate nature and extensive field observation indicates that the two types of plants interbreed freely."

Hitchcock's vars. *nuttallii, puniceus,* and *pilosellus,* cited above, are all regional minor flower color variants.

LATHYRUS NEVADENSIS var. PARKERI (H. St. John) C. Hitchc., Univ. Wash. Publ. Biol. 15:45. 1952.—*L. parkeri* St. John, Fl. Southeast. Washington and adjacent Idaho, p. 223. 1937.—*L. nevadensis* subsp. *lanceolatus* var. *parkeri* (St. John) C. Hitchc., Univ. Wash. Publ. Biol. 15:45. 1952. TYPE: USA, Idaho, Latah Co., Grizzly Camp, *Parker 511* (holotype, WS).

Lathyrus cusickii S. Watson, Proc. Amer. Acad. Arts Sci. 17:371. 1882.—*L. nevadensis* subsp. *cusickii* (S. Watson) C. Hitchc., Univ. Wash. Publ. Biol. 15:44. 1952.—TYPE: USA, Oregon, Union Co., dry mountain slopes, *Cusick s.n.* (holotype, presumably GH).

Var. *parkeri* differs from var. *nevadensis* regionally and morphologically as given in the key above. It is the ssp. *cusickii* of prior authors, which sadly must be replaced by the varietal epithet *parkeri.* Var. *parkeri,* sensu Hitchcock (1952) represents local Idaho populations in which the "banner [is] white, at most pinkish lined" (Hitchcock 1952, p. 45).

LATHYRUS VESTITUS Nutt. in Torrey & A. Gray, Fl. N. Amer. 1:276. 1838.—TYPE: USA, Columbia Plains near the sea, *Nuttall s.n.* (holotype, BM) (the type probably collected near Monterey, California [Hitchcock 1952]).

See varietal headings for pertinent synonymy and typification. Complete synonymy is provided by Broich (1987).

Lathyrus vestitus represents a complex that extends as a narrow band west of the Sierra Nevada and the Cascades almost the entire Pacific coast region of the United States. It includes numerous genetic-ecological forms that have been variously interpreted. Broich (1987) employed phenetic, taximetric analysis to revise the group. I recognize three varieties as in the following key.

a. Flowers dark purple-red to "wine red," 16–20 mm; standard recurved to 120°; southern California, Los Angeles Co., south to San Diego Co., also Santa Catalina Island. . . . . var. *alefeldii*
a′. Flowers various shades of lavender to purple, blue-purple, pink, or white, 14–18 mm; standard reflexed to ca. 90°; Washington to southern California (Los Angeles Co.; intermediates with var. *alefeldii* may extend further south).
  b. Washington to northern California (Del Norte and Humboldt cos.); plants glabrous or glabrate; flowers usually white. . . . . var. *ochropetalus*
  b′. Northern California (Humboldt Co.) to southern California (Los Angeles and southwest San Bernardino cos.); plants usually pubescent, but sporadically glabrous, especially adjacent to coast and inland in San Luis Obispo Co.; flowers rarely white. . . . . var. *vestitus*

LATHYRUS VESTITUS Nutt. var. VESTITUS

Lathyrus polyphyllus var. *insecundus* Jepson, Manual Fl. Pl. Calif. 582. 1925.—TYPE: USA, California, Marin Co., Olema, 28 Mar 1897, *Jepson 13644* (holotype, JEPS).

Lathyrus vestitus subsp. *bolanderi* (S. Watson) C. Hitchc., Univ. Wash. Publ. Biol. 15:19. 1952.—*L. bolanderi* S. Watson, Proc. Amer. Acad. Arts Sci. 20:363. 1885.—TYPE: USA, California, Oakland, thickets, creek banks, *Bolander 337* (holotype, GH).

Lathyrus vestitus subsp. *laetiflorus* (E. Greene) Broich, Syst. Bot. 12: 151. 1987.—*L. laetiflorus* E. Greene, Erythea 1:105. 1893.—TYPE: USA, California, seeds from Los Angeles, cultivated at Berkeley, May 1903 (holotype, UC).

Lathyrus vestitus subsp. *laevicarpus* Broich, Syst. Bot. 12:151. 1987.—TYPE: USA, California, Ventura Co., 2 Jun 1952, *C. L. Hitchcock 19573* (holotype, WTU).

Var. *vestitus,* broadly defined, is diverse in habit (short and erect to viny), leaflet proportions, flower size and color, pubescence, and the glandular condition of the ovary. There is a gradual trend, north to south of greater flower size, which culminates in var. *alefeldii.*

Amidst the plethora of local variation incumbent in *L. vestitus,* Broich's (1987) data provide two "modes" from Santa Barbara to

Los Angeles and western San Bernardino cos., California. These document subspp. *laevicarpus* and *laetiflorus,* which are distinguished from each other and var. *vestitus* on the basis of the presence or not of ovary pubescence and length of the style. These taxa possibly or probably have nomenclatural merit, but I include them under the umbrella var. *vestitus* for two reasons: (1) I have had difficulty identifying material and relating it to the assigned ranges of the taxa, and (2) the listing of categories such as these are discouraged for the purposes of the Jepson Manual: e.g.,"keys and descriptions should emphasize features visible with little or no magnification" (Jepson Manual Project, undated, p. 4). The serious student of California *Lathyrus* should of course consult Broich's paper (1987).

Lathyrus vestitus var. **alefeldii** (T. White) Isely, comb. nov.—*L. alefeldii* T. White, Bull. Torrey Bot. Club 21:449. 1894.—*L. laetiflorus alefeldii* (T. White) Bradshaw, Bot. Gaz. 80:261. 1925 (rank not given).—*L. laetiflorus* var. *alefeldii* (T. White) Jepson, Fl. Calif. 2:391. 1936.—*L. laetiflorus* subsp. *alefeldii* (T. White) C. Hitchc., Univ. Wash. Publ. Biol. 15:23. 1952 (attributed to Bradshaw).—*L. vestitus* (T. White) subsp. *alefeldii* Broich, Syst. Bot. 12:151. 1987.—TYPE: USA, California, San Diego, May 1852, *Thurber 524* (holotype, NY).

Lathyrus vestitus var. **ochropetalus** (Piper) Isely, comb. nov.—*L. ochropetalus* Piper, Proc. Biol. Soc. Wash. 31:189. 1918.—*L. vestitus* subsp. *ochropetalus* (Piper) C. Hitchc., Univ. Wash. Publ. Biol. 15:19. 1952.—TYPE: USA, Washington, Seattle, Jun 1918, *C. N. Piper 482* (holotype, NY).

L. peckii Piper, Proc. Biol. Soc. Wash. 31:190. 1918.—TYPE: USA, Oregon, Curry Co., Harbor, 31 Jul 1913, *M. E. Peck 4008* (holotype, WS).

As given in the above key, vars. *vestitus* and *ochropetalus* differ from one another in the usual association of both flower color and pubescence. By these criteria, var. *ochropetalus* extends from central Washington only to northern California, not to middle California as treated by prior authors.

This correlation fails to the degree that pubescence is a quantitative character. Glabrate extremes within the range of variety *vestitus* are most conspicuous contiguous to the coast where they have been called variety or subspecies *bolanderi.* Broich (1987, pp. 147–148) suggested that the glabrate condition reflects a coastal mesophytic habitat contrasting with the drier conditions of the chaparral to which the pubescent kinds are exposed. Be that as it may, it seems likely that glabrate plants or populations up to 250 miles distant from the primary range of the white-flowered, consistently glabrous var. *ochropetalus* are more closely related to the contiguous pubescent var. *vestitus* with which they share flower color. I have therefore referred them to var. *vestitus*. They include *L. bolanderi* and its nomenclatural derivatives that then become taxonomic synonyms of var. *vestitus*. Hence a new designation (i.e., var. *ochropetalus*) is needed for the northern phase of the species.

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I thank those who helped me with *Trifolium buckwestiorum*: Mélica Muñoz-Schick (SGO), for loan of specimens; Dr. Rupert Barneby (NY), who searched the South American holdings of that herbarium; and David Smith (ISC), who did likewise at the Missouri Botanical Garden. Roy Buck (JEPS) rechecked the Exsiccata citations and Earl Bishop wrote the Latin for *Trifolium buckwestiorum*. The figure was prepared by Beatriz Spalding.

Deborah Lewis, Patrick Herendeen, and Steve Broich read the manuscript and offered suggestions. My appreciation!

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CHROMOSOME NUMBERS IN SOME CACTI OF WESTERN NORTH AMERICA—VI, WITH NOMENCLATURAL CHANGES

DONALD J. PINKAVA, BRUCE D. PARFITT, MARC A. BAKER
Department of Botany, Arizona State University,
Tempe, AZ 85287

RICHARD D. WORTHINGTON
Department of Biological Sciences, University of Texas,
El Paso, TX 79968

ABSTRACT

Documented meiotic and mitotic chromosome counts are reported for 69 taxa, including interspecific hybrids, representing 11 genera of Cactaceae from the southwestern United States and northern Mexico. These include first reports for 16 taxa. New ploidy levels were determined for two additional taxa. These chromosome counts are all consistent with the base number for the Cactaceae, $x=11$.

Nomenclatural changes are: **Opuntia** ×**kelvinensis** V. Grant & K. Grant (pro sp.) (*O. fulgida* × *O. spinosior*), **O.** ×**vaseyi** (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* × *O. phaeacantha*), **O.** ×**occidentalis** Engelm. (pro sp.) (*O. littoralis* × [*O. engelmannii* × *O. phaeacantha*]), and **O. wolfii** (L. Benson) M. A. Baker, comb. et status nov.

RESUMEN

Se reportan conteos meióticos y mitóticos documentados de cromosomas para 69 taxa, representando 11 géneros de cactáceas del suroeste de los Estados Unidos y del norte de México. Estos incluyen los primeros reportes para 16 taxa. Neuvos niveles de ploidia fueron determinados para dos taxa adicionales. Estos conteos de cromosómas son todos consistentes con el número base para Cactaceae, $x=11$.

Cambios de nomenclatura son: **Opuntia** ×**kelvinensis** V. Grant & K. Grant (pro sp.) (*O. fulgida* × *O. spinosior*), **O.** ×**vaseyi** (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* × *O. phaeacantha*), **O.** ×**occidentalis** Engelm. (pro sp.) (*O. littoralis* × [*O. engelmannii* × *O. phaeacantha*]), y **O. wolfii** (L. Benson) M. A. Baker, comb. et status nov.

This report on chromosome numbers is part of a continuing effort to clarify taxonomic and evolutionary relationships among the Cactaceae. Polyploid chromosome numbers, especially in *Opuntia* and *Echinocereus,* aid in distinguishing closely related taxa and in verifying occurrences of hybridization. The base number of the family is established as $x=11$. Pinkava et al. (1985) reported that among the three subfamilies of Cactaceae the percentages of taxa known to include polyploids for the three subfamilies were: Pereskioideae—0.0% of 5 taxa; Opuntioideae—63.3% of 169 taxa; and Cactoideae—12.5% of 377 taxa.

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METHODS

Flower buds were collected in developmental series from plants growing in native habitats or in cultivation. Buds were killed and fixed in chloroform, 95% ethanol and glacial acetic acid (0.6:3:1) for at least 24 hours, transferred to 70% ethanol, and refrigerated. Anthers were squashed in acetocarmine and mounted in Hoyer's medium (Beeks 1955). Mitotic counts were obtained from root tips fixed, stained, and mounted according to the method of Parfitt (1979). Pollen stainability was based on 500+-grain samples stained in aniline blue in lactophenol (Maneval 1936).

RESULTS

Chromosome numbers were determined for 341 individual cacti representing 69 taxa in 11 genera (Table 1). First counts are reported for 14 taxa of 13 species plus two interspecific hybrids. New numbers are determined for two additional species, *Opuntia prolifera* and *Opuntia leptocaulis*.

The hexaploid number (Table 1) is new for *Opuntia prolifera,* previously known from diploid (Yuasa et al. 1973; Pinkava and Parfitt 1982) and triploid individuals (Yuasa et al. 1973). The triploid number for *Opuntia leptocaulis* is new. This species previously was known as diploid (Yuasa 1973; Pinkava et al. 1977, 1985) and tetraploid (Fischer 1962; Pinkava et al. 1973; Yuasa 1973; Conde 1975; Weedin and Powell 1978; and $2n$=ca. 44 by Ward 1984). The Sonoran Desert is now known to have both diploid and triploid individuals. Our diploid count from the Chihuahuan Desert (*Baker 5080 & Daniel*) is the first from that region.

New in our continuing series of studies are 26 taxa of which 16 were cytologically undescribed; the other 10 had been counted previously and all are consistent with our findings: 1) diploid *O. polyacantha* var. *trichophora* (Yuasa et al. 1973; Weedin and Powell 1978; Weedin et al. 1989); 2) *O. rosarica* (Yuasa et al. 1973); 3) hexaploid *O. stricta* var. *dillenii* (Carpio 1952; Yuasa et al. 1973); 4) diploid *O. strigil* (Weedin and Powell 1978; Weedin et al. 1989); 5) *Echinocereus engelmannii* var. *chrysocentrus* (Parfitt 1978); 6) *E. fendleri* var. *fendleri* (Weedin and Powell 1978); 7) *E. nicholii* (Parfitt 1987); 8) *Echinomastus warnockii* (Weedin and Powell 1978); 9) diploid *Coryphantha robertii* (Beard 1937, as *Escobaria runyonii*); and 10) *C. vivipara* var. *vivipara* (Fischer 1971).

Four of the above 10 taxa also have had discordant numbers reported: *O. polyacantha* var. *trichophora* as $2n$=ca. 44 (Weedin and Powell 1980); *O. stricta* var. *dillenii* as $2n=22$ (Spencer 1955) and as $2n=12, 22, 26, 36$, etc. (Sampathkumar and Navaneetham 1980a, b); *O. strigil* as $n=22$ (Weedin et al. 1989); and *Coryphantha vivipara* [var. *vivipara*] as $2n=44$ (Löve and Löve 1982).

Table 1. Chromosome Numbers Determined for Certain Cacti of Western North America. Voucher specimens are on deposit at ASU unless otherwise noted. Symbols: * = first chromosome count for taxon; ** = new number for taxon; *** = mitotic material. Percentages in parentheses after collector numbers represent pollen stainability. Collector names abbreviations: RA = R. Anthony; MAB = M. A. Baker; CMC = C. M. Christy; RKG = R. K. Gierisch; LAM = L. A. McGill; BDP = B. D. Parfitt; DJP = D. J. Pinkava; KLR = K. L. Roberts; AS = A. Sanders; NT = N. Trushell; RDW = R. D. Worthington.

OPUNTIOIDEAE

Opuntia acanthocarpa Engelm. & J. Bigelow var. *coloradensis* L. Benson
n=11. **Arizona.** La Paz Co., T1S R18W, 2 km W of Signal Peak, *MAB 7729.* Maricopa Co., T7S R1E, Vekol Valley, *MAB 7726A.* Pima Co., SW of Ajo, near Lime Hill. T14N R6W S7 NW¼–S6 SW¼, *BDP 3569 & Landrum* (counted by Eggers).

Opuntia acanthocarpa var. *major* Engelm. & J. Bigelow
n=11. **Arizona.** Pinal Co., ESE of Florence, ca. 20 mi E of jct US 80-89 and 289, *DJP 13811 et al., LAM 2287, 2288.*

Opuntia acanthocarpa var. *major* × *Opuntia spinosior* (Engelm.) Toumey
*n=11. **Arizona.** Pinal Co., ESE of Florence, T6S R12E S11, *LAM 2451* (92.7%); T6S R12E S30, *LAM 2468* (yellow-fld.).

Opuntia acanthocarpa var. *thornberi* (Thornber & Bonker) L. Benson
n=11. **Arizona.** Yavapai Co., ca. 11 mi E from I-17 along Bloody Basin Rd, T10N R4E S28, *NT 82-116, 82-122 & MAB.*

Opuntia arenaria Engelm.
n=11. **Texas.** El Paso Co., frontage road along E side of I-10, 0.5 mi N of junction with N end of Mesa Drive, *BDP 3473* (99.0%), *3475* (97.8%) *& KLR.*

Opuntia aurea E. Baxter
$2n=6x=66$. **Arizona.** Mohave Co., Cedar Ridge, T40N R6W S12, *RKG 5072-0* (ca. $2n$=66); SE of Lost Spring Mt., T41N R7W S35, *RKG 5082.*
Utah. Kane Co., 12.8 mi N of the jct US 89 & US 89A in Kanab, *BDP 3618 & KLR.*

Opuntia basilaris Engelm. & J. Bigelow var. *brachyclada* (Griffiths) Munz
n=11. **California.** Los Angeles Co., Trailhead at entrance to South Fork Campground, South Fork of Big Rock Creek, T4N R9W S33 NE¼, *BDP 3596 & MAB.*

Opuntia basilaris var. *heilii* Welsh & Neese
*n=11. **Utah.** Wayne Co.: ca. 12 mi W of Hanksville, T28S R9E S13 SW¼, *Anderson 88-14.*

Opuntia basilaris var. *treleasei* (J. Coulter) J. Coulter ex Toumey
$2n=3x=33$. **California.** Kern Co., NE of Bakersfield, T29S R28E S1, *R. Lewis 1, 2, 8.*

Opuntia chaffeyi Rose
*$2n=4x=44$. **Mexico.** Zacatecas, road from Nieves to Concepción del Oro, just N of Comacho on road to Cedros, *Glass & Foster 4038,* cultivated in Arizona by Parfitt as *BDP 3612.*

Opuntia chlorotica Engelm. & J. Bigelow
n=11. **Arizona.** Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.5–5.7 mi W of jct AZ 289, *BDP 4240, 4250 & CMC.*

Opuntia chlorotica × *Opuntia santa-rita* (Griffiths & Hare) Rose
*n=11. **Arizona.** Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.7 mi W of jct AZ 289, *BDP 4245, 4251 & CMC* (meiosis irregular).

TABLE 1. CONTINUED

Opuntia cholla F. A. C. Weber

$n=11$. **Mexico.** Baja California, Mex Hwy 1, 60 mi SE of Cataviña, *DJP 14226, et al.*; 14.2 mi N of turn in center of El Rosario, *DJP 14212, et al.*

Opuntia echinocarpa Engelm. & J. Bigelow

$n=11$. **Arizona.** Maricopa Co., T1S R6W S10 SW¼, 4 mi N of Centennial Wash, 6 mi NW of Gila R., *MAB 7734.*

California. San Bernardino Co., W bank of Mojave River, Victorville, T5N R4W S35 SE ¼, *MAB 7515 & BDP*; 10 km E of Goffs, T11N R17E S35 NE¼, *MAB 7507 & BDP.* San Diego Co., 5.3 km NW of Imperial Co. line, T15S R8E S34 SW¼, *MAB 7531 & BDP.*

Opuntia engelmannii Salm-Dyck ex Engelm. var. *engelmannii*

$n=33$. **Arizona.** Yavapai Co., 112°42′W, 34°23′N, *MAB 7547*; T12N R5W S1 NE¼, *MAB 7548*; N of Sunset Rest Area along I-17, T10N R2E S14, *BDP 3939.*

Opuntia fulgida Engelm. var. *fulgida*

$n=11$. **Arizona.** Maricopa Co., T6S R3W S16, I-8, ca. 10 mi E of Gila Bend turnoff, *MAB 7836, LAM 90-2, -3, -4, -6.* Pima Co., Organ Pipe Cactus Nat'l. Mon.: ca. 1.5 km S of Diablo Mts., *MAB 7829*; Estes Canyon trail head, *MAB 7835.* Pinal Co., ESE of Florence, T5S R11E S17, *MAB 3787* (97.4%), *3788*; T5S R12E S34, *DJP 13805 et al.* (52.7%); T6S R12E S3, *LAM 2459, 2460, DJP 13950, 13951 et al.*; T6S R12E S11, *MAB 3779, 3790, 3791, 3792*; T6S R12E S13, *MAB 3795* (99.4%), *3796, 3797, 3798,* (75.0%), *3799* (85.4%); T6S R13E S29, *MAB 3803* (97.4%), *3808*; T9S R12E S12, *MAB 3829*; 42.6 mi E of jct US 80-89 and 289, *DJP 13819 et al.* (69.5%). Pinal Co., Peralta Canyon: T1N R10E S31, *MAB 4593* (97.0%), *4588* (97.6%), *4589* (92.3%), *4590, 4591* (92.4%); T1S R9E S1, *4597* (62.4%), *4598* (84.7%); T1S R9E S11, *MAB 4603* (90.4%), *4606* (91.8%); T1S R9E S12, *MAB 4599* (45.9%), *4601, 4602* (98.5%); T1S R10E S6, *MAB 4595* (95.2%).

$2n=3x=33$. **Arizona.** Pinal Co., ESE of Florence, T6S R12E S3, *DJP 13807* (40.7%), *13807B, 13807C & LAM*; T6S R12E S11, *MAB 3704, 3705, 3770, 3772, 3778, 3793, 3794*; T6S R12E S12, *DJP 13954, 13955* (29.9%) *& LAM*; T6S R13E S29, *MAB 3800, 3801, 3802, 3805, 3807.*

Opuntia fulgida var. *mammillata* (A. C. V. Schott) J. Coulter

$n=11$. **Arizona.** Pinal Co., ESE of Florence: T9S R12E S12, *MAB 3827, 3828*; T9S R13E S21, *MAB 3826.* Pinal Co., Peralta Canyon: T1N R10E S31, *MAB 4592* (94.1%), *4594* (94.6%); T1S R9E S11, *MAB 4605* (80.8%).

Opuntia imbricata (Haw.) DC. var. *imbricata*

$n=11$. **Mexico.** Nuevo Leon, Huasteca Canyon, *MAB 5050 & Daniel.* Tamaulipas, Mex Hwy 101, 3 mi NNE of Juamave, *MAB 5075 & Daniel.*

Opuntia imbricata var. *imbricata* × *Opuntia spinosior* (Engelm.) Toumey

***$n=11$. **New Mexico.** Doña Ana Co., Organ Mtns., T24S R3E S12 SW¼, *RDW 8300-8301-8302* (69.5%) (pop. voucher) (ASU, UTEP) (counted by Fillipi).

Opuntia × *kelvinensis* V. Grant & K. Grant (pro sp.)

$n=11$. **Arizona.** Pinal Co., ESE of Florence: T6S R12E S34, *MAB 4318* (58.1%), *DJP 13952* (44.6%) *& LAM*; T6S R13E S34, *MAB 4340*; ca. 20 mi E of jct US 80-89 and 289, *DJP 13809* (78.7%), *13809A & LAM, LAM 2462 & DJP.*

$2n=3x=33$. **Triploid Morphotype A: Arizona.** Pinal Co., ESE of Florence: T5S R12E S27, *LAM 2454* (20.4%), *DJP 13802* (16.1%) *et al.*; T5S R12E S28, *LAM 2443, 2444, 2452, 2453* (20.2%) *& DJP, DJP 13800 et al.*; T5S R12E S34, *DJP 13804* (20.7%) *et al.*; T6S R12E S3, *LAM 2448* (20.0%), *2455* (15.3%), *2456* (21.6%), *2457*

TABLE 1. CONTINUED

(20.0%); T6S R12E S11, *MAB 3706* (16.4%), *3771, 3775, 4297, 4324*; T6S R13E S19, *MAB 4329* (20.0%), *4360* (30.1%); T6S R13E S29, *MAB 3806, 4332* (20.6%), *4334, 4335* (23.2%), *4336* (31.4%); T6S R13E S34, *MAB 4339*; T6S R13E S28, *MAB 3784* (26.4%); T6S R13E S35 *MAB 4349, 4350*; 1.7 mi NW of Bakerville Site Windmill near Cottonwood Hill, T7S R13E S2, *LAM 1363* (19.0%).

Triploid Morphotype B: Arizona. Pinal Co., ESE of Florence: T4S R13E S1, *MAB 4640 & DJP*; T5S R12E S35, *DJP 14002 & LAM*; T6S R12E S3, *MAB 4296* (17.7%), *DJP 14003 & LAM*; T6S R12E S11, *MAB 4298* (23.2%), *4304, 4305* (18.2%), *4306* (12.8%), *4307* (14.4%), *4313* (28.6%), *4316* (59.1%), *4317* (31.5%), *4319* (33.6%), *4320* (42.2%), *4322* (38.6%), *LAM 2450* (27.7%); 19.3 mi E of jct US 80-89 and 289, *LAM 2285* (39.5%), *DJP 13808* (23.0%) *et al.*

Opuntia kunzei Rose

*$2n=4x=44$. **Arizona.** La Paz Co., Hovatter Rd SW of I-10, *BDP 3839 & KLR*, (pop. voucher); US 60, 10 mi W of Gladden, T6N R12W S24, *MAB 7614.*

Opuntia leptocaulis DC.

$n=11$. **Arizona.** Maricopa Co., T1N R6W S28, Paloverde Power Plant, *MAB 7737.* Yavapai Co., Verde Valley, T13N R6E S30, *MAB 7039 & NT*; T10N R4E S15, 11 mi E of I-17 on Bloody Basin Rd, *NT 82-154 & MAB*; 0.5 km N of Rock Springs, T8N R2E S10, *MAB 7545, 7546.*

Mexico. Tamaulipas, Mex Hwy 101, 14 mi ENE of Jaumave, *MAB 5080 & Daniel.*

$2n=3x=33$. **Arizona. Yavapai Co., T6N R2E S10, *MAB 4549 et al.*

$2n=4x=44$. **Texas.** El Paso Co., Franklin Mts. NW of El Paso, *RDW s.n.* (ASU, UTEP).

Opuntia littoralis (Engelm.) Cockerell

$3n=6x=66$. **California.** Riverside Co., 5.1 mi W of I-15 at Temecula, *BDP 3499* (42.9%) *et al.*; S of Riverside and Lake Mathews, *BDP 3490* (67.6%) *et al.*

Opuntia macrocentra Engelm.

$2n=4x=44$. **Arizona.** Pima Co., T11S R9E S28, ca. 4 mi N of Silverbell, *Wiens 90-RT-64-04* (counted by S. Gama).

New Mexico. Doña Ana Co., Bishop's Cap, T24S R3E S25, *RDW 13592* (with up to 7 IV's) (ASU, UTEP).

Opuntia macrorhiza Engelm. var. *macrorhiza*

$2n=4x=44$. **Arizona.** Apache Co., Navajo Nation, Navajo Forest Rd 7700, E of Navajo Community College, 36°18′N, 109°9′W, *BDP 3552* (77.1%) *& Reeves.*

Opuntia nicholii L. Benson

$2n=6x=66$. **Arizona.** Coconino Co., Hwy 89A, 14.9 mi W of road to Lee's Ferry, *BDP 3634, 3635 & KLR.*

Opuntia oricola Philbr.

$2n=6x=66$. **California.** Santa Barbara Co., Montecito, San Ysidro Canyon, 0.1 mi E of San Ysidro Ranch (topotype), *BDP 3508* (72.1%) *& RA.* San Diego Co., S of Carlsbad, near Agua Hedionda Lagoon, *BDP 3529* (50.7%) *& KLR.*

Opuntia parishii Orc.

*$n=11$. **Arizona.** Maricopa Co., Vekol Valley Rd, 6 mi S of I-8, *BDP 4304, 4306, 4307.* Mohave Co., vicinity of Cottonwood Wash, T34N R16W S11, *RKG 5063A.*

Opuntia parryi Engelm. var. *parryi*

$n=11$. **California.** Riverside Co., S of Riverside and Lake Matthews, *BDP 3492 et al.*

TABLE 1. CONTINUED

Mexico. Baja California, 17.5 mi SW of turnoff to Rancho Mike from Mex Hwy 3, *DJP 14182 et al.*

Origin unknown. Cultivated at Rancho Santa Ana Bot. Gard., *MAB s.n.*

Opuntia parryi Engelm. var. *serpentina* (Engelm.) L. Benson

*n=11. **California.** San Diego Co., San Diego City, *Wolf 9472,* cultivated at Rancho Santa Ana Bot. Gard. as *RSA 3373, MAB s.n.*; Chula Vista, E Street Marsh, *BDP 3520 & KLR*; Telegraph Canyon, ca. 7 km E of ocean, T18S R1W S7 NE¼, *MAB 7522 & BDP.*

Opuntia phaeacantha Engelm.

$2n=6x=66$. **Arizona.** Santa Cruz Co., T23S R12E S19, Ruby Rd, 5.7 mi W of jct AZ 289, *BDP 4249 & CMC.*

California. Riverside Co., CA 371 2.5 mi E of Anza and 1.8 mi W of CA 74, T7S R3E S13, *BDP 3518* (88.2%) *et al.* San Bernardino Co., Cactus Flat, N side of San Bernardino Mtns., T3N R2E S30, *AS 6600 et al.*; N side of Baldwin Lake, ca. ¾ mi N of CA 18, road to Baldwin Mine, *AS 6604, 6605 et al.*

New Mexico. Luna Co., ca. 18 mi W of Columbus on Hwy 9, 1.7 mi E of Hermanas and 25 mi E of Hachita, *BDP 3483* (94.6%) *& KLR*; N end of Florida Mts., T25S R8W SW¼, *RDW 11924.*

Texas. El Paso Co., Three Sisters Hills, *RDW 17899* (ASU, UTEP).

Opuntia polyacantha Haw. var. *trichophora* (Engelm. & J. Bigelow) J. Coulter

n=11. **Texas.** El Paso Co., Hueco Mtns., 32°54′45″N, 106°08′15″W, *RDW 8068.*

Opuntia prolifera Engelm.

$2n=3x=33$. **California.** Orange Co., Laguna Beach, *Stark 139,* cultivated at Rancho Santa Ana Bot. Gard., *MAB s.n.*; San Diego Co., Chula Vista, H Street 1.7 mi E of I-805. *BDP 3521 & KLR*; 0.5 km N of Batiquitos Lagoon, T12S R4E S28 SE¼, *MAB 7520 & BDP*; ca. 4 km N of San Miguel Mt., *MAB 7524 & BDP*; Telegraph Canyon, ca. 7 km E of ocean, T18S R1W S7, *MAB 7521 & BDP.*

Mexico. Baja California, Mex Hwy 1, 19.3 mi S of San Vicente and 2.1 mi N of Colonet, *DJP 9006 et al.*; Mex Hwy 1, 11.7 mi SE of El Rosario, *DJP 9069 et al.*; 12.5 mi E of San Telmo, on fork to Rancho Buena Vista, *LAM 514 & Moulis*; 5.5 mi E of El Rosario, then 4.5 mi NE on left fork, *DJP 8787* (45.8%), *9140, 9149, 9154 et al.*; 8.3 mi on road to San Telmo from vicinity of Meling Ranch, *DJP 14198 et al.*

$2n=6x=66$. **Mexico. Baja California, 13 mi E of San Telmo, road to San Pedro Martir, *Gallagher 82-46.*

Opuntia ramosissima Engelm.

n=11. **Arizona.** La Paz Co., T4N R1W S4, US 60, W of Hope, *MAB 7741, 7743.* Maricopa Co., flats NE of Gila Bend Mts., *MAB 7738.* Mohave Co., US 93, ca. 19 mi S of Hoover Dam, *DJP 14370 et al.*

Mexico. Baja California Norte, Mex Hwy 5, 1.3 mi S of jct Mex Hwy 3, *DJP 14130 et al.*

$2n=4x=44$. **Arizona.** Maricopa Co., ca. 5 km NW of Gila R., T1S R6W, *MAB 7735, 7736*; flats NE of Gila Bend Mts., *MAB 7732.*

Opuntia rosarica G. Lindsay

n=11. **Mexico.** Baja California, 5.5 mi E of El Rosario, then 4.5 mi NE on left fork, *DJP 12143, 12147 et al.*

Opuntia rufida Engelm.

n=11. **Texas.** Hudspeth Co., S end of Quitman Mtns., *RDW s.n.*

Table 1. Continued

Opuntia santa-rita (Griffiths & Hare) Rose

$n=11$. **Arizona.** Santa Cruz Co., T23S R12E, Ruby Rd ca. 5 mi W of jct AZ 289, *BDP 4241, 4244 & CMC.*

Origin unknown. Cultivated at Payne Hall, Arizona State Univ. campus, *DJP 14368, 14369* (crested forms).

Opuntia spinosior (Engelm.) Toumey

$n=11$. **Arizona.** Gila Co., 1 km N of Young, T9N R14E S20, *MAB 7038 & NT.* Pinal Co., Oak Flat: T1S R6E S20, *MAB 4684* (96.5%), *4685* (82.7%), *4690* (95.2%); T1S R13E S28 SW¼, *MAB 4672* (96.8%), *4673* (96.9%), *4688* (89.9%), *4691* (92.1%); T1S R13E S20, *MAB 4674* (96.4%), *4680* (97.0%), *4682* (66.6%), *4683* (95.1%), *4687* (96.6%), *4689* (94.2%); T1S R13E S33 NE¼, *MAB 4677.* Pinal Co., ESE of Florence: T6S R12E S3, *MAB 3663, LAM 2446* (98.0%), *2447* (98.5%), *2449* (95.0%), *2461*; T6S R12E S11, *MAB 3774, 4302, 4309, 4312*; T6S R12E S10, *LAM 2464*; T6S R12E S13, *LAM 2466* (yellow-fld.); T6S R12E S12, *DJP 13815* (98.5%), *13816* (92.8%) *et al.* (both yellow-fld.); T6S R13E S19, *MAB 4314*; T6S R13E S29, *MAB 3674, 3676, 4331, 4333*; T6S R13E S34, *MAB 4337, 4341, 4342, 4343, 4344*; T6S R13E S28, *MAB 3780* (yellow-fld.), *3781*; T6S R13E S35, *MAB 4346, 4347, 4352*; T7S R13E S12, *MAB 4354, 4355, 4356*; ca. 20 mi E of jct US 80-89 and 289, *LAM 2463* (96.5%), *2465 & DJP* (87.9%).

New Mexico. Luna Co., Florida Mtns., Mahoney Park, T25S R8W S26 SW¼, *RDW 8124* (counted by Fillipi).

Opuntia stricta (Haw.) Haw. var. *dillenii* (Ker Gawler) L. Benson

$n=33$. **Origin unknown.** Cultivated at Desert Botanical Gard. as *DBG 80-291-03, Zimmerman s.n.*

Opuntia strigil Engelm.

$n=11$. **Texas.** Terrell Co., 2.5 mi E of Sanderson, *RDW 8007* (ASU, UTEP) (counted by Fillipi).

Opuntia ×*vaseyi* (J. Coulter) Britton & Rose (pro sp.)

$2n=6x=66$. **California.** Riverside Co., NNW of Lake Elsinore in Temescal Wash, *BDP 3495* (66.6%) *et al.*; Pauba Valley, CA 79 crossing of Temecula River, 4.6 mi E of jct with road to Pala, *BDP 3502* (67.7%), *3503* (27.9%) *et al.* San Diego Co., Chula Vista, H Street 1.1 mi E of I-805, *BDP 3526* (63.6%) *& KLR.* Ventura Co., W of Thousand Oaks ¼ mi N of Camarillo Park exit from US 101, *BDP 3507* (80.8%) *& RA.*

Opuntia whipplei Engelm. & J. Bigelow

$n=11$. **Arizona.** Mohave Co., head of Lime Kiln Canyon, T37N R16W S4, *RKG 5064A.* Yavapai Co., T10N R3W S24 NE¼, ca. 3 mi SE of Wagoner, *MAB 7826.*

Opuntia wolfii (L. Benson) M. A. Baker

*$2n=6x=66$. **California.** Imperial Co., T16S R9E S32 SE¼, 1 km SW of Sugarloaf Mt. (type locality), *MAB 7533* (86.1%), *7534 & BDP.* San Diego Co., T15S R8E S34, 3–4 km SE of Sweeney Pass, *MAB 4917, MAB 7532 & BDP.*

CACTOIDEAE

Carnegiea gigantea (Engelm.) Britton & Rose

$n=11$. **Arizona.** Pima Co., Organ Pipe Cactus Nat'l. Mon., ca. 1.5 km S of Diablo Mts., *MAB 7831.*

Coryphantha robbinsorum (W. Earle) A. Zimmerman

*$n=11$. **Origin unknown.** Cultivated at Desert Bot. Gard., *Eppele s.n.* (DES).

TABLE 1. CONTINUED

Coryphantha robertii A. Berger
$n=11$. **Texas.** Val Verde Co., ca. 10 mi NW of Del Rio at Amistad Reservoir, *RDW 8260,* cultivated by Worthington as *RDW 13879* (ASU, UTEP) (pop. voucher) (counted by Fillipi).

Coryphantha vivipara (Nutt.) Britton & Rose var. *vivipara*
$n=11$. **Colorado.** Pueblo Co., Univ. of Southern Colorado, Pueblo, N of heating plant, *BDP 3661 & KLR.*

Echinocereus bonkerae Thornber & Bonker
$n=11$. **Arizona.** Gila Co., jct US 60 and road to Chrysolite Mine, 110°32′W, 33°43′N, *MAB 4659 & BDP.* Maricopa Co., vicinity of Sunflower, *BDP 3214* (DES), *Nash 106* (ASU, DES); T6N R9E S9 NW¼, *BDP 3729 & Bricker.* Yavapai Co., Forest Service Rd 269, 16–20 mi E of I-17 en route to Bloody Basin, *BDP 3604, 3605* (counted by Eggers), *3606, 3607* (counted by Eggers), *3608* (counted by Eggers), *3609, 3611 & KLR.*

Echinocereus engelmannii (C. Parry ex Engelm.) Lemaire var. *acicularis* L. Benson
$2n=4x=44$. **Arizona.** Pima Co., 15.1 mi SSW of AZ 85 on Bates Well Rd, *BDP 3562 & Landrum*; Organ Pipe Cactus Nat'l. Mon., below base of Alamo Canyon, *MAB 7788*; Organ Pipe Cactus Nat'l. Mon., headwaters of Aguajita Wash, *MAB 7772A, 7792, 7796*; ca. 4 mi N of Silver Bell on Ragged Top Peak, *Wiens s.n.,* cultivated at Desert Bot. Gard. as *DBG-1989-0195-0101, Zimmerman s.n.*

Echinocereus engelmannii var. *chrysocentrus* (Engelm. & J. Bigelow) Engelm. ex Ruempler
$2n=4x=44$. **Arizona.** Mohave Co., Alamo Rd, 18.4 mi S of jct with Signal Rd (near type locality), *BDP 4184, 4185 & CMC.* **California.** San Bernardino Co., N of Ord Mt., ca. 1 mi N of Aztec Spring, T7N R1E S1 SE¼, *BDP 3591 & MAB* (counted by Eggers).

Echinocereus engelmannii var. *engelmannii*
$*2n=4x=44$. **California.** San Diego Co., W of Ocotillo, on E side of mts. Mountain Springs exit on south side of I-8, *BDP 3599 & MAB.*

Echinocereus engelmannii var. *howei* L. Benson
$*2n=4x=44$. **California.** San Bernardino Co., T10N R19E S31 NE¼ (topotype), *MAB 7503, 7504 & BDP.*

Echinocereus engelmannii var. *variegatus* (Engelm. & J. Bigelow) Engelm. ex Ruempler
$2n=4x=44$. **Arizona.** Coconino Co., US 89a below Vermilion Cliffs, 0.8 mi E of Cliff-Dwellers Lodge, *BDP 3983, 3984 & KLR.* Mohave Co., near Signal, *BDP 4179, 4182 & CMC.*

Echinocereus fasciculatus (Engelm. ex B. D. Jackson) L. Benson var. *boyce-thompsonii* (Orc.) L. Benson
$2n=4x=44$. **Arizona.** Yavapai Co.: Forest Rd 269, 20.5 mi E of I-17 en route to Bloody Basin, *BDP 3617 & KLR* (pop. voucher).

Echinocereus fasciculatus var. *fasciculatus*
$2n=4x=44$. **Arizona.** Graham Co., T6S R28E S29/30, 1.6 mi E of Sanchez (near type locality), *BDP 4212 & CMC.* Pima Co., Tucson, near Agua Caliente Regional Park *BDP 3918, 3919 & Bricker.*

Echinocereus fendleri (Engelm.) Ruempler var. *fendleri*
$n=11$. **Arizona.** Apache Co., T11N R24E S29, near jct US 60 & AZ 61 toward St.

TABLE 1. CONTINUED

Johns, *Abbot & Abbot s.n.*, cultivated at Desert Bot. Gard. as 1984-0782-01-04, *Zimmerman s.n.*

Echinocereus fendleri var. *rectispinus* (Peebles) L. Benson
n=11. **Arizona.** Santa Cruz Co., T22S R10E S26, ca. 8.5 mi SE of Arivaca, *BDP 4191 & CMC*; T22S R11E S32, 12 mi SE of Arivaca, *BDP 4199 & CMC.*

Echinocereus ledingii Peebles
n*=11. **Arizona. Graham Co., Pinaleno Mtns., 8 mi above jct of Swift Trail & US 666; above Noon Creek, *Valenciano 002, 004, 006.*

Echinocereus nicholii (L. Benson) Parfitt
n=11. **Arizona.** Pima Co., Organ Pipe Cactus Nat'l. Mon., headwaters of Aguajita Wash, *MAB 7793*; Organ Pipe Cactus Nat'l. Mon., below base of Alamo Canyon, *MAB 7789.*

Echinomastus erectocentrus (J. Coulter) Britton & Rose var. *erectocentrus*
n=11. **Arizona.** Pima Co., ca. 16 mi SE of Oracle, T11S R16E S12, *Hodgson 4527* (ASU, DES).

Echinomastus warnockii (L. Benson) Glass & Foster
n=11. **Texas.** Brewster Co., Hwy 170, 6.2 mi E of Lajitas, *RDW 8021.* Hudspeth Co., Indio Mtns., Upper Echo Canyon, 30°47'N, 104°59'40"W, *RDW 13563* (UTEP, ASU).

Ferocactus cylindraceus (Engelm.) Orc. var. *lecontei* (Engelm.) H. Brav.-Holl. (*F. acanthodes* var. *lecontei* (Engelm.) G. Lindsay).
n=11. **Arizona.** Pima Co., SW of Ajo. 9.4 mi SSW of AZ 85 on Bates Well Rd, then 2.4 mi W, then 0.5 mi NNW to Lime Hill, T14N R6W S6/7, *BDP 3568 & Landrum.*

Lophocereus schottii (Engelm.) Britton & Rose
n=11. **Arizona.** Pima Co., Organ Pipe Cactus Nat'l. Mon., T18S R5W S14 NW¼, east hill of Dos Lomitas, *MAB 7831A.*

In this six-part series as a whole, chromosome numbers have been determined for 773 individuals of 165 taxa in 106 species in 21 genera of cacti.

DISCUSSION

In Arizona, hybridization between *Opuntia spinosior* and *O. fulgida* was first cited in the literature by Britton and Rose (1919–1923). In 1936 Peebles described a population of hybrids near Sacaton. Benson (1969) cited two collections from near Tucson. Grant and Grant (1971), after a detailed study of populations near Kelvin, considered *O. fulgida* × *O. spinosior* to be an agamospermous microspecies, naming it *O. kelvinensis.* Baker and Pinkava (1987) studied a large population near Florence cytologically and morphometrically and found *O. kelvinensis* to consist of a few diploid individuals and many triploid plants, largely apomictic. The triploid hybrids were segregated into morphotypes A and B, both more similar to

TABLE 1. CONTINUED

Mammillaria carmenae Castañeda
*n=11. **Origin unknown.** Obtained from Abbey Garden and cultivated in Arizona State Univ. greenhouse, *BDP s.n.*

Mammillaria heyderi Muehlenpf. var. *bullingtoniana* Castetter, Pierce & Schwerin
*n=11. **Arizona.** Cochise Co., along AZ 90, 6 mi S of I-10, *Clark 1494 & BDP*; AZ 90, 8.6 mi N of jct with AZ 90/82, *Clark 1497 & BDP.*
New Mexico. Luna Co., Red Mountain, ca. 9 mi WSW of Deming, T24S R10W S17, *RDW 12999* (ASU, UTEP) (counted by Fillipi).

Mammillaria heyderi var. *macdougalii* (Rose) L. Benson
n=11. **Arizona.** Pinal Co., Mt. Lemmon Rd, 17.5 mi from AZ 77, *BDP 4175 et al.*

Pediocactus peeblesianus (Croizat) L. Benson var. *fickeiseniae* L. Benson
*n=11. **Arizona.** Mohave Co., Main Street Valley, T38N R11W S22/23, *RKG 5054.*

Sclerocactus cf. *spinosior* (Engelm.) Woodruff & L. Benson
*n=11. **Arizona.** Coconino Co., vicinity of Corral Valley, Paria Plateau, T40N R4E S20, *RKG 5055.*

Sclerocactus parviflorus Clover & Jotter var. *intermedius* (Peebles) Woodruff & L. Benson
n=11. **Arizona.** Mohave Co., Cedar Ridge, T40N R6W S12, *RKG 5045A*; vicinity of Cane Beds, T41N R5W S8, *RKG 5048.*

Stenocereus thurberi (Engelm.) F. Buxbaum
n=11. **Arizona.** Pima Co., Organ Pipe Cactus Nat'l. Mon., ca. 1.5 km S of Diablo Mts., *MAB 7830.*

Correction.

Echinocereus dasyacanthus (Engelm.) N. P. Taylor
n=22. **Texas.** El Paso Co., Franklin Mtns., *RDW 10290* (fig. 22), identified by A. Zimmerman; originally published as *E. pectinatus* (Scheidw.) Engelm. var. *minor* (Engelm.) L. Benson (Pinkava et al., 1985).

O. spinosior than to *O. fulgida,* morphotype A more so than morphotype B. Voucher specimens (Table 1) document these types of hybrids for which Baker and Pinkava herein propose the following:

Opuntia ×kelvinensis V. Grant & K. Grant (pro sp.) (*O. fulgida* Engelm. × *O. spinosior* [Engelm.] Toumey).—*O. kelvinensis* V. Grant & K. Grant, Evolution 25:154–155. 1971.—TYPE: USA, Arizona, Pinal Co., just southeast of Kelvin, 15 Jun 1970, *V. Grant 70-29* (holotype, TEX!).

Opuntia echinocarpa Engelm. & Bigelow var. *wolfii* L. Benson from Imperial Co. (type locality) and San Diego Co., California were found to be hexaploid. These differ from all other dry-fruited chollas of southern California (which are all $2x$ or $4x$) in having the following combination of characters: shrubby habit, dense and strict branching pattern, with thick stem segments (2.5–4 cm in diameter), and bronze flowers bearing bronze- to red-purple filaments. Baker herein proposes the following new combination and lectotypification:

Opuntia wolfii (L. Benson) M. A. Baker, comb. et stat. nov.—*O. echinocarpa* Engelm. & Bigel. var. *wolfei* L. Benson, Cact. Succ. J. 41:33. 1969.—Type: USA, California, Imperial Co., base of Mountain Springs Grade, W edge of Colorado Desert, U.S. 80 W of El Centro, 12 Jun 1938, *Carl B. Wolf 9429* (lectotype here designated, RSA 20700!; isolectotype, UC 592967! [box] and photo ASU 155254!, US [box]).

In the original protologue, Benson cited two different specimens as "holotype" [syntypes]: the specimen prepared in the field by Wolf (*Wolf 9429*); and a specimen later prepared (12 Apr 1954, *Balls 19004* RSA!, CAS! and photo ASU!, UC) from cultivated material (RSA propagation no. 3201) of Wolf's collection. The original, field-collected specimen is here chosen as lectotype.

Pinkava and Parfitt (1988) recognized as species the following two taxa that were treated (Benson 1969a, 1982) as varieties of *O. stanlyi* Engelm. ex B. D. Jackson (a superfluous name for *O. emoryi* Engelm.): diploid *O. parishii* and tetraploid *O. kunzei* (Table 1). *Opuntia stanlyi* var. *peeblesiana* L. Benson (1969a) was typified by a specimen of *O. kunzei,* and therefore is a synonym of that species. *Opuntia kunzei* consists of relatively robust plants, with very spiny fruits, from La Paz, western Pima and Yuma counties, Arizona. Benson's (1969a, 1982) concept of var. *peeblesiana* also included some specimens of *O. parishii* from Pima and Pinal counties, Arizona (relatively small plants, with spineless fruits). These south-central Arizona populations represent a southeastward disjunction of *O. parishii*; this species also has a southwestward disjunction in the vicinity of Joshua Tree National Monument, California.

Benson (1982) recognized five varieties comprising *Opuntia basilaris.* Two of these are consistently diploid: var. *basilaris* (Parfitt 1978; Pinkava and McLeod 1971; Pinkava et al. 1973, 1977), and var. *brachyclada* (Pinkava et al. 1977; Table 1). The var. *treleasei* is triploid (Pinkava et al. 1977; Table 1) except for one diploid report (Pinkava et al. 1977). *Opuntia basilaris* var. *aurea* (McCabe ex E. Baxter) W. Marshall is hexaploid (Pinkava et al. 1973; Pinkava and Parfitt 1982; Table 1); we treat it as *O. aurea,* specifically distinct from *O. basilaris.* Two recently described varieties remain under study: diploid var. *heilii* (Table 1), which may not be distinct from var. *basilaris,* and octoploid var. *woodburyi* W. Earle (Pinkava and Parfitt 1982), which is not closely related to *O. basiliaris.* We consider the cytologically unknown var. *longiareolata* (Clover & Jotter) L. Benson as an aberrant form of var. *basilaris.*

Benson (1982) recognized five varieties of *Opuntia violacea* Engelm.; three of these—var. *macrocentra* (Engelm.) L. Benson, var.

violacea and var. *castetteri* L. Benson—were reduced to synonymy under *O. macrocentra* by Pinkava and Parfitt (1988). They consider the remaining two taxa as distinct diploid species: *O. santa-rita* and *O. gosseliniana* F. A. C. Weber. *Opuntia macrocentra* has two ploidy levels that apparently are not separable morphologically. From El Paso, TX, to central Arizona all nine chromosome counts are tetraploid (Table 1; Pinkava and McLeod 1971; Pinkava et al. 1973, 1985); from Alpine, TX, to the Rio Grande of Big Bend National Park, all eleven counts are diploid (Pinkava and Parfitt 1982; Pinkava et al. 1985; Weedin et al. 1978, 1989).

In California there are two hexaploid hybrid complexes, *Opuntia occidentalis* (Pinkava et al. 1973) and *O. vaseyi* (Table 1), each involving numerous genetic segregates making identifications exceedingly difficult and somewhat arbitrary. *Opuntia occidentalis* is not a synonym of *O. ficus-indica* (L.) Miller as proposed by Benson and Walkington (1965) but apparently does include most of hybrid population "*occidentalis*" described by them. Parfitt herein proposes the following two changes:

Opuntia ×occidentalis Engelm. & J. Bigelow (pro sp.) (*O. littoralis* [Engelm.] Cockerell × [*O. engelmannii* Salm-Dyck ex Engelm. × *phaeacantha* Engelm.]).—*O. occidentalis* Engelm. & J. Bigelow, Proc. Amer. Acad. 3:219. 1856.—TYPE: USA, California, near Los Angeles (Benson [1982] places it near Cucamonga, 43 mi E of Los Angeles, San Bernardino Co.), 19 Mar 1854, *J. M. Bigelow* (lectotype designated by Benson and Walkington [1965], MO 2015200!; photos, ASU!, DS!, MO!, POM!, US!).

Opuntia ×vaseyi (J. Coulter) Britton & Rose (pro sp.) (*O. littoralis* × *O. phaeacantha*).—*O. mesacantha* Raf. var. *vaseyi* J. Coulter, Contr. U.S. Natl. Herb. 3:431. 1896.—*O. littoralis* (Engelm.) Cockerell var. *vaseyi*–Benson & Walkington, Ann. Mo. Bot. Gard. 52:268. 1965.—TYPE: USA, Arizona, Yuma Co., Yuma (presumably a labelling error [see Britton and Rose 1919–1923]), 1881, *G. R. Vasey s.n.* (lectotype designated by Benson and Walkington [1965], US 62105!; photos, ASU!, POM, NY!, US!; isolectotype, PH).

Coulter's syntype (AZ, Ft. Verde, Jun 1883, *H. H. Rusby 624* NY!, photo ASU!) is a different taxon, *O. chlorotica* Engelm. & J. Bigelow.

These two nothospecies may be distinguished from related species by the following key (Parfitt 1991):

KEY TO THE FLESHY-FRUITED PRICKLY-PEARS OF CALIFORNIA

a. Areoles more than 38 per ovary; base of plant a single erect trunk; branches ascending.

b. Ovary with well defined tubercles when fresh, areole wool dark brown; stem glochids 0–1 mm long, inconspicuous; mature plants more than 3 m tall (octoploid). .... *O. ficus-indica*
b′. Ovary smooth, areole wool tan; stem glochids 2–12 mm long, conspicuous; mature plants less than 2.5 m tall.
  c. Style red or pink when fresh; longest spines 19–25(–28) mm long; seeds 3.5–4 mm in diameter; southwestern California Floristic Province (hexaploid). .... *O. oricola*
  c′. Style white when fresh; longest spines (24–)32–47 mm long; seeds 3 mm in diameter; southeastern California Floristic Province northward and eastward to desert mountains (diploid). .... *O. chlorotica*

a′. Areoles fewer than 36 per ovary; base of plant generally obscured by several spreading to decumbent branches (hexaploids).
b. Style and filaments white.
  c. Stem segments more than 15 cm wide; perianth all yellow; fruit red-purple throughout. .... *O. engelmannii*
  c′. Stem segments less than 14 cm wide; perianth yellow with red base; fruit externally red-purple, internally green. .... *O. phaeacantha*
b′. Style pink and filaments yellow, or, if either style or filaments white then the other colored.
  c. Stem segments more than 15 cm wide. .... *O.* ×*occidentalis*
  c′. Stem segments less than 15 cm wide.
    d. Stem segments obovate; major spines usually flat, 1–4 per areole. .. .. *O.* ×*vaseyi*
    d′. Stem segments oblong-elliptic or narrowly obovate; major spines usually round, 4–11 per areole. .... *O. littoralis*

Three of the above names for fleshy-fruited species of *Opuntia* in California (Parfitt 1991) represent substantial changes from the concepts of Benson (1982). For names used in Table 1, these changes are as follows: 1) *O. engelmannii* var. *engelmannii* (*O. phaeacantha* var. *discata* (Griffiths) L. Benson & Walkington, not *O. ficus-indica*); 2) *O. littoralis* (*O. littoralis* var. *littoralis*); and 3) *O. phaeacantha* (*O. littoralis* var. *piercei* (Fosb.) L. Benson, *O. phaeacantha* var. *major* Engelm.); and *O.* ×*vaseyi* (*O. littoralis* var. *austrocalifornica* L. Benson and var. *vaseyi* (J. Coulter) L. Benson).

All five varieties of *Echinocereus engelmannii* reported here are tetraploid, two are first reports (vars. *engelmannii* and *howei*) and all are in agreement with earlier counts for the species (Parfitt 1978; Pinkava et al. 1977, 1985; Pinkava and McLeod 1971; Pinkava and Parfitt 1982; Stockwell 1935). Varieties *armatus, munzii,* and *purpureus* remain uncounted; var. *nicholii* is diploid and is considered a distinct species (Parfitt 1987). Specimens of var. *howei* from the type locality (Table 1) have multicolored spines, not all yellow as stated by Benson (1982). However, in spine number and robustness they correspond to Benson's description of the taxon. Varieties *howei* and *armatus* may be only minor variants of var. *chrysocentrus.*

CONCLUSIONS

Repeated counting of chromosomes in some species has revealed taxonomically useful variation in ploidy level, particularly in species groups already known to include polyploids. Careful comparison between morphology and chromosome number often leads to easier identification of previously unrecognized evolutionary lineages. When taxa of different ploidy levels hybridize, the progeny have intermediate ploidy levels in addition to morphological intermediacy.

Furthermore, our studies of *Opuntia* show that usually in 3*x* interspecific hybrids pollen stainability is about 20–25%; in 2*x*, 4*x*, 5*x*, and 6*x* interspecific hybrids, about 60–65%. For nonhybrid taxa, pollen stainability is about 85–95%. Besides hybridity, several factors may affect stainability percentages (e.g., inversions, translocations, and gametophytic lethal alleles); thus, sometimes results are difficult to interpret. In *Opuntia,* the meiotic chromosomes of triploid interspecific hybrids regularly form 11 trivalents per cell, rather than combinations of bivalents and univalents observed for interspecific hybrids in other families. We also caution against using seed set as an indicator of sexual fertility; adventive embryony in *Opuntia* has been reported for several taxa (see e.g., Davis 1966).

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ANNOUNCEMENT

Recent Publications

A Legacy of Change—Historic Human Impact on Vegetation of the Arizona Borderlands. 1991. Conrad Joseph Bahre. University of Arizona Press, Tucson. vii + 231 p. Hardcover. ISBN 0-8165-1204-3.

Environmental Restoration—Science and Strategies for Restoring the Earth. 1990. John J. Berger (ed.). Island Press, Covelo, CA. xxiv + 398 p. Softcover. ISBN 0-933280-93-9.

Marine Algae and Seagrasses of San Diego County. 1991. Joan G. Stewart. California Sea Grant College, University of California, La Jolla, CA. Report No. T-CSGCP-020.

Sensitive, Threatened and Endangered Vascular Plants of Montana. 1991. Peter Lesica and J. Stephen Shelly. Montana Natural Heritage Program, 1515 East Sixth Avenue, Helena, MT 59620. Occasional Publication No. 1. i + 88 p. Cost $5.00.

Manual of Vascular Plants of Northeastern United States and Adjacent Canada. 2nd ed. 1991. Henry A. Gleason and Arthur Cronquist. New York Botanical Garden, Bronx, NY. ixxv + 910 p. + xxii. ISBN 0-89327-365-1.

United Nations Environment Programme—Environmental Data Report. 1991. GEMS Monitoring and Assessment Research Centre, London, UK. 408 p. ISBN 0-631-18083-4.

THREE NEW SPECIES OF *STYLOCLINE* (ASTERACEAE: INULEAE) FROM CALIFORNIA AND THE MOJAVE DESERT

JAMES D. MOREFIELD
Rancho Santa Ana Botanic Garden,
1500 N. College Avenue, Claremont, CA 91711-3101 and
Nevada Natural Heritage Program,
123 W. Nye Lane, Carson City, NV 89710

ABSTRACT

Three new species of *Stylocline* are described and illustrated, bringing the number of species in this previously unrevised genus to seven. A key to the genus is provided. **Stylocline masonii** and **S. citroleum** are closely related to *S. psilocarphoides* and *S. gnaphaloides,* respectively, and are rare taxa of west-central California that were last collected in 1971 and 1935, respectively. *Stylocline citroleum* appears nearly restricted to oil-producing areas now highly disturbed; it may be extinct. Its character states suggest an origin via hybridization involving *S. gnaphaloides* and a *Filago* species. *Stylocline masonii* was previously identified as *S. gnaphaloides* by collectors, but appears instead to be a parapatric derivative of *S. psilocarphoides.* **Stylocline intertexta** combines character states, and may be a hybrid derivative, of *S. psilocarphoides* and *S. micropoides,* and has been the source of previous taxonomic confusion. It is found almost throughout the Mojave Desert, where the putative parents are sympatric. Both putative hybrid derivatives appear morphologically uniform and independently reproducing, and are thus treated as species. *Stylocline* species probably are almost obligately geitonogamous, insuring that any viable products of rare hybrid events would immediately be both isolated from their parents and capable of reproducing independently.

Ongoing systematic studies of *Stylocline* Nutt. (1840 p. 338) are generating new data regarding its distribution (Morefield 1988; Morefield and Taylor 1988), circumscription, and relationships and have revealed several previously undescribed taxa. So that treatments of *Stylocline* may be completed for the California Jepson Manual, Flora North America, Arizona Flora, and other projects, and so that rare and possibly endangered taxa may become better known, three new species are here formally described. Unfortunately, it was impossible to locate living material of two of the new taxa during the poor growing seasons of 1988–1990; the descriptions are thus based primarily on extensive analyses of herbarium material.

The previous literature on *Stylocline* consists solely of new species descriptions and floristic treatments. *Stylocline* has been placed in subtribe Filagininae Benth. in Benth. & Hook. (1873 p. 166; as "Filagineae") of Inuleae Cassini (Merxmuller et al. 1977) or Gnapha-

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lieae Benth. emend. A. Anderberg (1989, 1991). Its closest living relatives appear to be in *Filago* L. subgenus *Oglifa* (Cass.) Gren., which in turn appears derived from *Gnaphalium* L. and its relatives (Morefield unpublished cladistic data).

The type species of *Stylocline* is *S. gnaphaloides* Nutt. (the spelling has widely been changed to "*gnaphalioides*", based on the assumption that Nuttall derived the name from *Gnaphalium*). I consider *Stylocline* to exclude *S. filaginea* (A. Gray) A. Gray (=*Ancistrocarphus filagineus* A. Gray), *S. griffithii* A. Gray (=*Cymbolaena griffithii* (A. Gray) Wagenitz 1972), and *S. amphibola* (A. Gray) J. Howell (=*Micropus amphibolus* A. Gray; status uncertain and under investigation). The following characteristics are shared by all species remaining in *Stylocline,* justify placement of the genus in Filagininae, and collectively separate *Stylocline* from all other genera in the subtribe:

Diminutive gray arachnoid-tomentose annuals. Leaves simple, entire, alternate or seeming whorled below heads, lax, 1-nerved, evenly tomentose, sessile or with petiole short, broad, indistinct; uppermost leaves subtending the heads. Heads disciform, sessile in dense groups. Receptacle glabrous, 2.8–8 times longer than wide, with paleae subtending all the florets. Phyllaries none or few, grading into the paleae. Paleae in spiral ranks, deciduous with the mature florets or achenes; body parallel-veined, greenish to brownish, curved evenly inward, dorsally rounded, often partly sclerified; tips free, entire, acute to obtuse, erect at maturity; margin abruptly differentiated into a scarious wing with divergent striations, entire, glabrous, ± flat to concave. Middle (and usually outermost) paleae each subtending and tightly enclosing a pistillate floret; body dorsally woolly, the mass of wool dorsiventrally compressed; tips oriented inward over central florets during anthesis; wing reflexed from the line of closure, forming a complete or terminal ligule. Innermost paleae reduced, subtending central florets, concave or loosely folded; tips erect. Outermost and middle florets pistillate, arising in 3–6 series from the side of the receptacle; corolla narrowly tubular to filiform, barely exserted from the closed palea, whitish; style exserted, pressed against and exceeded by the palea wing, offset slightly inward from the geometric tip of the ovary, branches linear; achenes obovoid, curved inward, brown, glabrous, smooth, shiny, epappose. Central florets functionally staminate, in 1 series at tip of receptacle, surpassed and concealed by outer paleae; corolla narrowly funnelform, actinomorphic, lobes equal, triangular; style included; ovary vestigial or partially developed, abortive; pappus of (0–)1–12(–13) bristles.

In *Stylocline* the paleae subtending the pistillate florets provide many diagnostic characters for separating species. Cronquist (1950) suggested that the scarious wings of *Psilocarphus* paleae function in pollination, forcing the styles of the outer pistillate florets over the few central, functionally staminate florets of the same head during anthesis. My own observations of *Stylocline* specimens at many different developmental stages suggest that their palea wings perform the same function. Because the wings of *Stylocline* paleae usually cover the staminate florets throughout development, pollination *between* heads on the same or different plants is likely rare. Preliminary isozyme evidence in *Stylocline* confirms the very low allelic polymorphism expected of diploid selfers (Morefield unpublished data). As discussed further below, a prevalence of structurally enforced geitonogamy in *Stylocline* could have helped mediate two apparent cases of hybrid speciation.

As here conceived, *Stylocline* comprises seven species restricted to southwestern North America and distinguished by the key below. Descriptions of three new species follow the key. The terms *dorsal* and *ventral* are used synonymously with *abaxial* and *adaxial*, respectively. All descriptions are based on fully mature specimens:

KEY TO THE SPECIES OF *STYLOCLINE*

a. Longest palea scarious-winged for its full length, wing widest near or below middle of palea; phyllaries 2–4, slightly smaller than adjacent paleae, scarious throughout, persistent.
  b. Wing of largest palea broadly ovate, base round or cordate; ovaries of central florets vestigial, 0–0.2 mm long, pappus usually of 1–5 bristles; receptacle cylindric; heads shiny, appearing nearly glabrous, wool mostly concealed by the palea wings. . . . . *S. gnaphaloides* Nutt.
  b′. Wing of largest palea elliptic to slightly obovate, base acute; ovaries of central florets partially developed, abortive, (0.2–)0.3–0.6 mm long, pappus usually of 6–12 bristles; receptacle slightly clavate; heads evidently and copiously woolly. . . . . *S. citroleum* Morefield
a′. Longest palea scarious-winged only toward tip, wing widest well above middle of palea; phyllaries none, or 1–3, deciduous, either vestigial or partly sclerified.
  b. Receptacle strongly clavate, 2.8–3.5 times longer than wide; ovaries of central florets partially developed, abortive, 0.3–0.6 mm long; achenes 0.6–0.8 mm long; heads ± spheric, 3–4 mm wide; longest palea < 3.4 mm long; lowest leaves obtuse. . . . . *S. sonorensis* Wiggins
  b′. Receptacle ± cylindric in outline, >3.5 times longer than wide; ovaries of central florets vestigial, 0–0.3(–0.4) mm long; either achenes > 0.8 mm long *or* heads ovoid to ellipsoid *or* heads 5–9 mm wide *or* longest palea 3.4–4.5 mm long *or* lower leaves acute.
    c. Heads spheric, largest 5–9 mm wide; longest palea 3.4–4.5 mm long, body sclerified or membranous; outermost paleae closed, copiously woolly; achenes variously compressed.
      d. Body of longest palea (except midvein) membranous, tearing easily and irregularly as wool is pulled or scraped; achenes laterally compressed; longest leaves subtending the heads mostly 11–17 mm long, awl-like to lanceolate. . . . .*S. micropoides* A. Gray
      d′. Body of longest palea thickened and sclerified, splitting lengthwise if forced, wool easily scraped off; achenes dorsiventrally compressed; longest leaves subtending the heads mostly 4–10 mm long, elliptic to oblanceolate or obovate. . . . . *S. intertexta* Morefield

c′. Heads ovoid to ellipsoid, 1.5–4 mm wide; longest palea < 3.4 mm long, body thickened, sclerified; outermost paleae open, glabrous or thinly woolly; achenes dorsiventrally compressed.
  d. Heads 2.5–4 mm wide; longest palea 2.8–3.3 mm long; achenes 1.1–1.6 mm long; central corollas 1.1–1.7 mm long, 5-lobed; leaves mostly acute. .... *S. psilocarphoides* M. E. Peck
  d′. Heads 1.5–2.5 mm wide; longest palea 2.0–2.7 mm long; achenes 0.7–1.0 mm long; central corollas 0.8–1.1 mm long, mostly 4-lobed; leaves mostly narrowly obtuse. .... *S. masonii* Morefield

Stylocline masonii Morefield, sp. nov. (Fig. 1).—TYPE: USA, California, Kern Co., plains W of Bakersfield, 30 Mar 1935, *H. L. Mason 8241* (holotype, UC 581167, in particular the upper-right-most mounted plant just below the fragment packet on the sheet; isotypes, DS, GH).

Styloclinae psilocarphoidi M. E. Peck (1945) similis, sed capitulis 1.5–2.5(non 2.5–4) mm latis; bracteis longissimis receptaculi 2.0–2.7(non 2.8–3.3) mm longis; acheniis exterioribus maturitate 0.7–1.0(non 1.1–1.7) mm longis; corollis centralibus 0.8–1.1(non 1.1–1.7) mm longis, plerumque quadrilobatis (non quinquelobatis); foliis plus minusve anguste obtusis (non acutis); ramis inferioribus foliosis (non efoliosis) inter furcas; et habitatione ad California centrali-occidentali (non deserta interiora orientaliora).

