VOLUME 32, NUMBER 1 JANUARY 1985

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES AND NEWS

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to Barbara Keller, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118.

Editor—CHRISTOPHER DAVIDSON
Idaho Botanical Garden
P.O. Box 2140
Boise, Idaho 83701

Board of Editors
Class of:

1985—STERLING C. KEELEY, Whittier College, Whittier, CA
ARTHUR C. GIBSON, University of California, Los Angeles
1986—AMY JEAN GILMARTIN, Washington State University, Pullman
ROBERT A. SCHLISING, California State University, Chico
1987—J. RZEDOWSKI, Instituto Politecnico Nacional, Mexico
DOROTHY DOUGLAS, Boise State University, Boise, ID
1988—SUSAN G. CONARD, USDA Forest Service, Riverside, CA
WILLIAM B. CRITCHFIELD, USDA Forest Service, Berkeley, CA
1989—FRANK VASEK, University of California, Riverside
BARBARA ERTTER, University of Texas, Austin

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1984–85

President: ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542

First Vice President: DALE W. MCNEAL, Department of Biological Sciences, University of the Pacific, Stockton, CA 95204

Second Vice President: GREGORY S. LYON, 1360 White Oak Drive, Santa Rosa, CA 95405

Recording Secretary: ROBERT W. PATTERSON, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: BARBARA KELLER, Department of Botany, California Academy of Sciences, San Francisco, CA 94118.

Treasurer: CHERIE L. R. WETZEL, Department of Biology, City College of San Francisco, San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ISABELLE TAVARES, Department of Botany, University of California, Berkeley 94720; the *Editor* of MADROÑO; three elected *Council Members:* LYMAN BENSON, Box 8011, The Sequoias, 501 Portola Rd., Portola Valley, CA 94025; JAMES C. HICKMAN, Department of Botany, University of California, Berkeley 94720; THOMAS FULLER, 171 West Cott Way, Sacramento, CA 95825; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

A RECONSIDERATION OF THE NOMENCLATURE AND TAXONOMY OF THE *FESTUCA ALTAICA* COMPLEX (POACEAE) IN NORTH AMERICA

VERNON L. HARMS
The W. P. Fraser Herbarium and Biology Department,
University of Saskatchewan,
Saskatoon, Saskatchewan S7N 0W0, Canada

ABSTRACT

The recent taxonomic treatment of the North American members of the *Festuca altaica* complex by Looman (1979) is briefly reviewed and some nomenclatural problems are discussed. The nomenclatural histories of the included taxa are briefly summarized, and a revised taxonomic treatment is presented, recognizing three subspecies within the complex in North America, and including *F. altaica* subsp. **hallii**.

In Budd's Flora of the Prairie Provinces, Looman (1979) presented a revised taxonomic treatment, including some major taxonomic and nomenclatural changes, for the ecologically important *Festuca altaica* complex (rough-fescues) in North America. This was offered with minimal explanation. Although further elaboration may still be forthcoming from the author, four years have passed with only an unexplained nomenclatural correction (Looman 1981). Meanwhile, several comments with regard to this recent "revision" seem pertinent lest Looman's changes be too uncritically accepted.

Looman (1979) recognized three separate North American species in the *Festuca altaica* complex, as follows: (1) *F. altaica* Trinius of central to northeastern Asia and northwestern North America, occurring on this continent in the Alaskan and northern Rocky Mountains (=*F. altaica* sensu stricto of other treatments); (2) "*F. doreana* Looman" (a name that has never been validly published and that was replaced by *F. campestris* Rydb. without explanation in the "reprint" of Budd's Flora [1981]), applying to a species of the somewhat more southern Rocky and Cascade Mountains and foothills (*F. scabrella* var. *major, F. altaica* var. *major, F. scabrella* sensu lat., or *F. altaica* subsp. or var. *scabrella* sensu lat. of other modern treatments); and (3) *F. hallii* (Vasey) Piper, a species of the Northern Great Plains grasslands, extending southward to Colorado along the eastern foothills of the Rocky Mountains (=*F. scabrella* s. str., or *F. altaica* subsp. or var. *scabrella* of most other modern treatments). Looman's (1979) treatment contrasts with that of most other modern authors, who have recognized the latter two taxa as conspecific, either varietally distinguished or not, under *F. scabrella* Torrey, or

MADROÑO, Vol. 32, No. 1, pp. 1–10, 15 February 1985

else as one subspecies or two varieties of a more comprehensive *F. altaica.* The western mountain variant with larger, 3–5-floreted spikelets, unequal glumes, and taller culms (within the usually accepted North American species, *F. scabrella* sensu lat.), has often been distinguished as var. *major* Vasey (="*F. doreana*" and *F. campestris* sensu Looman 1977 and 1981, respectively), leaving the typical varietal epithet, *scabrella,* to refer to the northern Great Plains taxon (=*F. hallii* sensu Looman), with smaller, 2–3-floreted spikelets, sub-equal glumes, and shorter culms. Treated under an all-inclusive *F. altaica,* the two variants have either been merged under *F. altaica* subsp. *scabrella* (Torrey) Hultén or distinguished as *F. altaica* var. *major* (Vasey) Gleason and var. *scabrella* (Torrey) Breitung, respectively.

Looman's (1979) quite significant taxonomic revision of the North American members of the *Festuca altaica* complex represents an innovative contribution towards a better understanding of the morphological variations and taxonomic distinctions within this group. Presented therein for the first time are various clarifying taxonomic differences that are potentially useful in separating the included taxa of this complex. Unfortunately, because of its concise and unelaborated presentation in manual format, submerged within this regional flora, Looman's treatment of this group may easily be overlooked by interested agrostologists, plant taxonomists and ecologists.

Nevertheless, despite its value as a useful taxonomic contribution, there are some nomenclatural problems in Looman's (1979 and 1981) taxonomic treatment of the rough-fescue complex. In the first place, the name "*Festuca doreana* Looman" was not validly published in the original (1979) printing of Budd's Flora, nor has it been validated since. Latin diagnosis (as required under Article 36.1 *if* it was intended as a new species description) and bibliographic data for the cited synonym "*F. scabrella* var. *major* Vasey" (as required for a basionym under Articles 32.1 and 33.2 of the International Code of Botanical Nomenclature) are lacking. Furthermore, the name "F. doreana" would have been nomenclaturally superfluous even with the latter data, because it would have been based on the same basionym (viz. *F. scabrella* var. *major* Vasey, Contr. U.S. Natl. Herb. 1:278–279, 1897) as was the earlier species name, *F. campestris* Rydberg [Mem. N.Y. Bot. Gard. 1:57, 1900]. If the even older specific name, *Festuca scabrella* Torrey, should be ruled out as not applicable to this taxon of the Rocky and Cascade Mountains, as Looman (1979) did, then the next in priority is *F. campestris* Rydberg. There appears no valid reason to exclude the latter name, since Rydberg (1900) seems clearly to have based it on *F. scabrella* var. *major* Vasey, simultaneously citing as a usage synonym, "*F. scabrella* Coulter, Man. R.M., 424, not Torr."

Looman must have recognized the unacceptability of the name, "F. doreana," as shown by his substitution of the name *F. campestris* in the second printing (1981) of Budd's Flora and the use of the latter name in Looman (1983), although no nomenclatural explanations were given in either case. I believe that the still older specific name, *F. scabrella,* has priority over *F. campestris* for this western mountain taxon because Drummond's type material of the former appears best referred here. Looman (1979) evidently considered it necessary to find a new name for this taxon because of his view that the type of *F. scabrella* Torrey was referable instead to *F. altaica* s. str. He gave no explanation for this dispensation, which was reminiscent of the much earlier, similar referral by Piper (1906).

The taxonomic placement of Thomas Drummond's type material of *F. scabrella* Torrey is critical to the nomenclature of this group. An examination of the "Ex Herb. Torrey" holotype (now at GH), and the original "Gray Herb.!" isotype (also at GH) appeared readily enough to preclude their identification as the northern Great Plains–Eastern Foothills taxon, *F. hallii* sensu Looman because of the distinctly unequal glumes and the spikelets mostly with 4 florets and exceeding 8 mm in length. Furthermore, the leaves of the "Ex Herb. Torrey" holotype specimens varied from 1.5 to 2.5 mm wide and were only loosely involute, although the leaves on the "Gray Herb.!" isotype were more strongly involute. Unfortunately the quality of the type materials was too inadequate and the spikelets too immature to assure their unequivocal identification as either *F. altaica* sensu str. or the more southern mountain taxon that Looman called "F. doreana" (in 1979) and *F. campestris* Rydb. (in 1981). Most of the individual plants appeared depauperate for either taxon, and had rather scanty panicles. Coloration of herbage and spikelets was obscure. Although measurements of the lengths of spikelets, glumes and lemmas fell more into the expected range for *F. altaica* sensu str. than for the more southern mountain taxon, these are questionably reliable for the particular maturation stages. The rather contracted panicles with mostly ascending-erect upper branches, on the other hand, suggested the latter, as did the relatively inconspicuous glume-borders. Thus, identification of the available type material seemed inconclusive, although I was most inclined to place it with the more southern mountain taxon *F. campestris* sensu Looman 1981.

Neither does the original diagnosis in Hooker (1840) give conclusive clues to the proper taxonomic placement of the *F. scabrella* type material. The unequal glumes, 3–4-floreted spikelets, nearly glabrous and only loosely involute leaves, and (lower?) panicle branches spreading, would seem to exclude the northern Great Plains taxon, *F. hallii,* and rather imply either *F. altaica* s. str. or the more southern mountain taxon that Looman called "F. doreana" and *F. campestris* (in 1979 and 1981).

The spikelet size described as 0.75 in. (=1.9 cm), and the "upright" and "erect" panicles, seem best referable to the more southern mountain taxon, but the "purplish-green" spikelet color suggests *F. altaica* sensu str. Neither panicle shape nor spikelet color, however, seem very reliable diagnostic characters. The considerable emphasis given to the scabrous lemmas, leaf-sheaths, and culms, in the original species description, now seems unwarranted because such more or less pubescent forms occur in each of the three presently recognized taxa. *Festuca hallii* has the most consistently pubescent leaf-sheaths.

The taxonomic placement of Thomas Drummond's type collection of *F. scabrella* Torrey can be clarified by reference to its geographical source. Drummond's type was collected in 1825 or 1826, on the John Franklin Second Expedition, and is listed in Hooker (1840) as from "alpine districts of the Rocky Mountains." There has been frequent difficulty in confidently determining the locality, elevation, and habitat of many Drummond collections. But with the specimen label data and notations in Hooker (1840), supplemented by information from Drummond's own travel accounts (Drummond 1827, 1830; and in Franklin 1928, pp. 308–313), especially as clarified by the chronological and geographical tracing of his expedition by Bird (1967) and Ewan and Ewan (1981, pp. 63–64), it can be concluded with some confidence that Drummond's "Rocky Mountain" collections labelled as above came from the present-day Jasper National Park region. Drummond's collections from this region apparently ranged from "Jasper House" (53°20′N, 117°51′W), Rock Lake (called "Lac-la-Pierre" (53°27′N, 118°16′W), and the length of the Snake Indian (called "Assinaboyne") River (ca. 53°10–22′N; 118°00–50′W), southward along the upper Athabasca River (called "Red-Deer River, one of the branches of the Athapescow") to its headwaters near the Columbia Ice Fields (53°13–25′N, 117°15–20′W) and up the Whirlpool River toward Athabasca Pass (at 52°23′N, 118°11′W), on the Columbia Portage.

The collections made on Drummond's side-expedition northwestward to the headwaters of the Peace River in September 1826, seemingly were labelled from "north of Smoking (=Smoky) River" and/or "lat. 55°" or "lat. 56°." His collections from Athabasca Pass itself, in October 1926, appear labelled, "height of land," "summit" or "near summit of Rocky Mountains." His British Columbian collections, made during his brief October 1926 expedition through and southwest of Athabasca Pass along the Wood (called "Portage") River to the Columbia River, apparently bore the labels "Grande Cote," "Portage (River)," "sources of the Columbia," "the Columbia (River)" or "west side of the Rocky Mountains." Thus, at least tentatively discounting those Rocky Mountain collections by Drummond from the Peace River, Athabasca Pass and British Columbia, all presumably bearing the special label notations indicated above, the type locality of *F. scabrella* can be narrowed down with considerable assurance to the east (i.e., Alberta) side of the Continental Divide and to within the coordinates: 52°15′–53°30′N and 117°15′–118°50′W.

Interestingly, the presumed type locality of *F. scabrella* falls within the overlapping known ranges of the taxa that Looman (1981) called *Festuca hallii* and *F. campestris,* and somewhat less than 100 miles south of the known range of *F. altaica* sensu str. (as I interpret these three taxa). In this general area of east-central British Columbia and west-central Alberta, the three taxa are characteristic of lower, middle and high mountain elevations, respectively, so the altitudinal placement of the type collection of *F. scabrella* assumes importance. But, as his botanical colleague, John Richardson (1851, Pt. 3, p. 521), pointed out, "It is unfortunate that the vertical limits of the species gathered by Drummond in the mountains were not better noted . . . (as that) would have conveyed much information with respect to the distribution of plants." The habitat notation in Hooker (1840), "alpine districts," is not as unequivocal as it at first might seem. The word "alpine" was used frequently for Drummond collections in Hooker (1880) in references to "alpine woods," "marshes," etc., habitats, sometimes in apparent contrast to "open elevated places," "summits," or "barren places," and at other times in apparent contrast to "mountain woods." So the notation of "alpine districts" for Drummond's collections does not necessarily, if at all, imply an alpine tundra habitat at high elevations above tree-line, but quite possibly a sub-alpine zone. The habitat indication, "alpine districts," given in Hooker (1840) may also be queried because such a notation was not included on Drummond's exsiccatae labels.

The cumulative evidence from the characteristics of the type materials available of *Festuca scabrella* (viz., the holotype and an isotype, both in GH), the original species diagnosis, and the presumed geographical location and possible habitat of the type collection, allows its most likely, although still somewhat tentative, referral to the larger more southern mountain taxon that Looman called *F. campestris* Rydb. (in 1981). Such a taxonomic placement of the type material, would give the name *F. scabrella* Torrey priority over *F. campestris.*

Acceptance of these conclusions concerning the type of *F. scabrella* raises a nomenclatural problem with respect to the most frequent traditional taxonomic treatment (although not Looman's) that has recognized the two varieties, *scabrella* and *major,* within *F. scabrella.* A problem results because the names, *F. scabrella* Torrey (in Hooker, Fl. Bor.-Am. 2, 252, 1840; type from alpine districts of the Rocky Mountains, Canada, *Thomas Drummond s.n.*) and *F. scabrella* var. *major* Vasey (Contrib. U.S. Natl. Herb. 1:278–279, 1897; type from Spokane Co., Washington, *Suksdorf 118*), are both based on type specimens that are interpreted as belonging to the more southern Rocky and Cascade Mountain taxon rather than to the northern Great Plains–Eastern Foothills taxon. If the latter is recognized as distinct from the former, the epithet *scabrella* is unavailable for it. For this reason, rather than because of Looman's (1979) referral of the *F. scabrella* type to synonymy under *F. altaica* sensu str., I concur with Looman's substitution of the epithet *hallii,* which is based on *Melica hallii* Vasey (Bot. Gaz. 6:296, 1881; lectotype [indicated by Piper, 1906] from northern Colorado, *Hall and Harbour 621* [US]). Upon examination of the lectotype of *F. hallii* and duplicates of it, as well as several later collections by W. A. Weber et al. from Larimer and Huerfano Counties, Colorado, it seems apparent that all of these do indeed belong to the same taxon as does the rough-fescue of the northern Great Plains and Eastern Foothills grasslands. This identification seems definite despite their rather surprising occurrence at high alpine-meadow elevations. Some short rhizomes are even evident on the type materials, a taxonomic characteristic also noted by Weber (1961) on his Colorado collections.

Aside from the nomenclatural problems, Looman's recognition of the three taxa within the North American *F. altaica* complex seems basically well conceived and acceptable, although not necessarily with these variants treated as species. If they were to be treated as distinct species, the appropriate names for the (1) Beringian, (2) more southern Rocky and Cascade Mountain, and (3) northern Great Plains taxa of the rough-fescue complex as distinguished by Looman, would be, respectively: (1) *F. altaica* Trinius, (2) *F. scabrella* Torrey and (3) *F. hallii* (Vasey) Piper. If distinguished at the varietal level, the appropriate names would be, respectively: (1) *F. altaica* Trinius var. *altaica,* (2) *F. altaica* var. *major* (Vasey) Gleason, and (3) *F. altaica* var. *hallii* (Vasey), a combination that has never been made.

Recognition of these taxa at the subspecific level seems most preferable, however, for the following reasons. Although I agree that three North American taxa are at least broadly distinguishable within the *F. altaica* complex, personal experience in both field and herbarium strongly suggests to me that these are rather less discrete than is implied by Looman (1979). In many specimens, especially those from the mid-latitude (circa 49°–55°) in the Rocky Mountains and eastern foothills, the characters that distinguish the taxa may often appear overly subtle or seemingly intergradient. Thus it would seem preferable to accept these taxa at an infraspecific rather than a specific level. On the other hand, despite evidences of apparent intergradation (i.e., the presence of morphological intermediates), they occupy broadly separate geographical ranges for the most part.

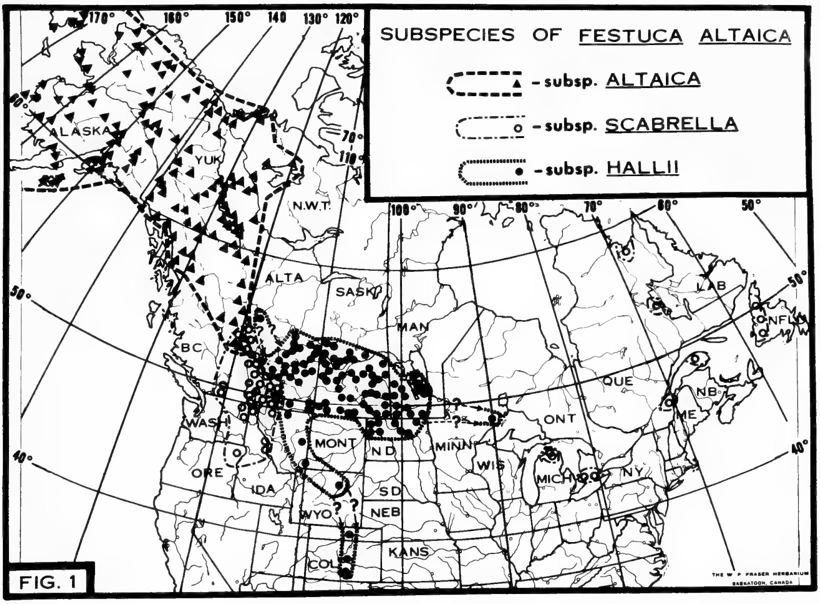


FIG. 1

FIG. 1. Distribution of the subspecies of *Festuca altaica* Trin. in North America.

The recognition of these taxa at a subspecies rank seems most appropriate.

The following taxonomic treatment (viz., key and nomenclatural summaries) is presented for *Festuca altaica* sens. lat. in North America, based largely on the diagnostic criteria given by Looman (1979), to distinguish and circumscribe the three recognized taxa, but at a subspecific level. The generalized distributional information appended for each taxon, and forming a partial basis for the ranges given in Fig. 1, has been extracted from Johnson (1958) and Hitchcock (1950), and a variety of regional floras including Gleason (1952), Harrington (1954), Scoggan (1957, 1978), Hultén (1968), Hitchcock et al. (1969), Voss (1972), Taylor and MacBryde (1977), Cronquist et al. (1977), McGregor et al. (1977), Porsild and Cody (1980), Boivin (1981), and Packer (1983), and from the numerous herbarium specimens personally reviewed.

Key to Subspecies of *Festuca altaica* in North America

1. Plants tufted, not at all rhizomatous; culms often over 6 dm high; spikelets over 10 mm long; fertile florets 3–6 per spikelet; glumes distinctly unequal, the first glume distinctly shorter than the first lemma; leaf-blades either flat or involute, 7-nerved; at least the

lower panicle branches spreading to somewhat reflexed or ± ascending.

2. Culms (3–)4–6(–8) dm high; herbage yellowish to dark-green; spikelets often ± reddish, (8–)9–13 mm long, with 3–5 florets; glumes with conspicuous translucent borders; lemmas 5–8 mm long; leaf-blades 1–2.5 mm wide; panicles open, lax, ± ovoid, with longer, spreading, and weaker branches, often ± secund .... subsp. *altaica*
2. Culms (3–)5–10 dm high; herbage more grayish to bluish-green; spikelets mostly green to stramineous, (8–)10–16 mm long, with 4–6 florets; glumes with less conspicuous translucent borders; lemmas 6–9 mm long; leaf-blades (1–)1.5–3 (–4) mm wide; panicles tending to be more erect, contracted, stiffer and narrower, not at all secund ..... subsp. *scabrella*

1. Plants less strongly tufted, somewhat rhizomatous and mat-forming; culms 2–6 dm high; spikelets mostly green to stramineous, 7–8 mm long; florets 2–3 per spikelet, the 3rd often sterile; glumes subequal, about equal to the first lemma; leaf-blades involute, less than 1.5 mm wide, obscurely 5-nerved; the lower panicle branches more strongly ascending to contracted-appressed .... subsp. *hallii*

1. FESTUCA ALTAICA Trinius subsp. ALTAICA. "Northern Rough Fescue."—*F. altaica* Trinius in Ledebour, Fl. Altaica, 1:109–110. 1829.—TYPE: Central Asia, Altai Mts.: "In summa alpe ad fontem fl. Acjulac rarissima," (tr.: "Very rare on mountain summit at source of Acjulac River"), *C. B. Trinius* (Holotype: LE).

Distribution. e.c.-n.e. Asia; Alaska, Yukon, w. Mack. Distr., s. to n. B.C. and in Rocky Mts. to e.c. B.C. and w.c. (and n.w.?) Alta.

2. FESTUCA ALTAICA Trinius subsp. SCABRELLA (Torrey) Hultén. "Mountain Rough Fescue."—*F. scabrella* Torrey, in Hooker, Flora Boreali-Amer. 2:252. 1840.—*F. altaica* subsp. *scabrella* (Torrey) Hultén, Flora Alaska and Yukon, v. 2, p. 241. 1942.—*F. altaica* var. *scabrella* (Torrey) Breitung, Amer. Midl. Naturalist 58:12. 1957 (as to basionym, not concept).—"*F. altaica* forma *scabrella* (Torrey) Looman," Budd's Flora Can. Pr. Prov., p. 128. 1979 (as to basionym, not concept; non rite publ.).—TYPE: Canada: "Alpine districts of the Rocky Mountains," 1827, *T. Drummond s.n.* (Holotype: the "Ex Herb. Torrey" specimen now at GH!; isotypes: the "Gray Herb.!" specimen at GH!; BM).

F. scabrella var. *major* Vasey, Contr. U.S. Natl. Herb. 1:278. 1893.—*F. altaica* var. *major* (Vasey) Gleason, Phytologia 4:21. 1952.—*F. campestris* Rydberg, Mem. N.Y. Bot. Gard. 1:57. 1900 (basionym: *F. scabrella* var. *major* Vasey).—"*F. doreana* Looman," Budd's Flora Can. Pr. Prov., pp. 128–129. 1979 (basionym indicated as *F. scabrella* var. *major* Vasey; non rite publ.).—TYPE: USA: Washington: Spokane Co.: "on prairies," 1884, *Suksdorf 118* (Holotype: US!).

Distribution. Rocky Mts. of w.c.-s.w. Alta., e.c. and s. B.C., s. in Rocky and Cascade Mts. to e. Ore., s. Ida., and w. Mont.; disjunct eastern isolates in Great Lakes region (n. Mich. and s. Ont.), the Gaspe Peninsula region (e. Que.), e.c. Que. (and w.c. Lab.?), Ungave Bay (n. Que.), and w. Newfoundland. The Michigan and e. Canadian disjunct populations of this complex seem best referred, at least tentatively, to subsp. *major,* but this conclusion needs verification, especially since, for reasons of geographical proximity, subsp. *hallii* might seem the more likely taxon to occur there. Yet the phytogeographical pattern of Cordilleran taxa with such eastern isolates is well known for various other groups.

3. FESTUCA ALTAICA Trinius subsp. **hallii** (Vasey) Harms comb. nov. "Plains Rough Fescue."—*Melica hallii* Vasey, Bot. Gaz. 6:296. 1881.—*Festuca hallii* (Vasey) Piper, Contr. U.S. Natl. Herb. 10: 31. 1906.—*F. altaica* subvar. *hallii* (Vasey) St. Yves, Candollea 2:271. 1925.—*F. scabrella* subsp. *hallii* (Vasey) W. A. Weber, Univ. Colo. Stud., Ser. Biol. 7:8. 1961.—TYPE: USA, Rocky Mountains, northern Colorado, Lat. 39°–40°, 1862, *Hall and Harbour 621* (Lectotype [as indicated by Piper, Contr. U.S. Natl. Herb. 10:31. 1906]: US!; isolectotypes: US–3!, F–photograph!).

F. scabrella auct. pro parte, non Torrey.

Distribution. This is the rough fescue variant of the northern Great Plains grasslands and parklands (w. Alta., c. Sask., to s.e. Man. and n.w. Dak.), apparently disjunct near Thunder Bay, Ont., extending s. along the eastern foothills of the Rocky Mts. in Mont. and Wyo., to s.c. Colo. (in Colorado, at high elevations, rare, and perhaps disjunct, as suggested by Weber, 1961).

LITERATURE CITED

BIRD, C. D. 1967. The mosses collected by Thomas Drummond in Western Canada, 1825–1827. Bryologist 70:262–266.

BOIVIN, B. 1981. Flora of the prairie provinces, Part 5—Gramineae. Mem. de l'Herbier Louis-Marie, Universite Laval, Quebec.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, and P. K. HOLMGREN. 1977. Intermountain flora, Vol. 6. New York Bot. Garden.

DRUMMOND, T. 1827. Letters (from Drummond). Linnaea 2:519–525.

———. 1830. Sketch of journey to the Rocky Mountains and to the Columbia River in North America. Hooker's Bot. Misc. 1:178–219.

EWAN, J., and N. D. EWAN. 1981. Biographical dictionary of Rocky Mountain naturalists. Bohn, Scheltema, and Holkema, Utrecht/Antwerpen.

FRANKLIN, JOHN. 1828. Narrative of a second expedition to the shores of the Polar Sea in the years 1825, 1826, and 1827. Charles E. Tuttle Co. Rutland, VT.

GLEASON, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. New York Botanical Garden, NY.

HARRINGTON, H. D. 1954. Manual of the plants of Colorado. Sage Books.

HITCHCOCK, A. S. 1950. Manual of the grasses of the United States (2nd ed., rev. by A. Chase). USDA Misc. Publ. 200.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1969. Vascular plants of the Pacific Northwest, Part 1. Univ. Wash. Press.

HOOKER, W. J. 1840. Flora Boreali-Americana, Vol. 2. H. G. Bohn, London.

HULTÉN, ERIC. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, CA.

JOHNSTON, ALEXANDER. 1968. Note on the distribution of Rough Fescue (*Festuca scabrella* Torr.). Ecology 39:536.

LOOMAN, J. 1979. *Festuca,* fescue. *In* J. Looman and K. F. Best, Budd's Flora of the Canadian prairie provinces, pp. 127–132. Research Branch, Agriculture Canada, Publ. No. 1662.

———. 1981. *Festuca,* fescue. *In* J. Looman and K. F. Best, Budd's Flora of the Canadian prairie provinces, pp. 127–132. Research Branch, Agriculture Canada, Publ. No. 1662. (Reprint with corrections of 1979 publication.)

———. 1983. 111 range and forage plants of the Canadian prairies, Publ. No. 1751, Agriculture Canada, Research Branch, Ottawa.

MARIE-VICTORIN, FRÈRE. 1964. Flore Laurentienne. Université de Montréal, Montréal, PQ.

MCGREGOR, R. L., T. M. BARKLEY, et al. 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.

PACKER, J. G. 1983. Flora of Alberta, 2nd ed. Univ. Toronto Press, Toronto.

PIPER, C. V. 1906. North American species of *Festuca.* Contr. U.S. Natl. Herb. 10: 1–48.

PORSILD, A. E. and W. J. CODY. 1980. Vascular plants of the continental Northwest Territories, Canada. Natl. Mus. Nat. Sci., Ottawa.

RICHARDSON, JOHN. 1851. Arctic searching expedition: a journal of a boat-voyage through Ruperts Land and the Arctic Sea in search of the Discovery ships under command of Sir John Franklin. Longman, Brown, Green and Longmans, London.

RYDBERG, P. A. 1900. Catalogue of the flora of Montana and the Yellowstone National Park. Mem. N.Y. Bot. Gard. 1: (No. 3835).

SCOGGAN, H. J. 1957. Flora of Manitoba. Natl. Mus. Canada, Ottawa.

———. 1978. The Flora of Canada, Part 2—Pteridophyta, Gymnospermae, Monocotyledonae. Natl. Mus. Canada, Ottawa.

TAYLOR, R. L. and B. MACBRYDE. 1977. Vascular plants of British Columbia, — A descriptive resource inventory. Techn. Bull. No. 4, The Botanical Garden, Univ. British Columbia.

VASEY, GEORGE. 1881. Some new grasses. Bot. Gaz. 6:296–298.

———. 1893. Descriptions of new or noteworthy grasses from the United States. Contr. U.S. Natl. Herb. 1:267–280.

VOSS, E. G. 1972. Michigan flora, Part 1—gymnosperms and monocots. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

WEBER, W. A. 1961. Additions to the flora of Colorado. Univ. Colorado Stud., Series in Biology, No. 7:1–26.

(Received 10 August 1982; accepted 8 May 1984.) (See note added in proof, p. 59.)

FULL-GLACIAL VEGETATION OF DEATH VALLEY, CALIFORNIA: JUNIPER WOODLAND OPENING TO *YUCCA* SEMIDESERT

Philip V. Wells and Deborah Woodcock
Department of Botany, University of Kansas,
Lawrence 66045

Abstract

Full-glacial (13,000–19,000 yr BP) wood rat (*Neotoma*) deposits from Death Valley establish a 1200–1500-m displacement of juniper woodland below modern, mountaintop relicts of *Juniperus osteosperma*. At an elevation of 425 m, however, there was full-glacial (19,550 yr BP) semidesert dominated by chaparral yucca (*Yucca whipplei*) with minor Joshua tree (*Y. brevifolia*). The late Pleistocene climate must have been much less arid and more equable with cooler summers than at present. Modern, hot-desert vegetation appeared at the 425-m site between 11,000 and 10,000 yr BP. The shift from pluvial woodland to hyperarid desert at 775 m was time-transgressive during 13,000–9000 yr BP, as is documented by three dated transitional stages of semidesert from this site.

Death Valley, California, a northern extremity of the Mohave Desert, is now one of the hottest and driest places on earth, but there is evidence that the extreme aridity of the modern climate is less than 11,000 years old. Wood rat (*Neotoma*) middens (Wells 1976) from very low elevations in Death Valley (Fig. 1) provide a detailed macrofossil record (thousands of leaves, twigs, seeds, etc., in many separate deposits) of late Pleistocene and Holocene vegetation over the past 20,000 years, whence the magnitude and nature of climatic change may be inferred. A more generalized indication of vegetational change during this time span is apparent from the pollen records at Tule Springs to the east in Nevada (Mehringer 1967) and at nearby Searles Lake, California (Roosma 1958).

Neotoma macrofossil records from the Amargosa Range, which flanks Death Valley on the east, indicate that late-Pleistocene Juniper Woodland (dominated by *Juniperus osteosperma*) grew in the elevational range 1130–1280 m (Fig. 1a, b), on slopes now occupied by creosote bush scrub. The highest site (a), on the northeast slope of Pyramid Peak at 1280 m, yielded a late-glacial (11,800 yr BP) record of relatively mesophytic juniper woodland with montane gooseberry, mountain mahogany, and shrubby ash (Wells and Berger 1967). A new and significant (though rare) component of this assemblage in the context of the other records reported here (Table 1) is *Yucca whipplei*.

At much lower elevations on the west flank of Death Valley (Fig.

Madroño, Vol. 32, No. 1, pp. 11–23, 15 February 1985

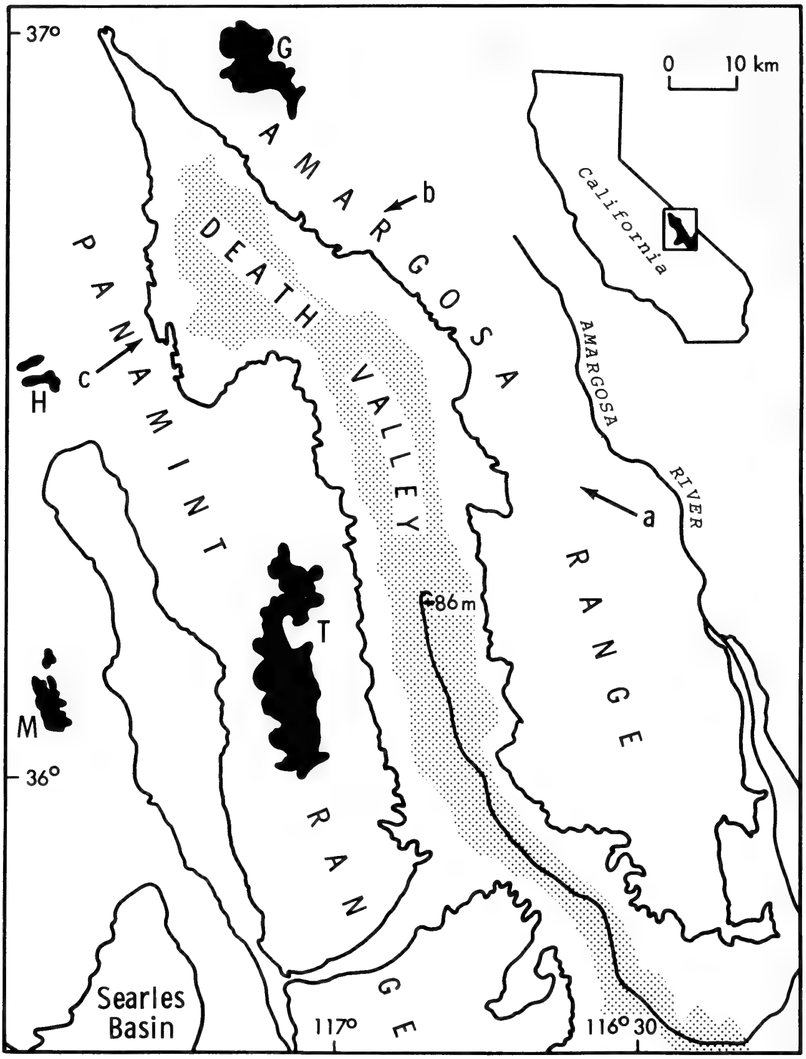


FIG. 1. Death Valley and surrounding region of eastern California (see inset). Solid line delimiting Death Valley and adjacent basins is the 610-m contour, which estimates the pleniglacial extent of juniper woodland. Stippled area in Death Valley approximates the high stands of Pleistocene Lake Manly (see text). Present-day woodlands and montane zones (black areas) are restricted to elevations above 1950 m on high mountains: G, Grapevine Pk., 2679 m (Grapevine Mts.); H, Hunter Mtn., 2272 m and T, Telescope Pk., 3368 m (Panamint Range); M, Maturango Pk., 2694 m (Argus Range). Locations of Quaternary *Neotoma* macrofossil records: (a,b) Amargosa Range: a, 1280 m (Wells and Berger 1967); b, 1130 m (M. D. Kelly, in Van Devender 1977); (c) Panamint Range, 775 m, 425/414 m, and 260 m (this report).

TABLE 1. PRINCIPAL WOODY PLANT SPECIES OF DATED MACROFOSSIL DEPOSITS FROM DEATH VALLEY, CALIFORNIA. Deposits are listed by elevation and age (^{14}C years BP). Relative abundances of species in deposits are indicated as high (principal constituent: +++); intermediate (++); and low (+). The two highest sites at 1280 m and 1130 m are from the Amargosa Range on the east side of Death Valley; all other sites in foothills of Panamint Range are on the west side (cf. Fig. 1). Direction of slope surrounding rock shelter or cave harboring *Neotoma* middens: north-facing (n.); south- (s.); east- (e.). Laboratory numbers for ^{14}C dates are in order given (left to right): UCLA-755, UCR-347, GX-7807, GX-7806, GX-7804, GX-7805, GX-7811, GX-7810, GX-7812, GX-7809, GX-7808.

	1280 m (n.)	1130 m (?)	775 m (n.)				425 m (s.)			414 m (s.)	260 m (e.)
Trees, shrubs	11,600 ±160	9680 ±300	13,060 ±460	11,210 ±380	9455 ±310	9090 ±300	19,550 ±650	17,130 ±550	10,230 ±320	900 ±130	1990 ±160
Juniperus osteosperma	+++	+++	+++				+				
Ribes montigenum	+										
Fraxinus anomala	+										
Cercocarpus ledifolius	+										
Yucca brevifolia		+					+				
Yucca whipplei	+			++			+++	++			
Atriplex confertifolia			+				+	+			
Chrysothamnus teretifolius				++	+			++			
Purshia glandulosa				++	++						
Haplopappus cuneatus					+	++					
Opuntia basilaris				+	+	++	+	+			
Ambrosia dumosa									+++	++	++
Larrea tridentata										+++	+++

1c) new *Neotoma* records extend the late-glacial (ca. 13,000 yr BP) lower limit of juniper woodland to below 775 m, a level that now supports an extremely sparse, hot-desert scrub of *Larrea* and *Ambrosia dumosa.* Pleniglacial (=full-glacial) deposits from a south-facing site at 425 m contain an unusual abundance of yucca leaves (chiefly *Y. whipplei*; some *Y. brevifolia*), a number of semidesert or cool-desert shrubs, and only occasional twigs of juniper in a large volume of matrix; two of these assemblages yielded dates of 19,550 and 17,130 yr BP (Table 1). The classical Wisconsinan glacial maximum is dated at 18,000 yr BP.

Juniperus osteosperma (cf. Fig. 2a) is now dominant only at elevations above 1950 m in the higher parts of the Panamint Range, some 15–20 km distant from its documented Pleistocene occurrences in the foothills bordering the western floor of Death Valley (Fig. 1). Junipers are no longer extant in the lower and drier Funeral Range (to 2040 m) on the east side of the valley. The late-glacial abundance of juniper (thousands of leafy twigs) at the 775-m, north-facing site, together with the recovery of a few traces of juniper twigs from the pleniglacial, *Yucca*-dominated deposits at 425 m (south-facing), indicates a Pleistocene displacement of 1200–1500 m for juniper. This is one of the most extreme and well-documented Quaternary shifts thus far established for any species or zone in western North America; the exceptional magnitude is especially significant because of the modern aridity of Death Valley.

The geographic extent of the vegetational change near Death Valley is indicated in Fig. 1, where the drastically shrunken mountaintop areas of the modern woodland and higher zones are shown in black; the minimal late-Pleistocene (Wisconsinan) extent of juniper woodland is estimated by the 610-m contour. Thus, most of the mapped area above the valley floor was probably wooded during the last glacial. The extraordinary vegetational displacement documented in Death Valley reflects both the magnitude of relatively recent climatic changes and the unusually large range of elevation locally available for their expression.

A ZONE OF CHAPARRAL *YUCCA* IN DEATH VALLEY

In contrast to the juniper-dominated woodland assemblages, the semidesert of yuccas indicated by the deposits at 425 m has no modern analog at higher elevations on nearby mountains, so far as is now known. The principal pleniglacial species at the lowest (425-m) site was *Yucca whipplei* (Fig. 2b), a mild-climate rosette-shrub with very distinctive, grooved leaf-surfaces (lacking a smooth cuticular sheath). This *Yucca* is now apparently absent in the Death Valley region, despite the extensive elevational/climatic gradients available on the higher mountain ranges. On the other hand, the

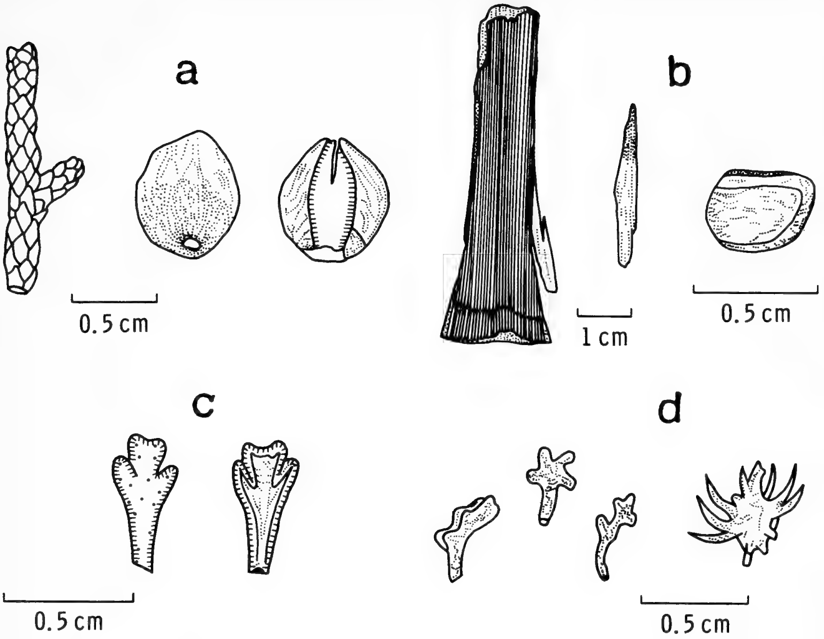


FIG. 2. Drawings of representative specimens among the many thousands of plant macrofossils in late Pleistocene *Neotoma* middens from near the floor of Death Valley: (a) *Juniperus osteosperma*: leafy twig and seeds. (b) *Yucca whipplei*: leaf base and tip, seed. (c) *Purshia glandulosa*: upper and lower surface of leaf. (d) *Ambrosia dumosa*: leaf fragments and fruit.

arborescent *Yucca brevifolia,* a more xerophytic and cold-tolerant species, was also present near the floor of Death Valley at 19,550 yr BP but now occurs only above about 1700 m on the slopes of some of the higher mountains. Of course, Joshua tree woodlands are the most characteristic modern feature of the higher or less arid sectors of the Mohave Desert, of which Death Valley is a northern extremity.

The pleniglacial combination of *Yucca whipplei* and *Y. brevifolia,* however, is decidedly unusual today, occurring on the extreme western margins of the Mohave Desert (e.g., foothills of Tehachapi Mountains) in a zone of transition to Mediterranean climate. Minor components of the pleniglacial *Yucca* community in Death Valley (Table 1) included *Chrysothamnus teretifolius* (a cool-desert species), *Atriplex confertifolia,* and *Opuntia basilaris.* The latter two species are favorite food plants of the desert wood rat, *Neotoma lepida*; therefore their scarcity in the pleniglacial assemblages at the 425-m site was undoubtedly real. The full-glacial *Neotoma* middens clearly indicate a relatively cool semidesert near the bottom of Death Valley, comparable to the "high desert" community of the western Mohave Desert that borders the Transverse Ranges of California.

The *Yucca*-dominated semidesert may have existed only locally, however. There are much more numerous macrofossil records of low-elevation coniferous woodland occurring throughout most of the Mohave Desert, even as late as 8000–10,000 yr BP (Wells and Berger 1967, King 1976, Van Devender 1977, Wells 1983). Under full-glacial conditions, juniper-Joshua tree woodland descended as low as 258 m, even in the northern Sonoran Desert, just to the southeast of the Mohave (Wells 1974, 1983). These low-elevation Mohavean woodlands were accompanied by semidesert shrubs, but there has been no firm pleniglacial evidence of *Larrea* and *Ambrosia,* the modern codominant shrubs of the hyperarid hot desert now prevalent at most of the low-elevation *Neotoma* sites in the Mohave Desert (Wells and Hunziker 1976). In fact, increasingly numerous late-Pleistocene *Neotoma* records establish a monotonous pattern of low-elevation woodland in the Southwest, from southern California to western Texas and adjacent areas of Mexico (Wells 1966, 1969, 1974, 1976, 1979, 1983; Van Devender and Spaulding 1979). The geography of the Chihuahuan Desert (relatively high base levels) permitted species-rich pluvial woodlands of pinyon, juniper and oaks to dominate the lowlands of most, if not all, of this modern desert region (Wells 1966, 1974). Only the more subtropical Sonoran Desert, with elevations descending to sea level at lower latitudes, provided a pleniglacial refugium for the more extreme xerophytes (Wells and Hunziker 1976).

Thus, the pleniglacial record of *Yucca* semidesert on the lower slopes of Death Valley is the first direct evidence that the ubiquitous Pleistocene woodlands of the arid Southwest did not descend to local base level everywhere during the glacial maximum. Restriction of the extent of any desert vegetation at that time is indicated by several limiting factors: 1) increasing basal elevations in all directions from the uniquely low and rain-shadowed trough of Death Valley; 2) greater lowering of the more mesophytic pinyon pine and evergreen oak (as well as juniper) components of the woodland zone toward the southeast at present (associated with the increasing proportion of summer rain in that direction); a very similar pattern is documented in the pleniglacial macrofossil record (Wells 1979), with juniper descending to local base level in the eastern Mohave, northern Sonoran, and probably all of the Chihuahuan Desert; and 3) occupation of the bottoms of enclosed basins by extensive glaciopluvial lakes (Hubbs and Miller 1948). A potentially extensive zone of semidesert or desert vegetation on the floor of Death Valley was preempted by Pleistocene Lake Manly (cf. Fig. 1); the highest stand of this lake is not well known, but it may have risen to within 250 m of the lowest *Neotoma* record of *Yucca* semidesert at 425 m above sea level (Hunt and Mabey 1966). Presence of *Atriplex confertifolia* in the full-glacial deposits at 425 m suggests the possibility of zones of *Atriplex* and other halophytes around the fluctuating margins of Lake Manly, comparable to the existing salt-desert vegetation bordering the shrunken remnants of Pleistocene lakes in the cooler, northern Great Basin (cf. Wells 1983).

TIME-TRANSGRESSIVE VEGETATIONAL SHIFTS

A major upward shift of the *Yucca* semidesert in Death Valley occurred during 13,000–11,000 yr BP, signifying a large climatic change. A deposit dated to 11,210 yr BP at the 775-m site is composed, not of juniper as at 13,060 yr BP, but of *Yucca whipplei* (previously unrecorded at this site) and of shrubs now characteristic of a cooler zone transitional between woodland and desert (Table 1). Absence of juniper from this still relatively early (11,210 yr BP) record at the 775-m site is doubly significant because this site is a relatively mesic, north-facing wall of a deep canyon, and *Juniperus osteosperma* is a very xerophytic woodland species. This juniper persisted at other localities in the Mohave Desert at comparably low or somewhat higher elevations as late as 10,000 yr BP, or even as late as 8000 yr BP at a few higher sites (Wells and Jorgensen 1964, Wells and Berger 1967, Van Devender 1977, King 1976, Wells 1983).