Stems to 10 cm long, branching above and usually at base; branches ± sympodial throughout or shortly monopodial at base, usually proliferating pseudo-dichotomously under the heads, ± evenly leafy below, usually ± leafless between the upper forks. Leaves mostly narrowly obtuse, tip herbaceous. Lowest leaves 2–3 mm long, ±0.5 mm wide, 1.5–3× as long as the internodes, ± imbricate, elliptic to oblanceolate. Middle leaves 5–9 mm long, ±1 mm wide, 1.5–2× as long as the internodes, linear to narrowly oblong or narrowly elliptic. Uppermost leaves 2–5 mm long, ±1 mm wide, shorter to barely longer than heads, linear-oblong to narrowly elliptic. Heads 2–5 per group, restricted to forks and tips of branches, 2–5 mm long, 1.5–2.5 mm wide, ovoid to ellipsoid, ± woolly. Receptacle 2–3 mm long, 0.3–0.4 mm wide, ± cylindric in outline, scars of paleae and florets elongate, peg-like, concentrated toward the base and tip of the receptacle. Phyllaries none, or 1–3, vestigial, unequal, scarious, deciduous, or a few of the outermost paleae sometimes not subtending florets and thus resembling phyllaries. Paleae in 4–5 series; body thickened and sclerified between the veins (splitting lengthwise if forced, any pubescence easily scraped off); wing terminal, narrowed and vestigial toward base, whitish to silvery. Outermost paleae each usually subtending a pistillate floret (sometimes empty), 1–2 mm long, open, concave, ± obovate; body dorsally glabrous or thinly woolly. Middle paleae 2.0–2.7 mm long; body lanceolate, its mass of wool broadly ± elliptic in outline; wing oblanceolate to obovate,

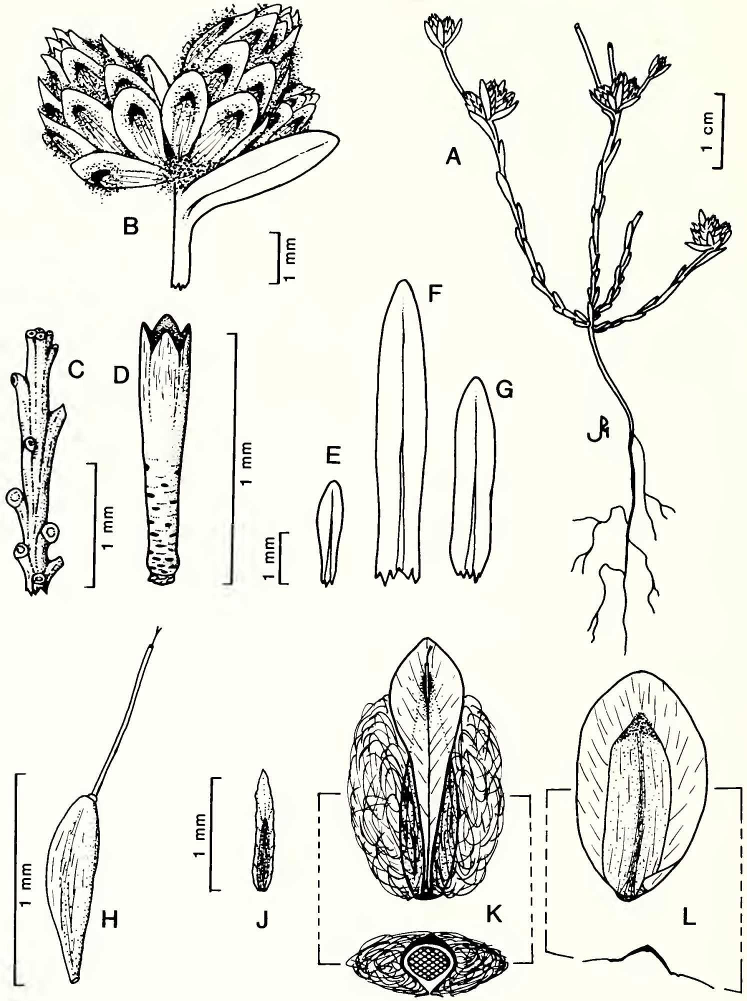

FIG. 1. *Stylocline masonii* (pubescence of stems and leaves not shown). A. Habit. B. Capitulescence. C. Receptacle. D. Central floret. E–G. Lower, middle, upperleaves. H. Lateral view of mature pistillate floret. J. Ventral view of innermost palea. K. Ventral view of middle palea with cross-section. L. Ventral view of outermost palea with cross-section.

obtuse, base acuminate. Innermost paleae 0.8–1.5 mm long, linear-lanceolate; body dorsally glabrous; wing acute. Pistillate florets in 3–4 series; corolla 3–4-denticulate; style branches 0.4–0.6 mm long; achenes 0.7–1.0 mm long, dorsiventrally compressed. Central florets 2–4; corolla 0.8–1.1 mm long, lobes mostly 4, yellowish to reddish-brown, throat whitish, tube maculate; style branches ±0.1 mm long, ± ovate; ovary vestigial, 0–0.1 mm long; pappus none, or of 1 smooth bristle 0.7–1.0 mm long.

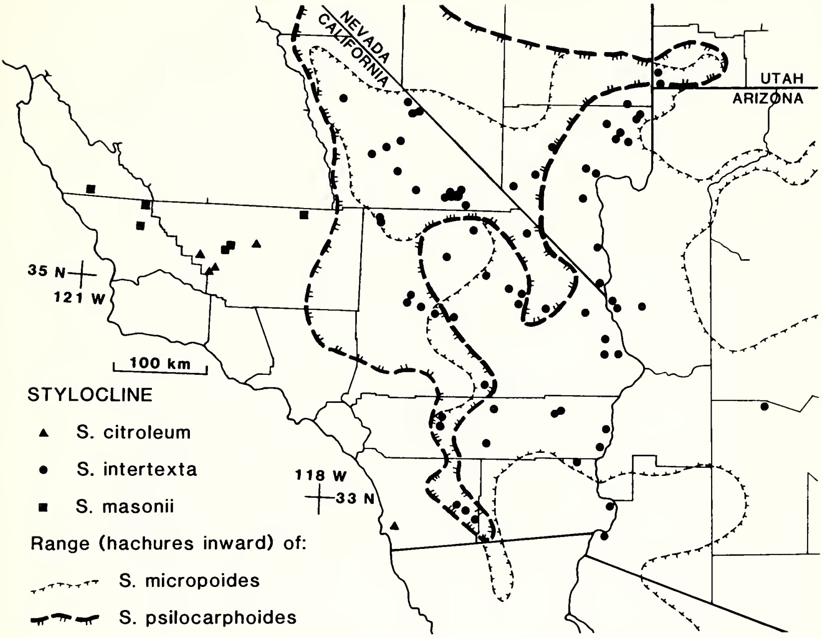

FIG. 2. Distributions of *Stylocline citroleum, S. intertexta,* and *S. masonii*; partial range outlines of *S. micropoides* and *S. psilocarphoides.*

PARATYPES: USA, California, Kern Co., plains W of Bakersfield, 30 Mar 1935, *Mason 8240* (UC); 5 mi W of Rosedale, 11 Apr 1937, *Hoover 1841* (JEPS); Sierra Nevada, Cyrus Canyon, scarce and scattered in light sandy soil in arid canyon bottom, California juniper association, 3900 ft, 26 Apr 1971, *Twisselmann 17572* (CAS). Monterey Co., Santa Lucia Mountains, sandy flat along San Antonio [River] near Pleyto, 29 Apr 1958, *Hardham 3092* (RSA). San Luis Obispo Co., Cholame Valley, 30 Mar 1935, *Mason 8252* (DS, UC); Commatti Canyon 11 mi S of Shandon, 16 May 1955, *Bacigalupi et al. 5126* (JEPS).

Distribution and habitat (Fig. 2). Known only from the above collections in west-central California; 100–400 (rarely to 1200) m. Dry, open sandy places (see further under *S. intertexta*). Last collected in 1971.

On average *Stylocline masonii* is the smallest and most inconspicuous species of *Stylocline,* and it is unclear whether the small number of specimens results from that fact or from genuine rarity of the species. To give it benefit of the doubt, rarity should be assumed until it can be disproven. Endangerment should also be assumed; 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.

TABLE 1. COMPARISON OF *STYLOCLINE INTERTEXTA* WITH ITS PUTATIVE PARENTS, AND OF *S. MASONII* WITH *S. PSILOCARPHOIDES*. "Longest" = longest structure(s) found on each mature plant.

Character	*S. micropoides*	*S. intertexta*	*S. psilocarphoides*	*S. masonii*
Interforks of lower branches	leafy	leafy	± leafless	leafy
Tips of leaves	acute	acute	acute	obtuse
Shape of uppermost leaves	lanceolate	elliptic–obovate	elliptic–obovate	elliptic
Longest uppermost leaves (mm)	11–17	5–11	4–9	3–7
Shape of head	spheric	spheric	ovoid	ovoid
Width of largest head (mm)	5–9	5–6	2.5–4	1.5–2.5
Scars of receptacle	low	low	elongate	elongate
Longest palea (mm)	3.4–4.5	3.4–4.5	2.8–3.3	2.0–2.7
Outermost palea closure	complete	complete	none	none
Outermost palea texture	membranous	sclerified	sclerified	sclerified
Length of achene (mm)	1.0–1.3	1.0–1.4	1.1–1.7	0.7–1.0
Compression of achene	lateral	dorsiventral	dorsiventral	dorsiventral
Length of central corolla (mm)	1.2–1.9	1.1–2.3	1.1–1.7	0.8–1.1
Lobes of central corolla	5	5	5	4
Pappus bristles/central flower	(2)3–5(10)	0–4(8)	0–3	0–1
Distribution	Mojave/Sonoran/ Chihuahuan deserts	Mojave Desert	Mojave/Great Basin deserts	west-central California

Relationships. Although specimens of *S. masonii* were previously determined as *S. gnaphaloides,* with which it is wholly sympatric, its closest relative appears instead to be *S. psilocarphoides.* It resembles the latter, and is separated from the former, by its heads ovoid; outermost paleae open, concave, obovate; each middle palea thickened and sclerified between veins, its winged margin vestigial or much narrowed and acuminate at base; and achenes dorsiventrally compressed (Table 1).

Stylocline masonii differs from *S. psilocarphoides* primarily in the smaller dimensions of its reproductive structures given in the diagnosis and in Table 1. The two species are allopatric and nearly parapatric, with *S. masonii* occurring in habitats similar to, but wholly to the west of, *S. psilocarphoides* (Fig. 2).

Given its strong similarities to *S. psilocarphoides,* varietal status might have been more justified for *S. masonii.* No morphologic or geographic connection could be found between the two taxa, though. Unlike most other Filagininae (see under *S. intertexta* and *S. citroleum* below), *S. masonii* specimens are only rarely intermixed with other species on herbarium sheets. Among the 10 sheets (representing 7 collections) examined, one was mixed with *S. gnaphaloides* and *Filago californica* Nuttall; the remainder were unmixed. This suggests that *S. masonii* is relatively distinct morphologically and/or ecologically in the field.

The epithet honors Dr. Herbert L. Mason (1896–), whose discerning collections of North American Filagininae provide the majority of the material on which *S. masonii* is based and contribute substantially to our understanding of many other taxa as well.

Stylocline intertexta Morefield, sp. nov. (Fig. 3).—TYPE: USA, California, Inyo Co., north end of Ibex Hills, along N side of California Highway 178, 0.3 mile W of Salsberry Pass, T21N R5E sect. 15, 990 m, 7 May 1991, *J. D. Morefield 5445* (holotype, RSA; isotypes to be distributed, ASU, BRY, MO, NSMC, NY, UC, UNLV).

Styloclinae micropoidi A. Gray (1853) similis, sed bracteis longissimis receptaculi dorsaliter incrassateae et firmae (non membranaceae); acheniis dorsiventraliter (non lateraliter) compressis; et foliis supremis longissimis plerumque 4–10(non 11–17) mm longis, ellipticis oblanceolatisve obovatisve (nec lanceolatis nec lesiniformibus).

Stems to 11 cm long, branching above and usually at base; branches essentially sympodial but often very unequal and appearing monopodial, usually not proliferating pseudo-dichotomously under the heads, ± evenly leafy throughout or less so above. Leaves acute, tip mucronate. Lowest leaves 4–12 mm long, 1.5–2 mm wide, 2–3 × as

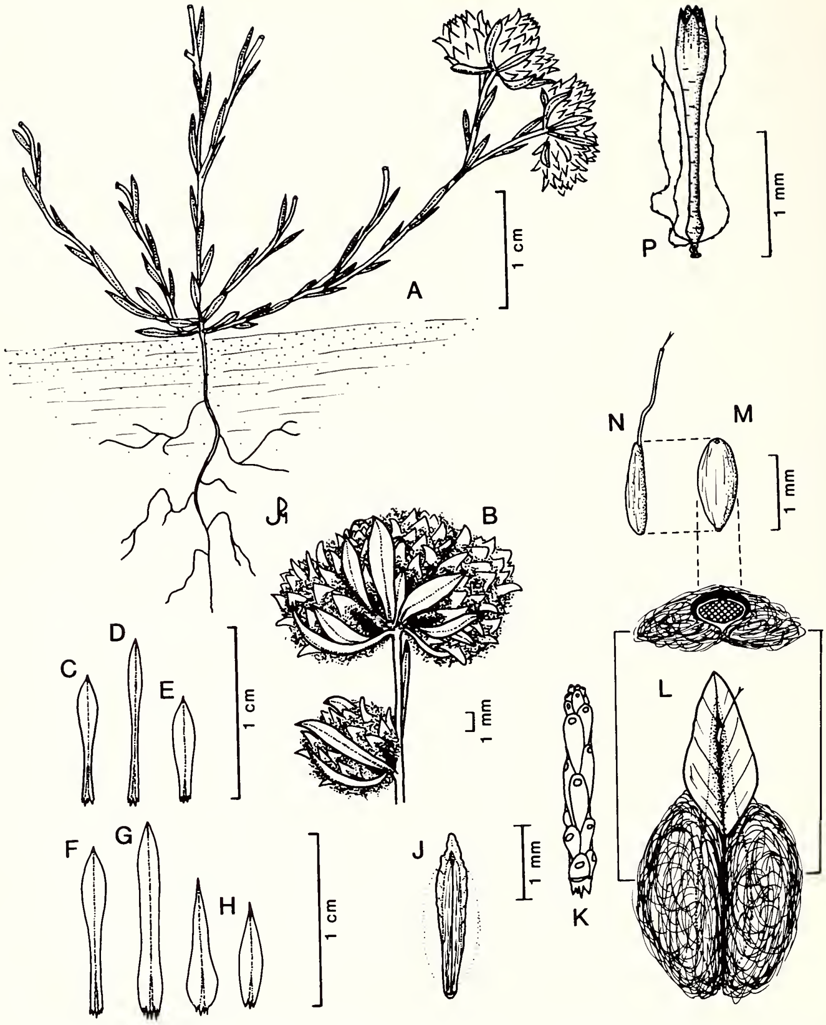

FIG. 3. *Stylocline intertexta* (except where stated otherwise; pubescence of stems and leaves not shown). A. Habit. B. Capitulescence. C–H. Lower, middle, upper leaves of *Stylocline intertexta* (C–E) and *Stylocline micropoides* (F–H). J. Ventral view of innermost palea. K. Receptacle. L. Ventral view of outer palea with cross-section. M. Ventral view of achene. N. Lateral view of achene. P. Central floret.

long as the internodes, ± imbricate, oblanceolate. Middle leaves 6–15 mm long, 1–1.5 mm wide, 1–2× as long as the internodes, narrowly oblanceolate. Uppermost leaves 4–11 mm long, 1–2.5 mm wide, shorter to barely longer than heads, elliptic to oblanceolate or obovate. Heads (1–)2–6 per group, mostly restricted to tips of branches, ± spheric, copiously woolly, the largest 5–6 mm in diameter. Receptacle 1.4–2.7 mm long, 0.3–0.5 mm wide, ± cylindric in outline, scars of paleae and florets low, rounded, ± evenly distributed. Phyllaries none, or 1–3, vestigial, unequal, scarious, deciduous. Paleae in 5–7 series; body thickened and sclerified between the veins (splitting lengthwise if forced, pubescence easily scraped off), copiously woolly; wing terminal, narrowed and vestigial toward base, yellowish to silvery, broadly acute. Outermost and middle paleae similar, the longest 3.4–4.5 mm long; body lanceolate to ovate, the mass of dorsal wool ovate in outline; wing elliptic to ovate, base acute. Innermost paleae 1.5–2.5 mm long, linear to lanceolate or oblanceolate; body lanceolate, the mass of dorsal wool elliptic in outline or none. Pistillate florets in 4–6 series; corolla 4–5-denticulate; style branches 0.4–0.6 mm long; achenes 1.0–1.4 mm long, dorsiventrally compressed. Central florets 3–6; corolla 1.1–2.3 mm long, lobes 5, yellowish to reddish, throat and tube whitish; style branches ±0.1 mm long, ± ovate; ovary vestigial, 0–0.3 mm long; pappus of 0–4(–8) bristles 1.1–2.0 mm long, smooth to minutely and antrorsely barbellate.

PARATYPE: USA, Nevada, Clark County, along the Virgin River, 3.5 mi SW from Riverside Bridge, 12 airline mi SW of Mesquite, T14S R69E sect. 26, 457 m, 5 May 1975, *Holmgren and Holmgren 7873* (ASU, BRY, MONTU, NY, UTC, WTU).

Distribution and habitat (Fig. 2). Northern and eastern Mojave Desert, northern and western Sonoran Desert; 40–1400 m (averaging 590 m). In open, often barren places on stable, sandy or gravelly, frequently calcareous soils, intolerant of recent disturbance but often on older, stabilized disturbance, often near bases of rocks, in small drainages or depressions, or under drip-lines of shrubs. With minor variations, this habitat description applies to all other *Stylocline* species I have observed in the field.

Relationships. This previously undetected taxon may have obscured the presence of *S. psilocarphoides* in California (Morefield and Taylor 1988) by seeming to link the latter with *S. micropoides.* It appears to share the most character states with *S. micropoides* and the remainder with *S. psilocarphoides* (Table 1). This suggests that *S. intertexta* was derived either from a hybrid between the other two or from their common ancestor. The epithet *intertexta* suggests this recombination of traits, as well as its intermediate geographic distribution.

Stylocline intertexta is outwardly so similar to *S. micropoides* that at first I planned to treat both as varieties of a single species. The differences described above, though, are constant for all specimens examined. The two species will at first have to be separated carefully and with magnification, but this does not alter the fact that they are entirely separate. After some experience, the shorter, elliptic to oblanceolate or obovate upper leaves of *S. intertexta* are easily separated in the field and herbarium from the larger, lanceolate to awl-shaped upper leaves of *S. micropoides* (Fig. 3).

Although *S. intertexta* occurs largely in the region of sympatry between its two putative parents (Fig. 2), it is clear from its abundance, broad range, frequent occurrence with neither or only one congener, and normally developed fruits and pollen, that it is now an independently reproducing species, whatever its origin may have been. Its present distribution may reflect retention of physiologic tolerances recombined from its parents.

Mixed collections of sympatric Filagininae seem the rule rather than the exception (Morefield 1988 and unpublished; Morefield and Taylor 1988). Of the 89 collections (represented by 122 sheets) of *S. intertexta* examined, 44 collections (49%) included sheets mixed with one or more additional taxa, including *S. micropoides* (found in 33 collections), *Filago depressa* A. Gray (15), *S. psilocarphoides* (8), *S. gnaphaloides* (2), *Filago californica* (1), and *S. sonorensis* (1). These numbers no doubt reflect some combination of the relative resemblance, and frequency of occurrence, of *S. intertexta* with each of the other taxa.

With *S. masonii* and *S. intertexta* recognized, *S. psilocarphoides* becomes a more clearly defined species centering in the western Mojave and Great Basin deserts (Fig. 2), extending northward to SE Oregon and SW Idaho. In California *S. psilocarphoides* has been misidentified most often as *S. micropoides* (Morefield and Taylor 1988) but has also been responsible for reports of *S. gnaphaloides* and *Filago arizonica* A. Gray from the northern and eastern Mojave Desert. *Stylocline gnaphaloides* is centered in the California Floristic Province (Hickman 1989), barely edges onto the California and Baja California deserts along the east slopes of the Tehachapi, Transverse and Peninsular ranges, and thence is disjunct to south-central Arizona and northern Sonora. *Filago arizonica* is similarly distributed, but is not known in California north of Riverside County.

Exsiccata (all collections early March to early May). USA, Arizona, Maricopa Co., *Palmer 603* (GH). Mohave County, *Jones s.n.,* 13 May 1884 (GH, POM); *Jones 3905* (ARIZ, NY, ORE, POM, UC); *Lemmon and Lemmon s.n.,* Apr 1884 (UC [2], US); *Mason 14240* (UC). Yuma Co., *Jones s.n.,* 25 Apr 1906 (POM).

California, county unknown, *Brandegee s.n.,* Apr 1905 (UC). Imperial Co., *McLaughlin and Bowers 2887, 2974* (ARIZ). Inyo Co., *Annable 566* (ARIZ, UNLV); *Boyd and Boyd 2007* (RSA, UCR); *Charlton and Pitzer 1678* (RSA); *Coville and Funston 673* (US); *Ferris et al. 4058* (DS); *Fosberg 5413* (PENN); *Gilman 1498* (US); *Gustafson and Herbst 2521a* (RSA); *Hall and Chandler 7049* (RM, UC); *Howell 3629* (CAS, JEPS); *Howell and True 49121* (CAS); *Jones s.n.,* 3 May 1897, 10 Apr 1907 (POM); *Keck and Ferris 5806*

(DS); *Neese and Welsh 12828* (BRY); *Parish 10091* (DS); *Peirson 7792* (DS); *Pinkava et al. 12554* (ASU); *Pinzl and Pinzl 4983* (NSMC); *Pitzer and Charlton 772* (UCR); *Raven 12113* (CAS, JEPS); *Stein 827* (MO); *Thorne et al. 42562* (RSA); *Tilforth and Dourley 747* (RSA); *Wright 1558a* (ORE, OSC). Riverside Co., *Boyd et al. 1316* (RSA), *2107* (RSA, UCR); *Boyd and Mistretta 1446* (RSA); *Hall 5917* (UC); *Ferris and Bacigalupi 13237* (JEPS), *13324* (DS, JEPS); *Mason 14208* (UC); *Munz 15688* (UTC); *Spencer 1629* (GH). San Bernardino Co., *Baldwin 112* (RSA); *Eastwood and Howell 8836* (CAS); *Ferris 12623* (DS); *Fosberg 5427* (PENN); *Gustafson and Keeley 2614* (RSA); *Hall 6150* (UC); *Hoffmann s.n.,* 16 May 1930 (SBBG); *Howell 3589* (CAS); *Jepson 17264* (JEPS); *Jones s.n.,* 2 May 1906 (POM); *Kellogg and Alexander 935* (K); *Liston and Zona 645-4* (RSA); *Mason 8233* (DS, GH, UC), *12248* (UC), *14236* (DS, UC), *14252* (SD); *Meebold 15517* (M); *Newlon 501* (JEPS); *Parish 9310, 10120* (DS); *Ripley and Barneby 3293* (CAS); *Sanders and Twitchell 166* (UCR); *Smith and Hansen 24* (FSC); *Wolf 3201* (RSA), *10215* (NY, RSA). San Diego Co., *Gander 176.44, 7117* (SD); *Jepson 8569* (JEPS).

Nevada, Clark Co., *Ackerman 3099* (UNLV); *Atwood and Thorne 11890* (BRY); *Bailey et al. 1914* (US); *Clokey 5961* (CM, DS, LL, NY, UC, WTU), *8610* (LL, NY, UC, US); *Kass and Neese 1549* (UNLV); *Kennedy 1120* (NESH); *Pinzl and Holland 2164, Pinzl 2557, 5051* (NSMC); *Pinzl and Knight 8189* (NSMC, RSA); *Swearingen 1025* (UNLV), *1409* (RSA); *Train 1425* (RENO). Lincoln Co., *Kennedy and Goodding s.n.,* 1906 (NESH).

Utah, Washington Co., *Neese 13026* (BRY); *Thorne et al. 4251A* (NY).

Stylocline citroleum Morefield, sp. nov. (Fig. 4).—TYPE: USA, California, Kern Co., flats at Taft, 2 Apr 1935, *P. A. Munz 13641* (holotype, POM 213346, in particular the upper-left-most mounted plant on the sheet; isotypes, DS, UC, UTC; all type sheets have *Filago californica* Nutt. intermixed).

Styloclinae gnaphaloidi Nutt. (1840) similis, sed bracteis receptaculi maturitate densius et copiosius lanatis, ambitu marginis scariosi elliptico vel parum obovato (non late ovato) et fundo acuto (nec cordato nec subcordato); ovariis flosculorum centralium evolutis ex parte, abortivis (non vestigialis), (0.2–)0.3–0.6(non 0–0.2) mm longis, setis pappi plerumque 6–12(non 1–5); receptaculo plus minusve clavato (non cylindrico); et foliis plerumque late acutis (non plerumque obtusis).

Stems to 13 cm long, branching above and at base; branches ± sympodial, often proliferating pseudo-dichotomously under the heads, ± evenly leafy below, mostly leafless between the upper forks.

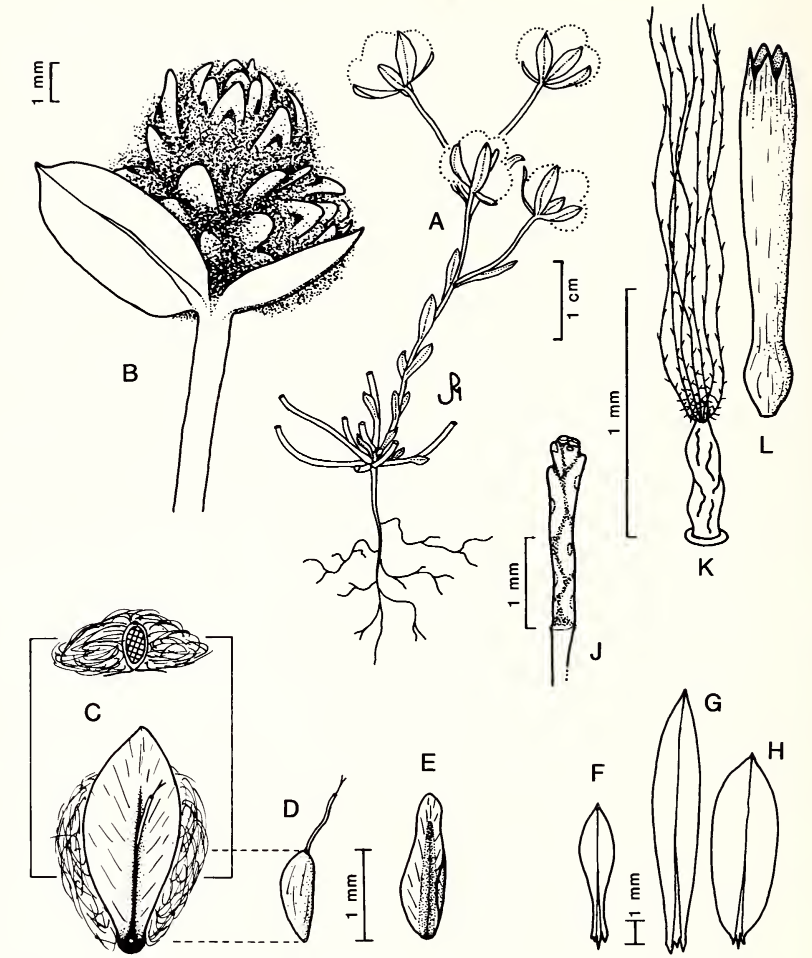

FIG. 4. *Stylocline citroleum* (pubescence of stems and leaves not shown). A. Habit. B. Capitulescence. C. Ventral view of middle palea with cross-section. D. Lateral view of achene. E. Ventral view of innermost palea. F–H. Lower, middle, uppermost leaf. J. Receptacle. K. Central floret with corolla removed. L. Central corolla.

Leaves ±1.5× as long as the internodes, broadly acute, tip mucronate. Lowest leaves 3–10 mm long, 1–2.5 mm wide, obovate. Middle leaves 6–13 mm long, 1–2 mm wide, oblanceolate. Uppermost leaves 4–12 mm long, 2–3.5 mm wide, shorter to barely longer than heads, broadly ± elliptic to oblanceolate. Heads 2–8 per group, mostly restricted to tips and forks of branches, 4–5.5 mm long, 3.5–5 mm wide, nearly spheric, copiously woolly. Receptacle 1.5–2.5 mm long, 0.3–0.5 mm wide, mostly narrowly clavate in outline, scars of paleae and florets slightly sunken at maturity, ± evenly distributed. Phyllaries 2–4, 1.5–2.5 mm long, elliptic to obovate, narrowly obtuse, slightly unequal, scarious, dorsally woolly, ± persistent, resembling and apparently derived from the paleae (by loss of associated floret, reduction of body, and expansion of the scarious margin). Paleae in 5–7 series; body membranous except at the midvein (tearing easily and irregularly as pubescence is pulled or scraped); wing developed along the full length of the palea, yellowish to silvery, narrowly obtuse. Outermost and middle paleae similar, the longest 2.5–3.5 mm long; body elliptic to lanceolate, the mass of dorsal wool ovate in outline; wing elliptic to slightly obovate, acute at base. Innermost paleae 1–2.5 mm long, lanceolate. Pistillate florets in 4–6 series; corolla 3–5-denticulate; style branches 0.3–0.5 mm long; achenes 0.8–1.0 mm long, laterally compressed. Central florets 3–6; corolla 1.0–1.6 mm long, lobes 5, yellowish to brownish, throat and tube whitish; style branches 0.1–0.2 mm long, ovate to oblong; ovary partially developed, abortive, (0.2–)0.3–0.6 mm long, glabrous; pappus of (5–)6–12(–13) bristles, 1.4–1.8 mm long, densely spreading-hispidulous at base, sparsely antrorse-barbellate above.

PARATYPES: USA, California, Kern Co., Buena Vista Hills [near Taft], 9 Apr 1893, *Eastwood s.n.* (UC); McKittrick, clay soil, brushy country, 4 Apr 1932, *Jepson 16234* (JEPS); 2 mi from Bakersfield, Kern River Canyon Road, 11 Apr 1935, *Esau s.n.* (DAV). San Diego Co., San Diego, Apr 1883, *Cleveland s.n.* (SD).

Distribution and habitat (Fig. 2). Known only from the above collections in southwestern California; 60–320 m. Open sandy flats and clay soils, mostly in areas with high levels of surface petroleum. Last collected in 1935. *Stylocline citroleum* appears nearly restricted to areas of heavy petroleum production and other developments in the southern San Joaquin Valley and is almost certainly endangered, if not already extinct. The epithet is derived from the Latin *citer,* indicating proximity or nearness, and *oleum,* oil.

I have observed petroleum welling to the surface naturally near two of the known localities. *Stylocline citroleum* could be adapted to or even dependent on these unusual environmental conditions. Other cases of endemism on substrates with high petroleum content have been documented (O'Kane and Anderson 1987). On the other hand, the apparent preference for petroleum-producing areas may be an artifact of the few samples available.

Relationships. Stylocline citroleum shares the most character states with *S. gnaphaloides* (Table 2), as which it was identified in the five known collections. But certain features, especially increased development of the ovaries and pappus of the central florets, suggest hybrid origin involving a member of *Filago* subgenus *Oglifa.* The central florets of the latter have fully developed achenes and pappus.

TABLE 2. COMPARISON OF *STYLOCLINE CITROLEUM* WITH ITS PUTATIVE PARENTAL TAXA AND WITH *S. SONORENSIS*. Measurements are in mm.

Character	*S. gnaphaloides*	*S. citroleum*	*Filago californica*	*S. sonorensis*
Branching pattern	sympodial	sympodial	monopodial	sympodial
Tip of lowest leaves	obtuse	acute	acute	obtuse
Tip of uppermost leaves	obtuse	acute	acute	acute
Shape of uppermost leaves	obovate	elliptic	elliptic	elliptic
Shape of head	spheric	± spheric	ovate	± spheric
Phyllaries	present	present	absent	absent
Outermost palea closure	complete	complete	partial	complete
Outermost palea texture	membranous	membranous	sclerified	membranous
Innermost pistillate paleae	deciduous	deciduous	persistent	deciduous
Paleae of central florets	present	present	absent	present
Palea wing development	complete	complete	terminal	terminal
Palea wing base	± cordate	acute	acute	acute
Receptacle tip	cylindric	± clavate	much expanded	clavate
Receptacle length : width	6–7	5–6	0.7–0.9	2.8–3.5
Compression of achene	lateral	lateral	lateral	none
Central ovary development	none	partial	complete	partial
Central ovary length	0–0.2	0.2–0.6	0.7–0.9	0.3–0.6
Lobes of central corolla	5	5	4	5
Pappus bristles/central flower	1–4(–6)	(5–)6–12(–13)	19–23	(0)1–6(7)

Of the eight sheets of *S. citroleum* examined, five are mixtures with *Filago californica,* and one with *S. gnaphaloides. Filago californica* is thus suggested as the second parent and is also included in Table 2. The spotty, disjunct occurrences of *S. citroleum,* and its apparent restriction to highly disturbed areas, further support a hypothesis of recent and perhaps multiple hybrid origin (Anderson 1948).

The new taxon is treated as a species of *Stylocline* rather than a nothotaxon for the following reasons: 1) hybrid origin is unproven (studies are in progress), 2) a clear majority of its diagnostic character states unite it with *S. gnaphaloides* and the remainder of *Stylocline* (Table 2), 3) mature specimens possess normally-developed achenes that appear to have been once viable, and 4) the known specimens are highly uniform among themselves and occur in multiples on most sheets. These last three observations suggest that, even if *S. citroleum* arose from the products of one or more hybrid events, it has since become a uniform and independently reproducing entity. The disjunct locality in San Diego County could represent an independent hybrid origin of the taxon, or simply a fragmented distribution.

Stylocline sonorensis (Wiggins 1950) was known only from its holotype until recently (Morefield 1988). It is widely distributed in southeast Arizona and northeast Sonora, with one disjunct occurrence near Hayfields Dry Lake in the Sonoran Desert of Riverside County, California. Superficially it is very similar to *S. citroleum,* and shares with it the appearance of hybrid origin involving *Filago* (Table 2). In this case, though, frequencies of mixed collections suggest *S. micropoides* and *F. depressa* as possible parents.

As structurally unlikely as inter-plant pollination seems in most Filagininae, the new taxa recognized above suggest that rare hybridization events could have played a significant role in the origin of new species in *Stylocline.* If viable, the products of such events would be immediately both isolated from their parents and capable of reproducing independently. Studies at the molecular level are under way to test these possibilities.

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A NEW SPECIES OF *UROSKINNERA* (SCROPHULARIACEAE) FROM SOUTHERN MEXICO

Thomas F. Daniel and Dennis E. Breedlove
Department of Botany, California Academy of Sciences,
Golden Gate Park, San Francisco, CA 94118, USA

Abstract

Uroskinnera almedae, a new species from north-central Oaxaca, Mexico, is described and illustrated. The species is unique in the genus by virtue of its relatively long, red corolla and exserted stamens. The distributional range of *Uroskinnera flavida* is extended from Tabasco to Chiapas. The range of *U. hirtiflora* is extended from Oaxaca and Veracruz to northern Puebla. A key to all species of *Uroskinnera* that incorporates data from recent collections of *U. flavida* and *U. hirtiflora* is presented. The known distribution of each species is plotted on a map.

Resumen

Se describe e ilustra **Uroskinnera almedae** como especies nueva de la parte norte-central de Oaxaca, México. El especies se distingue por su corola larga y roja y sus estambres exertas. *Uroskinnera flavida* se reporta por primera vez para el estado de Chiapas; tambien *U. hirtiflora* se registre del estado de Puebla. Una clave de todas las especies de *Uroskinnera,* que incluye informaciones recientes de colecciones de *U. flavida* y *U. hirtiflora* es presentada. Se provee un mapa que muestra la distribucion de cada una de las especies.

Four species have been described and three are currently recognized in *Uroskinnera* Lindley, a genus of southern Mexico and northern Central America. *Uroskinnera* has been included in the tribe Cheloneae (Thieret 1954, 1967) and is characterized by its racemose inflorescence, well-developed staminode, and distinct stigmas. Distinct stigmas are somewhat anomalous in the Cheloneae; thus the tribal position and relatives of the genus are uncertain. Keys to genera in Thieret (1954) and Standley and Williams (1973) are nearly identical in their treatment of *Uroskinnera, Tetranema* Benth., and *Penstemon* Mitch. In both keys, the leads for *Uroskinnera* and *Tetranema* appear to have been inverted. Correct information is provided in the generic descriptions and illustrations of Standley and Williams (1973).

Schultes (1941) recognized four species of *Uroskinnera* and provided a synopsis of the genus. Unfortunately, the species were known to him from relatively few wild collections (i.e., *U. flavida* Lundell, 1; *U. spectabilis* Lindley, 1; *U. watsonii* Schultes, 2; and *U. hirtiflora* Hemsley, 4). The distinctions between *U. watsonii* and *U. spectabilis,* which could be found growing together, appeared particularly tenuous. Standley and Williams (1973) combined the two species and

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reduced *U. watsonii* to synonymy of *U. spectabilis.* Although they provided little rationale for combining the two species, their conclusion appears justified. Schultes (1941) had distinguished these species on the basis of foliar, corollar, and androecial size and stylar form. He recorded overlap in measurements of most of the quantitative characters, and we were unable to detect differences in the relative flatness of the style. It seems likely that the distinctions noted by Schultes (1941) were based on too small a sample and that additional collections from eastern Guatemala will further link the two species he recognized.

Recent field activities in southern Mexico have resulted in additional collections of *Uroskinnera.* Tom Wendt and colleagues, working in the Uxpanapa region of the Isthmus of Tehuantepec, collected a variant of *U. hirtiflora* (Wendt 1983) in Veracruz. A recent collection of typical *U. hirtiflora* from northern Puebla (Mpio. Zapotitlan de Méndez, Atehuiztita, 4.7 km SE de Zapotitlan, 28 February 1987, *P. Tenorio L. et al. 12747,* TEX) extends the distributional range of that taxon about 350 kilometers northwest of its previously known westernmost occurrence in Oaxaca. *Uroskinnera flavida,* previously known only from the type collected in Tabasco in 1939, has recently been collected in another region of Tabasco (Mpio. Teapa, Cerro del Coconá, 6 April 1980, *C. Cowan 2894,* CAS) and in three regions of Chiapas (Mpio. Las Margaritas, Laguna Miramar E of San Quintín, 11 February 1973, *D. Breedlove 33245,* CAS; Mpio. Ocosingo, 70 km SW of Palenque, 12 April 1981, *D. Breedlove 50872,* CAS; same locality, 4 December 1980, *D. Breedlove and F. Almeda 48336,* CAS; Mpio. Palenque, Agua Azul, 24 May 1973, *D. Breedlove 35343,* CAS; same locality, 8 November 1980, *D. Breedlove 47315,* CAS). It is likely that this species will also be found in adjacent regions of the Petén in Guatemala where similar habitats occur.

Two recent collections from north-central Oaxaca possess the diagnostic characteristics of *Uroskinnera* but do not represent any of the previously described taxa. They are described below as a new species, *U. almedae.* In all, we examined 38 specimens representing 24 collections of the genus from CAS, F, GH, LL, and TEX. Study of the specimens utilized by Schultes (1941) and more recent collections show that species of *Uroskinnera* can be distinguished by the following key:

a. Corolla dark red, 50–55 mm long; stamens exserted beyond limb of corolla. . . . . *U. almedae*

a.′ Corolla white, yellow, or purple, 22–40 mm long; stamens included within corolla tube or if exserted from tube then not surpassing limb.

  b. Corolla white to yellow; floral bracts 1–2.3 mm long; calyx lobes broadly triangular, 0.3–1 mm long; inflorescence rachis pubescent with trichomes less than 0.5 mm long. . . . . *U. flavida*

b.′ Corolla purple (usually with white markings); floral bracts 3–6 mm long; calyx lobes narrowly triangular to subulate, 1–7 mm long; inflorescence rachis pubescent with trichomes 0.5–2.5 mm long.
  c. Calyx 5-lobed; corolla externally densely pubescent over entire surface with glandular trichomes 0.2–1 mm long; staminode glabrous. .. *U. hirtiflora*
  c.′ Calyx 4-lobed; corolla externally very sparsely pubescent proximally with glandular trichomes 0.05–0.1 mm long and glabrous distally; staminode glandular pubescent (at least distally). .... *U. spectabilis*

Uroskinnera almedae T. Daniel & Breedlove, sp. nov. (Fig. 1).—TYPE: MEXICO, Oaxaca, 15 km N of Valle Nacional along road to Cd. Oaxaca, 150 m, 5 Jan 1982, *D. Breedlove and F. Almeda 56695* (holotype, CAS!; isotypes, GH!, MEXU!, NY!).

Frutex debilis usque ad 1.5 m altus. Laminae foliorum ovatae vel ellipticae, 55–165 mm longae, 31–81 mm latae, 1.4–2.1-plo longiores quam latiores. Inflorescentiae racemosae usque ad 150 mm longae. Calyx 4–5 mm longus, 4-lobatus. Corolla atrorubra, 50–55 mm longa, extus glandulosa. Stamina corolla exserta; staminodium glabrum. Capsula 4.5–5 mm longa. Semina 0.8–1.1 mm longa, 0.6–0.8 mm lata, reticulata-foveata.

Weak shrub to 1.5 m tall. Young stems evenly pubescent with flexuose-antrorse eglandular trichomes to 0.7 mm long. Leaves opposite, petiolate, anisophyllous; petioles to 90 mm long; blades ovate to elliptic, 55–165 mm long, 31–81 mm wide, 1.4–2.1 times longer than wide, subacute to rounded at base, acute at apex, the surfaces sparsely pubescent with the trichomes becoming mostly restricted to major veins on older leaves, the margin coarsely dentate to crenate-dentate. Inflorescence of terminal (sometimes appearing axillary) unbranched racemes to 150 mm long; rachis pubescent like young stems; flowers solitary, alternate, pedicellate, subtended by a bract and 2 bractlets; bracts linear-subulate, 1.5–2 mm long, 0.3–0.4 mm wide; bractlets borne along proximal portion of pedicel, subulate or toothlike, 0.6–0.9 mm long, 0.1–0.2 mm wide; pedicels 2.5–5 mm long (accrescent and up to 6 mm long in fruit), pubescent with a mixture of eglandular and stipitate glandular trichomes. Calyx 4–5 mm long, shallowly 4-lobed, externally densely pubescent with antrorsely appressed eglandular trichomes, shattering irregularly when capsules dehisce and with proximal portion often remaining attached to pedicel; lobes broadly triangular, up to 1 mm long. Corolla dark red, 50–55 mm long, externally pubescent with stipitate glandular trichomes; tube 46–49 mm long, ± gradually ampliate distally; limb ± bilabiate, 12–13 mm in diameter, the upper lip 3–6 mm long with 2 lobes 1–3 mm long and wide, the lower lip 3–5.5 mm long with 3 lobes ± reflexed, 2–5 mm long and 2–4.5 mm wide. Stamens inserted about midway up corolla tube, exserted, didynamous, the longer pair 31–40 mm long, the shorter pair 29–37 mm long; fila-

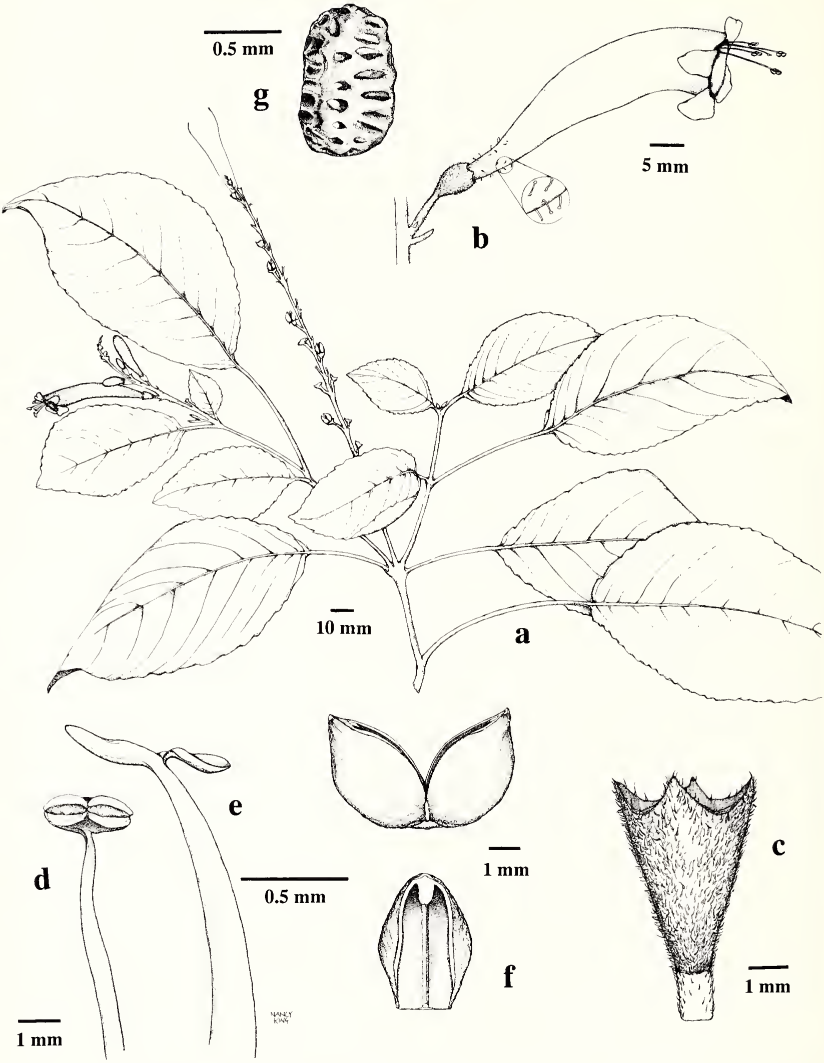

FIG. 1. *Uroskinnera almedae.* a. Habit. b. Inflorescence node with flower. c. Calyx. d. Distal portion of stamen. e. Distal portion of style and stigma. f. Dehisced capsule (top), interior view of single valve with seeds removed (bottom). g. Seed. (a. Drawn from *Fryxell and Lott 3222.* b–g. Drawn from *Breedlove & Almeda 56695.*)

ments flattened, pubescent with downward-pointing eglandular trichomes near base; thecae cream tinged with red, 1.2–1.5 mm long, the pair oriented end-to-end on a dark and broad connective; staminode filamentous, 15 mm long, glabrous. Style 54–57 mm long, glabrous; stigma with 2 unequal lobes 0.2–0.5 mm long. Capsule

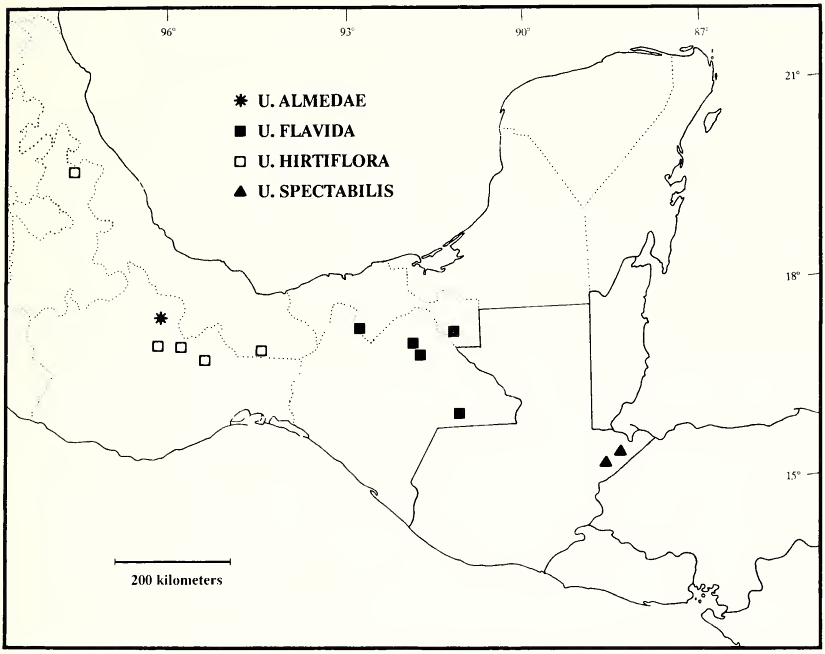

FIG. 2. Map of southern Mexico and northern Central America showing the known distribution of *Uroskinnera.*

ovoid to ellipsoid, 4.5–5 mm long, external surface roughened, lacking trichomes. Seeds numerous, blackish, subellipsoid, 0.8–1.1 mm long, 0.6–0.8 mm wide, the surface reticulate-foveate, lacking trichomes.

PARATYPE: MEXICO, Oaxaca, 21 mi S of Tuxtepec on Hwy. 175 to Oaxaca, 30 Oct 1980, *P. Fryxell and E. Lott 3222* (CAS).

Distribution and habitat. Southern Mexico (north-central Oaxaca; Fig. 2) where plants occur on shaded slopes in lower montane rain forest at elevations from 50–150 m.

Phenology. Flowering and fruiting: October and January.

The sister species of *Uroskinnera almedae* is not readily identifiable at this time. The species resembles *U. hirtiflora* by its linear, glaborus staminode (vs. clavate and glandular in other species) and *U. flavida* and *U. spectabilis* by its four-lobed calyx (vs. five-lobed in *U. hirtiflora*). In features of pubescence, form of the calyx lobes, and seed form, *U. flavida* is most similar to *U. almedae.* Both *U. flavida* and *U. hirtiflora* var. *breviloba* Wendt occur in habitats similar to those of *U. almedae.* The floral features that are unique in *Uroskinnera* to *U. almedae* (i.e., long, tubular, and red corollas with exserted stamens) are common adaptations for pollination by hummingbirds.

The epithet of this species honors the co-collector of the type, our colleague and friend, Frank Almeda.

ACKNOWLEDGMENTS

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ANNOUNCING THE GÖTE TURESSON MEMORIAL SYMPOSIUM

"Eco-Geographic Races: from Turesson to the Present"

To be held *June 24, 1992* at the meeting of the Pacific Division, AAAS at U.C. Santa Barbara, California

CHROMOSOME NUMBERS OF SOME NORTH AMERICAN SCROPHULARIACEAE, MOSTLY CALIFORNIAN

T. I. CHUANG
Department of Biological Sciences, Illinois State University,
Normal, IL 61761

L. R. HECKARD
Jepson Herbarium, University of California,
Berkeley, CA 94720

ABSTRACT

Chromosome counts are reported for 55 collections of 38 species representing eight genera in Scrophulariaceae, mostly from California. Chromosome numbers of 17 species are reported here for the first time, including *Collinsia linearis, Lamarouxia dasyantha, Mimulus arenarius, M. bicolor, M. bolanderi, M. breweri, M. filicaulis, M. layneae, M. latidens, M. pictus, M. pilosellus, M. pygmaeus, M. torreyi, M. tricolor, Pedicularis attolens, P. semibarbata, and Penstemon purpusii.* The species of *Lamarouxia* do not appear to be cytologically uniform as haploid numbers of $n=7$, 14, 15, and 16 have been recorded. The counts of $n=9$, 18 for *Mimulus primuloides* differ from a previous report of $n=17$. Consistency of chromosome number appears to be characteristic of certain genera of Scrophulariaceae whereas variation due to polyploidy and aneuploidy occurs in others, especially the large, polymorphic genera *Mimulus* and *Veronica.*

The Scrophulariaceae (Figwort or Foxglove Family), a large family of about 4000 species of mostly herbs or small shrubs, is distributed worldwide, but especially in the northern temperate zone. Some herbaceous genera (tribe Pediculareae) are root hemi-parasites, obtaining water and mineral nutrition from the host plants. A few genera, such as *Lathraea, Harveya,* and *Hyobanche,* are without or almost devoid of chlorophyll, and represent the most truly parasitic members in the family; these have been transferred back and forth between Scrophulariaceae and Orobanchaceae (Boeshore 1920; Kuijt 1969). These holoparasitic genera have usually been retained in Scrophulariaceae because they possess a bilocular ovary and axile placentation, rather than a unilocular ovary and parietal placentation as found in Orobanchaceae. The family is usually characterized by possession of an herbaceous habit, a more or less zygomorphic corolla, 2–4 stamens (plus occasionally a staminodium), a superior ovary with 2 united carpels and axile placentae, and seeds containing endosperm. Variation of these features, however, leads to uncertainty regarding proper delimitation of the family. Knowledge of Scrophulariaceae and its internal and external relationships is still far from satisfactory, as clearly pointed out by Thieret (1967). He

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remarked that, "New and detailed research on the family, using whatever tools are available, and a re-evaluation of past research are necessary before a logical taxonomic treatment of the family can be realized."

On the basis of corolla aestivation and leaf arrangement, the family has traditionally been divided into three subfamilies since the treatment proposed by Bentham (1846, 1876), and later modified by Wettstein (1891). These three subfamilies are: 1) Verbascoideae (=Pseudosolanoideae, two tribes and about 10 genera, characterized by the upper corolla lip covering the lateral lobes in bud, alternate leaves, and a fifth stamen often present); 2) Scrophularioideae (=Antirrhinoideae, seven tribes and more than 100 genera, characterized by the upper corolla lobes covering the lateral lobes in bud, at least the lower leaves opposite, and a fifth stamen becoming staminodial or absent); 3) Rhinanthoideae (three tribes and more than 100 genera, characterized by the upper corolla lobes being covered by one or both lateral lobes in bud, either alternate or opposite leaves, and a fifth stamen absent).

In a broad review of chromosome numbers in angiosperms, Raven (1975) pointed out that, "Scrophulariaceae are extremely diverse cytologically and the overall pattern is difficult to determine. Many of the tribes appear to be characterized by descending aneuploidy, but it is not certain whether any of the original diploids persist in most of them or not." Published reports of chromosome numbers of western North American Scrophulariaceae, particularly from California, are numerous, consisting either of scattered data on individual species or in taxonomic revisions and monographs of certain genera. Especially significant contributions to the cytotaxonomy of western American Scrophulariaceae have been those of Keck (1945) on *Penstemon,* McMinn (1951) on *Diplacus* (=*Mimulus*), Garber (1956) on *Collinsia,* Vickery (1978, summarized the reported counts) on *Mimulus,* Heckard (1968) on *Castilleja,* Chuang and Heckard (1982) on *Orthocarpus,* Chuang and Heckard (1973, 1975, 1986) on *Cordylanthus,* and Thompson (1988) on *Antirrhinum.*

Our study of *Cordylanthus* showed diversity in chromosome number that proved useful in infrageneric classification (Chuang and Heckard 1986). Each chromosome number, except $n=14$, coincides well with a particular group of related species (subgenus *Dicranostegia* $n=16$; subgenus *Hemistegia* $n=14$, 15, 21; subgenus *Cordylanthus,* $n=14$ for section *Cordylanthus,* $n=13$ for section *Anisocheila,* and $n=12$ for section *Ramosi*). The observed differences in base chromosome numbers ($n=11$, 12, and 14) in *Orthocarpus* (Chuang and Heckard 1982), and correlation of cytological information with different corolla morphology, stigma shape, ovule type, and seed coat morphology strongly support our contention that the genus as previously defined (sensu Keck 1927) is a heterogeneous and probably polyphyletic group (Chuang and Heckard 1991). We realigned the members of *Orthocarpus* into three genera: 1) *Orthocarpus,* restricted to the type section and subgenus with *n*=14; 2) *Castilleja* section *Oncorhynchus,* including Keck's (1927) sections *Castillejoides* and *Cordylanthoides,* with *n*=12; and 3) *Triphysaria,* an elevation of subgenus *Triphysaria* to generic status, with *n*=11 (Chuang and Heckard 1991). Our continuing survey of chromosome number in *Castilleja* (Heckard 1968; Heckard and Chuang 1977, and unpublished data) shows that over one-half of 100 species examined are either polyploid or are diploid plus one or more polyploid levels. For example one species complex, *Castilleja affinis-litoralis,* has diploids plus 5 levels of polyploidy from 4*x* to 12*x*. The widespread *C. miniata* of western United States and Canada has diploids and four additional levels of ploidy from 4*x* to 10*x*. Our preliminary study of the relationship of polyploidy to morphological variation indicates that hybridization and the widespread occurrence of polyploidy have resulted in formation of extensive pillar polyploid complexes, often with intergradation on a large scale.

A steady increase in knowledge of chromosome numbers may play an important role in placing taxa of uncertain affinities, in suggesting realignments, and corroborating other lines of evidence in formulating a more meaningful and useful classification of the family. More importantly it will help elucidate modes and mechanisms of speciation within the family.

MATERIALS AND METHODS

Cytological materials were obtained from the wild and fixed in Farmer's solution (3 anhydrous ethanol : 1 glacial acetic acid, v/v) or modified Carnoy's (Bradley 1948; Turner 1956) fluid (4 chloroform : 3 anhydrous ethanol : 1 glacial acetic acid, v/v/v). Fixed flower buds were immediately cooled on ice in the field and stored under refrigeration in the laboratory. All counts were made from acetocarmine squashes of pollen mother cells and observed with Zeiss phase contrast microscope. Chromosome drawings were made by camera lucida at magnifications of ×2600 and ×2100. Voucher specimens are deposited in the Jepson Herbarium, University of California at Berkeley, except where noted.

RESULTS AND DISCUSSION

In this study we present chromosome counts for 55 collections of 38 species representing eight genera (see Table 1). Included are what we believe to be the first counts for 17 species, indicated by an asterisk. In the following discussion, our counts are compared with the previously reported chromosome numbers for each genus. The

TABLE 1. GAMETIC CHROMOSOME NUMBERS OF WESTERN NORTH AMERICAN SCROPHULARIACEAE.

Taxon	Gametic chromosome number	Voucher
Collinsia		
C. greenei A. Gray	*n*=7	CALIFORNIA. Tehama Co.: Tedoc Mt., *Heckard 2957.*
**C. linearis* A. Gray	*n*=7 (Fig. 1)	CALIFORNIA. Del Norte Co.: Middle Fork Smith River, below Patrick Creek, *Heckard 6158.*
**Lamarouxia dasyantha* (Cham. & Schldl.) W. R. Ernst	*n*=15 (Fig. 2)	Mexico. OAXACA: 10 km N of Huajuapan de Leon, *Breedlove 39190* (DS).
Linaria		
L. dalmatica (L.) Miller	*n*=6	ARIZONA. Coconino Co.: just E of Ashfork, *Chuang & Chuang 7806.*
L. vulgaris Miller	*n*=6	IDAHO. Blaine Co.: along US 95, 2 mi S of Custer Co. line, *Heckard et al. 3471.*
Mimulus		
**M. arenarius* Grant	*n*=16 (Fig. 3)	CALIFORNIA. Fresno Co.: N Fork Kings River, *Heckard & Chuang 3198.*
**M. bicolor* Hartweg ex Benth.	*n*=8 (Fig. 4)	CALIFORNIA. Mariposa Co.: Jersey Road, 8 mi NE of Mariposa, *Heckard & Chuang 4062.* Fresno Co.: 2 mi below Shaver Lake, *Heckard & Chuang 5869.*
**M. bolanderi* A. Gray	*n*=8	CALIFORNIA. Fresno Co.: Jose Basin road, NE of Auberry, *Walker 66012.*
**M. breweri* (E. Greene) Cov.	*n*=16 (Fig. 5)	CALIFORNIA. Colusa Co.: Snow Mt., *Heckard & Hickman 5056.*
**M. filicaulis* S. Watson	*n*=8 (Fig. 6)	CALIFORNIA. Tuolumne Co.: S of Mather, *Chuang & Chuang 7526.*
M. floribundus Douglas ex Lindley	*n*=16	CALIFORNIA. Colusa Co.: Snow Mt., *Heckard & Hickman 5729.* Madera Co.: Ahwahnee, *Heckard & Chuang 4067.*
M. guttatus Fischer ex DC.	*n*=14	CALIFORNIA. Lassen Co.: S of Adin, *Heckard & Chuang 5530.* Lake Co.: W of Crockett Peak, *Heckard & Hickman 5661.*
**M. layneae* (E. Greene) Jepson	*n*=8 (Fig. 7)	CALIFORNIA. Fresno Co.: Dinkey Creek road to McKinley Grove, *Heckard & Chuang 3193.*

TABLE 1. CONTINUED.

Taxon	Gametic chromosome number	Voucher
**M. latidens* (A. Gray) E. Greene	*n*=16 (Fig. 8)	CALIFORNIA. Stanislaus Co.: SE of Warnerville, *Heckard & Chuang 4746.*
M. moschatus Douglas ex Lindley	*n*=16	CALIFORNIA. Tuolumne Co.: Stanislaus River, 3 mi NW of Columbia, *Heckard & Chuang 5500.*
M. nanus (E. Greene) Jepson	*n*=8	CALIFORNIA. Tehama Co.: Tedoc Mt., *Heckard 2979.*
**M. pictus* (Curran) A. Gray	*n*=8 (Fig. 9)	CALIFORNIA. Kern Co.: Lilly Canyon, near Miracle Hot Springs, *Bacigalupi & Hickman 9342.*
**M. pilosellus* E. Greene	*n*=9 (Fig. 10)	CALIFORNIA. Lake Co.: Snow Mt., *Heckard & Hickman 5268.* Mariposa Co.: Vogelsong Lake, Yosemite Natl. Park, *Heckard 6781.* Shasta Co.: King Creek Meadow, Lassen Volcanic Natl. Park, *Heckard & Chuang 5148a.*
M. primuloides Benth.	*n*=9 (Fig. 11)	CALIFORNIA. Mono Co.: Crowly Lake, *Heckard & Chuang 4927.*
	n=18 (Fig. 12)	CALIFORNIA. Shasta Co.: King Creek Meadow, Lassen Volcanic Natl. Park, *Heckard & Chuang 5148b.* Mariposa Co.: Bridalveil Campground, Yosemite Natl. Park, *Heckard 5872.*
**M. pygmaeus* Grant	*n*=9 or 10 (Fig. 13)	CALIFORNIA. Plumas Co.: Lake Almanor, *Heckard 5203* (plants raised from seed collected by J. T. Howell), *Heckard 5250.*
**M. torreyi* A. Gray	*n*=10 (Fig. 14)	CALIFORNIA. Lassen Co.: NE of Westwood, *Heckard 5255.*
**M. tricolor* Lindley	*n*=9 (Fig. 15)	CALIFORNIA. Stanislaus Co.: SE of Warnerville, *Heckard 4745.*
Parentucellia viscosa (L.) Carnel.	*n*=24	CALIFORNIA. Sonoma Co.: Pitkin Marsh, *Chuang & Heckard 6904.*
Pedicularis		
**P. attolens* A. Gray	*n*=8 (Fig. 16)	CALIFORNIA. Lassen Co.: NE of Westwood, *Heckard & Chuang 5259.*
P. densiflora Benth. ex Hook.	*n*=8	CALIFORNIA. Marin Co.: 1 mi SW of Fairfax, *Chuang & Chuang 7489.*

TABLE 1. CONTINUED.

Taxon	Gametic chromosome number	Voucher
**P. semibarbata* A. Gray	$n=8$ (Fig. 17)	CALIFORNIA. San Bernardino Co.: Bluff Lake, *Heckard & Chuang 4091.*
Penstemon		
P. deustus Douglas ex Lindley	$n=8$	OREGON. Josephine Co.: Elijah Mt., Oregon Cave Natl. Monument, *Chuang & Chuang 7776.*
**P. purpusii* Brandegee	$n=8$ (Fig. 18)	CALIFORNIA. Lake Co.: Snow Mt., *Heckard & Hickman 5102.*
Veronica		
V. alpina L.	$n=9$	CALIFORNIA. Alpine Co.: Woods Lake, *Heckard & Chuang 3772, 3779*; Ebbetts Pass, Sangre de Cristo Range, *Heckard & Chuang 3562.* NEVADA. Elko Co.: E Humboldt Mts., Angel Lake, *Heckard & Chuang 4957.*
V. americana (Raf.) Benth.	$n=18$	CALIFORNIA. Mono Co.: 3 mi SE of Bridgeport, *Heckard 2714a*; 2 mi W of Bridgeport, *Heckard 2817, 2818.* Sonoma Co.: Pitkin Marsh, *Chuang et al. 6905.*
V. anagallis-aquatica L.	$n=18$	CALIFORNIA. San Joaquin Co.: 7 mi SW of Manteca, *Heckard 2803.* Siskiyou Co.: Shasta River, 5 mi N of Yreka, *Heckard 2781.*
V. catenata Pennell	$n=18$	CALIFORNIA. Siskiyou Co.: Shasta River, 5 mi N of Yreka, *Heckard 2782.* OREGON. Klamath Co.: 2 mi NE of Keno, *Heckard 2698.*
V. copelandii Eastw.	$n=9$	CALIFORNIA. Trinity Co.: Mt. Eddy, Middle Deadfall Lake, *Heckard 2690.*
V. cusickii A. Gray	$n=9$	CALIFORNIA. Alpine Co.: Wood Lake, *Heckard 3778, 6774.*
V. peregrina L. subsp. *xalapensis* (Kunth) Pennell	$n=27$	OREGON. Marion Co.: 1 mi NW of Aumsville, *Heckard 2915.*
V. persica Poiret	$n=14$	CALIFORNIA. Alameda Co.: Berkeley, *Heckard 4068.*
V. scutellata L.	$n=9$	CALIFORNIA. Sonoma Co.: Pitkin Marsh, *Chuang et al. 6906.* OREGON. Marion Co.: 1 mi NW of Aumsville, *Heckard 2926.*

TABLE 1. CONTINUED.

Taxon	Gametic chromosome number	Voucher
V. serpyllifolia L. var. *humifusa* (Dickson) Vahl	$n=7$	CALIFORNIA. Colusa Co.: Snow Mt., *Heckard & Hickman 5276.* Modoc Co.: Cedar Pass, Warner Mts., *Heckard 5241.*

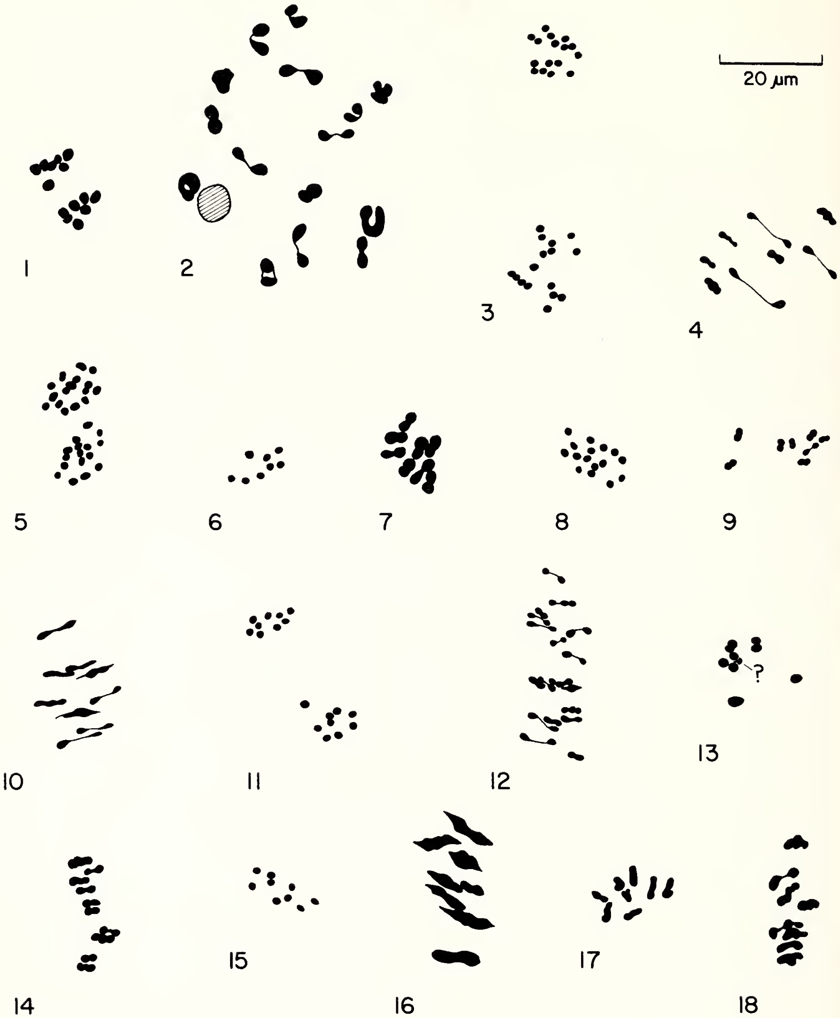
systematic implications based on chromosome number are briefly discussed where appropriate.