The explanation for the much earlier upward shrinkage of juniper woodland in Death Valley probably lies in the great vertical relief of the graben and the extreme intensity of rain-shadow induced by the mountain barriers around it. No other valley within the Mohave Desert has so great an elevational span between existing lower limit of juniper woodland (at ca. 1900 m) and local base level (−86 m at Badwater) as now obtains in Death Valley, a span of nearly 2000 m. In most other sectors of the Mohave, the span is considerably less than 1000 m, well within the robust tolerance limits of *Juniperus osteosperma* under the glaciopluvial climate. In Death Valley, the uniquely wide environmental gradient from mountain slope to valley bottom apparently exceeded the tolerance limits of *Juniperus osteosperma* even under the cooler climate of the glacial maximum. Populations of the juniper growing as much as 1200–1500 m below their present lower limits were probably near the end of their tether; and they could have been trimmed back by climatic oscillations too small to affect junipers growing at slightly higher and less marginal levels elsewhere in the Mohave.

An outstanding feature of the 11,210-year-old deposit at the 775-m (north-facing) site in Death Valley is the similarity in composition to the full-glacial (19,550 yr BP) semidesert assemblage at the lowest (and south-facing) site at 425 m (Table 1). Shared dominant species include *Yucca whipplei* and *Chrysothamnus teretifolius*; presence of *Purshia glandulosa* (Fig. 2c) at the 775-m site suggests that woodland was not far above at 11,210 yr BP. The time-transgressive consistency of this *Yucca*-semidesert community seems to be an example of a simple cliseral shift of 350 m along this segment of the elevational gradient. A nearly contemporaneous (11,600 yr BP) record from 500 m higher (at 1280 m) shows *Yucca whipplei* coexisting with juniper woodland (Table 1).

The further shift to modern vegetation at the 775-m site involved at least two other stages (Table 1). About 1500 years later, at 9455 yr BP, *Yucca whipplei* had dropped out locally, but *Purshia glandulosa, Chrysothamnus teretifolius,* and other shrubs of the high desert/woodland transition still persisted. By 9090 BP, however, only two transitional species, *Haplopappus cuneatus* and *Opuntia basilaris,* remained; of the Pleistocene species, only *O. basilaris* survives in the modern creosote bush scrub at the 775-m site today.

The unfolding in ordered time sequence at this location of three transitional phases of semidesert vegetation, almost entirely distinct from both late-glacial juniper woodland and modern desert scrub, is strong evidence of a slow, secular upward shift of the woodland/desert boundary past this site in the interval 13,000–9000 yr BP. A gradual and protracted warming and desiccation of climate during this late-glacial/Holocene phase of transition is clearly indicated here. Thus, the suggestion (Van Devender 1977) of an abrupt shift from woodland to desert throughout the Southwest at about 8000 yr BP (on the basis of a few coincidental dates at scattered sites) is refuted by the present evidence and by a more detailed review of the whole Mohavean data set (Wells 1983).

The earliest appearance of vegetation similar to the existing, hot-desert scrub in Death Valley was prior to 10,000 yr BP. At the lowest and most xeric (south-facing) 425-m site, which supported *Yucca* semidesert during the full-glacial (17,000–19,500 yr BP), there is a hiatus of seven millennia, followed by a *Neotoma* record of *Ambrosia dumosa,* dated at 10,230 yr BP (Table 1). This deposit is composed entirely of remains of this *Ambrosia* (Fig. 2d), but lacks *Larrea tridentata. Larrea* and *Ambrosia* dominate the existing desert scrub at the 425-m site and throughout Death Valley from below sea level (except on saline deposits) upward to 1500 m or more.

Only the absence of *Larrea* denies characterization of the 10,000-yr BP desert scrub community as really modern; the absence of *Larrea* at 10,230 yr BP, however, may not be of climatic significance at the latitude of Death Valley. This is merely another instance, already indicated by the weight of macrofossil evidence throughout the Southwest (Wells and Hunziker 1976), of the late arrival of *Larrea* over much of its present range in North America. Within the Mohave Desert region, the earliest firmly established *Neotoma* record of *Lar-*

rea tridentata is from the Mohave River valley at 670 m (west-facing), just north of Ord Mountain and east of Daggett; the radiocarbon date of 7400 ± 100 yr BP (UCLA-759) was on a branch and leaves of *Larrea* itself, which dominated the deposit (Wells and Berger 1967). Woodland conifers were lacking in this record, but *Juniperus osteosperma* still dominated as late as 7800 yr BP at higher elevations (1006 m, south-facing site) on the south side of Ord Mountain, as indicated by the *Neotoma* records of King (1976). This juniper is now absent on Ord Mountain, which lacks woodland despite its substantially high elevation (to 1920 m), and *Larrea* ascends the mountain from all sides.

The oldest records of *Larrea* are from the much lower elevations and latitudes of the more subtropical Sonoran Desert. The *Larrea*-dominated *Neotoma* deposits from the low Wellton Hills (at 162 m), in southwestern Yuma County, Arizona, have been dated to at least 10,580 yr BP, but this does not establish the earliest possible occurrence of *Larrea* at elevations approaching sea level (see review in Wells and Hunziker 1976). It should be emphasized that these early, low-elevation records of *Larrea* are about 4° south of the substantially higher Death Valley *Neotoma* sites reported here. A time-transgressive development of the *Larrea* scrub zone in the Sonoran and Mohave Deserts is apparent. In Death Valley, two very late Holocene *Neotoma* middens dated to 900 yr BP (very close to the 425-m site) and 1990 yr BP (at 260 m) serve as a control on the unusual composition of pure *Ambrosia* at 10,230 yr BP. Both of the very recent deposits contain *Larrea* and *Ambrosia* in subequal amounts (Table 1). Thus, there is no indication of *Neotoma* discrimination against *Larrea.* Although the timing of arrival for *Larrea* is yet to be established in Death Valley, it seems clear that it was preceded by its ubiquitous modern associate in the Mohave, *Ambrosia dumosa.*

LATE-GLACIAL/HOLOCENE CLIMATIC CHANGE IN DEATH VALLEY

With regard to the magnitude and nature of late Quaternary climatic change in Death Valley, the evidence presented here sheds some light on the perennial temperature vs. precipitation controversy (Brakenridge 1978, Wells 1979). A pluvial increase in precipitation is apparent from the present moisture requirements of *Juniperus osteosperma* and its 1200–1500-m displacement as the dominant species of the late-Pleistocene woodlands in Death Valley. This juniper is a relatively xerophytic species, descending at its lower limits to semidesert of *Artemisia tridentata, Atriplex confertifolia,* or *Coleogyne ramosissima*; but rarely does *J. osteosperma* descend into the hot desert of *Larrea* and *Ambrosia. Juniperus osteosperma* forms woodlands (even in the cooler, northern Great Basin) only

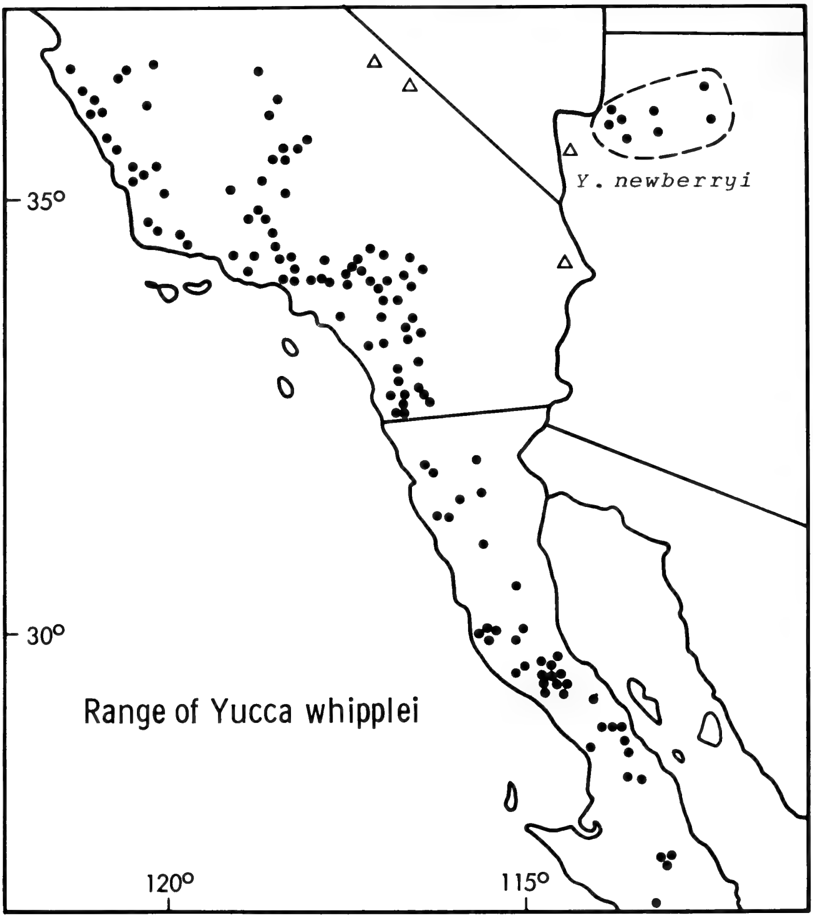


FIG. 3. Distribution of yuccas of the *Yucca whipplei* group (sect. *Hesperoyucca*). Modern records of *Y. whipplei* are in southern California and Baja California; the closely related (if not conspecific) *Y. newberryi* is restricted to northwestern Arizona; documented occurrences indicated by dots (after McKelvey 1938, Hastings et al. 1972). Late Pleistocene macrofossil records of yuccas with the highly distinctive leaf morphology of the *Yucca whipplei* group are indicated by "△"; occurrences at very low elevations indicate continuity of range then.

under mean annual precipitation of 200 mm or more (Beeson 1974). Today, much of Death Valley below 775 m receives 75–100 mm or less of precipitation per year; and there are frequent years with 25 mm or less. The late Pleistocene (13,060 yr BP) record of juniper woodland at 775 m in Death Valley suggests that the precipitation then was about twofold greater than today and probably less variable.

The late-Pleistocene climate was undoubtedly cooler than today; but limits to cooling are set by the pleniglacial (19,500 yr BP) dominance of *Yucca whipplei* at the lowest site (425 m) and late-glacial (11,600 yr BP) occurrences of the same yucca as high as 1280 m. At present, *Y. whipplei* appears to be absent in the Death Valley region, despite a large available elevational gradient of over 3000 m on the adjacent Panamint Range (Telescope Peak: 3368 m). It is now widely distributed in chaparral vegetation under the mild, Mediterranean isoclime (winter rain, summer drought) of cis-montane California. But *Y. whipplei* (the polycarpic subsp. *caespitosa*) extends to the extreme western margins of the Mohave Desert, where there is a transition from woodland/chaparral to high desert under a similar climatic rhythm (Fig. 3). It (chiefly as the polycarpic subsp. *eremica*) occurs also in the relatively cool, foggy desert of northern Baja California.

There is one outstanding exception to this restriction of *Y. whipplei* to the Mediterranean isoclime of the Pacific slope: an aberrant, widely disjunct population in the lower, western end of the Grand Canyon, Arizona under a hot-desert climate (Fig. 3). It differs in having reduced placental wings and has been regarded as a distinct species, *Y. newberryi* McKelvey. Furthermore, the Grand Canyon population appears to be entirely monocarpic (McKelvey 1938). The low-elevation *Neotoma* records from Death Valley and the lower Colorado River valley (Wells and Hunziker 1976) document a much wider and more continuous distribution of yuccas of *Y. whipplei* affinity (*Hesperoyucca*) as recently as the last (Wisconsinan) glacial of the Pleistocene (Fig. 3). The climatic characteristics of regions with modern populations of *Yucca whipplei* include very mild winter temperatures and substantial winter rain; and for most populations, summer temperatures are only mildly hot (relative to Death Valley).

Thus, the abundance of *Y. whipplei* under a full-glacial (19,500 yr BP) climate in Death Valley is an indication of cool but relatively mild winters then, coupled with greater precipitation; summers were almost certainly cooler then. A cold, dry pleniglacial climate (Brakenridge 1978) in Death Valley, cold enough to account for juniper woodland 1200–1500 m below its present lower limits, would have been too cold for *Yucca whipplei.* A cool and equable, pleniglacial climate (Wells 1979) with greater precipitation better explains the present evidence. *Yucca whipplei* may have disappeared in the Death Valley region because montane elevations moist enough for its survival are too cold in winter; and the area of mild winter climate near the valley floor now becomes too hot and dry in summer.

At the close of the last (Wisconsinan) glacial, the climate of Death Valley suffered a drastic but gradual decline in equability and precipitation during the interval 11,000–9000 yr BP, giving rise to the extremely hot summers and limited precipitation of the modern desert. The macrofossil evidence indicates that the desertification process began on the floor of Death Valley (already a *Yucca* semi-desert during the last glacial) and spread gradually up the slopes of adjacent mountains in the wake of the shrinking juniper and Joshua tree woodlands.

ACKNOWLEDGMENTS

Research support from the National Science Foundation (DEB-78-1187 to P.V.W.) is gratefully acknowledged.

LITERATURE CITED

BEESON, C. D. 1974. The distribution and synecology of Great Basin pinyon-juniper. M.S. thesis, Univ. Nevada, Reno.

BRAKENRIDGE, G. R. 1978. Evidence for a cold, dry, full-glacial climate in the American Southwest. Quaternary Res. 9:22–40.

HASTINGS, J. R., R. M. TURNER, and D. K. WARREN. 1972. An atlas of some plant distributions in the Sonoran Desert. Technical Reports on the Meteorology and Climatology of Arid Regions No. 21, Univ. Arizona, Tucson.

HUBBS, C. L. and R. R. MILLER. 1948. The Great Basin, with emphasis on glacial and postglacial times. The zoological evidence. Univ. Utah Bull. 38:18–144.

HUNT, C. B. and D. R. MABEY. 1966. Stratigraphy and structure, Death Valley, California. U.S. Geol. Surv. Prof. Paper 494-A.

KING, T. J. 1976. Late Pleistocene-early Holocene history of coniferous woodlands in the Lucerne Valley region, Mohave Desert, California. Great Basin Naturalist 36:227–238.

MCKELVEY, S. D. 1938. Yuccas of the Southwestern United States: Part One. Arnold Arboretum, Jamaica Plain, Mass.

MEHRINGER, P. J. 1967. Pollen analysis of the Tule Springs area, Nevada. Nevada State Museum, Anthropological Papers 13:129–200.

ROOSMA, A. 1958. A climatic record from Searles Lake, California. Science 128: 716.

VAN DEVENDER, T. R. 1977. Holocene woodlands in the southwestern deserts. Science 198:189–192.

——— and W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

WELLS, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153:970–975.

———. 1969. Preuves paléontologiques d'une végétation tardi-Pleistocène (datée par le ^{14}C) dans les régions aujourd'hui désertiques d'Amérique du Nord. Rev. Géogr. Phys. Géol. Dynam. 11:335–340.

———. 1974. Postglacial origin of the present Chihuahuan Desert less than 11,500 years ago. *In* R. H. Wauer and D. H. Riskind, eds., Transactions of Symposium on the Biological Resources of the Chihuahuan Desert Region, pp. 67–83. U.S. Govt. Print. Office, Wash., D.C.

———. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quaternary Res. 6:223–248.

———. 1979. An equable glaciopluvial in the West: pleniglacial evidence of increased precipitation on a gradient from the Great Basin to the Sonoran and Chihuahuan Deserts. Quaternary Res. 12:311–325.

———. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecol. Monogr. 53:341–382.

——— and R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science 155:1640–1647.

——— and J. H. HUNZIKER. 1976. Origin of the creosote bush (*Larrea*) deserts of southwestern North America. Ann. Missouri Bot. Gard. 63:843–861.

——— and C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in Mohave Desert: a record of juniper woodlands. Science 143:1171–1174.

(Received 9 June 1983; accepted 25 July 1984.)

ANNOUNCEMENT

To Madroño authors:

The California Botanical Society Council has adopted a new policy of assessing page allotments. Co-authors may now split the total page number, rather than each author's being charged with the full page total. Thus, co-authors of a 20-page paper will each be debited for 10 pages.

In addition, Madroño will now give Society members 10 free pages each year or 20 pages in a two-year period. This policy will begin with volume 32, January 1985, and the slate will be cleaned. Thus, beginning on 1 January 1985, all members of the Society will be eligible to publish a 10-page paper without an editorial fee. On 1 January 1986, those who have not used any of this allowance will be able to publish a 20-page paper without a fee. Pages published in 1985 will be deducted from this free allotment of 20. An author publishing a 20-page paper in 1986 would be eligible to publish a 10-page paper in 1987, but would not be able to publish a 20-page paper free until 1988. In other words, page allotments are granted on an annual basis and may be accumulated for two years only. The cycle begins in the first full year of membership.

SALE OF SURPLUS COPIES OF MADROÑO

A certain number of surplus issues have been set aside for sale at half price, first come, first served. Available are full sets of volume 1 and some numbers in volumes 2, 11–21, and 23 (including vol. 11, no. 2 and vol. 20, no. 3). Write to the corresponding secretary for a complete list of available issues and prices.

BOTANICAL SYSTEMATICS SYMPOSIUM

The Rancho Santa Ana Botanic Garden will sponsor and host a symposium on Trends in Systematic and Evolutionary Botany on 25–26 May 1985, at the Garden in Claremont, California. The purpose of this symposium is to examine current trends and, if possible, suggest and identify promising trends in systematic and evolutionary botany in the coming decade. Invited papers will be presented on pollination biology (H. Baker), chemical systematics (T. Swain), morphology (J. Skvarla), cladistics (M. Donoghue), physiological ecology (P. Rundel), aspects of modern floristics and traditional systematics (G. Prance), and research in botanical gardens (P. H. Raven). Low-cost housing will be available at nearby Pomona College. Attendance will be limited. For further information write: Systematics Symposium, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711.

This will be the first of an annual series of symposia planned at the Rancho Santa Ana Botanic Garden and is intended to provide a forum primarily for botanists in the southwestern United States and adjacent regions of Mexico.

A CYTOTAXONOMIC CONTRIBUTION TO THE WESTERN NORTH AMERICAN ROSACEOUS FLORA

E. DURANT MCARTHUR and STEWART C. SANDERSON
USDA Forest Service, Intermountain Forest and
Range Experiment Station,
Shrub Sciences Laboratory, Provo, UT 84601

ABSTRACT

New chromosome counts are reported for *Cercocarpus montanus* Raf. var. *montanus* and *C. ledifolius* Nutt. (2 varieties), $x = n = 9$; *Chamaebatia australis* (Brandg.) Abrams and *C. foliolosa* Benth., $x = n = 9$; *Chamaebatiaria millifolium* (Torr.) Maxim., $x = n = 9$; *Coleogyne ramosissima* Torr., $x = n = 8$; *Holodiscus dumosus* (Nutt.) Heller, $2x = n = 18$; *Kelseya uniflora* (Wats.) Rydb., $x = n = 18$; *Peraphyllum ramosissimum* Nutt., $x = n = 17$; and *Petrophytum caespitosum* (Nutt.) Rydb., $x = n = 18$. The counts are related to rosaceous subfamilial taxonomy. All taxa are relatively narrowly (geographically or ecotypically) distributed endemics. *Cercocarpus* and *Holodiscus* are the most wide ranging taxa.

Rosaceae, consisting of four subfamilies (Rosoideae, Prunoideae, Spiraeoideae, and Pomoideae), is pandemic but most common in the northern temperate region—especially western North America and eastern Asia (Raven and Axelrod 1974, Robertson 1974, Goldblatt 1976, Jones and Luchsinger 1979). In this paper we report chromosome counts for 10 species in 8 genera for three of the subfamilies. These counts are first reports for three varieties, nine species, and seven genera. Base chromosome numbers of the four subfamilies of Rosaceae are summarized in Table 1.

MATERIALS AND METHODS

Chromosome counts were made from root tips of germinated seedlings or from plants brought from the field to a mist bench and stimulated to produce additional roots; or from pollen mother cells (PMCs). Fixation was in 5% acetic acid or 1 N HCl. Roots were hydrolyzed in 1 N HCl for four hours at room temperature. Staining was by iron acetocarmine, air-evaporated on the slide to increase its concentration. Preparations were mounted in Hoyer's medium and examined microscopically under light field (meiosis) or phase contrast (mitosis) (Sanderson et al., in review). Counts were made from several plants (2–5) for each sampled population. Voucher herbarium specimens of representative samples were placed in the herbarium at the Intermountain Station's Shrub Sciences Laboratory (SSLP).

MADROÑO, Vol. 32, No. 1, pp. 24–28, 15 February 1985

TABLE 1. SUBFAMILIES OF ROSACEAE WITH CHARACTERISTIC CHROMOSOME NUMBERS AND GENERIC EXAMPLES. References: Ornduff (1967), Federov (1969), Moore (1973, 1974, 1977), Robertson (1974), Goldblatt (1976, 1981), McArthur et al. (1983), Baker et al. (1984), and Table 2. *New generic counts, Table 2.

Subfamily	Common x's	Other x's	Representative genera (x)
Rosoideae	7, 9	8, 14	*Fragaria, Geum, Potentilla, Rosa, Rubus, Sanguisorba* (7); *Alchemilla, Coleogyne** (8); *Adenostoma, Cercocarpus, Chamaebatia**, *Cowania, Dryas, Purshia* (9); *Fallugia* (14).
Prunoideae	8	—	*Exochorda, Oemleria, Prunus* (8).
Spiraeoideae	9	7	*Physocarpus, Spiraea, Aruncus* (7, 9); *Chamaebatiaria**, *Holodiscus**, *Kelseya**, *Petrophytum**, *Luetkea* (9).
Pomoideae	17	14, 15	*Quillaja* (14); *Vauquelinia* (15); *Amelanchier, Cotoneaster, Crataegus, Malus, Peraphyllum**, *Pyracantha, Pyrus, Sorbus* (17).

RESULTS AND DISCUSSION

The counts reported in Table 2 reveal no major surprises. Each corresponds to a base number consistent with previous records in its subfamily, unlike the new base numbers recently reported for *Fallugia* ($x = 14$) (Rosoideae) (McArthur et al. 1983, Baker et al., 1984) and for *Quillaja* ($x = 14$) and *Vauquelinia* ($x = 15$) (Pomoideae) (Goldblatt 1976).

Each generic count is new except for *Cercocarpus,* which had been reported $x = n = 9$ for one population of *C. betuloides* Nutt. (Morley 1949)—best referred to as *C. montanus* Raf. var. *glaber* (Wats.) F. L. Martin (Martin 1950). We report original counts for the typical variety of *C. montanus* Raf. and two varieties of *C. ledifolius* Nutt. Both species of *Chamaebatia* (Rosoideae) and its namesake genus *Chamaebatiaria* (Spiraeoideae) are $x = n = 9$.

Perhaps our most interesting new count is that of *Coleogyne ramosissima* Torr. (Rosoideae), a relictual endemic from the Mohave-Cold Desert ecotone (Bowns and West 1976). This species had $x = n = 8$ chromosomes. This is only the second unequivocal $x = 8$ count for Rosoideae (Table 2; Robertson 1974). *Coleogyne* is quite different from most other Rosoideae (and Rosaceae) in having 4- rather than 5-merous flowers. *Alchemilla,* the other $x = 8$ Rosoideae genus, is also 4-merous.

Holodiscus dumosus (Nutt.) Heller, $2x = n = 18$, was the lone new count we uncovered above the diploid basic number. Higher base numbers are not unexpected among the Rosaceae, where polyploidy is quite common in some groups (references cited for Table 1).

TABLE 2. CHROMOSOME COUNTS OF ROSACEOUS SHRUBS. *First report for taxon.