Collinsia Nutt. This genus, comprising 21 annual species, is restricted to western North America. All reported species are $n=7$, except *C. torreyi,* which is polyploid with $n=21$ (Garber 1956, 1958). Our count of $n=7$ for *C. greenei* agrees with the previously reported count by Garber (1958). The count of $n=7$ for *C. linearis* (Fig. 1) is the first for this species and confirms the base chromosome number of $x=7$ for the genus. Although Moldenke (1973) listed $2n=42$ for *C. linearis,* we are unable to find it in Garber's (1958) original report.

Lamourouxia Kunth. This genus, distributed from Mexico south to Peru, includes 24 perennial species (Ernst 1972). The three species reported thus far each has a different chromosome number: *Lamourouxia longiflora* (section *Lamourouxia*), $n=7$ (Ernst 1972); *L. viscosa* (section *Hemispadon*), $n=14$ (Ernst 1972); and *L. multifida* (section *Lamourouxia*), $n=16$ (Cruden 1972). Our count of $n=15$ for *L. dasyantha* (section *Adelphidion*; Fig. 2) is the first for this species and section. It appears that higher numbers of $n=14$–16 are polyploid, perhaps derived from amphiploid of ancestral forms with a base number of $x=7$, followed by aneuploid increase. More chromosome counts are needed for the genus, especially from Mexico, before any attempt to explore the utility of chromosome number in relation to the infrageneric classification can be realized.

Linaria Miller. This genus, composed of more than 100 species, is mostly Eurasian; only one species is native to North America. Two base chromosome numbers of $n=6$ and 7 have been reported for the genus, the former representing the prevalent number. Several polyploids based on $n=6$ have been reported (see Sutton 1980 for summary). Our counts of $n=6$ for both *L. dalmatica* and *L. vulgaris* agree with previous reports (Valdes 1970).

Mimulus L. This large genus of approximately 150 species of annual and perennial herbs and shrubs (section *Diplacus*) is distributed principally in western North America, especially California. Munz (1959) listed 77 species in that state and undoubtedly the California floristic province is a center of diversity of the genus.



FIGS. 1–18. Meiotic chromosome figures of first counts of western North American and Mexican Scrophulariaceae (H = Heckard; C = Chuang). 1. *Collinsia linearis*, $n=7$, TI (*H-6158*). 2. *Lamarouxia dasyantha*, $n=15$, Diak. (*Breedlove 39190*). 3. *Mimulus arenarius*, $n=16$, TI (*H&C-3198*). 4. *M. bicolor*, $n=8$, MI (*H&C-4062*). 5. *M. breweri*, $n=16$, ½ portion of TII (*H & Hickman 5056*). 6. *M. filicaulis*, $n=8$, ¼ portion of TII (*C&C-7526*). 7. *M. layneae*, $n=8$, MI (*H&C-3193*). 8. *M. latidens*, $n=16$, ¼ portion of TII (*H&C-4746*). 9. *M. pictus*, $n=8$, MI (*Bacigalupi & Hickman 9342*). 10. *M. pilosellus*, $n=9$, MI (*H&C-5148a*). 11. *M. primuloides*, $n=9$, TI (*H&C-4927*). 12. *M. primuloides*, $n=18$, MI (H&C-5148b). 13. *M. pygmaea*, $n=9$ or 10?, MI (*H-5250*). 14. *M. torreyi*, $n=10$, MI (*H-5255*). 15. *M. tricolor*, $n=9$, ¼ portion of TII (*H-4745*). 16. *Pedicularis attolens*, $n=8$, MI (*H&C-5259*). 17. *P. semibarbata*, $n=8$, ¼ portion of TII (*H&C-4091*). 18. *Penstemon purpusii*, $n=8$, MI (*H & Hickman 5102*).

Recently, two additional species, *M. norrisii* and *M. shevockii,* were described from California by Heckard and Shevock (1985) and Heckard and Bacigalupi (1986), respectively. A comprehensive survey of pollen morphology of the genus was conducted by Argue (1980). He reported 117 species and varieties, classified them into five major and eight more tentative, minor pollen types, and concluded that, "The pollen morphological data correlate well with geographical and macromorphological data and, where the latter are ambiguous, often provide important clues toward the resolution of conflicting interpretations of infrageneric classification and generic delimitation." Available cytological information (Vickery 1978) reveals great diversity of chromosome number in the genus, with gametic numbers of *n*=7, 8, 10, 11, 12, 14, 15, 16, 17, 23, 24, 28, 30, 31, 31, 32, and 46. He reports that sections *Erythranthe* and *Diplacus* have the same number throughout (*n*=8 and *n*=10, respectively) whereas section *Simiolus* has an extensive mixoploid series of *n*=13, 14, 15, 16, 24, 28, 30, 31, 32, and 46 (Vickery 1978).

Included in the present study are counts of 16 species, 11 of which are reported here for the first time. Four species agree with and one differs from previously reported counts.

Five species (*M. dudleyi, M. floribundus, M. moschatus, M. norrisii,* and *M. shevockii*) of section *Paradanthus* have been previously reported from California; all have *n*=16. We report here *n*=16 also for *M. floribundus* and *M. moschatus,* in agreement with earlier reported counts. Our counts of *n*=9 and 18 for *M. primuloides* differ from that of McArthur and Vickery (1970) who reported *n*=17 for this species from plants collected 1.5 km above Bumpass Hell, Mt. Lassen, Shasta Co., California, very near the locality where we obtained our material. The counts of *n*=8 for *M. bicolor* (Fig. 4) and *M. filicaulis* (Fig. 6), *n*=9 for *M. pilosellus* (Fig. 10), and *n*=16 for *M. arenarius* (Fig. 3) and *M. latidens* (Fig. 8) represent the first reports for these species. *Mimulus pilosellus* E. Greene was reduced to varietal status under *M. primuloides* by Smiley (1921) and completely synonymized to that species by Grant (1924); subsequent workers have followed this treatment. *Mimulus pilosellus* (*Heckard and Chuang 5148a*) and *M. primuloides* (*Heckard and Chuang 5148b*) grow together in Lassen Volcanic National Park. They can be distinguished by the small and densely pilose leaves and small flowers of the former versus the larger and less densely pilose leaves and large flowers of the latter. The fact that these two taxa frequently grow together in many localities in the Sierra Nevada, and that *M. pilosellus* has a chromosome number of *n*=9 (Fig. 10) and *M. primuloides n*= 18 (Fig. 12) leads us to reinstate the former as a distinct species.

Four species of section *Eunanus* have been reported previously: *M. brevipes, M. cusickii,* and *M. nanus* with *n*=8 and *M. bigelovii* with $n=16$. Our count of $n=8$ for *M. nanus* confirms the previous count for this species. We report here first counts for the following: $n=8$ for *M. bolanderi* and *M. layneae* (Fig. 7) and $n=10$ for *M. torreyi* (Fig. 14). *Mimulus mohavensis,* treated in the monotypic section *Mimulastrum* by Gray (1884) and subsequently followed by Grant (1924), was submerged in section *Eunanus* by Pennell (1951). The chromosome number of $n=7$ (Carlquist 1953) and tricolpate pollen (Argue 1980) found in *M. mohavensis,* along with its distinct corolla morphology and stylar pubescence, readily distinguish this species from members of section *Eunanus,* which have $n=8$ or 10, 5–7 stephanocolpate pollen, and different corolla morphology. Based on these facts, it seems desirable to retain the monotypic section *Mimulastrum* for *M. mohavensis.*

Mimulus breweri, included in section *Paradanthus* by Grant (1924), was assigned to a monotypic section *Monimanthe* by Pennell (1947), who considered it to be intermediate between the subgenera *Synplacus* and *Schizoplacus* in having an unsplit capsule septum of the former and persistent corolla of the latter. We report here the first count for this species as $n=16$ (Fig. 5). This chromosome number and possession of tricolporate pollen grains further confirm the close affinity of this species with subgenus *Synplacus,* especially section *Paradanthus* as suggested earlier by both Grant (1924) and Argue (1980).

Mimulus pictus (Fig. 9) and *M. tricolor* (Fig. 15), both with $n=9$, represent not only first counts for these two species but also for section *Oenoe.* The gametic chromosome number of $n=9$ is a new base number of the genus. *Mimulus pygmaeus,* a much reduced species from NE California, was treated in a monotypic section, *Microphyton,* by Pennell (1947), who suggested that, "It is presumably derived from section *Eunanus* ancestry." We present here the first report for this species with $n=9$ or 10? (Fig. 13). The uncertainty owes to the fact that there were always 2 or 3 pairs of sticky chromosomes at metaphase I. This difficulty is compounded by the extremely small- and solitary-flowered plants, of which we were unable to collect sufficient bud material for a good count. Based on the probable chromosome number of $n=9$ and its 5–7 stephanocolpate pollen grains, we follow Grant (1924) in placing *M. pygmaeus* in section *Oenoe,* rather than section *Eunanus,* as suggested by Pennell (1947) and Argue (1980).

More chromosome counts, especially in sections *Eunanus* and *Oenoe,* are needed in order to clarify the sectional relationships of the genus and for placement of species of uncertain affinity.

Parentucellia Viv. This is a small genus of two species, native to the Mediterranean region. *Parentucellia viscosa* is an introduced weed in western North America and has been reported to be $n=24$ (Hambler 1954, 1955). Our count of $n=24$ confirms this earlier count. *Parentucellia latifolia* has also been reported as $n=24$ (Markova and Ivanova 1973).

Pedicularis L. This, the largest genus of Scrophulariaceae with about 500 species, occurs chiefly in northern temperate and boreal regions, especially in the Old World. Approximately 23 species are indigenous to western North America. The great majority of species thus far reported are diploid with $n=8$, plus a few tetraploid of $n=16$. Only one species, *P. verticillata,* has been reported several times by various investigators to be $n=6$ (see Carr 1971 for summary). We report here $n=8$ for *P. densiflora,* which is in agreement with previous counts by Carr (1972) and Spellenberg (1971). Our counts of $n=8$ for *P. attolens* (Fig. 16) and *P. semibarbatus* (Fig. 17) represent the first reports for these two species.

Penstemon Schmidel. This, the largest genus of North American Scrophulariaceae, is composed of over 250 species and is native to North America with the vast majority of species occurring in western United States. According to Freeman (1983), the chromosome numbers of 39.6% of the species of *Penstemon* have been reported, with $n=8$ representing the number most commonly encountered. He estimated that fewer than 20% of the species counted are polyploid, with $n=16$, 24, 32, and 48. We report here $n=8$ for both *P. deustus* and *P. purpusii* (Fig. 18), the former agreeing with the previously reported count (Keck 1945) and the latter representing the first count.

Veronica L. This genus is composed of over 200 species, distributed in the North Temperate Zone, especially in the Old World. Ownbey (1959) listed 14 species of *Veronica* occurring in the Pacific Northwest, five native and the remainder introduced from the Old World. The great amount of cytological information available to date reveals a diversity of chromosome number, with base numbers of $x=7$, 8, and 9 and varying levels of polyploidy up to $n=32$ and 34. Polyploidy is common in the genus, with many species consisting of 2 or 3 ploidy levels (see Index to Plant Chromosome Numbers 1966–1987). Obviously, polyploidy has played an important role in evolution in the genus. We report here $n=7$ for *V. serpyllifolia* var. *humifusa*; $n=14$ for *V. persica*; $n=9$ for *V. alpina, V. copelandii, V. cusickii,* and *V. scutellata*; $n=18$ for *V. americana, V. anagallis-aquatica,* and *V. catenata*; and $n=27$ for *V. peregrina* subsp. *xalapensis.* All counts agree with earlier reported counts.

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MUHLENBERGIA PILOSA (POACEAE: ERAGROSTIDEAE), A NEW SPECIES FROM MEXICO

PAUL M. PETERSON
Department of Botany, National Museum of Natural History,
Smithsonian Institution, Washington, DC 20560

J. K. WIPFF and STANLEY D. JONES
S. M. Tracy Herbarium,
Department of Rangeland Ecology and Management,
Texas A&M University, College Station, TX 77843

ABSTRACT

Muhlenbergia pilosa from Mexico is described and illustrated. The new species is distinguished by its densely pilose florets; hirsute internodes; hairy sheath summits; membranous, deeply lacerate to short ciliate ligules, 0.5–2.5(5.0) mm long; and awned, pilose, second glumes. A tabular comparison with *M. lucida* Swallen and *M. versicolor* Swallen is given.

RESUMEN

Muhlenbergia pilosa de Mexico, se describe e ilustra. La nueva especie se distingue por sus flósculos densamente pilosos; entrenudos hirsutos; ápice de las vainas pubescentes; lígulas membranáceas, profundamente laceradas a cortamente ciliadas, 0.5–2.5(5.0) mm de longitud; y segunda gluma aristada, pilosa. Se presenta una tabla comparativa con *M. lucida* Swallen y M. *versicolor* Swallen.

The genus *Muhlenbergia* is represented in Mexico by about 115 species, of which 47% are endemic (Beetle 1987). Morphological characters that delimit the genus are spikelets with single perfect florets and lemmas with three, usually prominent, nerves.

There has been considerable floristic work in the state of México (Reiche 1926; Sánchez 1969) and more recently, 22 additions have been reported to the grass flora from the valley of Mexico, including the following four species of *Muhlenbergia*: *M. hintonii* Swallen, *M. orophila* Swallen, *M. polycaulis* Scribn., and *M. seatonii* Scribn. (Herrera 1988). While making routine determinations at TAES the junior authors noted the unusual morphological features of a new species and sent it to the senior author for clarification. The new species is presented prior to completion of the revision of the entire genus in Mexico (Peterson in preparation) so others working in that country may become aware of its existence and perhaps search for additional locations. The specific epithet of the new species refers to the dense covering of epidermal hairs on the dorsal surface of the lemma and the palea.

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Muhlenbergia pilosa P. Peterson, Wipff, & S. D. Jones, sp. nov. (Fig. 1).—TYPE: MEXICO, Mexico, Municipio Tejupilco, 17 km NE of Tejupilco on road to Temascaltepec, 18°59′N, 10°04′W, 30 Oct 1982, *S. D. Koch and P. A. Fryxell 82256* (holotype, CHAPA; isotypes, CHAPA, IEB, MEXU, MICH, TAES!, US, XAL).

A *Muhlenbergia lucida* culmis (50)90–130 cm altis, internodiis hirsutis, vaginis pilis ad apicem, ligulis membranis laciniis ad apicem 0.5–2.5(5.0) mm longis, antheris 1.3–1.9 mm longis recedit.

Caespitose perennial without rhizomes. Culms (50–)90–130 cm tall, erect, rounded and purplish near base, hirsute just below and above the mostly basal nodes, the hairs appressed; internodes glabrous to antrorsely scaberulous. Sheaths (5–)20–50(–70) cm long, many times longer than the mostly basal internodes, antrorsely scaberulous, in age becoming somewhat fibrillate and shredded below, often brown; sheath margins with a few, hyaline hairs, the hairs up to 2.5 mm long and more numerous near the summit. Ligules 0.5–2.5(–5.0) mm long, delicate, hyaline, deeply lacerate the entire length or reduced to a short ciliate membrane in age; apex obtuse to truncate. Blades 15–35 cm long, 1–3.1 mm wide, flat to tightly involute, antrorsely scaberulous below to scabrous and sparsely hirsute above; margins with intermittent hairs. Panicles 20–45 cm long, 3–8 cm wide, somewhat loosely flowered, the ascending branches 0.8–4.7 cm long, purplish, spreading 20–60° from the culm axis with a tuft of hairs in the axils; pedicels 1–7 mm long, delicate, purplish, short hispidulous to glabrous. Spikelets 2.4–3.7 mm long, erect, 1-flowered. Glumes (1.8)2.1–3.2 mm long, shorter to longer than the lemma, usually equal in length, 1-nerved, pilose on the back, sometimes sparingly near the apex; first glume narrowly lanceolate, unawned, the second more broadly lanceolate, awned; apex acuminate, the awn up to 0.6 mm long, delicate, hyaline. Lemma 2.1–3.7 mm long, lanceolate to oblong-elliptic, 3-nerved, awned, densely pilose on the dorsal surface, the hairs up to 1.6 mm long, whitish; apex acute to acuminate, sometimes minutely bifid with acute teeth, the teeth up to 0.2 mm long; lemma awn 18–31 mm long, flexuous, delicate, often purplish. Palea 2.0–3.5 mm long, oblong-elliptic, 2–nerved, densely pilose on the dorsal surface, the whitish hairs up to 1.5 mm long; apex acute to acuminate. Stamens three; anthers 1.3–1.9 mm long, purplish yellow. Caryopsis 1.1–1.4 mm long, fusiform, light brownish. Chromosome number unknown.

PARATYPES: MEXICO, Mexico, 5 km NE of Tejupilco on Mex 134 to Temascaltepec, 18°57′N, 100°8′W, 6 Oct 1991, *Peterson and Annable 11061* (ANSM, CHAPA, ENCB, IEB, K, MEXU, MO, RSA, TAES, UC, US, UTC, WIS); 26 km NE of Tejupilco on Mex 134 and 2.4 km S of Temascaltepec, 19°01′N, 100°3′W, 6 Oct 1991,

FIG. 1. *Muhlenbergia pilosa,* Mexico, Mexico (*Koch and Fryxell 82256*). A. Habit. B. Ligule. C. Inflorescence. D. Inflorescence branch. E. Spikelet. F. Glumes. G. Lower glume, ventral view. H. Upper glume, ventral view. I. Floret. J. Lemma, ventral view. K. Palea, dorsal view. L. Palea enclosing the stamens, pistil, and lodicules. M. Caryopsis.

TABLE 1. SALIENT CHARACTERS DISTINGUISHING *MUHLENBERGIA PILOSA, M. LUCIDA,* AND *M. VERSICOLOR.*

Characters	*M. pilosa*	*M. lucida*	*M. versicolor*
Culm height (m)	(0.5–)0.9–1.3	0.25–0.6	(0.8–)1–1.5(–2)
Internode	hirsute	glabrous to puberulent	glabrous to puberulent
Sheath auricles	absent	absent	well-developed
Sheath summit	hairy	puberulent	puberulent
Blade	flat to involute	involute	folded
Ligule	delicate below, lacerate above	firm below, entire above	firm below, entire above
Ligule length (mm)	0.5–2.5(–5.0)	3–6	(5–)10–22
Inflorescence branches	spreading 20–60° from culm axis	spreading 20–80° from culm axis	ascending and appressed
Second glume	awned, pilose	unawned, pilose	awned, scaberulous
Anther length (mm)	1.3–1.9	2.1–2.4	1.6–2.0

Peterson and Annable 11072 (ANSM, CHAPA, ENCB, IEB, MEXU, MO, US).

DISTRIBUTION, HABITAT, AND RELATIONSHIPS

Muhlenbergia pilosa is known only from the state of México northeast of Tejupilco along the road to Temascaltepec. It occurs in open, oak and pine-grass savannahs on steep rocky slopes and roadcuts in clayish soils between 1530 and 1810 m. It is found associated with species of *Stevia* Cav., *Bouteloua* Lagasez, *Heteropogon* Pers., *Stipa* L., *Trachypogon* Nees, *Pennisetum* Rich. in Pers., and *Aegopogon tenellus* (DC.) Trin., *Rhynchelytrum repens* (Willd.) C. E. Hubb., *Pereilema crinitum* Presl, and *Muhlenbergia ciliata* (Kunth) Kunth. The morphological characters that can consistently be used to distinguish among *M. pilosa, M. lucida* Swallen, and *M. versicolor* Swallen are listed in Table 1. *Muhlenbergia pilosa* differs from the latter two species by possessing hirsute internodes, hairy sheath summits, and membranous, deeply lacerate to short-ciliate ligules, 0.5–2.5(5) mm long.

Muhlenbergia pilosa superficially resembles *M. lucida,* a species known only from the Sierra Madre Occidental of western Chihuahua (Swallen 1936). *Muhlenbergia lucida* occurs in a very different habitat from *M. pilosa.* The former is found on gray to reddish or white volcanic pumice, lapilli tuff, and altered rhyolite lava flows in dry rocky sites among boulders at elevations between 2000 and 2600 m (Peterson et al. in review). Characteristics shared by both species are flat to involute leaf blades; whitish, densely pilose florets that are borne on delicate pedicels; and pilose glumes.

The new species seems most closely related to *M. versicolor,* a member of section *Epicampes,* which ranges in Mexico from Guanajuato, Michoacán, Morelos, Guerrero, México, Distrito Federal, Veracruz, Oaxaca, and Chiapas to Guatemala and Honduras (Swallen 1950; Soderstrom 1967; Breedlove 1986). *Muhlenbergia versicolor* occurs sympatrically with *M. pilosa* and is found in slightly more mesic sites, in pine-needle or oak-leaf litter. Besides the gross morphological differences observed between the leaf blades, i.e., folded in *M. versicolor* verses flat to involute in *M. pilosa,* the adaxial ribs are angled with a pointed apex in the former and flat-topped with a flattened apex in the latter.

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NOTES

NOTES ON THE STATUS OF *PSILOCARPHUS BERTERI* (ASTERACEAE: INULEAE).—James D. Morefield, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711-3101 (present address: Nevada Natural Heritage Program, 123 W. Nye Lane, Carson City, NV 89710).

Psilocarphus Nuttall consists of 3–5 ill-defined species most widely distributed in temperate western North America, with smaller, disjunct populations of two taxa in temperate South America. The genus is currently in need of detailed systematic investigation. No such study is contemplated here, but detailed examination of over 1000 sheets and types of *Psilocarphus* (mostly at BM, CAS, DS, JEPS, POM, RSA and UC) in conjunction with the Jepson Manual Project, along with field collections and observations during 1988–1990, have revealed a geographic range extension for one taxon and suggest a nomenclatural change.

Cronquist (1950; see synonymy below for literature citations) recognized *Psilocarphus berteri* I. M. Johnston as a species endemic to central Chile. Three herbarium collections from California (*Jepson 8310* [JEPS!], *Howell 28323* [RSA! UC!], both from the Point Reyes area, Marin Co., and *Mason and Lee 9104* [UC!] from Point Lobos State Park, Monterey Co.) all contain plants that I cannot distinguish from specimens of *P. berteri.* The *Howell* specimen, furthermore, includes a complete set of intergrades to typical *P. tenellus* Nuttall var. *tenuis* (Eastwood) Cronquist. The *Mason and Lee* collection was cited by Cronquist (1950) as *P. tenellus* var. *tenuis.*

The condensed habit and increased pubescence of Californian *P. berteri* over *P. tenellus* var. *tenuis* is typical of ecotypes of other taxa inhabiting seashore and other relatively severe habitats. This is my interpretation of the *P. berteri* collections in California.

I agree with Cronquist (1950) that the two *Psilocarphus* taxa with disjunct populations in temperate South America likely originated in North America as *P. brevissimus* Nuttall var. *brevissimus* and *P. tenellus.* My own field observations show that *P. brevissimus* var. *brevissimus* and (contrary to Cronquist 1950) *P. tenellus* var. *tenuis* inhabit the wettest areas of any taxa in the genus (generally vernal pools). Accidental transport of their small, woolly-bracted achene-complexes between the two continents by migratory waterfowl is plausible and perhaps frequent.

Unlike Cronquist (1950), however, I am unable to separate South American and Californian *P. berteri* from the variation now observable in *P. tenellus* var. *tenuis.* The character he used to distinguish *P. berteri* from *P. tenellus* var. *tenuis,* "Leaves . . . closely enfolding and often hiding the heads" versus "Leaves not closely enfolding the heads" appears inconstant within both taxa.

My own observations of about 120 additional characters in preparation for detailed cladistic analyses reveal no other differential characters. Some specimens of *P. berteri* tend to have a dense grayish pubescence, spreading or very short branches, and leaves longer than the internodes, whereas *P. tenellus* var. *tenuis* tends to have thinner greenish pubescence, more erect and elongate branches, and leaves shorter than the internodes. Unfortunately, these tendencies are also inconstant in both North America and South America. I therefore propose that the two taxa be united.

With the inclusion of *P. berteri* in *P. tenellus* var. *tenuis,* an older varietal epithet becomes available, and must be used. I propose the following treatment for *Psilocarphus tenellus* in anticipation of the Jepson Manual Project:

PSILOCARPHUS TENELLUS Nutt., Trans. Amer. Philos. Soc. (ser. 2) 7:341. 1840.—*Micropus tenellus* (Nutt.) Walp., Repert. Bot. Syst. 2, part 4:600. 1843.—TYPE: USA, California, Santa Barbara, probably Apr 1836, *Nuttall s.n.* (holotype, BM-herb. Nutall!; isotype, K-herb. Hooker 1867!).

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KEY TO THE VARIETIES OF *PSILOCARPHUS TENELLUS*

a. Uppermost leaves oblanceolate to obovate, mostly 2 times as long as wide or longer, spreading; corollas of central, functionally staminate flowers 5-lobed. .... var. *tenellus*

a′. Uppermost leaves ovate to broadly elliptic, less than 2 times as long as wide, more or less appressed to the heads, corollas of central, functionally staminate flowers 4-lobed. .... var. *globiferus*

PSILOCARPHUS TENELLUS var. *TENELLUS*.

Common on usually dry slopes and flats, often along paths, on burns, or where otherwise disturbed, from near sea level to 2000 m elevation. W California, NW Baja California, and SW Oregon, widely scattered to SW British Columbia and NW Idaho. Tending to merge with *P. oregonus* Nuttall, especially in the Sierra Nevada southward to Baja California.

Psilocarphus tenellus var. **globiferus** (Bertero ex DC.) Morefield, comb. nov.—*Micropus globiferus* Bertero, Mercurio Chileno 15:700. 1829 (nom. nud.); Bertero ex DC., Amer. J. Sci. Arts 23:254. 1833 (nom. nud.); Bertero ex DC., Prodr. 5: 460. 1836.—*Bezanilla chilensis* E. J. Remy in C. Gay, Fl. Chil. 4, part 1:110. 1849. (nom. illegit.!).—*Psilocarphus chilensis* (E. J. Remy) A. Gray, Syn. Fl. N. Amer., 2nd ed., vol. 1, part 2:448. 1886.—*Psilocarphus globiferus* (Bertero ex DC.) Speg., Anales Soc. Ci. Argent. 48:330. 1899.—non *Psilocarphus globiferus* Nutt., 1840 (=*P. brevissimus* Nutt. var. *brevissimus*).—*Psilocarphus berteri* I. M. Johnston, J. Arnold Arbor. 19:261. 1938.—TYPE. Chile, Rancagua, 1833, *Bertero 433* (holotype, G-DC, fiche RSA!).

Because Remy (1849) cited "*Micropus globiferus* Bertero, Herb.!—DC., *Prodr.*" as an unequivocal synonym of *Bezanilla chilensis,* the latter becomes an illegitimate nomenclatural synonym of the former (ICBN Art. 63). It thus cannot be a taxonomic synonym of *P. brevissimus* Nutt. sensu Johnston (1938) and Cronquist (1950).

Psilocarphus tenuis Eastw., Bot. Gaz. (Crawfordsville) 41:292. 1906.—*Psilocarphus tenellus* Nutt. var. *tenuis* (Eastw.) Cronq., Res. Stud. State Coll. Wash. 18:88. 1950.—TYPE: USA, California, Monterey, Jul 1905, *Mrs. Joseph Clemens s.n.* (holotype, CAS [lost?]; fragments, UC! US).

?*Psilocarphus globiferus* (Bertero ex DC.) Speg. var. *minimus* Cabrera, Revista Chilena Hist. Nat. 40:231. 1937. Type not seen.

According to the ICBN Arts. 32.6 and 57.3 Note 1, the autonym var. *globiferus* has a legitimate basionym and takes priority over both var. *minimus* and var. *tenuis,* even though *P. globiferus* (Bertero ex DC.) Speg. is illegitimate.

Infrequent (or rarely collected), low moist places, mostly in vernal pools or among coastal dunes, sea level to 700 m elevation. W-central California, W-central Chile. Depauperate, broad-leaved, often glabrate forms of *P. brevissimus* var. *brevissimus* (*Parish s.n.,* 16–20 June 1895 [UC]; *Thorne et al. 53496* [RSA, UC]; *Thorne 53233* [RSA, UC], etc.) occur at higher elevations in the San Bernardino Mountains of S California, and might be confused with *P. tenellus* var. *globiferus.*

The characters separating var. *globiferus* from var. *tenellus* appear relatively constant. Only a very few intermediate specimens have been seen, and these may merely be aberrant forms of var. *tenellus.* Further systematic study may show the two taxa to be separate species.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

NERIUM OLEANDER L. (APOCYNACEAE).—Shasta Co., well established in riparian corridor along the Sacramento River, between Redding and Keswick Dam, elevation 180 m, T32N R5W, 6 Nov 1991, *J. Keeley 14145* (LOC).

Previous knowledge. Not previously reported in the California flora (Munz, A California flora and supplement, 1968; Hickman (ed.), The Jepson manual, in press).

Significance. Although extensively planted throughout the state, this is the first report of oleander being naturalized in the wild. This species is native to the Mediterranean Basin where it is largely restricted to riparian communities similar to the site described above.

—JON E. KEELEY, Biology Department, Occidental College, Los Angeles, CA 90041.

AMBROSIA PUMILA (Nutt.) A. Gray. (ASTERACEAE).—Riverside Co., ca. 1 km S of Tucalota Creek and 0.8 km E of San Diego Aqueduct in Skunk Hollow, 40 m W of N end of large vernal pool. Population of ca. 500 individuals in clearing of annual grassland dominated by *Avena fatua*; associated with *Erodium* sp. and *Bromus rubens*; 30 May 1991, *D. B. Zippin* 138 with C. C. Patterson. Confirmed by S. Boyd and G. H. Levin. Specimens at SD, RSA.

Previous knowledge. Floodplains, valley grasslands and dry lake bed fringes from the San Luis Rey River, San Diego Co. to vicinity of Calmalli and El Arco, Baja California, Mexico (Wiggins, Flora of Baja California, 1980; California natural diversity data base, 1991).

Significance. First record for Riverside Co. and a northward range extension of ca. 20 km. This species is a Category 2 candidate for federal listing and is considered rare and endangered throughout its range by the California Native Plant Society. This species is very close to several other rare species at Skunk Hollow including *Orcuttia californica* (state-listed endangered) and *Navarettia fossalis. Eryngium aristulatum* subsp. *parishii* (state-listed endangered) is also reported from the Skunk Hollow vernal pool (S. Boyd personal communication), but has not been relocated in 1991 (P. Zedler personal communication). This site is currently privately held and will soon be surrounded by a housing development. This discovery lends additional support for permanent protection and management of this significant area.

—DAVID B. ZIPPIN, Department of Botany, University of Texas, Austin, TX 78713-7640.

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IDAHO

CRUCIANELLA ANGUSTIFOLIA L. (RUBIACEAE).—Clearwater Co., flowering plants on S slope above Clearwater River, 10 km west of Orofino, on both sides of county road between Orofino and Cavendish, T37N R1E NW¼ SE¼ sect. 32, 435 m, 9 Jul 1991, *C. J. T. Roché 1479.* Native vegetation: open *Pinus ponderosa* over *Crataegus douglasii* and *Agropyron spicatum.* Associated vegetation: *Bromus tectorum, B. japonicus, Centaurea solstitialis, Torilis arvensis,* and *Lotus purshiana.* Fruiting specimens, same location, 2 Aug 1991, *C. Roché, B. F. Roché, and R. R. Old 1494* (WS).

Previous knowledge. The first North American collection of narrow-leaved crosswort was by A. A. Beetle from scrub oak thickets on dry hills near Igo, Tehama County, California, 22 May 1944 (Leaflets of Western Botany 6:64. 1945). By 1962 it had spread to Shasta, Butte, and Yuba counties (Leaflets of Western Botany 9:233–242. 1962). Although listed in Jepson (A flora of California. Rubiaceae by Lauramay T. Dempster, 1979) and by Kartesz and Kartesz (A synonymized checklist of the vascular flora of the United States, Canada and Greenland, 1980), *Crucianella* was not included in Jepson (Manual of flowering plants of California, 1925), Munz (California flora, 1959), or the National list of scientific plant names (USDA Soil Conservation Service, 1982). Narrow-leaved crosswort is an annual forb native to stony hillsides, open forests, and macchie in southern Europe, northwest Africa, and southwest Asia (Flora of Turkey and the East Aegean Islands, Vol. 7, 1982, p. 730).

Significance. This is the first record of *Crucianella* in Idaho. Although not listed as a noxious weed in California, this extension of its range indicates that crosswort is yet another Mediterranean species capable of invading grasslands in the western US.

—CINDY ROCHÉ and B. F. ROCHÉ, JR., Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410; and R. R. OLD, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83843.

MEXICO

IOSTEPHANE HETEROPHYLLA (Cav.) Hemsley (ASTERACEAE).—Chihuahua, La Guitarra, 28°40′N, 108°35′W, elevation 2000 m, 10 Aug 1988, *Laferrière 1650* (ARIZ).

Previous knowledge. Southwestern Chihuahua to Oaxaca (Sharp, Annals of the Missouri Botanical Garden 22:51–152, 1935; McVaugh, Flora Novo-Galiciana, Vol. 12: Compositae, 1984).

Significance. Range extension of approximately 350 km.

—JOSEPH E. LAFERRIÈRE, Herbarium, Department of Botany, Washington State University, Pullman, WA 99164.

NEVADA

LEPTOCHLOA FILIFORMIS (Lam.) Beauv. (POACEAE).—Clark Co., intersection of I-15 and Nevada State Highway 40, California Wash, small restricted population in sandy loam of flood channel with *Ambrosia dumosa, Gutierrezia sarothrae, Atriplex canescens, Larrea tridentata,* and *Chloris virgata,* ca. 610 m, 6 Nov 1982, *P. M. Peterson 795* (UNLV).

Significance. First collection from Nevada. *Leptochloa filiformis* extends from the southern third of the United States through much of South America and frequently occurs as a weed in agricultural areas. Because it prefers relatively mesic growing conditions, populations are unlikely to persist in arid climates such as that of Nevada. The depauperate specimens from this collection are atypically small.

—Neil Snow, Department of Biology, Washington University, St. Louis, MO 63130; and Paul M. Peterson, Department of Botany, Smithsonian Institution, Washington, DC 20560.

OREGON

ASARUM WAGNERI Lu and Mesler (ARISTOLOCHIACEAE).—Douglas Co., Lemola Lake, 0.1 mi W of Bunker Hill campground on rd 999, T26S R5E sect. 11 SE¼, elev. ca. 1400 m, in understory of *Pseudotsuga-Pinus* forest, 6 Jul 1991, *Mesler and Lu 9103* (HSC).

Significance. A range extension of about 100 km N from Mt. McLoughlin, Jackson Co., Oregon. A rare endemic previously known from Jackson and Klamath cos., in the vicinity of Mt. McLoughlin and Lake of the Woods (Lu and Mesler, Brittonia 35:331–334, 1983).

—M. R. Mesler and K. Lu, Department of Biological Science, Humboldt State University, Arcata, CA 95521.

SATUREJA VULGARIS (L.) Fritsch (syn. *Clinopodium vulgare* L.) (LAMIACEAE).—Polk Co., McTimmonds Valley, about five airline km N of Pedee, in a shady, moist *Fraxinus* swale with *Oemleria, Pseudotsuga, Rubus, Prunella, Agrostis, and Lupinus,* T9S R6W sect. 15, 108 m, 6 Jul 1990, *R. Halse 4057* (CAS, NY, OSC, US), determined by K. L. Chambers.

Significance. First report for Oregon. This Eurasian species has been reported from southern British Columbia and from Ontario to Nova Scotia, Canada (Scoggan, The flora of Canada IV, 1979) southward to North Carolina, Tennessee, Kansas, Colorado, New Mexico, Arizona, and southern Utah (Cronquist et al., Intermountain flora IV, 1984). Whether this species has a native American element, as suggested by Fernald (Rhodora 46:388, 1944), or does not, as suggested by Doroszenko (unpubl. Ph.D. dissertation, Edinburgh University, 1985), has yet to be determined.

WASHINGTON

ARTEMISIA STELLERIANA Besser (ASTERACEAE).—Jefferson Co., Quimper Peninsula, Fort Worden State Park, on sand dunes along Admiralty Inlet with *Grindelia integrifolia, Elymus mollis, Carex macrocephala, Ambrosia chammissonis,* and *Cakile* spp., T31N R1W sect. 35, 1–2 m, 12 Aug 1990, *R. Halse 4103* (OSC, WTU); Clallam Co., Washington Harbor, tuft on a sand spit, 14 Sept 1921, *H. St. John 5867* (WS).

Significance. First report for Washington. This species is a native of northeast Asia from Japan, Korea, Sakhalin, Kamchatka, and the Ochotsk Sea region (Ohwi, Flora of Japan, 1965) and possibly Shemya Island, Alaska (Scoggan, The flora of Canada IV, 1979). It has been cultivated and is now naturalized on the seashores of eastern North American from Quebec, Canada, to Virginia, and inland on the shores of the Great Lakes to Minnesota (Fernald, Gray's manual of botany, 8th ed., 1950) and has been reported from British Columbia, Canada (Boivin, Nat. Can. 93:1048, 1966).

—Richard R. Halse, 4535 North West Big Oak Place, #3, Corvallis, OR 97330.

REVIEW

Plant Biology of the Basin and Range. By C. B. Osmond, L. F. Pitelka, and G. M. Hidy (eds.). 1990. Springer-Verlag, Berlin. xii + 375 pages. ISBN 3-54051219-5.

Plant Biology of the Basin and Range is a valuable and well-written collection, and it fulfills the intent of its editors to review the literature with an emphasis on physiological plant ecology. The book has nine chapters, most of these with multiple authors, and the subject of plant biology is approached from a variety of temporal and spacial scales.

The opening chapter briefly considers human impact on Great Basin ecosystems, although the treatment is more an intriguing introduction to the topography and history of the region than a full review of the subject. The second chapter gives a rather thorough overview of the climate of the Great Basin in the context of broad regional weather patterns across the North American Continent. The figures and text put the climate of the Great Basin in perspective with the rest of the continent and consider a large number of parameters ranging from wind, temperature, and precipitation to variability of weather and the impact of anthropogenic pollutants. Chapter 3 is by Dwight Billings, to whom the book is also dedicated, and considers the floristics and vegetation zones of mountains throughout North America. After a thorough discussion of slope effects and regional variation, Billings points out that while the Cascades, Rocky Mountains, and Appalachians have major floristic affinities with the transcontinental taiga, the forest trees of the Great Basin show more floristic affinities with the Southern Rocky Mountains and mountains of Mexico. Chapters 4 through 8 deal more specifically with ecophysiological studies and for many readers will represent the heart of the book. A chapter on high elevation forests stresses microsite and plant habit and morphology as key factors affecting water relations and productivity along elevational gradients. The importance of an unusual bedrock material and its influence on contrasting vegetation types is explored in Chapter 5, by DeLucia and Schlesinger. Both water and nutrient relations are analyzed for an impact on the type of vegetation developed on contrasting soils. Chapter 6 by Smith and Nowak and Chapter 7 by Dobrowolski, Caldwell, and Richards provide particularly valuable reviews of productivity and water relations from the perspective of shoots and roots, respectively. The concluding chapters return to broad-scale considerations with an analyses of long-term temporal patterns. Chapter 8, "Isotopic Assessment of Vegetation Changes," actually has little data directly on the Great Basin and is more interesting for its discussion of techniques of assessing historical plant community succession. The last chapter considers the sensitivity of the internal drainage basins to subtle shifts in climate. Past climatic fluctuations are evaluated extensively, and it is concluded that the Great Basin might be extremely sensitive to future climatic changes.

While the topics covered are covered well, many aspects of plant biology such as plant–animal interactions, herbivory, and pollination ecology are barely touched upon and must be sought elsewhere, while others, such as population biology, are not covered so extensively as is the physiological literature. Several chapters, such as that by Dobrowolski et al. on basin hydrology and plant root systems, provide insightful and thorough syntheses of topics that are rarely treated so well. The various contributions are generally well written and informative, and the book represents a valuable summary of data, techniques, and theory as they apply to plant physiological ecology in the Great Basin. Typographical errors are few, and the presentation of text is attractive and easy to read. Color illustrations are numerous, and graphical data presentations are abundant and clear. I recommend the volume strongly for those

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interested in plant adaptations and physiological behavior, and also for those interested in broad ecosystem processes.

—Jonathan Comstock, Department of Biology, University of Utah, Salt Lake City, UT 84102.

ANNOUNCEMENT

MT. TAMALPAIS—TO BURN OR NOT TO BURN?

A Vegetation Management Plan is being developed for Mt. Tamalpais by public land owners in Marin County. The Tamalpias Ecological Committee has been formed as a biological board of trustees to oversee and "watchdog" the process. At issue is whether there should be prescribed burning on the Mountain and, if so, why, where, when and how? The Committee invites your input by writing to TEC, % Dr. Edward S. Ross, Entomology Department, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, (415) 383-5343, FAX (415) 381-9214.

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NEW COMBINATIONS IN THE GENUS *CLARKIA* (ONAGRACEAE)

Harlan Lewis
Department of Biology, University of California,
Los Angeles, CA 90024

Peter H. Raven
Missouri Botanical Garden,
Saint Louis, MO 63166-0299

Abstract

The monotypic genus *Heterogaura* is combined with *Clarkia,* resulting in the new combination **Clarkia heterandra** that is placed in a new section *Heterogaura.* Plants previously described as *Clarkia nitens* and *C. parviflora* are assigned subspecific status in *C. speciosa* and *C. xantiana,* respectively. The rationale for these changes is presented and possible origins of **C. heterandra** are discussed.

Investigations by various workers since the genus *Clarkia* was last monographed (Lewis and Lewis 1955) indicate the desirability of publishing new combinations for three taxa and establishing a new section to accommodate one of them. The most significant change involves combining the monotypic genus *Heterogaura* Rothrock with the genus *Clarkia* Pursh and recognizing the former as a separate section; the other two changes reduce taxa published as species to subspecific rank.

Clarkia heterandra (Torrey) Lewis & Raven, comb. nov.—*Gaura heterandra* Torrey, Pacif. Railr. Rep. 4(5):87. 1857. *Heterogaura californica* Rothrock, Proc. Amer. Acad. Arts 6:354. 1864. *Heterogaura heterandra* (Torrey) Coville, Contr. U.S. Natl. Herb. 4:106. 1893.—Type: USA, California, Calaveras Co., River banks, Mokelumne Hill, 17 May 1854, J. M. Bigelow (NY).

When first described, *Clarkia heterandra* was placed in the genus *Gaura* by Torrey, undoubtedly on the basis of its small indehiscent fruits, but he recognized it as "a very peculiar one." When Rothrock later described a new genus, *Heterogaura,* to accommodate this species, he commented that it has a ". . . habit entirely different from *Gaura,* rather that of *Clarkia.*" Others have since recognized that *Heterogaura heterandra* is so similar to *Clarkia* that it could be considered a specialized derivative of that genus (e.g., Raven 1979). However, the small nut-like indehiscent fruit differs so conspicuously from the many-seeded dehiscent capsules of all other species of *Clarkia* that the retention of the monotypic genus *Heterogaura*

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seemed appropriate. A study by Sytsma and Gottlieb (1986), however, provided convincing evidence that plants of *Heterogaura heterandra* are more closely related to *Clarkia dudleyana* with respect to chloroplast DNA than *C. dudleyana* is to any other species of *Clarkia.* Consequently, if taxonomy is to reflect closeness of genetic relationship, as we think it should, it seems only logical to combine the two genera.

Clarkia heterandra has several traits in common with species of *Clarkia* section *Sympherica* (formerly *Peripetasma*) to which *C. dudleyana* belongs, including chromosome number of $n=9$, duplication of the gene encoding the cytosolic enzyme phosphoglucoisomerase (Gottlieb 1988), sepals that remain fused at anthesis, and stamens in two very distinct series, the inner being much smaller. These same traits, however, also characterize two other sections of *Clarkia,* namely, *Phaeostoma* and *Fibula.*

In contrast to the similarities to *C. dudleyana* and other species in section *Sympherica, C. heterandra* differs from them in several conspicuous ways, the most significant of which are traits that characterize species of sections *Phaeostoma* and *Fibula,* suggesting a possible close relationship to these sections, perhaps through hybridization. Seedlings of *C. heterandra,* for example, are scarcely distinguishable from those of *C. unguiculata* (section *Phaeostoma*) but would never be confused with those of *C. dudleyana* or any other species of section *Sympherica.* The axis of the inflorescence in bud is straight as it is in sections *Phaeostoma* and *Fibula,* whereas the axis of species in *Sympherica* is curved down in bud and becomes erect as the flowers open. The leaves of *C. heterandra* are lanceolate to ovate as they are in *C. unguiculata,* rather than linear to narrowly lanceolate like those characteristic of all species in section *Sympherica.* Leaf shape is particularly significant according to Keating (1982) who has shown that broader leaves in *Clarkia* have a more complex pattern of vein organization than do narrower leaves. Furthermore, he finds that in *Clarkia,* simple organization is derived from more complex patterns. This indicates that the more complex pattern of venation found in the leaves of *C. heterandra* almost certainly did not develop following its origin from a species like *C. dudleyana.*

The close relationship between *C. heterandra* and *C. dudleyana* is unquestionable on the basis of chloroplast DNA data, and the possibility cannot be excluded at present that *C. heterandra* represents a significantly modified self-pollinating derivative of *C. dudleyana* or a closely related taxon. Self-pollination in *Clarkia* and in a number of other genera may be associated with conspicuous morphological differences that can obscure actual relationships. The derivatives may look so strikingly different from their progenitors that they have often been placed not only in different species but in different higher categories as well. *Clarkia epilobioides,* for example, is a highly self-pollinating species that is unique in the genus in having small, white, unmarked petals. Although it clearly belongs to section *Sympherica,* the cylindric immature fruits are unlike any others in the section in that they are not obviously grooved. These differences led to its placement in its own subsection, *Micranthae* (Lewis and Lewis 1955). Chloroplast DNA and isozyme data indicate unequivocally, however, that *C. epilobioides* is very closely related to *C. rostrata* in subsection *Sympherica* and that the relationship is much closer than between *C. rostrata* and other morphologically very similar species in subsection *Sympherica, C. lewisii* and *C. cylindrica* (Sytsma et al. 1990).

Although the evidence for the close relationship between *C. heterandra* and *C. dudleyana* is indisputable on the basis of chloroplast DNA data, chloroplast DNA is transmitted in *Clarkia* only through the female parent (Sytsma et al. 1990), which means that the pollen progenitor may have come from quite a different source. Given this possibility, we suggest that the origin of *C. heterandra* may have involved intersectional hybridization between *C. dudleyana,* or a closely related species, and a species in section *Phaeostoma* such as *C. unguiculata.* Intersectional hybridization between these two sections is known to be involved in the origin of the tetraploid species *C. delicata* (Lewis and Ernst 1953), and intersectional hybridization has been postulated in the origin of section *Fibula* (Lewis and Lewis 1955). Section *Fibula* consists of two morphologically very similar species, *C. bottae* and *C. jolonensis,* that have vegetative characteristics that would place them in section *Phaeostoma,* whereas the flowers and immature fruits are so similar to those of *C. lewisii* in section *Sympherica* that *C. bottae* and *C. lewisii* were at one time considered conspecific. *Clarkia bottae* in now known on the basis of chloroplast DNA studies to be very closely related to *C. xantiana* in section *Phaeostoma* (Sytsma et al. 1990). Although these data show only that the two sections are closely related, the possibility of intersectional hybridization being involved in the origin of section *Fibula* is certainly not ruled out.

Intersectional hybrids between species in section *Sympherica* and section *Phaeostoma* have been produced in crossing experiments, including hybrids between *C. dudleyana* and *C. unguiculata* (Lewis and Lewis 1955). Furthermore, intersectional hybrids between these two sections have appeared spontaneously in experimental mixed populations and in one area have been observed in natural populations.

Natural hybrids between *C. cylindrica* (section *Sympherica*) and *C. exilis* (section *Phaeostoma*) have been observed by F. C. Vasek and H. Lewis where the two species grow together in Tulare County, California (Deer Creek Road, three miles south of its junction with the road to the Tule Indian Reservation; photographs on file at LA). Spontaneous hybrids were also found after a population of *C. unguiculata* was established by broadcasting seeds on a roadside fill in 1952 adjacent to a natural population of *C. dudleyana* in the foothills of the San Gabriel Mountains, Los Angeles County, California. The *C. unguiculata* population thrived and increased in area until the site was destroyed by construction and filling after the plants were last scored in 1965. The first hybrid between the two species was observed in 1956 and a total of 15 hybrids were recorded through 1965, although the site was not visited during five of the intervening years. Most of the hybrids appeared to be F_1 but they were variable and at least two, on morphological grounds, could have been backcrosses. A hybrid between *C. xantiana* and *C. dudleyana* was observed in an experimental mixed population of species in Oiler Canyon, Kern County, California, where *C. xantiana* occurs naturally. Spontaneous hybrids between *C. bottae* (section *Fibula*) and species in sections *Phaeostoma* and *Sympherica* have also been observed in the Oiler Canyon experimental population.

None of the hybrids mentioned above are known to have set seed, and all that have been examined have had less than five percent visibly good pollen. No effort has been made to obtain F_2 or backcross progeny. Essentially sterile hybrids such as these may seem unlikely candidates as forebearers in the origin of any taxa save polyploid derivatives. Grant (1966), however, has shown experimentally that fertile lineages, at the same chromosome level, that are intersterile with the parental species, can be extracted by self-pollination of hybrids of very low fertility where infertility is due primarily to chromosomal rearrangement. Homoploid speciation in this manner from essentially sterile hybrids is undoubtedly infrequent in nature and highly improbable following any given hybridization. We believe, however, that speciation in *Clarkia* has often involved highly improbable events (Lewis 1973).

Regardless of the origin of *C. heterandra,* the conspicuous difference in fruit from the rest of the genus warrants placing it in a separate section of *Clarkia.*

Clarkia Pursh section **Heterogaura** (Rothrock) Lewis & Raven, comb. nov.—*Heterogaura* as a genus, Rothrock, Proc. Amer. Acad. Arts 6:354. 1864.—TYPE SPECIES: *Clarkia heterandra* (Torrey) Lewis & Raven. Fruit indehiscent, nut-like; seeds 1 or 2.

Clarkia speciosa Lewis & Lewis subspecies **nitens** (Lewis & Lewis) Lewis & Raven, comb. nov.—*Clarkia nitens* Lewis & Lewis, Univ. Calif. Publ. Bot. 20:287. 1955.—TYPE: USA, California, Fresno County, 2.8 miles north of Highway 168 on the road to Auberry, *Lewis & Thompson 954* (holotype, LA).

Clarkia speciosa is a polytypic species that occurs in the South Coast Ranges and the foothills of the Sierra Nevada in California. Two subspecies (*speciosa* and *immaculata*) occur near the coast and two other subspecies (*polyantha* and *nitens*) occur in the Sierra Nevada foothills. Subspecies *nitens* occurs from San Joaquin County south into Fresno County and characteristically has lanceolate leaves that are longer than the internode above, a congested inflorescence, petals that are pink or lavender at the upper margin shading to pale yellow at the base, and stigmas that are yellow. Subspecies *polyantha,* which occurs from Fresno County south, is characterized by linear or narrowly lanceolate uncrowded leaves, lax wand-like inflorescences, purple to lavender petals, and stigmas that are lavender to deep purple. These two taxa were considered distinct species (Lewis and Lewis 1955) not only because of the conspicuous morphological differences but because hybrids between them were sterile. Subsequent study (Bloom and Lewis 1972; Bloom 1976) has shown that these two taxa, which replace each other geographically, are interfertile and intergrade morphologically where they meet in Fresno County and are, therefore, conspecific.

The disparity in fertility observed in different hybrids between the two taxa has its explanation in chromosomal differentiation with respect to reciprocal translocations (Bloom 1974). Hybrids between subsp. *nitens* and individuals of subsp. *polyantha* from the southern part of its range (e.g., Kern County) always form a large ring of chromosomes at meiosis, usually a ring of 16 and one pair. These large rings mostly segregate non-disjunctionally, resulting in very low fertility. On the other hand, when subsp. *nitens* is crossed with morphologically typical individuals of subsp. *polyantha* from the northern part of its range (e.g., northern Tulare County) the hybrids form 9 pairs of chromosomes or have a small ring of 4 or sometimes 6. Segregation of the chromosomes is almost invariably disjunctional and the hybrids are fertile. This is the situation in the area where the two taxa intergrade. At the same time, when individuals of subsp. *polyantha* from the northern part of its range are crossed with morphologically comparable individuals from the southern part of its range the hybrids are as sterile, due to chromosomal rearrangement, as those between subsp. *nitens* and individuals of subsp. *polyantha* from the south. Hybridization between individuals from adjacent populations throughout the range of the two subspecies produces only fertile individuals with at most small rings of chromosomes, which permits the migration of genes from one subspecies to the other.

Clarkia xantiana Gray subspecies **parviflora** (Eastwood) Lewis & Raven, comb. nov.—*Clarkia parviflora* Eastwood, Bull. Torrey Bot. Club 30:492. 1903.—Type: USA, California, Kern County, Kernville. *T. S. Brandegee* (holotype, CAS).

Clarkia xantiana subsp. *parviflora* is a self-pollinating derivative of *C. xantiana* subsp. *xantiana* and differs primarily in flower size and in the position and time of maturation of the stigma. Subspecies *parviflora* has petals 6 to 12 mm long whereas those of subsp. *xantiana* are generally 15 to 20 mm long, although petals as short as 12 mm have been observed in some populations. The stigma of subsp. *parviflora* is receptive and in contact with the anthers at anthesis and some pollen is deposited directly on the stigma. Both subspecies are self-compatible but subsp. *xantiana* is strongly protandrous; the anthers begin to dehisce two to three days before the stigma becomes receptive. Furthermore, the mature stigma is held about 3 mm above the anthers. Subspecies *parviflora* includes two color forms, one lavender-pink and the other white, whereas the petals of subsp. *xantiana* range from lavender to reddish-purple.

Subspecies *parviflora* is known primarily from a small area in the Kern River Canyon about 40 km north of Kernville where it grows sympatrically with subsp. *xantiana.* Where they grow in the same area, subsp. *parviflora* begins to flower about two weeks earlier than subsp. *xantiana.* Pink and white forms of subsp. *parviflora* from adjacent populations in this area and a sympatric population of subsp. *xantiana* have been studied genetically (Moore and Lewis 1965) and an electrophoretic analysis of enzyme variation has been made of the same populations (Gottlieb 1984). The latter study indicates that there is essentially no gene exchange between any of the populations, although hybrids made in any combination are highly fertile. Materials for these studies came from populations on a west-facing slope just north of a bridge over the Kern River at South Creek. Construction of a new bridge just north of the old bridge has completely destroyed the site and the studied populations. A few other localities for subsp. *parviflora* and many for subsp. *xantiana* are known in the Kern River drainage.

The relationship of subsp. *parviflora* to subsp. *xantiana* is comparable to that of self-pollinating subspecies in several other species of *Clarkia,* such as *C. amoena, C. concinna, C. gracilis, C. purpurea,* and *C. tenella.*

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LOCAL VARIATION IN FLORISTICS AND DISTRIBUTIONAL FACTORS IN CALIFORNIAN COASTAL SAGE SCRUB

Sandra A. Desimone and Jack H. Burk
Department of Biological Science, California State University,
Fullerton, CA 92634

Abstract

Californian coastal sage scrub, a soft-leaved mediterranean-climate shrubland, is disappearing rapidly as urbanization spreads. Previous researchers classified the community on a regional spatial scale: three associations within the full range of southern coastal sage scrub and 11 subassociations within two of the geographic associations were identified. Ordination analysis of 54 sites at Starr Ranch in Orange County, CA, revealed that subassociations similar to some regional groupings are found at the local level. Whereas gradients in temperature and precipitation are the strongest predictors of distribution at the regional scale, topographic and edaphic variables were most influential at our site. Five subassociations of coastal sage scrub and their environmental relationships were derived: *Salvia apiana–Artemisia californica–Eriogonum fasciculatum* dominated sites with southerly aspects and coarser soils; *Artemisia californica–Lotus scoparius* was prevalent on northerly aspects; no correlation with environmental factors was found for *Salvia mellifera.* There were two transitional groups. The variation in floristics and habitat found at our relatively small study site has strong implications for conservation planning. We urge land managers to identify local subassociations in order to protect the variability over short distances (±50 m) characteristic of southern coastal sage scrub.

Coastal sage scrub is a half-woody, facultatively drought deciduous and seasonally dimorphic, shallow-rooted, soft-leaved shrubland that is entirely confined to the mediterranean-climate zone in North America. Its range extends from the San Francisco Bay Region, Alta California, USA, to El Rosario in Baja California, Mexico (Westman 1981b).

Of the several classification systems proposed for coastal sage (Thorne 1976; Kirkpatrick and Hutchinson 1977; Axelrod 1978; Westman 1981b; Mooney 1988), only those of Westman and Kirkpatrick and Hutchinson are derived from quantitative studies. All systems except that of Kirkpatrick and Hutchinson include the full geographic range of the community and are based on latitudinal changes in species composition from Baja California to northern California.

A northern and southern division of coastal sage scrub are recognized (Thorne 1976; Axelrod 1978; Westman 1981b; Mooney 1988). The southern coastal sage scrub comprises three floristic associations: the coastal Venturan, the cismontane inland Riversidian,

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and the Baja-influenced Diegan (Axelrod 1978; Westman 1981b, 1983a). Westman distinguished two Venturan subassociations.

Kirkpatrick and Hutchinson (1977), using data from 120 sites from coastal Santa Barbara 266 km inland to Banning, described 11 subassociations (their "associations") distributed between an inland basin and a coastal region. Their study area, approximately 140 km northwest and 50 km east of the present study area, lies within the central part of coastal sage scrub distribution in what appear to be the Venturan and Riversidian associations.

There have been only two quantitative studies of the habitat factors associated with coastal sage scrub distribution. Kirkpatrick and Hutchinson (1980) found that the variable best correlated with distribution patterns of their 11 "subassociations" is mean annual range in temperature. Although nine subassociations are concentrated within altitudinal zones, they found few strong relationships with other environmental factors (aspect, slope, substrate).

The four Alta California associations of Westman (Diablan, Venturan, Riversidian, and Diegan) reflect a geographic/climatic gradient of increasing evapotranspirative stress from northern to southern and coastal to inland sites (Westman 1981b, 1983a). Sharp species segregation was detected only in the Venturan association in which distributions of dominant species were related to moisture preference as influenced by aspect and soil texture.

Conclusions about both community and species level distributions are dependent upon the size of the study area (Lepart and Debussche 1980). Differences in scale produce differences in conclusions about the degree of community structure, importance of stochastic effects, and roles of distributional factors (Wiens et al. 1986). Although the urgency of coastal sage scrub preservation has been recognized (Kirkpatrick and Hutchinson 1977; Axelrod 1978; Westman 1981a, b, 1982), there is a need for more information on variability within each association. The major geographical associations are not designated by distinguishing species because each one has several distinct communities whose composition depends on such factors as exposure and soil depth (Axelrod 1978). Identification of such component communities has become increasingly important since, as a result of habitat decline, several animal species associated with sage scrub are candidates for listing at federally endangered status. One such bird species, the California Gnatcatcher, has been found in a limited number of studies to be associated with certain floristic and structural coastal sage scrub sub-types (Atwood 1990).

The goals of this research were to explore the pattern of coastal sage scrub distribution on a local scale, generate hypotheses to explain habitat effects upon local community structure, then contrast results to the two regional scale studies of sage scrub classification and environmental relationships.

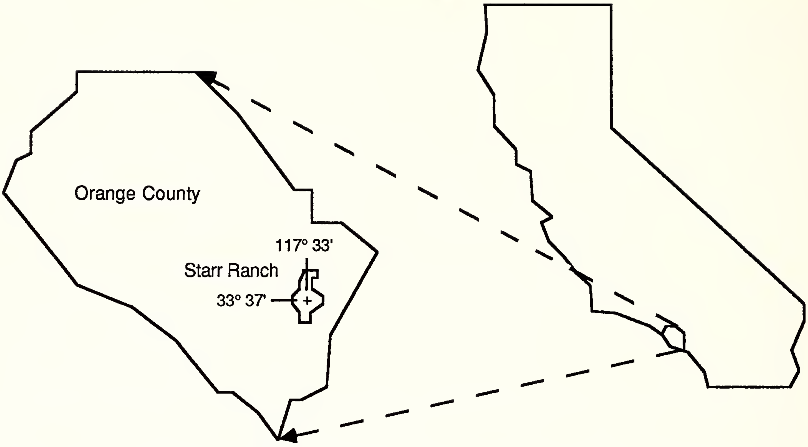

FIG. 1. The location of Starr Ranch Sanctuary in Orange County, California.

STUDY AREA

Starr Ranch was selected as the study site because of its extensive expanses of coastal sage scrub. It is a 1585-ha National Audubon Society Sanctuary located in the foothills of the Santa Ana Mountains in southeastern Orange County, California (Fig. 1). Elevation ranges from 182 m to 533 m. Mean annual precipitation is 360 mm, and as rainfall is typical of a mediterranean climate, almost all falls between November and April. Winter mean temperature is 12°C and summer temperatures average 21°C. Fog is common in early summer.

Until 1963, Starr Ranch was a working cattle operation, with up to 1200 animals grazing at one time (County of Orange 1974 unpublished). Within the last 30 years, there have been two fires that swept over the entire ranch: December 1958 and November 1980 (County of Orange 1974 unpublished; J. Froke personal communication 1986).

There are several expanses of river terrace deposits at Starr Ranch. Bedrock units are all Upper Cretaceous (Morton 1970). Coastal sage scrub is found predominantly on two soil phases at Starr Ranch that differ primarily in surface texture and color and depth (D. Estrada personal communication 1987): Cienaba sandy loam is shallow, usually <38 cm to bedrock, while the Gabino gravelly clay loam is moderately (76–101 cm) deep and brown to reddish after the first 25 cm. The less extensive Yorba cobbly sandy loams are found on steep terrace escarpments and have pinkish gray surface layers underlain by red subsoil (Wachtell 1978).

Little (1977) described vegetation mosaics at Starr Ranch typical of southern California: southern oak woodland, riparian woodland, chaparral, southern California grassland, and coastal sage scrub. Although Orange County coastal sage has been placed in both the Diegan (Westman 1983a) and the Venturan (Axelrod 1978; Westman 1982) associations, the Starr Ranch flora, when compared with species lists of Axelrod and Westman, has elements of both Riversidian and Venturan associations.

METHODS

Data collection. Sampling began 1 March 1987 and was completed 31 May 1987. To reduce sampling error from seasonality, all March sites were revisited in May and early June and cover of new herbaceous species was recorded and combined with earlier data. A 0.5-km grid was superimposed on a topographic map and a unique site was located within each grid section. Criteria for individual sites were that they be dominated by low, soft-leaved shrubs; free from disturbance (away from roads and without gullies, ravines, and rock outcrops); and representative of the stand. After review of county records for grazing and fire history (County of Orange 1974 unpublished) and aerial photographs taken after the 1980 fire, we concluded that major disturbances such as frequency of fire and grazing were similar for all coastal sage scrub within Starr Ranch boundaries for the last 30 years. Fire intensities among sites, however, were most likely varied and are unknown.

The sampling intensity of Westman (1981a) was found sufficient for Starr Ranch in species-area curves for data from a preliminary study in fall, 1986. At each of the 54 sites along a 25-m baseline, four 25-m transects were randomly located and run parallel to the slope direction. Cover of all shrubs and herbs intercepting the transect was recorded. Subsequent exclusion of annuals from data sets to reduce sampling error from seasonality was not considered serious since by seven years following fire, there is a dramatic decline in annual herb species (Westman 1981a). Nomenclature follows Munz (1974) and is updated, where necessary, from Roberts (1989).

Elevation, slope, and aspect were recorded for each site. The "medium-scale patchiness" ($\approx$0.1 ha) characteristic of coastal sage scrub demands that an unusually large number of sites must be sampled to characterize fully the floristic variation within a community type (Westman 1981b). To sample as many sites as possible, we performed on-site soil phase identification by superimposing the Soil Conservation Service soil survey map of Orange County (Wachtell 1978) on to the Starr Ranch topographic map (Fig. 2). Map soil types were confirmed by auger checks of depth and color.

Although soil surveys include data on substrate, depth, texture, pH, water-holding capacity, and permeability for soil series and phases, chemical composition must be determined in the laboratory.

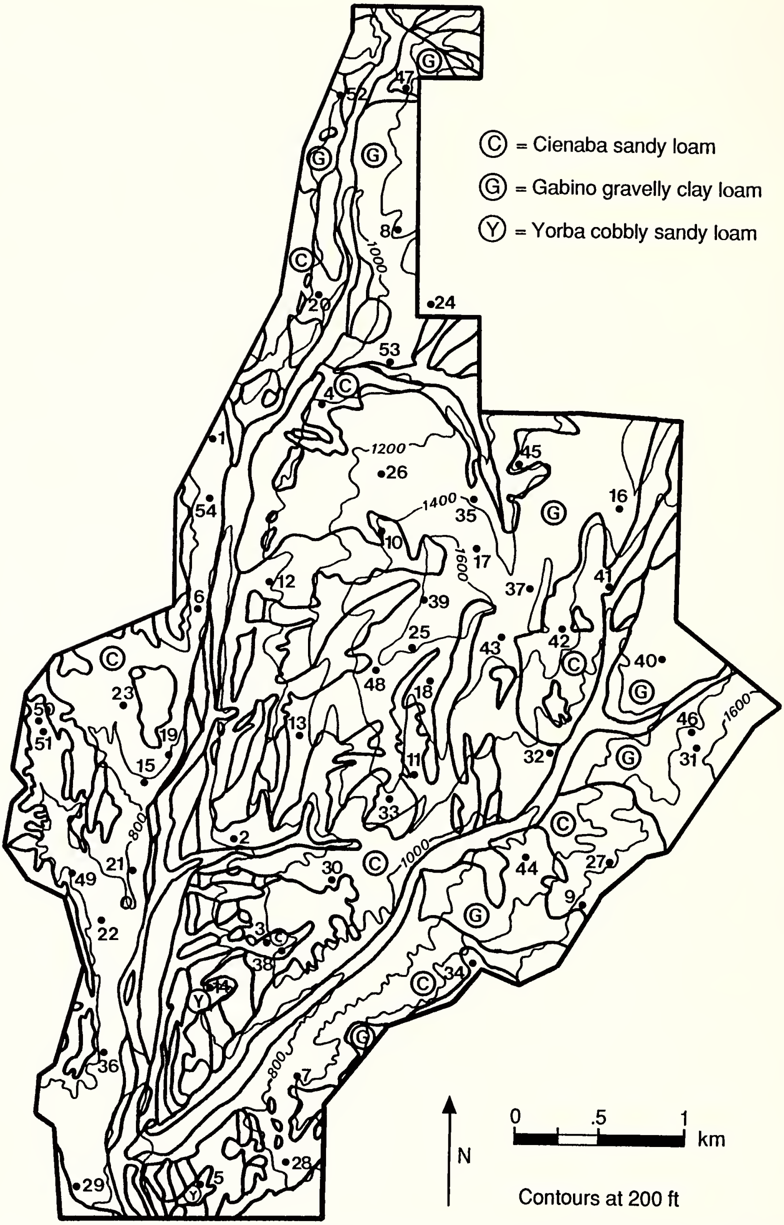

FIG. 2. Locations of 54 sites of coastal sage scrub at Starr Ranch Sanctuary on a topographic map of Starr Ranch Sanctuary (sections of Santiago Peak and Cañada Gobernadora quadrangles of the U.S. Geological Survey topographic map series) with the Soil Conservation Service soil survey map of Orange County (Wachtell 1978) superimposed.