Taxa	Location, collection number	Chromosome count
Cercocarpus ledifolius Nutt. var. *intercedens* C. K. Schneider	Big Horn Mts., near Dayton, Sheridan Co., WY, 1230 m, *S. B. Monsen s.n.,* Jun 1982.	$2n = 18$*
Cercocarpus ledifolius Nutt. var. *ledifolius*	Near Adin, Lassen Co., CA, 1370 m, *J. A. Young s.n.*	$2n = 18$*
	Near Soda Springs, Caribou Co., ID, 2120 m, *J. N. Davis AB 849.*	$2n = 18$
	Near Verdi, Washoe Co., NV, 1520 m, *J. A. Young s.n.*	$2n = 18$
	Mineral Mountain Pass, Beaver Co., UT, 2050 m, *J. N. Davis S-12.*	$2n = 18$
	Near Cedar City, Iron Co., UT, 2100 m, *W. R. Stewart s.n.* (U 23).	$2n = 18$
	Weber Canyon, Morgan Co., UT, 2000 m, *J. N. Davis AB 681.*	$2n = 18$
Cercocarpus montanus Raf. var. *montanus*	Salt Creek Canyon, Juab Co., UT, 1800 m, *M. Black s.n.,* 6 Jun 1961 (U 8).	$2n = 18$*
Chamaebatia australis (Brandg.) Abrams	Tecate Peak, San Diego Co., CA, 760 m, *M. Kottman s.n.,* 20 Dec 1982.	$n = 9$*
Chamaebatia foliolosa Benth.	Near Auburn, Placer Co., CA, 500 m, *McArthur 1361.*	$2n = 18$*
Chamaebatiaria millifolium (Torr.) Maxim.	Marysvale Canyon, Sevier Co., UT, 1800 m, *McArthur and Sanderson 1339* (U 1).	$n = 9$*
	Ophir Canyon, Oquirrh Mtns., Tooele Co., UT, 2000 m, *McArthur 1370.*	$n = 9$
Coleogyne ramosissima	Tobin Wash, Washington Co., UT, 1250 m, *T. B. Moore s.n.,* 29 Jun 1978 (U 4).	$2n = 16$*
	Motoqua, Washington Co., UT, 1250 m, *J. E. Bowns s.n.*	$2n = 16$
Holodiscus dumosus (Nutt.) Heller	Chalk Cr., Pavant Range, Millard Co., UT, 1860 m, *S. Goodrich 16897.*	$n = 18$*
Kelseya uniflora (Wats.) Rydb.	Pass Canyon, Lost River Range, Custer Co., ID, 1840 m, *Sanderson 1367.*	$2n = 18$*
Peraphyllum ramosissimum Nutt.	Near Monticello, San Juan Co., UT, 2130 m, *W. R. Stewart s.n.,* 18 Aug 1965 (U 9).	$2n = 34$*

TABLE 2. CONTINUED.

Taxa	Location, collection number	Chromosome count
Petrophytum caespitosum (Nutt.) Rydb.	Rock Canyon, Wasatch Range, Utah Co., UT, 1700 m, *McArthur and Sanderson 1365.*	$n = 9$*
	Pass Canyon, Lost River Range, Custer Co., ID, 1840 m, *Sanderson 1366.*	$n = 9$
	Valley Mts., near Gunnison, Sanpete Co., UT, 1920 m, *S. Goodrich s.n.*	$n = 9$

Kelseya uniflora (Wats.) Rydb. and *Petrophytum caespitosum* (Nutt.) Rydb. (Spiraeoideae) are restricted western North American endemics; both have $x = n = 9$ chromosomes. *Peraphyllum ramosissimum* Nutt. (Pomoideae), in common with the mainstream members of its subfamily, has $x = n = 17$ chromosomes. We suggested earlier (McArthur et al. 1983) that the shrubby $x = 9$ Rosoideae (*Adenostoma, Cercocarpus, Chamaebatia, Cowania, Dryas, Purshia*) of western North America might be closely allied with the shrubby $x = 9$ Spiraeoideae (*Chamaebatiaria, Holodiscus, Kelseya, Luetkea, Petrophytum, Physocarpus, Spiraea*) of the same area. Both groups are characterized by high endemism and monotypicism and by sclerophyllous or microphyllous leaf habit. These six Rosoideae may have more in common with the seven Spiraeoideae than with mesic, $x = 7$ Rosoideae, such as *Fragaria, Potentilla, Rosa, Rubus,* and *Sanguisorba.* For example, *Chamaebatia* of Rosoideae and *Chamaebatiaria* of Spiraeoideae resemble one another closely in their unusual leaf form, although they differ in fruit type. However, one unifying factor for the $x = 9$ Rosoideae is presence of actinomycete root nodulation (Klemmedson 1979, Nelson 1983). Spiraeoideae are not nodulated. We also point out that *Physocarpus* and *Spiraea* have $x = 7$ members in Asia in addition to their more common $x = 9$ North American and Asian taxa (McArthur et al. 1983).

ACKNOWLEDGMENTS

This work was facilitated by funds from the Pittman Robertson Wildlife Restoration Project W-82-R. We thank J. E. Bowns, J. N. Davis, S. Goodrich, M. Kottman, S. B. Monsen, and H. C. Stutz for plant materials and stimulating discussion.

LITERATURE CITED

BAKER, M. A., D. J. PINKAVA, B. PARFITT, and T. J. RIGHETTI. 1984. On *Cowania* and its intergeneric hybrids in Arizona. Great Basin Naturalist 44:484–486.

Bowns, J. E. and N. E. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Utah Agric. Exp. Sta. Res. Report 27, Logan, UT.

Federov, A. A. 1969. Chromosome numbers of flowering plants. Izdateyur Nauk, Leningrad.

Goldblatt, P. 1976. Cytotaxonomic studies in the tribe Quillajeae (Rosaceae). Ann. Missouri Bot. Gard. 63:200–206.

———, ed. 1981. Index to plant chromosome number 1975–1978. Monogr. Syst. Bot. Missouri Bot. Gard. No. 5. St. Louis.

Jones, S. B., Jr. and A. E. Luchsinger. 1979. Plant systematics. McGraw-Hill Book Co., NY.

Klemmedson, J. O. 1979. Ecological importance of actinomycete-nodulated plants in the western United States. Bot. Gaz. (Suppl.) S91–S96.

Martin, F. L. 1950. A revision of *Cercocarpus*. Brittonia 7:91–111.

McArthur, E. D., H. C. Stutz, and S. C. Sanderson. 1983. Taxonomy, distribution and cytogenetics of *Purshia, Cowania,* and *Fallugia* (Rosoideae, Rosaceae). *In* A. R. Tiedemann and K. L. Johnson, compilers, Proceedings—research and management of bitterbrush and cliffrose in western North America, pp. 4–24. USDA Forest Service, Gen. Techn. Report INT-152, Ogden, UT.

Moore, R. J., ed. 1973. Index to plant chromosome numbers 1967–71. Regnum Vegetabile, vol. 90. Utrecht.

———. 1974. Index to plant chromosome numbers 1972. Regnum Vegetabile, vol. 91. Utrecht.

———. 1977. Index to plant chromosome numbers 1973–1974. Regnum Vegetabile, vol. 96. Utrecht.

Morley, T. 1949. *In* Documented chromosome numbers of plants. Madroño 10: 95.

Nelson, D. L. 1983. Occurrence and nature of actinorhizae on *Cowania stansburiana* and other Rosaceae. *In* A. R. Tiedemann and K. L. Johnson, techn. compilers, Proceedings—research and management of bitterbrush and cliffrose in western North America, pp. 225–239. USDA Forest Service Gen. Techn. Report INT-152, Ogden, UT.

Ornduff, R., ed. 1967. Index to plant chromosome numbers 1956. Regnum Vegetabile, Vol. 50. Utrecht.

Raven, P. H. and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61:539–673.

Robertson, K. R. 1974. The genera of Rosaceae in the southeastern United States. J. Arnold Arbor. 55:303–332, 344–401, 611–662.

(Received 12 March 1984; accepted 26 July 1984.)

ANNOUNCEMENT

All-expense-paid Trip to Berkeley

Yes, people desiring one or even two free trips each year to Berkeley, California may apply for the position of editor, MADROÑO, A West American Journal of Botany. The president of the California Botanical Society is accepting applications at this time. Qualifications include 3–5 hrs per day of free time during Dec., Mar., June, and Sept. (work load varies during other months); proficiency in English; and a very durable red pencil. Office expenses incurred while editing MADROÑO will be reimbursed by the Society.

I have found the experience of working on MADROÑO educational and highly rewarding, and I recommend the job to anyone who is interested.—C. Davidson

SEROTINY AND CONE-HABIT VARIATION IN POPULATIONS OF *PINUS COULTERI* (PINACEAE) IN THE SOUTHERN COAST RANGES OF CALIFORNIA

MARK BORCHERT
Los Padres National Forest, Goleta, CA 93117

ABSTRACT

The cone habit of *Pinus coulteri* exhibits considerable variation among plant communities in the southern Coast Ranges of California. Serotiny is prevalent in *P. coulteri*/chaparral, *P. coulteri*/*Quercus chrysolepis,* and *P. coulteri*/*Cupressus sargentii* communities that are periodically burned by wildfire. The bulk of pine regeneration in these types occurs in the first year after a fire, after which it rapidly declines, and ceases within 20 years. By contrast, in the *P. coulteri*/*Q. agrifolia* community nearly all cones open at maturity or soon thereafter. Pines in this habitat are generally less subjected to fire-caused mortality; regeneration, although sporadic, is continuous.

The quantity of stored viable seed is reduced in all community types by animal depredations and varying degrees of spontaneous cone opening. Despite these losses, the amount of stored, viable seed retained in serotinous stands is 50 times greater than quantities stored in nonserotinous stands.

Three closely related species of the genus *Pinus, P. torreyana, P. sabiniana,* and *P. coulteri,* constituting the subsection *Sabinianae,* show tendencies toward seed retention (McMaster and Zedler 1981; Critchfield, pers. comm.). *Pinus torreyana* retains seed for up to 15 years in cones that open gradually over time (McMaster and Zedler 1981). Minnich (1980) suggested that the often abundant regeneration of *P. coulteri* following wildfire originates from seed stored in partially open cones and maturing cones persistent on fire-killed trees. Despite these tendencies, however, serotiny, defined as the retention of mature seeds in closed cones, is not known to occur in this group.

In this study I describe serotiny, cone-habit variation in relation to plant community types, and factors that influence seed retention in *P. coulteri* growing in the southern Santa Lucia and La Panza Ranges, part of the southern Coast Ranges of California. I also discuss the possible adaptive value of canopy-stored seed in fire-prone habitats and management implications of seed storage and other life history traits of *P. coulteri.*

THE STUDY AREA

The study area includes a highly fragmented *P. coulteri* distribution in part of the Los Padres National Forest (Fig. 1). The tree ranges in elevation between 610 m and 1525 m, and average annual

---

MADROÑO, Vol. 32, No. 1, pp. 29–48, 15 February 1985

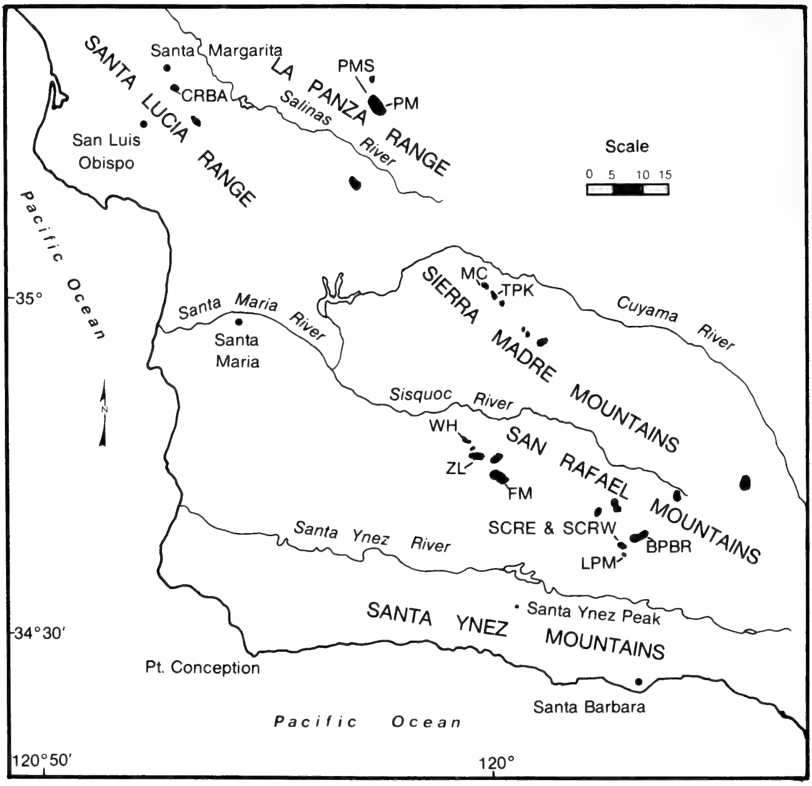


FIG. 1. The distribution of *Pinus coulteri* and the location of sampling sites in the study area.

precipitation generally exceeds 450 mm. Stands grow on a variety of soil types (Table 1), but gravelly loams derived from marine bedrock parent material are the most common.

The climate of the region is Mediterranean. At lowland localities like Santa Barbara (36 m) and San Luis Obispo (60 m), most precipitation falls from November–April. Mean monthly precipitation and temperature range from 30–100 mm and 11–15°C, respectively. May–October is dry and warm: mean monthly precipitation and temperature for this period vary from 0.5–10 mm and 16–20°C, respectively. Data from Santa Ynez Peak (1310 m) and Figueroa Mountain (FM; 960 m) (Fig. 1) indicate that precipitation at higher elevations extends into May and ranges from 30–186 mm for the six month period.

Wildfires are very frequent in the region. Since 1912, major fires (>4000 ha) have burned on the average of once every three years,

TABLE 1. LOCATION AND HABITAT DETAILS OF *P. coulteri* SAMPLE SITES IN THE STUDY AREA. Key: D, density in no. plants/ha; and, BA, basal area in m^2/ha.

Sample site	Elevation, aspect, slope, soil family	*Pinus coulteri*		Other tree species	D	BA	Shrub cover %
		D	BA				
Big Pine-Buckhorn Road (BPBR)	1438 m, se., 5–40% Supan	45	1.3				70
Cuesta Ridge Botanical Area (CRBA)	806 m, n., 50% Cuesta-Henneke	239	8.2	*Cupressus sargentii*	1458	50.0	2
Figueroa Mountain (FM)	1244 m, se., 60% Witzel-Skalan	154	0.5	*Q. agrifolia*	60	2.9	
Little Pine Mountain (LPM)	1341 m, sw., 35% Witzel	148	20.0	*Q. agrifolia*	46	2.2	25
Miranda Canyon (MC)	1304 m, nnw., 64% Morical and Konocti	900	29.0	*Q. chrysolepis*	208	8.1	
Pine Mountain (PM)	975 m, wsw., 45% Supan	936	0.1				77
Pine Mountain Summit (PMS)	1137 m, e., 50% Supan	242	31.4				96
Santa Cruz Road East (SCRE)	1335 m, e., 35% Witzel	72	1.6				98
Santa Cruz Road West (SCRW)	1335 m, w., 60% Witzel	2754	0.2				15
Timber Peak (TPK)	1448 m, nnw., 65% Morical and Konocti	307	20.0	*Q. chrysolepis*	320	11.9	
Wildhorse (WH)	945 m, nw., 50% Witzel	230	11.6	*Q. agrifolia*	141	4.6	
Zaca Lake (ZL)	729 m, ene., 5–20% Witzel-Skalan	68	6.5	*Q. agrifolia*	65	50.6	22

and most (60%) spread through chaparral older than 40 years. Because 52% of the vegetation is currently older than 40 years, large-scale conflagrations are inevitable in future dry seasons (U.S. Forest Service data on file at the Supervisor's Office, Goleta).

Chaparral, semidesert chaparral, and coastal sage scrub collectively cover 73% of the study area, followed by 5% oak woodland and 3% conifer forest. Three *P. coulteri* communities are common in the study area: *P. coulteri*/chaparral, *P. coulteri/Quercus agrifolia* and *P. coulteri/Q. chrysolepis.* Fifty-five percent of *P. coulteri* forests occur with chaparral. This community occupies a variety of exposures on slopes ranging from 5–81%. *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* are the most common understory species, although richer mixtures of brush species are encountered on more mesic sites. Shrub cover usually exceeds 70%, but is often lower in dense pine stands, or where soils are thin on outcroppings.

Pinus coulteri/Q. agrifolia forest is the next most common community (23%), and occurs mostly on gentler slopes (<50%), southerly exposures (Campbell 1980) and ridgetops. Exotic annual (*Bromus* spp., *Festuca* spp., and *Avena* spp.) and indigenous perennial grasses (*Bromus carinatus* and *Elymus glaucus*) dominate the understory with several subshrubs in *Lupinus* spp. Shrub cover is less than 30%.

Pinus coulteri/Q. chrysolepis forest (20%) is confined almost entirely to steep (>60%) north-facing aspects. *Toxicodendron diversilobum* is the only common understory species, but its cover is low (Campbell 1980). The *P. coulteri/C. sargentii* forest grows at a single locality in the area (CRBA) (Fig. 1).

STUDY METHODS

Twelve stands were sampled from most parts of the *P. coulteri* distribution in the study area (Fig. 1). The stands were selected subjectively to represent a variety of community types of differing ages. Each stand had to be native (i.e., unplanted), relatively accessible, undisturbed, and homogeneous in vegetation. It is estimated that at least 50% of the major *P. coulteri* stands are represented. The CRBA stand is anomalous because it straddled a sheltered fuelbreak. However, there were no signs of pine cutting in this stand, although *C. sargentii* was thinned.

Elevation, slope angle, and aspect were recorded at each site. Soil classification was taken from a third order soils map (U.S. Forest Service data on file on file at the Supervisor's Office, Goleta). Depending on the size and density of the stand, tree density was estimated with circular plots or by the plotless point-center-quarter method (Cottam and Curtis 1956). Small (<0.75 ha) or relatively dense stands were sampled with plots varying in size from 0.05–0.2 ha. Each plot was made large enough to include 30–60 pines ≥2.5

cm in diameter measured at 1.4 m (dbh). Larger sample sizes were necessary to characterize multi-aged stands. In low-density stands larger than one hectare (SCRE, ZL), the point-center-quarter method was employed. In each stand a total of 12–15 points was sampled along 2–3 transects oriented parallel to the contours. Tree density estimates using this method had standard errors less than 10% of their mean values.

All *P. coulteri* seedlings ($\leq$2.5 cm dbh), saplings (2.5 cm–10 cm dbh) and trees ($>$10 cm dbh) were counted in plots and at sampling points on the transects. Fewer than 5 seedlings were encountered in each of the WH, ZL, and LPM stands. Stems $\geq$5 cm were cored at 60 cm to determine age. In addition, two to four stems were cut at ground level in several stands to estimate the number of years required to reach 60 cm; as a result, four years were added to the core-height age of trees in all stands. No attempt was made to estimate the mean and variance in the age required to reach 60 cm in each stand. All other tree species $\geq$2.5 cm dbh were counted and measured.

Shrub cover was visually estimated in 2.3 m^2 circular subplots taken at each sampling point along transects or at 8–15 locations within the plots. Total herbaceous cover also was recorded for each subplot and the dominant species noted.

Open and closed cones were censused and aged with binoculars. Since over 95% of cones in 15- to 50-year trees are borne on the bole, cone age can be determined indirectly by counting the number of branch whorls. Generally, trees in this age class produce whorls annually. Nevertheless, in order to verify the accuracy of whorl counts, one to two branches were cut from a sample of 5–15 trees per site, and the branch ages compared to their corresponding whorl counts. The two were highly correlated ($r = 0.948$, $p < 0.01$, $n = 14$, SCRW; $r = 0.974$, $p < 0.01$, $n = 31$, SCRE; $r = 0.947$, $p < 0.01$, $n = 19$, CRBA).

Branch cones in trees older than 50 years could not be aged accurately using binoculars because branch growth had slowed enough to prevent distinction between recent cones, which remain closed during the normal maturation period, and those that remained closed longer. Accurate aging could only have been accomplished by counting bud-scale scars, which would have required tree felling or branch cutting. Thus, only the number of open and closed cones was recorded in these trees. All stand samples had at least 10 trees 15–50 years old.

To simplify analysis of cone age data, cones were grouped into one-year age class intervals. Thus, cones 0–12 months are in the first age class, 13–24 months in the second, and so on. Cone production is assumed to have commenced on 1 June, when pollination first was observed in the SCR and PM stands.

A total of 251 closed cones, varying in age from 16 months to 24 years, was gathered from trees in PM and SCRE stands: 156 cones from 26 trees in the SCRE stand, and 95 cones from 25 trees in the PM stand. Cones were selected from trees that appeared visually to have an adequate number of cones in certain size classes. Cones remaining closed for more than two years after pollination are termed serotinous in this study. Each cone was first measured and examined for external signs of animal damage, and then immersed in boiling water for 60–75 seconds to melt the resinous bonding material that seals the scales together. Once the scales had separated, the seeds were hand-extracted. In addition, residual seeds were removed from 28 open cones (5–17 years) gathered from the SCRE stand. Empty seeds were removed by floating in water.

Germination trials were conducted on a random sample of 20 filled seeds from each cone. Because of the small number of filled seeds in each open cone, they were combined into one lot from which three samples were tested. After soaking in an aerated water bath for 24 hours, each sample was dipped in a captan solution and sown on a moist layer of cotton in a petri dish. Following a stratification period of 60 days at 10°C in continuous light, the light-temperature regime of the samples was altered to 8 hours of light at 25°C and 16 hours of darkness at 15°C. A seed was considered germinated if it produced a radicle at least 3 mm long after 14 days. The small sample size of cones in some age classes required the grouping of germination results for analysis.

A description of cone maturation was constructed from small samples of cones (4–10 at each sample age) collected 12, 14, 16, 18, and 22 months after pollination (1 June) in the LPM and SCRE stands, and 16-month cones in the PM stand.

RESULTS

Age structure and establishment. Stand age data indicate two general types of age structures: unimodal, bell-shaped distributions indicative of even-aged stands, and pulsed distributions suggesting irregular episodes of successful regeneration (Figs. 2–3).

Most *P. coulteri* stands growing in association with chaparral (SCRE, SCRW, PM), *Q. chrysolepis* (MC, TPK), or *C. sargentii* (CRBA) are characterized by an even-aged structure that results from a stand-killing wildfire. Evidence corroborating this explanation is provided by Minnich (1978, 1980), who noted high levels of fire-caused pine mortality in both *P. coulteri*/chaparral (90%) and *P. coulteri*/*Q. chrysolepis* (81%) types in the eastern Transverse Ranges. Comparable pine losses probably occur in *C. sargentii* thickets, which are prone to crown fires (Vogl et al. 1977).