However, there is minor variation for the important macronutrients, nitrogen and phosphorus, in southern California soils (except for serpentine, limestone, or metavolcanic soils) (P. Riggan personal communication 1987) in which they are largely in forms unavailable for plant growth (Rundel 1983).

Data analysis. We applied two environmental scalars. The composite moisture-availability index of Westman (1980, 1981b) [Index = mean annual ppt × aspect × (slope + half-saturation percentage soil)] was modified by removing mean annual precipitation, which is relatively uniform within our study site. With the exception of soils, factors were ranked on an eight-point scale. Available water capacity data for the three soil phases went into rankings for soil water-holding capacity, from lowest to highest: Yorba cobbly sandy loam, Cienaba sandy loam, and Gabino gravelly clay loam. Aspect values were ranked according to Whittaker (1982). An index of annual potential direct-beam solar irradiation (Frank and Lee 1966) was used to check its significance against related variables (aspect and slope).

In ordination, the spatial arrangement of samples reflects their similarity. Ordination was accomplished using detrended reciprocal averaging (DRA) (Pimental and Smith 1986), which follows the methodology of detrended correspondence analysis (Hill and Gauch 1980), a technique that corrects the problems of compression of first-axis ends and arch effect in reciprocal averaging (Gauch 1982). We then classified sites into groups using both DRA and manual table sorting techniques (Westman 1981b; Abrams 1986) to accomplish "detrended correspondence analysis space partitioning" or DCASP, a polythetic divisive classification method (Gauch and Whittaker 1981; Gauch 1982). Tentative groups of adjacent sites in the DRA plot were placed together in a table of species cover so that dominant (highest cover) species could be identified. Sites were then placed in a revised table and groups were further distinguished by identifying those species that reached maximum cover values and ≥50% frequency within a group. Using the table as a guide, we drew lines on the ordination graph to group sites with similar high cover of dominant and maximum cover species. We adjusted difficult group boundaries with another polythetic divisive classification technique, TWINSPAN (Hill 1979), which is a more objective and automatic complement to DCASP (Gauch 1982). The program was run using all default options. The divisions at a given level of the TWINSPAN dendrogram are derived from successive refinements of the first axis of a reciprocal averaging ordination and reflect gradients along a single dimension only so that an approach that combines TWINSPAN and DCASP unites the summarizing power of classification with the effectiveness of the coordinate system of an ordination in displaying directions of gradients (Gauch and Whittaker 1981; Gauch 1982). The DCASP method is as robust as TWINSPAN because it is based on the robust DCA ordination method (Gauch and Whittaker 1981).

Since strong clustering of community data is rare and community variation is ordinarily relatively continuous, classification is imposed on data (Gauch 1982). Well-defined clusters and transitions between recurring plant patterns were, therefore, equally emphasized (sensu Mueller-Dombois and Ellenberg 1974).

Relationships between ordination axes and both life history types and environmental factors were analyzed using Spearman's rank correlation with a correction for ties. The Kruskal-Wallis test was applied to environmental data for differences among Starr Ranch groups. Although the efficiency of Kruskal-Wallis decreases with unequal sample sizes, it is never <86.5% that of analysis of variance (Pimental and Smith 1990). Factors significant in the Kruskal-Wallis test were subjected to nonparametric analogs of Tukey-Kramer and Student-Newman-Keuls' multiple range tests, both appropriate for unequal sample sizes, though efficiency weakens with numbers of ties (Pimental and Smith 1990). Spearman rank correlation coefficients were computed for 17 of the most widespread and abundant species and the eight environmental variables (aspect, proportion of bare ground, composite moisture index, elevation, soil phase, radiation index, amount rock, and slope). Criteria for species to be included in the analysis were occurrence in >10 sites (Westman 1980) and with >15% cover.

RESULTS

Ordination and classification. Starr Ranch groups are shown in the DRA plot in Figure 3; species distinguishing each group are marked in Table 1. There was a gradient in species cover along both DRA axes one and two so that groups shared one dominant species while differing in another. With the exception of group 4, TWINSPAN divisions at the second dichotomy generally coincided with DCASP groups. We partitioned off group 4 because of intermediate cover values of dominant species along axis one between sites of absence or low cover of *Salvia mellifera* and dominance or presence of *S. apiana* in groups 1a, 2, and 3 at the negative end of the axis to dominance of *S. mellifera* and absence or low cover of *S. apiana* in group 5 at the positive end of axis one. Group 4 sites had a combination of moderate *S. apiana* cover (<15%) and intermediate cover of *S. mellifera* (<40%) as well as >20% cover of *A. californica,* which further distinguished it from group 5 (<10% *A. californica* in all but one site).

Groups at axes extremes (1, 3, and 5) were most floristically dis-

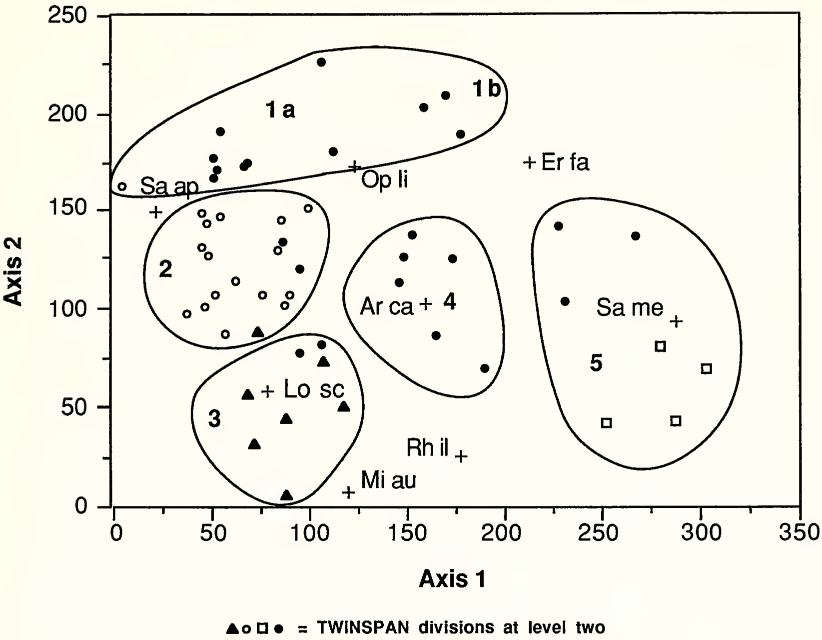

FIG. 3. Detrended reciprocal averaging ordination of 54 sites using 68 species. Sites were divided into five groups according to the cover values of dominant and maximum cover species (see Table 1) then difficult boundaries were adjusted with TWINSPAN output. + = locations of dominant and maximum cover species in the species ordination. Groups 2 and 4 are transitional (see "Results" and Table 1). Eigenvalues for axes one and two were 0.560 and 0.227, respectively. Gradient lengths were 2.981 and 2.213 standard deviation units for DRA axes one and two, respectively. Species abbreviations: Op li = *Opuntia littoralis,* Er fa = *Eriogonum fasciculatum,* Sa ap = *Salvia apiana,* Ar ca = *Artemisia californica,* Sa me = *Salvia mellifera,* Lo sc = *Lotus scoparius,* Rh il = *Rhamnus ilicifolia,* Mi au = *Mimulus aurantiacus.*

tinct. Groups 2 and 4 at mid axis two and one, respectively, were transitional in nature as codominants shifted between the extreme groups. Along axis two, groups 1 and 3 were characterized by several species that were not dominant but reached maximum cover. Along DRA axis one, a single species (*S. mellifera*) had highest cover at the positive axis extreme. The following five groups of Starr Ranch coastal sage scrub were named by their dominant or codominant species in order of decreasing cover:

Group 1 (*Salvia apiana–Artemisia californica–Eriogonum fasciculatum*). There is a subgroup (1b) of three sites in which codominance shifts from *S. apiana* to *E. fasciculatum. Opuntia littoralis* reached maximum cover in group 1.

Group 2 (*Artemisia californica–Salvia apiana*).

Group 3 (*Artemisia californica–Lotus scoparius*). *S. apiana* showed

TABLE 1. AVERAGE COVER (%) AND FREQUENCY (%) OF THE MOST WIDESPREAD AND ABUNDANT SPECIES FOR FIVE STARR RANCH COASTAL SAGE SCRUB GROUPS. Species are arranged in order of descending total % cover. ● = dominant species; ◇ = maximum cover species.

	Group 1 (n = 12)		Group 2 (n = 21)		Group 3 (n = 8)		Group 4 (n = 6)		Group 5 (n = 7)	
Species	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.
Shrubs										
Artemisia californica	●22.5	100	●31.9	100	●35.9	100	●35.8	100	9.8	100
Salvia apiana	●31.9	75	●30.2	100	13.0	100	3.8	50	1.3	29
Lotus scoparius	6.4	83	16.3	95	●26.9	100	11.9	83	1.2	43
Salvia mellifera	0.6	25	0.2	14	2.2	38	●21.8	100	●68.5	100
Eriogonum fasciculatum	●17.0	83	2.4	62	1.5	38	6.0	67	5.1	43
Rhamnus ilicifolia	0.0	0	1.9	52	◇11.1	75	0.8	33	1.7	29
Malosma laurina	1.5	33	1.1	52	0.1	13	4.0	50	4.5	71
Galium angustifolium	0.9	50	2.9	52	0.5	50	0.9	67	0.2	14
Mimulus aurantiacus	0.0	0	0.4	33	◇4.5	50	0.7	50	0.2	14
Mirabilis californica	0.4	50	0.8	33	0.3	38	0.4	17	0.0	14
Herbs and succulents										
Stipa lepida	11.2	100	8.5	95	1.0	88	5.6	100	4.7	71
Opuntia littoralis	◇7.5	83	1.0	33	0.6	25	3.2	67	0.5	29
Calystegia macrostegia	0.4	58	0.5	52	0.1	13	0.6	100	0.7	29
Cuscuta spp.	1.0	42	0.0	10	0.0	13	1.3	17	0.3	29
Stipa pulchra	0.6	50	0.4	29	0.0	13	0.4	50	0.0	0
Melica imperfecta	0.1	17	0.4	43	0.8	25	0.2	17	0.0	14
Brassica geniculata	0.0	0	0.7	43	0.0	13	0.3	50	0.0	0

lower cover (<17%) than in groups 1 and 2 in all but one site. Group 3 maximum cover species (*Rhamnus ilicifolia* and *Mimulus aurantiacus*) were not present in group 1. Twenty-seven species, 13 shrubs and 14 herbs, were not held in common between groups 1 and 3.

Group 4 (*Artemisia californica–Salvia mellifera*).

Group 5 (*Salvia mellifera*). *S. mellifera* was present in all sites at >43% cover, while *S. apiana* was present in only two sites at relatively low (0.3 and 8.6%) cover. *Salvia mellifera* was the single dominant species in six of the seven sites, reaching 90% of the total cover in an individual site.

Group characterizations. Two of the Starr Ranch groups were clearly distinguished by differences in habitat variables (Table 2). Groups 1 and 3 differed significantly in aspect, amount of bare ground, composite moisture index, and radiation index. Environmental factors for group 2, although closer in mean values to group 3, had relatively wide ranges and were ± intermediate between groups 1 and 3. Most of the same factors found significant in the Kruskal-Wallis test were also significant in the correlations with axes component scores (Table 3). Although there was a tendency for coarser soils (Cienaba sandy loam and Yorba cobbly sandy loam) to be associated with group 1 sites at the positive end of DRA axis two, group 3 at the negative end of axis two showed a relatively weak soil texture affinity: in 67% of group 1 sites soils were coarse-textured, whereas only 50% of group 3 sites occurred on finer-textured soils (Gabino gravelly clay loam). Composite moisture index was the singular factor found to be significantly related to axis one.

Groups 1 and 3 were further distinguished by cover differences in life history types. Shrub cover decreased significantly along DRA axis two ($r_s = -0.356$, $P < 0.001$) from group 3 to group 1 and perennial herb cover ($r_s = 0.525$, $P < 0.001$) and succulent cover ($r_s = 0.515$, $P < 0.001$) increased along the same axis. There were no significant relationships between life history types and DRA axis one.

As expected, there were correlations among several environmental factors. Aspect is a component of the radiation index ($r_s = -0.821$, $P < 0.001$) and is the most influential factor (with mean annual precipitation) in the composite moisture index ($r_s = 0.849$, $P < 0.001$) (Westman 1980). Correlation of both indices with aspect and with the axis two gradient support the strong influence of aspect on DRA axis two site differences.

Results of the statistical analyses are summarized in the following environmental relationships for the five groups. Group 1 (*Salvia apiana–Artemisia californica–Eriogonum fasciculatum*) sites were found on southerly aspects and coarser soil phases. Shrub cover was lower, succulent cover (especially *Opuntia littoralis*) and perennial

TABLE 2. MEAN VALUE, STANDARD DEVIATION, RANGE AND SIGNIFICANCE OF THE KRUSKAL-WALLIS (KWL) STATISTIC FOR HABITAT FACTORS AMONG FIVE STARR RANCH GROUPS. AS = aspect rank (1 = SW, 8 = NE), BG = % bare ground, CI = composite moisture index, EL = elevation (m), SL = % slope, RI = radiation index, RK = % rock, SO = soil rank (1 = Yorba cobbly sandy loam, 2 = Cienaba sandy loam, 3 =

		Group 1 (n = 12)			Group 2 (n = 21)		
	KWL	Mean ± SD		Range	Mean ± SD		Range
AS	*	2 ± 1	●	1–3	5 ± 2		1–8
BG	*	9.59 ± 5.57	●	5.38–25.45	2.16 ± 1.46	◇	0.80–5.60
CI	*	16 ± 9	●	5–30	38 ± 16	◇	7–80
EL	n.s.	331 ± 106		213–506	362 ± 101		213–500
SL	n.s.	20 ± 8		9–31	21 ± 6		7–30
RI	*	0.56 ± 0.04	●	0.45–0.60	0.48 ± 0.05		0.39–0.55
RK	n.s.	2.79 ± 2.01		0–6.35	1.04 ± 1.18		0–4.30
SO	n.s.	1 and 2 (67%)			2 (62%)		

herb cover were higher, and there was more bare ground than in group 3 sites. Site factors for group 2 (*Artemisia californica–Salvia apiana*) were ±intermediate between groups 1 and 3. Twelve of 16 sites found on east- or west-facing slopes were included in group 2. Group 3 (*Artemisia californica–Lotus scoparius*) was found on northerly aspects. There were no interpretable environmental relationships for group 4 (*Artemisia californica–Salvia mellifera*) or group 5 (*Salvia mellifera*).

Species distributions. Proportion of bare ground was correlated with the most species (8), followed by aspect (6), composite moisture index (6), and radiation index (6) (Table 4). There were no environmental factors correlated with the cover of *Salvia mellifera.* With the exception of *Salvia apiana,* the dominant and maximum cover species for each of DRA axis two extreme groups 1 and 3 tended to be correlated with the same environmental factors significantly associated with their respective groups. *Opuntia littoralis* and *Eriogonum fasciculatum* (group 1 species) were associated with south aspects, high proportion of bare ground, low composite moisture index, and high radiation index. Group 3 species showed inverse associations: *Artemisia californica, Rhamnus ilicifolia,* and *Mimulus aurantiacus* were associated with north aspects; *A. californica, Lotus scoparius, R. ilicifolia,* and *M. aurantiacus* were significantly correlated with a low proportion of bare ground and a low radiation index; and *L. scoparius, R. ilicifolia,* and *M. aurantiacus* were associated with a high composite moisture index. Thirty-four (50%) of the 68 species were "rare," that is "occurred in only one or two sites or attained a maximum cover value of <3%" (Westman 1983a).

TABLE 2. CONTINUED.

Gabino gravelly clay loam). Numbers in parentheses after soil ranks signify percentage of sites in a group. Means with different symbols (●, ◇) were significantly different in nonparametric multiple range tests; all unmarked means were not significantly different. * $P < 0.05$.

Group 3 (n = 8)		Group 4 (n = 6)		Group 5 (n = 7)	
Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
6 ± 1 ◇	4–8	3 ± 2	1–6	3 ± 2	1–6
0.98 ± 0.59 ◇	0.30–1.80	3.88 ± 2.81	0.60–8.90	4.72 ± 4.80	0.5–13.95
37 ± 7 ◇	28–48	26 ± 12	10–40	20 ± 14	6–45
376 ± 81	259–478	332 ± 81	244–457	366 ± 83	229–451
26 ± 7	12–35	22 ± 6	13–23	24 ± 8	13–40
0.42 ± 0.08 ◇	0.30–0.54	0.51 ± 0.08	0.48–0.58	0.52 ± 0.09	0.33–0.60
1.01 ± 1.55	0–4.00	0.88 ± 0.87	0–1.20	1.99 ± 1.83	0–4.90
3 (50%)		3 (67%)		3 (57%)	

DISCUSSION

Affiliations with regional floristic groupings. Some of the subdivisions of coastal sage scrub at Starr Ranch correspond to species groupings identified in regional research. Kirkpatrick and Hutchinson's (1977) *Artemisia californica–Eriogonum fasciculatum–Salvia apiana,* found mostly inland, is similar to Starr Ranch group 1. Dominance of *Salvia mellifera* in Kirkpatrick and Hutchinson's *Salvia mellifera–Malosma laurina* (found near the coast) and Westman's (1983a) Venturan I subassociations is comparable to Starr Ranch group 5. Dominance of *Artemisia californica* and *Lotus scoparius* in a "floristic class" of Westman (1981b) parallels Starr Ranch group 3. Similarities in floristic groupings among study areas that differ in scale and geographic location suggest the possibility of iden-

TABLE 3. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN HABITAT FACTORS AND COMPONENT SCORES FROM DRA AXES. * $P < 0.05$.

Habitat factor	Axis 1	Axis 2
Aspect (1 = SW, 8 = NE)	−0.273	−0.426*
Bare ground (%)	−0.102	0.711*
Composite moisture index	−0.402*	−0.281*
Elevation (m)	−0.243	−0.261
Radiation index	0.141	0.559*
Rock (%)	0.201	0.266
Slope (%)	0.224	−0.268
Soils (1 = Yorba cobbly sandy loam, 3 = Gabino gravelly clay loam)	−0.113	−0.280*

TABLE 4. SPEARMAN RANK CORRELATION COEFFICIENTS FOR COVER OF 17 OF THE MOST WIDESPREAD AND ABUNDANT SPECIES AND HABITAT FACTORS. See Table 2 for environmental factor abbreviations. * $P < 0.05$.

	AS	BG	CI	EL	SL	RI	RK	SO
Shrubs								
Artemisia californica	0.310*	−0.323*	0.093	−0.082	0.190	−0.343*	−0.019	−0.128
Salvia apiana	0.213	0.148	0.347*	0.105	−0.293*	0.003	−0.144	0.020
Lotus scoparius	0.201	−0.378*	0.298*	0.344*	−0.076	−0.274*	−0.123	0.248
Salvia mellifera	−0.192	0.106	−0.196	−0.193	−0.063	0.172	−0.129	0.082
Eriogonum fasciculatum	−0.468*	0.531*	−0.373*	−0.027	−0.190	0.538*	0.311*	−0.123
Rhamnus ilicifolia	0.477*	−0.478*	0.300*	0.041	0.374*	−0.531*	−0.075	−0.082
Malosma laurina	−0.178	−0.018	−0.036	−0.090	−0.107	0.200	−0.021	0.050
Galium angustifolium	0.183	0.107	0.118	0.045	0.083	−0.139	−0.074	−0.072
Mimulus aurantiacus	0.477*	−0.396*	0.324*	0.108	0.353*	−0.542*	−0.351*	0.080
Mirabilis californica	−0.122	0.085	−0.212	−0.092	0.135	0.268	0.056	−0.278*
Herbs and succulents								
Stipa lepida	−0.081	0.536*	−0.017	−0.295*	−0.161	0.150	0.136	−0.131
Opuntia littoralis	−0.475*	0.456*	−0.436*	0.068	−0.073	0.521*	0.305*	−0.030
Calystegia macrostegia	−0.205	0.130	−0.079	−0.095	−0.326*	0.131	−0.022	0.139
Cuscuta spp.	−0.226	0.334*	−0.255	0.099	0.155	0.145	0.555*	0.016
Stipa pulchra	−0.217	0.172	−0.084	0.249	−0.334*	0.227	0.170	0.270*
Melica imperfecta	0.333*	−0.165	0.169	−0.237	0.209	−0.191	0.101	−0.426*
Brassica geniculata	0.134	−0.244	0.104	0.145	−0.004	−0.077	−0.124	0.209

tifying dominants and associated species that consistently occur together throughout the southern coastal sage scrub.

Environmental relationships of groups. We consider the combination of significant variables that distinguish DRA axis two groups 1 and 3 to be preliminary evidence of a moisture availability gradient from more xeric (group 1) to more mesic (group 3) sites. Relatively high proportions of bare ground occur on drier, "desertic" sites in chaparral (Keeley and Keeley 1988); thus, the high amount of bare ground in group 1 sites is likely a good indicator of a xeric environment. The relatively high succulent and relatively low shrub cover of group 1 sites may also be related to more xeric conditions. Total shrub cover generally increases in coastal sage scrub with decreasing evapotranspirative stress (Westman 1983a), whereas succulent cover is strongly associated with increasing aridity (Westman 1983a; Mooney 1988). Although perennial herb cover was higher at the xeric end of the Starr Ranch moisture gradient, differences in yearly precipitation affect understory herb production versus production in the open in coastal sage (Poole et al. 1981; Westman 1983b); thus, data for one year's herb production are not indicative of general site moisture conditions.

Westman (1981b, 1983a) cites mean temperature of the warmest month and decreasing annual and monthly maximum precipitation along a latitudinal gradient from north to south (evapotranspirative stress) as the strongest predictors of coastal sage scrub distribution on a regional scale. Although evapotranspirative stress also appears to influence Starr Ranch community composition, the contributing factors are distinct.

Change in aspect has been associated with postfire differences in coastal sage scrub composition and diversity patterns (Keeley and Keeley 1984; O'Leary 1988, 1990). We found aspect to be a strong determinant of distribution on a local scale. At Starr Ranch, all group 1 sites were south-facing; 75% of group 3 sites were north-facing (none were south-facing). In a study area ±6 km from Starr Ranch, stands with measured attributes of groups 1 and 3 were observed within 50 m of each other as aspect shifted from south to north across a slope (DeSimone 1990 unpublished). Southern exposures at Starr Ranch are hypothesized to contribute to xeric conditions. In contrast, Westman (1983a) proposed that the north-facing slopes of Venturan II subassociation sites offer drier conditions for more xeric-adapted species than south-facing slopes (Venturan I sites) since higher transpirational water loss from greater vegetation cover on north-facing slopes results in similar or earlier soil drying and similar or less soil moisture throughout the summer than on south-facing slopes (Poole and Miller 1975). However, the influence of aspect is probably greatest during the early stages of recovery after fire (Mooney and Miller 1985) when north-facing slopes, with lower evaporational losses, have more water available (Miller et al. 1981) for growth, establishment, and survival than south-facing slopes. Such conditions favor species that are less drought-adapted (Barbour et al. 1987). Mesic species on north-facing slopes in mature coastal sage scrub might then be somewhat immune to dry season soil moisture differences between north and south slopes since shrub species initiate vigorous growth in early winter after the first rains (Gray and Schlesinger 1981) and then absciss many or all leaves during summer in response to drought and/or photoperiod (Westman 1981c, 1982).

Substrate influence on local community structure is somewhat weaker in our analyses than that of aspect. However, we hypothesize that the coarser-textured soils associated with group 1 sites offer drier conditions for shrub species than finer soils. Since dominants are most photosynthetically active before soils begin to dry (Harrison et al. 1971; Gray and Schlesinger 1981), the higher moisture-holding capacity of finer-textured soils would contribute to a more mesic environment for shallow, fibrous roots than coarser-textured soils. The two major soil phases differ not only in surface texture but also in depth. We expect that shallow depth exacerbates the low water holding capacity of the Cienaba sandy loam soil (Miller and Hajek 1981); however, the effects of soil depth on shrubs that are seasonally active and with roots that can be concentrated in the upper 8–30 cm of soil (Hellmers et al. 1955; Kummerow et al. 1977) is uncertain and requires further investigation.

There was little similarity between our results and those of Kirkpatrick and Hutchinson (1980), whose subassociations similar to Starr Ranch groups were associated only with altitude. Continentality is a major correlate of coastal sage scrub distribution, which reflects the resolution at the larger spatial scale of their study area.

Our hypotheses that, given uniform time since last fire, coastal sage scrub distribution at a local scale reflects a moisture gradient influenced by aspect and substrate remain speculative until tested. Present moisture conditions of Starr Ranch sites can be known only after direct measurement of water relations in the field (Miller and Poole 1979). The capability of most dominants to respond to drought with varying degrees of leaf abscission, dimorphism, and/or poikilohydric behavior (Westman 1981c, 1982) confers flexibility of response to heterogeneity in moisture availability. Future research on coastal sage scrub at a local scale will combine observations of drought response of dominants with measurements of plant water potentials and such habitat variables as aspect, soil texture, soil depth, and soil water potential. There is evidence from the Venturan subassociations (Malanson 1984) that habitat factors (especially aspect) are more important than fire history in determining mesoscale pattern-ing; however, with increasing fire frequency habitat factors may be of less predictive value (Zedler et al. 1983). The effects of differences in fire intensities at a local scale could be significant (Westman et al. 1981) and require further research.

Factors influencing species distributions. Complementary to the findings of Westman (1981b), *Artemisia californica* had the broadest distribution among dominants; *Lotus scoparius* was associated with sites of greater available moisture and *Eriogonum fasciculatum* with relatively xeric habitats. *Eriogonum fasciculatum* was found by Kirkpatrick and Hutchinson (1977) to be most abundant on recently disturbed sites. All three sites of subgroup 1b, in which *E. fasciculatum* reached its highest cover, were steep with surface cobbles. Occasional slides of loose cobble could cause the disturbance that would favor *E. fasciculatum.*

The low cover of *S. apiana* in group 5 (*S. mellifera*-dominated) cannot be ascribed to known habitat differences. Grant and Grant (1964) conclude that, though the two *Salvia*'s have definite habitat preferences (*S. apiana* on drier sites), their range of tolerance is widely overlapping. The volatile toxins of *S. mellifera* are more inhibitory than those from *S. apiana* (Muller and Muller 1964). However, there is no experimental evidence for the ability of different *Salvia* species to inhibit each other (Westman 1981b).

Both the high number of rare species and the medium-scale patchiness of the coastal sage scrub community in this study are similar to the findings of Westman (1981a, b, 1983a). He suggests that reserve planners should seek maximum representation of the diversity of coastal sage associations. This research has shown that when regional climatic variation is held constant, species composition shifts over short distances along gradients in topographic and edaphic variables. The detection of five groups within a relatively small area such as Starr Ranch has important implications for planning preserves in the topographically diverse southern Californian region: the Venturan, the Riversidian, and probably all other associations, contain subassociations that can be identified at local scales. The methods for floristic and ecological analysis employed in this study are time- and cost-efficient. We urge land managers and biological consultants to identify coastal sage scrub subassociations for an adequate conservation effort.

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TOWNSENDIA MICROCEPHALA (ASTERACEAE: ASTEREAE): A NEW SPECIES FROM WYOMING

ROBERT D. DORN
Box 1471, Cheyenne, WY 82003

ABSTRACT

Townsendia microcephala, a new species from Wyoming, is described and illustrated. It appears most closely related to *T. spathulata* Nutt., with its deciduous pappus and tiny heads. It differs in having glabrous or glabrate and epapillate achenes, smaller heads, and longer and narrower and less copiously pubescent leaves. It occurs about 125 km beyond the known range of *T. spathulata.*

While conducting field work in southwest Wyoming, I encountered a *Townsendia* with unusually tiny heads less than 17 mm in diameter including the spreading rays. It also had a deciduous pappus, a characteristic of only two other species of *Townsendia* (Beaman 1957). One of these species, *T. condensata* Parry ex A. Gray, has rather large heads 25–80 mm in diameter. The other, *T. spathulata* Nutt., has small heads 15–40 mm in diameter but most plants have shorter and broader leaves and often oddly colored rays (Table 1). Further study indicated significant differences in achene pubescence and surface texture.

Townsendia microcephala Dorn, sp. nov. (Fig. 1)—TYPE: USA, Wyoming, Sweetwater Co., T13N R112W W½ of W½ of Sect. 22, Cedar Mtn., rocky slope, 8500 ft (2590 m), 19 Jul 1989, *Dorn 5034* (holotype, RM; isotype, NY).

Herba perennis; foliis plerumque oblanceolatis, pubescentibus, 3–18 mm longis, 1–2.5 mm latis; capitulis sessilibus vel prope sessilibus; involucro 6–8 mm longo, 4–8 mm lato, tegulis 3–4 seriatis; radiis 13–17, albis, 5–8 mm longis; pappo deciduo; acheniis oblanceolatis, glabris vel prope glabris, epapillosis.

Rosulate, taprooted perennial herb with much branched caudex; leaves mostly oblanceolate, moderately to densely pubescent with multicellular hairs, 3–18 mm long, 1–2.5 mm wide; heads sessile or nearly so, less than 17 mm in diameter including rays, old ones tending to persist; involucres 6–8 mm long, 4–8 mm wide; phyllaries in 3–4 series, mostly lanceolate, acute, margins scarious and lacerate-ciliate, pubescent on back with multicellular hairs, 4–8 mm long, mostly 1–1.5 mm wide; ray corollas 13–17, white, 5–8 mm long; disk corollas yellow, about 4 mm long; pappus of ray and disk flowers

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Table 1. Selected Characteristics of *Townsendia microcephala* and Similar Species.

Species	Leaf length (mm)	Leaf width (mm)	Leaf pubescence	Involucre width (mm)	Ray length (mm)	Ray color	Achenes glabrous-glabrate	Achenes papillate
T. microcephala	3–18	1–2.5	villous	4–8	5–8	white	yes	no
T. spathulata	3–12 (–22)	1.5–5	woolly to villous	(5–)8–16	5–10(–12)	*	no	yes
T. condensata	4–30	1.5–5	woolly to villous	10–40	8–16(–20)	white, pink, lavender	no	yes

* The following colors have been noted: white, pink, lavender, brownish orange, coppery, bronze, yellowish green.

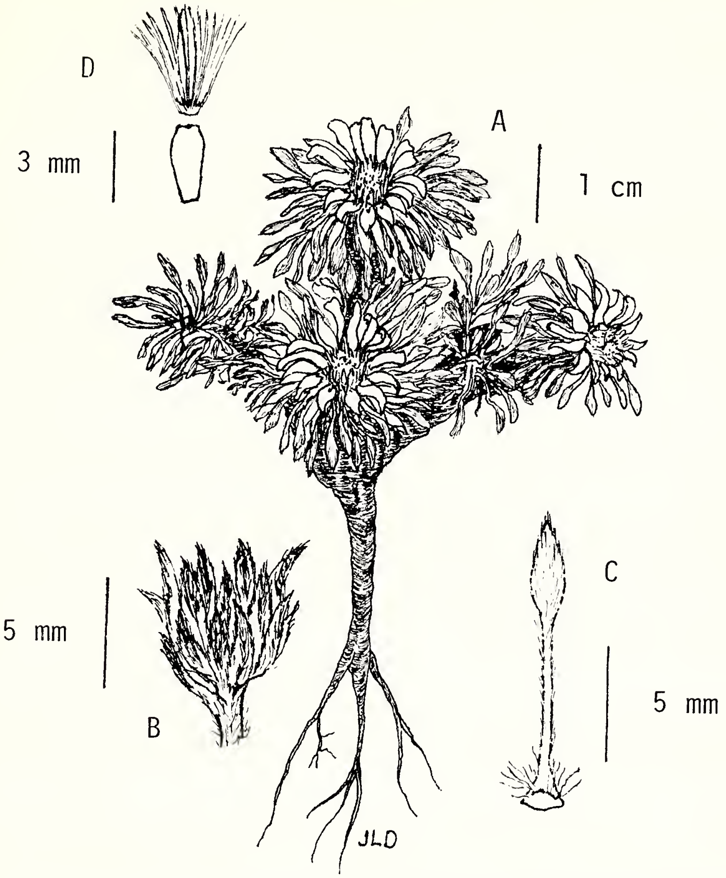

FIG. 1. *Townsendia microcephala.* A. Habit. B. Involucre. C. Leaf. D. Achene and pappus.

similar, of mostly 15–20 barbellate bristles, 3–5 mm long, deciduous; achenes oblanceolate, compressed, glabrous or nearly so, epapillate, 3–4 mm long, about 1 mm wide.

Townsendia microcephala is most similar to *T. spathulata* but the achenes are glabrous or nearly so and not papillate, the heads are smaller, and the leaves are generally longer and narrower and less copiously pubescent (Table 1). *Townsendia spathulata* is usually found on a calcareous substrate; *T. microcephala* grows on the Bishop Conglomerate which is not calcareous. *Townsendia spathulata* occurs to the north and east of *T. microcephala* in Wyoming and Montana. The closest known population of *T. spathulata* is about 125 km ENE of the *T. microcephala* population. The similarities of *T. microcephala* and *T. spathulata* suggest that *T. microcephala* is derived from *T. spathulata,* although the reverse cannot be ruled out.

Townsendia microcephala will key to *T. spathulata* in Beaman (1957). The collection of much more material since Beaman's monograph has increased our understanding of the variability of *T. spathulata* and *T. condensata* so that his key for separating them is no longer useful. The three species can be separated with the following key.

a. Achenes glabrous or glabrate, epapillate; involucre 4–8 mm wide. . . . . *T. microcephala* Dorn
a′. Achenes pubescent, papillate; involucre (5–)8–40 mm wide.
  b. Involucre (5–)8–16 mm wide, 6–10 mm long; stems rarely apparent; leaves mostly copiously pubescent. . . . . *T. spathulata* Nutt.
  b′. Involucre of largest heads 17–40 mm wide, 8–18 mm long, or if smaller, then stems usually apparent and leaves becoming glabrate, especially the upper surface.
    c. Involucre of largest heads 17–40 mm wide; stems rarely apparent; heads often solitary. . . . . *T. condensata* Parry ex A. Gray var. *condensata*
    c′. Involucre usually 10–17 mm wide, rarely wider; stems often apparent; heads rarely solitary, usually 3–15. . . . . *T. condensata* Parry ex A. Gray var. *anomala* (Heiser) Dorn

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TAXONOMIC ASSESSMENT OF *ASTRAGALUS TEGETARIOIDES* (FABACEAE) AND A NEW RELATED SPECIES FROM NORTHERN CALIFORNIA

ROBERT J. MEINKE and THOMAS N. KAYE
Restoration Ecology and Plant Conservation Biology
Cooperative Project,[1]
Department of Botany and Plant Pathology,
Oregon State University, Corvallis, OR 97331

ABSTRACT

Astragalus tegetarioides is taxonomically redefined following recent discoveries of several new sites for this uncommon milkvetch in eastern Oregon. Consequently, disjunct populations previously reported from ash beds in Lassen County, California, are described as the new species **Astragalus anxius**, distinguished by root, inflorescence, pubescence, and floral characters. The morphology, natural history, and putative relationships of the two species are contrasted.

Astragalus tegetarioides M. E. Jones is a local endemic of the northern Great Basin, occupying open pine forests and occasionally sagebrush-juniper steppe. Until recently, the species was poorly known in the field and sparsely represented in herbaria. During the last few years, however, biological inventories associated with federal timber harvest in Oregon have resulted in the discovery of several rather large populations of *A. tegetarioides*. This has renewed taxonomic interest in the species, whose phylogenetic relationships have been considered by Barneby (1964, 1984) to be enigmatic.

Foremost in any reassessment of *Astragalus tegetarioides* is the disposition of an intriguing set of outlying populations reported from northern California. Formerly believed to be a southeast Oregon endemic, *A. tegetarioides* was identified by Nelson and Nelson (1981) from a single locality in Lassen County, California, approximately 325–450 kilometers southwest of the previously known range of the species. The California plants were deemed different in minor ways from Oregon specimens, the main discrepancies being a slightly larger, purplish banner (versus white to lilac-streaked) and longer calyx teeth. Nelson and Nelson (1981) and Barneby (1989) considered these variations to be taxonomically insignificant, although until the last two years very little material of the California or Oregon populations was available for comparison.

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[1] A collaborative research unit of Oregon State University and the Oregon Department of Agriculture.

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The recent discovery of new populations of *Astragalus tegetarioides* in Oregon has allowed us to clarify the circumscription of the species. In 1990 and 1991 visits were made to all known population centers to re-evaluate the differences previously noted for the California plants, and to determine if these or other traits were outside the range of variation for the species in Oregon. These initial studies strongly suggested that the Lassen County plants are consistently and strikingly dissimilar from those in Oregon. Taxonomically significant variation within the species in Oregon was not evident, as these populations appeared to be morphologically uniform.

To further investigate phenotypic variation in *A. tegetarioides,* seeds from California plants were germinated in a climate-controlled greenhouse and grown together with plants from the three largest Oregon populations. Twenty-six plants (10 from California and 16 from Oregon) were cultivated through early autumn, each developing several inflorescences prior to senescence. The unique characters observed in the field remained constant in the greenhouse, supporting the recognition of the Lassen County, California populations as taxonomically distinct.

In this paper we provide a description for the new species, amend the current description of *Astragalus tegetarioides,* and compare the two species with each other and potentially related taxa.

Astragalus anxius Meinke & Kaye, sp. nov. (Figs. 1, 2)—TYPE: USA, California, Lassen Co., Ash Valley, ca. 25 km west of Madeline and U.S. Hwy. 395, immediately south of Ash Valley Rd., in loose gravel overlying volcanic bedrock, on the boundary of T38N R11E Sect. 32 and T37N R11E Sect. 5, ca. 1550 m, 16 Jul 1991, *Meinke and Lantz 6108* (holotype, OSC; isotypes, CAS, ISC, MO, NY, RM, UC, US).

Herba perennis ± prostrata striguloso-villosula; *radices* diffusae non profundae; *caules* graciles 0.3–2.0 dm longi; *folia* 2.0–5.0(–7.0) cm longa, foliolis 4–6(–7)-jugis (2.5–)4–9(–12) mm longis (1.5–) 2.5–7.0(–10.5) mm latis; *racemi* breves densi floribus (7–)9–13 (–15); *calyx* 3.2–4.7(–5.0) mm longus, dentibus subulatis 1.7–2.7 mm longis; *vexillum* purpurascens vel lilacinum 6.5–10.0(–12.0) mm longum 3.0–5.5(–6.5) mm latum; *alae* albae 4.5–8.8 mm longae; *carina* purpurea 4.7–6.6 mm longa; *legumen* sessile 3.5–4.5 mm longum 3.2–4.2 mm latum angulis lateralibus obtusis valvulis chartaceis strigulosis, ovulis 2–3(–4); *semina* (1–)2–3, 1.7–2.1 mm longa.

Decumbent to weakly prostrate perennial; *stems* slender, trailing, few to many, 0.3–2.0 dm long, freely branching beginning with the lower nodes, arising from a weak, suffruticulose caudex; *roots* diffuse, taproot short with proliferous secondary and tertiary roots, these spreading horizontally in the loose, shallow substrate, with larger

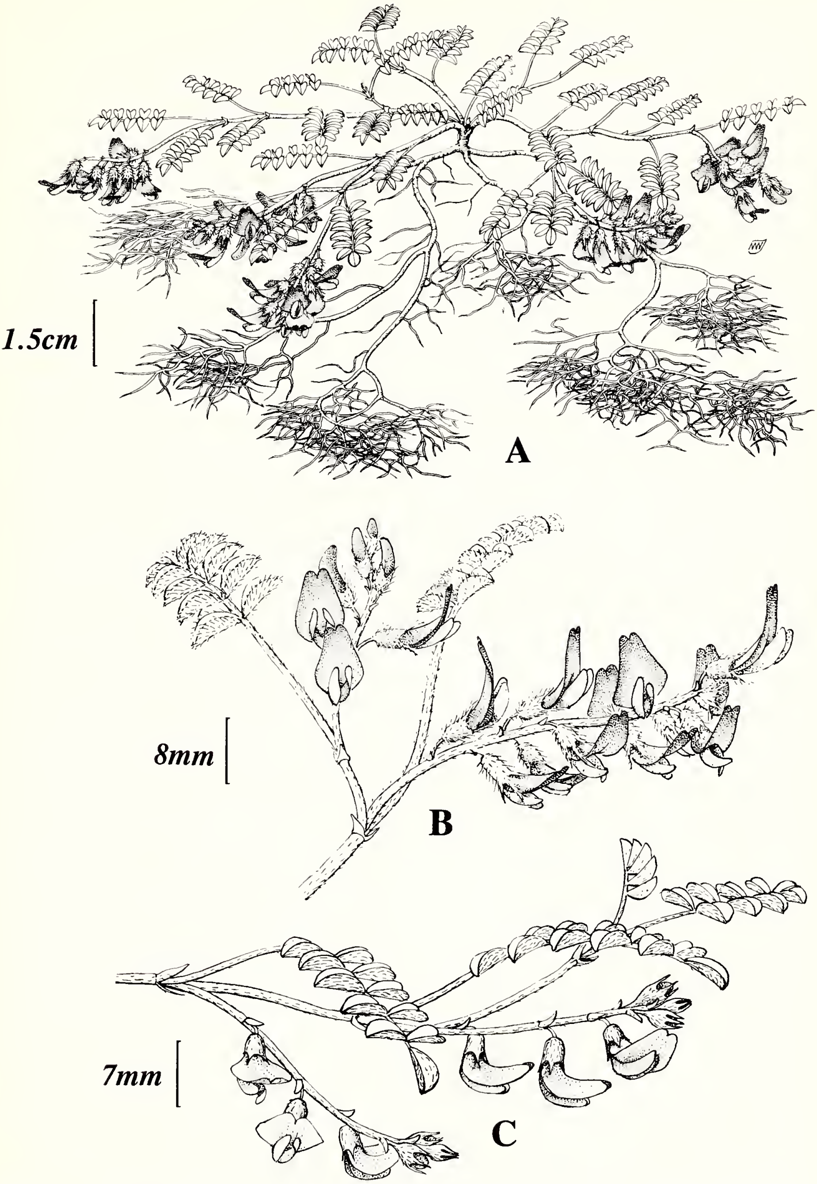

FIG. 1. *Astragalus anxius.* A. Prostrate habit and shallow root masses. B. Close-up of flowering branch. *Astragalus tegetarioides.* C. Close-up of flowering branch.

plants ultimately developing densely branched clusters or mats of pubescent, capillary rootlets up to 10 cm across, possibly with mycorrhizal connections, forming nodules; *pubescence* of short semi-appressed hairs on the lower stems, hoary to subvillous on the new growth, becoming loosely villous with numerous straight to sinuous hairs up to 1.2 mm long on the stipules, petioles, and particularly the leaflets, the latter pilosulous below and glabrous and green above, occasionally with scattered hairs 1–2 mm inside the dorsal margin; *stipules* 1–4 mm long, thinly herbaceous, becoming papery with age, ovate-acuminate to lanceolate, the blades mostly recurved at the tip, generally completely free but occasionally ± amplexicaul and weakly united by a stipular line at the lowest nodes; *leaves* 2.0–5.0 (–7.0) cm long, with filiform petiole approximately equalling the blade, leaflets crowded, sessile to obscurely petiolulate, 9–13(–15) per leaf, (2.5–)4–9(–12) mm long, (1.5–)2.5–7.0(–10.5) mm wide, flat or partially folded, obovate-cuneate, obtuse to truncate or with a slight apical notch; *peduncles* slender, spreading to erect, 0.5–3.5 cm long, shorter than the leaf; *racemes* congested, 0.8–2.2 cm long in flower, with 0.5–2.0 mm spacing between pedicels, the (7–)9–13 (–15) flowers spreading to ascending, usually declined in post-anthesis; *floral bracts* herbaceous, lance-linear, 1–3 mm long, ciliate; *pedicels* slender, ascending to arcuate, 0.5–1.5 mm long; *calyx* 3.2–4.7 (–5.0) mm long, the tube 1.5–2.2 mm long, pubescence spreading, with straight to wavy hairs 0.7–1.1 mm long, the subulate teeth ciliate, 1.7–2.7 mm long; *corolla* dull lavender in bud, purple and white at anthesis; *banner* rose-purple to deep lilac when fresh, often with darker striations and a pale eye at the base, drying deep violet in well-preserved specimens, narrowly obovate-cuneate, 6.5–10.0(–12.0) mm long, 3.0–5.5(–6.5) mm wide, the blade reflexed 60–80°, notched at the apex, the claw 2.0–3.5 mm long; *wings* white, drying white to faintly lilac, 1.5–3.0 mm shorter than the banner, 4.5–8.8 mm long, ± asymmetric, frequently bent or sigmoidally twisted to the right, the blades narrowly oblong to ligulate, obtuse, 3.8–6.8 mm long, the claws 1.7–2.1 mm long; *keel* pale lilac proximally and dark purple at the tip, 4.7–6.6 mm long, the claws 1.5–2.2 mm long, the oblong blades 3.3–4.4 mm long, incurved ca. 100° at the broad, deltoid apex; *anthers* 0.20–0.30 mm long, pollen orange; *pod* spreading to declined, sessile, dehiscent from the receptacle, uniloculate, lenticulate, 3.5–4.5 mm long, 3.2–4.2 mm wide, plumply ovoid to weakly compressed laterally in cross-section, the papery valves silky-villous, not inflexed, usually glabrescent with age, revealing thin cross-reticulations, beakless or with beak less than 0.5 mm, style persistent, ovules 2–3(–4); *seeds* (1–)2–3, dull black, smooth, 1.7–2.1 mm long.

The epithet "*anxius*" has both passive and active meanings, i.e., troubled or troublesome. Considering the probable correlation between public lands grazing and the long-term prospects for this potentially endangered species, either common name may be appropriate, depending on the point of view.

Paratypes. USA, California, Lassen Co., type locality, 6 Jul 1980, *Nelson and Nelson 5988* (HSC, NY); 29 Jun 1985, *Shelly & King 1028* (OSC); 27 Jun 1990, *Kaye and Meinke 1252* (OSC).

Distribution. Astragalus anxius is believed to be endemic to Ash Valley in extreme north-central Lassen County, California, at 1540–1660 meters elevation. The species is scattered sporadically over a few square kilometers northwest of Spooner Reservoir, occurring on arid flats in or near juniper-sagebrush steppe or *Pinus jeffreyi* woodland. Common associate species include *Artemisia tridentata, Juniperus occidentalis, Eriogonum prociduum, Phacelia hastata, Mentzelia albicaulis, Ipomopsis congesta, Senecio canus, Ivesia paniculata, Ranunculus testiculatus, Alyssum alyssoides, Sisymbrium altissimum,* and *Bromus tectorum.*

Astragalus tegetarioides M. E. Jones, Contrib. West. Bot. 10:66. 1902 (Figs. 1, 2)—TYPE: USA, Oregon, southern Blue Mountains, in sandy soil in the Buck Range, 28 Jun 1901, *Cusick 2619* (holotype, POM!; isotypes, G, GH, K, MO, ND, NY, ORE!, P, RM, US).

Prostrate to matted perennial 0.5–4.0 dm across; *stems* few to many, freely branching throughout, arising from a suffruticose caudex; *taproot* vigorous, elongate, secondary and tertiary roots not prominent, nodules not observed; *pubescence* grayish, ± strigose, the hairs straight to wavy, 0.2–0.6 mm long, appressed-ascending on stems, petioles, and peduncles, the leaflets strigillose, completely pubescent below and medially glabrescent above; *stipules* 1–5 mm long, ovate- to lance-acuminate, the blades recurved at the tip, thinly herbaceous to papery with age, often amplexicaul and united by a stipular line or connate at lower nodes; *leaves* 1.5–4.0(–6.0) cm long, the slender petiole approximately equalling the blade, leaflets loosely arranged, distinctly petiolulate, (5–)7–11 per leaf, 1.5–5.5(–7.0) mm long, obovate-cuneate, obtuse, apically notched or emarginate, seldom conduplicate; *peduncles* slender, ± humistrate, (0.3–)0.6–2.5 cm long, shorter than the leaf; *racemes* loosely (2–)4–6(–8) flowered, 1.3–1.8 cm long, with 1.5–6.0(–8.0) mm spacing between the pedicels, the flowers spreading-ascending, typically declined in fruit; *floral bracts* herbaceous, lanceolate to lance-linear, 1.2–2.7 mm long, pubescence appressed; *pedicels* filiform, spreading to ascending, 0.4–1.3 mm long; *calyx* (2.2–)2.6–3.7 mm long, strigulose, the tube 1.1–2.0 mm long, the teeth subulate, 1.0–1.9 mm long; *corolla* dirty white to olivaceous in bud, whitish to ochroleucous at anthesis; *banner* broadly obovate-cuneate, sometimes lilac-veined, 4.4–5.9 (–7.0) mm long, 3.5–5.1(–6.0) mm wide, the blade reflexed 70–100°, often notched at the apex, the claw 1.0–2.0 mm long; *wings* 4.3–

5.9(–7.2) mm long, ± asymmetric, often bent or twisted to the right, the blades broadly lunate-oblanceolate, obtuse, 3.6–4.1 mm long, the claws 1.1–1.8 long; *keel* 3.3–4.1 mm long, pale- or purplish-tipped, the claws 1.1–1.7 mm long, the broadly lunate blades 2.0–2.5 mm long, the deltoid apex abruptly incurved to 130°; *anthers* 0.2–0.3 mm long, pollen orange; *pod* spreading to declined, sessile, dehiscent from the receptacle, uniloculate, oblong-ovoid to sublenticulate, 3.3–4.5 mm long, 1.5–2.8 mm wide, slightly compressed laterally as seen in cross-section, obscurely dorsiventrally compressed, the valves weakly appressed-pubescent, pale green to somewhat stramineous, not inflexed, becoming generally glabrescent with age, smooth or occasionally with scattered cross-reticulations running vertically between the sutures (as seen under magnification), beakless but usually with the curved style firmly attached, ovules 2–3; *seeds* 1–2, tan to dark brownish or black, smooth, 1.6–2.1 mm long.

Representative specimens. USA, Oregon, Harney Co., yellow-pine slopes 25 mi north of Burns, 15 Jul 1936, *Thompson 13289* (WS, WTU, WILLU!); 18 mi north of Burns, 13 Jul 1938, *Peck 2010* (WILLU!); 2 mi east of Little Juniper Mtn., 21 Jun 1941, *Peck 20853* (WILLU!); open yellow-pine, Malheur National Forest, 18 mi north of Burns along John Day Hwy. (=U.S. 395), 30 Jul 1946, *Maguire and Holmgren 26735* (UTC, WTU); 2.5 mi east-northeast of Little Juniper Mtn., T28S R25E Sect. 7, 30 May 1985, *King 137* (OSC!); along Oregon State Highway Division right-of-way, ca. 29 km north of Burns along U.S. Hwy. 395, T20S R31E Sect. 22, 20 Jun 1991, *Meinke, Lantz, and Clark 6078* (OSC; to be distributed); Dry Mtn., Ochoco National Forest northwest of Riley, T21S R25E Sect. 27, 20 Jun 1991, *Meinke, Lantz, and Clark 6085* (OSC; to be distributed); near the terminus of Smoke Out Canyon, 4.1 km due east of Little Juniper Mtn., T28S R25E Sect. 8, 21 Jun 1991, *Meinke, Lantz, and Clark 6098* (OSC; to be distributed).

Distribution. Astragalus tegetarioides is endemic to northern Harney County, Oregon, at 1500–1630 meters elevation. The species extends irregularly along the extreme southern edge of the Blue Mountains, in the Malheur and Ochoco National Forests. Populations are distributed from near U.S. Hwy. 395 west to the Dry Mountain area near Riley, usually in or near *Pinus ponderosa* woodland. Common associate species include *Artemisia arbuscula, A. tridentata, Purshia tridentata, Allium acuminatum, Calochortus macrocarpus, Ipomopsis aggregata, Mimulus nanus, Collinsia parviflora,* and *Gayophytum diffusum.* An unusual disjunct station, comprised of mostly depauperate individuals, is located near Little Juniper Mountain immediately east of the Lake County line. The population here occurs in a rimrock-scrub community characterized

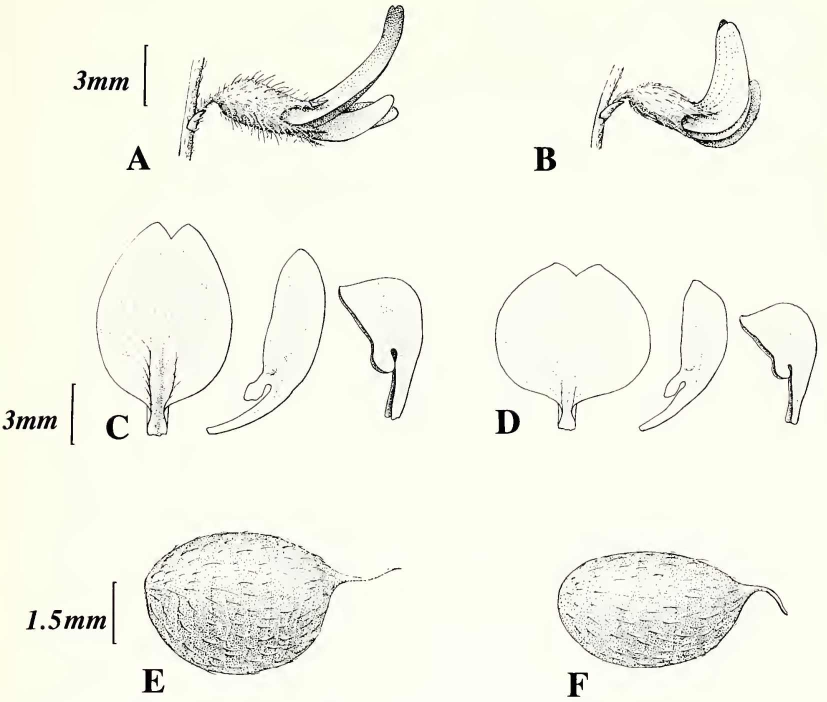

FIG. 2. Comparisons of *Astragalus anxius* (A, C, E) and *Astragalus tegetarioides* (B, D, F). A, B. Flower profile. C, D. Banner, wing, and keel petals. E, F. Pod profile.

by *Juniperus occidentalis, Artemisia tridentata, Chrysothamnus nauseosus, Trifolium gymnocarpum, Astragalus purshii, Lomatium nevadense, Lewisia rediviva, Agropyron spicatum, Poa sandbergii, P. bulbosa, Bromus tectorum,* and *Taeniatherum caput-medusae.*

COMPARISON OF THE SPECIES

Morphology. Salient morphological differences between *Astragalus tegetarioides* and *A. anxius* are summarized in Table 1 and illustrated in Figures 1 and 2. While the two microphyllous species share many traits there are a number of features that separate them, including aspects of root development, floral morphology, inflorescence architecture, and pubescence. Plants of *A. anxius* are typically more robust vegetatively, with larger and more numerous leaflets and a somewhat procumbent (as opposed to strictly prostrate) habit. The new species is also more obviously pubescent, with longer, spreading foliage hairs that are clearly visible to the unaided eye. The longer, bicolored corolla of *A. anxius* is another striking feature, with the combination of rose-purple banner and clear white wings not approached by any populations of *A. tegetarioides.*

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *ASTRAGALUS ANXIUS* AND *A. TEGETARIOIDES.*

Character	*A. anxius*	*A. tegetarioides*
Root system	weak taproot; secondary roots prolific, spreading	strong central taproot; secondary roots scant
Vegetative pubescence	hairs spreading, evident, conspicuous on underside of leaflet, 0.8–1.2 mm long	hairs inconspicuous and strigillose on leaflets, up to 0.6 mm long
Leaflets	4–9 mm long, scarcely petiolulate; 9–15 per leaf	1.5–5.5 mm long, clearly petiolulate; 7–11 per leaf
Inflorescence	racemes 0.8–2.2 cm long, congested, flowers (7–)9–13(–15)	racemes 1.3–1.8 cm long, loosely arranged, flowers (2–)4–6(–8)
Calyx	3.2–4.7(–5.0) mm long, the teeth spreading-ciliate, 1.7–2.7 mm long	(2.2–)2.6–3.7 mm long, the teeth short-strigose, 1.0–1.9 mm long
Banner petal	rose-purple with a pale basal eye, reflexed 60–80°, narrowly obovate, 6.5–10.0(–12.0) mm long by 3.0–5.5(–6.5) mm wide	whitish, often with pale lilac veins, reflexed up to ca. 100°, broadly obovate, 4.4–5.9(–7.0) mm long by 3.5–5.1 (–6.0) mm wide
Pod	lenticulate, 3.5–4.5 mm long by 3.2–4.2 mm wide, 2–3(–4) ovulate	oblong-ovoid, 3.3–4.5 mm long by 1.5–2.8 mm wide, 2–3-ovulate

Phenology. Both species are primarily summer bloomers, with flowering beginning in early to mid-June and peaking from late June to mid-July. *Astragalus anxius* is largely in fruit by late July, while *A. tegetarioides* may continue to bloom into September or even October, depending on moisture availability.

Reproductive ecology. No fruit developed on plants of either species grown in the greenhouse, although fruits and filled seeds are commonly observed on plants in nature. Anthers in greenhouse plants developed and dehisced normally, and dissections showed that pollen coated the stigmas of both species within 24 hours after anthesis. These observations imply that *Astragalus anxius* and *A. tegetarioides* are incapable of setting seed without pollinators, and are probably self-incompatible. Preliminary field inspection suggests that *A. anxius* receives more insect visitors than *A. tegetarioides,* perhaps due to the showier, more plentiful flowers. Several native bees, primarily species of *Bombus, Osmia, Mellisodes,* and *Lasioglossum,* gather pollen and possibly nectar from *A. anxius* flowers. Insect visitors observed foraging on *A. tegetarioides* flowers are primarily small pollen-gathering bees, including several species of *Lasioglossum* and *Chrysis.* The floral life span for both species averages about three days.

First-year plants of *Astragalus tegetarioides* appear to devote comparatively more resources to vegetative development than to flowering and reproduction. Greenhouse grown plants of both species were cultivated under a spring/summer photoperiod, resulting in an average germination to flowering time of four months for *A. anxius* and six to seven months for *A. tegetarioides.* In addition to producing half again to twice as many flowers per raceme, first year *A. anxius* plants also bloom more prolifically, developing inflorescences at two to three times the rate of *A. tegetarioides.* In the field, large established plants of the two species were observed to produce comparable numbers of inflorescences, although *A. anxius* retained the advantage in flowers per raceme.

Astragalus anxius usually produces two, or occasionally three, seeds per pod, while *A. tegetarioides* often produces only one. Seeds of both species germinate readily after scarification, usually within three days. No pre-dispersal seed predators were observed for either species.

Microsite variation and adaptation. Astragalus anxius and *A. tegetarioides* are found in basin and range plant communities, occurring in volcanic soils associated with openings in the forest or scrub. The substrate occupied by *A. anxius* is unique, however, in consisting of a spongy, ash-gravel aggregate overlying semi-exposed bedrock. The soils here are relatively well-drained, loose, and often only a few centimeters deep. *Astragalus tegetarioides* also occurs in shallow, stony soils, but these tend to be poorly to moderately drained, comprised of ashy clays surmounting heavily fissured bedrock. Populations of *A. tegetarioides* are sometimes found in deeper loams or in crevices of exposed basalt outcrops.

The differences in the root systems of the two species may be related to substrate and microclimatic adaptations. *Astragalus anxius* plants grow from a short taproot and a matrix of secondary and tertiary roots spreading just below the gravelly soil surface. These produce scattered mats of capillary roots, stabilizing the substrate immediately surrounding the plants and presumably facilitating the rapid uptake of water during infrequent spring and summer storms. The emphasis on early flower and fruit production by *Astragalus anxius* may also represent adaptation to periodic drought. *Astragalus tegetarioides,* conversely, has few significant lateral roots but develops a deep taproot capable of penetrating heavy soils and subsurface cracks and fissures. This allows plants access to less ephemeral moisture sources, thereby enabling a longer flowering season and promoting a greater ratio of vegetative to reproductive biomass.

Relationships. The evolutionary relationships of *Astragalus anxius* and *A. tegetarioides* are difficult to assess. Barneby (1964) aligned *A. tegetarioides* with the New Mexico endemic *A. micromerius* (section *Humistrati*), based on fruit and flower size, keel characters, and ovule numbers. He implied that this is a somewhat arbitrary alliance, however, and noted that an affiliation with *A. microcystis* or *A. vexilliflexus* in section *Ervoidei* might be equally appropriate. *Astragalus anxius* is morphologically similar to these taxa as well, particularly *A. microcystis,* a species of northeast Washington to western Montana. Several features of *A. anxius,* including flower number per raceme, leaflet size, pubescence, flower coloration, and pod compression, are more or less intermediate between *A. microcystis* and *A. tegetarioides.*

Barneby (1984) also suggested a relationship between *Astragalus tegetarioides* and the recently discovered *A. tiehmii,* a xerophytic mat-forming perennial from northwestern Nevada. In addition to a microphyllous, prostrate habit, *Astragalus tiehmii* parallels *A. anxius* and *A. tegetarioides* in possessing a tiny, few-seeded pod. It is likewise endemic to ashy substrates, which are comparable, although apparently not identical, to those inhabited by *A. anxius* in Ash Valley (Barneby 1984). *Astragalus anxius* shares a number of traits with *A. tiehmii* that are not found in *A. tegetarioides,* most notably the weak taproot, essentially free stipules, pilosulous foliage, obovate banner, and 3–4-ovulate pods. *Astragalus anxius* differs from both species in its purple flowers, larger banner, more floriferous racemes, pubescence length, and more numerous leaflets. Barneby (1984) speculated that *A. tiehmii* may form an evolutionary connection between *A. tegetarioides* and *A. pulsiferae,* another Great Basin species of uncertain affinities. Further study of *Astragalus anxius* may assist in clarifying the phylogeny of this group.

If *Astragalus anxius* and *A. tegetarioides* are most closely related to each other, there is evidence to suggest that *A. anxius* is the derived member of the pair. *Astragalus tegetarioides* has a broader ecological amplitude, and the discontinuous range of this species indicates it may once have been more plentiful. For example, the disjunct population persisting on rock outcrops near Little Juniper Mountain almost certainly is a relict occurrence, based on the improbability of recent dispersal across 80–100 kilometers of desert to such an ecologically marginal site. *Astragalus anxius* is also isolated from the main range of *A. tegetarioides,* and may represent a modification of that species selected through past climatic changes. Now restricted to a single substrate, *A. anxius* has developed a more specialized, xerophytic life history, exemplified by the diffuse root system, denser pubescence, and precocious reproduction. Although clearly a perennial species, *A. anxius* appears capable of functioning as a facultative annual, and may routinely flower and set seed the first year. During July field inspections an estimated 98% of *A. anxius* plants, regardless of size, were in flower. Populations of *A. tegetarioides* were far less homogeneous, consisting of reproductive and sterile individuals. Despite numerous leafy branches (in late June) most nonflowering plants were considered prereproductive, defined by the presence of green cotyledons.

Conservation status. All known populations of *Astragalus tegetarioides* are under public ownership, primarily administered by the U.S. Forest Service (USFS) or Bureau of Land Management (BLM). Observations on the Ochoco National Forest show that, in the short term at least, *A. tegetarioides* populations appear to recover from the effects of moderate habitat disturbance associated with timber harvest. Preparations are underway for a demographic study by the USFS to evaluate impacts of logging on the species over several years (A. Kratz, personal communication). In the meantime the agency is protecting the majority of populations. On BLM land domestic overgrazing of *A. tegetarioides* habitat is widespread, evidenced by soil compaction and infestations of pernicious weeds such as *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead wildrye). Data on the effects of grazing and habitat degradation on the biology and demography of *A. tegetarioides* have never been gathered.

Grazing may also be a hazard for *Astragalus anxius,* since all reported sites for this species occur on federal range or privately owned pastures. Impacts from livestock and off-road vehicle use were conspicuous at the type locality in 1991. However, the severity of the substrate appears to be moderating the proliferation of competing exotics that often coincides with such land uses. Trampling by cattle could be the most serious threat to *A. anxius* populations and the unique plant assemblages occurring locally in Ash Valley. Other rarities here include the subshrub *Eriogonum prociduum* and the herbaceous perennial *Ivesia paniculata,* a second narrow endemic.

Another potential effect of habitat disturbance on *Astragalus anxius* and *A. tegetarioides* may be a reduction or elimination of insect pollinators needed for fertilization and seed set. Most of the floral visitors observed foraging on the two species are ground-nesting, and may be particularly sensitive to surface disturbances. Grazing, logging, and pesticide applications can devastate native pollinators, and small populations of either *Astragalus* species could be vulnerable to reproductive failure under these circumstances.

Astragalus tegetarioides is presently a candidate for listing as threatened or endangered under Oregon and federal law. Considering the current efforts of the Forest Service to conserve and study populations in Oregon, formal listing could ultimately prove unnecessary for this species. *Astragalus anxius,* on the other hand, appears to exist under more precarious circumstances. Its taxonomic separation from *A. tegetarioides* may compel an administrative and biological review, to evaluate the propriety of protecting the new endemic under the federal Endangered Species Act.

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MORTALITY AND AGE OF BLACK COTTONWOOD STANDS ALONG DIVERTED AND UNDIVERTED STREAMS IN THE EASTERN SIERRA NEVADA, CALIFORNIA

JULIET C. STROMBERG and DUNCAN T. PATTEN
Center for Environmental Studies,
Arizona State University,
Tempe, AZ 85287

ABSTRACT

Effects of stream flow diversion on riparian vegetation can range from extreme to subtle. Extreme effects include extensive loss of riparian vegetation, such as has occurred along portions of Bishop Creek, Rush Creek, and other eastern Sierra Nevada streams diverted for hydropower production and municipal water use. Some diverted reaches of these and other streams, however, have relatively dense vegetation. This study revealed the presence of subtle diversion effects within such reaches of Bishop Creek, as indicated by younger age and size, higher mortality, and lower canopy foliage density of black cottonwood stands (*Populus trichocarpa*) in comparison to black cottonwood stands along a nearby free-flowing river (Pine Creek). Tree ring analysis implicated chronic drought and episodic floods as causes of this reduced biotic integrity. Droughts have become more frequent and intense, as a result of greater flow diversion during dry and normal years than in wet years. The frequency of flood flows has been diminished, but the magnitude of rare extreme flood events has been little affected. Restoration of biotic integrity depends, in part, on restoration of minimum and maximum flows that approximate natural conditions.

Damming of rivers for hydropower production, flood control, or water supply often results in substantial change in the downstream flow regime (Chien 1985). Annual flow volume may be reduced; seasonal flow peaks may shift from spring to summer if flows are released after reservoir filling; and annual fluctuation in flow volume may increase if flow diversion is greater during dry and normal years than in wet years. The effects of these changes on downstream riparian vegetation range from extreme to subtle (Williams and Wolman 1984; Risser and Harris 1989). The extreme effects, notably widespread loss of low elevation riparian ecosystems, have stimulated research on restoration and maintenance of endangered riparian ecosystems, including development of instream flow methodologies for riparian vegetation (Stromberg and Patten 1990). The less apparent subtle changes have engendered controversy over the effects of stream diversion while also stimulating research on identification of streams that are least sensitive to diversion (Kondolf et al. 1987).

Within California, the riparian ecosystems of the eastern Sierra Nevada have been extensively managed for their water resources.

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At Bishop Creek, for example, streamflow has been diverted for hydropower production for nearly a century (Stromberg and Patten 1991). This has reduced the extent of riparian vegetation in many stream reaches. Out-of-basin flow diversion for municipal use at Rush Creek similarly has caused loss of riparian vegetation (Stine et al. 1984; Stromberg and Patten 1990). As is true for many diverted streams, however, some diverted reaches on both Bishop and Rush creeks support stands of cottonwoods (*Populus* spp.) and other riparian vegetation. The mere presence of riparian trees, though, cannot be used as the sole indicator that flow regimes are providing for a high degree of biological integrity (Karr 1991). Although ecosystem level changes indicative of extreme stress may not be present (e.g., changes in species composition), there may be population level changes indicative of a lower level of stress (Taub 1987). For example, riparian cottonwood populations may recruit infrequently or have high mortality as a result of altered flow pattern or reduced flow volume. Recruitment is particularly sensitive to flow conditions, and often depends on a particular sequence of flows such as high spring flows followed by reduced summer flooding (Stromberg et al. 1991). Mortality in riparian systems also is strongly influenced by flow regimes. Flood flows and low flows alike are primary causes of mortality, particularly for juvenile and senescent trees (Albertson and Weaver 1945; McBride and Strahan 1984; Hunter et al. 1987; Smith et al. 1991). Thus, parameters indicative of biotic integrity, such as population age structure and mortality, should be assessed along diverted and regulated streams (Karr 1991).

Studies of vegetational parameters such as age structure and mortality can be useful in understanding ecological processes and thereby avoiding adverse environmental impacts (Franklin et al. 1987). Within riparian ecosystems, for example, if tree mortality is found to be caused by a particular flow regime, this information can be useful in prescribing appropriate instream flows for managing riparian vegetation. This study was undertaken with the primary objective of comparing: (1) vegetation structure; (2) black cottonwood (*P. trichocarpa*) size and age structure, including maximum tree size and age; and (3) extent and causes of mortality for mature black cottonwood; between a partially diverted stream (Bishop Creek) and a nearby free-flowing stream (Pine Creek) in the eastern Sierra Nevada of California. A secondary objective was to identify flow regimes associated with mortality of black cottonwood along diverted Rush Creek, also in the Sierra Nevada. Such information is important because of the rarity and value of riparian cottonwood ecosystems in the American West, and because of the utility of the data in helping to define appropriate flow regimes for riparian ecosystem maintenance.

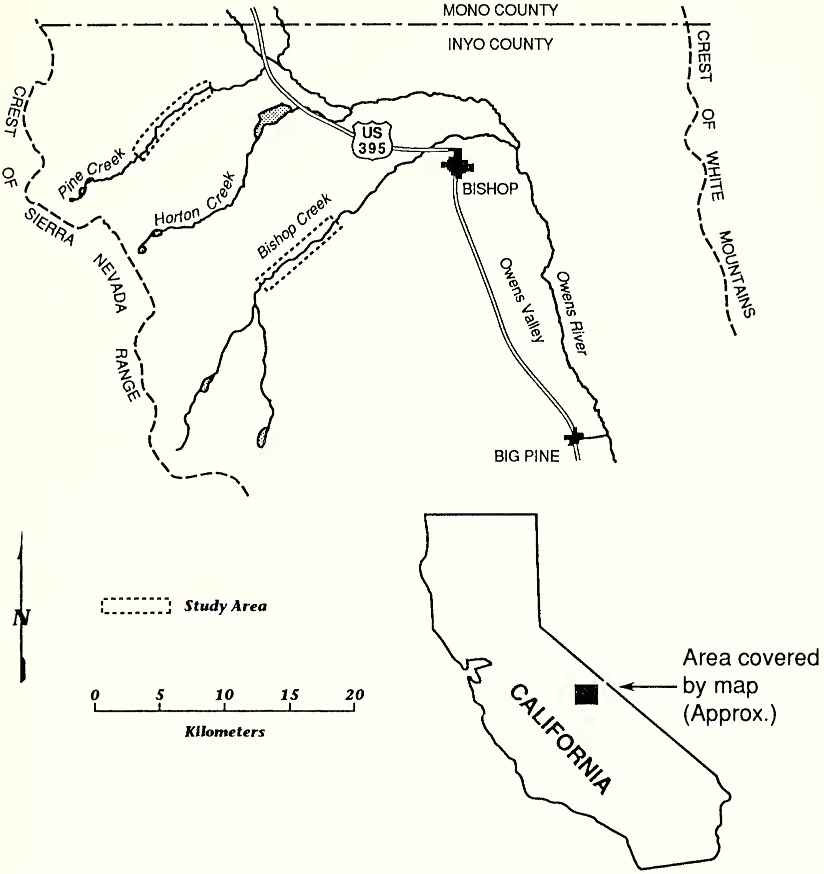

FIG. 1. Location map for study areas along Bishop and Pine creeks. The Rush Creek study area is located about 75 km north of Pine Creek within the Mono Basin.

STUDY AREAS

Bishop Creek drains a 180 km^2 watershed in the rainshadow of the eastern Sierra Nevada (Fig. 1). In its upper reaches, Bishop Creek flows over bedrock and glacial till through steep alpine and coniferous landscapes in a glacially carved canyon. The stream in its mid and lower reaches is surrounded by Great Basin shrub desert and flows over an alluvial fan before entering the Owens River Valley. Riparian vegetation in the mid-elevation reaches (ca. 1500–2000 m) is dominated by black cottonwood, water birch (*Betula occidentalis*), willow (*Salix* spp.), Jeffrey pine (*Pinus jeffreyi*), and mountain rose (*Rosa woodsii ultramontana*). Vegetation cover decreases with elevation, and black cottonwood gradually gives way to Fremont cottonwood (*Populus fremontii*) hybrids at about 1500 m.

Five hydroelectric power plants operate on Bishop Creek. In dry and normal snow pack years, all of the water is diverted from the channel into a series of pipelines and reservoirs, and used to generate power. At these times, any water present in the stream arises from dam leakage and/or groundwater input; often no surface flow is present in the lower reaches. In wet years, snowmelt delivers water at a rate that exceeds the capacity of the facilities and the excess flow spills into the stream. At each power plant a small intake dam collects the water exiting the plant plus any flows in the stream. The dam delivers the water to the next power plant through another pipeline. Flows are ultimately released into the stream channel below the lowermost power plant.

Pine Creek is a free-flowing stream located 15 km north of Bishop Creek (Fig. 1). The stream drains a 98 km^2 watershed and flows over deep sedimentary fill through a glacially carved U-shaped valley (Kondolf et al. 1987). In its mid-elevation reaches (1500–2000 m), Pine Creek is dominated by water birch and black cottonwood, with a shrub understory of mountain rose. Fremont cottonwood is present at low elevations, but in a landscape highly modified by ranching activities.

Rush Creek is the largest tributary to Mono Lake. It flows from the eastern slope of the Sierra Nevada through a narrow mountain valley until it is impounded in Grant Lake Reservoir, from which water is diverted to the City of Los Angeles. Diversion was limited during the first few years after construction of the reservoir (1942), but from 1948 on releases were minimal except in wet years. The riparian vegetation below Grant Lake is dominated by black cottonwood, several species of willow, and Jeffrey pine.

METHODS

Our research approach included assessment of: (1) vegetation structure; (2) black cottonwood size and age structure; and (3) extent and causes of mortality for mature cottonwood trees. The first parameters were measured in each of three diverted reaches of Bishop Creek and three elevationally matched reaches of Pine Creek. The second parameters were measured for these same reaches and for an additional high-elevation diverted reach of Bishop Creek. The third parameters were determined for one reach of Bishop Creek with high mortality, and for a diverted reach of Rush Creek at ca. 2000 m. The Bishop creek reaches range in elevation from 2380 m (reach 1) to 1470 m (reach 4) and are numbered based on the number of the nearest upstream powerplant. Numbers of Pine Creek reaches (2, 3 and 4) correspond to numbers of elevationally matched Bishop Creek reaches.

Vegetation structure. Vegetation structure was assessed by measuring canopy foliage density (i.e., leaf area index) and by identifying the dominant woody plants. Canopy foliage density was measured in 1991, by sampling fifty points per reach with a LICOR 2000 plant canopy analyzer. Measurements were taken in early morning or under shaded sky conditions to minimize error (Welles 1990). Canopy foliage densities were compared between elevationally matched reaches of Pine and Bishop creeks using Student's t-tests. To identify dominant woody species, woody plant density by species was sampled within four, 10 m × 50 m quadrats per reach. Species names follow Munz and Keck (1973).

Size and age structure. Black cottonwood size structures were generated based on stem diameters measured in four, 10 m × 50 m quadrats per reach. To generate age structure, increment cores (two per tree) and stem diameters were taken for 14 to 50 trees per reach. After cross-dating the increment cores, the trees were aged by counting the number of growth rings and adding the estimated number of years to grow to the 1.5 m coring height (2 years at low elevations, 3 years at high elevations). Prior studies have indicated that black cottonwoods produce one growth ring per year (Stromberg and Patten 1990). Linear regression equations relating tree age to tree diameter were then developed with SPSS/PC+. These reach-specific equations were used to estimate ages of all trees measured for stem diameter.

Mortality. Mortality was calculated in 1989 as the percentage of standing dead or downed trees among the population of mature trees (those >10-cm dbh). Sample size for the mortality count was 100 trees, except in reaches with very small cottonwood populations. At this time, 15 to 50 live trees per reach were marked. The sites were revisited in Fall 1991 (during the fifth year of a drought) to assess mortality among the marked population of trees. To determine causes of past tree death, increment cores (two per tree) were collected from 10 randomly selected mature, dead black cottonwoods at Bishop Creek reach 2 and from 15 dead black cottonwood trees at Rush Creek. Dead trees were not cored at Pine Creek because there were few trees that had died from unknown causes. The diameter of each cored tree was measured, and the cores were mounted and sanded following standard procedures (Fritts and Swetnam 1989). Because of cellular decomposition, only 11 trees per stream had interpretable annual rings. The annual ring widths of these trees were measured with a Bannister type incremental measuring machine and standardized to remove age-related growth trends. To identify the year of death, the ring chronologies were cross-dated against reach chronologies developed previously for live trees (Stromberg and Patten

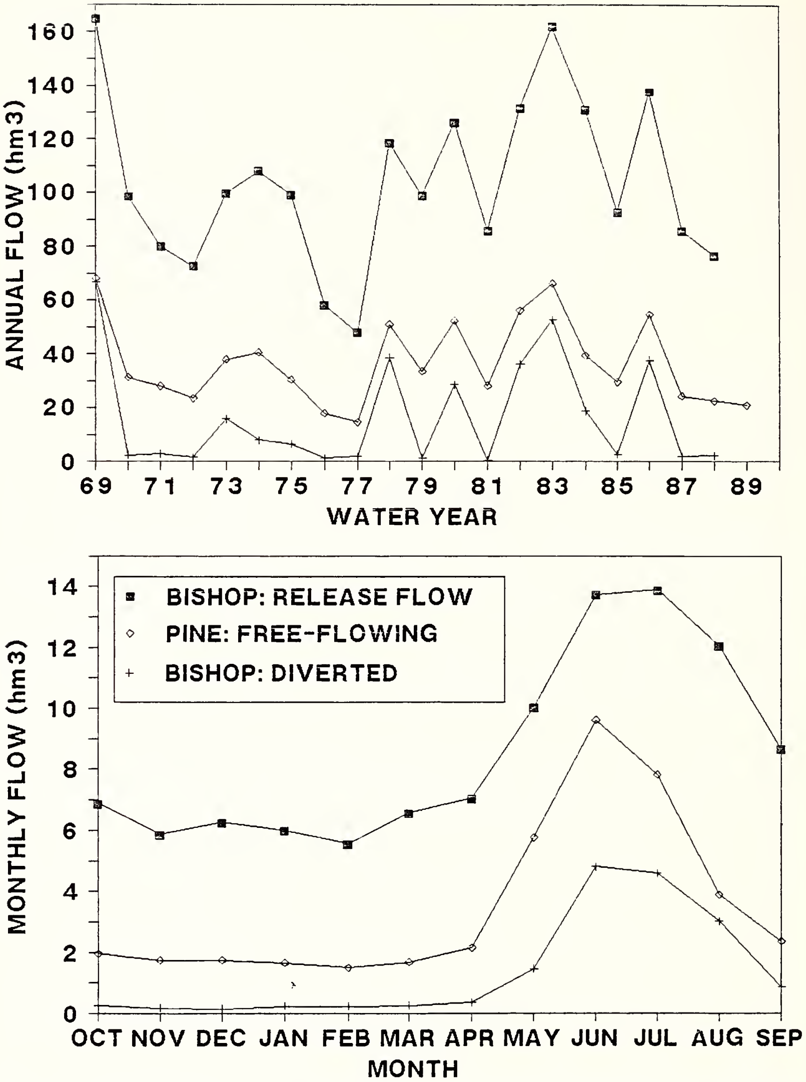

FIG. 2. Annual and monthly flow volume in free-flowing Pine Creek (1580 m), in a diverted reach of Bishop Creek (1390 m), and in the reach of Bishop Creek that receives the return flows (1380 m).

1990, 1991). Flow volume during the year of death was determined from data supplied by Southern California Edison Co. (Bishop Creek) and by Los Angeles Department of Water and Power (Rush Creek). The chronologies of the dead trees were also measured for annual growth rate and for mean sensitivity, an indicator of the degree of annual growth fluctuation (Fritts and Swetnam 1989). Growth rates and mean sensitivities were also measured for live trees within each

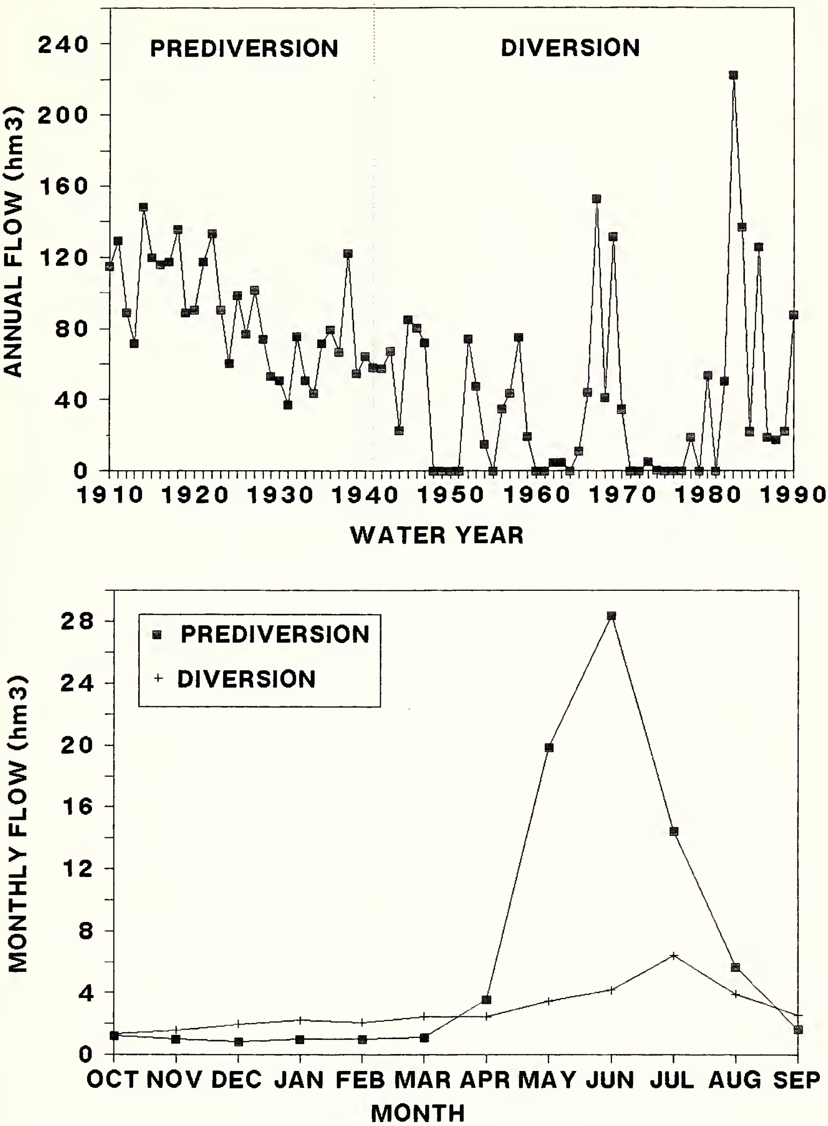

Fig. 3. Annual and monthly flow volume at Rush Creek (2180 m) during prediversion and diversion (post-1941) periods.

reach. Student's t-tests were used to compare values between live and dead trees, and between live trees on Bishop and Pine creeks.

Results

Flow patterns. The diverted reaches of Bishop Creek have had extended periods of low flow punctuated by flood years (Fig. 2).

TABLE 1. STAND CANOPY FOLIAGE DENSITY, MORTALITY, DENSITY, AND ANNUAL VARIATION IN GROWTH RATE FOR *POPULUS TRICHOCARPA* AT DIVERTED BISHOP CREEK AND FREE-FLOWING PINE CREEK REACHES. Values are means ± standard deviations.

Reach	Elev. (m)	Canopy foliage density[1]	Tree mortality[2] (%)	Tree density (no. 0.1 ha^{-1})	Juvenile density[3] (no. 0.1 ha^{-1})	Annual growth variation[4]
Bishop 2	2020	1.73 ± 0.16	27	28	98	35 ± 13
Bishop 3	1800	0.51 ± 0.12	14	33	93	39 ± 14
Bishop 4	1470	0.35 ± 0.12	33	6	42	49 ± 29
Pine 2	2100	2.52 ± 0.25	9	41	199	30 ± 11
Pine 3	1850	2.14 ± 0.19	0	45	170	24 ± 09
Pine 4	1580	3.13 ± 0.37	11	38	125	22 ± 05

[1] Leaf area index (m^2 m^{-2}).
[2] Dead trees as a percent of the total.
[3] Juveniles are plants <10-cm stem diameter.
[4] Mean sensitivity of the ring chronologies.

Flow volume ranged annually from <1 to >50 hm^3 (in 1983), with an annual coefficient of variation of 116% to 139% among reaches. Instantaneous flows were very high in 1982 (>40 m^3 s^{-1}), exceeding the 100-year flood rate. Average annual flow volume in the diverted reaches ranged from 9 hm^3 at 2020 m to 16 hm^3 at 1390 m, and was considerably lower than in the return flow reach (76 hm^3 at 1380 m). Average annual flow volume in Pine Creek (50 hm^3 at 1580 m) was intermediate between that in the diverted and return flow reaches of Bishop Creek. Pine Creek flows ranged annually from 24 to 83 hm^3, but on average were more constant than at Bishop Creek (coefficient of variation in annual flow volume of 41%). Seasonal flow patterns in Pine Creek and the diverted Bishop Creek reaches showed the spring (June) peak characteristic of snowmelt fed eastern Sierra Nevada streams.

Annual flows in Rush Creek were considerably more erratic during the diversion period than the prediversion period (Fig. 3). Flows during the diversion period were characterized by extended periods of low or no flow during drought years to >221 hm^3 (180,000 acre-feet) per year. Flows in recent years have been relatively high as a result of court orders requiring sufficient flows to maintain the stream's fisheries. Seasonal flow peaks at Rush Creek shifted from June (prediversion) to July (diversion period).

Vegetation structure. Canopy foliage density differed significantly between all three elevationally matched reaches of Bishop and Pine creeks ($P < 0.01$) (Table 1). The difference was most pronounced at low elevation reach 4, where values were 0.35 ± 0.12 for Bishop Creek and 3.13 ± 0.37 for Pine Creek. Black cottonwood density also was lower at Bishop Creek reaches, particularly at reach 4. Reach 4 at Pine Creek was dominated by black cottonwood, water birch, and mountain rose. Reach 4 at Bishop Creek was dominated by these same species as well as by several upland species: *Purshia tridentata, Artemisia tridentata,* and *Chrysothamnus nauseosus.* Mid and upper reaches Bishop and Pine creeks supported similar species: black cottonwood, water birch, mountain rose, *Shepherdia argentea,* and various willow species (e.g., *Salix lasiolepis* and *Salix lasiandra*). Jeffrey pine was present within all Bishop Creek reaches.

Size and age structure. Age of black cottonwood could be predicted from stem diameter with only a moderate degree of confidence (Figs. 4, 5). Most regression equations relating tree age to stem diameter had relatively high scatter (e.g., Pine reach 3, $R^2 = 0.12$), while others had lower scatter (e.g., Pine reach 2, $R^2 = 0.67$). All regressions were significant at $P < 0.05$.

Age and size structure data showed the same trends. On both streams, maximum stem diameter, maximum tree age, and number of age classes increased with elevation (Figs. 6, 7). However, maximum age and size at Bishop Creek was lower at all elevations, particularly for the lowest elevation reach. The maximum age of black cottonwood trees at the high, mid and low elevation reaches at Pine Creek was 129, 113, and 98 years, respectively, compared to 103, 74, and 39 for elevationally matched reaches of Bishop Creek. In all reaches of both streams black cottonwoods were most abundant in the smallest size class (<10-cm dbh; data not shown) and youngest age class (<20 years of age) (Fig. 7).

Mortality. The percentage of standing dead cottonwood trees differed substantially between elevationally matched reaches of Pine and Bishop creeks (Table 1). At Pine Creek, <11% of the mature trees were dead, and most of these had died as a result of beaver (*Castor canadensis*) activity. Within Bishop Creek, the percentage of dead trees within the mature population ranged from 14 to 33% between reaches. Return visits in 1991 revealed additional mortality within some Bishop Creek reaches but not within Pine Creek. Highest mortality was within Bishop Creek reach 4, where 60% of the marked black cottonwood trees had died. Seven percent of the marked trees in Bishop reach 2 had died.

Of the cored dead trees in Bishop Creek reach 2, three were determined to have died during drought periods (1972–1973 and 1976–1977 (Fig. 8) and one during a high-flow year (1982); one tree could not be assigned a year of death. Annual flow volumes during the drought periods ranged from <1 hm^3 to <7 hm^3. The dead trees grew more slowly in the years prior to death than they did over their lifetime, and on average grew slower than living trees of similar age (Table 2). The dead trees did not have significantly higher annual growth fluctuation than live trees, although the Bishop Creek trees as a group had greater annual growth fluctuation than did Pine Creek

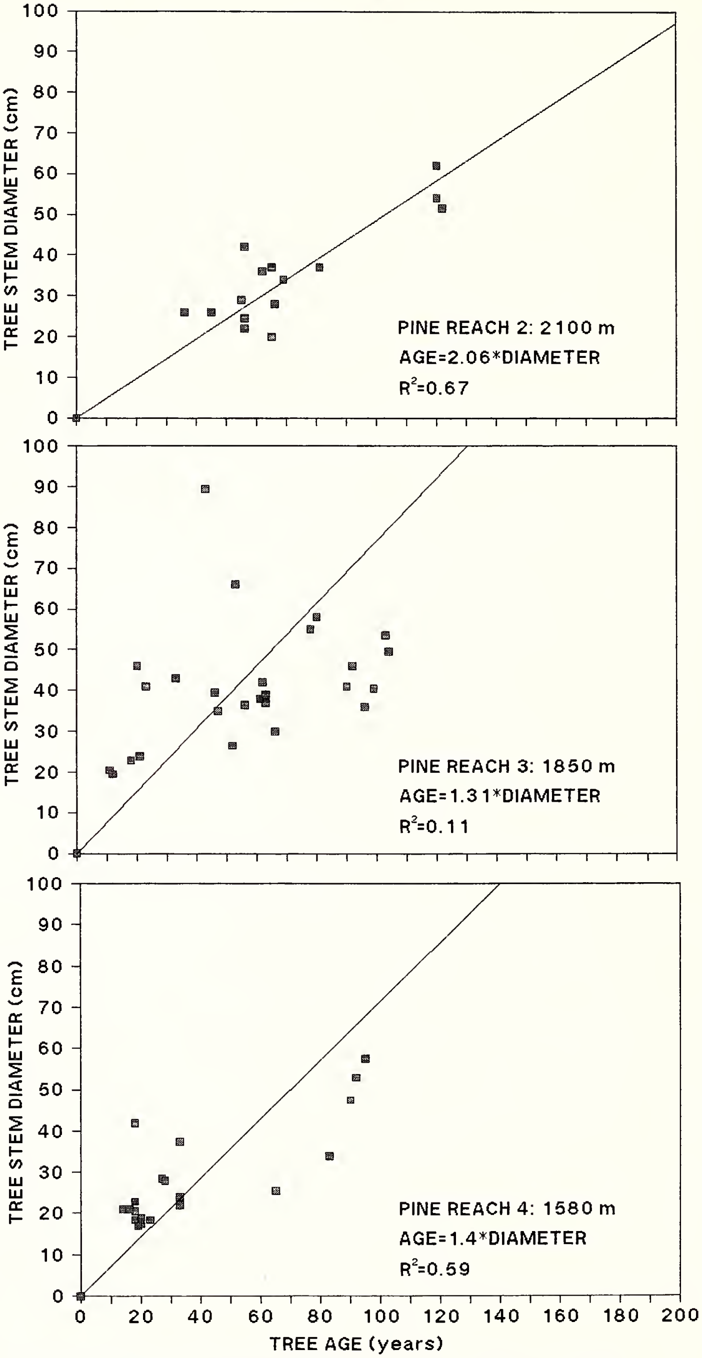

FIG. 4. Size-age plots for *Populus trichocarpa* at Pine Creek, by reach.

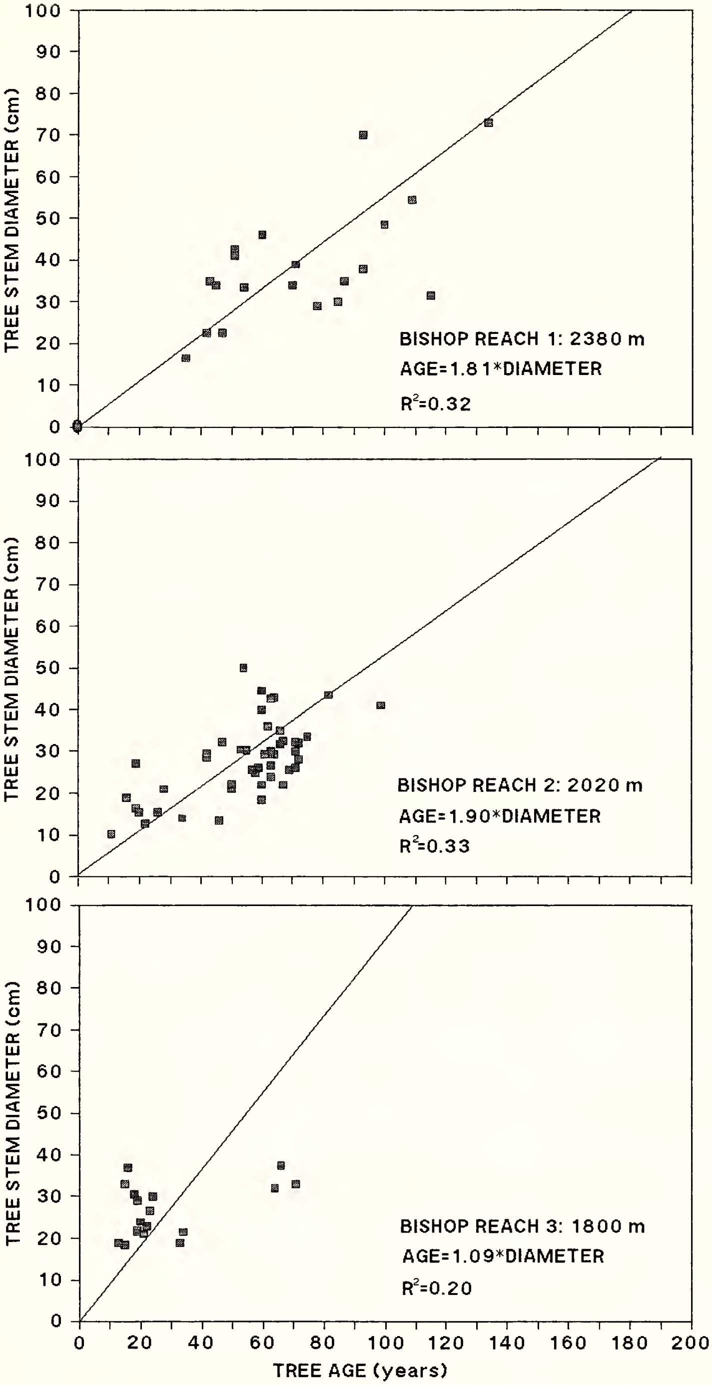

FIG. 5. Size-age plots for *Populus trichocarpa* at Bishop Creek, by reach.

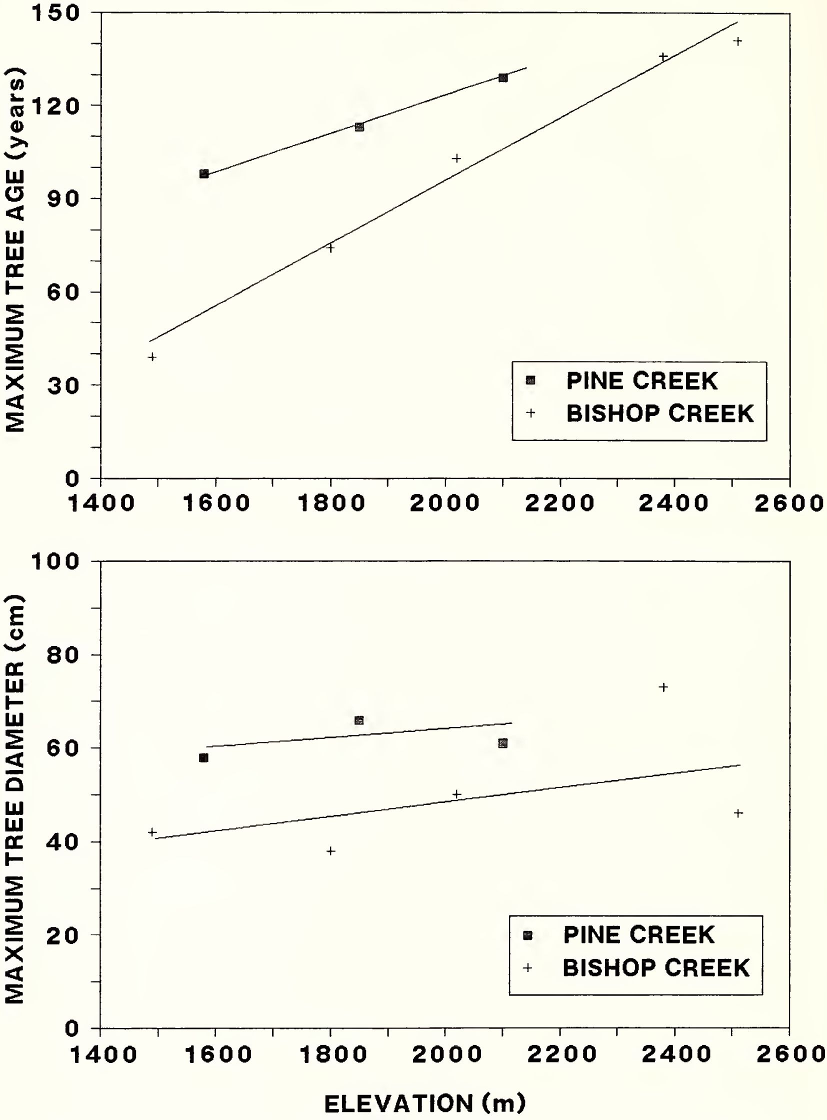

FIG. 6. Maximum size and age of *Populus trichocarpa* at Pine and Bishop creeks, as a function of elevation.

trees ($P < 0.05$; Table 1). The average age of the dead trees (57 ± 11) was somewhat younger than the present age of most of the older cohorts in the reach (60 to 80 years). At the time of their deaths 8 to 17 years ago, the dead trees were among the oldest in the reach. Spatially, the dead black cottonwoods were found near the stream

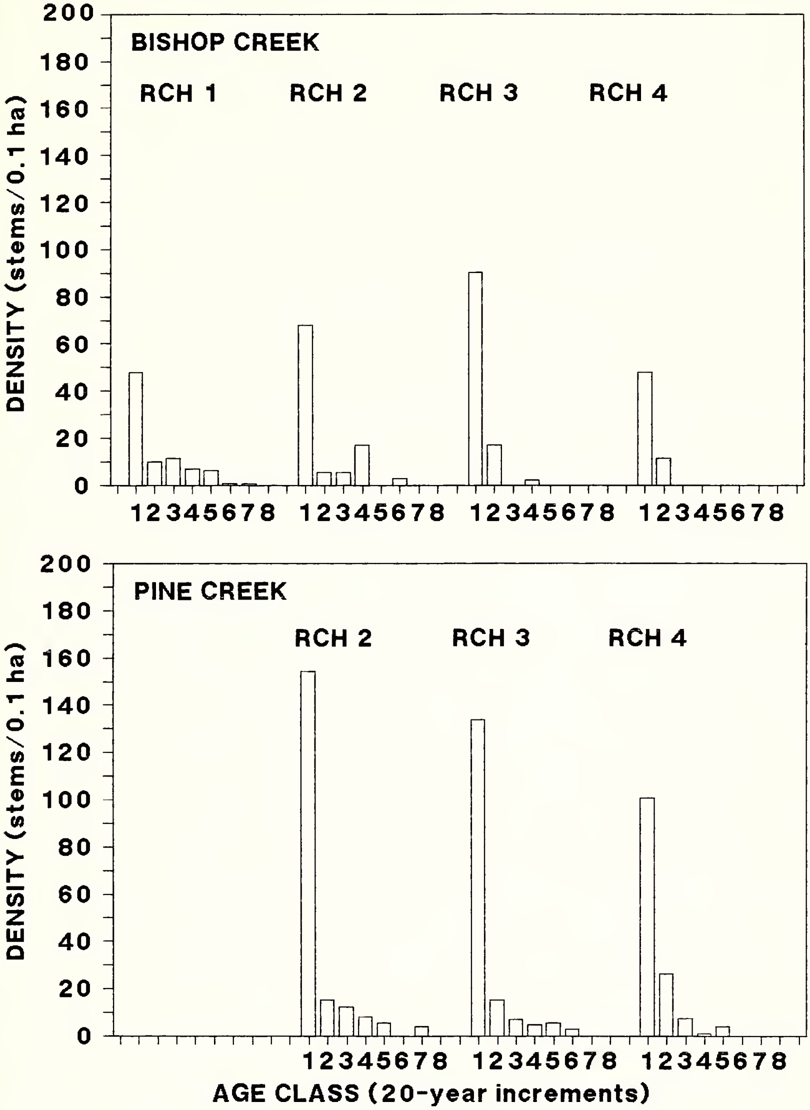

FIG. 7. Age structure of *Populus trichocarpa* at Pine and Bishop creeks, by reach.

edge to the perimeter of the floodplain (up to 20 m from the stream edge).

At Rush Creek, year of death was determined for 9 of 11 dead black cottonwood trees. Of these, 7 died during drought periods (1972–1973 and 1976–1977) (Fig. 8) and 2 died during or immediately after high flow years (1967, 1983). Average age of the dead

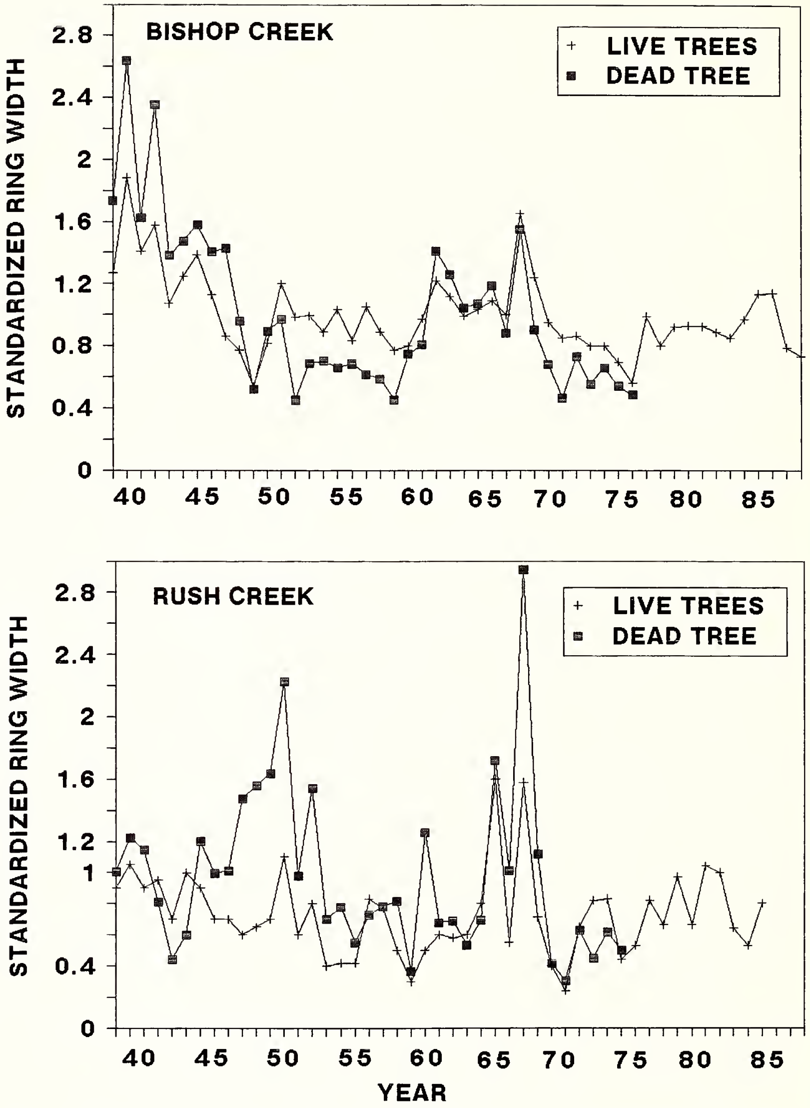

FIG. 8. Ring width chronologies of representative dead *Populus trichocarpa* at Bishop and Rush creeks, overlain on the chronologies of live trees.

trees was 47 ± 9 years. Spatially, the dead trees were present throughout the floodplain, from the streamedge to the floodplain perimeter. Similar to the Bishop Creek trees, recent and lifetime growth rates were lower for dead trees than live trees. Annual growth fluctuation (i.e., mean sensitivity of the tree-ring chronologies) did not differ between dead and live trees at Rush Creek (Table 2).

TABLE 2. RADIAL GROWTH RATE (ANNUAL RING WIDTH) AND EXTENT OF ANNUAL GROWTH VARIATION FOR LIVE AND DEAD *POPULUS TRICHOCARPA* AT BISHOP AND RUSH CREEKS. Growth during the five years prior to tree death is also indicated.

Stream	Status	Sample size	Lifetime growth (mm yr^{-1})	Pre-death growth (mm yr^{-1})	Annual growth variation[1]
Bishop Creek	Live	20	1.88 ± 0.47	–	35 ± 13
	Dead	5	1.32 ± 0.32	0.46 ± 0.44	39 ± 03
Rush Creek	Live	18	1.85 ± 0.77	–	43 ± 11
	Dead	10	1.65 ± 0.74	1.08 ± 0.81	43 ± 09

[1] Mean sensitivity of the ring chronologies.

DISCUSSION

The data in this study indicate that changes in natural flow regimes have reduced the biological integrity of riparian cottonwood stands along Bishop Creek. Riparian stands differed in dominant species composition between low elevations of Bishop Creek and free-flowing Pine Creek, indicating that extreme stress had resulted in ecosystem-level changes (Taub 1987). Population-level changes indicative of moderate stress were apparent in all stream reaches, including higher elevations were diversion effects were less visually apparent. In comparison to black cottonwood stands along Pine Creek, those along Bishop Creek were younger, had lower tree density, higher tree mortality, and lower canopy foliage density. Tree ring analysis at Bishop Creek and another diverted stream, Rush Creek, suggested that episodic floods and chronic droughts have been at least partly responsible for these biotic changes, by increasing the incidence of cottonwood mortality and preventing trees from living out their natural lifespans.

Floods and droughts are natural phenomena in aridland riparian systems. Floods often are a driving variable in riparian ecosystems, and although they can trigger recruitment events they also can cause tree death by physiologically stressing the trees or physically removing them (Stromberg et al. 1991). Sustained low flows during prolonged natural droughts also cause death of aridland riparian trees (Albertson and Weaver 1945). At Bishop and Rush Creeks, low flow periods have become lower in flow magnitude and longer in duration, because flows are completely diverted from the stream in normal and below normal water years. Extreme events, however, have been little altered. As a result, mortality incidence is high for cottonwoods along the diverted streams, particularly at low elevations. Flood magnitude is known to increase with elevation (Leopold 1964), while drought effects can be increased at low elevations because of high temperature and evaporative demand.

The data in this study specifically implicate the 1982–1983 flood years as mortality years for Bishop Creek cottonwoods. We speculate that the damaging effects of large floods are high at Bishop Creek and other diverted streams because: (1) reduced base flows have allowed cottonwood establishment in flood-prone near-stream sites; and (2) reductions in vegetative cover arising from flow diversion have decreased the extent of vegetation-related attenuation of flood flows. At Bishop Creek, the restriction of many cottonwoods to a narrow strip (<5 m) along the streamedge may be a result of diverted streamflow, predisposing the trees to greater impact from flood flows. Although dams and diversions may reduce the frequency of low magnitude flood flows and allow encroachment of trees into the channel (Harris et al. 1987), they do not necessarily eliminate the infrequent large-magnitude flood flows. This may ultimately increase the damage to riparian trees.

Flood-related mortality may be compounded by chronic drought stress, which weakens the resistance of the trees. Drought, however, also independently contributed to cottonwood death at Rush Creek and Bishop Creek. Mortality periods corresponded to drought periods (e.g., early and mid 1970's), which were periods of very low flow release. The present drought period (1987–1991) also correlates with a period of mortality at Bishop Creek. Similar drought-related mortality was not observed at Pine Creek. The trees that died from drought at Bishop and Rush creeks had very low radial growth rates in the years prior to death. Both of these streams have been shown to be "sensitive" rather than "complacent" sites in the sense that growth of cottonwood trees fluctuates with annual flow volume (Stromberg and Patten 1990, 1991). Thus it is not surprising that very low flows reduced growth rates to lethal levels. Besides having low radial growth in the years prior to death, the dead trees also grew more slowly than the population as a whole. We did not attempt to determine whether lower growth rates were a result of genetic factors or environmental factors (e.g., the dead trees may have been growing on drier microsites within the riparian zone). Whatever the cause, lower growth may have rendered the trees more susceptible to extreme hydrological events (e.g., droughts and floods). Greater annual growth fluctuation of the Bishop Creek trees (a result of higher flow fluctuation) also may have increased their susceptibility.

The contributions of juvenile mortality or reduced recruitment to the low canopy foliage density at Bishop Creek were not directly addressed in this study. Other studies have indicated that young cottonwoods are more sensitive to diversion than are mature trees (Smith et al. 1991). The size structure data collected in our study, however, revealed a high relative abundance of saplings. Cottonwood establishment may be facilitated at Bishop Creek by the openness of the canopy (a factor that may stimulate root sprouting), combined with seasonal flow peaks that still follow natural patterns (a factor that would favor seedling recruitment). This contrasts with the situation at streams such as Rush Creek, where altered seasonal flow peaks (July vs. June) may be preventing sexual seedling recruitment by desynchronizing the periods of flow peaks and seed germination (Fenner et al. 1985; Stromberg and Patten 1989).

MANAGEMENT IMPLICATIONS

Prior studies have indicated that release of a certain average volume of seasonal or annual flow is necessary for maintaining riparian cottonwoods (Stromberg and Patten 1989, 1990). This present study suggests that flow minima and maxima also need to be managed at diverted or regulated streams. Adherence to specific minima and maxima would help to reduce drought-related mortality and to encourage establishment in areas less susceptible to flood damage, and would thus help to restore the biological integrity of the riparian trees.

The following techniques could be used to establish minimum flows. First, the relative difference between mean (or median) flows and minimum annual flows in free-flowing streams in the region could be used as an index. At Pine Creek, for example, the lowest annual flow during the last 20 years was about 2.5 times lower than the mean. By extrapolation, this would mean that low flows should not be less than 5 $hm^3\ yr^{-1}$ in the diverted Bishop Creek reaches. This approach is validated by another approach, that being the use of flows during lethal drought periods as an index of insufficient flows. Data in this study suggest that flows $<5\ hm^3\ yr^{-1}$ have been lethal to mature cottonwoods at Bishop Creek. Thus, 5 hm^3 is perhaps a good first approximation of non-lethal flows for this stream. Whatever values are selected, subsequent monitoring of vegetation response should be an integral component of riparian management.

With respect to maximum flows, a prudent approach would be to allow floods to occur with a magnitude, timing, and frequency characteristic of natural flow regimes (Stromberg et al. 1991). At Bishop Creek, for example, the frequency of small floods should be increased while at the same time there should be a decrease in the range between the mean annual flow and the maximum annual flow, as well as between the mean and maximum instantaneous flow. Assuming that maximum flows can not be reduced (due to reservoir constraints), then mean annual flows must be increased. This should reduce flood damage by reducing tree establishment in flood prone sites and increasing vegetative cover that moderates downstream flood effects.

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RESPONSE OF *SALIX LASIOLEPIS* TO AUGMENTED STREAM FLOWS IN THE UPPER OWENS RIVER

JULIET C. STROMBERG and DUNCAN T. PATTEN
Center for Environmental Studies,
Arizona State University,
Tempe, AZ 85287-3211

ABSTRACT

The upper Owens River channel has been used for decades as an aqueduct to deliver flows from the Mono Basin to the Los Angeles Aqueduct. This out-of-basin diversion has tripled the volume of flow in the upper Owens River and altered channel and floodplain morphology (e.g., channels have become wider, deeper, and straighter). These changes have influenced density, distribution and growth response of the dominant riparian tree, *Salix lasiolepis* (white willow). Compared to an upstream control reach, juvenile *S. lasiolepis* had significantly lower density in the reach receiving the additional flows. Mature *S. lasiolepis* trees in the augmented-flow reach had significantly lower areal cover and had high relative abundance of dead trees. The trees tended to be located farther from the stream and to be more abundant on floodplains higher above the stream water level. These patterns may result from physiological intolerance of wetter soils, and from avulsive channel straightening and physical removal of seedlings and trees from near-stream recruitment areas during high flood flows.

Radial growth rates of mature *S. lasiolepis* did not differ between reaches, but annual growth patterns did differ. Growth of the willow in the control reach increased significantly with annual flow volume and was frequently limited by low flows. Growth of willow in the augmented reach decreased with annual flow volume and was limited by very high flows. Flows that produced greatest growth were at the high range of the natural flows and low range of the augmented flows. Very high flows may produce saturated conditions that are not conducive to growth or survival. If flows were restored to natural levels, we speculate that *S. lasiolepis* would ultimately increase in density. Density would remain low, however, until the river-floodplain system reequilibrated and until other factors that limit willow abundance (i.e., cattle browsing) were minimized.

Stream flow diversion has contributed to regional decline of riparian vegetation in the western United States. Within California, for example, most riparian vegetation along the Owens River (the main drainage of the eastern Sierra Nevada) had been lost because of flow diversion into the Los Angeles Aqueduct (Brothers 1984). This regional loss has stimulated study on the effects of flow diversion and on instream flow needs of riparian vegetation (Risser and Harris 1989; Stromberg and Patten 1990). However, far less is known about the effects of flow augmentation, a less common form of flow manipulation. The upper Owens River provides an example of this type of flow manipulation. A 17 km segment of the upper Owens River has been used for the last 50 years as an aqueduct that receives

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and delivers flows from nearby Mono Basin to downstream Crowley Lake and ultimately to the Los Angeles Aqueduct. Ongoing adjudication has called for examination of the impacts of this out-of-basin transfer on the diverted Mono Basin rivers as well as on the flow-augmented upper Owens River. This study had two objectives: (1) to document effects of flow augmentation on the dominant riparian tree (*Salix lasiolepis*) along the upper Owens River; and (2) to identify factors other than flow volume that are related to willow abundance within the study area.

STUDY AREA

The upper Owens River arises in the eastern Sierra Nevada foothills (Mono Co., California) and meanders through a broad valley along a shallow gradient for much of its length. The wide floodplains are vegetated mainly by hydrophilic herbaceous species, tree willows (primarily *Salix lasiolepis,* white willow), and shrub willows (primarily *S. exigua,* coyote willow), with incursions of Great Basin shrubs (*Artemisia* spp., *Chrysothamnus* spp.; nomenclature according to Munz and Keck [1973]). A few kilometers after it emerges from the foothills, the river is augmented by flows diverted from the Mono Basin (Rush, Lee Vining, Parker, and Walker creeks) through Mono Craters Tunnel (Fig. 1). Flow augmentation began in 1940 and increased in volume in the early 1970's. Below the augmentation point, the river continues to flow through broad valleys for about 17 km before being impounded in Crowley Lake and diverted into the Los Angeles Aqueduct.

The study was divided into two reaches with similar valley morphology (Fig. 1). The control reach extends for ca. 2 km upstream from Mono Craters Tunnel, and the augmented-flow reach extends for about 2 km downstream from the tunnel. The area in the first few hundred meters below the tunnel was excluded from study, because local springs and beaver ponds have produced vegetation that is not representative of the general area. Reaches farther upstream and downstream were also excluded because their floodplain morphology differed from that within the study area (e.g., floodplains were wider in downstream reaches, while stream gradient was steeper in upstream reaches).

METHODS

Response of the willow species to flow augmentation was documented by comparing the following parameters between *S. lasiolepis* stands in the control reach and augmented-flow reach: (1) abundance and distribution of juvenile and mature willows; (2) annual radial growth rates of mature willows; and (3) relationships between stream

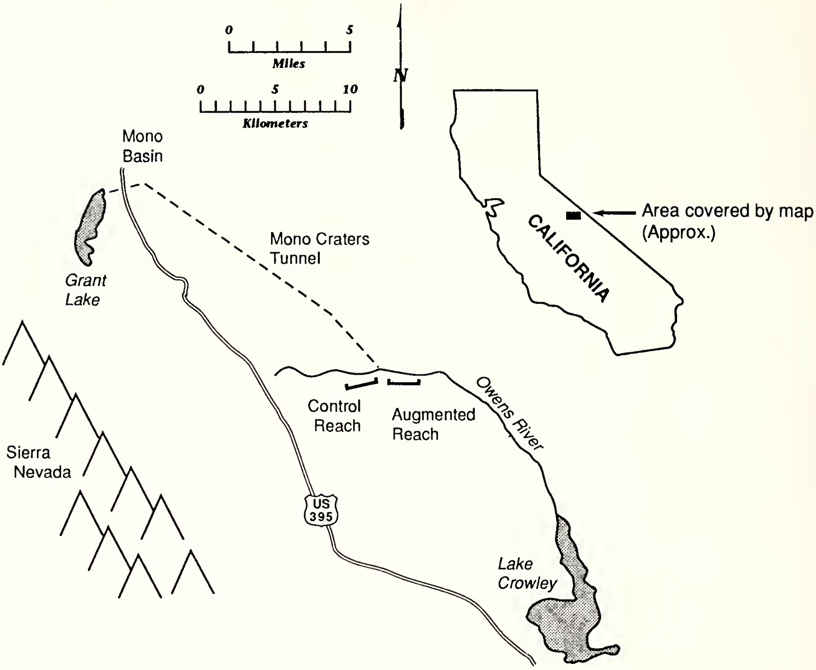

FIG. 1. Location of study reaches along the upper Owens River, Mono County, California.

flow volume and radial growth rates of mature willows. Data were also analyzed to determine to what extent factors other than flow augmentation were related to willow abundance. These factors included grazing intensity and factors potentially varying along a downstream distance gradient.

Density and distribution. Nine transects per reach were randomly selected and sampled in fall 1990 for density of willows. The transects spanned the width of the riparian floodplain and varied in width from 25 to 180 m. Willows were divided into two classes: juvenile plants (<1 m tall) and mature plants (>1 m tall). Density of the juveniles was sampled within 1-m wide belt transects (divided into 1 × 5 m plots) that spanned the width of the riparian zone. Plot number thus varied from 5 to 36, depending on floodplain width. Density of the juveniles also was sampled in an additional 50 streamside plots (1 × 2 m) randomly selected per transect, to obtain density values within main recruitment zones. Density and areal cover of live and dead mature willows were sampled in one large plot per transect that spanned the width of the floodplain and extended for 100 m in length. This unusually large plot size was chosen because of the low abundance of mature willows. Areal cover was calculated based on two canopy diameter measurements per tree. For the density calculations, multiple-stemmed "plants" were considered as one individual.

Juvenile and mature willow abundances were compared between reaches and transects with analysis of variance to test the null hypotheses that abundances did not differ significantly between reaches. Within-reach relationships between juvenile and mature willow densities and five environmental variables (floodplain width, elevation of the near-stream floodplain relative to the stream, distance downstream within the reach, cow dung density) were determined with Pearson correlation analysis, using average values per transect ($n = 9$). Floodplain elevation was measured at five random locations per transect during a period of natural (i.e., unaugmented) flows (fall 1990). Density of cow dung "units," an index of recent grazing intensity, was sampled within the same floodplain plots sampled for juvenile willow density.

Radial growth. Increment cores were collected from ten mature *S. lasiolepis* trees per reach. The cored trees were randomly selected and had average canopy diameters of 7.1 ± 1.4 m (control group) and 7.2 ± 0.8 m (augmented-flow group). The cored trees had multiple stems, a common growth form for *S. lasiolepis.* Five cores were collected per tree, from large stems and from the main stem, if discernable. In the laboratory, the cores were mounted and sanded with a graded series of sandpaper (from 60 to 12 micrometers). The cores were cross-dated and measured for annual ring width with a Bannister-type incremental measuring machine. Many of the cored trees had "heart-rot" and only one of the chronologies pre-dated the onset of flow augmentation (1940). Fourteen of the 20 trees had chronology rings that extended through 1955, and these were used for subsequent analysis.

Average annual radial growth rate (over the period 1955–1989) was compared between reaches using analysis of variance to test the null hypothesis that growth rate did not differ significantly between reaches. Relationships between radial growth rate and stream flow (seasonal and annual flows) were analyzed by reach with univariate linear regression analysis. Streamflow data were obtained from Los Angeles Department of Water and Power. Flow data in the augmented-flow reach were for a gauge located immediately downstream from Mono Craters Tunnel. Data for the control reach were obtained by subtracting tunnel flows from augmented-reach flows.

RESULTS

Flow regimes. Natural flows in the upper Owens River averaged 52 hm^3/yr (42,200 acre-feet/yr) and ranged from ca. 37 to 90 hm^3/yr over the period 1941 to 1989 (Table 1, Fig. 2). During this period,

TABLE 1. COMPARISON OF FIVE ENVIRONMENTAL VARIABLES BETWEEN THE CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Control reach $\bar{x} \pm$ SD	Augmented-flow reach $\bar{x} \pm$ SD
Annual flow in water year (hm^3)	52 ± 12	150 ± 43**
Coefficient of variation in annual flow	24%	30%
Floodplain width (m)	101 ± 38	103 ± 54
Floodplain elevation above stream (cm)	34 ± 03	41 ± 8*
Cow dung density (no. m^{-2})	0.43 ± 0.15	0.36 ± 0.16

** $P < 0.01$.
* $P < 0.05$.

an average of 98 hm^3/yr (range from ca. 17 to 180) were diverted from the Mono Basin through the Mono Tunnel. This tripled the flow volume in the augmented-flow reach, bringing the annual average to 150 hm^3/yr (range from ca. 65 to 240). Annual fluctuation in flow has been higher in the augmented-flow reach, as indicated by coefficients of variation in annual flow: 30% for augmented-flow reach, 24% for control reach. Flow-augmentation has not altered seasonal flow patterns. In both reaches, more than half of the annual flow occurred during the May–October growing season (55% for control, 59% for augmented-flow reach), with peak flows in June.

Density and distribution of mature trees. Areal cover and density of mature *S. lasiolepis* were low in both the control and augmented-

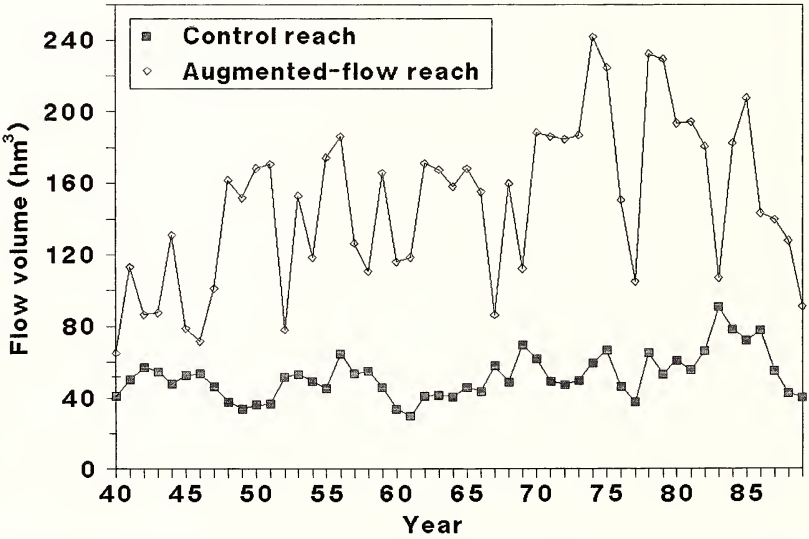

FIG. 2. Annual flow volume for the control and augmented-flow reaches of the upper Owens River.

TABLE 2. COMPARISON OF WILLOW VARIABLES BETWEEN CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Control reach $\bar{x} \pm$ SD	Augmented reach $\bar{x} \pm$ SD
	Mature *Salix lasiolepis*	
Areal cover (m^2 ha^{-1})	750 ± 798	210 ± 197*
Density (no. ha^{-1})	14 ± 15	8 ± 10
Live/dead density ratio	5.6 ± 5.6	2.3 ± 2.6
Distance to water's edge (m)	8.7 ± 6.1	10.2 ± 8.5
Radial growth rate (mm yr^{-1})	2.43 ± 0.75	2.82 ± 0.63
	Juvenile *Salix lasiolepis*	
Floodplain density (no. ha^{-1})	158 ± 301	36 ± 73
Streamedge density (no. ha^{-1})	2089 ± 1789	233 ± 283**
Juvenile/mature density ratio	209 ± 221	67 ± 128

** $P < 0.05$.
* $P < 0.08$.

flow reach. Cover values were significantly lower in the augmented-flow reach at $P < 0.08$, but densities of live trees did not differ significantly (Table 2). There were 2.3 live willows per dead willow in the augmented-flow reach compared to 5.6:1 for the control reach, but these values did not differ significantly. Willow trees on average occurred about 2m farther from the streamedge within the augmented-flow reach than in the control reach.

Density of mature *S. lasiolepis* decreased significantly with distance downstream within each reach (Table 3). These correlations were not significant, however, when the data were analyzed without three outliers with high willow density (Fig. 3). Density of the willow decreased with floodplain width within both reaches ($r = -0.75$ and -0.54). Within the augmented-flow reach, *S. lasiolepis* density was significantly correlated with floodplain height. Both reaches were heavily grazed (based on abundance of cow dung), and willow density

TABLE 3. CORRELATION COEFFICIENTS FOR *SALIX LASIOLEPIS* DENSITY AND FOUR ENVIRONMENTAL VARIABLES, FOR CONTROL AND AUGMENTED-FLOW REACHES OF THE UPPER OWENS RIVER.

	Distance downstream	Floodplain width	Floodplain elev.	Cow dung density
		Control reach		
Mature density	−0.71*	−0.75*	0.18	−0.48
Juvenile density	−0.11	−0.33	0.06	−0.36
		Augmented-flow reach		
Mature density	−0.63*	−0.54	0.63*	−0.19
Juvenile density	−0.01	0.18	−0.34	−0.23

* = $P < 0.05$.

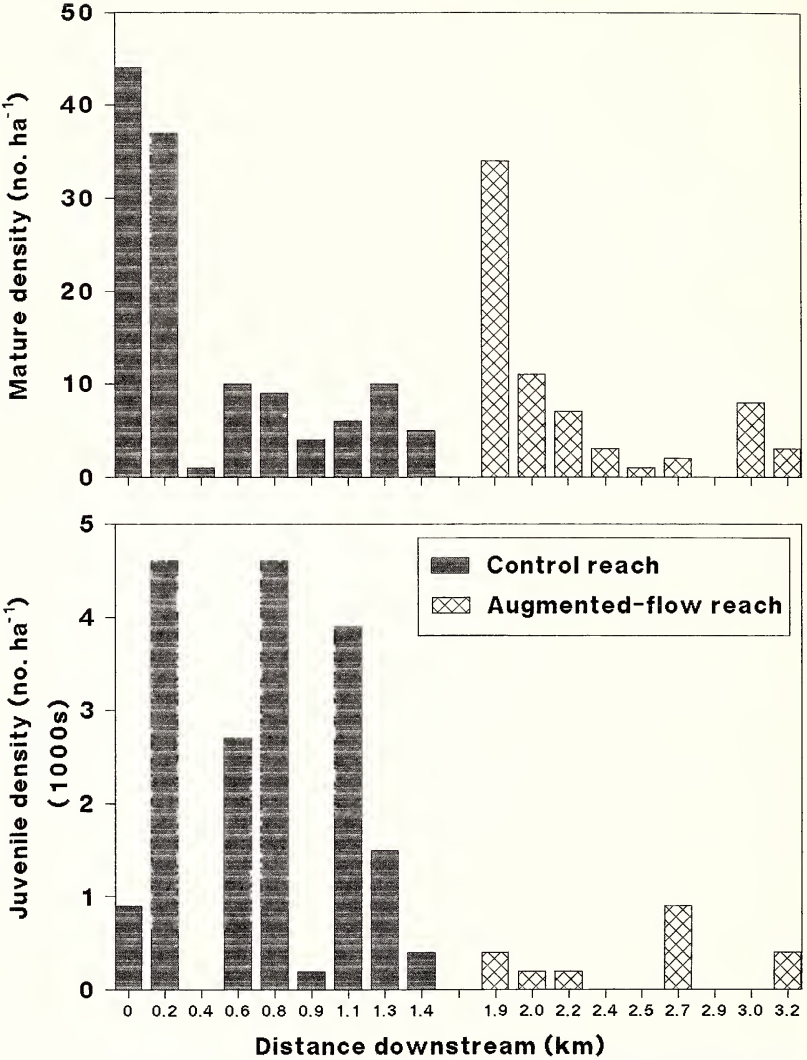

FIG. 3. Density of mature and juvenile *Salix lasiolepis* in relation to distance downstream from the upper end of the study area, for control and augmented-flow reaches of the upper Owens River.

tended to decrease with increasing density of cow dung in both reaches.

Density and distribution of juveniles. Densities of juvenile *S. lasiolepis* in both reaches were 10-fold higher along streamedges than in the floodplain as a whole (Table 2). Densities within this streamside recruitment zone were significantly lower in the augmented-

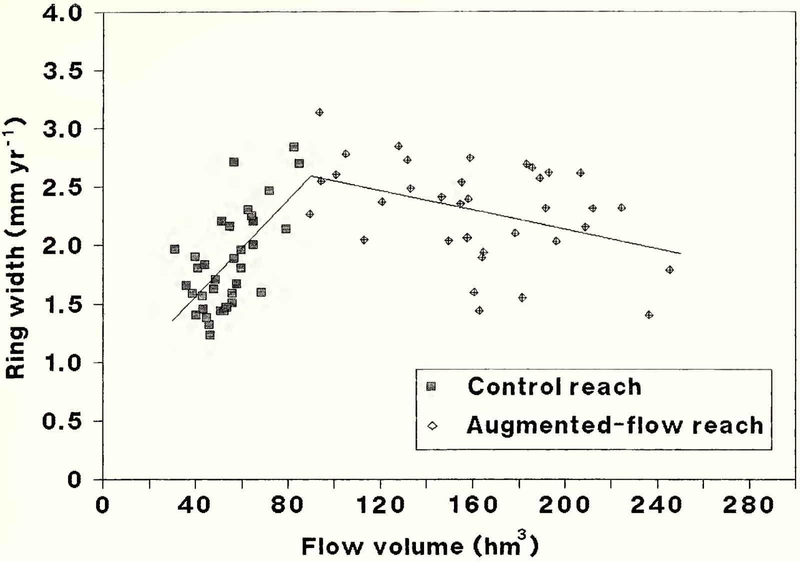

FIG. 4. Annual radial growth rate of *Salix lasiolepis* in relation to annual volume of flow in the water year (October–September), for control and augmented-flow reaches of the upper Owens River. Regression equations are: $y = 1.33 \pm 0.021x$, $r^2 = 0.49$, df = 34, $P < 0.01$ (control reach); $y = 3.48 - 0.004x$, $r^2 = 0.11$, df = 34, $P < 0.06$ (augmented-flow reach).

flow reach than in the control reach. The ratio of juvenile to mature individuals was >3-fold higher in the augmented-flow reach than in the control reach.

Observation indicated that most juvenile willows were browsed in both reaches. Many had relatively large diameter stems for their height, suggestive of repeated browsing. Juvenile willow density tended to decrease as cow dung density increased in both reaches, but correlations were not statistically significant (Table 3). Juvenile willows also tended to increase in density as floodplain height decreased within the augmented-flow reach, but again relationships were not significant. Density of juvenile willows did not vary with distance downstream in either reach (Fig. 3, Table 3).

Radial growth. Radial growth of *S. lasiolepis* in both reaches varied significantly as a function of stream flow volume, although in different fashion (Fig. 4). Growth rate of the willows in the control reach, where flow volumes were comparatively low, increased significantly with volume of flow during the October–September water year ($r^2 = 0.49$, $P < 0.01$, df = 34) and during the April–September growing season ($r^2 = 0.30$, $P < 0.01$, df = 34). In contrast, growth rate of trees in the augmented-flow reach declined as flow increased to high volumes, although relationships were less significant than in the control reach ($r^2 = 0.11$, $P < 0.06$, for water year; $r^2 = 0.09$, $P < 0.08$, for April–September flow). Trees in both reaches had highest growth rates at "overlapping" flow volumes, i.e., those at the high range of the natural flows and low range of the augmented flows. Average annual radial growth rates did not statistically differ between reaches (Table 2).

DISCUSSION

Salix lasiolepis stands in the augmented-flow reach of the upper Owens River differed in several ways from that in the control reach. Juvenile willows had significantly lower densities in the augmented-flow reach. Mature trees had lower cover and tended to be present in lower proportion relative to dead trees. The trees in the augmented-flow reach had greatest abundance on floodplains highest above the stream water level, and grew somewhat farther from the stream than trees in the control reach. Growth of trees in the control reach increased with flow volume, and was often limited by low flows. The reverse was true for trees in the augmented-flow reach. Trees in both reaches attained highest growth rates at similar flow ranges (ca. 60–120 hm^3/yr).