The PMS stand is anomalous. It is an old-aged pine stand in

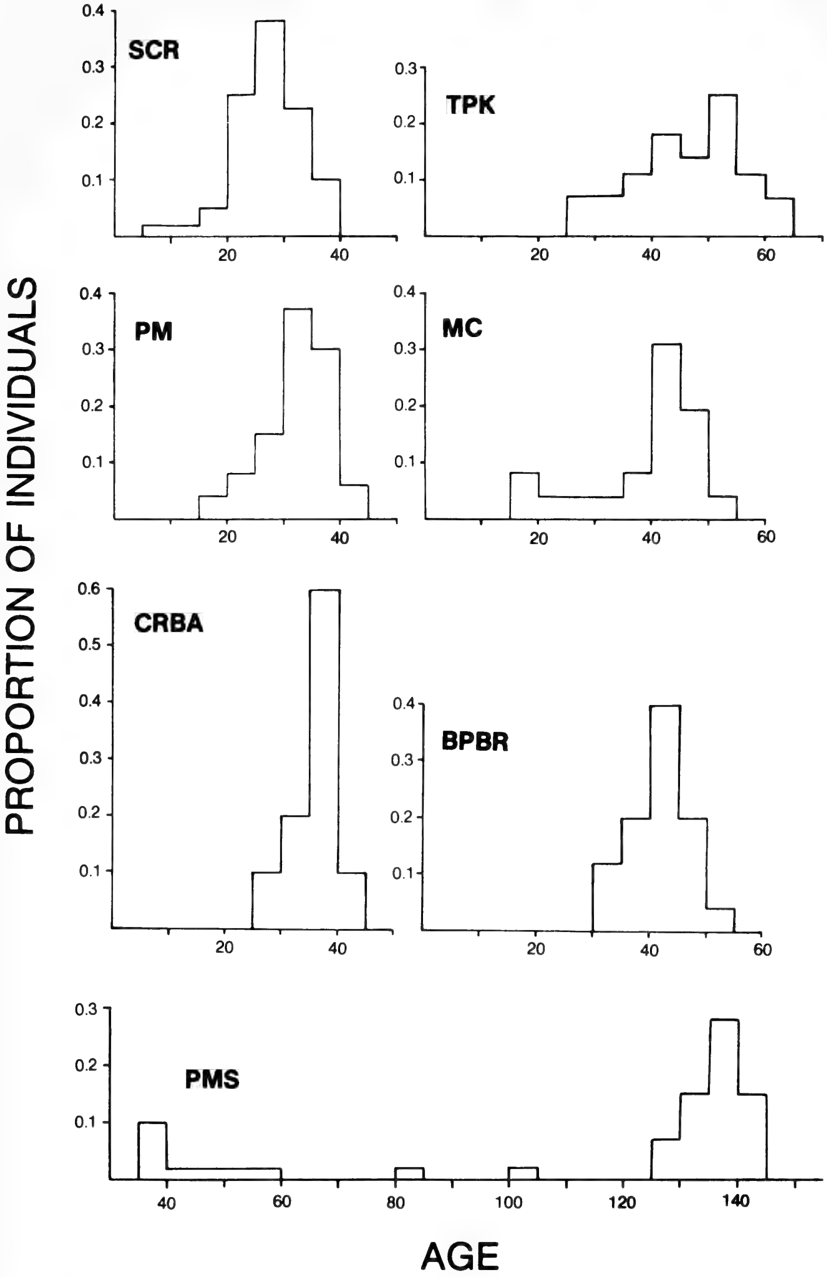


FIG. 2. Age-frequency histograms for the *P. coulteri*/chaparral (BPBR, PM, PMS, and SCR); *P. coulteri/Q. chrysolepis* (MC, TPK); and *P. coulteri/C. sargentii* (CRBA) stands. The SCRE and SCW are nearly identical and have been combined into SCR.

chaparral with several episodes of pine establishment. The oldest cohort likely originated after a fire in the 1830s. Another documented fire swept the area in 1921, but evidently spared most of the 90-year-old trees. Fire scar analyses of 140-year-old trees indicate that a fire that burned an adjacent area in 1939 also spread to the PMS site. The isolated 80- and 100-year-old trees suggest that chaparral stands relatively well-protected from stand-converting fires may exhibit pulsed regeneration at an advanced age. In a discussion of 40-year-old, south-slope, montane chaparral of the type often associated with *P. coulteri,* Hanes (1971) noted the formation of openings in the canopy resulting from shrub mortality. These openings were colonized by *Salvia mellifera* seedlings. Similarly, *P. coulteri* seedlings may establish in these sites. My observations of canopy openings in comparatively young stands (<60 years), however, suggest that such establishment is probably rare and most likely occurs on the periphery of the stand.

Complete or nearly complete stand destruction is followed within a year by a burst of pine regeneration (Minnich 1977, Griffin 1982). Seeds fall from heat-opened, maturing cones, residual seed in open cones, and older closed cones stored in the canopy. Age-frequency histograms (Fig. 2) show the appearance of new trees consistently later than the first year after the fire. To a large extent, this discrepancy can be attributed to the variable growth period necessary for seedlings to reach the core height. In dense stands, for example, numerous seedlings do not reach 60 cm even after 6 years (Griffin, pers. comm.). Inadequate precipitation and poor site conditions may also retard seedling growth.

As vegetative cover increases with stand age, tree establishment declines and eventually ceases. Despite the variety of species associated with *P. coulteri* among the even-aged stands, the length of establishment, as determined by the age difference between the oldest and youngest trees in each stand, was remarkably constant, averaging 23 ± 1.86 years ($n = 7$). The actual establishment period is probably around 20 years, since very late appearing trees would likely require more time to reach the core height. Vale (1979) found that successful regeneration of *P. coulteri* in a chaparral stand on Mt. Diablo spanned 19 years.

Although first-year seedlings originate from fire-released, cone-stored seed, later pine regeneration probably developed from other sources. These include: (a) occasional trees that survived fires. Some trees, especially those on ridgetops, are undamaged by fire and continue to supply seed to burned areas for decades. Such survivors were present in both the SCR and TPK stands; (b) singed, but unopened cones on fire-killed trees. After a recent fire (1981) in a *P. coulteri/Q. agrifolia* stand, some large, heavily scorched pines had unburned or lightly singed cones on the tips of high branches. Con-

TABLE 2. CONE AND SEED CHARACTERISTICS OF THE PM AND SCRE STANDS. All attributes are significantly different ($p < 0.05$, one-way ANOVA) between the two stands, except full seeds/undamaged cone. Cone size is length × maximum width. Means are presented ± one standard error.

Cone and seed characteristics	Study site			
	PM	n	SCRE	n
Cone size	209.3 ± 4.2	133	159.0 ± 5.3	44
Seed length (cm)	1.43 ± 0.02	75	1.26 ± 0.03	75
Seed weight (gm)	0.35 ± 0.01	2420	0.29 ± 0.01	1780
Full seeds/undamaged closed cone	150.5 ± 5.6	111	151.3 ± 5.9	88
Percent empty seeds/ closed cone	15.7 ± 1.3	134	9.8 ± 1.1	82
Full seeds/open cone	2.2 ± 0.4	28	no data	

ceivably, these cones might open slowly enough to furnish viable seed to the area for several years after the fire; (c) early reproducing trees of the immediate post-burn cohort. Reproduction can occur in trees as young as 10 years (Minnich 1980). Seed released from precociously reproducing trees appeared to be the likely source of trees where no obvious survivors were observed (PM, CRBA, MC); and (d) residual seed trapped in the basal scales of open cones (Table 2).

Irregular pulses of pine regeneration characterize the *P. coulteri*/*Q. agrifolia* stands (Fig. 3). Some even-aged cohorts date back to fires, whereas others probably coincide with years of good precipitation and seed production. Typically, small groups of pine seedlings appear in grassy openings or at the edge of the oak canopy. Saplings are often spindly, and some heavily shaded individuals die. Nevertheless, many manage to reach a fire-resistant size. Because ground fuels in this habitat consist of grasses and discontinuous patches of shrubs and subshrubs, wildfires are generally lower in intensity, and crown fires are probably rare. For example, fire-caused pine mortality averaged only 30% in a similar *P. coulteri*/*Q. kelloggii* type in the eastern Transverse Ranges (Minnich 1977). Both forests are open, free of brush and *Q. chrysolepis.*

Age of first reproduction. Based on the age of the oldest serotinous cones in the SCRE and PM stands, as well as observations of saplings at other locations, reproduction in most *P. coulteri* begins 12–15 years after germination. Published figures range from 8–20 years (Krugman and Jenkinson 1974) to 15–20 years (Minnich 1980). High tree density may significantly delay reproduction. Thus, although the two SCR stands are the same age, reproduction in the extremely dense SCRW stand began five years after the adjacent low-density SCRE stand. Late-establishing trees often grow poorly because of

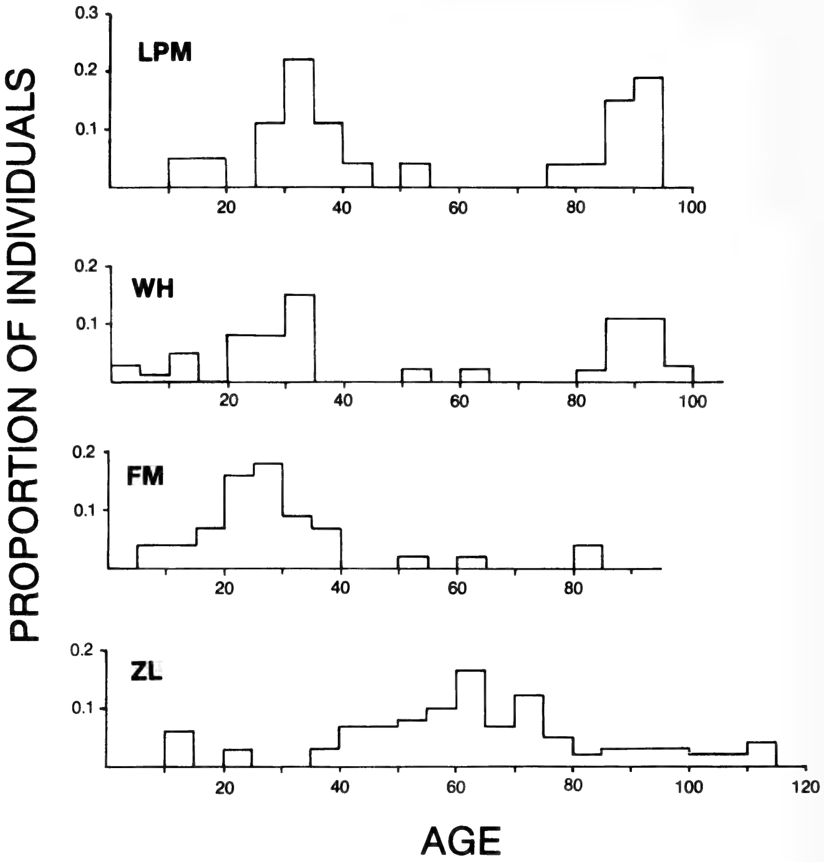


FIG. 3. Age-frequency histograms for the *P. coulteri*/*Q. agrifolia* stands.

brush competition or suppression by overstory trees. Thus, cones are infrequently encountered in trees of reproductive age.

Trunk and branch cone production. Young trees typically bear whorls of up to four cones (rarely five) on the bole. Cones do not appear at the ends of branches until limbs are strong enough to support the heavy cones (the heaviest in the Pinaceae). The age of first branch-cone production differed markedly among stands. Trees in the low-density, fast-growing SCRE stand produced branch cones 20–25 years after germination, whereas cones occurred in small numbers on 36- to 40-year-old trees in the considerably denser CRBA, PM, TPK and MC stands. Limb cones were not produced in the extremely dense SCRW stand. As the stand ages, cone production shifts almost entirely to tips of the major branches and apex of the crown (Minnich 1980). It is not uncommon, however, to find tiers of serotinous cones dating back 20 years on the trunks of trees as old as 50 years.

Cone maturation. Twelve-month (June) cones are similar in size to mature cones. However, 12-month cones are green, firm, and pulpy compared to mature cones, which are hard, brittle, and light caramel in color. Seeds at this stage are full-sized, but white and soft, lacking any trace of a hard seed coat.

By 14 months (August), the umbos of outward-facing scales begin to turn dark brown. Cones are typically moist, but the scales are fibrous and separate individually when heated. The seed coat is hard and light brown instead of black. Only 11% of the seeds were solid; of these, 50% were viable. Cones burned at this stage of ripening probably contribute only marginally to pine regeneration.

Most cones turned to mature-cone color after 16 months, although some retain a reddish hue. Seeds are fully formed and, despite the somewhat milky texture of the endosperm, have a high germination rate (Table 3).

By 18 months (December), cones have completely matured, and judging by the degree of cone development at 16 months, most probably reach full maturity between 15 (September) and 16 months (October) after pollination.

Cone weathering. Serotinous cones retain a light-caramel color for 2–3 years. Almost invariably by the fifth year, however, outward-facing scales show signs of weathering as the apophyses begin to gray. In succeeding years the signs of weathering spread, and the abundant resinous covering of newly-ripened cones gradually wears away. Fifteen-year cones are almost entirely gray and usually devoid of external resin. Cones reaching 24–26 years are heavily weathered, usually to the point of disintegrating. This weathering sequence conforms closely to that described for *Pinus banksiana* cones (Roe 1963).

Cone and seed characteristics. Table 2 summarizes cone and seed characteristics of the PM and SCRE stands. Cone size, seed length and weight, and the percent empty seeds per cone differ significantly between the two populations. Despite these differences, however, the mean number of full seeds per undamaged cone is similar in the two stands.

Seed viability. The viability of seeds from closed cones of all ages from the SCRE and PM stands is high, 83–100%, and shows no decline with cone age. This trend contrasts with similar studies of other serotinous pines, *P. clausa* (Cooper et al. 1959), *P. banksiana* (Schantz-Hansen 1941, Beaufait 1960) and *P. pungens* (Barden 1979), in which seed viability decreases with cone age. High viability appears to be related to protection afforded by the tightly sealed scales that cover the seed with a hard, woody layer 1–1.5 cm thick. High

Table 3. Cone-habit Characteristics and Stored Viable Seed Estimates for the Two *P. coulteri* Plant Community Groups. Stored viable seed estimates assume 138 solid seeds/cone and 91% viability. Open cones are assumed to have 2.2 solid seeds/cone and 97% viability.

Study site	Open cones/tree	Closed cones/tree	% open cones	Viable seeds/tree	Stored viable seeds/ha
Q. agrifolia stands					
FM	0.23	0.30	43.4	38.2	5878
LPM	0.73	0.35	67.5	45.5	6735
WH	0.02	0.10	16.7	12.6	2898
ZL	0.77	0.45	63.1	58.2	3954
$\bar{x}$ ± S.E.	0.44 ± 0.18	0.30 ± 0.07	47.7 ± 11.6	38.6 ± 9.6	4866 ± 876
Chaparral, *Q. chrysolepis,* and *C. sargentii* stands					
BPBR	0.64	7.64	7.7	960.8	43,236
CRBA	0.00	5.71	0.0	717.1	210,100
MC	0.16	2.37	5.4	678.1	610,319
PM	0.06	4.29	1.4	538.8	504,371
PMS	0.13	14.20	0.9	1783.5	431,610
SCRE	1.29	8.60	13.0	1082.7	77,957
SCRW	0.06	0.18	25.0	22.7	62,605
TPK	0.00	3.14	0.0	394.3	121,057
$\bar{x}$ ± S.E.	0.29 ± 0.16	5.77 ± 1.55	6.7 ± 3.1	772.3 ± 185	257,657 ± 79,377

seed viability (97%) from open cones suggests that the seed coat may also provide additional protection, although it was not possible to determine how long seeds in open cones were exposed at the time of collection.

Insect damage to cones. In early stages of development (<16 months), cones are highly susceptible to insect attack. For example, 71% of the SCRE cones in the 2–4-year age classes were infested by *Dioryctria auranticella* (ponderosa pine coneworm). Damage was complete in 25% of the collected cones. However, in the 5–7-year age classes partially damaged cones decreased to 36%, 11%, and 9%. Insect damage was absent in cones older than 7 years. Directly or indirectly, insect infestations caused an average loss of 67 full seeds per attacked cone, or a 45% reduction. Seed losses may have been elevated further by the mining of *Camponotes anthrax* (carpenter ants), a frequent inhabitant of damaged cones.

Complete cone losses to insects in the PM stand were far less frequent than in the SCRE stand (<1%). Insect-damaged cones in 2–9-year age classes varied from 25–40%, whereas cones older than 9 years showed no signs of recent insect attack. Altogether, there was a reduction of 57 full seeds per damaged cone, or a 38% seed loss. Nearly all the cones in the PM collection were infested by larvae of *Chrysophana canocola* (flatheaded cone borer). Although this species is not known to attack pine seeds (Essig 1958), its extensive tunneling may weaken the cone's resistance to weathering.

The diminishing percentage of insect-attacked cones in increasingly older age classes indicates that damaged cones probably weather, disintegrate and fall before unattacked cones. However, there was no evidence to suggest that insect tunneling caused serotinous cones to open or encouraged squirrel consumption.

Variation in serotiny. The degree of serotiny differed markedly among the *P. coulteri*/chaparral, *P. coulteri/Q. chrysolepis, P. coulteri/C. sargentii* stands (Fig. 4). The highest degree of serotiny was exhibited by the PM stand; fully 52% of the cones 6 years or older were closed. By contrast, none of the MC cones was closed after 4 years. Between these extremes the other stands form a gradient, but exhibit no discernible pattern of variation.

Attempts to assess serotiny in the *P. coulteri/Q. agrifolia* stands were only partially successful. Trees younger than 50 years were present in all the stands and were particularly abundant in the WH and FM stands. These stands were notable for their scarcity of cones in comparison to the even-aged stands regardless of tree age (Table 3). The small cone populations suggest that either (a) they opened at maturity and were blown from the trees, or (b) they remained closed at maturity but were cut by *Sciurus griseus anthonyi* (western gray squirrels) before they could age further.

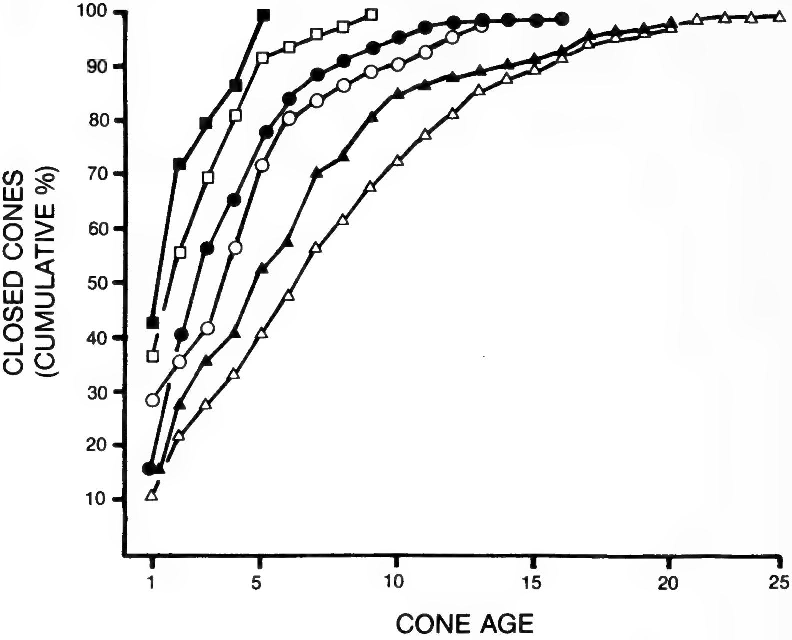


FIG. 4. Cumulative cone-age distributions for the serotinous BPBR (▲), CRBA (○), MC (■), PM (△), SCR (●), and TPK (□) stands. The SCRE and SCRW stands have identical distributions displayed as SCR.

Several lines of evidence point to cone opening at maturity. Few trees in the age class 15–50 years with an adequate sample of attached cones had closed cones older than 2 years. On the periphery of the LPM and FM stands in chaparral, pines appeared less prone to squirrel depredations than those in the central portion of the stand, judging by the numerous attached cones in the older age classes (4–6). Significantly, nearly all the cones in these outlying trees were open. And finally, the percentage of open cones/trees in these stands was nearly 8 times ($p < 0.01$; one-way ANOVA, arcsine transformation) that of the even-aged stands (Table 3).

There are at least three factors that clearly influence the length of time that cones stay closed and attached to the tree: (a) insect damage, (b) cone cutting by squirrels, and (c) spontaneous cone opening. As discussed previously, insect-attacked cones diappear from the cone population before undamaged cones. Because coneworm infestations are generally widespread, insect damage probably has a significant but highly variable effect on cone persistence.

Squirrel cone cutting and consumption was observed in all stands.

Both green and mature cones were cut and consumed on the ground, or less frequently, partially consumed while attached to the tree bole or limbs. Scales of some cones were partially or entirely stripped from the main axis while others appeared to be excavated with only the half shell remaining.

Western gray squirrels are known to depend heavily on acorns and pine seeds for winter food supplies (Stienecker and Browning 1970, Stienecker 1977). Evidence for this dependence was readily observed in the *P. coulteri/Q. agrifolia* habitat. For example, a random sample of 125 ground cones in the ZL stand showed that 44% had signs of squirrel damage, including removal of basal scales, partial excavation, or complete scale removal. Seventy-five percent of a sample of 108 cones on the ground in the FM stand were squirrel-damaged. In most the scales had been stripped completely from the cone axis. Observations suggest that *P. coulteri* cones are a relatively dependable year-round food source for squirrels. Moreover, squirrel population density and stability may be closely tied to cone production by this pine in southern California, a relationship perhaps comparable to that of serotinous *P. contorta* and squirrels of the genus *Tamiasciurus* in the Cascade Mountains of Washington (Smith 1970).

Spontaneous cone opening occurred in varying degrees in nearly all stands (Table 3). Perry and Lotan (1977) cited three factors explaining differential cone opening: differences in scale tension, environmental effects on bonding strength, and genetic differences in the bonding oleoresin. In a study of *P. contorta,* they found opening differences between new and old serotinous cones from the same tree, suggesting that melting characteristics of the resin seal may be influenced by the environment. A complex interaction of genetic and environmental factors probably determines cone opening in *P. coulteri,* but differentiating between the two will require further study.

Stored viable seed. Table 3 gives estimates of stored viable seed for sampled stands. The number and viability of seeds in open and closed cones in the *Q. agrifolia* stands are assumed to be the same as the chaparral stands. A comparison of seed populations between the two community groups reveals a marked difference. Although there is considerable within-group, interstand variability, the *P. coulteri*/chaparral, *P. coulteri/Q. chrysolepis, P. coulteri/C. sargentii* stands taken together average 50 times the number of stored viable seeds in the *P. coulteri/Q. agrifolia* stands ($p < 0.01$; one-way ANOVA, logarithmic transformation). I attribute most of this between-group difference to the higher incidence of both squirrel cone cutting and spontaneous cone opening (i.e., less serotiny) in the *P. coulteri/Q. agrifolia* stands.

DISCUSSION

There is a discernible pattern of cone-habit variation among sample stands in the study area. The open-cone habit predominates in the *P. coulteri/Q. agrifolia* forest, where fire-caused mortality is low and pine regeneration relatively unrestricted by competing vegetation. Serotiny tends to be well developed in communities subject to killing crown fires. Previous studies (Minnich 1977, Griffin 1982) indicate that pine establishment in fire-prone communities is relatively synchronous, peaking in the first post-fire year. Thereafter, establishment declines and eventually ceases within 20 years as competing vegetation gradually dominates the site.

Habitat-related cone-habit variation similar to that described above has been recorded for a number of pine species (Little and Dorman 1952; Lotan 1967, 1968; Givnish 1981). Indeed, several investigators have proposed that serotiny has evolved in direct response to fire (Perry and Lotan 1979, Givnish 1981, McMaster and Zedler 1981). Extensive evidence linking fire frequency and serotiny was presented for *P. rigida* in the Pine Barrens of New Jersey (Givnish 1981). Similarly, results of this study suggest that cone-habit variation in *P. coulteri* is strongly influenced by fire. Indeed, the pattern of variation corresponds favorably to that predicted by a model for the evolution of serotiny in Mediterranean-climate conifers proposed by McMaster and Zedler (1981). They argue that serotiny is selected for when: (a) stand-killing fires burn over extensive areas, (b) interfire intervals are too short for reproduction by second-generation trees, and (c) fire size is too large for seed dispersal from adjacent unburned areas to be a significant factor for recolonization of burned areas. As discussed previously, stand-immolating fires are common in the *P. coulteri*/chaparral, *P. coulteri/Q. chrysolepis* and *P. coulteri/C. sargentii* communities, and average fire size is usually large relative to the seed dispersal abilities of *P. coulteri.* The average fire-free interval, however, is often long enough (Byrne 1979) to permit some reproduction by second generation trees. Thus, limited seed release is favored, as was observed in even the most serotinous stands.