Many of these differences in willow density and distribution may be attributable to flow augmentation. However, other factors also must be considered. Cattle effects, for example, complicate assessment of flow augmentation effects. Evidence in this study (i.e., the trend for negative correlations between cow dung and willow abundance) suggests that cattle grazing, browsing, and trampling has prevented willows in both reaches from attaining maximum potential densities. If true, this may have "dampened" changes wrought by altered flow regimes. Additionally, although the data is inconclusive, the possible trend for declining willow tree density with distance downstream raises the possibility that abiotic conditions are not uniform throughout the study area. For example, subtle changes in stream gradient or soil chemistry, or availability of suitable habitat for seedling establishment, may contribute to differences in willow trees within and between reaches. Thus, the weak trend for lower abundance of mature willows in the augmented-flow reach may not strictly be attributed to the altered flow regime. However, the low ratio of live to dead willow trees in the augmented-flow reach suggests that flow augmentation has played some role in increasing willow mortality. Mortality may have resulted from adverse physiological effects of excessive water or from physical removal of streamside trees in areas where flood flows have caused bank slumping and erosion. This latter phenomenon, combined with avulsive channel straightening, also may explain why trees were somewhat farther from the stream edge in the augmented-flow reach.

Juvenile willows, in contrast to mature willows, were significantly less abundant in the augmented-flow reach and did not decrease in abundance with downstream distance within reaches. Furthermore, the ratio of juvenile to mature willows was several-fold more abundant in the control reach than in the augmented-flow reach. These data implicate flow augmentation as a primary factor that has reduced the abundance of juvenile *S. lasiolepis* below Mono Craters Tunnel. There are several possible mechanisms for this reduction. First, channel meanders have straightened and streambanks have undergone erosion and mass wasting (i.e., "slumping") as the river has adjusted to the new flow volume. This has physically removed sites where seedlings have established. Additionally, the high degree of flow fluctuation within the augmented reach may have increased seedling mortality rates (Strahan 1987). Another explanation may relate to availability of seedling habitat. Sand and gravel "point" bars are typical recruitment areas for *Salix* spp. (McBride and Strahan 1984), as was observed to be the case in this study (subjective observation). Such areas were not abundant in the augmented-flow reach, which has become an erosive rather than depositional environment, and which is characterized by steep banks, incised channels, and low rates of channel meandering.

Altered flow volumes are undoubtedly the primary cause for between-reach differences in annual radial growth patterns. Within the control reach, growth rate increased as flows increased, and flows never attained growth-suppressing levels. Such positive relations between flow volume and tree growth rate indicate that water availability can be a limiting factor in some riparian systems, as has been documented for riparian trees along streams in the eastern Sierra Nevada (Stromberg and Patten 1990, 1991) and elsewhere (Reily and Johnson 1982). This was not the case for the flow-augmented reach, where excess water availability apparently was a limiting factor. Reduced growth rates for *S. lasiolepis* at high flows may be a result of increased saturation within the riparian floodplain and reduced oxygenation to the root zone (Dionigi et al. 1985). Positive correlations between mature willow density and floodplain height in the augmented-flow reach support the idea that high flows have adversely affected growth and survival and suggest that growth and survivorship have been greater in higher, less saturated areas or areas subject to less erosive forces. The high degree of "scatter" between annual growth and flow in the augmented-flow reach may reflect topographical differences in annual saturation extent or genetic differences in saturation tolerance.

MANAGEMENT IMPLICATIONS

Although flow diversion is a more common scenario than is flow augmentation, there are many cases where an existing river channel is utilized as a natural aqueduct to deliver water between drainage basins. In Arizona, for example, water from a tributary of the Little Colorado River is diverted into the East Verde River, as part of a system of water transfers designed to increase water supply at mining sites. Impacts of such water transfers on channel response (e.g., width and meander rate) have occasionally been addressed (Kellerhals et al. 1979; Bradley and Smith 1984), but impacts on riparian vegetation have received less study (Henszey et al. 1991). Effects of existing or proposed water transfers on riparian and aquatic ecosystems should be studied on a case-by-case basis, until generalizations are available relative to riparian community type, stream geomorphic type, and extent of change in stream flow regimes (Kondolf et al. 1987).

The data presented in this study indicate that flow augmentation has had adverse effects on the upper Owens River willow community. However, removal or reduction of the augmented flows would not instantaneously restore the upper Owens River willow community to its pre-perturbation state. We speculate that willow establishment will not become abundant until the river-floodplain system has re-equilibrated, which may take decades (Leopold 1964; Petts 1985). Reduction of high flows should decrease rates of willow mortality, but new recruitment depends on restoration of suitable floodplain morphology. Recovery of the willow population would be enhanced if cattle were at least temporarily removed from willow recruitment zones. In addition to allowing for new recruitment, removal of cattle would allow the existing juvenile willows to increase in size, thereby increasing their ability to stabilize banks and accelerate channel recovery (Armour et al. 1991). Further, this would ameliorate the adverse effects (e.g., increased water temperatures) on fish and other aquatic organisms that occur when riparian vegetation are not present to moderate stream temperatures (McGurk 1989).

Willow growth patterns should revert to "normal" once flows are restored to natural levels. Instead of being frequently limited by high flows, growth of the trees would be frequently limited by low flows as is presently the case in the control reach. Prediction of the extent of growth change is complicated by the changes in channel depth and floodplain height within the augmented-flow reach. These changes may have altered the relationship between stream flow volume and riparian water table depth, and between stream flow volume and growth rate. Nevertheless, existing information suggests that optimum growth of the willow trees would result from partial reduction in flow augmentation, to levels similar to those in the high range of natural flows.

ACKNOWLEDGMENTS

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NOTES

Pollination of *Platanthera dilatata* var. *dilatata* in Oregon by the Noctuid Moth *Discestra oregonica*.—Ronald J. Larson, U.S. Fish and Wildlife Service, 801 Gloucester St., Brunswick, GA 31520.

In the Pacific Northwest, the orchid *Platanthera dilatata* (Pursh) Lindley ex Beck var. *dilatata* occurs from sea level to above treeline. It (or its varietal segregates) is especially abundant in montane meadows, fens, and bogs, where it can number in the thousands at a single site. Although very common, surprisingly little is known about its pollination. There have been anecdotal reports of moths being the pollen vectors (Luer, The Native Orchids of the United States and Canada excluding Florida. New York Botanical Garden, 1975), but descriptions of pollination are lacking.

At 1500 hr on 15 July 1990, chance observations of diurnal moths visiting *Platanthera dilatata* var. *dilatata* were made at Three Creeks Meadow (elev. 1950 m) in the Three Sisters Wilderness Area in Deschutes Co., Oregon. At the 1-ha graminoid-dominated fen, >500 orchids were observed in clusters of 2 to >25 plants. Most of the blossoms on the white racemes were open and unpollinated as indicated by the position of the lip (pollinated flowers have a recurved lip blocking the entrance to the spur).

An estimated 15–20 ash-gray, hairy *Discestra oregonica* (Grote) noctuid moths, about 2 cm in length, were seen visiting the blossoms. The moths apparently selected a raceme at random, using visual cues. After landing, a moth probed few-to-many blossoms before moving to a nearby or distant plant. The relatively large size of the moths necessitated grasping several adjacent perianths while feeding. The orientation of the moths while feeding was mostly head up, but other postures were also noted. Probing was sometimes done with the head close to the opening of the spur, and at other times several millimeters distant. Perhaps the amount of available nectar determined both the numbers of flowers probed on a spike and the depth of probing. Gross dissection of several spurs showed that nectar levels varied; some were nearly empty and others were full.

Spur orientation may force moths to insert their mouthparts so that pollination in *Platanthera* is assured (Inoue, Journal of the Faculty of Science, University of Tokyo III 13:285–374, 1983). In general this may be true, but my photographs showed *Discestra oregonica* moths probing using a variety of orientations, suggesting that its proboscis is highly flexible. In fact, one photo showed a moth standing head down and inserting its proboscis around the recurved lip of a previously pollinated flower. The curved spur of *P. dilatata* var. *dilatata* may prevent long-tongued bumblebees from reaching the nectar, since none were observed at the flowers. Nonetheless R.J. bumblebees are known to occasionally pollinate *Platanthera* species (Catling and Catling, Lindleyana 4(2):78–84, 1989; Patt et al., American Journal of Botany 76(8): 1097–1106, 1989).

Although *Discestra oregonica* moths were wary, I observed several of them with pollinia attached to their proboscides. Three moths collected at random had 1 to 5 pollinia attached to the dorsal side of the proboscis, several millimeters from the head. In situ photos showed the pollinium stipe was erect and bent slightly forward, ready to brush against the stigma of another flower.

In *Platanthera dilatata* var. *dilatata,* the paired viscidia are located on the roof and to each side of the rectangular spur opening (0.8–1.0 mm high and 1.2–1.5 mm wide). The elliptical viscidia (approx. 0.15 mm wide × 0.4 mm long) are oriented with the long axis parallel to that of the spur, probably to insure that they become securely attached to an insect's tubular proboscis. After removal, the flat viscidium becomes

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concave below. The stigma is located medially on the roof of the spur entrance where pollen would contact it as an upright moth inserts or withdraws its proboscis.

Spur length and orientation were important characters determining insect pollinators of Japanese *Platanthera* spp. (Inoue loc. cit.). *Platanthera* species with short spurs (1–2 mm long) were pollinated by beetles; those with 4–6 mm long horizontal spurs were pollinated by small pyralid moths; those with 10–20 mm long decurved spurs were pollinated by medium-sized noctuid and geometrid moths; and those with >20 mm long spurs, by sphingid moths. In *Platanthera dilatata* var. *dilatata,* the spur is about 10 mm long and decurved; it is pollinated by medium-sized noctuids, which agrees with the observations on Japanese *Platanthera* spp.

A number of moth species may pollinate *Platanthera dilatata* var. *dilatata.* Studies in Sweden showed that one *Platanthera* species was pollinated by 28 moth species, of which 80% were medium-sized noctuids (Nilsson, Bot Notiser 131:35–51, 1978). In Japan, most *Platanthera* spp. were pollinated by at least 2 to 3 insect species (Inoue loc. cit.). This note is the first record of *Discestra oregonica* moths pollinating *P. dilatata* var. *dilatata.* Most likely nocturnal observations or collections of moths near this orchid would provide additional pollinators.

I would like to thank J. Donald Lafontaine of the Biosystematics Research Centre in Ottawa, Canada for identifying the moths. Paul Catling, of the same institution, made useful comments on the manuscript. I also wish to acknowledge two anonymous reviewers and Kathy Larson for their help.

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MICRODISSECTING EQUIPMENT FOR BOTANICAL WORK.—

Martin F. Ray, Department of Integrative Biology, University of California, Berkeley, CA 94720.

Securing a botanical specimen is generally a major difficulty when an investigator is dissecting and manipulating small plant material. The delicacy of some plant structures makes them very susceptible to damage by crude instruments or poor cutting techniques. For holding, fingers are relatively large and awkward and can easily ruin fine structures. Holding with the fingers also leaves only one hand free. Double-sided tape has been used, but the specimen is not easily reoriented. Fine forceps are an improvement, yet they also leave only one hand free to operate other instruments. In cutting, a scalpel or a razor blade is usually satisfactory for larger, tougher structures or specimens, but the tendency of a single blade, no matter how sharp or fine, is to put pressure on the tissue being cut. This often results in tearing the specimen or other inability to selectively control the dissection. Since one generally is interested in observing fine details, methods of holding the specimen and manipulating or cutting its delicate parts without undesirable damage are advantageous. This paper describes techniques and equipment for holding and cutting botanical specimens which are useful in fine manipulation under the dissecting microscope. These techniques and equipment are based on those developed primarily for use with insects, and in some medical work.

Specimen holding. For holding the specimen, petri dishes of various sizes filled with a material that allows for pin placement have been used for insect dissection. The smallest type of insect pins, known as "minuten" pins, are very suitable for work with fine plant structures. For example, I have been able to dissect and observe the interior of male florets from *Soliva sessilis* R.&P. (Asteraceae), which are about 2 mm long, using these techniques. Another example is preparation of a dissection of a flower for photography. Even a larger flower can be laid out nicely using minuten pins. Although various types of wax are often used for pin emplacement, the best material I have seen is a form of liquid silicone that is heat cured, marketed as Sylgard 184 Resin by Dow Corning. This material can be left clear or colored with various materials, the most common being pure powdered carbon to render the Sylgard black. The carbon is mixed into the resin prior to pouring into petri dishes and heat curing. If the Sylgard is left clear, it is far superior to wax for transmitted illumination. The Sylgard is quite long lasting, although after years of use it may need to be replaced because of loss of clarity or resiliency. A Sylgard-filled petri dish combined with stainless steel minuten pins (thinnest grade) allows the use of both hands for instrument manipulation, photography, etc. If the dish is small or light it can be held down with double-sided tape. The minuten pins are handled entirely by means of forceps; they are too small to be placed with bare hands. These pins are approximately 0.1 mm in diameter and 5–10 mm long. They can be cut down to any desired length by means of fine wire cutters.

Pins must be stored by placement in the Sylgard. Because of their minute size they are more dangerous, in terms of possible puncture wounds, than larger pins or needles. They are also very hazardous if dropped or misplaced; a minuten pin caught in an article of clothing could cause a very painful injury.

Dissection. Iris scissors are used in entomological dissections and also in some medical work. They are also useful for fine plant work. Different sizes of iris scissors are available from surgical supply houses. Although various types of scissors are called "iris scissors," the type of interest have blades approximately 3–10 mm long, or less, and are sold under the names Weiss, Martin, Vannas, Castroviejo, and others. They are also referred to as "microdissecting scissors." These are operated by squeezing the spring-like handles with two fingers. They are quite expensive, but the control they allow is worth every penny. The ability to selectively snip rather than tear makes it possible to perform the very finest detail work. The only limiting factor becomes manual dexterity. Using the holding techniques described above, one can use a fine forceps in one hand and the iris scissors in the other, or use two pairs of forceps.

All these fine instruments respond to very light pressure. Make sure that there is sufficient support for the hands, as movement is mostly via the fingers. Often the best way to achieve this is with a microscope with no stage, working instead directly on the bench, where the hands can rest. If transmitted illumination is desired, one might set up a large piece of clear glass or plexiglass as a bench top.

It is useful to have a couple of pairs of iris scissors, one larger and one finer. Other types of fine surgical scissors of larger size are also useful for larger structures or in cases where the specimen material is hard enough to damage iris scissors. The larger surgical scissors are less expensive and more easily sharpened if damaged. I have not yet tried any operations on plant material that seemed hard enough to be harmful to my instruments, but this may be the case with some members of the Poaceae, Cyperaceae, Juncaceae, and *Equisetum,* and some woody materials.

Instrument repair and modification. If fine instruments such as forceps or iris scissors are damaged at the tips, they may be repaired by careful work under the stereoscope. Any bending can be slowly and gently correlated by light pressure on a bench surface or by the use of forceps of an appropriate (usually larger) size, this second pair acting as a pair of pliers. Tips can be repaired, sharpened, or customized using a fine oilstone and a small amount of light oil. Carefully rub the tips, one at a time, over the oilstone in oil, back and forth in a filing motion, working under the dissecting microscope. The oilstone removes material from the instrument tip as a fine file. Renew the oil occasionally. Iris scissors, or probes with dull points, may be sharpened or have their tips modified for custom purposes in the same way. When doing this, take care to maintain the original blade angle. I have one pair of iris scissors which had sustained damage on one blade only, and I created a new instrument by filing down and sharpening the damaged blade so that it was shorter than the other. This unequal blade length scissor allows one to lift up and probe or slide under a delicate object prior to cutting. There are many other possibilities for custom instruments.

(Received 2 Sept 1991; revision accepted 21 Nov 1991.)

LECTOTYPIFICATION OF *QUERCUS EMORYI* AND *Q. HYPOLEUCA* (FAGACEAE).—Leslie R. Landrum, Department of Botany, Arizona State University, Tempe, AZ 85287.

In my studies of Arizona oaks, I have found two species that need lectotypification, *Quercus emoryi* Torr. and *Q. hypoleuca* Engelm.

Quercus emoryi Torr. in W. H. Emory, Not. milit. reconn. 152. pl. 9. 1848.—TYPE. USA, "common in the elevated country between the Del Norte and the Gila [rivers]," *W. H. Emory s.n.* (leaves and twig on type specimen from the Torrey herbarium at NY!, hereby designated as lectotype).

The type specimen is a mixed collection: the twig and leaves are of the species commonly known as *Q. emoryi* and the fruits are probably of *Q. turbinella* Greene or *Q. grisea* Liebm. The illustration and original description of Torrey are based on both elements. Therefore, it is necessary to lectotypify *Q. emoryi* with the twig and leaves portion of the type specimen and exclude the acorns.

The scales on the acorn cup on the type sheet have attenuate, non-lustrous tips and raised, warty bases and the peduncle is 14 mm long. These characteristics are typical of the white oaks *Q. turbinella* and *Q. grisea.* Acorns of the black oak traditionally known as *Q. emoryi,* represented by the twig and leaves on the type sheet, have scales with blunt to truncate, lustrous tips and thin, non-warty bases and the peduncles are rarely over 2 mm long.

The fact that the type sheet of *Quercus emoryi* is a mixed collection seems to have been known for years. There are penciled notes in two handwritings (one of which is probably George Engelmann's) that indicate this. Furthermore, Engelmann stated in his paper on oaks in 1876 (Transactions of the Academy of Science, St. Louis 3: 372–400) that "the peduncled acorn of Torrey's figure may belong to . . . [*Q.*] *undulata,*" a white oak. Sargent (Silva of North America, 1895), in his citation of Torrey's original publication, excluded that part of the illustration containing the fruit with a long peduncle.

Quercus hypoleuca Engelm., Trans. Acad. Sci. St. Louis 3:384. 1876.—*Quercus hypoleucoides* Camus, Bull. Mus. Nat. Hist. Paris, ser. 2, 4: 124. 1932. A new name for *Q. hypoleuca* Engelm., proposed because of the prior existence of *Q. hypoleuca* Miquel.—TYPE. USA and northern MEXICO. "I name an Arizona oak which Torrey, in Mex. Bound. Rep. p. 207, refers to *Q. confertifolia,* H.B.K." *Wright 1869* at GH, representing one of the collections mentioned by Torrey and a specimen annotated by Engelmann, is hereby designated as the lectotype.

Torrey (in W. H. Emory, Report on the United States and Mexican Boundary Survey, 1859) mentions four collections: "Near Copper Mines, New Mexico; *Thurber*; No. 1869, *Wright.* Sierra del Pajarito, Sonora; *Schott.* San Francisco mountain; *Captain E. K. Smith.*" I am uncertain which of these collections George Engelmann saw and in which herbaria he saw them. Fortunately, a lectotype can be chosen from two sheets he annotated: one at GH (*Wright 1869*) and another at MO (with both *Wright 1869* and *Schott s.n.*). Both were annotated by him as *Q. confertifolia,* so it is clear that he saw them before his publication of *Q. hypoleuca.* (The handwriting has been compared with a photocopy of a handwritten description of *Cereus giganteus* by Engelmann in his papers at MO). The sheet at GH has the name crossed out and is re-annotated by Engelmann (in the same handwriting) as *Q. hypoleuca* with the pertinent literature citation. It also has a note, signed "G.E." on the duration of the acorns, which Engelmann considered taxonomically important. The sheet at MO (3377694) is a mixture of Wright and Schott collections and there is no way to know confidently what part was collected by which collector. The sheet at GH is entirely of the Wright collection. Given the above information, I have chosen the sheet at GH, a syntype, as the lectotype of *Q. hypoleuca.* Another mixed Wright and Schott sheet is housed at NY and comes from the Torrey herbarium. It was never annotated by Engelmann.

The name *Q. hypoleuca* Engelm. was a later homonym at the time of publication, and was renamed *Q. hypoleucoides* by Camus.

I thank Donald J. Pinkava and two anonymous reviewers for helpful comments.

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LEPYRODICLIS HOLOSTEOIDES (CARYOPHYLLACEAE), "NEW" TO NORTH AMERICA.— Richard K. Rabeler, University of Michigan Herbarium, North University Bldg., Ann Arbor, MI 48109-1057 and Richard R. Old, Department of Plant, Soil, and Entomological Sciences, University of Idaho, Moscow, ID 83843.

During a conversation with Francis E. Northam of the University of Idaho concerning *Apera* in Michigan, the senior author mentioned his interests in weedy Caryophyllaceae. Northam asked if he was familiar with *Lepyrodiclis*; it was an agricultural weed in his area. Rabeler said he was and that he thought it had been reported elsewhere in North America. Further investigation revealed the latter statement incorrect.

The genus *Lepyrodiclis* includes three annual species native to southwestern and central Asia. Although the plants resemble some species of *Stellaria,* the presence of but two styles, two entire capsule valves, and (usually) apically-notched petals allies *Lepyrodiclis* with *Minuartia* (McNeill, Notes from the Royal Botanical Gardens, Edinburgh 24:79–155, 1962).

Lepyrodiclis holosteoides (C. Meyer) Fenzl ex Fisch. & C. Meyer (Fig. 1) (lepyrodiclis or pashenick) is a large, often sprawling, annual. Since it was first found in 1959 by Lambert C. Erickson "10 miles S of Lewiston" [Nez Perce Co.], Idaho (seed collection, idps), *L. holosteoides* has become a serious problem in green pea and wheat fields in Nez Perce County, Idaho, and Whitman County, Washington; "it climbs up and spreads as a canopy over the top of wheat" (Roché et al., Pacific Northwest Extension Publication PNW-349, 1990). It is classified as a "Class B noxious weed" in Washington, requiring officials to take actions aimed at restraining its further advance (Roché et al., Pacific Northwest Extension Publication PNW-349, 1990). This is not altogether unexpected since it is a weedy species in its native environs: found "commonly among crops, . . . surroundings of villages, wasteland, vegetable gardens" in the Caucasus region of the USSR (Gorshkova *in* Komarov and S[c]his[c]hkin, Flora of the USSR, 6:368–369, 1936 [1970]); "widely distributed and common as a field weed" in Pakistan (Ghazanafar *in* Nasir and Ali, Flora of Pakistan, 175:18–20, 1986).

The following collections of *Lepyrodiclis holosteoides* are known (herbarium abbreviations follow Holmgren et al. [Index Herbariorum, part I, 8th ed., 1990] except for idps = University of Idaho Plant Science Department, Moscow, and wsda = Washington State Department of Agriculture, Pullman).

IDAHO. Nez Perce Co.: Disturbed steppe, slope in Coyote Gulch, ca. 1.75 mi N of Clearwater River, 10 mi E of Lewiston, NE¼ of NW¼ of Sec. 16, T36N, R4W, May 1985, *R. R. Old s.n.* (NY); Coyote Canyon, 20 May 1986, *R. R. Old s.n.* (ID, idps, MICH, RM, WS, wsda). WASHINGTON, Whitman Co.: roadside gravel, Union Flat Creek, 2 mi E of Uniontown, Sec. 9, T12N, R46E, 29 May 1991, *Northam 91-3* (ID, idps, MICH, RM, WSU).

In spite of the above-mentioned agricultural awareness, it appears that *Lepyrodiclis holosteoides* has escaped attention in the North American botanical literature. Regional floras that have appeared since 1959 (Hitchcock and Cronquist, Vascular Plants of the Pacific Northwest, Part 2, 1964; Hitchcock and Cronquist, Flora of the Pacific Northwest, 1973; St. John, Flora of Southeastern Washington and of Adjacent Idaho,

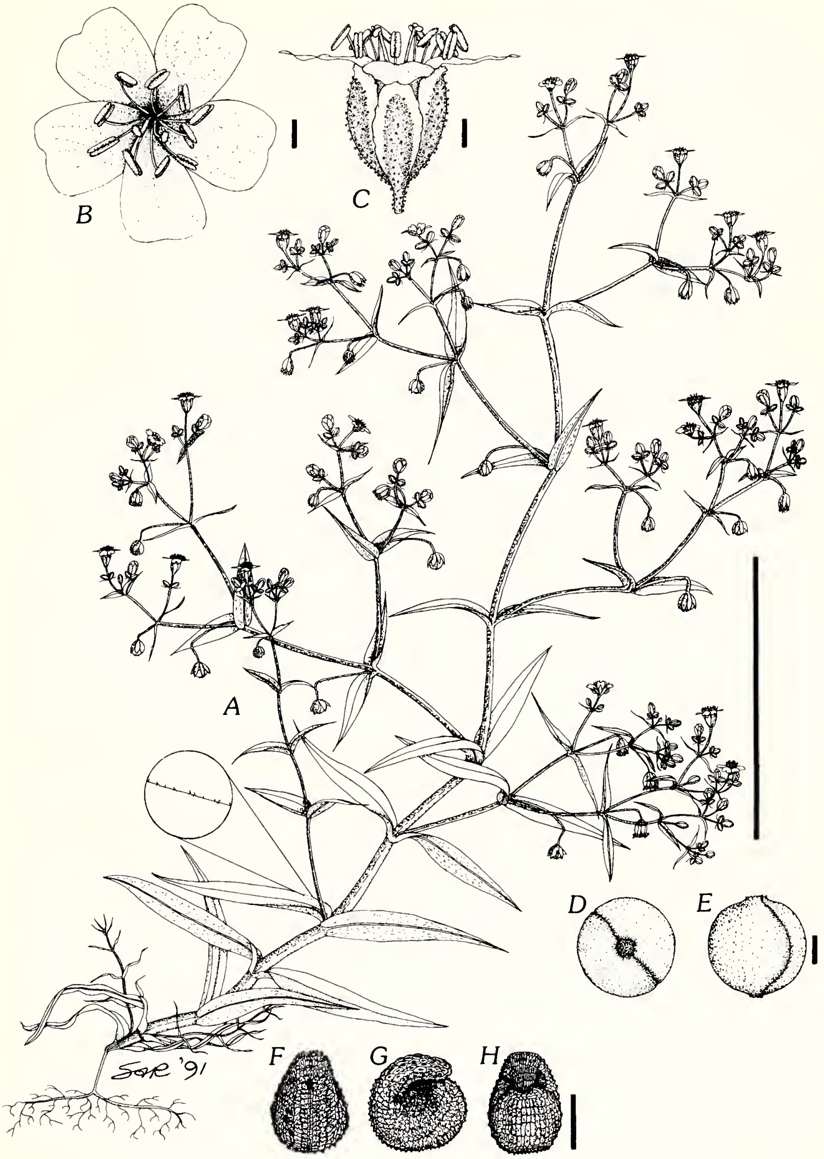

FIG. 1. *Lepyrodiclis holosteoides,* drawn from *Old s.n.,* 20 May 1986 (MICH). A. Habit. B. Top view of flower. C. Side view of flower. D. Top view of fruit. E. Side view of fruit. F. Marginal face of seed. G. Lateral view of seed. H. Hilar face of fruit. Bars equal 10 cm for A, 1 mm for B–H.

1963) make no mention of it. Nor do the two recent national checklists (Rice et al., National List of Scientific Plant Names, 1982; Kartesz and Kartesz, A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, 1980).

Although all reports thus far are from, or adjacent to, agricultural fields, its annual habit and weedy tendency suggests that *L. holosteoides* should be expected in disturbed areas of the Palouse Country and possibly elsewhere in the Pacific Northwest.

We thank Pat Holmgren for the loan of the NY specimen and Francis Northam for his collection from Whitman Co., Washington. Susan Reznicek prepared the illustration.

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NOTEWORTHY COLLECTIONS

MONTANA

CLAYTONIA ARENICOLA Henderson (PORTULACACEAE).—Sanders Co., Cascade Creek [no other data available], *Lesica 4808* (MONTU). Siegel Creek E of Hwy. 46 [no other data available], *Lesica 1401* (MONTU). During the course of monographic studies of *Claytonia* in collaboration with K. L. Chambers (Oregon State University) I found these collections as two misidentified sheets at MONTU which constitute noteworthy collections of a species not known in the flora of Montana.

Previous knowledge. Not previously known from the State of Montana. The occurrence of *C. arenicola* in the Kootenai Region of western Montana is a significant range extension of the species which was known previously from bluffs, terraces and woods around Spokane, Washington (e.g., *Piper 2290,* NY, ORE, US, WS) and from the Snake and Clearwater River Canyons of Idaho, Oregon and Washington (e.g., *Constance et al. 992,* MONTU, NY, OSC, UC, US, WS, and *Baker 6591,* (ID, NY, WTU). Federal and State land managers and the Montana Natural Heritage Program might consider the special status listing of this species in Montana.

—JOHN M. MILLER, BioSystems Analysis, Inc., 303 Potrero Street, Suite 29-203, Santa Cruz, CA 95060.

OREGON

CENTAUREA VIRGATA Lam. subsp. *SQUARROSA* Gugl. (CYNAREAE: ASTERACEAE).—Malheur Co., plants in bud with a few flowers open, in a population about 0.1 ha in size, 61 km west of Vale on Highway 20, on rangeland approximately 20 m away from highway between the highway and the Malheur River in a seasonally used hunter campsite, T20S, R39E, NW¼ sect. 32, W.M., 20 June 1991, *Bill Decker s.n.,* Native vegetation: *Artemisia tridentata/Agropyron spicatum,* associated vegetation: *Bromus tectorum, Chrysothamnus.* Det. R. Halse (OSC specimen not retained), Fruiting specimens, same location, 11 December 1991, *Bill Decker s.n.* (WS).

Previous knowledge. Although squarrose knapweed has been present in northern California since 1950 (California Department of Agriculture Bulletin 41:61–63, 1952; Leaflets of Western Botany 9:17–32, 1959) and Utah since 1954 (Utah State University Experiment Station Bulletin No. 432, 1960), it was not known in the Pacific Northwest until found in Grant County, Oregon, by Dan Sharratt in 1988 (Northwest Science 63:246–252, 1989).

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Significance. This second record of squarrose knapweed in Oregon is approximately 215 km distant from the first population, via State Highways 395 and 20. Because squarrose knapweed's diffusely branched stems and urn-shaped capitula are similar to those of diffuse knapweed (*Centaurea diffusa* Lam.), an invader that is already widespread on Oregon rangelands, it is likely that other populations of squarrose knapweed remain undetected. Squarrose knapweed is easily distinguished from diffuse knapweed by its woody perennial crown and its deciduous capitula with spreading or recurved phyllaries. Diffuse knapweed, normally a biennial, often breaks off at the base of the stem and tumbles about with the seedheads intact. Stems of squarrose knapweed persist as bare "twigs" following capitula dispersal, the characteristic which earned it the adjective *virgate.*

—CINDY ROCHÉ, Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410.

EUPHORBIA OBLONGATA GRISEB. (EUPHORBIACEAE).—Marion Co., Salem, grounds of the Oregon State Penitentiary near the junction of State and Hawthorne streets, forming a dense patch 9 × 4.5 m by the edge of a pond, with *Alnus rubra, Cirsium arvense, Hypericum perfoliatum, Plantago major, Rubus discolor, Salix* sp., *Solanum dulcamara,* T7S, R3W, sect. 25, 58 m, 26 Sept. 1991, *R. Halse 4334* (OSC, DAV, duplicates to be distributed); same location, 30 Aug. 1991 and 4 Sept. 1991, *E. Coombs s.n.* (OSC); identification confirmed by Grady L. Webster.

Significance. First record for OR; previously known from CA (Munz, Supplement to A California Flora, 1968); introduced from Europe.

—RICHARD R. HALSE, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2910; ERIC COOMBS, Oregon Department of Agriculture, Commodity Inspection Division, 635 Capitol Street N.E., Salem, OR 97310-0110.

WASHINGTON

CENTAUREA NIGRESCENS Willd. (ASTERACEAE: CYNAREAE).—Pend Oreille Co., a few flowering plants along roadside near Mill Pond, 6.5 km east of Metaline Falls, on the Sullivan Lake Road, T39N, R43E, SE¼ SE¼ sect. 24, ca. 800 m, 30 September 1991, *J. McCroskey and S. Sorby s.n.,* Det. *C. Roché* (WS).

Previous knowledge. The first collection of *Centaurea nigrescens* (short-fringed knapweed) in the Pacific Northwest was by W. N. Suksdorf from low wet ground along roadsides and fields at Odell, Hood River County, Oregon, 25 August 1919 (WTU, WS). It was collected again at that location in June 1921, *Peck 9886* (WILLU). The first Washington collection was at Bingen, Klickitat County, *Suksdorf 12415,* 12 September 1928 (WS). Later collections included Hood River, Hood River County, Oregon, *Marble s.n.,* 1932 (OSC); Wahkiakum County, Washington, *Weyrich s.n.,* 1932 (WS) and Trout Lake, Klickitat County, Washington, *Talbott 1188,* 1985 (WS) (The Collection History of *Centaureas* Found in Washington State, Wash. State Univ. Agric. Research Center Res. Bull. XB0978, 1986). In addition, Howell recorded it from Idaho County, Idaho, and Manchester, Kitsap County, Washington, *Wheeler 35* (CAS, DS) (Leaflets of Western Botany 9:17–32, 1959). The only record from British Columbia is Vancouver Island, 1966 (The Thistles of Canada, 1974). No distribution is given in Hitchcock and Cronquist (Flora of the Pacific Northwest, 1973) under the synonym, *Centaurea dubia* Suter, only that it is an occasional weed. *Centaurea nigrescens* is a perennial forb native to south central and eastern Europe, with 5 named subspecies (Flora Europaea, Vol. 4, 1976, p. 292).

Significance. This is the first record of *Centaurea nigrescens* east of the Columbia

Gorge region in Washington. Because it is a Class A noxious weed in Washington (RCW17.10, Ch. 16-750 WAC), the intention is to eradicate the two known populations in the state (Trout Lake and Sullivan Lake) while this goal is still achievable.

—CINDY ROCHÉ, Department of Natural Resource Sciences, Washington State University, Pullman, WA 99164-6410.

SIDALCEA NELSONIANA Piper (MALVACEAE).—Cowlitz Co., in a meadow/pasture dominated by *Festuca arundinacea, Anthoxanthum odoratum, Holcus lanatus,* and *Poa* sp., between Coal Creek and Carlon Loop Road, silt loam to silty clay loam soil, native soil profile disturbed by cultivation, T9N, T3W, SE¼ of SW¼, sect. 35, 80 m, 10 June 1991, *C. J. Antieau s.n.* (OSC); in a roadside ditch at the junction of Carlon Loop and Coal Creek roads, with *Holcus lanatus, Fraxinus latifolia, Juncus effusus, Chrysanthemum leucanthemum, Cirsium arvense,* and *Festuca arundinacea,* about 3 airline miles north of Longview, T9N, R3W, sect. 35, 85 m, 4 July 1991, *R. R. Halse 4209, 4210* (OSC, duplicates to be distributed).

Previous knowledge. Sidalcea nelsoniana was thought to be endemic to the Coast Range and Willamette Valley of Oregon (Madroño 33:225–226, 1986). In the Coast Range it is known from western Yamhill and eastern Tillamook counties; in the Willamette Valley it is known from Washington County south to central Benton and Linn counties.

Significance. First record for WA and a northward range extension of about 90 km from Tillamook and Washington Counties, OR. This range extension suggests that *S. nelsoniana* may be present elsewhere in the Coast Range and southwestern part of WA. However, human introduction of *S. nelsoniana* into Cowlitz Co. cannot be ruled out, as most of the species at the sites are exotic. In any case *S. nelsoniana* is well established and reproducing in the Coal Creek area.

—RICHARD R. HALSE, 4535 NW Big Oak, #3, Corvallis, OR 97330; JUDITH B. GLAD, 1400 N Holman, Portland, OR 97217; CLAYTON J. ANTIEAU, Ebasco Environmental, 10900 NE 8th St., Bellevue, WA 98004.

YUKON TERRITORY

CASTILLEJA MINIATA DOUGLAS EX HOOK. (SCROPHULARIACEAE).—Along Top of the World Hwy. (Yukon Hwy. 9), 49.8 km WNW of ferry dock on western side of Yukon River across from Dawson, ca. 64°10′N, 140°30′W, ca. 600 m, single robust, multistemmed plant in moist, gravelly roadbank ditch with bushy *Salix* sp., 4 July 1991, *M. Egger 432* (TWU).

Significance. A northward range extension of over 400 km and third report for Yukon Terr. Likely from seed carried on an automobile tire from a population to the south.

—MARK EGGER, 9521 49th Ave. N.E., Seattle, WA 98115.

OBITUARY

ANNETTA MARY CARTER
(1907–1991)

On 28 June 1991, southern California was rattled by the 6.0 Sierra Madre earthquake, exactly 84 years after Annetta Mary Carter was born in the town for which the quake was named, the town founded by her grandfather and where her ashes had recently been laid to rest in the family cemetary. The next day, following the earthquake, numerous of her friends and relatives gathered in the University of California Botanical Garden to remember and reflect on the life of a person whose warmth, generosity, and indomitable spirit had touched so many.

Annetta Carter was born and raised in Sierra Madre, now part of Greater Los Angeles suburbia, at the foot of the San Gabriel Mountains. Much of Annetta's lifelong love of the out-of-doors reflects the interests of and her close ties with her father, Arthur N. Carter, who would often take his family to the mountains for the summer when he worked as a fire guard.

Her mother unfortunately died when Annetta was 11, but she had the good fortune to have several excellent women role models in Pasadena High School/Pasadena Junior College, including the botany teacher. Their influence encouraged her to come to the University of California in Berkeley in 1928 to study botany. She received her A.B. in botany in 1930 with 7 other women; no men. One of her classmates at both Pasadena and Berkeley was Mary L. Bowerman, who attained her own fame as the authority on the flora of Mount Diablo.

Carter entered the Master's program and did an experimental morphology study of the floating liverwort *Riccia fluitans* ("Carter's little liverworts"), under the supervision of W. A. Setchell. She received her M.A. in 1932, at which time her intention of finding a teaching position was stymied by the Depression. Instead, Carter continued to work in the University Herbarium, where she had initially obtained a position as plant mounter during her senior year. She eventually was in charge of all the day-to-day operations of the herbarium, retiring in 1968 with the title of Principal Herbarium Botanist. She continued as Research Associate for the rest of her life, for an unbroken span of 61 years of association with the herbarium!

During the first 16 years of her career, Carter collected plants extensively throughout California, retaining her interest in cryptogams in addition to vascular plants. She had a diversity of field companions on these pursuits, including Helen Sharsmith, Ethel Crum, and Edward Lee. During this period she made nearly 1850 collections, often with enormous numbers of duplicates for exchange. Many of these collections remained unprocessed upon her death, because in 1947 she was invited on an expedition that totally changed and set the pattern for the rest of her life.

Annie Alexander, heiress of a Hawaiian sugar cane fortune, had a strong interest in natural history. She explored extensively with her life-long travelling companion and friend Louise Kellogg (whose niece-by-marriage, Alice Howard, became Carter's successor in the herbarium). Alexander had previously founded and endowed both the Museum of Vertebrate Zoology and the Museum of Paleontology on the Berkeley campus; in her later years, plants were added to her interests. In October 1947, as Carter was getting disgruntled from helping several other botanists prepare for faraway field trips without going on any herself, Alexander invited her on a 3-month expedition to Baja California. Carter was 40 at the time; Alexander would celebrate her 80th birthday while on the trip. Driving the length of Baja California with Alexander and Kellogg, at a time when a high clearance vehicle was essential, left a deep impression on Carter, to the extent that she made a New Year's vow to return every year, a vow she very nearly kept.

Even a summary of Carter's 40 years in Baja California justifies a separate publication, and anyone undertaking a biographical study will have a wealth of details available as a result of her meticulously kept logs. These logs, although unpublished,

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were typed, duplicated and made available in several herbaria, including the University of California. The logs, beginning in 1962, include detailed descriptions of itineraries, commentaries on happenings, and maps. Later logs of trips also contain photographs, selected from a vast number taken and accumulated by Carter. Also of interest are taped interviews with ranchers and residents of Loreto.

One anecdote illustrating the exploratory nature of these expeditions is related in a commemorative letter written by George Lindsay (25 June 1971), a long-time associate and supporter of Carter's work. "Once, in 1950, I packed into the Sierra Laguna south of La Paz, thinking I was really exploring. When we got down off the mountains to our vaquero's ranch he brought out an old photograph, wrapped in buckskin, of Annetta and Miss Alexander and Miss Kellogg who he had guided to the peak years before."

Alexander, who died in 1950, was on only the first of Carter's trips. Kellogg continued going on and funding many subsequent trips before her own death in 1967. Other field companions over the years included Roxana Ferris, Helen Sharsmith, Reid Moran, and Mario Sousa S. The guide most frequently mentioned in her logs is Franco Murillo; other guides include Carlos Rubio, Pancho Romero, and Juan Mesa. She frequently recounted the story of how the guide on one of her early trips, Marcos Fuerte O., exasperatedly told her either she was going to have to learn Spanish or he was going to have to learn English. Her success in the former endeavor was such that she would sometimes lapse into Spanish during the last weeks of her life.

After 1959, at least the major trips to Baja California were funded by the Belvedere Scientific Fund out of the California Academy of Sciences. These funds allowed occasional cooperative expeditions with Mexican botanists. Starting in 1971, Carter also led several natural history tours to Baja California under the auspices of the California Academy of Sciences.

After several trips to the mountains of the Cape Region, where her ribs were cracked in a rock-fall, Carter's interest eventually focused on the Sierra de la Giganta, a 200-mile-long rugged volcanic range between La Paz and Loreto. She had climbed the highest point, Cerro Giganta, on her first trip with Alexander, but failed to make it to the top of Cerro Muchado, suffering a broken arm on the third attempt when her horse stumbled and fell (on the 25th anniversary of her first trip to Baja California). In addition to these major injuries, there were the numerous inevitable logistical problems, assorted ailments, and car break-downs.

Reminiscences of Carter's journeys frequently include fond memories of the old panel truck that she inherited from her father. It withstood the rigors of numerous field trips, both to Baja California and with the California Botanical Society, before succumbing to a sand storm in Baja California.

In preparation for her retirement, Annetta and her brother Robert dug a well and built a small one-room brick bungalow with a thatched roof on a hectare of land leased near Loreto. It had a large front porch with the roof supported by two palm tree trunks and was named "Las Lomas de Anita." Carter used the "casita" as a base for much of her continued exploration of the Sierra de la Giganta and intended the land to become a native vegetation park. Tragically, she arrived in April 1978 to find the place being bulldozed by the government as part of proposed tourism development. Ironically, the plans called for a park, which never came into being.

As a result of her years in Baja California, Carter made over 5000 collections, the last in 1986 being additional material of the lovely rubiaceous shrub *Carterella alexanderae* (Carter) Terrell. This genus was named for Carter in 1987, based on a species she herself had named in honor of Alexander in 1955. Other plants named after Carter include the *Eupatorium* segregate *Carterothamnus anomalochaeta* R. M. King in 1967, *Abronia carterae* Ferris in 1950, *Abutilon carterae* Kearney in 1953, *Galium carterae* Dempster in 1970, *Amauria carterae* Powell in 1972, and *Viguiera carterae* Schilling in 1990.

Carter described several new species herself based on her collections, including *Acacia kelloggiana,* and published numerous other articles. *Acacia* and other legumes drew her attention, as did the genus *Alvordia* in the Compositae. She also became an authority on the history, biogeography, ethnobotany, and economic botany of the Sierra de la Giganta, and occasionally collected bulk samples for pharmaceutical analysis. She published numerous articles and gave talks at meetings of various Mexican botanical societies. Apparently she did not plan to publish a flora of the Sierra de la Giganta, at least not after I. Wiggins' *Flora of Baja California* was published in 1980. She was, however, working with R. Thorne to compile a list of additions to Wiggins' flora.

Until her retirement in 1968, Carter's trips to Baja California were "the ice cream and cake" sandwiched among her responsibilities for the curation and administration of the herbarium. She effectively set the standards for this vocation, such that when New York Botanical Garden was looking for a person to fill an equivalent position in 1967, Art Cronquist wrote to C. L. Hitchcock asking if he had a student who could be the "Annetta Carter" for New York (P. K. Holmgren, personal communication, who was hired to fill the position). Carter's talents in herbarium curation had previously been "borrowed" by the University of Michigan when it needed to process the collections amassed by H. Bartlett, former director of their botanic garden. She was in Michigan for two 6-month periods: April–October 1957 and July 1958–January 1959.

The Bartlett herbarium included the collections of Mary Clemens, the wife of an army chaplain stationed in the Philippines, Borneo, and New Guinea. Carter eventually published an article on Clemens, and also became an authority on I. G. Voznesenskii, a Russian naturalist who collected in Baja California in the winter of 1841–1842, as part of a salt-collecting expedition. Carter's interest in botanical history was further expressed in her pride in possessing the desk and bookcase that formerly belonged to T. S. Brandegee. His significant western North American (including Baja California) collections and library were donated to the University Herbarium in 1906, where he worked until his death in 1925.

As if these interests and responsibilities were not a sufficient demand on her time and energies, Carter was also heavily involved in numerous organizations and other activities. She had a long commitment to the California Botanical Society and was secretary of the editorial board of its journal *Madroño* for 20 years, from 1943 until 1963. Although Dr. H. Mason was editor, the bulk of getting issues ready for press fell on the secretary's shoulders. Carter was then elected president for 1965, continued as an active member, and served on the council from 1985 to 1988. Volume 18 of *Madroño,* in 1966, was dedicated to her, with a lovely dedication written (at least in part) by Lincoln Constance.

In 1974 Carter joined The Society of Woman Geographers, an international organization. She was co-chair of the San Francisco Bay Area Chapter from 1978 to 1984 and afterwards remained involved with student fellowship awards. At the 1984 triennial meeting in Washington, D.C., she was invited to speak on "Plants and man in the Sierra de la Giganta." Her dedication to the group was demonstrated by her regular attendance, up to several months before her death. Along with her faithful visits to Baja California, her foreign travel also included three trips to the Yucatan Peninsula and trips to Europe in 1954, 1969, and 1972.

In the 1970's, Carter became one of the first female members of the Biosystematists, an informal gathering of systematic biologists centered in the San Francisco Bay area. The group began in the 1930's, at a time when the famous Clausen, Keck, and Hiesey transplant experiments of the Carnegie Institute of Washington were at their peak. The purpose was to encourage no-holds-barred arguments in the new field of biosystematics; women (and graduate students) were excluded for many years for fear that their presence would inhibit such rough-and-tumble discussions.

Carter was a long-standing member of the Sociedad Botanica de Mexico, and attended almost every three-year congress. She was awarded a life membership at the 6th Congress in 1975, and was further distinguished with a highly prestigious honorary membership at the 10th Congress in 1987. Other memberships included

Sigma Xi, San Diego Society of Natural History, California Native Plant Society, American Society of Plant Taxonomy, and American Bryological and Lichenological Society. She also attended Botanical Congresses at Seattle, Leningrad, and Sydney, participating in field trips offered at each.

The significance of Carter's contributions to California and Mexican botany did not go unrecognized. In addition to the aforementioned honors from the California Botanical Society and the Sociedad Botanica de Mexico, she was elected a Fellow of the California Academy of Sciences in 1957. Further recognition came in 1985, when she was selected as one of the first women to be interviewed as part of a series on "California Women in Botany" by the Regional Oral History Office of The Bancroft Library, University of California at Berkeley. There are plans to name the herbarium in La Paz and a street in Loreto after Carter, and to dedicate an issue of *Acta Botanica Mexicana* to her. These honors accurately reflect the depth of the respect and affection that was held for "Señorita Anita" south of the border.

Carter retained her vigor until the age of 80, even participating in a tour to China around that time. Unfortunately, her health began to decline not long after, and she was eventually diagnosed as having an atypical form of multiple myeloma. Dialysis failed to halt the steady decline, and after a prolonged hospitalization she chose to discontinue the treatments. She died at home, attended by friends, on the morning of 8 May 1991, 1½ months before her 84th birthday.

News of her passing elicited condolence letters from as far away as Australia, Argentina, Japan, and Spain—a reflection of the diversity of people around the world who had experienced her hospitality at Berkeley. During Carter's tenure, the Berkeley herbarium had a reputation for being an exceptionally warm, friendly place, a herbarium where visitors truly felt welcome. Carter's urge to care for and assist others was legendary, even at the expense of her own research and other obligations. Many visitors (including the author when she first arrived in Berkeley) stayed in the apartment in the basement of the house which Carter shared with her companion of many years, Florence Little. Little, a professional librarian and long-standing participant in the Guild for Psychological Studies, accompanied Carter on several of her trips.

The dedication written for Annetta Carter in *Madroño* Vol. 18, remains as appropriate as when it was written in 1966:

> During your long association with the University Herbarium, from student assistant to Principal Museum Scientist, you have been the trusted advisor of faculty and administrative officers, a generous counselor and confidante of successive generations of grateful students, and an esteemed friend to your associates and herbarium visitors.
>
> Champion of human rights and friend of the friendless; intrepid field botanist and indefatigible collector and interpreter of the plants of the remote ranges of Baja California, especially of the Sierra de la Giganta, gracious ambassadress to our Mexican botanical friends—you have shown in all your broad and varied responsibilities over the years an unfailing skill and competence which is overshadowed only by your personal warmth and outstanding human spirit.

—BARBARA ERTTER.

APPENDIX I.

LIST OF PUBLICATIONS BY ANNETTA CARTER

1935. *Riccia fluitans* L.—a composite species. Bulletin of the Torrey Botanical Club 62:33–42.

1939. Two new species of *Ranunculus S flammula.* American Journal of Botany 26: 555–557. [With L. Benson.]

1955. Observaciones sobre los encinos de Baja California. Boletín de la Sociedad Botánica de Mexico 18:39–42.

1955. A new species of *Bouvardia* (Rubiaceae) from Baja California, Mexico. Madroño 13:140–144.
1964. The genus *Alvordia* (Compositae) of Baja California, Mexico. Proceedings of the California Academy of Science 30:157–174.
1966. Una forma nueva de *Lophocereus* en Baja California, Mexico. Cactaceas y Suculentas Mexicanus 11:13–17.
1970. Some ethnobotanical notes on the plants of the Sierra de la Giganta, Baja California Sur. Pacific Coast Archeological Survey Quarterly 6(1):29–33.
1974. Evidence for the hybrid origin of *Cercidium sonorae* (Leguminosae: Caesalpinoideae) of northwestern Mexico. Madroño 22:266–272.
1974. The genus *Cercidium* (Leguminosae: Caesalpinoideae) in the Sonoran Desert of Mexico and the United States. Proceedings of the California Academy of Science 40:17–57.
1974. Pollen studies in relation to hybridization in *Cercidium* and *Parkinsonia* (Leguminosae: Caesalpinoideae). Madroño 22:303–311. [With N. Rem.]
1975. The Ynez Mexia collections and N. Floy (Mrs. H. P.) Bracelin. Madroño 23: 163–164.
1976. Notas el el genero *Cercidium* (Caesalpinoideae) en Sud America. Darwiniana 20:305–311. [With A. Burkhart.]
1979. I. G. Voznesenskii, early naturalist in Baja California, Mexico. Taxon 28: 27–33.
1980. Edward Lee [obituary]. Madroño 27:143.
1981. A new species of *Acacia* (Leguminosae: Mimosoideae) from Baja California Sur, Mexico. Madroño 28:220–225. [With V. Rudd.]
1982. Lectotypification of *Cercidium floridum* (Leguminosae: Caesalpinoideae). Taxon 31:333–335.
1982. The itinerary of Mary Strong Clemens in Queensland, Australia. Contributions, University of Michigan Herbarium 15:163–169.
1983. *Acacia pacensis* (Leguminosae: Mimosoideae), a new species from Baja California Sur, Mexico. Madroño 30:176–180.
1986. Aspectos generales de la flora de Baja California. Cactaceas y Suculentas Mexicanus 31:79–96.
1986. Vesta Florence Hesse [obituary]. Madroño 33:307.

APPENDIX II.

BOOK REVIEWS AND INTRODUCTIONS

1965. "A selected guide to the literature on the flowering plants of Mexico," by I. K. Langman. Madroño 18:126.
1973. "The prairie, swell and swale," by T. Korling. Pacific Discovery 26:32.
1974. "Historia natural y cronica de la Antigua California," by M. del Barco. Pacific Discovery 27(6):32.
1979. "The agaves of Baja California," by H. S. Gentry. Madroño 26:193.
1980. "Flora of Baja California," by I. L. Wiggins. Fremontia 8(3):26–29.
1982. Foreword for republication of "Flora of the Mount Hamilton Range of California," by H. Sharsmith.
1982. "The California islands: proceedings of a multidisciplinary symposium," edited by D. M. Power. Madroño 29:64.
1983. "Imagenes de la Flora Quintanarroense," by O. Telez Valdes and M. Sousa S. Madroño 30:198–199.
1983. Editor for appendix "Plants of the Cape Region." Pp. 328--358 *in* A. Zwinger, A desert country near the sea, a natural history of the Cape Region of Baja California. Harper & Row.
1986. "Manual de herbario, administracion y manejo de coleccions, tecnicas de recoleccion y preparacion de ejemplares botanicos," by A. Lot and F. Chang. Madroño 33:232–233.

1987. "Xantus, the letters of John Xantus to Spencer Fullerton Baird from San Francisco and Cabo San Lucas, 1854–1861," by A. Zwinger. Madroño 34: 269–271.
1988. "Atlas cultural de Mexico. Flora," by J. Rzedowski and M. Equihua. Madroño 35:75–76.

NOTE

The California Botanical Society has established an Annetta Carter Memorial Fund for doing field work on the botany of Baja California. The core of the fund is a generous donation by Florence Little. If you wish to honor Annetta Carter by donating to this fund, please send your check to Treasurer, California Botanical Society, % University Herbarium, University of California, Berkeley, CA 94720.

OBITUARY

BAKI KASAPLIGIL

1918–1992

Baki Kasapligil, a structural botanist and professor emeritus at Mills College, Oakland, California, and a research associate in the University Herbarium, University of California at Berkeley, died April 22nd in his home in Berkeley. He was 73 years old and died of cancer.

Born on 13 November, 1918, in Çankaca, Turkey, and raised in Istanbul, he received his B.Sc. from the University of Istanbul in 1941, served in the Turkish army from 1941 to 1944, was an assistant botanist at the Higher Institute of Agriculture, Ankara, from 1944 to 1946, and attended the University of California, Berkeley, from 1947 to 1950, where he received his Ph.D.

From 1950 to 1954 he held botanical positions at the University of Ankara, which awarded him a post-doctoral habilitation degree in 1953. While serving in 1954 to 1956 as a forest botanist, Food and Agriculture Organization (FAO) of the United Nations, Dr. Kasapligil headed an ecological and vegetational mapping survey of forest and grazing lands in Jordan.

In 1956 Dr. Kasapligil assumed Howard Earnest McMinn's (1891--1963) position at Mills College and remained there until his retirement in 1984. At Mills he taught courses in basic biology, basic botany, economic botany, and plant taxonomy. One of the most popular professors on campus, and affectionately known as "Dr. K," he maintained even through his retirement years at the University Herbarium at Berkeley an active correspondence and contact with many colleagues and former students.

Dr. Kasapligil is the author of several monographs and numerous botanical papers on fossils, anatomy, morphology, and taxonomy. He also contributed to *Hortus Third* (1976) and other horticultural publications. His doctoral thesis done at Berkeley is now regarded as a classic piece of work and was on the structure and development of the vegetative and reproductive organs of California bay (*Umbellularia californica*) and European bay (*Laurus nobilis*), both members of the laurel family. He also wrote on such diverse plant groups as the pines (*Pinus*), oaks (*Fagus*), filberts (*Corylus*), as well as on past and present floras of Asia Minor.

Dr. Kasapligil is survived by two sons, David and Danyal, his brother Vehbi Kasapligil, and sister Şahika Ozon, both of Istanbul, Turkey.

—RUDOLF SCHMID.

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CALIFORNIA BOTANICAL SOCIETY

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Department of Biology
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THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

SHORT FIRE INTERVALS RECORDED BY REDWOODS AT ANNADEL STATE PARK, CALIFORNIA

MARK A. FINNEY
Research Division, Sequoia National Park,
Three Rivers, CA 93271

ROBERT E. MARTIN
Department of Forestry and Resource Management,
University of California, Berkeley, CA 94720

ABSTRACT

Fire intervals were derived from analysis of fire scars on samples taken from 14 redwood (*Sequoia sempervirens* D. Don (Endl.)) stumps throughout Annadel State Park, California. Samples were obtained from small redwood groves that are isolated within other forest types. Dating before the mid-1800's, mean fire intervals between 6.2 and 23.0 years were found on individual stumps, with single intervals as low as 2 years. Although the sources of these fires are uncertain, fire usage by Native Americans is a plausible explanation given the archeological evidence at Annadel and sparse lightning activity in areas like Annadel near the coast.

The historical presence of fire among the oak woodland (Sawyer et al. 1977) and mixed evergreen forests (Griffin 1977; Wainwright and Barbour 1984) near the coast in northern California has been little studied. Records predating fire exclusion are scarce because most tree species in these forests are poor long-term recorders of fire scars. Nevertheless, several studies in similar vegetation types throughout northern California suggest substantial fire activity prior to the mid-1800's (Talley and Griffin 1980; Rice 1985; McClaran and Bartolome 1989; Wills 1991). This paper reports fire history evidence obtained from fire scars recorded on coast redwood trees which grow in isolated clumps within oak and mixed evergreen forests.

STUDY AREA

Annadel State Park is approximately 2000 hectares in size, located 3 km east of the city of Santa Rosa in Sonoma County, California (Fig. 1). Elevations range from approximately 90 meters to 550 meters at the summit of Bennett Mountain, the tallest point at Annadel. Much of the park is elevated several hundred meters above valley bottoms which surround the Park on the North (Melita and Rincon Valley), East (Valley of the Moon), and West (Bennett Valley and Santa Rosa).

Dominant vegetation cover includes Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) which forms closed stands throughout the

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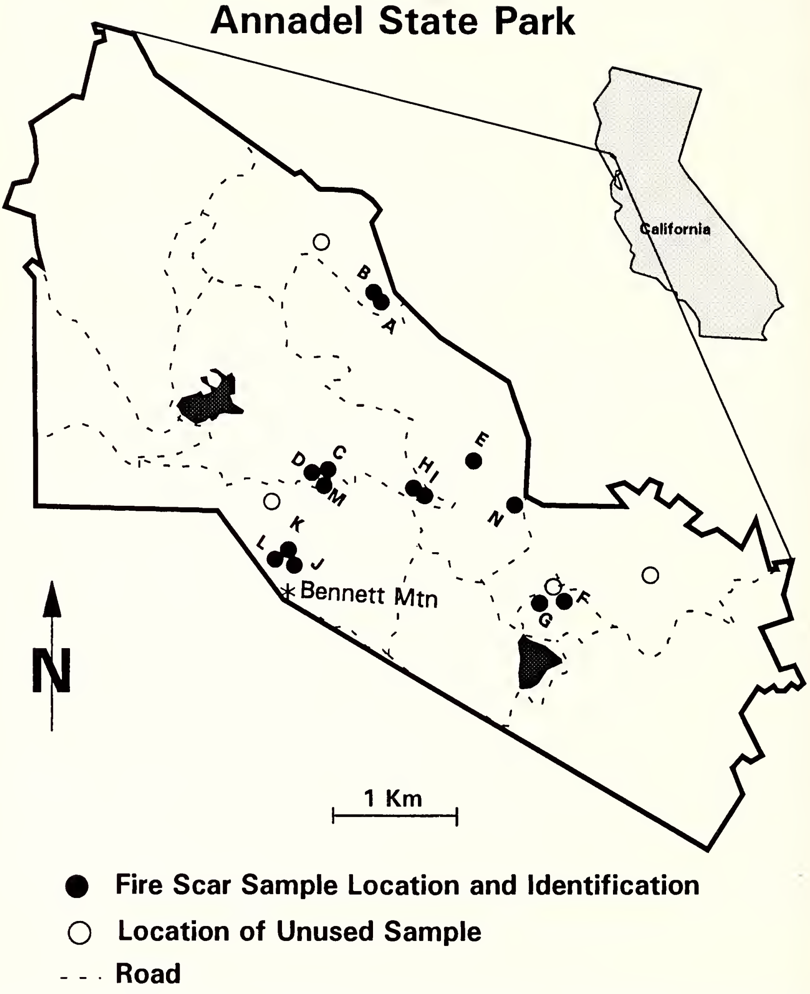

FIG. 1. Location of Annadel State Park and fire scar samples removed from redwood stumps.

area and is an obvious invader of the oak woodlands and oak savannahs (Barnhardt et al. 1987; Wainwright and Barbour 1984). Madrone (*Arbutus menziesii* Pursh), California laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), and Douglas-fir comprise the mixed evergreen forests (Sawyer et al. 1977) which occupy much of the park. Oak woodlands contain various proportions of blue oak (*Quercus douglasii* Hook. & Arn.), black oak (*Q. kelloggii* Newb.), valley oak (*Q. lobata* Nee), or interior live oak (*Q. wislizenii* A. DC.). Coast redwood is found typically in small groves (<5 ha) on northerly aspects and as isolated clumps in drainages. Areas of chaparral, grassland, and various wetlands are interspersed throughout the forested areas of Annadel.

The coast redwood, in contrast to most co-occurring tree species, is renowned for its relative fire resistance, longevity, and resistance to heart-rot. Redwood is thus a potentially useful and important source of fire history information. To date, information on fire history obtained from redwood has been reported by Fritz (1931), Veirs (1981), Greenlee (1983), Jacobs et al. (1985), Stuart (1987), Swetnam (1987), Finney and Martin (1989), Brown (1989), and Finney (1990).

Evidence of fire specifically at Annadel has been restricted to written records (Amme 1987) which indicate only two lightning ignitions since 1939. No investigations at Annadel have quantified fire occurrence prior to these records. Land use by settlers began with cattle grazing in the 1830's, and by the 1870's logging and quarrying were initiated (Futini 1976).

METHODS

Following a reconnaissance of the redwood clumps in drainages and redwood stands growing along northerly aspects, samples were removed from any redwood stump showing fire history evidence (Fig. 1). Redwood was the only species from which fire scar evidence could be obtained, since Annadel State Park contains few other species that can or have survived to offer fire history information. Usable redwood evidence at Annadel was scarce because the long time since early logging has allowed natural deterioration (including insect damage and rot) of stumps and fire scar evidence. Stumps found in acceptable condition were sectioned with a chainsaw in order to locate the best recorded series of fire scars; up to three wedges or full slabs were removed to the laboratory from each stump.

At one stump in each grove, the largest individual stem among the youngest definite generation of redwood sprouts was selected for age determination. One increment core was extracted from that sprout as close to the base as possible (<30 cm). Redwood often sprouts when damage occurs to the above ground organs during fire or harvesting, with sprout growth sometimes exceeding two meters per year during the first few growing seasons (Olson et al. 1990). Post-harvest sprouts are usually distinguishable from older pre-harvest generations by 1) their size, 2) their relatively uniform sizes and arrangement around the stump, and 3) the usual absence of fire scarring at the juncture between sprout and the parent tree (stump). Scarring is often present at these locations on sprouts which survived previous fires. High fuel accumulations around redwood clumps and radiative heat exchange between sprouts contribute to inward-facing fire scars.

Fire scar samples were sanded to a smoothness of 400 grit. Fire scars were identified by the characteristic disruption and healing patterns of radial tree ring growth. Fires were assigned a tree ring based on the position of the fire-caused growth disruption relative to the pattern of earlywood and latewood production. A fire year was assigned to a given ring if the growth disruption appeared to precede termination of latewood formation during that growing season or if the callus healing tissue began with earlywood in the year (ring) following that ring. The latter assumes a late season fire which occurred after latewood production had ceased, rather than an early season fire before earlywood formed the following year.

Intervals between fire scars were obtained by counting rings using a binocular dissecting microscope. No attempts were made to cross-date for correcting ring dating problems common to redwood (see Swetnam 1987; Brown 1989). Annual rings were counted along radii with the widest increment; often this involved tracing individual rings from zones of narrow growth to those with wider increment. Scar dates were then assembled for each stump individually. Where multiple sample cross-sections existed from a given stump, fire scar dates were compiled from all sections as one chronology by matching fire intervals common between sections. Discrepancies between scar intervals on separate sections were resolved by recounting; where necessary the most complete count was used because missing rings are more common than false rings (Brown 1989). Mean fire intervals were calculated from all fire intervals found on individual stumps.

In the laboratory, increment cores were mounted in a groove cut in a wooden lath and sanded to a smoothness of 400 grit. Dates of sprout origination were obtained by counting growth rings on the increment cores and were used to estimate the date of harvest. Given the typically rapid height growth of sprouts, no correction was made for the time required for a redwood sprout to reach core height.

Redwood harvest dates were used as the upper bound on the time-period covering the fire scar chronologies. More precise estimates of fire dates were not possible because the sapwood, and recent heartwood on some samples, had rotted away.

RESULTS

A total of 18 redwood partial sections or whole slabs were removed from stumps in the Park (Fig. 1). Fire scar evidence on four samples was rendered unusable by rot. Increment cores were removed from trees belonging to 6 separate groves. Ring counts on increment cores from all groves suggested that ages of the dominant generation of redwood sprouts at the time of sampling were between 124 and 134 yr. This suggests that logging of the previous redwood trees occurred between 1856 and 1866.

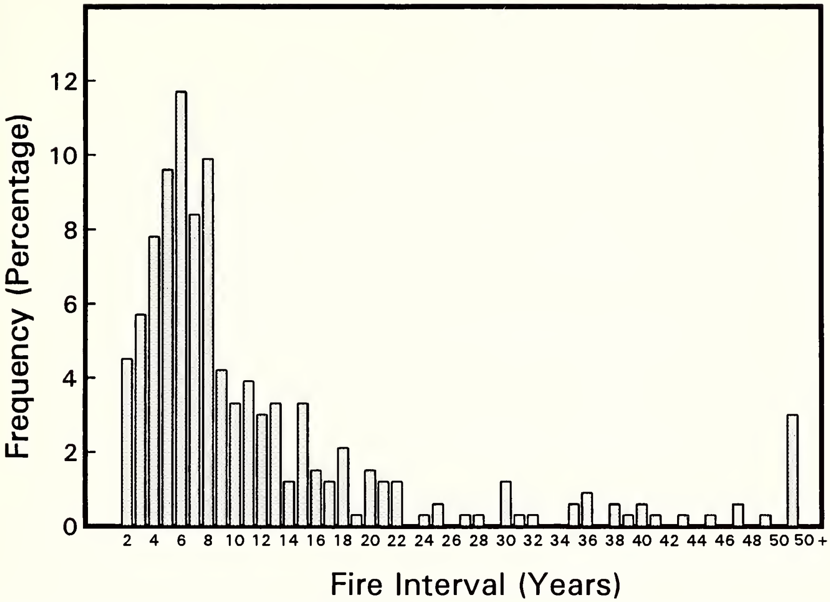

FIG. 2. Distribution of fire intervals from all samples combined. Fire intervals shorter than 10 years comprised 67.39% of all intervals.

Mean fire intervals among all individual stumps varied from 6.2 to 23.0 years (Table 1). All fire scars are believed to predate European settlement in the early 1800's. The most recent scar on each sample was typically older (by up to 106 yr) than the outermost ring (Table 1). Also, the most recent ring on each sample was actually several decades older than the harvest date because an unknown number of rings were contained in the decomposed sapwood. Fire intervals between 2 and 10 years comprised 67.39% of all intervals (Figs. 2 and 3), and often occurred in multiple sequences (Table 1, Fig. 4). Longer fire intervals (up to 131 yr) are evident on some samples. Summing the ring counts by sample suggests the earliest scar records date from about the 14th century (Table 1).

DISCUSSION

The short fire intervals found on many redwood samples at Annadel suggest a fire regime in sharp contrast to the modern era. Fires underburned redwood groves and probably the surrounding forests at intervals shorter than a decade throughout at least 4 centuries before settlement. Since the early 1900's fire suppression has limited the spread of both lightning and human caused fires.