When any of the above conditions are sufficiently relaxed, open-cone behavior is favored. Hence, the generally low fire intensity in *P. coulteri/Q. agrifolia* forests assures that open-cone trees can leave offspring that survive and reproduce. Closed-cone behavior, on the other hand, is not favored in this fire regime because seed-releasing crown fires are infrequent.

The retention of substantial quantities of viable seed has obvious adaptive value to fire-killed pine stands that regenerate in the face of heavy post-burn tree and chaparral competition. The accumulation of seed in serotinous cones insures that the maximum number of seed is available to take advantage of a transient post-burn environment conducive to seedling growth. In addition, cone-stored seed acts to buffer year-to-year fluctuations in seed production (McMaster and Zedler 1981). If stand regeneration were dependent entirely on seed in ripening cones, a crown fire coincident with a poor cone year could severely curtail stand replacement. Serotinous cones guarantee that at least some seed will fall after the fire.

An abundant seed rain may also be crucial to pine reestablishment in habitats with a limited supply of microsites sufficient for seed germination and seedling growth. In this regard, Wilson and Vogl (1965) noted locales in the Santa Ana Mountains where successful *P. coulteri* establishment was confined to rivulets, channels, and eroded areas. The dissemination of large numbers of propagules may enhance the chances of seed encounter with these "safe sites" (Harper et al. 1965).

Finally, serotiny may confer superior competitive status to *P. coulteri* in mixed conifer stands burned by recurrent fire. In at least one stand in the Santa Lucia Mountains, Griffin (1982) recorded a very high post-burn *P. coulteri*/*P. lambertiana* seedling-to-tree ratio (6.65) compared to the prefire ratio (0.15). He attributed this inversion of relative species abundances in part to the release of stored seed by *P. coulteri.* Lotan (1976) cites the serotinous cone habit as a major reason for the aggressive reinvasion of disturbed sites by *P. contorta* at the expense of other conifers.

Understanding the variation in cone habit as well as other life history traits of *P. coulteri* is vital to the management of this species. In southern California fire suppression activities have created extensive tracts of old, highly flammable vegetation subject to catastrophic fires (Minnich 1983). In recent years, land management agencies have introduced prescribed burning as a means of creating a less flammable vegetation mosaic of younger age classes. This means that *P. coulteri* in its various habitats will be managed increasingly under controlled burn conditions (Dougherty and Riggan 1981).

Burn objectives, of course, vary depending on the desired outcome whether it be complete or partial stand regeneration. When the goal is complete stand turnover, knowing whether there is adequate stored seed for natural regeneration is essential (Lotan 1976). Another consideration is timing the burn so that it coincides with maximum viability of seeds in maturing cones. The limited data presented here suggest that ripening seed would not contribute measurably to pine regeneration until after mid-September. Obviously, the quantity of stored viable seed is but one factor affecting the post-burn abundance of *P. coulteri.* Others include fire intensity, precipitation, and postfire competition.

One aspect of seed retention not adequately investigated in this study is the relationship between canopy storage of seed and stand age. In many serotinous species stored viable seed increases with stand age (Roe 1963, Vogl 1973, Zedler 1981). In this study, the sample size of stands of differing age growing in similar environmental settings is too small to observe clear trends. My general impression from field observations, however, is that stored viable seed decreases rather than increases with stand age. In older trees, most cones are bunched at the crown apex or grow singly at the ends of branches. Branch-cone production tends to be spotty, and closed cones seldom accumulate well back on the limbs in the same way they do on the trunks of young trees. Additionally, there appears to be more active cone cutting in older stands, perhaps because large old trees furnish an abundance of denning sites resulting in higher squirrel densities.

If net seed accumulation diminishes with stand age, then it may become increasingly difficult to secure natural pine regeneration by prescribed burning. Further, trees in excess of 100 years appeared especially susceptible to insect and disease attack as well as to wind breakage. Consequently, excessive periods of protection from fire may be detrimental to stand persistence.

ACKNOWLEDGMENTS

I thank Drs. Richard Minnich, Robert Haller, W. B. Critchfield, and James Griffin for reviewing this manuscript. My special thanks to James Griffin for suggesting seed retention as a research topic and Valdo Calvert for his diligent field assistance.

LITERATURE CITED

ANONYMOUS. 1972. Decennial census of the United States climate. Climatic summary of the United States. California. Supplement for 1951 through 1960. NOAA/EDIS, Washington, D.C.

BARDEN, L. S. 1979. Serotiny and viability of *Pinus pungens* in the southern Appalachians. Castanea 44:44–47.

BEAUFAIT, W. R. 1960. Some effects of high temperatures on the cones and seeds of jack pine. Forest Sci. 6:194–199.

BYRNE, R. 1979. Fossil charcoal from varved sediments in the Santa Barbara Channel: an index of wildfire frequencies in the Los Padres National Forest (735 AD to 1520 AD). USDA For. Serv., Pacific Southwest Range Exp. Sta., Unpubl. Rep., Res. Agreement PSW-47.

CAMPBELL, B. 1980. Some mixed hardwood communities of the coastal ranges of southern California. Phytocoenologia 8:297–320.

COOPER, R. W., C. S. SCHOPMEYER, and W. H. DAVIS. 1959. Sand pine regeneration on the Ocala National Forest. USDA For. Serv., Southeastern For. Exp. Sta., Res. Rep. 30.

COTTAM, G. and J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

DOUGHERTY, R. and P. J. RIGGAN. 1981. Operational use of prescribed fire in southern California. *In* E. C. Conrad and W. C. Oechel, eds., Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, pp. 502–510. USDA For. Serv., Pacific Southwest Range Exp. Sta., Gen. Techn. Rep. PSW-58.

Essig, E. O. 1958. Insects and mites of western North America. McMillan, NY.

Givnish, T. J. 1981. Serotiny, geography and fire in the Pine Barrens of New Jersey. Evolution 35:101–123.

Griffin, J. R. 1982. Pine seedlings, native ground cover, and *Lolium multiflorum* on the Marble-Cone burn, Santa Lucia Range, California. Madroño 29:177–188.

Hanes, T. L. 1971. Succession after fire in chaparral in southern California. Ecol. Monogr. 41:27–52.

Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. Behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol. 53:273–286.

Krugman, S. L. and J. L. Jenkinson. 1974. *Pinus* L., Pine. *In* C. S. Schopmeyer, techn. coordinator, Seeds of woody plants in the United States, pp. 598–638. USDA For. Serv. Agric. Handb. 450.

Little, E. L., Jr. and K. W. Dorman. 1952. Geographic differences in cone opening in sand pine. J. Forest. 50:204–205.

Lotan, J. E. 1967. Cone serotiny of lodgepole pine near West Yellowstone, Montana. J. Forest. (Washington) 13:55–59.

———. 1968. Cone serotiny of lodgepole pine near Island Park, Idaho. USDA For. Serv., Intermountain For. Range Expt. Sta. Res. Pap. INT-52.

———. 1976. Cone serotiny–fire relationships in lodgepole pine. Proc. Tall Timbers Fire Ecology Conf. 14:267–278.

McMaster, G. S. and P. Zedler. 1981. Delayed seed dispersal in *Pinus torreyana* (Torrey pine). Oecologia 51:62–66.

Minnich, R. A. 1977. The geography of fire and bigcone Douglas-fir, Coulter pine and western conifer forests in the eastern Transverse Ranges. *In* H. A. Mooney and E. C. Conrad, techn. coordinators, Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems, pp. 443–450. USDA For. Serv. Gen. Techn. Rep. WO-3.

———. 1978. Fire and the biogeography of conifer forest in the eastern Transverse Ranges, California. Ph.D. dissertation, Univ. California, Los Angeles.

———. 1980. Wildfire and the geographic relationships between canyon live oak, Coulter pine, and bigcone Douglas-fir forests. *In* T. R. Plumb, techn. coordinator, Proceedings of the symposium on the ecology, management and utilization of California oaks, pp. 55–61. USDA For. Serv., Pacific Southw. For. Range Exp. Sta., Gen. Techn. Rep. PSW-44.

———. 1983. Fire mosaics in southern California and northern Baja California. Science 219:1287–1294.

Perry, D. A. and J. E. Lotan. 1977. Opening temperatures in serotinous cones of lodgepole pine. USDA For. Serv., Intermountain For. Range Exp. Sta., Res. Note INT-228.

——— and ———. 1979. A model of fire selection for serotiny in lodgepole pine. Evolution 33:958–968.

Roe, E. I. 1963. Seed stored in some jack pine stands, northern Minnesota. USDA For. Serv., Lake States For. Exp. Sta., Res. Pap. LS-1.

Schantz-Hansen, T. 1941. A study of jack pine seed. J. Forest. 39:980–990.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349–371.

Stienecker, W. 1977. Supplemental food habits of the western gray squirrel. California Fish and Game 63:11–21.

——— and B. M. Browning. 1970. Food habits of the western gray squirrel. California Fish and Game 56:36–48.

Sudworth, G. B. 1908. Forest trees of the Pacific Slope. Dover, NY.

Vale, T. R. 1979. *Pinus coulteri* and wildfire on Mount Diablo, California. Madroño 26:135–140.

Vogl, R. J. 1973. Ecology of knobcone pine in the Santa Ana Mountains, California. Ecol. Monogr. 43:125–143.

———, W. P. Armstrong, K. L. White, and K. L. Cole. 1977. The closed-cone pines and cypresses. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, pp. 295–358. Wiley-Interscience, NY.

WILSON, R. C. and R. J. VOGL. 1965. Manzanita chaparral in the Santa Ana Mountains, California. Madroño 18:47–61.

ZEDLER, P. H. 1981. Vegetation change in the chaparral and desert communities in San Diego County, California. *In* D. C. West, H. H. Shugart, and D. B. Botkin, eds., Forest succession: concepts and applications, pp. 406–430. Springer Verlag, NY.

(Received 1 June 1984; accepted 27 July 1984.)

ANNOUNCEMENT

ASPT HERBARIUM TRAVEL AWARDS

The American Society of Plant Taxonomists is pleased to announce the availability of competitive awards for travel by graduate students to the nation's herbaria. The awards will not exceed $500 and will be used to help pay expenses to and from any herbarium (or herbaria) in the United States and per diem expenses during the visit. Competitions for awards will be held twice a year: The first competition deadline is 1 January 1985, with the second deadline 1 July 1985. The grants program will last a minimum of three years (six competitions). Interested Master's or Ph.D. graduate students should send a curriculum vitae, two letters of recommendation (including one from the major professor), a two or three page outline of the proposed research emphasizing the role that the visit to the herbarium will play, and a letter from the Head Curator, Chairman or Director of the institution(s) to be visited indicating willingness to receive the visitor. Awards will be announced by 1 March from the January competition and during the annual banquet of the ASPT from the July competition. Students are encouraged to obtain additional funds from their home institutions (or elsewhere) to extend their research visits even further. This competition is open to students of both cryptogamic and phanerogamic groups. Completed applications and additional questions should be directed to TOD F. STUESSY, Chairman, ASPT Committee for Systematics Collections, Department of Botany, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210. (Phone: (614) 422-5200 or (614) 422-8952.)

BERKELEY HERBARIUM

Severe space limitations require that the Herbarium of the University of California, Berkeley (UC) box and store all vascular plant specimens originating from Europe, Africa, Asia, and the Pacific Basin. Specimens from these areas will be unavailable for loan or routine consultation. However, special arrangement can be made to see them. Please write to the Director of the Herbarium to arrange to use these collections. Collections from North and South America remain unaffected; exchange programs will also remain unaffected. We regret the inconvenience that the inaccessibility of these collections may cause researchers and will try to resolve our space problems so that Eastern Hemisphere specimens will be available again as soon as possible. UC has acquired additional space to house these collections and hopes to obtain storage cases within the next year. For the next decade, the collection at UC will be housed in two locations within close proximity. As the University of California completes the renovation that began this year of all biological science facilities, the collections of the University Herbarium will be brought together in a single expanded and modernized facility.—THOMAS DUNCAN, Director—UC and JEPS.

A NEW SPECIES OF *ERYTHRONIUM* (LILIACEAE) FROM THE COAST RANGE OF OREGON

Paul C. Hammond
2435 E. Applegate St., Philomath, OR 97370

Kenton L. Chambers
Department of Botany and Plant Pathology,
Oregon State University, Corvallis 97331

Abstract

A new species, **Erythronium elegans,** is described from three sites in the northern Coast Range of Oregon. On morphological grounds the species is closely allied with *E. montanum* of the Olympic Mountains and northern Cascade Range, and with *E. klamathense* of the southern Cascades. Its variability in certain traits such as flower color, stamen width, and leaf mottling is suggestive of past hybridization with the geographically associated species, *E. revolutum.*

During 1982, the U.S. Forest Service initiated a project to study the distribution and ecology of *Erythronium revolutum* Smith along the Oregon Coast in order to assess conservation requirements for the species (Bierly and Stockhouse 1982). In the course of this study, large populations of a distinctly different *Erythronium* were discovered on the top of Mt. Hebo (945 m) in Tillamook County just 10 miles inland from the Pacific Ocean. Two additional populations of this taxon have since been found, one on Saddleback Mountain in northern Lincoln County 15 miles south of Mt. Hebo, and another on Fanno Ridge north of Valsetz in Polk County. The species exhibits a combination of characteristics seen in no other described taxon, and it forms a link between sections *Concolorae* and *Pardalinae* as defined by Applegate (1935). In this paper we describe this *Erythronium* as new and examine evidence concerning its origin and relationships.

Erythronium elegans Hammond & Chambers, sp. nov.

Herba perennis, foliis duo concoloris raro maculosis petiolo subterraneo lamina lanceolata prostrata, scapo 16–30 cm alto, floribus 1–2(–4) cernuis tepalis reflexis lanceolatis 2–4(–5) cm longis albis basi luteis dorsaliter plerumque roseis, filamentis 0.5–2.0 mm latis, antheris luteis, stylo 1–3 cm longo, stigmate profunde trifurcato, capsula clavata 2.5–3.5 cm longa.

Corm 2.0–5.5 cm long, 8–15 mm wide, enclosed in papery sheaths and producing new cormlets laterally; subterranean stem between

---

Madroño, Vol. 32, No. 1, pp. 49–56, 15 February 1985

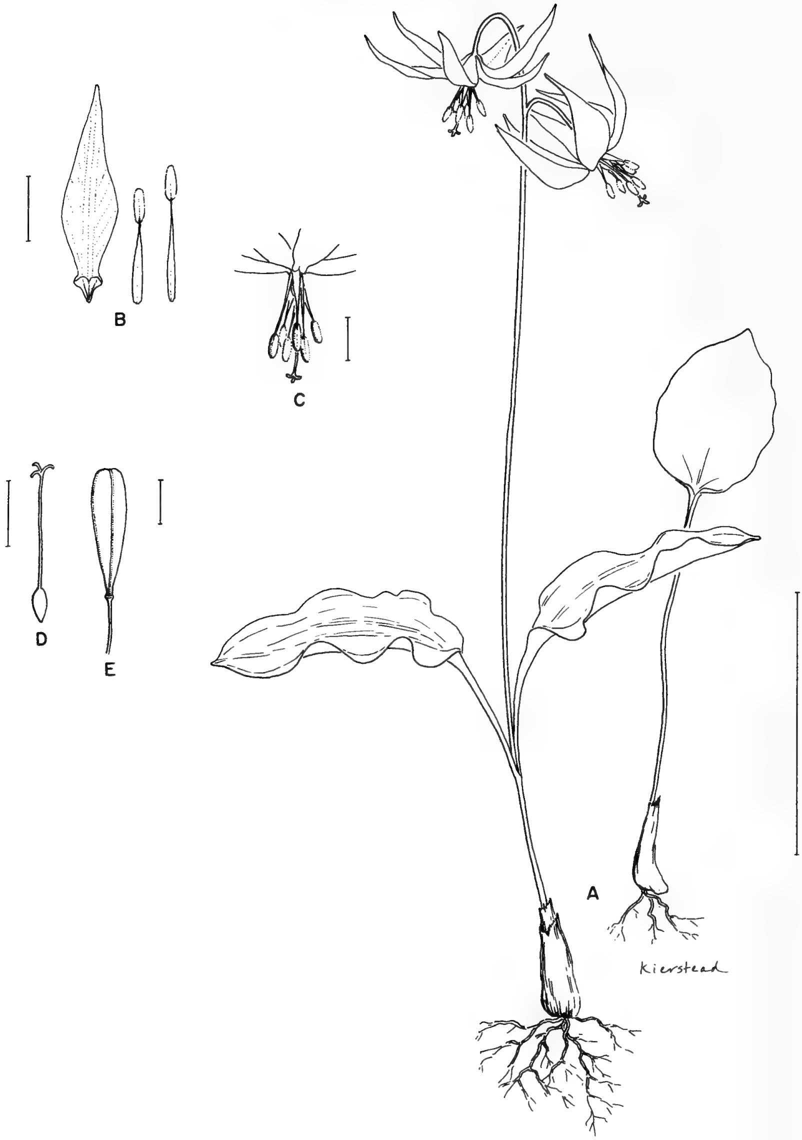


FIG. 1. *Erythronium elegans*. A. Habit of flowering and non-flowering individuals. B. Inner tepal and pair of stamens. C. Androecium and exserted style. D. Gynoecium. E. Capsule. Scale equals 10 cm in A, 1 cm in other Figs.

leaves and corm 3.5–10 cm long; leaves usually uniformly deep green or mottled with a few pale lines, rarely with well-developed brown mottling; leaf of non-flowering plants single, 6–8 cm long, 4–5 cm wide, the blade broad, ovate-lanceolate, usually abruptly narrowed to a slender, nearly wingless petiole; leaves of flowering plants two, more or less prostrate, 7–13(–15) cm long, 2–4(–8) cm wide, the blade narrowly lanceolate, usually with strongly undulate margins, gradually narrowed to a short, evidently winged petiole; scape 16–30 cm tall; flowers 1–2(–4), nodding, with perianth strongly reflexed in bright sunshine to only slightly spreading under shady or cloudy conditions; perianth segments lanceolate, 2–4(–5) cm long, (3–)5–10(–15) mm wide, with well-developed basal appendages, white or pale pink with bright yellow stripes at the base, often reddish on abaxial surface; filaments narrow to somewhat dilated, 0.5–2.0 mm wide; anthers golden yellow, not connivent around style; style filiform, 1–3 cm long; stigma deeply divided with recurved lobes; capsule broadly clavate, blunt, 2.5–3.5 cm long, 6–8 mm wide.

TYPE: USA, OR, Tillamook Co.: Mt. Hebo, T 4 S R 9 W S 13, ca. 945 m, open sites on rocky slopes and cliffs, *P. Hammond s.n.,* 28 May 1982 (Holotype: OSC; isotype: UC).

PARATYPES: OR, Tillamook Co.: Mt. Hebo, open slopes with *Gaultheria* and *Vaccinium, Pseudotsuga* belt, 945 m, *Constance and Beetle 2656* (ORE, WILLU); Mt. Hebo, 914 m, plentiful under *Pseudotsuga, Thuja, Picea* and in open meadows with *Gaultheria, Vaccinium,* grasses, *Lupinus, Fragaria,* mosses, *Greenleaf 1301* (OSC, ORE, NY); Mt. Hebo, *A. M. Phillips s.n.,* 24 May 1954 (OSC). Lincoln Co.: Lost Prairie, Saddleback Mtn. at edges of bog, T 7 S R 9 W S 2, *S. Lofton s.n.,* May 1982 (MOC). Polk Co.: Fanno Ridge, bog at headwaters of Little Luckiamute River, T 8 S R 8 W S 14, *L. Scofield s.n.,* 25 May 1983 (MOC).

Populations of this species extend over the entire length of the Mt. Hebo escarpment, an area of some three square miles, and occupy meadows, rocky cliffs, brushland, and open coniferous forest. In many areas thousands of plants carpet the ground in a manner like that of *E. montanum* in subalpine meadows of the northern Cascade Range. The Saddleback Mountain and Fanno Ridge populations of *E. elegans* are much smaller and are largely restricted to the edges of sphagnum bogs. Additional populations of the species may be expected in mountain bogs, meadows, or rocky balds of northern Lincoln County and in Polk and Tillamook Counties.

Populations of *E. elegans* show considerable variation in leaf mottling, flower color, and stamen filament width. Most plants have completely unmottled leaves that are uniformly deep green or exhibit a few pale lines along the veins. Well-developed brown mottling is found in occasional plants, however, and may be so extensive that the leaves are almost entirely brown. The frequency of such extreme mottling is roughly estimated at about one in 10,000 plants on Mt. Hebo, but some local colonies consist largely of mottled plants. The majority of individuals have a pinkish-white perianth, often with deeper pink on the abaxial side of the tepals. However, flower colors vary from deep rose-pink at one extreme to pure white at the other. The dilation of the stamen filaments is also variable. In a sample of 174 flowers on Mt. Hebo, 62 (36%) had thin filaments about 0.5 mm wide, and 112 (64%) had dilated filaments of 1.0–2.0 mm. In most plants the stamens spread away from the style, but in a few plants they are constricted around the style, as in *E. revolutum.*

Sympatric with *E. elegans* on the rocky cliffs of Mt. Hebo is *E. grandiflorum* Pursh var. *pallidum* St. John. Its leaves are similar in shape to those of *E. elegans* but differ in their blue-green color. The two species exhibit floral differences as well, and there is no evidence of hybridization between them. In western Oregon there are four additional species of *Erythronium* with which *E. elegans* can be compared. These are *E. revolutum, E. montanum* Watson, *E. oregonum* Applegate, and *E. klamathense* Applegate. Applegate (1935) divided the genus *Erythronium* into two sections: the *Pardalinae,* found in lowland habitats and having mottled leaves and white to lavender flowers; and the *Concolorae,* occurring in mountain habitats and having unmottled leaves and white to yellow flowers. *Erythronium montanum* and *E. klamathense* belong to sect. *Concolorae,* while *E. oregonum* and *E. revolutum* belong to sect. *Pardalinae.* However, *E. elegans,* as described here, is intermediate between the two sections in certain of its characteristics. In order to understand this relationship, it is useful to review the biogeography and ecology of the five allied species.

Both *E. montanum* and *E. klamathense* have white flowers, narrow filaments, and unmottled leaves. They occupy habitats at high elevations in the Cascade Range, including subalpine meadows and wet forests. *Erythronium montanum* is distributed from Vancouver Island and the Cascades of southern British Columbia southward to the Olympic Mountains and through the Cascades to Monument Peak in northern Linn County, Oregon. It differs from *E. klamathense* by the larger size of the plants and flowers (tepals 25–40 mm long), deeply divided stigma lobes, erect flowers, long and slender aerial petioles that raise the leaves above the ground, and abruptly expanded leaf blades. In contrast, *E. klamathense* is restricted to the southern Cascade Range extending from Black Rock Lookout in Douglas County, Oregon, south to the Mt. Shasta region of Siskiyou County, California. The species is smaller than *E. montanum* (tepals 15–25 mm long) and has entire stigmas, pendulous flowers, short subterranean petioles, prostrate leaves, and gradually expanded leaf blades.