The short fire intervals recorded in the isolated redwood groves

TABLE 1. FIRE INTERVAL DATA FROM REDWOOD STUMP SAMPLES. Intervals in parentheses are the number of rings between outermost ring and the most recent scar and were not included in calculating mean fire intervals. Other intervals represent the rings between fire scars.

Samples													
A	B	C	D	E	F	G	H	I	J	K	L	M	N
Means													
6.2	23.0	10.6	20.9	17.4	14.1	9.9	13.8	10.2	6.2	10.4	7.5	10.8	6.5
Intervals (most recent at the top)													
(13)	(75)	(47)	(35)	(106)	(30)	(53)	(35)	(67)	6	(36)	(71)	7	4
9	7	17	131	3	7	16	12	8	6	13	11	18	6
7	38	18	22	5	3	24	20	38	7	13	7	36	9
6	12	32	18	13	6	5	15	7	5	30	3	21	8
3	28	21	12	5	7	8	78	7	8	9	6	16	2
4	6	2	45	8	53	7	6	8	4	11	8	25	5
3	101	5	8	14	7	5	9	17	4	6	4	12	3
3	4	10	6	21	10	11	7	8	6	6	4	5	13
5	39	14	47	13	6	6	3	6	7	11	6	12	6
11	12	9	15	5	13	7	11	4	6	2	4	14	14
2	5	7	2	8	41	10	10	5	5	8	7	9	10
3	9	3	27	36	57	8	2	4	7	7	7	10	2
6	15	3	30	30	18	15	2		9	8	7	3	6
7		5	11	4	6	8	5			15	15	8	3
4		3	11	22	4	16				13	6	5	
16		5	9	40	9	19				8	9	7	
6		5	6	40	4	8				10	10	4	
6		2	6	10	4	8				2	3	6	
3		10	5	15	7	5				18	8	4	
3		4	8	43	6	3				15	5	8	
7		4	22	13	17	7				3	11	12	
5		4	13		5	4					10	2	
6		7	5		20	8					8	15	
9		8				20					5	12	

TABLE 1. CONTINUED

Samples													
A	B	C	D	E	F	G	H	I	J	K	L	M	N
Means													
6.2	23.0	10.6	20.9	17.4	14.1	9.9	13.8	10.2	6.2	10.4	7.5	10.8	6.5
Intervals (most recent at the top)													
4		18									7	6	
15		8									2	16	
5		18									5	8	
4		4									7	6	
13		20									20	12	
6		11									2	5	
5		9									17	9	
6		6									6	11	
5		2									12	8	
8		49									6	5	
8		8										11	
4		11										22	
		5										8	
		6										6	
		15										31	
		25										21	
												4	
												8	
												8	
												2	
												6	
Totals													
230	351	460	494	454	340	281	215	179	80	244	319	484	91

FIG. 3. A sample redwood cross-section from Annadel State Park that contains fire scars separated by 2 years.

at Annadel probably reflect the fire regimes of the surrounding vegetation types and fuels rather than the redwood forest type itself. Unlike the expansive forests of more coastal redwood study sites, the inland redwood groves at Annadel are presently isolated within more open forests (e.g., oak woodlands) which support considerable understory vegetation. Regrowth of grasses and herbaceous vegetation following fires in these forests can form continuous surface fuel cover sooner than forest litter and woody debris deposited beneath closed forest canopies.

The mean fire intervals from individual stumps at Annadel are somewhat shorter than mean fire intervals from wetter and more coastal redwood forests (Table 2), and the 10 to 15 year intervals from mixed evergreen forests of northern California (Rice 1985; Wills 1991). Direct comparisons between studies, however, are made difficult by the different methods used for obtaining fire dates and for computing mean fire intervals. The mean fire intervals computed for individual samples at Annadel are likely to be conservative because all fires may not scar a tree and scars may be destroyed by later fires, rot, and insects. Mean fire intervals computed from fire dates on more than one sample are generally shorter.

The impact of consistently short fire intervals as recorded at Annadel would have markedly influenced the vegetation. The distribution and composition of most plant communities have changed

FIG. 4. A sample redwood cross-section from Annadel State Park exhibiting a well preserved sequence of fire scars.

Table 2. Summary of Mean Fire Intervals from Fire History Studies in Coast Redwood Forests. Size of the sampling area is presented where mean fire intervals were computed using fire dates from more than one sample.

Location	Mean fire intervals (years)	Source
Humboldt Co. and Del Norte Co.	~25	Fritz (1931)
Marin Co.	22–27	Jacobs et al. (1985)
Humboldt Co.	11–44/190–430 ha	Stuart (1987)
Sonoma Co.	9–11/200 ha	Finney and Martin (1989)
Humboldt Co.	8–12/unknown	Brown (1989)
Marin Co.	5–15/5–10 ha	Finney (1990)

since settlement through conversion of chaparral to Douglas-fir forests, invasion of oak woodlands by Douglas-fir, and increasing canopy density of other forest types (Barnhardt et al. 1987). The boundaries of existing redwood groves, however, have apparently remained relatively static since settlement. No redwood evidence (stumps, sprouts, etc.) was found between extant groves to suggest a recently constricted distribution.

Without having direct evidence, the source(s) of the pre-settlement fires cannot be determined with certainty. Lightning, however, is unlikely to have been the primary cause of consistently short fire intervals given the modern record. In fact only two lightning ignitions at Annadel are recorded since 1939 (Amme 1987). Lightning ignitions surrounding the park were probably of similar frequency given the relatively low lightning densities of coastal California (Keeley 1982). Some fires, however, undoubtedly originated outside the present park boundaries.

Ignitions by Native Americans (intentional and accidental) could, however, account for the consistently short fire intervals recorded on redwoods. Aboriginal uses of fire throughout grassland and forested areas in northern California have been documented, often in association with acquiring food and other vegetal materials (Lewis 1973; Sugihara and Reed 1986; Reed and Sugihara 1987; Veirs 1987). Archeological evidence including bedrock milling stations, basalt metates, and obsidian quarries, suggests that Annadel had been used intensively for procuring food and stone implements (Parkman and McGuire 1981; Porter and Wilbur 1987). Prehistoric camp sites within the park suggest temporary or seasonal occupancy, and the largest of several nearby permanent village sites is within a few hundred meters of the park boundary (J. Charles Whatford personal communication).

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CHROMOSOME NUMBERS AND GEOGRAPHIC DISTRIBUTION IN *CHAENACTIS DOUGLASII* (COMPOSITAE, HELENIEAE)

JOHN S. MOORING
Biology Department, Santa Clara University,
Santa Clara, CA 95053

ABSTRACT

A report of $2n=15$ II is new for *Chaenactis douglasii* (Hook.) Hook. & Arn., as are 12 II and 18 II for *C. douglasii* var. *montana* M. E. Jones. The frequency of meiotic aberrations (11%) was 33% of that found in a larger 1980 study. The correlation between ploidy level and age of substrate was highest in the Sierra Nevada and lowest in the Intermontane Plateaus.

Chaenactis douglasii (Hook.) Hook. & Arn. ranges from near sea level to over 3000 m from the Pacific Coast states to British Columbia, Montana, Wyoming, Colorado, and Arizona. These winter annuals, biennials, or short-lived perennials occur in dry and often disturbed sites in diverse soils and plant communities. Taxonomic treatments differ widely, from ten species and six varieties (Stockwell 1940) to one species and five varieties (Abrams and Ferris 1960). Gillet (1954), Alava (1959), and Raven and Kyhos (1961) reported chromosome counts of $2n=24$, $2n=12$, and $2n=12$, 24 and 36, respectively. In a study of 500+ plants Mooring (1965, 1980) reported triploids ($2n=18$) and many tetraploids and hexaploids with rings or chains of chromosomes, as well as diploids or polyploids with one or more extra, full-sized chromosomes.

The geographic distribution of diploid and polyploid populations was correlated with age of the substrate. Evidence suggested that the *C. douglasii* complex evolved in late Cenozoic time as major climatic and geologic changes induced migration and hybridization. Polyploidy stabilized the hybrid derivatives, and, tolerant of increasing aridity, they colonized newly available habitats in areas disturbed by volcanic activity and glacial or glacial-related processes (Mooring 1980).

The 1980 study rested on uneven geographic sampling. British Columbia, Wyoming, and Colorado were represented by a total of only ten populations, and few samples elsewhere came from mountains projecting above arid or geologically recent intermountain plateaus. Since then I have sporadically sampled more populations while traveling, and also have undertaken a hybridization program.

My purpose here is to describe the results of the additional sampling, especially in British Columbia, Wyoming, and Colorado.

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METHODS

One count came from buds collected in the field, 14 from field plants transplanted to the greenhouse, and 20 from greenhouse or garden plants grown from field-collected fruits. Microsporocytes or, in four cases, root tips were squashed in acetocarmine, the former after fixation in 1:3 acetic ethanol, the latter after 6–8 minutes in concentrated HCl-95% ethanol (Mooring 1975). Meiotic studies were of cells during diakinesis or metaphase I; determinations rest on at least 12 clear cells. Root tip counts generally were of prophase stages and rest on 4–6 clear cells. Nine counts are not accompanied by voucher specimens because the plants died suddenly or were used in artificial hybridizations. Identities of the plants are certain. Information about the age of the substrates at population sites in the U.S. came from USDI Geological Survey maps, scaled at 1:500,000 for Colorado, Nevada, Oregon, and Washington, and at 1:750,000 for California. The scale for British Columbia was 1:1,267,200.

RESULTS AND DISCUSSION

Some populations of this complex do not fit nicely in one or another of the various varieties. If pressed, I would place all but two of the populations in this report in var. *achilleifolia* (Hook. & Arn.) A. Nels. The exceptions are populations *302* and *316,* which are assignable to var. *montana* M. E. Jones.

Cytological aberrations were relatively infrequent (11%) in these samples (Table 1). In contrast, about 33% of the individuals studied previously (Mooring 1980) had multivalents, chromosomes in excess of the basic complement, an unusually large or an unusually small bivalent, secondary associations between bivalents, unpaired chromosomes, or a fragment chromosome. In the present study one tetraploid occasionally formed an association of 4 chromosomes, another had a fragment chromosome. In the 1980 study 50% of the tetraploids had multivalents, extra chromosomes, or both. The 300% difference in the frequency may be sampling error or attributable to greater diploidization of the tetraploids in this sample. At the diploid level one plant had an extra, full-sized chromosome and another had two, which generally paired. These chromosomes in excess of the basic complement will be referred to as supernumerary chromosomes.

The count of 15 bivalents seems to be a new report for this species, and those of 12 and 18 bivalents are new reports for var. *montana* (Table 1). Another member of that population had 12 II, and 13 II and 14 II counts have been obtained in other populations (Mooring 1980). Supernumerary (=B or accessory) chromosomes occur in many species. In some they can be transmitted through the maternal or paternal line, and sometimes multiplied, as in the female line in *Clarkia unguiculata* (Mooring 1960). Stuessy (1990, p. 292) commented that *Chaenactis douglasii* has a great range of variation in number of chromosomes; the 15 II count adds to that range. The presence of one to six supernumerary chromosomes in *C. douglasii* individuals, and their presence in many populations (Mooring 1980) suggest that they persist for one or several reasons; they can be multiplied or at least transmitted, they have adaptive value, or they are not harmful enough to be eliminated by selection.

Mooring (1980) reported that diploids predominated in the Pacific and Rocky Mountain systems, and polyploids in the intermontane plateaus comprising the Columbia Plateau, Basin-and-Range, and Colorado Plateau provinces. After comparing soil, vegetation, altitude and what climatic data could be applied, it became apparent that a correlation existed between the ploidy level of populations and the age of underlying or nearby substrate (Mooring 1980). Generally, polyploid populations were on Quaternary or occasionally on Pliocene or Miocene substrates, whereas diploids were on soils derived from older rocks. Most polyploid populations occupied naturally disturbed regions—former glacial lakes (Montana), lands scoured by the Spokane Flood(s) (Washington), regions where the soils were derived from Quaternary or late Tertiary lava flows (eastern Washington and Oregon, southern Idaho, northeastern California, northern Sierra Nevada), or moraines (California). Diploid populations, on the other hand, were on older substrates undisturbed by volcanic and glacial or glacial-related forces. The ploidy level-substrate correlation was not 1:1. See Mooring (1980, pp. 1311–1314) for a more complete description.

The distribution pattern of the 14 diploid, 11 tetraploid, and two hexaploid populations in this study (Table 2) is consistent with that described (1980) for 68 diploid, 110 tetraploid, and 19 hexaploid populations. The degree of correlation between ploidy level and substrate age and disturbance varied regionally, as it did in the 1980 study. This time it was highest in the Sierra Nevada and lowest in the Intermontane Plateaus.

In the Sierra Nevada the correlation between diploid populations on soils derived from geologically older rocks and polyploids on younger ones was perfect: two diploids on Mesozoic granite and four tetraploids on Miocene volcanic material (Table 2).

In the Basin-and-Range Province portion of the Intermontane Plateaus two of the three California and Nevada diploid populations did not fit the diploid-old substrate hypothesis. Population *280*, on soils derived from Pliocene or Pleistocene sedimentary rocks, is 16 km down Long Valley Creek from diploid population *208* and on the same substrate. Mooring (1980) noted that *208* was an ex-

TABLE 1. CHROMOSOME COUNTS AND MEIOTIC ASSOCIATIONS IN *Chaenactis douglasii.* Locations are approximate. The bolded 3-digit number immediately preceding a location is the population number; 4-digit numbers indicate my collection numbers. I collected all populations but *286* and *287.* My voucher specimens have been deposited in SACL, those for *286* and *287* in CS. Numbers in parentheses indicate numbers of individuals counted, if more than one. An asterisk denotes the plant died before furnishing a herbarium specimen, and RT means root tip count.

Location	Chromosome count
California	
Alpine Co., **285,** Highland Lakes Road, *	2*n*=12 II
Fresno Co., **282,** Mono Creek, *	2*n*=6 II, 2*n*=11–12 (RT)
Mariposa Co., **278,** Sentinel Dome, Yosemite N. P. *	2*n*=6 II
Mono Co., **316,** Sonora Pass, *3653*	2*n*=12 II
Sierra Co., **281,** Sierraville, *3474*	2*n*=12 II
Lassen Co., **280,** Constantia, *3745*	2*n*=6 II (2)
276, SW flank, Skeedaddle Mt. *3473*	2*n*=12 II
Nevada	
Eureka Co., **288,** 30 mi W of Eureka, *3547*	2*n*=6 II 1 I
Nye Co., **283,** Grantsville, *3494*	2*n*=6 II (2)
Oregon	
Sherman Co., **315,** Moro, *3700*	2*n*=12 II
Colorado	
Archuleta Co., **290,** Arboles, *3528*	2*n*=6 II (2)
Rio Blanco Co., **286,** T1S R100W S 28, *Kelley & Waters 82-190* (CS)	2*n*=6 II, 2*n*=12 (RT)
287, T2S R99W S 25, *O'Kane & Sigstedt 82-425* (CS)	2*n*=12 II, 15 II
San Miguel Co., **289,** Norwood Hill, *3633*	2*n*=12 II
Grand Co., **298,** Kremmling, *3548*	2*n*=12 II
Gunnison Co., **295,** Monarch Pass, *	2*n*=6 II
293, Powderhorn, *	2*n*=7 II
Hinsdale Co., **292,** Lake City, *	2*n*=6 II
Jackson Co., **300,** Walden, *	2*n*=12 II, 1 fragment
Pitkin Co., **297,** Thomasville, *	2*n*=6 II
Wyoming	
Teton Co., **277,** Gros Ventre R., Teton N. P., *3476*	2*n*=18 II
Carbon Co., **302,** Lincoln Park, *3534*	2*n*=18 II
Sweetwater Co., **305,** Point of Rocks, *3743,*	2*n*=6 II, 2*n*=12 (RT)
British Columbia	
312, Bear Creek Provincial Park, *3679*	2*n*=6 II (2)
314, Penticton, *	2*n*=12 (RT)
308, Spence's Bridge, *3638*	2*n*=12 II
309, Princeton, *3675*	2*n*=12 II

ception to the ploidy level-substrate age correlation. Population *288* was on Quaternary alluvium, but within 13 km of Cretaceous and older rocks on Antelope Peak (3144 m). Mooring (1980) described a similar situation for Nevada diploid populations *154* and *218.*

The single Columbia Plateau population (*315,* tetraploid, on Pliocene gravels) fit the polyploid-young substrate hypothesis, but the two Colorado Plateau tetraploid populations (*287, 289*) did not (Table 2).

The ploidy level-substrate age correlation held in the Rocky Mountains. The four diploid populations were in soils underlain by Eocene to Precambrian igneous or volcanic rock, and the single hexaploid (*277*) was on Quaternary alluvium (Table 2). The two tetraploid populations (*298* and *300*) were on Cretaceous or Eocene substrates, but were in "parks," unforested basins in a syncline between mountain ranges (Fenneman 1931). The parks probably are geologically quite recent compared to the mountains that contribute their erosion products to these basins.

The Wyoming Basin populations are represented by a diploid (*305*) on a Cretaceous sandstone ridge between basins, and a seemingly out-of-place hexaploid (*302*) on a Precambrian substrate in the Carbon Basin. These and other Wyoming basins, like the Colorado "parks," probably are much younger than the surrounding mountains. The North Platte River (8 km from *302*) drains the Carbon Basin and North Park, where population *300* (tetraploid) occurs (Table 2).

It was difficult to decide which substrates were present under the British Columbia populations because many substrates were present and the map scale was 1:1,267,200. The two diploid populations, on very dry and shallow-soiled sites under *Pinus ponderosa* and *Pseudotsuga menziesii,* appeared to be on Eocene or Precambrian sedimentary or metamorphic substrates. Tetraploid population *309,* in sandy soil under the same conifers, appeared to be on Pleistocene glacial lake deposits. These three fit the ploidy level-substrate age hypothesis. Tetraploid population *308,* in heavy clay soils derived from a Cretaceous sedimentary rock substrate, did not. It was along the Nicola River in an *Artemisia tridentata* community, however, probably a much more recent environment than conifer forest.

One would predict imperfect correlations in this study for the following reasons. First, it is sometimes difficult or impossible to locate precisely a population on a geological map where substrates of very different ages and kinds are jumbled together ("eggbeater geology"). Second, these maps may not identify small, geologically different sites speckling an extensive and monotonous surface. Third, highway building and other disturbances facilitate the establishment of *Chaenactis.* Fourth, the existence of polyploids in a diploid region may result from the fusion of unreduced gametes. (I regard the origin of diploids from tetraploids as considerably less likely.)

The correlation between ploidy level and substrate age and disturbance in *C. douglasii* might, of course, represent a correlation between ploidy level and climate, rather than ploidy level and geo-

Table 2. Comparison of Ploidy Level, Substrate, Soil, Elevation, and Plant Community.

Population	Substrate	Soil	Elevation (m)	Plant community
Sierra Nevada				
California				
diploid				
282	Mesozoic granite	sandy	2500	Jeffrey Pine Forest
278	Mesozoic granite	sandy	2000	Red Fir/Jeffrey Pine
tetraploid				
285	Miocene volcanics	clay	2500	Jeffrey Pine Forest
276	Miocene volcanics	clay	1500	Sagebrush Steppe
316	Miocene volcanics	clay	2935	Whitebark Pine Forest
281	Miocene volcanics	clay	1860	Jeffrey Pine Forest
Intermontane Plateaus				
Basin-and-Range, California				
diploid				
280	Pliocene or Pleistocene	sandy	1400	Sagebrush Steppe
Basin-and-Range, Nevada				
diploid				
288	Quaternary alluvium	clay	1980	Sagebrush Steppe
283	Jurassic volcanic?	clay	2135	Pinyon-Juniper Woodland
Columbia Plateau, Oregon				
tetraploid				
315	Pliocene gravels	talus	150	Sagebrush Steppe
Colorado Plateaus, Colorado				
diploid				
290	Eocene sedimentary	shale	1905	Pinyon-Juniper Woodland
286	Eocene sedimentary	shale	2950	Mountain Shrub
tetraploid				
287	Eocene sedimentary	loam	2145	Mountain Shrub
289	Cretaceous sandstone	sandy	2195	Pinyon-Juniper Woodland

TABLE 2. CONTINUED.

Population	Substrate	Soil	Elevation (m)	Plant community
		Rocky Mountains		
Colorado				
diploid				
292	Eocene volcanics	loam	2560	Ponderosa Pine Woodland
293	Precambrian granite	coarse sand	2740	Sagebrush Steppe
295	Precambrian granite	coarse sand	3025	Subalpine Forest
297	Pennsylvanian	sandy	2548	Subalpine Forest
tetraploid				
298	Cretaceous limestone	chalky fine	2432	Sagebrush Steppe
300	Eocene	clay	2500	Sagebrush Steppe
Wyoming				
hexaploid				
277	Quaternary	sandy	1950	Sagebrush Steppe
		Wyoming Basin		
diploid				
305	Cretaceous sandstone	fine sand	1984	Sagebrush Steppe
hexaploid				
302	Precambrian	fine sand	2280	Sagebrush Steppe
		Thompson Plateau, British Columbia		
diploid				
312	Eocene sedimentary	clay	442	Ponderosa Pine Forest
314	Precambrian metamorphic	clay	343	Ponderosa Pine Forest
tetraploid				
309	Pleistocene glacial	fine sand	868	Ponderosa Pine Forest
308	Cretaceous sedimentary	clay	460	Sagebrush Steppe

logically recent disturbance. In this view, diploids predominate on geologically older substrates because these substrates tend to occur in more mesic montane or riparian environments. Similarly, polyploids predominate on younger substrates because they occur in more arid environments on younger volcanic and alluvial substrates. The examples in Table 2 frequently contradict the climate hypothesis. Compare, for example, Wyoming Basin populations *305* and *302*. The diploid was in the Red Desert, the hexaploid in the Medicine Bow Mountains. Climatic explanations, it seems to me, too often have become a panchestron, an explain-all. Myriads of local climates exist in western North America, but reliable data describing them do not. Reliable data on rock and soil factors are easier to obtain, and can offer better explanations for distributions of ploidy levels in *C. douglasii.*

Substrate age hypotheses and other hypotheses need not be mutually exclusive. I suggested (Mooring 1980, p. 1317) that polyploid populations on geologically ancient, rather than recent, substrates could represent secondary adaptation to increasing aridity, particular soils, or both.

The observed correlation between ploidy level and age of substrate is a first step in explaining diploid-polyploid patterns in *Chaenactis douglasii*; it is a generalization that has predictive value. Much more often than not I have been able to predict the ploidy level of a population upon seeing it in the field for the first time.

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ECOLOGICAL STUDY OF THE RARE *CHORIZANTHE VALIDA* (POLYGONACEAE) AT POINT REYES NATIONAL SEASHORE, CALIFORNIA

LIAM H. DAVIS and ROBERT J. SHERMAN
Biology Department, Sonoma State University,
1801 East Cotati Avenue, Rohnert Park, CA 94928

ABSTRACT

The only known population of the rare Sonoma spineflower, *Chorizanthe valida,* is a colony within a coastal grassland subjected to cattle grazing. Exclosures were constructed and baseline data taken in and outside of the exclosures over four years. Inside the exclosures, *C. valida* demonstrated considerable phenotypic plasticity and experienced a remarkable population decline. Percent cover transects inside the exclosures revealed a 65% non-native plant cover. Outside the exclosures *C. valida* continued to thrive with cattle apparently grazing the non-native plants but not *C. valida.* A cattle grazing regime therefore had a positive influence on the perpetuation of a rare, endemic plant. *C. valida* seeds were sown into nearby grazed plots and monitored for three years. *C. valida* continues to reproduce on these sites. Soil analyses were performed for nutrients, pH, texture, and salinity. Recommendations for the management of this rare species are given.

The Sonoma spineflower, *Chorizanthe valida* Wats. (Polygonaceae), is known from a single population in Marin County, California. The flower is a California state listed endangered plant (Davis and Sherman 1990) and was recently granted federal endangered status (Federal Register 1992). The colony is located in a coastal grassland 200 m south of Abbotts Lagoon within Point Reyes National Seashore.

The first known collection of *Chorizanthe valida* was by Ilya G. Voznesensky who collected in northern California in 1840–1841 (Alekseev 1987). Watson (1877) first described *C. valida* from the holotype in the Russian collection (Davis and Sherman 1990; Howell 1937). While the genus has undergone considerable revision (Bentham 1836; Parry 1884; Goodman 1934; Reveal and Hardham 1989), *C. valida* has been regarded as a distinct species since its initial description in 1877. Reveal and Hardham (1989) recognize about 50 taxa of *Chorizanthe.* Most are predominantly cismontane and distributed on the west coasts of North and South America.

Chorizanthe is among the 20 largest genera in California (Noldeke and Howell 1960) but none of the *Chorizanthe* found in temperate North America is widespread or abundant (Stebbins 1974). The reasons for narrow geographical ranges of some California endemics are not clear (Ornduff 1974). Barbour et al. (1987) suggest that endemic plants are poor competitors. Stebbins (1974) considers *Chori-*

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zanthe to be a recently derived genus of Polygonaceae and a plant pioneer on xeric sites where little or no competition with other plants would occur.

The narrow endemism of *Chorizanthe,* coupled with urbanization and agriculture, has promoted local extirpations and extinctions. Several species from the Pacific coast of North America have not been collected for years and some species are known from only one or a few populations (Reveal and Hardham 1989). Fifteen taxa are considered rare in California (Smith and Berg 1988). *Chorizanthe valida* was thought extinct for 77 years until a population was rediscovered in 1980 at Abbotts Lagoon (Davis and Sherman 1990). Historically *C. valida* was more widespread within the National Seashore. The plant was collected by Elmer in 1903 about 1.5 km south of the Abbotts Lagoon colony, northwest of Schooner Bay near the site of the Point Reyes Post Office and F Ranch (Fig. 1). Our surveys (1988–1991) and surveys by others (Fellers and Norris 1990) indicate that this population is extirpated.

The prehistory and ecology of grazing in California and the benefits of grazing to native plants are discussed by Edwards (1992). The ability of a plant to withstand grazing varies by species (Stoddart et al. 1975). Quantitative studies by Willoughby (1987) in central California demonstrated the negative impact of livestock grazing on two rare, endemic plant species. Fiedler and Leidy (1987), in a study of Ring Mountain Preserve, Marin County, CA, reported seven rare species in a serpentine bunchgrass community with a history of cattle grazing. Their study did not compare grazed with non-grazed sites. Heady (1956) demonstrated the positive influence of moderate grazing on *Stipa pulchra* Hitchc. but we know of no study that has quantified the positive influence of a livestock grazing regime on a rare, endemic California plant. In fact, few population studies have been carried out on endemic plants (Major 1988). At Point Reyes National Seashore most rare, endemic plants occur in the pastoral zone and livestock grazing may have had either a negative or positive influence on national seashore rare plants (Clark and Fellers 1986, 1987; Fellers and Norris 1990). In response to questions raised by the above discussion, we designed a field study to: establish a baseline for the *C. valida* population, monitor the influence of grazing, investigate other factors such as soils that may limit the population, and explore the potential to expand the colony.

STUDY AREA

The Abbotts Lagoon colony is located in western Marin County in Point Reyes National Seashore in northern California 38°6′N and 122°57′W. The terrestrial vegetation surrounding Abbotts Lagoon

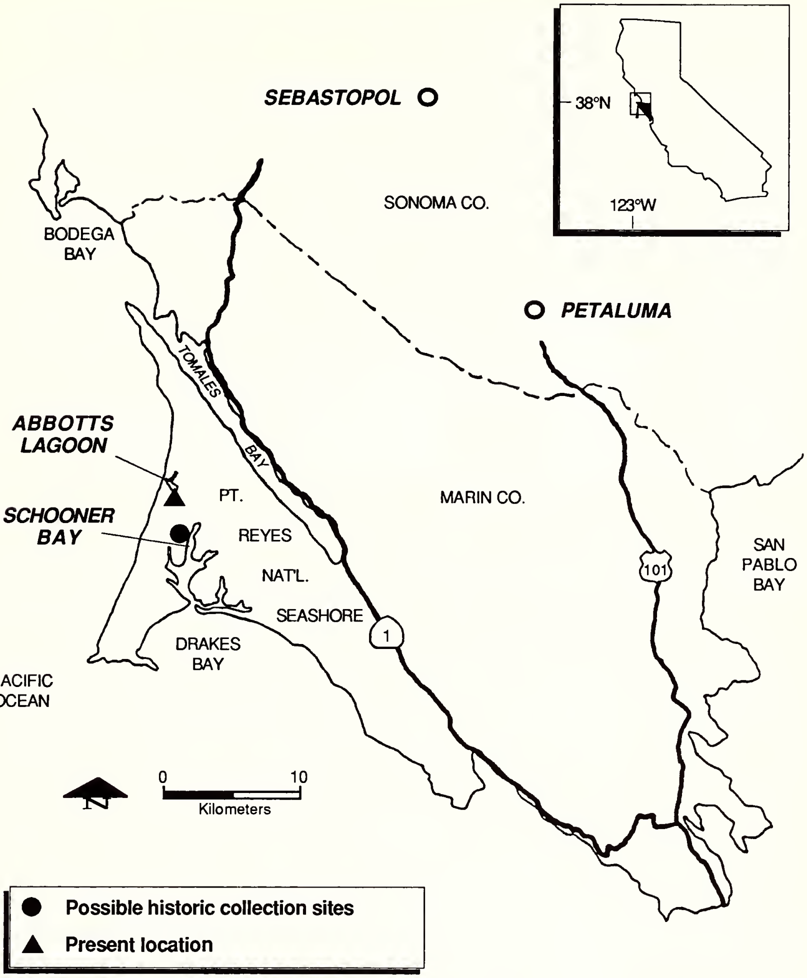

FIG. 1. Distribution of *Chorizanthe valida.*

is a mosaic of coastal grassland, coastal scrub, and sand dune (Barbour and Major 1988) and coastal swale.

The *C. valida* colony is located in coastal grassland, approximately 15 m above sea level. The total population exists within approximately 17,000 m^2 and is well defined within the larger coastal grassland community. The predominate grasses are *Vulpia bromoides* [=*Festuca dertonensis* (All.) Asch. & Graebn.], *Bromus mollis* L., and *Aira caryophyllea* L. and the predominate forbs are *Cardionema ramosissimum* (Weinm.) Nels. & Macbr. and *Rumex acetosella* L. Two shrub species, *Lupinus arboreus* Sims. and *Baccharis pilularis* ssp. *consanguinea* (D.C.) C. B. Wolf., also occur in the colony but appear stunted at heights of <1 m.

According to the Soil Survey of Marin County, California (Kashiwagi 1985), the soil where the *C. valida* colony occurs is Sirdrak sand. This soil has low to moderate available water capacity and plants found there are drought tolerant.

Pastoralism was introduced to the Point Reyes Peninsula in the 1830's (Gogan et al. 1986). The site is a federally-leased cattle pasture that has a grazing history extending over a century (S. Phelan personal communication).

The area has a typical Mediterranean coastal climate. Records from the University of California Bodega Marine Laboratory, 23 km north, indicate mean temperatures are: January, 9.5°C; July, 13.6°C; annual, 11.5°C; and annual precipitation is 793 mm.

METHODS

Exclosures. During the June 1988 summer bloom two 4 m × 6 m cattle exclosures were constructed in different portions of the colony that contained large numbers of *C. valida.* Two circular plots with a radius of 0.81 m (area = 2.0 m^2) were established in each exclosure. Two plots were also established in grazed areas within 22 m of each exclosure. *Chorizanthe valida* population counts were taken in 1988 (baseline) and over the next three consecutive summers (1989–1991) during the bloom. Also, in early June 1989 before a *C. valida* bloom, percentage cover baseline measurements were made along transects inside each non-grazed exclosure and the resulting plant species and percentages were recorded. Previous to this investigation there was year-around grazing and this practice continued during the course of our study.

Introduction plots. In September 1988 *C. valida* seeds were collected from the colony and 1000 seeds were selected for introduction in December 1988 into each of three 2 × 2 m plots located within the coastal grassland cattle pasture. The areas were devoid of *C. valida,* but within 100–200 m of the colony. The soil surface was exposed to a depth of 2–3 cm using a small hand shovel. The seeds were broadcast into the plots and pressed into the soil by foot pressure. *Chorizanthe valida* counts were made, both inside and outside of the plots, during the bloom over the next three years (1989–1991).

Soils. Soil samples were taken from the exclosures, from sample plots outside exclosures in the colony at points 10 m beyond the distinct periphery of the colony (*C. valida* $< 1\ m^{-2}$) in the four cardinal directions, and from the three introduction sites. Soil analyses were made for levels of nitrates, phosphorus, and potassium; pH; texture; and salinity.

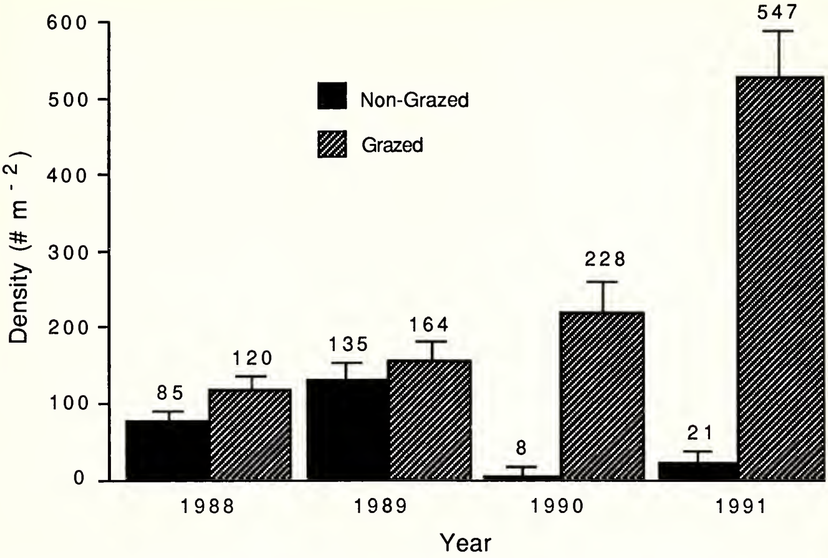

FIG. 2. Population densities of *C. valida*, non-grazed and grazed, over four years. Values above the bars indicate density. Error bars represent ±1 SE of the mean.

Specimens were examined from CAS and from photocopies (GH, MO, and US). Nomenclature conforms to Munz (1968) except for *Vulpia bromoides* (Fellers et al. 1990).

RESULTS

Vegetation. After the 1988 baseline density counts, the colony showed an increase in both non-grazed and grazed spineflower populations (Fig. 2). A crash occurred, however, in the non-grazed populations from a density of 135 m^{-2} in 1989 down to 8 m^{-2} in 1990, but with a slight recovery in 1991 to 21 m^{-2}. The grazed population density continued to increase in 1991, up to 547 m^{-2}.

There are 236 non-native plant species recognized on the approximately 295 km^{-2} at Point Reyes National Seashore (Fellers et al. 1990). Our percent cover measurements taken from transects inside exclosures for the 1989 growing season averaged 65% cover by non-native species, particularly non-native grasses (Table 1). Measurements were taken in early June before a significant *C. valida* bloom occurrence.

Differences in *C. valida* morphology inside and outside the exclosures were apparent in 1989 (Davis and Sherman 1990). Most plants in the non-grazed population were 3–4 times taller, had many more inflorescences, and greater crown diameters than the plants in the

TABLE 1. PLANT AND LITTER COVER INSIDE EXCLOSURES AFTER ONE YEAR OF NON-GRAZING.

Species	Native or non-native	Percentage cover
Vulpia bromoides	non-native	25.5
Bromus mollis	non-native	11.5
Aira caryophyllea	non-native	11.5
Cardionema ramosissimum	native	8.5
Chorizanthe valida	native	7.0
Rumex acetosella	non-native	6.0
Hypochoeris radicata	non-native	5.0
Hordeum brachyantherum	native	4.0
Litter	—	4.0
Plantago lanceolata	non-native	3.0
Deschampsia caespitosa ssp. *holciformis*	native	2.5
Bare ground	—	2.5
Clarkia davyi	native	2.0
Lupinus arboreus	native (?)	1.5
Lupinus bicolor	native	1.5
Achillea borealis	native	1.0
Cynosurus echinatus	non-native	1.0
Lolium perenne	non-native	1.0
Danthonia californica	native	0.5
Layia platyglossa	native	0.5

Cover summary
65.0% from 8 non-native species
28.5% from 10 native species
6.5% litter/bare ground

grazed population (Fig. 3). In 1991 one plant inside an exclosure measured 0.5 m in diameter and had 44 inflorescences.

Successful reproduction occurred within all three introduction plots and by 1991 two plots had reproduction outside of the original 2 × 2 m seeded area (Table 2).

Soils. Soil nutrients and textures in the colony, at the 10 m distant sample sites, and at the introduction sites were compared. There were no statistically significant differences. Within the colony, the means and ranges were as follows: nitrates 9 kg ha^{-1} (8–10), phosphorus 19 kg ha^{-1} (13–25), potassium 278 kg ha^{-1} (200–390), soil pH 4.9 (4.6–5.4), and conductivity 347 μmhos (240–490). The soil texture was sand 91% (89–93), silt 5% (3–5), and clay 4% (3–5).

DISCUSSION

Halligan (1974) noted that cattle do not graze on *C. coriacea* associated with California sagebrush in annual grassland. Cattle do not appear to graze on *C. valida* or *C. cuspidata* var. *villosa* at Abbotts Lagoon. The reluctance of cattle to graze on *Chorizanthe* is no doubt

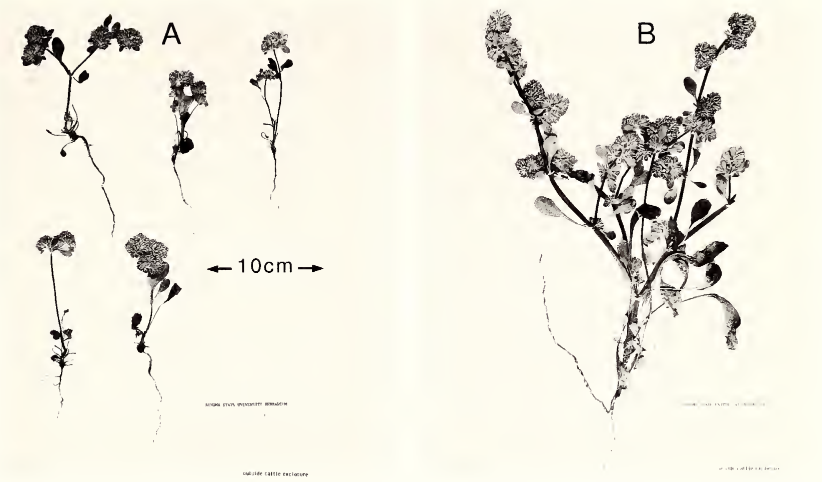

FIG. 3. *Chorizanthe valida* from (A) grazed and (B) non-grazed populations. *L.H. Davis 9002* and *9003* (NCC), both collected 29 June 1989/mounted 1990.

due to the highly modified involucres abundant on each inflorescence. These spines, a major taxonomic feature for classification of the spineflower genus (Reveal and Hardham 1989; Howell 1985; Munz 1968), possibly represent an evolutionary adaptation for dispersal and/or grazing.

The remarkable differences in morphology between the grazed colony and the non-grazed colony demonstrate the phenotypic plasticity of *C. valida.* Major (1988), in response to the suggestion that restricted endemics lack plasticity, state, "Many apparently stenotopic endemics show extreme morphological variations when relieved of competition." In the case of *C. valida* it appears the reverse is true, extreme morphological variations occur when the species is subjected to apparent competition with other plants, when grazing pressures are removed.

During the course of this study the grazed population of *C. valida*

TABLE 2. RESULTS FROM THE INTRODUCTION OF *C. valida* SEEDS ON THREE PLOTS IN COASTAL GRASSLAND CATTLE PASTURE. Numbers in parentheses indicate additional plants found outside of the 2 × 2 m plots.

2 × 2 m plots	December 1988 seeds sown	Summer 1989 plant count	Summer 1990 plant count	Summer 1991 plant count
X	1000	38	3	16+ (3)
Y	1000	22	193	159+ (23)
Z	1000	98	2	9

increased remarkably, more than doubling from 1990 to 1991. Most populations fluctuate, either due to environment, or to intrinsic oscillatory properties (Ricklefs 1990). Changes in weather may have influenced *C. valida* population densities. The period from 1986–1991 was one of drought conditions. According to records from the University of California, Bodega Marine Laboratory, rainfall during our study was only 71% of normal.

Changes in grazing intensity would certainly contribute to density fluctuations. The National Seashore keeps grazing intensity records for each ranch unit. The ranch with the *C. valida* colony showed range management improvements from 1987 to 1990, however, the records are not sufficiently detailed to allow analysis of the specific *C. valida* site. We did not observe any changes in grazing intensity in our site visits over the four years of the study.

It may be that animals other than cattle have historically influenced this species. Edwards (1992) discusses the vast array of late Pleistocene (12,000 years ago) grazing-browsing-trampling mammalian megafauna of the Bay Area of central California. Today this megafauna is locally extinct, with the exception of deer and elk. Elk were extirpated and reintroduced. Large herds of Tule elk (*Cervus elaphus nannodes*) on Point Reyes in the last century are referred to by McCullough (1971). Evermann (1915) comments on elk inhabiting openlands up to five to six miles wide along the coast in Marin County. Presently an introduced elk herd exists 7 km north of the colony on Tomales Point within the National Seashore. The food habits of cattle overlap those of elk almost completely (McCullough 1971) and grazing by elk may have been an important factor in the earlier perpetuation of *C. valida,* however, the proportions of native and non-native plant species would have been different from those we observed in this study.

Other endemic animal associations are more evident. Stebbins (1974) stated that transport by animals is probably the most effective method for passive transport of the spiny hooked *Chorizanthe* seeds. Badger (*Taxidea taxus*), pocket gopher (*Thomomys bottae*), and blacktail jackrabbit (*Lepus californicus*) activity was observed in and near the colony. These mammals demonstrate some proclivity for coastal grassland habitat and emigration from the colony with attached seeds into nearby habitats would be expected. Also, during the summer bloom *C. valida* flowers attracted many hymenopteran species. We observed the solitary ground nesting wasp (*Bembix americana comata*), the yellow-faced bumble bee (*Bombus vosnesenkii*), and the non-native Italian honey bee (*Apis mellifera*) visiting *C. valida* flowers. Any or all of these insects may provide the means for outcrossing within the colony.

Recommendations for management. The apparent last remaining colony of *C. valida* is managed in a cooperative rare plant monitoring program between Point Reyes National Seashore and The California Native Plant Society (Fellers and Norris 1990). Consideration should be given to expansion of the colony into the nearby coastal grassland mosaic on appropriate soils. An introduction program should consider the colony seed source as limited. The success of the three initial introduction plots demonstrates the potential for expansion of the colony. A small scale introduction program of one site per year may be appropriate.

Ornduff's (1974) discussion of successional disclimax plant communities refers to the Central Valley grasslands as being no longer dominated by native perennials but not replaced by an unnatural community of introduced annuals. The coastal grassland community at Abbotts Lagoon is also a disclimax (Elliott and Wehausen 1974). If livestock grazing were removed from these grasslands it is uncertain what successional changes would take place. Our study suggests that non-native plants would replace a rare, endemic plant that is apparently a poor competitor. A program that reassociates *C. valida* and native elk could be beneficial. Whichever programs are implemented, the perpetuation of *C. valida* will be a matter of constant human endeavor.

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OPUNTIA DENSISPINA (CACTACEAE): A NEW CLUB CHOLLA FROM THE BIG BEND REGION OF TEXAS

BARBARA E. RALSTON
Department of Biological Sciences,
Northern Arizona University, Flagstaff, AZ 86011

RICHARD A. HILSENBECK
Florida Natural Area Inventory,
1018 Thomasville Rd, Suite 200-C,
Tallahassee, FL 32303

ABSTRACT

Opuntia densispina (Cactaceae) a new species in the series *clavatae* from Texas is described and illustrated. The new species has close affinity to *O. emoryi* of the *Opuntia schottii* complex in Texas. Morphological, chromosomal and phenological characters which distinguish this species from other taxa in the *Opuntia schottii* complex are provided.

A recent systematic study of *Opuntia* series *clavatae* (sensu Benson 1982) subgenus *Cylindropuntia* included the taxa *Opuntia schottii* Engelm., *O. grahamii* Engelm., and a newly recognized species, *O. aggeria* Ralst. & Hils. (Ralston and Hilsenbeck 1989). These taxa composed a part of the *O. schottii* complex in Texas as defined by Benson (1982) and Ralston (1987). Observations made from both herbarium collections and field work indicated that large variation existed within populations of *O. aggeria* found in Big Bend National Park. Further critical study of this variation, involving both morphological and chromosomal analysis, determined that another entity, found sympatrically with *O. aggeria,* deserves specific taxonomic rank. The species is proposed here.

Opuntia densispina Ralston & Hilsenbeck, sp. nov. (Fig. 1).—TYPE: U.S.A., Texas: Brewster County, Big Bend National Park, 5.3 mi NE of Solis' Ranch on Old River Rd, on clay slopes. 15 May 1989, *Ralston 200* (holotype SRSC, isotypes TEX, ASC).

Opuntia schottii Engelm. et *O. emoryi* Engelm. similis sed ab utroque differt articulis in catenis brevioribus et areolis minoribus (a 4 mm longis) glochides numerosas a 1 cm longas ferentibus. Differt a *O. schottii* spinis sine marginibus carinitis. Differt a *O. emoryi* articulis et tuberculis brevioribus angustioribus.

Plants forming low sprawling mats to 12 cm high, 3 m wide. Roots fibrous. Branches forming short chains, new growth emerging from lateral areoles of previous year's growth; joints 45–70 mm long, 35

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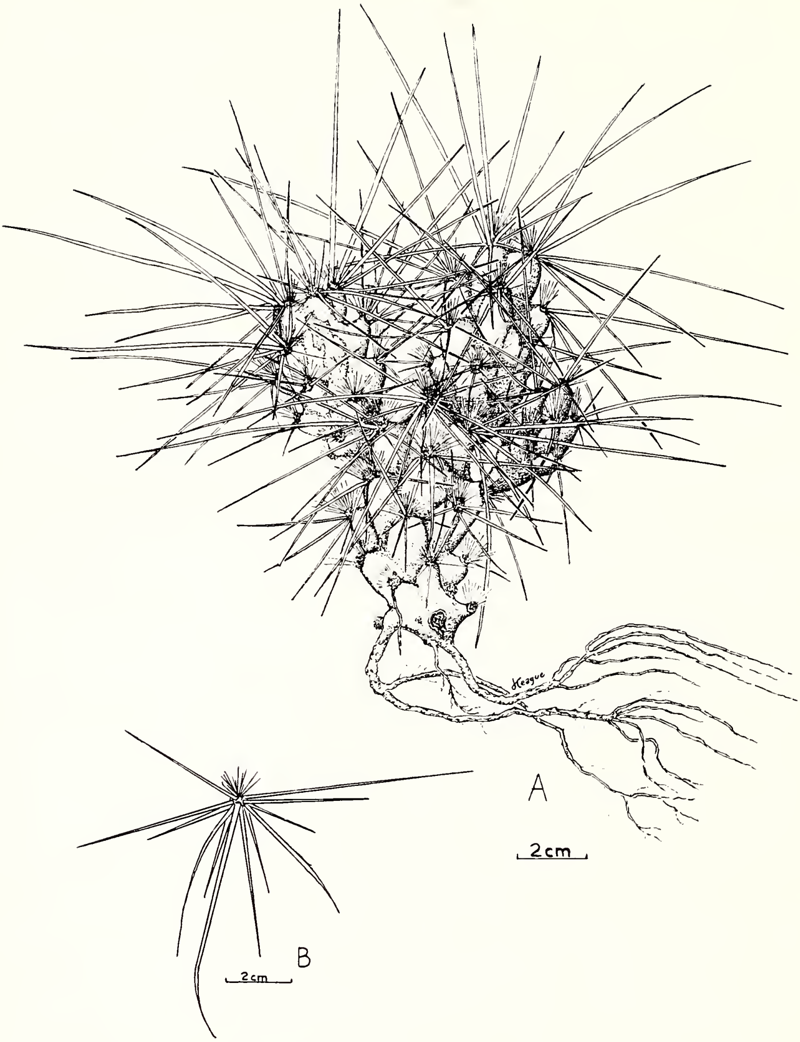

Fig. 1. *Opuntia densispina* Ralston and Hilsenbeck. A. Habit showing fibrous roots, and branching pattern of clavate stem-joints. B. Detail of spine cluster. Illustrated from live specimen *Ralston 200.*

mm wide; obovate to clavate; tubercles prominent, 15–20 mm long, 5–7 mm wide, 5 mm high, green; areoles ovate to 4 mm wide. Spines 11–14, flattened pink/white; 6–9 spines per areole 30–70 mm long with 1 central spine; 4 spines per areole shorter, 15–25 mm long, spreading, 2 spines deflexed; glochids abundant to 10 mm long. Flowers 50–70 mm long, 30–45 mm wide; petaloids in 3–4 whorls

TABLE 1. COMPARISON OF TAXA IN THE *Opuntia schottii* COMPLEX.

	O. densispina	*O. aggeria*	*O. emoryi*	*O. schottii*	*O. grahamii*
Root type	fibrous	tuberous	fibrous	fibrous	tuberous
Joint length (mm)	45–70	45–65	70–150	45–65	35–45
Tubercle size (mm)					
Length	15–20	10–20	35–50	15–20	8–12
Width	5–7	8–10	10–15	6–8	4–6
Height	5	5–7	10–12	6–8	4–6
Areole diameter (mm)	3–4	3–4	5–7	5–7	3–4
Spines/areole	11–14	7–9	11–16	8–14	7–14
Spine length (mm)	30–70	55–90	35–70	40–60	30–35
Central spine	yes	no	yes	yes	no
Chromosome number (*n*)	22	11	22	22	22
Phenology	May–Jun	Mar–Apr	May–Jun	Jun–Jul	May–Jun

grading from yellow green with central pink tinge to bright yellow in innermost petaloids; petaloids to 22 mm long, 15 mm wide, spatulate, apiculate; filaments red, 10 mm long; style cream, to 25 mm long; pericarpel obconic, 35–50 mm long, 10–25 mm wide with glochids to 5 mm long. Seeds cream to brown, 5 mm wide. $n=22$. Flowering mid May to early June.

The specific epithet is chosen to describe the dense appearance of the spine clusters of this species. As noted above, *Opuntia densispina* occurs sympatrically with *O. aggeria* in southern Brewster County, Texas, specifically in the extreme southern portion of Big Bend National Park. At first glance, *O. densispina* appears similar to *O. aggeria.* However, morphological and chromosomal differences exist between these two taxa, as well as between *O. densispina* and other taxa in the complex (Table 1).

Comparisons between *Opuntia densispina* and *O. aggeria* indicate that these taxa differ in root morphology, fibrous vs. tuberous; spines per areole, 11–14 vs. 7–9; spine length, *O. densispina* having shorter spines; chromosome number, $n=22$ vs. $n=11$; and phenology, *O. aggeria* flowering earlier than *O. densispina.* In addition, *O. aggeria* is found on loosely consolidated igneous or calcareous desert alluvium (Ralston and Hilsenbeck 1989) while *O. densispina* appears restricted to a clay substrate. *Opuntia densispina* differ from other taxa in the complex in the number of spines per areole, tubercle dimensions, root morphology, joint length, and phenology (Table 1). These differences are not uniform (i.e., in some cases such as spine length or number, there is overlap among taxa), but with respect to *O. aggeria,* the taxon found sympatrically with *O. densispina,* these characters do not overlap.

Pollen studies of the *Opuntia schottii* complex show only slight interspecific variation, mostly in grain size, number of pores and angularity of the grains (Ralston 1987). Grain size differs between *O. densispina* and *O. aggeria,* with *O. aggeria* pollen measuring 70 m in diameter and *O. densispina* measuring 105 m in diameter (Hilsenbeck and Ralston unpublished). Pollen stainability, determined by using cotton blue in lactophenol (Radford et al. 1974), and inferred viability indicate that stainability and corresponding fertility of *O. densispina* grains vary from 93 to 85%, with some samples registering 0% stainability (based on five samples at 200 grains per sample). The viable and morphologically distinctive pollen further supports the recognition of this species.

Of the remaining taxa in the complex, *Opuntia densispina* shows closest affinity to *O. emoryi* and to *O. schottii.* All three taxa possess fibrous roots, numerous spines per areole and all are tetraploid species. These species differ in joint length, tubercle dimensions and spine length with dimensions for *O. densispina* usually falling between the two other taxa (Table 1). *Opuntia densispina* is clearly a distinctive taxon worthy of specific rank. Because this cactus has been found only at its type locality, further surveys for this species is southwest Texas and adjacent Mexico are warranted, both to document variation that exists in this species and to supplement information concerning the geographic distribution of cacti found in the series *clavatae.*

ACKNOWLEDGMENTS

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GROWTH FORM DICHOTOMY IN SUBSPECIES OF *ARCTOSTAPHYLOS PENINSULARIS* FROM BAJA CALIFORNIA

Jon E. Keeley, Allen Massihi, and Robert Goar
Department of Biology, Occidental College,
Los Angeles, CA 90041

Abstract

Arctostaphylos peninsularis subsp. *peninsularis* is a crown sprouting species with massive burls that dominates much of the Sierra San Pedro Martir of northern Baja California. In the adjacent Sierra Juarez, ***A. peninsularis*** subsp. ***juarezensis*** is a non-burl-forming arborescent obligate seeder. Hypotheses are proposed to account for this marked difference in fire response.

Resumen

Arctostaphylos peninsularis subesp. *peninsularis* es una especie poseedora de tubérculo lignoso que rebrota despues de incendios y se encuentra por todo la Sierra San Pedro Martir de Baja California norte. Encuentran en las montanas adyacientes, la Sierra Juarez, ***A. peninsularis*** subesp. ***juarezensis.*** Es esta una especie arborescente la cual no posee un tuberculo lignoso ni puede rebrotar despues de los incendios. Hipotesis son proponer para explicar esta differencia en respuesta regeneracion del fuego.

Arctostaphylos peninsularis Wells has been described as a crown-sprouting species "tending to develop massive burls" or "in some individuals the burl apparently absent" (Wells 1972). Field studies reveal that this description does not adequately describe the pattern of variation present throughout the range of this species in Baja California. Extensive collections from much of the range of *A. peninsularis* indicates a remarkable geographical pattern in the presence or absence of the basal burl and it is proposed that these taxa are best treated as burl-forming and non-burl-forming subspecies.

Throughout the western face of the Sierra San Pedro Martir, between 1200 m and 2400 m, *A. peninsularis* is a burl-forming, multi-stemmed, postfire resprouting shrub. Thousands of individuals have been examined and all plants in the San Pedro Martir are burl-forming resprouting shrubs (Keeley unpublished data). In marked contrast, throughout the adjacent Sierra Juarez to the north, *A. peninsularis,* is a non-burl-forming, typically arborescent, postfire obligate-seeder; extensive collections from the central to northern portion of the Sierra Juarez plateau have revealed no exceptions to this rule.

This growth form difference is the only characteristic that consistently separates these taxa; herbarium specimens from the Sierra

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San Pedro Martir and the Sierra Juarez are indistinguishable. In light of the importance of the burl to *Arctostaphylos* taxonomy and the well-defined geographical distribution of sprouters and seeders, these differences are best treated as subspecies.

ARCTOSTAPHYLOS PENINSULARIS P. V. Wells subsp. PENINSULARIS, Madroño 21:268. 1972.—TYPE: MEXICO, Baja California, gravelly hillside 1 mile east of Corral de Sam, elevation 2200 m, Sierra San Pedro Martir, near 31°03′N, 115°33′W, *Reid Moran 15531* (SD).

Burl-forming shrub that resprouts vigorously after fire, often forming large clones on the western face of the Sierra San Pedro Martir, from 1200 m to 2400 m, interspersed with other chaparral shrubs at the lower elevations, but often dominating entire slopes at the higher elevations.

Arctostaphylos peninsularis subsp. **juarezensis** J. E. Keeley, subsp. nov.—TYPE: MEXICO, State of Baja California, Cerro Hanson, 1625 m, Sierra Juarez, 32°04′N, 115°55′W, 14 May 1989, *J. E. Keeley 11145* (holotype, LOC).

Frutices arborescentes, 2–4 m alti, caudex basi etumescens, trunco manifeste; cortex laevis ruber.

Non-burl-forming shrub, either single-stemmed to 4 m or lower and multi-stemmed and mounded due to rooting of branches. Obligate-seeder, not resprouting after fire. In other respects as in the nominal subspecies. Restricted to boulder-strewn rocky outcrops scattered throughout the Sierra Juarez plateau.

PARATYPES: MEXICO, State of Baja California, growing amongst boulders of Cerro El Toro, 20 km N of Cerro Hanson, 1540 m, Sierra Juarez, 32°13′N, 115°59′W, 26 July 1992, *J. E. Keeley, A. Massihi, R. Goar 18174* (LOC); boulder-strewn outcrop, 10 km S of Cerro Hanson, 1640 m, Sierra Juarez, 31°59′N, 115°51′W, 25 July 1992, *J. E. Keeley, A. Massihi, R. Goar 18054* (LOC).

The striking difference in postfire response of these two taxa in adjacent mountain ranges requires closer analysis. The Sierra San Pedro Martir is a rugged range of steep slopes, much of the crestline extending to 2900 m. Here, *Arctostaphylos peninsularis* subsp. *peninsularis* dominates in a belt between 1500 and 2200 m, in places creating pure stands of resprouting manzanita.

The Sierra Juarez is a plateau of about 1500 m with widely disjunct peaks of 1600–1700 m. ***Arctostaphylos peninsularis*** subsp. ***juarezensis*** is restricted to the disjunct boulder-strewn peaks, often separated by 10 km or more. On the flats of the plateau, between the peaks, *A. peninsularis* is absent and is replaced by *A. pungens* H.B.K. On some outcrops, *A. peninsularis* coexists with two other congeneric species, *A. pringlei* Parry (subsp. *pringlei*) and *A.* cf. *parryana* Lemmon. It is curious that all four of the manzanita species in the Sierra Juarez share, not only the same initial letter in the epithet, but the feature of being non-burl-forming obligate-seeders; crown-sprouting manzanitas are apparently absent from the main portion of this mountain range.

We hypothesize that the obligate-seeding mode has been selected in the Sierra Juarez due to a lower probability of burning than is the case in the Sierra San Pedro Martir. It is to be expected that the much lower elevation of the Sierra Juarez leads to a lower fire frequency due to a lesser incidence of lightning ignitions (Keeley 1982). Regardless of the frequency of ignitions, *A. peninsularis* in the Sierra Juarez are unlikely to burn very frequently because of their restriction to boulder-strewn peaks, where more than 30% of the ground cover is rock. Thus, ***A. peninsularis*** subsp. ***juarezensis*** remains undisturbed by fire for much longer periods than is likely the case for *A. peninsularis* subsp. *peninsularis* in the Sierra San Pedro Martir.

Field observations confirm these ideas as most ***A. peninsularis*** subsp. ***juarezensis*** are quite massive, often with trunks in excess of 50 cm diameter and probably greatly exceeding 50 yr of age. This is noteworthy in light of the fact that Baja California has no active program of fire suppression (Minnich 1983), and thus these manzanitas are not currently experiencing an unnaturally low frequency of fires; indeed, because fire prevention is not practiced, the frequency of fires may be even higher than prior to human occupation of the region. In contrast, observations in the Sierra San Pedro Martir reveal that most populations of *A. peninsularis* subsp. *peninsularis,* particularly at the higher elevations, have experienced fire within the last decade or two. Nowhere were massive, ancient individuals observed as seen in the Sierra Juarez.

These observations support the hypothesis (Keeley and Zedler 1978) that, in these relatively slow growing woody plants, the obligate-seeding mode is well adapted to withstand long fire-free periods and poorly adapted to very high fire frequencies.

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A NEW ANNUAL SPECIES OF *MINUARTIA* (CARYOPHYLLACEAE) FROM OREGON AND CALIFORNIA

ROBERT J. MEINKE
Restoration Ecology and Plant Conservation
Biology Cooperative Project,[1]
Department of Botany and Plant Pathology,
Oregon State University, Corvallis, OR 97331

PETER F. ZIKA
Herbarium, Oregon State University,
Corvallis, OR 97331

ABSTRACT

Minuartia cismontana is described as a new species from the lower slopes of the Cascade Mountains, Sierra Nevada, and Coast Ranges of Oregon and California. It appears most closely related to *Minuartia californica* and *M. pusilla,* as suggested by macromorphological traits and seed microsculpture. The new species is distinguished chiefly by a stiffly erect habit, elongate pedicels and internodes, narrowly attenuate and prominently nerved sepals, hyaline sepal apices, and petals that equal or only slightly exceed the calyx. The flowering phenology of *M. cismontana* is overlapped by *M. pusilla* but is normally later than *M. californica.* Extant occurrences of the new species in Oregon are known only from ultramafic substrates. The range of *M. cismontana* in California appears largely coincidental with the distribution of serpentine outcrops, based on herbarium records and geologic maps.

Recent botanical investigations of ultramafic outcrops in the North Umpqua River basin have resulted in an increased understanding of rare and localized species of southwestern Oregon (Godfrey and Callahan 1988; Fredricks 1989; Shelly 1989). During a field trip associated with one of these studies several populations of a locally common annual *Minuartia* were discovered and tentatively identified as *M. californica.* The plants deviated from published descriptions of that species, however, and were growing farther north than *M. californica* had been previously reported (Maguire 1951; Peck 1961; Munz 1968). Moreover, they were restricted to serpentine substrates, leading to speculation that they might represent another North Umpqua endemic.

Specimens of the putative new species were collected for study, including seeds that were used to cultivate plants in the greenhouse. Pressed material and live plants were compared with herbarium collections of known annual species of *Minuartia* from North America, particularly *M. californica* and *M. pusilla,* the two taxa that most

[1] A collaborative research unit of Oregon State University and the Oregon Department of Agriculture.

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resembled the unknowns based on the literature. It was concluded that the Oregon plants were members of an undescribed species that, rather than being a local endemic, occurs intermittently from the southern foothills of the Cascade Mountains to central California. The present paper provides a description for the new species, contrasts it with similar and potentially related taxa, and includes a key to the annual species of *Minuartia* native to western North America.

Minuartia cismontana Meinke and Zika, sp. nov. (Fig. 1).—TYPE: USA, Oregon, Douglas Co., gravelly serpentine meadow, Ace Williams Mountain, T26S R3W Sect. 27 NE¼, ca. 630 m, 30 May 1989, *Meinke 5757* (holotype, OSC; isotypes, CAS, MO, NY, RM, RSA, UC, US).

Plantae annuae, glabrae; *caulibus* (5–)8–20(–25) cm longis, erectis; *foliis* 2–7(–9) mm longis, 0.5–1.2(–1.8) mm latis, lance-linearibus, (1–)3-nervis; *inflorescentiis* dichotomis; *pedicellis* (7–)10–30(–35) mm longis, capillaribus; *sepalis* 3.2–5.5 mm longis, linearibus vel lanceolatis, scarioso-marginatus, 3(–5)-nervis; *petalis* 4–6.5 mm longis, oblanceolatis-cuneatis vel elliptico-oblongis; *capsulis* 3.5–5.8 mm longis, valvis 3; *seminibus* 0.7–1.0 mm longis, subreniformis, minute papillatis.

Glabrous *annual,* herbage green or reddish-purple, well-developed specimens wiry and freely branched above; *stems* erect, (5–)8–20(–25) cm tall, dichotomously branched from near the base, with middle and upper internodes ranging from 1.5–3.5 cm long; *leaves* few, green to bluish-green, scarious-margined below, withered or often ± tenacious at the stem base, scattered and persistent along the axes, 2–7(–9) mm long, 0.5–1.2(–1.8) mm wide, lance-attenuate to linear, acute to mucronate, 1–3-nerved; *inflorescence* an open cyme; *flowers* nyctitropic; *pedicels* capillary, elongate, (7–)10–30(–35) mm long in fruit, erect or occasionally arcuate; *sepals* 3.2–5.5 mm long, lance-linear to lanceolate, tips sharp and hyaline, colorless or rarely anthocyanic, narrowly acute to long-attenuate, scarious-margined the entire length, possessing 3(–5) prominently ridged nerves that predominate the middle chlorophyllous portion of the sepal, these especially raised at the thickened, ± squarrose base, the primary nerve extending to the hyaline apical portion, the lateral nerves nearly as long, ± immediately adjoining the scarious margins; *petals* clear white, persistent after pollination, 4–6.5 mm long, oblanceolate-cuneate to oblong-elliptic, equal to or up to ca. one-fourth (–one-third) longer than the sepals, inserted with the stamens on a thickened receptacle; *nectaries* present, alternating with the stamens on the floral disk; *styles* 3; *capsule* 3.5–5.8 mm long, ± ovoid, 3-valved, ca. equalling the length of the sepals or slightly shorter; *ovules* 15–25; *seeds* 5–15, 0.7–1.0 mm long, brown or reddish, asym-

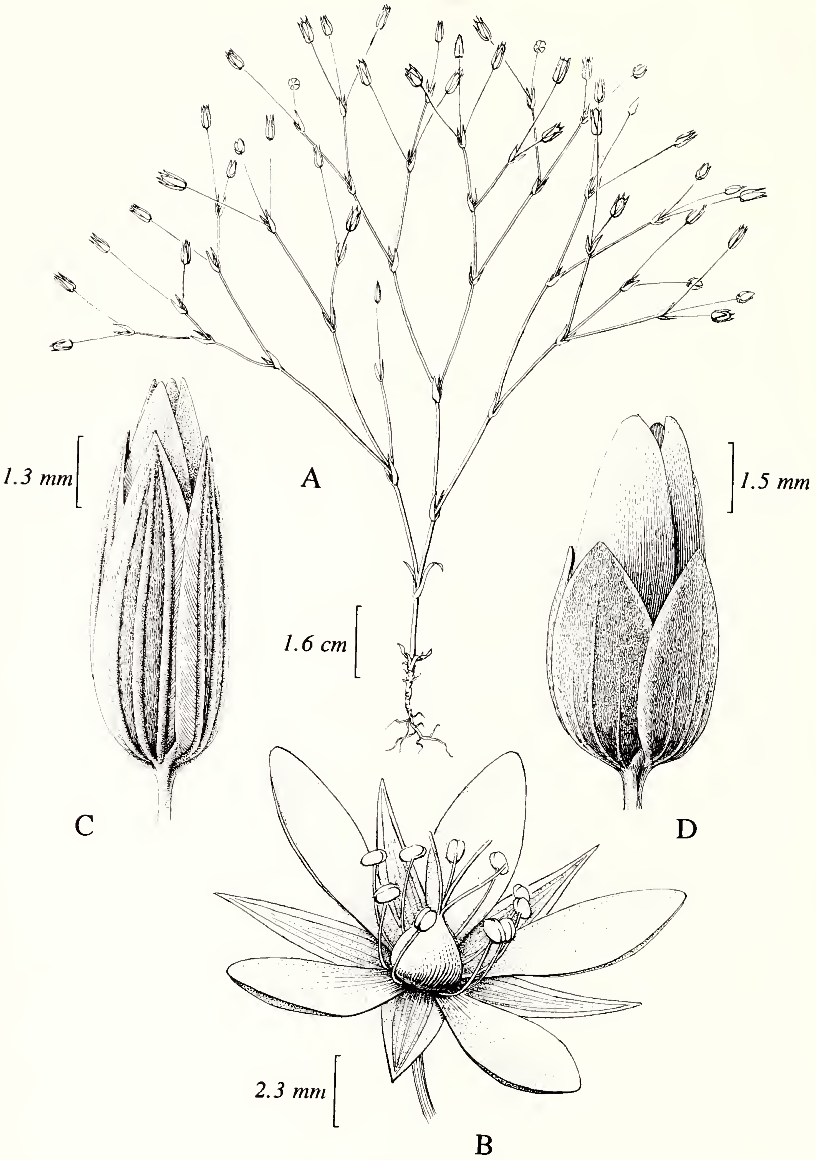


FIG. 1. *Minuartia cismontana.* A. Habit. B. Close-up of open flower. C. Close-up of closed flower, detailing petal length and sepal morphology. In extreme specimens, the ribbed nerves of the sepals become crowded and closely parallel. *Minuartia californica.* D. Close-up of closed flower.

metrically reniform with a prominent radicle, testa minutely foveolate-papillate, cell margins sinuous.

Paratypes. USA, California: Amador Co., Hamm's (Station), 5000 ft, May 1895, *Hansen 1100* (DS, MO). Calaveras Co., Mokelumne Hill, *Blaisdell s.n.* (CAS). El Dorado Co., Armstrong's Station, 5300 ft, 13 Jun 1895, *Hansen 1100* (DS); Institute of Forest Genetics, 3 mi E of Placerville, 2500 ft, 28 Apr 1943, *Robbins 1043* (CAS); 2 mi W of Georgetown, on road to Greenwood, 28 Apr 1956, *Raven and Robbins 9077* (CAS); E slopes of Bass Lake, 2 mi NE of Clarksville, 21 May 1959, *Crampton* 5252 (AHUC). Humboldt Co., Kneeland Prairie, 2500 ft, 4 May 1913, *Tracy 4068* (WTU, US), 30 May 1921, *Tracy 5479* (UC, WS, POM); Trinity River Valley, near Willow Creek, 500 ft, 30 Apr 1922, *Tracy 5991* (UC); McClellan Mountain, 2700 ft, 30 May 1925, *Tracy 7040* (UC); Laribee Valley, 25 May 1930, *Parks and Tracy 866* (NY, CAS, DS, MO, UC, RSA); ridge top near Harris, 3000 ft, 13 Jun 1948, *Tracy 18055* (WTU, UTC). Lake Co., near Lakeport, 12 May 1903, *Baker 2957* (US, POM, MO, RM, UC, JEPS [on UC 75355]); Jordan Park, 1 May 1932, *Jussell s.n.* (POM); near Lakeport, 23 May 1933, *Henderson 15238* (ORE). Mendocino Co., Tomki Road, 11 km N of Calpella, 550 m, 26 May 1981, *Smith 6410* (HSC). Merced Co., 5 mi N of Snelling, 4 May 1937, *Hoover 2055* (UC). Monterey Co., Santa Lucia Mountains SW of Junipero Serra Peak, 2300 ft, 13 May 1980, *Ertter and Strachan 3377* (CAS, WTU, UTC, RM, RSA, NY). Placer Co., E end of Ralston Ridge (T14N R13E Sect. 28), 5100 ft, 28 May 1978, *Stebbins 7895* (CAS). San Francisco Co., Lake Merced, 26 Apr 1895, *Cannon s.n.* (CAS). San Luis Obispo Co., 3.2 mi NE of Highland School, 1500 ft, 26 Apr 1937, *Hendrix 98* (UC, RSA); Yazo Creek district, N of Pozo, 20 Apr 1947, *Hoover 6990* (DS, CAS, SD, RSA); road between El Dorado School and Pozo, 7 mi N of Pozo, 25 May 1955, *Ferris 12836* (DS, WTU, RSA); N Traffic Way, Atascadero, 20 Apr 1958, *Hardman 3055* (CAS, SBBG); hills between the San Juan River and the Carissa Plains, 28 Apr 1958, *Hardman 3136* (POM); Bee Rock Canyon, 12 May 1960, *Bacigalupi 7429* (RM, WTU, UTC). Tehama Co., 9 mi E of Paynes Creek, 3300 ft, 12 May 1954, *Barneby and Howell 11484* (CAS). Trinity Co., Weaverville, 3400 ft, 30 May 1880, *Kleeburger s.n.* (CAS). Oregon: Douglas Co., Umpqua Valley, Apr 1881, *Howell s.n.* (ORE); Oakland, Apr 1881, *Howell s.n.* (NY); along BLM Road 13.0 in T28S R4W Sect. 1, 23 Jun 1978, *Crowder 440* (BLM—Roseburg District); NE of Watson Mountain, above Douglas Co. Road 17, 1200 ft, 10 Jun 1984, *Fredricks 263* (OSC); type locality, 29 Apr 1987, *Zika and Holmes 10216* (BLM—Roseburg District); Beatty Creek Research Natural Area, T30S R6W Sect. 19, 1200 ft, 5 Jun 1987, *Hopkins 1448* (Douglas County Museum). Lane Co., near Eugene, 2 May 1925, *Constance s.n.* (DS); Lorane Road, 11 May

1930, *Henderson 12258* (ORE), 17 May 1931, *Henderson 13540* (UC); Crowe Road, Jun 1933, *Henderson 15182* (DS).

TAXONOMIC RELATIONSHIPS

Vegetative and floral morphology. Previous collections of *Minuartia cismontana* have usually been identified as *M. pusilla* or *M. californica* and both of these taxa bear a resemblance to the new species. While *M. cismontana* has floral dimensions reminiscent of *M. californica,* it could be best described as a larger, open-flowered version of the poorly known *M. pusilla,* an inconspicuous and apparently autogamous species with which it shares the consistently lance-linear, attenuate sepals and elongate pedicels and internodes. Sepals of *Minuartia cismontana* are distinctive in combining a sharp, narrow, hyaline sepal apex with a prominently tri-nerved, chlorophyllous center; the species is also unique in having petals that equal or only slightly exceed the calyx (Fig. 1B, C).

Minuartia cismontana plants have capillary, often wiry stems and branches (Fig. 1A) and are typically several times larger than *M. pusilla.* The stiffly dichotomous branching of the new species is a prominent feature in mature specimens not stunted by drought. The diminutive *M. pusilla* differs further in having petals that are considerably shorter than the small calyx (or absent) and single-nerved sepals and leaves. *Minuartia californica* is decidedly polymorphic. However, most examples of this species also tend to be smaller than *M. cismontana,* even when apparently well-watered, and typically possess blunt, inconspicuously nerved sepals that invariably have pigmented, non-hyaline tips (Fig. 1D). Although *M. californica* is described as having rounded, obtuse, or "acutish" sepals (Maguire 1951; Peck 1961; Munz 1968), a few, mostly depauperate individuals have been collected with narrowly acuminate calyx segments, particularly near the southern Sierra Nevada and along the central California coast. These plants are distinguished from *M. cismontana* by the corolla length, which surpasses the calyx by one-half or more, the relatively small sepals that rarely exceed 3 mm and lack a hyaline tip, and a diffuse habit less than 7 cm high.

Minuartia cismontana might also be mistaken for *M. douglasii* and occasionally co-occurs with this species. *Minuartia douglasii* is recognized by glandular pubescence (which is sometimes sparse), broadly ovate sepals, and flexible, linear leaves up to 25 mm long. It has wafer-like, prominently wing-margined seeds (Fig. 6), an unusual trait for the genus that suggests *M. douglasii* is not a particularly close relative of *M. cismontana. Minuartia tenella* (=*M. stricta* var. *puberulenta*), an annual or short-lived perennial of mesic sites in the Pacific Northwest, has acuminate sepals and petal length comparable to *M. cismontana.* It can be distinguished by a glandular-pubescent inflorescence and conspicuous axillary leaves.

TABLE 1. MORPHOLOGICAL CHARACTERS USED IN PRINCIPAL COMPONENTS ANALYSIS OF *Minuartia cismontana* AND *M. californica*. Sixteen populations of *M. cismontana* and 32 populations of *M. californica* were sampled. The numbers following each trait indicate the sample size used to calculate an average score for each population. See discussion in text.

1. Sepal length (10).
2. Ratio of sepal length to petal length (10).
3. Length of internode beyond first stem branch (10).
4. Post-anthesis pedicel length (10).
5. Plant height (2).
6. Ratio of sepal length to capsule length (10).
7. Capsule length (10).
8. Style length (10).
9. Length of leaf at first stem branch (10).
10. Sepal length to width ratio (10).
11. Length of basal stem prior to first branch (2).
12. Ratio of lateral sepal nerve length to primary nerve length (10).
13. Width of scarious sepal margin (10).
14. Shape of sepal tip (1 = long-attenuate or acuminate; 2 = acute; 3 = obtuse to rounded) (10).
15. Shape of cauline leaf tip (1 = acute; 2 = mucronate; 3 = obtuse) (10).

Phenetic analysis. Minuartia cismontana is most often confused with *M. californica* and will generally key to this species using most floristic references. To evaluate the morphological relationship of these taxa a principal components analysis (PCA) of 48 populations was conducted, using 15 vegetative and floral attributes commonly employed in *Minuartia* taxonomy (Table 1). Sixteen collections of *M. cismontana* and 32 of *M. californica* were included, selected from across the range of both species. Each population sample was represented by a single herbarium sheet having a minimum of two complete specimens.

The selected morphological traits were measured for each population and the taxa ordinated along the axes of the first two principal components. The resulting PCA diagram (Fig. 2), describing 57.4% of the variation contained in the original data set, clearly indicates that *M. cismontana* and *M. californica* are separable phenetically on the basis of the traits used in the analysis. Characters heavily (and more or less equivalently) weighted along the first axis are 1) the ratio of lateral sepal nerve length to primary nerve length; 2) the ratio of sepal to petal length; 3) plant height; and 4) post-anthesis pedicel length. This confirms the value of sepal, pedicel, and stem measurements in classifying collections of the two species.

Seed morphology. Seed coat microsculpture and seed shape, conservative traits successfully used in the taxonomy of *Minuartia* (Wofford 1981), are in agreement with a proposed alliance of *M. cismontana, M. pusilla,* and *M. californica.* Seeds of the three species are unequally reniform and foveolate-papillate (Figs. 3–5), often with

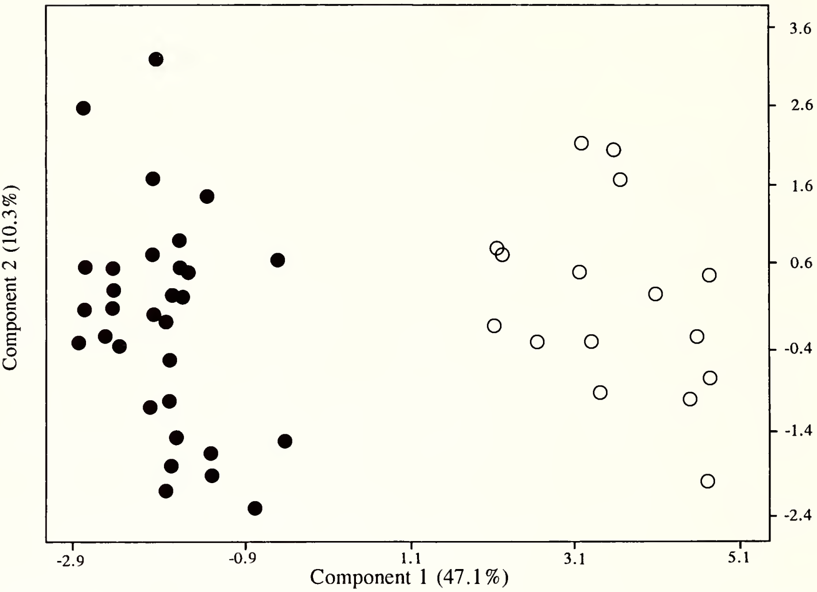
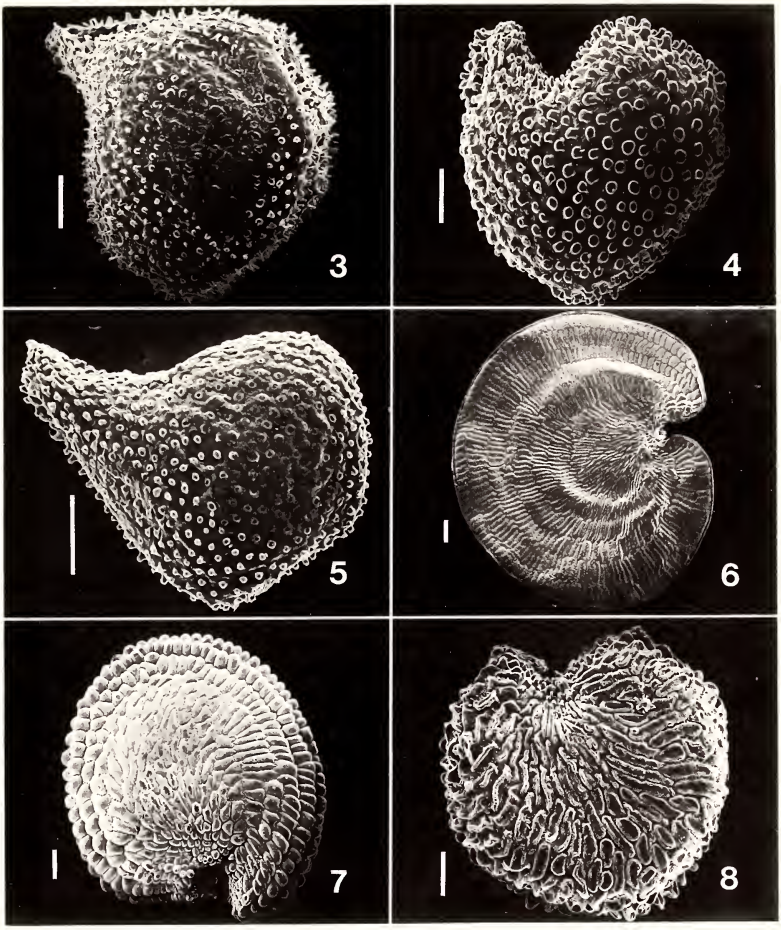


FIG. 2. Plot of the first two principal components resulting from the phenetic analysis of 15 morphological traits (Table 1) of *Minuartia cismontana* and *M. californica.* Open circles = *M. cismontana*; solid circles = *M. californica.* The first axis depicts 47.1% and the second 10.3% of the variation represented in the original data set. See discussion in text.

a prominent radicle. They are commonly angled on the edges due to being pressed together in the capsule but are usually terete and never significantly flattened. Those of *M. californica* appear to be distinctive in having fewer, and notably larger, testal processes. The seeds of the other annual *Minuartia* in western North America are readily distinguished from the preceding three species, being broadly reniform to somewhat asymmetric and lacking tubercles (Figs. 6–8). They are more or less lenticulate and range from moderately to severely compressed.

Reproduction and phenology. Seeds of *Minuartia cismontana* collected at the type locality were dormant when capsules dehisced. They germinated readily at room temperature after undergoing moist, dark stratification for three to eight weeks at 2–3°C. It is not known how the germination ecology of *M. cismontana* compares with related species.

Observations of field and cultivated *Minuartia cismontana* plants suggest that the species is a facultative outcrosser. Flowers open on sunny days and attract small flies and bees to the nectar glands located along the receptacle. Nectar droplets accumulated in flowers



FIGS. 3–8. Scanning electron micrographs of seeds of annual *Minuartia* species from western North America (scale bars = 0.2 mm). 3. *M. cismontana.* 4. *M. californica.* 5. *M. pusilla.* 6. *M. douglasii.* 7. *M. howellii.* 8. *M. tenella.*

of greenhouse grown plants and were evident to the unaided eye. Anthers dehisce one to two days after anthesis, at which time self-pollination may occur when corollas close during the evening. Seeds were produced by *M. cismontana* plants in the greenhouse, indicating that the species is genetically self-compatible.

The tiny flowers of *Minuartia pusilla* are probably exclusively self-pollinated since they lack nectar glands and occasionally petals, and their anthers open prior to floral expansion. The chasmogamous-flowered *M. californica* may have a breeding system similar to that postulated for *M. cismontana* but there was no opportunity to examine living plants of this species. Inspection of herbarium material of *M. californica* shows that flowers preserved shortly after opening often have undehisced anthers.

Minuartia cismontana blooms from late April through mid-June, depending on elevation and latitude. This contrasts with *M. californica,* which usually flowers from late February to mid-April, or occasionally into early May. *Minuartia pusilla* has been collected in flower from April through July. All three species are strict ephemerals, their germination and longevity greatly dependent on precipitation before and during the growing season.

Distribution and habitat. Minuartia cismontana is known from Douglas County, in southwestern Oregon, south to at least the vicinity of San Luis Obispo in central California. Historical collections place *M. cismontana* as far north as Lane County, Oregon, south of Eugene near the Douglas County line. Populations are widely but sporadically distributed and have been recorded from the west slope of the southern Cascade Range in Oregon, the southern Oregon Coast Range, the west slope of the north-central Sierra Nevada, and in or near the southern and northern Coast Ranges of California. The relative distributions of *Minuartia cismontana, M. californica,* and *M. pusilla* in Oregon and California are mapped in Figure 9.

Reported elevations for *Minuartia cismontana* extend from (150–) 400–1700 m. Low elevation sites (below 500 m) generally exist at the northern end of the range, mostly beyond the geographic limits of *M. californica.* Two unusual lower elevation collections of *M. cismontana,* from San Francisco and Merced counties, California, are mixed with specimens of *M. californica* on the same herbarium sheet. These are the only accounts of potential sympatry between the species. Scrutiny of the San Francisco County material, however, shows that the *M. cismontana* plants were infected with a mold while those of *M. californica* were not. This implies differences in the storage times for the two species prior to pressing, suggesting they may have actually been collected at different localities. Label data for both the San Francisco and Merced County collections are sparse and lack significant habitat information and precise elevations.

Minuartia cismontana frequents vernally moist slopes and ridges,

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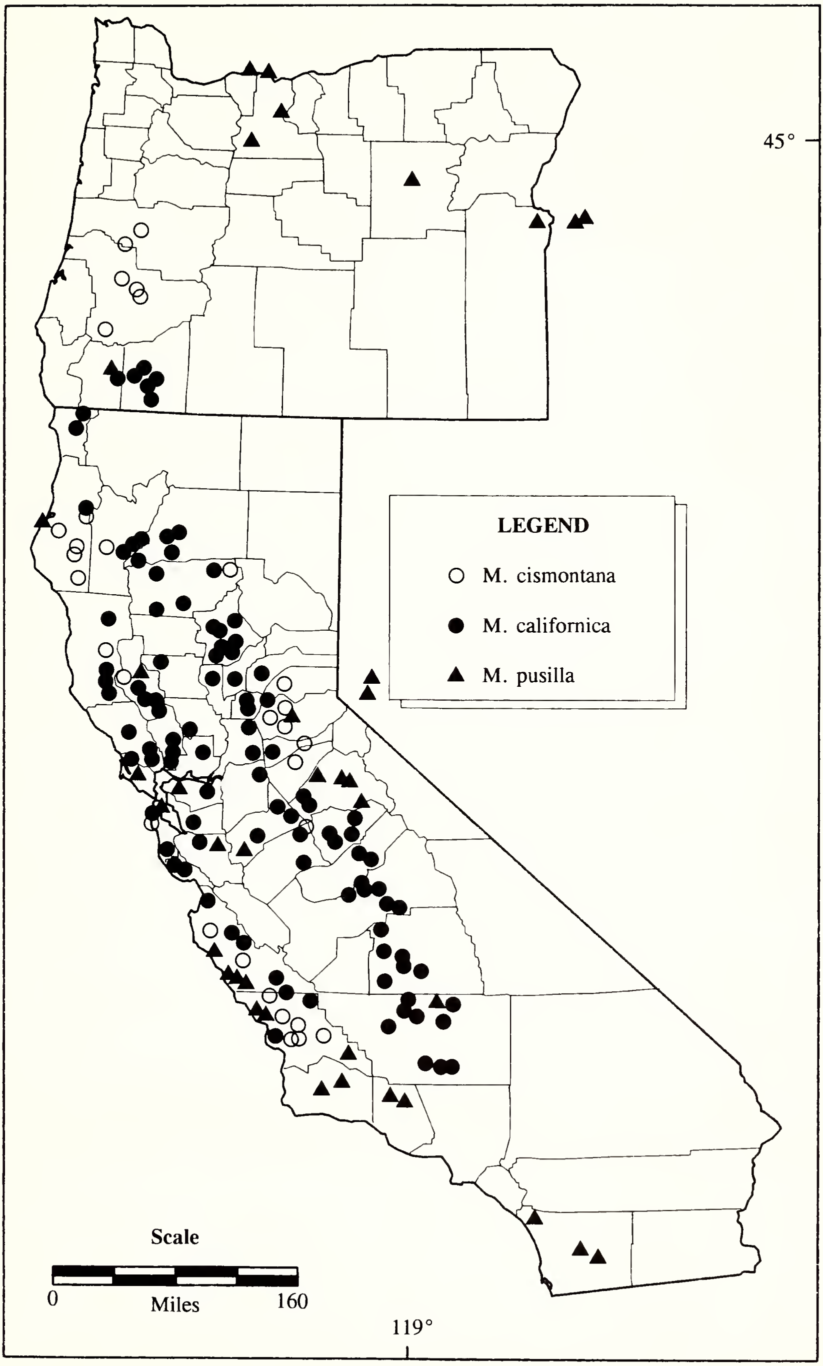
FIG. 9. Distribution of *Minuartia cismontana, M. californica,* and *M. pusilla* in Oregon and California, based on herbarium data. Each symbol may represent one or more populations. *Minuartia cismontana* and *M. californica* are endemic to Oregon and California. The range of *M. pusilla* includes a few scattered stations in the Great Basin, not all of which are shown here.


45°
LEGEND
○ M. cismontana
● M. californica
▲ M. pusilla
Scale
0
Miles
160
119°

apparently in well-drained microsites subject to extended drought by late spring or early summer. It is typically a foothill to low montane species, occurring in or near dry woodland or chaparral. In Oregon, common associates include *Agoseris heterophylla, Alchemilla occidentalis, Allium parvum, Calochortus tolmiei, Cerastium arvense, Epilobium minutum, Minuartia douglasii, Sagina occidentalis,* and *Silene hookeri,* as well as the rare endemics *Calochortus umpquaensis* and *Phacelia capitata. Minuartia californica* is primarily a lowland species, found throughout the Central Valley and adjacent areas of California, then irregularly north to the Rogue and Illinois River valleys of extreme southern Oregon. Recorded habitats include vernal pools, rocky fields, roadsides, and grassy slopes, occasionally on serpentine. Although the geographic ranges of *M. cismontana* and *M. californica* coincide to some extent, particularly towards the Pacific Coast, populations of the two species are generally separated by elevation and phenology in areas of apparent overlap, with *M. californica* mostly occurring below 650 m and senescing by early May. *Minuartia californica* is occasionally reported up to ca. 1400 m, but this is limited to a few localities in the southern Sierra Nevada, from Fresno County south. *Minuartia pusilla* has a broader distribution, ranging through much of California and Oregon into Washington, Idaho, Nevada, and southwestern Utah. It is infrequently recorded and occurs in a variety of primarily xeric habitats, often in waste areas or otherwise sterile sites.

In Oregon, extant populations of *Minuartia cismontana* occur only on serpentine outcrops. Herbarium labels confirm that some of the California populations are from serpentine as well, or suggest such an affiliation by describing topography and substrata consistent with serpentine landscapes. Additional circumstantial evidence supporting an ultramafic association for the new species is derived from its geographic pattern in California (Fig. 9). The range of *M. cismontana* largely coincides with the general distribution of serpentine as recorded on geologic maps (Kruckeberg 1984), both in the Coast Ranges and the Sierra Nevada foothills. It is interesting that many of the sites for the new species appear to correlate with comparatively minor ultramafic outcrops, and that no populations have been recorded from the botanically rich and heavily collected Klamath-Siskiyou serpentines.

Conclusions. Minuartia cismontana has been overlooked as a distinct taxon since it was first collected in 1880. The scattered occurrence of the new species and its similarity to the variable *Minuartia californica* probably has contributed to this. Morphological evidence also suggests an affinity between *M. cismontana* and *M. pusilla.* On the basis of floral, seed, and phenological characters, these species may be the most closely related of the trio. Further study is required to evaluate this, and to estimate the relationships of *M. cismontana* and its annual relatives with perennial members of the genus. Although apparently not rare in California, *M. cismontana* is uncommon and local in Oregon, and may merit designation as a sensitive species in that state.

KEY TO ANNUAL SPECIES OF *MINUARTIA* IN WESTERN NORTH AMERICA

a. Plants glandular-pubescent above; cauline leaves (5–)10–30 mm long; seeds ± flattened, reniform and often lenticular, lacking a prominent radicle, tessellate to crested, never papillate
  b. Sepals ovate, acute to obtuse; cauline leaves simple or with reduced axillary fascicles; from southwest Oregon to northern Baja California, mostly away from the immediate coast
    c. Leaves and sepals evidently 3-nerved; petals broad, obovate; stems greenish; seeds flat, smooth, broadly winged; widespread .... *M. douglasii* (Fenzlex Torr. & Gray) Mattf.
    c′. Leaves and sepals obscurely nerved, or lacking nerves altogether; petals oblong; stems reddish; seeds not strongly flattened, never winged, with crested cell margins; local in Josephine County, Oregon and Del Norte County, California .... *M. howellii* (S. Wats.) Mattf.
  b′. Sepals lance-attenuate; cauline leaves prominently fasciculate; often coastal, from central Oregon north to British Columbia ... *M. tenella* (Nutt.) Mattf.
a′. Plants glabrous throughout; cauline leaves 3–8(–10) mm long; seeds terete, sometimes with angled edges, not flat or lenticular, asymmetrically reniform with a prominent hooked radicle, distinctly papillate
  d. Petals inconspicuous, < sepals or absent; plants dwarf, rarely > 5 cm in height; leaves and sepals generally with a single, often faint nerve; a widespread species, usually in dry habitats .... *M. pusilla* (S. Wats.) Mattf.
  d′. Petals conspicuous, ≥ the sepals; plants (3–)5–25 cm tall; leaves and sepals-prominently to obscurely 3-nerved
    e. Petals exceeding calyx by ≥ one-half; sepals green-tipped, obtuse to weakly acute or occasionally ± acuminate, faintly 3-nerved, the lateral nerves or ribs often obscured, rarely extending to the apex, separated from the scarious border by a strip of green tissue; longest fruiting pedicels 5–15(–20) mm long; flowering mostly March to April *M. californica* (Gray) Mattf.
    e′. Petals equal to or exceeding the calyx by about one-fourth; sepals sharply hyaline tipped, narrowly acute to usually attenuate, boldly 3(–5) nerved, the dorsal ribs raised and ± crowded, parallel below and converging near the apex, the lateral nerves bordering the scarious margin; fruiting pedicels (7–)10–30(–35) mm long; flowering mostly May to early June .... *M. cismontana* Meinke & Zika

ACKNOWLEDGMENTS

We thank Nancy Fredricks and Patricia Turcotte for field assistance in the North Umpqua River area; Teresa Magee, Ken Chambers, Ron Hartman, and Tom Kaye for commenting on the manuscript; John Megahan, for preparing the line illustrations; the staff of the Douglas County (Oregon) Natural History Museum, for permitting the evaluation of herbarium specimens; Russell Holmes, for permitting study and collection of *M. cismontana* from federal lands in Oregon; Al Soeldner, for technical assistance with electron microscopy; and Aaron Liston, for providing access to the Oregon State University (OSC) and the Willamette University (WILLU) herbaria.

We are grateful to the curators of the following institutions for loaning specimens or providing label data: AHAC, BRY, CAS, CHSC, CPH, DAV, DS, FSC, HSC, ID, JEPS, LA, MO, NY, OBI, ORE, POM, RM, RSA, SBBG, SD, SOC, UC, US, WS, and WTU. The Oregon Department of Agriculture supported this research through Plant Systematics and Conservation Biology Program funding.

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A RE-EVALUATION OF THE GENUS *CREMASTOPUS* (CUCURBITACEAE)

DENIS M. KEARNS[1]
Department of Botany, University of Texas,
Austin, TX 78713

C. EUGENE JONES
Department of Biological Science,
California State University,
Fullerton, CA 92634

ABSTRACT

Cremastopus, a small cucurbit genus, differs from *Cyclanthera* by only one character, single-seeded fruits. The presence of numerous shared characters between the two taxa indicates that the species of *Cremastopus* should be transferred to *Cyclanthera.*

RESUMEN

Cremastopus, un genero pequeño de Cucurbitaceae, se distingue de *Cyclanthera* por solo un caracter, frutos de una sola semilla. La presencia de caracteristicas numerosas en comun entre los dos grupos indica que las especies de *Cremastopus* deben de transferirse a *Cyclanthera.*

Cremastopus P. Wils., established in 1962, is said to differ from the closely related *Cyclanthera* Schrader by the possession of single-seeded fruits. The two taxa share many distinctive characters, however, and the maintenance of the former entity as a distinct genus is not justified. The only difference between *Cremastopus* and *Cyclanthera* is that the former usually is single-seeded. Both have the same unique stamen morphology, the same type of oblique fruits with elongate placentae, and a very similar overall aspect.

Cyclanthera and *Cremastopus* are the only taxa in the tribe Cyclanthereae with the anther thecae in a single, unfolded ring. Single anther thecae are found in other Cyclanthereae (*Pseudocyclanthera* Mart. Crov. and *Rytidostylis* Hook. & Arn.), but in these genera the thecae are variously folded. The androecium in the African *Cyclantheropsis* Harms (tribe Zanonieae) has a superficial resemblance to that of *Cyclanthera,* but instead of being a single unbroken ring, it is composed of two thecae joined end to end (Jeffrey 1967). The similar appearance of the anthers of the two distantly related genera is obviously a case of convergent evolution.

The name *Cremastopus* apparently is in reference to the structure that Wilson calls an elongate funiculus. This is equivalent to the

[1] Present address: Missouri Botanical Garden, POB 299, St. Louis, MO 63166

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placental arm found in *Cyclanthera* and the related genera *Elateriopsis* Ernst, *Hanburia* Seemann, *Pseudocyclanthera,* and *Rytidostylis* (Kearns in preparation). These genera have explosively dehiscent fruits in which the placental arm functions as a catapult, thereby dispersing the seeds. The fruits of *Cremastopus rostrata* Paul G. Wilson and *C. minimus* (S. Watson) Paul G. Wilson are also explosively dehiscent.

The slight difference in ovule number between *Cyclanthera* and *Cremastopus* breaks down upon close examination. In some species of *Cyclanthera,* the fruits are few to single-seeded, while the fruits of *Cremastopus rostrata* have either one or two seeds (Jones 1969).

Because the two genera share many unique characters and have no major character differences, the two named species of *Cremastopus* are hereby placed in synonymy under *Cyclanthera.*

Cyclanthera minima (S. Watson) Kearns & C. Jones, comb. nov.—*Sicyos minimus* S. Watson, Proc. Amer. Acad. 23:274. 1888. *Brandegea minima* (S. Watson) Rose, Contr. U.S. Natl. Herb. 5:121. 1897. *Cremastopus minimus* (S. Watson) Paul G. Wilson, Hooker's Icon. Pl. 36:t.3586. 1962. *Heterosicyos minimus* (S. Watson) Cockerell, Bot. Gaz. (Crawfordsville) 24:378. 1897. nom. illegit., non Welw. ex Hook. f.—TYPE: MEXICO, Chihuahua, canyons of the Sierra Madre, under cliffs, 2 Oct 1888, *Pringle 1871* (holotype, US; isotypes, K!, MICH!, MO!).

Additional specimens examined: MEXICO: Chihuahua: Casada de Basaseachic, 1960 m, *Torres and Tenorio 3792* (MO); Chuhuichupa, *LeSueur 949* (MO); near Colonia Garcia, 7300 ft, *Townsend and Barber 190* (MO); Loreto, Rio Rayo, *Gentry 2556* (MO). Durango: Barranca of Rio Jaral, bluffs 15 mi NW of Coyotes, 2100 m, *McVaugh 21722* (MICH). Sinaloa: 6 km W of El Palmito, 2200 m, *Dieterle 3837* (MICH); Ocurahui, Sierra Surutato, *Gentry 6265* (MICH, MO); Sierra Surutato, 2 mi S of El Triquito, 5800 ft, *Breedlove and Kawahara 17014* (MICH); Sierra Surutato, 3 mi SE of Los Ornos, 7200 ft, *Breedlove and Thorne 18454* (MICH).

Cyclanthera rostrata (Paul G. Wilson) Kearns & C. Jones, comb. nov.—*Cremastopus rostratus* Paul G. Wilson, Hooker's Icon. Pl. 36:t.3586. 1962.—TYPE: MEXICO, Mexico, Dist. Temascaltepec, Cumbre de Tejupilco, 10 October 1932, *Hinton 2045* (holotype, K!; isotype, GH!).

Additional specimens examined: MEXICO: Mexico: Temascaltepec, near Tejupilco, *Hinton 8458* (GH, MICH, NY, UC); Temascaltepec, Vigas, *Hinton 4805* (GH), *8616* (F, GH, MO, NY). Michoacán: Vicinity of Motel de la Sierra, ca. 6 km N of Uruapan, *Dieterle 4413* (MICH); Uruapan, *Hinton 15528* (MICH, NY, UC, US); 2 mi S of Tancitaro, *Leavenworth 565* (F, NY).

Jeffrey (1978, 1990) indicated that there is a third, as yet unnamed, species of *Cremastopus.* Having not yet seen the specimen on which Jeffrey based his decision (*Breedlove 15135*), we are unable to evaluate his conclusion. The proper disposition of the Breedlove specimen will be addressed in a forthcoming treatment of *Cyclanthera* (Jones and Kearns in preparation).

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ANNOUNCEMENT

THE RUPERT BARNEBY AWARD

The New York Botanical Garden invites applications for the 1992 Rupert Barneby Award. The ward of $500.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought and how the collections at NYBG will benefit their research. Travel to NYBG should be planned between Jan. 1, 1993 and Jan. 30, 1994. The letter should be addressed to Dr. Brian M. Boom, Vice President for Botanical Science, The New York Botanical Garden, Bronx, NY 10458, USA, and received no later than December 4, 1992. Announcement of the recipient will be made by December 20. Anyone interested in making a contribution to The Rupert Barneby Fund in Legume Systematics, which support this award, many send their check, payable to The New York Botanical Garden, to Dr. Boom.

The recipient of the 1991 Rupert Barneby Award is Edith Gómez-Sosa, a legume taxonomist from the Instituto de Botánica Darwinion in Argentina. Professor Gómez-Sosa will use the award to further her studies of the genus *Astragalus* through the consultation of collections at The New York Botanical Garden during July and August of 1992. She will also have the opportunity to work together with Dr. Barneby during her stay in New York.

NOTES

PLANT NATURALIZATION IN SEMI-ARID AREAS: A COMPARISON OF ARIZONA WITH VICTORIA, AUSTRALIA.

—R. F. Parsons, Botany Department, La Trobe University, Bundoora, Victoria 3083, Australia.

Burgess et al. (Madroño 38:96–114, 1991) give a detailed account of plant introductions to an area of 352 ha where mean annual rainfall is 250 mm and which is now on the edge of suburban Tucson, Arizona. They found the dominant plant naturalization process to be 'Mediterraneanization', with annual herbs from the Mediterranean being most significant. In this note, I use data from a southern Australian area of very similar rainfall to find out to what extent Mediterraneanization there involves the same plant species as it does in Arizona. Species nomenclature follows Burgess et al. (1991).

The Australian data are from a reliable, recent species list for major grid rectangle A, an area of 12,720 sq. km which is the driest, most northwestern grid rectangle of the Victorian Plant Mapping Scheme (Beauglehole, Victorian Vascular Plant Checklists. 1980). This area includes irrigated and non-irrigated crops, sheep and cattle grazing, towns and tracts of predominantly native vegetation.

Both the Desert Laboratory, Tucson and northwestern Victoria have mild winters and hot summers, with Tucson being slightly drier and with lower absolute minimum temperatures (Table 1). The rainfall distribution in northwestern Victoria is of the Mediterranean type with 60% of the rain falling in the six coolest months (May to October). In sharp contrast, at the Desert Laboratory, rainfall is biseasonal with 51% falling in summer, and 27% in winter, with the driest months in between (Bowers and Turner, Madroño 32:225–252, 1985).

Of the 36 exotic species listed for the Desert Laboratory, Tucson, I will regard *Schismus barbatus* as present, but not *S. arabicus* (see Burgess et al. 1991, p. 114). Also, I will assume that the *Salsola australis* of Burgess et al. is conspecific with the '*Salsola kali*' of Beauglehole (1980), as is very likely. This leaves only 15 species recorded from the Desert Laboratory which have not also been recorded from Victorian grid rectangle A.

These 15 can be broken down as follows:

(i) forbs which are escapes from cultivation, namely *Dimorphotheca sinuata, Matthiola longipetala, Molucella laevis* and *Phacelia campanularia* (four species).

(ii) grasses which are escapes from introductions by the Soil Conservation Service, namely *Eragrostis lehmanniana* and *Pennisetum ciliare* (two species) (see Burgess et al. 1991).

(iii) tall shrubs or trees which are escapes from cultivation, namely *Caesalpinia gilliesii, Lantana horrida, Melia azederach, Opuntia microdasys, Parkinsonia aculeata, Rhus lancea* and *Tamarix ramosissima* (seven species).

This leaves just two species unaccounted for, namely *Lepidium oblongum* and *Pennisetum setaceum.* The latter is a garden escape in the Tucson area (Bowers and Turner 1985) as it is in southern Victoria (N. G. Walsh personal communication). *Lepidium oblongum* is most unlikely to have been cultivated. Although I follow Burgess et al. (1991) in treating this American species as an exotic, I note that Al-Shehbaz (Journal of the Arnold Arboretum 67:265–311, 1986) regards it as native to Arizona. Whilst it appeared in Australia in the 1880s, it has not persisted there (Hewson, Brunonia 4:217–308, 1981).

Thus, of the 35 exotic species listed by Burgess et al. (1991), 14 of the 15 species not found in northwestern Victoria turn out to be escapes from cultivation. Presence of such species at the Desert Laboratory, Tucson will often merely reflect local factors

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TABLE 1. CLIMATIC DATA FOR THE DESERT LABORATORY, TUCSON, AND NORTHWESTERN VICTORIA. [1]Data from Burgess et al. (1991). [2] Data from Rowan and Downes (Victoria: Soil Conservation Authority Technical Communication No. 2, 1963) and Australia: Bureau of Meteorology (unpublished) giving the range of values for all meteorological stations present.

	Desert Laboratory[1]	NW Victoria[2]
Mean annual rainfall (mm)	250	265 to 355
Absolute minimum temperature (°C)	−8.9	−4.0 to −5.8

like fashions in suburban garden plantings or introduction of species for special purposes by the Soil Conservation Service.

Nineteen of the 20 species shared by the two areas are herbaceous and are not escapes from cultivation; *Nicotiana glauca* is the exception on both counts. Thus, if we compare the exotic flora of the two areas but exclude escapes from cultivation, a striking 95% of the Desert Laboratory, Tucson species occur in northwestern Victoria, the only unshared species being *Lepidium oblongum.* It is also striking that all 19 species except for *Cynodon dactylon* are annuals, biennials or short-lived perennials (Table 2), the majority being annuals.

Once the escapes from cultivation are set aside, it is very striking that all 19 Desert Laboratory exotics except for *Lepidium oblongum* occur also in northwestern Victoria, despite significant climatic differences between the two areas. This emphasizes the rapidly increasing tendency towards homogeneity of the world's flora caused by intentional and unintentional human activities (Elton, The Ecology of Invasions by Animals and Plants. 1958).

As pointed out by Burgess et al. (1991), the dominant naturalization process in their area is the successful establishment of winter annuals from the Mediterranean,

TABLE 2. EXOTIC SPECIES SHARED BY THE DESERT LABORATORY, TUCSON AND NORTHWESTERN VICTORIA, EXCLUDING ESCAPES FROM CULTIVATION. Life spans from Jessop and Toelken (Flora of South Australia. 1986).

Species	Life span	Species	Life span
Asteraceae		Geraniaceae	
Centaurea melitensis	annual	*Erodium cicutarium*	annual
Lactuca serriola	biennial	Malvaceae	
Sonchus oleraceus	annual	*Malva parviflora*	annual or perennial
Brassicaceae		Poaceae	
Brassica tournefortii	annual	*Avena fatua*	annual
Sisymbrium irio	annual or biennial	*Bromus catharticus*	short-lived perennial
S. orientale	annual or biennial	*B. rubens*	annual
Chenopodiaceae		*Cynodon dactylon*	perennial
Chenopodium murale	annual	*Hordeum murinum* ssp. *glaucum*	annual
Salsola australis	annual	*Phalaris minor*	annual
Fabaceae		*Polypogon monspeliensis*	annual
Melilotus indica	annual	*Schismus barbatus*	annual

or 'Mediterraneanization'. This is also true of the northwestern Victorian flora as a whole. That general area has predominantly annual exotics of which 76% originated in Europe, the Mediterranean and the Middle East (Wapshere *in* Noble and Bradstock, Mediterranean landscapes in Australia. 1989).

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A NEW COMBINATION IN *CALOCHORTUS* (LILIACEAE).—Randy K. Zebell and Peggy L. Fiedler, Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132.

A taxonomic investigation of the *Calochortus venustus* complex suggests that *Mariposa argillosus* R. F. Hoover is a coherent, distinct species belonging to the sect. *Mariposa* within the genus *Calochortus.* While the binomial *C. argillosus* has been used on herbarium labels, it has never been formally proposed. Thus, the combination is formally proposed.

Calochortus argillosus (Hoover) R. Zebell and P. Fiedler. comb. nov. Basionym: *Mariposa argillosa* R. F. Hoover, Leafl. West. Bot., IV(1):3, 1944. *Calochortus argillosus,* the clay mariposa, grows in open to partially canopied grasslands, on hard clay soils in areas of volcanic or metamorphic rock, from San Mateo to San Luis Obispo counties. It has three-angled, non-winged capsules, membranaceous bulb coats, and slightly depressed to non-depressed glands that lack surrounding membranes. These characters clearly place it within subsect. *Venusti* of sect. *Mariposa. Calochortus argillosus* most closely resembles *C. venustus,* with which it is most often confused, and from which it is distinguished by its color pattern. In *C. argillosus,* the inner perianth segments are adaxially cream-colored with a single vertical band of dark purple below the base of the gland, with a nearly central dark purple to maroon blotch above a small region of yellow to yellow-green located distal to the gland and proximal to (and occasionally above) the blotch. Abaxially, the inner perianth segments of *C. argillosus* are distally dark lavender to cream with a central band of cream and the proximal half streaked with dark red or dark green. This color pattern is comparatively stable and significant, especially when it is contrasted with the striking array of floral colors present in *C. venustus,* e.g., cream, crimson, rose, purple, yellow, and blood red, in various patterns such as one or two spots, solid colors without spots, and with or without streaks. *Calochortus argillosus* is also distinguished from *C. venustus* by its transversely-oriented, narrow-rectangular to lunate glands, its stouter capsules, and its more cuneate, less clawed petals. It differs from *C. luteus,* a bright yellow-flowered species to which Hoover thought it most closely related, by its cream colored flowers. Munz (California flora, University of California Press, 1959) considered *C. argillosus* as a synonym of *C. superbus,* but *C. superbus* has inverted V-shaped glands and a more intense orange-yellow region above the central blotch.

Calochortus argillosus was described by Hoover in 1944. In the protologue, he elevated all members of sect. *Mariposa* occurring in San Luis Obispo County to genus level. In the forthcoming revision of Jepson's Manual of Flowering Plants of California, P. L. Fiedler recognizes *Mariposa* as a section of *Calochortus,* as has been done in all previous comprehensive *Calochortus* treatments.

Research in progress by one of us (RKZ) suggests that there are two distinct groups within *C. argillosus.* One group occurs near the coast in San Luis Obispo County around Morro Bay and Point Sal, while the other group ranges more broadly through the central coastal ranges. The flowers of the coastal group consistently lack yellow above the central dark purple blotch, and the central blotch is consistently square to circular. The flowers of the interior group have pale yellow above the dark purple to maroon central blotch, and the central blotch is often elongated into a colored cresent or horizontal band. The flowers of the coastal group are more cuneate and less clawed than those of the interior group. Also, the interior group is more variable in gland shape, ranging from narrowly rectangular to lunate to weakly inverted V-shaped. Regardless, *C. argillosus* is morphologically distinct from *C. superbus, C. luteus,* and *C. venustus.*

(Received 4 Mar 1992; revision accepted 8 Apr 1992.)

NEW CHROMOSOME COUNTS IN MADIINAE (ASTERACEAE) AND THEIR SYSTEMATIC SIGNIFICANCE.—Bruce G. Baldwin, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

Chromosome numbers have been reported from all but five of the ca. 116 species of tarweeds (cf. Kyhos et al., Biodiversity and cytogenetics of the tarweeds [Asteraceae: Heliantheae-Madiinae], Ann. Missouri Bot. Gard. 77:84–95, 1990). New chromosome records from *Hemizonia martirensis, Layia platyglossa* [*L. ziegleri*], and *Madia stebbinsii* reported herein leave only one extant species of Madiinae uncounted: *Hemizonia streetsii* A. Gray, from the remote San Benito Islands of Baja California. The systematic significance of these new counts is assessed in light of the nearly comprehensive record of chromosome numbers in Madiinae and pertinent morphological evidence.

Floral buds were fixed in modified Carnoy's solution (6:3:1; chloroform : 100% ethanol : glacial acetic acid) for five days. Cells were stained in acetocarmine and cleared with Hoyer's solution prior to squashing. All counts were from microsporocytes at diakinesis, metaphase I, or anaphase I.

Hemizonia martirensis Keck, $n=12$, Mexico, Baja California, Sierra de San Pedro Martir, Valladares, 0.4–0.8 km E of the ranch site, *Baldwin, S. N. Martens, & S. J. Bainbridge 771* (ARIZ).

The modal, and possibly basal, chromosome number in *Hemizonia* sect. *Madiomeris,* to which *H. martirensis* belongs, is also $n=12$. This count, therefore, offers little insight into infrasectional relationships of *H. martirensis.*

Layia platyglossa (Fischer & C. A. Meyer) A. Gray [*L. ziegleri* Munz], $n=7$, CA, Riverside Co., San Jacinto Mts., 1.3 km N of Keen Camp Summit along Hwy 74, *S. J. Bainbridge 91-3* (ARIZ); $n=7$, Garner Valley, 0.3 km N of Morris Ranch Road, *S. J. Bainbridge 91-4* (ARIZ).

Layia ziegleri was described by Munz (Supplement to A California Flora, Univ. California Press, 1968) as a new species with probable close affinities to *L. glandulosa* (Hook.) Hook. & Arn. ($n=8$) or *L. pentachaeta* A. Gray ($n=8$). *Layia ziegleri* is indeed readily distinguished from all $n=8$ *Layia* species by its pappus of scabrous, non-plumose bristles. Later, Munz (A Flora of Southern California, Univ. California Press, 1974) only hesitantly recognized *L. ziegleri* by indicating that it was an "uncertain taxon" that might be conspecific with the highly polymorphic *L. platyglossa* ($n=7$). *Layia ziegleri* has been accorded status as a List 1B (rare or endangered) species by the California Native Plant Society (Smith Jr., J. P. and K. Berg, Inventory of Rare and Endangered Vascular Plants of California, CNPS, 1988) and as a Sensitive species by the U.S. Forest Service (Shevock, J. personal communication).

Morphologically, *Layia ziegleri* falls well within the range of variation in *L. platyglossa.* The uniform yellow rays and yellow anthers in *L. ziegleri,* which superficially suggest placement within the $n=8$ group, are infrequent but widespread character states in *L. platyglossa* (cf. Clausen, J., Stages in the Evolution of Plant Species, Hafner, 1951). Although it is widely documented that uniformly yellow-rayed individuals predominate in scattered populations of *L. platyglossa* throughout its range, the occurrence of yellow anthers in this species is not reported in existing floristic treatments of *Layia.* Clausen (loc. cit.) recorded *L. platyglossa* with yellow anthers in much of its southern Californian distribution and in Baja California. I have observed collections of *L. platyglossa* with both uniform yellow rays and yellow anthers from Riverside County, outside of the San Jacinto Mountains, and San Diego County. Conversely, a small proportion of individuals in the *L. ziegleri* populations sampled had black anthers and yellow rays or black anthers and white-tipped rays (*Bainbridge 91-3*), as in typical *L. platyglossa.*

These counts of $n=7$ from two populations referable to *Layia ziegleri,* in addition to a count by Peter H. Raven [$n=7$, Riverside Co., San Jacinto Mountains, Hemet Meadows, *Raven 12971* (RSA)], corroborate morphological evidence that *L. ziegleri* is conspecific with *L. platyglossa.* Because the yellow-anthered and yellow-rayed condition in *L. platyglossa* does not mark a discrete sublineage, I hesitate to recognize the San Jacinto Mountains plants as a subspecies. These populations are noteworthy, however, as the highest known elevational occurrences of *L. platyglossa.*

Madia stebbinsii T. W. Nelson & J. P. Nelson, $n=9$, CA, Trinity Co., 7.5 km E of Wildwood-Mad River Road along U.S. Forest Service Road 28N10, *Baldwin 611* (DAV).

This chromosome count for *Madia stebbinsii* provides further evidence that this species, *M. doris-nilesiae* T. W. Nelson & J. P. Nelson, *M. hallii* Keck, and *M. nutans* (E. Greene) Keck, all with $n=9$, belong to the same sublineage within *Madia* (cf. Nelson, T. W. and J. P. Nelson, A new *Madia* of sect. *Anisocarpus* [Compositae: Heliantheae] from Trinity County, California, Brittonia 37:394–396, 1985). These four species are among only eight in all of Madiinae with $n=9$, the others being *Hemizonia kelloggii* E. Greene, *H. pallida* Keck, *H. pungens* (Hook. & Arn.) Torrey & A. Gray [including *H. laevis* (Keck) Keck], and *Osmadenia tenella* Nutt. In *Madia,* $n=9$ appears to have been derived from $n=8$, the modal diploid number, by ascending aneuploidy. The four $n=9$ *Madia* species are North Coast Range endemics restricted to serpentine (*M. doris-nilesiae, M. hallii, M. stebbinsii*) or weathered volcanic (*M. nutans*) soils. Morphologically, they are distinguished from other annual *Madia* species by their yellow anthers and pappose disk florets.

I thank Susan Bainbridge and Scott Martens for critical field assistance; Donald Kyhos and Wayne Maddison for use of microscope facilities; and Christopher Campbell, John Mooring, and Robert Robichaux for helpful comments on the manuscript.

Present address: Botany, Duke University, Durham, NC 27706

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NOTEWORTHY COLLECTIONS

ARIZONA

BOEHMERIA CYLINDRICA (L.) Swartz (URTICACEAE).—Gila Co., Tonto National Forest, Sierra Ancha Wilderness Area. Collected twice on 7 Aug 1991: (1) at Devil's Chasm, along stream just below road, 21.8 mi N on FS 203 (Cherry Creek Road) from junction with Hwy. 288, T6N, R15E, NW ¼ sect. 31, elev. ca. 1000 m, *Imdorf & Landrum 37* (ASU, GH); and (2) in wet area along road at 34.4 mi N on FS 203 from junction with Hwy. 288, T7N, R14E, NE ¼ sect. 28, elev. ca. 1200 m, *Imdorf & Landrum 74* (ASU).

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Significance. Previously known in Arizona from only two collections, both made about 100 years ago: Gila Co., Catalpa (now covered by Roosevelt Lake), ca. 750 m, 6 Sep. 1891, *D. T. McDougal 746* (US), and Cochise Co., Fort Huachuca, July 1893, *J. E. Wilcox s.n.* (NY), as reported by one of the authors (DEB) in a manuscript in press on the Urticaceae of Arizona. Knowledge of this manuscript led the other authors to search for the species in an area ca. 18 mi NE of the original Catalpa locality. There has apparently been no previous published report of this species in Arizona. The Arizona plants are distantly disjunct from the nearest known populations in Utah (see below) and New Mexico, Chaves Co., Roswell, ca. 3800 ft., *F. S. & E. S. Earle 265* (MINN, NY, US; cited as *B. scabra* (Porter) Small in Martin & Hutchins, A Flora of New Mexico, vol. 1, 1980). The New Mexico location is about 1100 km ENE of the Fort Huachuca site and about 1300 km E of the Sierra Ancha. The Utah site is ca. 350 km N of Sierra Ancha. The main portion of the range of the species in the United States is almost entirely east of the 100th meridian.

—LESLIE R. LANDRUM and GREG IMDORF, Department of Botany, Arizona State University, Tempe, AZ 85287, and DAVID E. BOUFFORD, Harvard University Herbaria, 22 Divinity Ave., Cambridge, MA 02138.

CALIFORNIA

GAUDINIA FRAGILIS (L.) P. Beauv. (GRAMINEAE).—Sonoma Co.: T10N R10W S3 SE ¼ of NW ¼, 0.2 km W of Hwy. 101, 2 km S of the Asti exist, elev. ca. 100 m, low grassy hills with *Quercus,* 20 May 1991, *J. Guggolz & B. Guggolz 1142* (CAS).

Previous knowledge. This distinctive genus of 4 species is native to southern Europe, the Middle East, northern Africa, the Azores, and the Canary Islands (Bot. J. Linn. Soc. 76:353–356, 1978). *Gaudinia fragilis* is the most widely distributed species in the genus (circum-Mediterranean) and is known as a frequent casual in NW and E Europe where it occasionally persists (Fl. Europaea 5:217, 1980).

Significance. This collection represents the first report of the establishment of both this genus and species in the Western Hemisphere. Plants were collected on an open grassy hilltop in thin, rocky soil. The locality is in a general region of open oak woodland but much of the nearby land has long been used for farming (currently viticulture) and/or livestock pasture. The origin of *G. fragilis* at this locality remains unknown; however, it is not unlikely that seeds were inadvertently introduced in conjunction with past or present agricultural pursuits associated with this portion of Sonoma County.

Gaudinia is classified in subfamily Pooideae, tribe Aveneae, subtribe Aveninae where it is aligned with the *Helictotrichon* Schult. group of genera, all of which have hairy ovaries. The genus is recognizable by its spicate inflorescence with a disarticulating rachis and a caryopsis with a very short stylopodium. The inflorescence of *Gaudinia* is unusual among Aveneae with the result that the genus does not "key" in existing American grass keys. Because there are no descriptions of this genus and species in North American manuals and because the taxon will not be included in the forthcoming revision of the California flora (D. Wilken personal communication), a description of *G. fragilis,* based on North American plants, is provided below.

Annual; culms to 3.5 dm tall, erect or ascending, usually clustered; leaves (sheaths and blades) villous, the blades flat, the ligule short, truncate; inflorescence a solitary terminal distichous spike to 15 cm long, the rachis disarticulating at prominent joints; spikelets sessile, 9–20 mm long (excluding awns), laterally flattened with flat side ± appressed to concave rachis; glumes unequal, the lower 3–5 mm long, the upper 7–11 mm long (the lower ca. ½ the length of the upper), both scabrous on nerves, awnless, the margins hyaline; florets 3–6; lemmas (3–)5–8 mm long, scabrous on midnerve, dorsally awned above the middle with a single twisted or geniculate scabrous awn to 15 mm long; anthers 2–4 mm long. Caryopsis not seen.

—THOMAS F. DANIEL and CATHERINE BEST, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, JACK GUGGOLZ and BETTY GUGGOLZ, 1123 Palamino, Cloverdale, CA 95425.

SEDUM OBLANCEOLATUM Clausen (CRASSULACEAE).—Siskiyou Co., Klamath National Forest, ssw. slope of ridgeline 1.2 air km wnw. of summit of Copper Butte, or 2.8 air km due e. of Cook and Green Butte, Pacific Crest Trail above the headwaters of East Fork Seiad Creek, a tributary of the Klamath River, T47N R11W S9 se.¼ of ne.¼, Mt. Diablo meridian, ca. 380 genets, sunny xeric green phyllite-schist outcrops, associated with *Sedum obtusatum* ssp. *retusum, S. stenopetalum, Lewisia cotyledon* ssp. *cotyledon, Selaginella wallacei, Eriogonum nudum, Orobanche uniflora, Eriophyllum lanatum, Holodiscus discolor,* etc., ca. 1615–1735 m, 11 Jun 1991, *Zika & Mumblo 11198* (OSC).

Significance. First collection from the Klamath River drainage for this species, previously believed to be endemic to a small portion of the upper Applegate River drainage in California and Oregon. A range extension of 2.8 km s. of the nearest known site in the Applegate basin. Clausen (*Sedum* of North America, 1975) and Denton (Brittonia 34:48–77, 1982) reported the taxon was restricted to igneous diorite, here it is on metamorphic rock. Unpublished field studies by the Rogue River National Forest have shown *S. oblanceolatum* also grows on Applegate metavolcanic and metasedimentary outcrops, as well as on ultramafic serpentinite and peridotite in the Applegate basin. Denton (Taxon 28:149–155, 1979) found sympatry in *Sedum* section *Gormania* was extremely rare, here thousands of the tetraploid *Sedum obtusatum* ssp. *retusum* are found with the diploid *Sedum oblanceolatum,* in places within a few meters of each other on the same ledges on the ridgeline.

—PETER F. ZIKA, Oregon Natural Heritage Program, 1205 NW 25th Ave., Portland, OR 97210.

WASHINGTON

SAXIFRAGOPSIS FRAGARIOIDES (Green) Small (SAXIFRAGACEAE).—Chelan Co., Wenatchee National Forest, ca. one mile west of Leavenworth on U.S. Route 2, T24N, R17E, S10. Growing in rock crevices of Castle Rock climbing area, elevation ca. 1700 feet, 3 June 1991, *Burnett & Arnot 346a, 346b* (WTU). Determination confirmed by Patrick Elvander.

Significance. First record for WA. Formerly known only from northern California and southwestern Oregon, a disjunction of ca. 400 miles. The popularity of Castle Rock as a climbing area creates the possibility that this population may have been introduced to Washington.

—SARAH GAGE, Herbarium, Department of Botany, KB-15, University of Washington, Seattle, WA 98195.

REVIEWS

Plant Reproductive Ecology: Patterns and Strategies. Edited by J. LOVETT DOUST and L. LOVETT DOUST. 1988. Oxford University Press, New York. xiii + 344 pages. Softcover: $24.95, ISBN 0-19-506394-5.

This book is a collection of fifteen reviews of plant reproductive ecology. Because of the diversity of topics that are covered and the diversity of approaches taken by the contributors, this book is a valuable introduction to current concepts and research in the ecology and evolution of plant reproduction. Seven chapters address conceptual issues in this field, five consider ecological forces affecting reproduction, and three survey the reproductive ecology of non-angiosperms. Together, they are an attempt to present a cohesive and synthetic review of the field for both researchers and newcomers. Despite the book's title, many of the authors also consider genetic, population genetic and phylogenetic approaches in order to address the evolution of plant reproductive characteristics, perhaps signalling a greater synthesis than even the editors had envisioned.

Chapters range from purely factual summaries of a topic (Meagher) to synthetic reviews incorporating many avenues of research. The evolution of reproductive traits and strategies arises in most chapters but is addressed in a variety of ways. Some authors rely on verbal arguments of fitness and selection. Others use the concept of inclusive fitness to examine reproductive traits (Haig and Westoby, in a chapter on parent-offspring conflicts in seed provisioning). Game theory and evolutionarily stable strategies (ESS) are featured in several contributions (Cox and others). An ESS is a phenotype such that, if almost all individuals have it, no alternative phenotype can invade the population. This approach assumes an asexual population in which phenotypes breed true. ESS reasoning is attractive because complex evolutionary situations are made manageable by being reduced to a consideration of alternative states. When applied to sexual organisms, however, this simplification is achieved at the price of ignoring the question of transmission of phenotypes from one generation to the next (the province of population and quantitative genetics). Sexual populations do not necessarily evolve to an ESS, and therefore ESS arguments, while illuminating, do not by themselves provide a convincing evolutionary scenario.

The genetic considerations necessary to understand the evolution of reproductive traits are, however, included in a number of chapters, thus expanding the scope of the book beyond reproductive ecology alone (Barrett and, to a lesser degree, others). The conceptual section begins with an overview by the editors of this volume. Provocatively entitled "The sociobiology of plants: an emerging synthesis", Lovett Doust and Lovett Doust discuss the transfer of concepts from animal sociobiology to plant ecology and provide a brief overview of theory and data on topics ranging from sex allocation to incompatibility and the sociobiology of the seed. This is followed by more detailed chapters on male fitness and evolution of paternal strategy (Bertin), inclusive fitness and maternal care (Haig and Westoby), monomorphic and dimorphic sexual strategies (Cox), the evolution, maintenance, and loss of self-incompatibility systems (Barrett), sex determination (Meagher), and gender modification and gender choice (Schlessman). The ecological section includes some chapters that focus on specific stages of the reproductive process and others that consider more general issues. Zimmerman examines the ways in which plants can manipulate their pollinators and Lee discusses factors influencing fruit and seed production. Waller investigates the relationship of plant morphology and reproduction. Chapters on the effects of competition (Weiner) and herbivory (Hendrix) on reproduction conclude this section. The chapters describing the reproductive biology on non-angiosperms are valuable for their exposition of the diversity of reproductive patterns in plants. These have generally been neglected by plant reproductive biologists. All of the authors, however, go beyond a mere description of reproductive strategies.

Mishler reviews the reproductive ecology of bryophytes and concludes that their reproductive abilities are far from optimal. In contrast to some of the other authors in this volume, Mishler cautions against an adaptationist approach to plant reproduction and emphasizes the utility of a phylogenetic framework for approaching the assumption of adaption in evolutionary ecology more rigorously. DeWreede and Klinger describe reproductive strategies in algae and discuss resource allocation and sex ratio theory in these organisms. Cousens describes reproductive strategies of pteridophytes, including quantitative studies of mating systems and genetic structure of pteridophyte populations, and discusses features of reproductive allocation, phenology and demography influencing pteridophyte reproduction. The contributors to this book have provided useful and comprehensive surveys of disparate topics. Typographical errors are rare. The deliberate inclusion of material on non-angiosperms is admirable, and the population genetic and phylogenetic approaches used by some authors broadens the appeal and increases the value of this book. Although now several years old, this collection of reviews provides an excellent introduction to current concepts and research in the ecology and evolution of plant reproduction.

—KAIUS HELENURM, Department of Biology, San Diego State University, San Diego, CA 92182.

Global Patterns—Climate, Vegetation, and Soils. By WALLACE E. AKIN. 1990. University of Oklahoma Press, Norman. ix + 370 pages. ISBN 0-8061-2309-5.

Consistent with the title, this book is divided into three sections: Global patterns of 1) Climate, 2) Vegetation, and 3) Soils. The strength of the book is the thorough and very readable coverage of climatic pattern and processes. This section is nicely illustrated and, in itself, makes the book worth purchasing. Soils are well described, however, the section on vegetation is rather disappointing in that it merely describes global patterns but does not adequately relate these to processes under climatic or edaphic control.

—JON E. KEELEY, Ed.

EDITOR'S REPORT FOR VOLUME 39

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on the journal. Between 1 July 1991 and 30 June 1992, 65 manuscripts were received. These comprised 35 articles (9 published, 7 in press, 4 in review, 10 in revision and 5 rejected), 8 notes (4 published, 2 in press and 2 in review) and 22 noteworthy collections (17 published, 2 in press and 3 in review). Volume 39 was composed of 27 articles (17 systematic and 10 ecological) 12 notes, 20 noteworthy collections, 3 book reviews, 2 obituaries and several announcements.

I thank the Board of Editors for editorial assistance, Steven Timbrook for his continuing contribution of the annual Index and Table of Contents, Barbara Ertter for assistance with the dedication and John Strother for his continued assistance with taxonomic details.

This year has seen more than a 20% increase over the previous year in submissions and a continued high quality of manuscripts. Also, I am pleased with the thorough, tactful and helpful comments by reviewers and, although high levels of community service normally set the research sciences apart from other professions, the reviewers I have dealt with this year have been very generous in their time. Lastly, I acknowledge the excellent job done by the Allen Press staff in the production of our high quality journal.—J.E.K. 1 Oct 1992.

Reviewers of Manuscripts

As Editor, I thank all reviewers for their contribution to the continued excellence of the journal. Special thanks are extended to those who review more than one manuscript published in 1991 (*). The California Botanical Society appreciates the generosity of time and ideas of the following reviewers for volume 39:

Barbara H. Allen-Diaz
Kelly W. Allred
Mark Baker
Mary E. Barkworth
Rupert C. Barneby
Ellen Bauder
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Dennis Breedlove
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Number 4, pages 251–318, published 19 November 1992

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CALIFORNIA BOTANICAL SOCIETY

Schedule of Speakers
1992–1993

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October 15	Robert Patterson, San Francisco State University "Patterns of adaptive radiation using examples from the Polemoniaceae, Hydrophylaceae, and Goodeniaceae"
November 19	Robert Haller, University California, Santa Barbara "A botanical odyssey through Chile"
January 21	Linda Vorobik, University California, Santa Barbara "The distribution and delimitation of species in the *Arabis macdonaldiana* group (Brassicaceae)"
February 20*	**Robert Thorne, Rancho Santa Ana Botanic Garden** "Principles of Plant Biogeography"
March 18	Dale McNeal, University of the Pacific "The biogeography and taxonomy of *Allium* (Liliaceae)"
April 15	Bruce Bartholomew, Department of Botany, California Academy of Sciences "Plant collecting in China"
May 20	Tom Daniel, Department of Botany, California Academy of Sciences "Reproductive biology of tropical Acanthaceae"

***Annual Banquet—Santa Barbara Botanic Garden, Santa Barbara**

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DEDICATION

Eleven years ago, on that fateful trip to Snow Mountain, Jim Hickman and Larry Heckard decided the time had come to fulfill Jepson's wish to have his 1925 *Manual of the Flowering Plants of California* revised. Although the project rapidly expanded to include staff members, volunteers, and numerous collaborators, Jim remained Editor while Larry served as Principal Consultant and Chairman of the Editorial Board.

James Hickman came to the Jepson Herbarium after a circuitous route and with diverse interests, beginning in Iowa where he spent more time with snakes and butterflies than with plants. He then vacillated between music, chemistry, and marine biology before settling on botany as a career. He studied plant ecology in the Oregon Cascades, taught for eight years at Swarthmore College, studied annual *Polygonum* while on a sabbatical leave at Stanford, served as program officer for Systematic Biology for NSF, and edited *Madroño* for three years. This broad background, combined with his personal warmth and contagious enthusiasm that inspired numerous Swarthmore students, pre-adapted Jim for the complex challenges that faced him as editor of a new *Manual.*

Lawrence R. Heckard had originally come to Berkeley from Oregon as a doctoral student, two years after Jepson's death. After completing a dissertation on the *Phacelia magellanica* complex and teaching for five years in Illinois, he returned to Berkeley for good to work in the Jepson Herbarium, eventually replacing Rimo Bacigalupi as Curator. His primary interest by this time focused on Scrophulariaceae, especially *Castilleja, Cordylanthus,* and *Orthocarpus.* Larry was honored and respected for his unstinting willingness to share his impressive knowledge of the California flora with professional and amateur botanists alike, resulting in his being named a fellow of both CNPS and the California Academy of Sciences. His death in 1991 left a deep gap felt by colleagues and friends throughout the state and elsewhere.

It is fitting that the 1992 volume of *Madroño* be dedicated to Jim Hickman and Larry Heckard, the year that what began as "a gleam in the eye" of Jim and Larry becomes "the light at the end of the tunnel", when *The Jepson Manual: Higher Plants of California* is submitted for publication. It is only regrettable that Larry did not live to see either the finished *Manual* or this dedication.

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