Erythronium revolutum and *E. oregonum,* the closest geographical associates of *E. elegans,* both have dilated stamen filaments and distinctly mottled leaves. The flowers of *E. oregonum* are creamy-white, with the stamens spread away from the style (contrary to the illustrations in Hitchcock et al. 1969, p. 792), whereas those of *E. revolutum* are deep pink and the filaments are appressed to the style (as illustrated by Hitchcock et al. 1969, and Gilkey 1945). These two taxa occupy mostly lowland habitats west of the Cascades from southern British Columbia to southern Oregon; *E. revolutum* continues south to Mendocino County, California. Except in the northern part of this range, the two species are rarely sympatric because *E. revolutum* occupies the coastal rain-forest zone and *E. oregonum* occurs in drier forests and woodlands of the interior. As observed by us in Oregon, *E. revolutum* is best developed in low-lying riparian habitats in the portion of its range south of the Siuslaw River, Lane County. These habitats include streamside benches above the high-water line, rotting log-jams, and rocky ledges. North of the Yaquina River, Lincoln County, the species shifts to moist coniferous forests on mountain slopes, reaching 900 m elevation on Onion Peak, Clatsop County. In the vicinity of Mt. Hebo, *E. revolutum* occurs on mountainsides above Powder Creek and Limestone Creek on the north and east sides of the peak below the main escarpment, where it is separated by 600 m elevation from the main population of *E. elegans.* It should be noted that *E. oregonum* is sometimes present in open meadows or "balds" on the tops of high Coast Range peaks, including Roman Nose Mountain in Douglas County, Marys Peak in Benton County (elevation 1200 m), and Rickreall Ridge in Polk County. These meadow habitats are superficially similar to those occupied by *E. montanum* in the Cascade Range, and by *E. elegans* on Mt. Hebo. The population of *E. oregonum* on Rickreall Ridge is ecologically isolated from *E. elegans* on nearby Fanno Ridge, however, since the former is on an exposed rocky ridge and the latter is in a cold bog.

In summary, the habitats of *E. elegans* are more similar overall to those of *E. revolutum* in this part of Oregon than to the habitats of *E. oregonum.* There may have been sympatry between *E. revolutum* and *E. elegans* at some time in the past, with an opportunity for introgression into the latter species of such traits as pink flower color, dilated filaments, and mottled leaves. These traits are found in all three disjunct populations of *E. elegans,* suggesting that introgression is not a recent event. There is presently no evidence that *E. elegans* and *E. oregonum* have had genetic contact through hybridization, however.

The morphological traits that suggest introgression by *E. revolutum* affect only a small minority of the plants of *E. elegans,* and we do not believe that the new species is itself of hybrid origin. The basic affinities of *E. elegans* appear instead to be with *E. montanum* and *E. klamathense.* The habitats of the three taxa are similar, although at present they are widely separated geographically. *Erythronium elegans* is like *E. montanum* in its flower size and its deeply

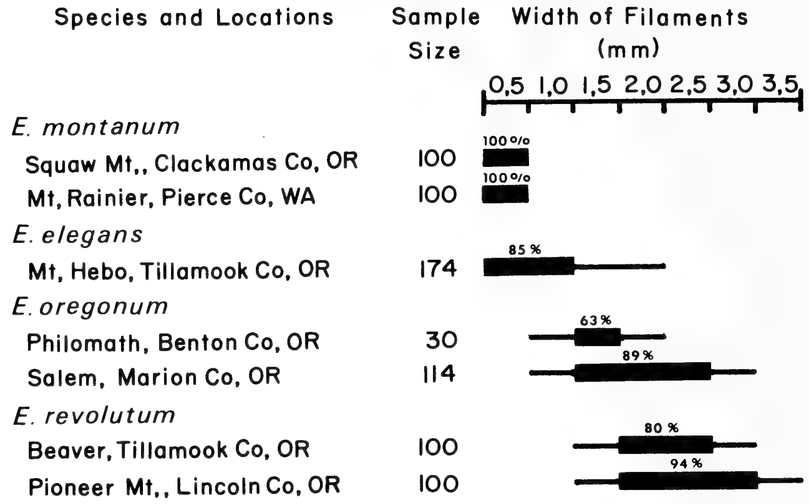


FIG. 2. Width of stamen filaments in four species of *Erythronium*. Range of variation is given for each population, with the frequency of the most common class shown as a labeled rectangle.

divided stigma lobes; it resembles *E. klamathense* in having pendulous flowers, prostrate leaves with short subterranean petioles, and blades tapering gradually at the base. Figures 2 and 3 illustrate the variation in two critical morphological features, the width of the stamen filaments and the angle formed by the tapering base of the leaf blade, in selected populations of four species under discussion. All measurements were taken from living plants in the field. The filament width in *E. elegans* is commonly in the range of *E. montanum* but varies toward the broad filaments of *E. revolutum* and *E. oregonum.* The basal angle of the leaf blades of *E. montanum* is variable, but the most frequent condition is to have a larger angle (that is, a more abruptly tapering blade) than in *E. elegans.* Figure 2 also illustrates that filament width cannot be used to separate *E. oregonum* from *E. revolutum,* despite the assertion by Applegate (1935, p. 100).

In the above discussion, *E. elegans* has been compared with its congeners for all the characteristics commonly used by taxonomists to distinguish species of *Erythronium.* We hypothesize that some of the present variability of this new taxon derives from past hybridization with *E. revolutum,* but that the origin of the species lies in an ancestral complex from which both *E. montanum* and *E. klamathense* are also derived. Putatively primitive traits recognizable in *E. elegans* are its separate stigma lobes, its pendulous flowers, and

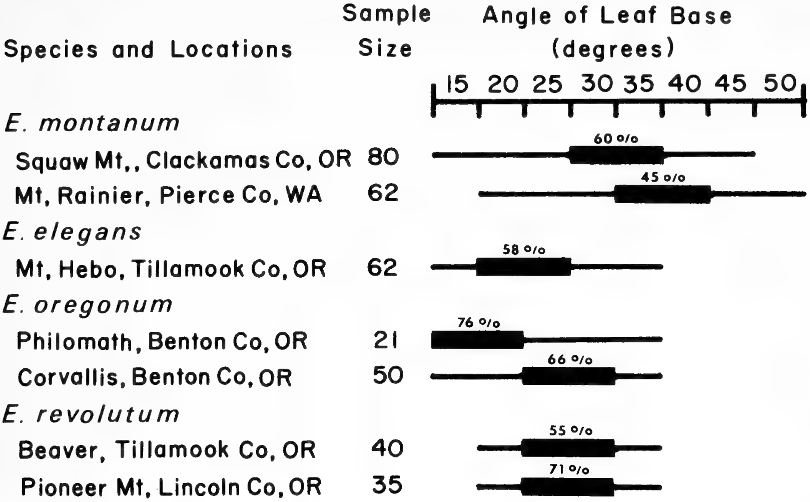


FIG. 3. Angle of leaf base in four species of *Erythronium.* Measurements are the angle, in increments of five degrees, from the petiole midline along the diverging margin of the blade at its base. Range of variation is given for each population, with the frequency of the two most common classes shown as a labeled rectangle.

its tapering, short-petioled leaves; advanced traits in the complex may be the united stigma lobes of *E. klamathense,* and the erect flowers and long-petioled leaves of *E. montanum.* It is reasonable to find a species with Cascadian affinities growing at high elevations in the northern Oregon Coast Range. In Clatsop County, Saddle Mountain (Detling 1954), Onion Peak (Chambers 1973) and Sugarloaf Mountain (Chambers 1974) harbor plant species that are disjunct from the Olympic Mountains and the Cascade Range. *Erythronium elegans* may once have had a wider range in the coastal mountains of the Pacific Northwest, and have been reduced to a few relict populations by postglacial climatic changes. Although modified by genetic contact with *E. revolutum,* it is recognizable as a distinct and phylogenetically interesting species.

ACKNOWLEDGMENTS

We thank the following persons for advice and assistance with this study: K. Bierly, H. Chrostowski, M. Johnson, S. Lofton, and L. Scofield. The illustration was prepared by Julie Kierstead.

LITERATURE CITED

APPLEGATE, E. I. 1935. The genus *Erythronium*: a taxonomic and distributional study of the western North American species. Madroño 3:58–113.

BIERLY, K. F. and R. E. STOCKHOUSE. 1982. Coast fawn lily (*Erythronium revolutum*) sensitive species conservation status report. USDA For. Serv., Pacific Northwest Region, Siuslaw Natl. For., Corvallis, OR. 82 pp.

CHAMBERS, K. L. 1973. Floristic relationships of Onion Peak with Saddle Mountain, Clatsop County, Oregon. Madroño 22:105–114.

———. 1974. Notes on the flora of Clatsop County, Oregon. Madroño 22:278–279.

DETLING, L. R. 1954. Significant features of the flora of Saddle Mountain, Clatsop County, Oregon. Northwest Sci. 28:52–60.

GILKEY, H. M. 1945. Northwestern American plants. Oregon State Coll. Monogr., Studies in Botany, No. 9.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1969. Vascular plants of the Pacific Northwest. Part 1. Univ. Washington Press, Seattle.

(Received 9 April 1984; accepted 30 July 1984.)

NOTES AND NEWS

YELLOW JACKETS DISPERSE *Vancouveria* SEEDS (BERBERIDACEAE).—During a field study in Lewis and Clark State Park (WA: Lewis Co.) in early July 1983, I had the opportunity to study seed dispersal in *Vancouveria hexandra* (Hook.) Morr. & Dcne. (inside-out-flower). Observations were made on 3 and 4 July, at which time plants were in all stages, from open flowers to ripe seeds. The common yellow jacket *Vespula vulgaris* (L.) was fairly abundant in the area, and on eight occasions individuals were observed collecting seeds of *V. hexandra.* When an insect searching through an area covered by the plant found a dehisced pod, it alighted on the pod stalk next to it. It then bit loose the seed and its large, white appendage and flew a few meters before alighting on a low branch. It then bit the appendage off within a few seconds and dropped the seed to the ground. The yellow jacket then disappeared carrying the appendage. Apart from the eight successful searches I observed, there were also four occasions when yellow jackets searched in vain for seeds in sterile patches or in patches with unripe pods. Attempts to bite open unripe pods were never observed to be successful. Searches lasted for up to four minutes before the yellow jacket left the study area. The chemical nature of the appendage appears to be unknown, but may possibly consist of polysaccharides.

Berg (Amer. J. Bot. 59:109–122. 1972), in an extensive experimental study, showed that ants are effective seed vectors of *Vancouveria.* In repeated experiments, where seeds were put out within a few meters from nests of ant species in three genera, all seeds were dragged by the appendages to the nests within 0.5–2.5 h.

In contrast to other members of the genus, the pods of *V. hexandra* dehisce while the seeds are still green; this leaves some time before they fall spontaneously to the ground. My observations suggest that this can be an adaptation to allow seed dispersal by vespids. It should result in a more random distribution of the seeds than that provided by ants, which drag them to their nests along their trails. Berg observed ant-mediated transport up to 2.5 m from the starting point. Dispersal by the winged yellow jacket also increases the possibility of dispersal over a somewhat longer range.

To my knowledge, this is the first reported case of seed dispersal by yellow jackets. Vance Tartar (pers. comm.) has observed vespids collecting seeds of *Trillium,* another myrmecochorous genus. Further studies of vespids as seed vectors in ant-dispersed species may prove this phenomenon to be of wider occurrence.

The support of B. J. D. Meeuse during the work in the Pacific Northwest is gratefully acknowledged. This study was made while on a joint travel grant from the Swedish Natural Science Research Council (NFR) and the Royal Swedish Academy of Sciences.—OLLE PELLMYR, Dept. of Entomology, Uppsala Univ., Box 561, S-751 22 Uppsala, Sweden. (Received 6 April 1984; accepted 24 May 1984.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

DICENTRA PAUCIFLORA Wats. (PAPAVERACEAE).—Ventura Co., 2 km ne. of Reyes Peak (34°39′30″N, 119°16′15″W). Few small scattered colonies observed on steep n.-facing slope immediately above Beartrap Cr. Plants growing in deep leaf mold within dense forest of *Calocedrus decurrens, Pinus ponderosa, Abies concolor, Quercus chrysolepis,* 1500 m, 12 Jun 1983, *Odion 68* (UCSB), *67* (RSA). Verified by K. R. Stern, Calif. State Univ., Chico. (Voucher)

Significance. Previously known from northern California and southern Oregon. Small populations also occur in the Greenhorn Mts. (Twisselman, Fl. Kern Co. 1967) and San Emigdio Range (*Emmel 562,* RSA), both in Kern Co. This is the first record in Ventura Co. and within the areas covered by floras of Munz 1974 (Southern Calif.) and Smith '76 (the Santa Barbara Region).—DENNIS C. ODION, Dept. Biol. Sci., UCSB.

SPIRODELA PUNCTATA (G. F. W. Meyer) Thompson (LEMNACEAE).—USA, CA, Humboldt Co., Clam Beach, 15 km n. of Arcata, e. side Hwy 101 (T7N R1E S17 nw. ¼), 8 m, 25 May 1980, *Richards 101* (HSC). Dense population at north end of pond, associated with *Spirodela polyrrhiza* and *Azolla filiculoides.*

Previous knowledge. Known from Asia, s. Pacific, se. US, MO, IL. Reported in CA from San Diego, Fresno, Yolo, Madera and Santa Clara Counties and from the UC Berkeley campus (Alameda Co.). This species is listed as *S. oligorrhiza* (Kurz) Hegelm. by Daubs (Ill. Biol. Monogr. 34. 1965; Rhodora 64. 1962) and Mason (A Fl. Marshes Calif. 1957). It is distinguished from *S. polyrrhiza* by its smaller size and the presence of only 2–3 roots, and from *Lemna* spp. by purple lower surface of frond and multiple roots. Without close examination, however, these features can easily be overlooked and the plants mistaken for *Lemna.*

Significance. Northernmost occurrence in CA and range extension of ca. 480 km n. of Berkeley. This species was also collected on the UC Davis campus in1967 and mislabeled *S. polyrrhiza.* I looked for this population in June 1983 and am doubtful it still exists. I found another population of *S. punctata* in 1980 ca. 5 km w. of Blue Lake, CA (ca. 25 km se. of Clam Beach), *Richards 102* (HSC). Winter storms in 1982 destroyed this population and it has not recovered. *Spirodela punctata* from both Humboldt Co. locations have been observed in flower between June and early November.

WOLFFIA BOREALIS (Engelm.) Landolt (LEMNACEAE).—USA, CA, Mendocino Co., 11.2 km s. of Willits, w. side of Hwy 101 (T17N R13W S16 se.¼), 442 m, 25 Oct 1981, *Richards 104* (HSC). Dense population at surface of small pond, mixed with *Lemna minor* and *Azolla filiculoides.* Verified by W. P. Armstrong.

Previous knowledge. Known from WA, OR, s. Canada, c. and ne. US. In CA reported from Shasta and San Diego Counties. This species has been listed incorrectly as *W. punctata* Griseb. by most Amer. authors. The original *W. punctata* described by Grisebach was synonymous with *W. brasiliensis* Weddell, a species native to s. US and in C. and S. America.

Significance. First record of this sp. in Mendocino Co., a sw. range extension of ca. 250 km from Fall River Mills, Shasta Co.—DANIEL V. RICHARDS, Humboldt State Univ., Dept. of Biol. Sci., Arcata, CA 95521.

COLORADO

PHACELIA CONSTANCEI Atwood (HYDROPHYLACEAE).—San Miguel Co., ne.-facing slopes in gypsum soils, 2.5 km se. of Gypsum Gap (T43N R16W S6, 38°02′N, 108°39′W), 1830 m, 16 Aug 1983, *Kelley 83-147* (Mesa College Herb., CS).

MADROÑO, Vol. 32, No. 1, pp. 57–58, 15 February 1985

Previous knowledge. Common on soils derived from the Moenkopi formation in se. UT and ne. AZ.

Significance. This is the first record of the species in CO.—WALT KELLEY, Dept. of Biology, Mesa College, Grand Junction, CO and DIETER H. WILKEN, Dept. of Botany, Colorado State Univ., Ft. Collins 80523.

REVIEW

Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A. Volume 4. By ARTHUR CRONQUIST, ARTHUR H. HOLMGREN, NOEL H. HOLMGREN, JAMES L. REVEAL, and PATRICIA K. HOLMGREN. The New York Botanical Garden, New York. 1984. $77.50 (U.S.), $79.00 (non U.S.). ISBN 0-89327-248-5.

The publication of volume 4 of the Intermountain Flora represents another landmark of botanical excellence for western United States. The Flora, this time published by the New York Botanical Garden, is the third volume of their proposed six volume series, covers Cronquist's Subclass Asteridae and includes 28 families, leaving the Asteraceae for volume 5. This volume was written largely by Cronquist and Noel Holmgren. Cronquist authors 13 families and co-authors four others, two with Jim Reveal (Lamiaceae, Cuscutaceae), and one each with Arthur Holmgren (Caprifoliaceae), and C. L. Hitchcock (Solanaceae). Noel Holmgren authors nine families including the Scrophulariaceae, the largest in the book (215 species, including 104 species of *Penstemon*!). Pat Holmgren contributes the Campanulaceae and, with Noel, the Asclepiadaceae.

The format used is the same as in the preceding volumes, complete with excellent illustrations of each species contributed largely by Jeanne R. Janish, Bobbi Angell and Robin Jess. The book provides complete citation of synonymy, very readable, well-written descriptions, ample discussions of distribution, and perhaps most importantly, comments on past treatments of groups and the rationale for the present treatments. These commentaries, to me, are the best part of the book because they provide historical perspectives and often in-depth discussions of nomenclatural problems; and when coupled with the references, allow for direct access to literature of a group. Even if a person has no direct interest in the Intermountain area, the book is an important reference bringing together much information on the plants of western North America. While the book is invaluable to practicing botanists, it will also be very useful to beginning botanists, non-botanical professionals and amateurs who can use the illustrations to help them through the keys (or one may rely entirely on the pictures to identify plants in question). In this regard the Intermountain Flora is potentially useful to a large segment of the Intermountain population. The book is also, to some degree, user friendly in that both technical and artificial keys are provided in some large genera and species that are known outside the area, but that may eventually be found in the region.

Regarding taxonomy, *Neogaerrhinum* is separated from *Antirrhinum, Fraseria* from *Swertia, Gentianella* and *Gentianopsis* from *Gentiana,* and *Leucophysalis* from *Chaemaesaracha. Tiquilia* replaces our *Coldenia.* However, *Glandularia* is not distinguished from *Verbena.* The careful work of Dempster and Erhendorfer in the *Galium multiflora* complex has been critiqued and reduced to a more "practical" taxonomy (3 varieties) in a lengthy discussion by Cronquist. Likewise, Grant's *Gilia inconspicua* complex has been reduced and *Ipomopsis* is not distinguished from *Gilia.* While Grant admits some elements in the *Gilia inconspicua* complex may be disregarded in favor of more easily discernable morphotaxa, he (pers. comm. 1984) feels that the reduction has gone too far and that taxa such as *Gilia opthalmoides* and *G. clokeyi*

MADROÑO, Vol. 32, No. 1, pp. 58–59, 15 February 1985

are recognizable, morphologically and ecologically. *Ipomopsis* has been accepted as distinct from *Gilia* by all recent workers in Polemoniaceae, and in all but one recent western flora, and its recognition leaves a much "cleaner" *Gilia*. But we are reminded that taxonomy still consists mostly of opinion. At least their preferences have been openly discussed and not proposed by fiat. As in past works from the New York Botanical Garden, infraspecific taxa are recognized primarily at the rank of variety and 38 new combinations are made at that level, only three of which represent simple subsp.-to-var. changes.

The volume is very well edited and has a list of new combinations and an index in the back. It represents a fine contribution to systematic botany that reflects well on the authors, their institution and on the field of systematic botany as a whole. While some may feel the price is high, we must remember what happened to the nickle candy bar. One should consider it an investment. The Flora is sure to have a strong influence on plant systematics in the years to come.—JAMES HENRICKSON, Biology Department, California State University, Los Angeles 90032.

PUBLICATION ANNOUNCEMENT

LAS GRAMINEAS DE MÉXICO

Alan Ackerman Beetle and collaborators. Secretaría de Agricultura y Recursos Hidráulicos under the auspices of COTECOCA [Comisión Técnico Consultiva par el Determinación Regional de los Coeficientes de Agostadero]. 260 pp., 1983. This first of four volumes includes a key to the subfamilies, tribes and genera, and treats genera and their species through the letter A. The following three volumes, intended for publication in 1984, will complete the taxonomic treatment and in addition contain bibliography, synonymy, glossary and general index. Species treatments include full page illustrations and maps giving distributions within states.

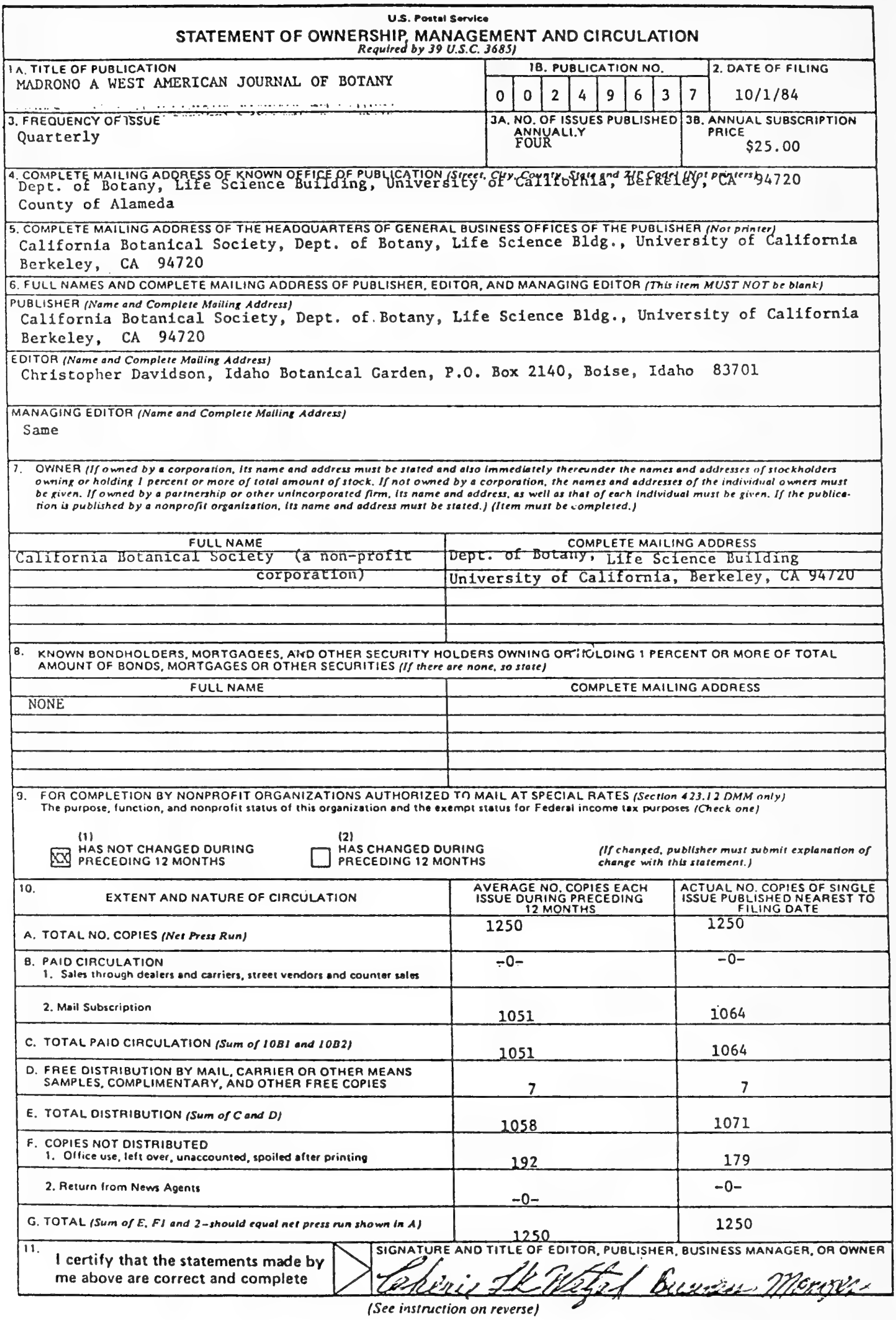
According to a notice in *Macpalxochitl* [newsletter of the Sociedad Botánica de México], institutions or investigators interested in obtaining a copy of this book may address their request to Ing. Horacio García Aguilar, Secretario de Agricultura y Recursos Hidráulicos with a copy for Victor Jaramillo Villalobos [Director General de COTECOCA]. Such a letter should state the reasons for wishing to have a copy of the work.—ANNETTA CARTER

Note added in proof (See Harms, pp. 1–10, this issue):

The following article was published too late to be incorporated into the text of Harms, Madroño 32(1):1–10:

> PAVLICK, L. E. and J. LOOMAN. 1984. Taxonomy and nomenclature of rough fescues, *Festuca altaica, F. campestris* (*F. scabrella* var. *major*), and *F. hallii,* in Canada and the adjacent part of the United States. Canad. J. Bot. 62(8):1739–1749.

Although not taken into account, it is not believed to alter the premises and conclusions of the paper in Madroño. The reader is referred to the Pavlick and Looman paper in conjunction with the present paper for amplified morphological (specifically anatomical) and cytological data, and for differing taxonomic interpretations.



U.S. Postal Service

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

Required by 39 U.S.C. 3685)

1A. TITLE OF PUBLICATION MADRONO A WEST AMERICAN JOURNAL OF BOTANY	1B. PUBLICATION NO. 0 0 2 4 9 6 3 7	2. DATE OF FILING 10/1/84
3. FREQUENCY OF ISSUE Quarterly	3A. NO. OF ISSUES PUBLISHED ANNUALLY FOUR	3B. ANNUAL SUBSCRIPTION PRICE $25.00

4. COMPLETE MAILING ADDRESS OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP Code) (Not printers)*
Dept. of Botany, Life Science Building, University of California, Berkeley, CA 94720
County of Alameda

5. COMPLETE MAILING ADDRESS OF THE HEADQUARTERS OF GENERAL BUSINESS OFFICES OF THE PUBLISHER *(Not printer)*
California Botanical Society, Dept. of Botany, Life Science Bldg., University of California
Berkeley, CA 94720

6. FULL NAMES AND COMPLETE MAILING ADDRESS OF PUBLISHER, EDITOR, AND MANAGING EDITOR *(This item MUST NOT be blank)*

PUBLISHER *(Name and Complete Mailing Address)*
California Botanical Society, Dept. of Botany, Life Science Bldg., University of California
Berkeley, CA 94720

EDITOR *(Name and Complete Mailing Address)*
Christopher Davidson, Idaho Botanical Garden, P.O. Box 2140, Boise, Idaho 83701

MANAGING EDITOR *(Name and Complete Mailing Address)*
Same

7. OWNER *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated.) (Item must be completed.)*

FULL NAME	COMPLETE MAILING ADDRESS
California Botanical Society (a non-profit corporation)	Dept. of Botany, Life Science Building University of California, Berkeley, CA 94720

8. KNOWN BONDHOLDERS, MORTGAGEES, AND OTHER SECURITY HOLDERS OWNING OR HOLDING 1 PERCENT OR MORE OF TOTAL AMOUNT OF BONDS, MORTGAGES OR OTHER SECURITIES *(If there are none, so state)*

FULL NAME	COMPLETE MAILING ADDRESS
NONE	

9. FOR COMPLETION BY NONPROFIT ORGANIZATIONS AUTHORIZED TO MAIL AT SPECIAL RATES *(Section 423.12 DMM only)*
The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes *(Check one)*

☒ (1) HAS NOT CHANGED DURING PRECEDING 12 MONTHS
☐ (2) HAS CHANGED DURING PRECEDING 12 MONTHS
(If changed, publisher must submit explanation of change with this statement.)

10. EXTENT AND NATURE OF CIRCULATION	AVERAGE NO. COPIES EACH ISSUE DURING PRECEDING 12 MONTHS	ACTUAL NO. COPIES OF SINGLE ISSUE PUBLISHED NEAREST TO FILING DATE
A. TOTAL NO. COPIES *(Net Press Run)*	1250	1250
B. PAID CIRCULATION 1. Sales through dealers and carriers, street vendors and counter sales	-0-	-0-
2. Mail Subscription	1051	1064
C. TOTAL PAID CIRCULATION *(Sum of 10B1 and 10B2)*	1051	1064
D. FREE DISTRIBUTION BY MAIL, CARRIER OR OTHER MEANS SAMPLES, COMPLIMENTARY, AND OTHER FREE COPIES	7	7
E. TOTAL DISTRIBUTION *(Sum of C and D)*	1058	1071
F. COPIES NOT DISTRIBUTED 1. Office use, left over, unaccounted, spoiled after printing	192	179
2. Return from News Agents	-0-	-0-
G. TOTAL *(Sum of E, F1 and 2—should equal net press run shown in A)*	1250	1250

11. I certify that the statements made by me above are correct and complete

SIGNATURE AND TITLE OF EDITOR, PUBLISHER, BUSINESS MANAGER, OR OWNER
Business Manager

(See instruction on reverse)

For his brilliant contributions to plant physiology, ecology, and our understanding of life on Earth, in a career that has spanned more than half a century, we take great pleasure in dedicating volume XXXI of Madroño to FRITS WARMOLT WENT. Born in 1903 in Utrecht, the son of a professor of botany in the University there, Frits Went first found employment at the Botanical Gardens in Bogor (then Buitenzorg) from 1927 to 1933. While still a graduate student, he initiated the first quantitative studies of plant hormones, one of the fields of investigation in which his work has been most successful. He spent the next quarter century at the California Institute of Technology, where he developed the first Phytotron and continued to make distinguished scientific contributions, especially in the areas of plant growth and desert plant ecology. As Director of the Missouri Botanical Garden from 1958 to 1963, he was responsible for the first geodesic-dome greenhouse, the Climatron, still a splendid display of tropical plants and an important element in the rejuvenation of that 125-year-old institution.

For the past two decades, Frits Went has been pursuing questions of desert ecology at the Desert Research Institute of the University of Nevada. We salute him in his 82nd year for the genius that he has brought to bear on the science of botany during the course of a long and distinguished career.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

VOLUME 32, NUMBER 2 APRIL 1985

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES AND NEWS

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Science, San Francisco, CA 94118.

Editor—CHRISTOPHER DAVIDSON
Idaho Botanical Garden
P.O. Box 2140
Boise, Idaho 83701

Board of Editors
Class of:

1985—STERLING C. KEELEY, Whittier College, Whittier, CA
ARTHUR C. GIBSON, University of California, Los Angeles
1986—AMY JEAN GILMARTIN, Washington State University, Pullman
ROBERT A. SCHLISING, California State University, Chico
1987—J. RZEDOWSKI, Instituto Politecnico Nacional, Mexico
DOROTHY DOUGLAS, Boise State University, Boise, ID
1988—SUSAN G. CONARD, USDA Forest Service, Riverside, CA
WILLIAM B. CRITCHFIELD, USDA Forest Service, Berkeley, CA
1989—FRANK VASEK, University of California, Riverside
BARBARA ERTTER, University of Texas, Austin

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928

First Vice President: RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

Second Vice President: DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403

Recording Secretary: VIRGIL THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: WAYNE SAVAGE, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542; the *Editor* of MADROÑO; three elected *Council Members:* JAMES C. HICKMAN, Department of Botany, University of California, Berkeley, CA 94720; THOMAS FULLER, 171 West Cott Way, Sacramento, CA 95825; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

SOUTHERN CALIFORNIA WHITE FIR (PINACEAE)

FRANK C. VASEK
Department of Botany and Plant Sciences,
University of California, Riverside 92521

ABSTRACT

Three lines of evidence are evaluated to determine the varietal relationships of southern California white fir. Based on nine seedling traits studied by Hamrick and Libby, southern California populations first cluster with those from Arizona and Utah, then later cluster with those from northern California. Based on relative amounts of camphene and 3-carene, three equivalent chemical races were found by Smedman et al. (1969) and Zavarin et al. (1975). A greater similarity of the southern California race to the Rocky Mountain race is rather tenuous and depends on the significance of rather small differences in four sesquiterpenes. Based on leaf morphology of adult trees (this study), two broad groups were defined. Northern California populations have long leaves with an emarginate to rounded tip, few stomatal rows on the upper surface, and a definite twist at the leaf base. The other populations have more stomatal rows on the upper leaf surface, acute tips, and very little to no twist at the base. They are distributed from Colorado-New Mexico with long, thin, narrow leaves, to Baja California with short, thick, wide leaves. The southern California populations largely fall within the latter group, are clearly more similar to the Rocky Mountain populations, and hence are referable to *Abies concolor* var. *concolor.*

White fir, *Abies concolor* (Gord. and Glend.) Lindl., is a common and widespread montane forest tree in the western United States (Fowells 1965, Hamrick and Libby 1972, Markstrom and Jones 1975, Sudworth 1908, 1916). Regionally-correlated variation has been formalized by the recognition of two varieties: *A. concolor* var. *lowiana* in California, and *A. concolor* var. *concolor* in the Rocky Mountain region. The pertinent nomenclature has been reviewed by Lamb (1914), Fowells (1965), Liu (1971), and Hamrick and Libby (1972).

On a broader view, the white fir complex is interpreted by Hamrick (1966) and by Hamrick and Libby (1972), on the basis of seedling morphology and growth characteristics in experimental nursery plots, to consist of four population groups: I, *A. grandis* in Oregon and northwest California; II, *A. concolor* var. *lowiana* in the Sierra Nevada and northeastern California; III, *A. concolor* var. *concolor* in southern California and Arizona; and IV, another form of *A. concolor* var. *concolor* in Utah and southern Nevada.

All the California white fir have been included in var. *lowiana* by Griffin and Critchfield (1972) except those in the high mountains of the eastern Mojave Desert. Griffin and Critchfield do not assign varietal names, but they clearly imply a "California" form and a

---

MADROÑO, Vol. 32, No. 2, pp. 65–77, 26 April 1985

"Rocky Mountain" form on map 3 and on page 10. The Rocky Mountain white fir extends intermittently from the Wasatch Plateau region (Markstrom and Jones 1975, Vasek and Thorne 1977) to the Kingston and Clark Mountains of eastern San Bernardino County, California (Henrickson and Prigge 1975, Miller 1940, Mehringer and Ferguson 1969, Munz 1959). The influence of the Rocky Mountain white fir extends into southern California and is evident to some extent in populations as far north as the Tehachapi Mountains (Griffin and Critchfield 1972).

Southern California white fir has been interpreted as var. *lowiana* by Griffin and Critchfield (1972) and as var. *concolor* by Hamrick and Libby (1972). The taxonomic and phytogeographic relationships of southern California white fir therefore remain unsettled. This paper addresses the question of varietal classification of southern California white fir and briefly speculates on its paleohistory.

METHODS AND MATERIALS

Two approaches were used. First, information about morphology and growth of seedlings (Table 1) and terpenoid chemistry of mature trees (Table 2) was gathered from the literature for evaluation.

Second, new information about the morphological variation of mature trees was gathered via small population samples from representative localities throughout the range (Table 3). For each sampled tree, an exposed sun branch was selected and cut off with a pole pruner. Ten consecutive leaves were removed from the center of a stem growth segment at least 1 year old (i.e., current season leaves were not sampled). The branch was pressed as a voucher and later scored for degree of pubescence. The leaves were transported in labeled coin envelopes, air dried, and then measured or scored in the laboratory for the first six traits listed in Table 4. The average of 10 leaves was used to represent the plant.

The first three characteristics—leaf width, leaf thickness, and leaf length—were measured to the nearest 0.1 mm with the aid of vernier calipers. The shape of the leaf tip was rated on a scale of 1 to 4 from acute to obtuse to rounded to emarginate after Hamrick (1966). The twist at the base of the leaf was rated on a scale of 1 to 5 progressively from no twist to twists of 90°, 180°, 270°, and 360°. The number of rows, or partial rows, of stomata on the upper leaf surface was counted several times under a dissecting microscope until a consistent maximum count was obtained.

The seventh trait, degree of stem pubescence, was rated on a scale of 0 to 4 respectively for no pubescence, a few scattered hairs, small intermittent patches of hairs, uniformly distributed but not dense (hairs shorter than the spaces between), uniform and dense (hairs longer than the spaces between). A stepwise discriminant analysis was used to analyze the data (BMDP7M).

RESULTS

Seedling morphology. A study of variation in 43 test populations was conducted (Hamrick and Libby 1972) by growing seedlings in a nursery. An interpopulation difference index was compiled based on the sum of significant differences for nine characteristics. A matrix of such difference indexes sorts the test populations into four groups. Group I (*Abies grandis* from Oregon and northwest California) is not of direct concern to the present question.

Groups II (*A. concolor* var. *lowiana* from northern California), III (*A. concolor* var. *concolor* from southern California and Arizona), and IV (*A. concolor* var. *concolor* from Utah and eastern Nevada) are of present concern. These groups are each less homogeneous (by inspection of Hamrick and Libby's 1972 data) than Group I. One or two, or very few, populations contribute toward high interpopulation difference indexes within each group (Table 1, lower left). Nevertheless, Groups II and III are about equally homogeneous as judged by the average within-group interpopulation difference index (Table 1, upper right). But Group IV is more heterogeneous and can readily by separated into two components: Utah (BF, BG) and Nevada (AW, AX, AY). Furthermore, Arizona population BB is somewhat anomalous and could be separated out. Nevertheless, both Utah and Arizona cluster with southern California as one group using the available interpopulation difference index as a clustering tool. Arizona joins first if BB is omitted, and Utah joins first if BB is included. The combined group, an expanded Group III, then clusters next with northern California, leaving the Nevada populations unclustered. On this analysis, the southern California, Arizona, and Utah populations form one group assignable to *A. concolor* var. *concolor.* The northern California populations form one group assignable to *A. concolor* var. *lowiana.* The Nevada populations, the reduced Group IV, are the most different but could be considered another form of *A. concolor* var. *concolor* because of reasonable similarity to the Utah populations.

Terpenoid chemistry. The terpenes in several species of *Abies,* specifically including the three groups of *A. concolor* under concern here, were studied by Smedman et al. (1969). Chemical differences support the interpretation that three groups of populations are included in *A. concolor.* However, the method employed used bulk resin samples from up to 50 trees, in unspecified sample areas, which permits "good averaging" but precludes any test of significance between averages. Consequently, the results (Table 2) are difficult to interpret.

TABLE 1. INTERPOPULATION DIFFERENCE INDEXES FOR THREE GEOGRAPHIC GROUPS OF WHITE FIR. II, northern California (AA to AL); III, southern California (AQ to AV)–Arizona (BA to BC); and IV, Utah (BF to BG)–Nevada (AW to AY). Lower left, data from Hamrick and Libby (1972), based on the sum of differences for nine characters. Double letters at left and on diagonal designate seed collection localities. Upper right, average of interpopulation differences calculated for convenience of description. The dashed line separates an expanded Group III from a reduced Group IV.

		II														III	IV
II	AA	AA															
	AB	0	AB														
	AE	3	0	AE				3.15								6.98	12.20
	AG	1	0	2	AG												
	AH	0	0	1	0	AH											
	AJ	0	0	2	0	0	AJ										
	AM	2	1	0	1	0	1	AM									
	AN	4	0	0	2	1	3	0	AN								
	BD	7	2	2	2	1	7	0	0	BD							
	BE	5	3	1	0	2	4	0	0	1	BE						
	AO	3	0	0	0	3	0	0	2	3	1	AO					
	AP	7	3	0	2	2	5	0	0	1	0	1	AP				
	AK	3	4	8	10	8	2	8	8	16	9	6	9	AK			
	AL	5	5	9	11	8	3	10	10	16	11	5	10	0	AL		

TABLE 1. CONTINUED.

		II														III									IV				
III	AQ	9	7	4	3	2	5	3	6	5	6	4	8	15	16	AQ													
	AR	12	9	6	7	5	9	7	10	14	18	7	19	14	14	2	AR												
	AS	4	3	1	4	2	2	1	0	4	4	2	2	10	10	1	0	AS											
	AT	7	3	2	3	3	3	4	3	7	5	2	6	10	11	0	0	0	AT			3.29					13.33		
	AU	8	7	5	7	5	4	3	5	10	8	4	6	7	7	1	2	0	0	AU									
	AV	7	6	4	8	4	4	4	7	10	12	6	12	10	9	2	0	0	0	0	AV								
	BA	3	5	4	5	3	2	0	4	7	5	4	6	8	7	0	3	0	1	1	0	BA							
	BC	8	7	8	10	7	5	3	9	13	9	6	10	5	7	6	6	12	3	0	2	2	BC						
	BB	8	13	15	13	10	5	11	14	21	13	12	16	5	3	12	12	13	11	7	8	5	5	BB					
IV	BF	8	5	1	5	3	7	3	3	2	7	8	8	14	16	4	10	2	2	8	5	4	11	17	BF				
	BG	4	4	1	2	3	6	1	2	2	4	3	5	13	15	0	5	0	5	4	4	2	5	13	0	BG			
		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		5.10	
	AW	26	21	14	17	17	24	15	15	9	19	22	17	35	33	8	23	13	17	22	18	15	29	33	7	10	AW		
	AX	15	11	3	9	7	14	2	4	2	10	9	8	21	22	5	15	1	7	10	10	6	16	23	0	2	0	AX	
	AY	25	22	14	16	20	27	16	9	6	17	21	13	36	37	9	33	17	23	29	27	22	30	38	6	13	7	6	AY

TABLE 2. TERPENOIDS OF *Abies concolor*. A, Monoterpenes. Data from Smedman et al. (1969) and Zavarin et al. (1975). B, Sesquiterpenes. Data from Smedman et al. (1969). Southern California populations are similar to: C, Northern California; D, Rocky Mountains; E, both; or F, neither. Key: x = trace; — = none; ( ) = tenuous similarity.

	1969			1975			Similarity
	NC	SC	RM	NC	SC	RM	
A							
α-Pinene	9	10	23	8.9	10.0	16.4	
β-Pinene	53	42	28	66.3	41.2	22.7	
(α + β-Pinene)	62	52	51	75.2	51.2	39.1	D
Camphene	x	x	12	1.3	x	9.4	C
3-Carene	0.5	20	11	0.7	13.1	0.6	D
Myrcene	0.5	0.5	8.0	0.4	0.6	1.3	(C)
Limonene	2	2	2	2	2	2.6	E
β-Phellandrene	35	26	16	17	25.4	6.8	C
Terpineole	—	0.5	x	—	0.1	0.2	E
B							
Farnesene	—	3	4				(D)
β-Elemene	5	14	6				F
α-Selinene	14	10	10				(D)
β-Selinene	15	—	6				(F)
β-Bergamotene	8	2	3				D
γ-Cadinene	1	8	3				F
α-Muurolene	1	3	9				C
α-Cubabene	2	21	9				F
α-Copaene	1	3	8				C
Longifolene	5	2	1				(D)
Longicyclene	3	—	—				(D)

The monoterpenes were studied by Zavarin et al. (1975) in resin from individual trees in widely distributed and amply described sample populations of all three groups (Table 2A).

The monoterpene components varied extensively (Zavarin et al. 1975), but medial differences confirmed three population groups. Trees from northern California populations (var. *lowiana*) produce little camphene and little 3-carene. Trees from Rocky Mountain populations (var. *concolor*) produce fairly large amounts of camphene and 3-carene. Trees from southern California populations produce large amounts of 3-carene but no camphene.

The three chemical races were compared by means of a non-weighted similarity index. In terms of monoterpenes, the southern California populations were more similar to var. *lowiana* (Zavarin et al. 1975) with a similarity index of 0.64. However, inspection of Table 2A indicates significant similarity only in amounts of camphene, β-phellandrene, and perhaps myrcene. The southern California populations were more similar to var. *concolor* in amounts of 3-carene and the total of α- and β-pinene. (Since α- and β-pinene are stereo-isomers, one increases as the other decreases. Hence, they are better combined as one chemical trait.) The greater similarity to var. *lowiana* is therefore reduced to a tenuous similarity in one component (myrcene).

In terms of sesquiterpenes, the southern California populations approach var. *concolor* (Rocky Mts.) "being overall closer to the latter" (Zavarin et al. 1975). However, the sesquiterpene similarity index was calculated from the Smedman et al. (1969) data for which no test of significance is available.

Given the extreme variability of terpenoid data (see Zavarin et al. 1970, Zavarin 1975), differences in sesquiterpenes (Table 2B) of less than 5–10% are probably not significant. Therefore, similarity of southern California samples to northern California samples seems fairly certain for two compounds, α-muurolene and α-copaene. Similarity of southern California populations to Rocky Mountain populations seems fairly certain for only one compound, β-bergamotene, and somewhat tenuous for four other compounds (Table 2B). The overall greater similarity of southern California to Rocky Mountain populations, as claimed by Zavarin et al. (1975), is demonstrated only if the rather small differences in farnesene, α-selinene, longifolene, and longicyclene are significant.

Morphology of mature trees. Two groups of samples are evident (Table 4). The northern California populations stand out in having rather long leaves with a definite twist at the base (sun branches), a rounded to emarginate leaf tip, and a low number of stomatal rows on the upper surface. The other populations are distributed along a line from Colorado-New Mexico to Baja California. The Colorado-New Mexico populations have the narrowest, thinnest, and longest leaves with the most acute tips but with little twist. The Baja California population has the widest, thickest, and shortest leaves with the very least twist.

All the extreme values for the six leaf traits occur in the geographically extreme populations: northern California, or Colorado-New Mexico, or Baja California. The other populations fall in between the above extremes except for the contrasting pattern in stem pubescence for which the southern California populations score the lowest and the desert mountain populations score the highest.

The variation and distribution patterns for the seven characteristics were analyzed by a stepwise discriminant analysis that ranked the average values for each character for each region. The program selected the most discriminating characters in the sequence: leaf twist, leaf thickness, stomatal rows, leaf length, pubescence, leaf width, and leaf tip shape. The cumulative proportion of the total dispersion was respectively 0.721, 0.898, 0.949, and 0.978 for the

TABLE 3. COLLECTION SITES.

County	Locality	Date	Sample size
Northern California (including Kern Co.):			
Alpine	W. Woodfords	Sep 1979	8
Alpine	Ebbetts Pass Rd.; Silver Crk. C. G.	Sep 1979	5
Alpine	Ebbetts Pass Rd.; Alpine Lake	Sep 1979	5
Calaveras	Ebbetts Pass Rd.; Hell's Kitchen Vista	Sep 1979	5
Kern	Greenhorn Mts.	May 1977	17
Lassen	5W Susanville	Sep 1976	5
Mariposa	8N Wawona	Oct 1981	6
Mariposa	15S Wawona	Oct 1981	12
Tulare	Giant Forest	Sep 1979	6
Tulare	General's Highway	Sep 1979	7
Tuolumne	Sonora Pass Rd.; Strawberry	Sep 1979	8
Tuolumne	Sonora Pass Rd.; 5E Strawberry	Sep 1979	7
Tuolumne	Sonora Pass Rd.; 12E Strawberry	Sep 1979	5
Tuolumne	Sonora Pass Rd.; 19E Strawberry	Sep 1979	5
Southern California:			
Riverside	San Jacinto Mts.	Jul 1976	5
Riverside	San Jacinto Mts.	Nov 1977	12
Riverside	Santa Rosa Mts.	Jul 1979	10
San Bernardino	San Bernardino Mts.	Sep 1976	10
San Diego	Palomar Mts.	Sep 1977	18
Desert Mts. (Nevada-California):			
Clark (Nev.)	Charleston Mts.	Aug 1976	2
Clark (Nev.)	Charleston Mts.	Mar 1977	10
Clark (Nev.)	Charleston Mts.	Sep 1979	6
San Bernardino (Cal.)	Clark Mts.	May 1978	5
San Bernardino (Cal.)	New York Mts.	Jul 1979	2
Baja California (Mexico):			
Norte	Sierra San Pedro Martir	Oct 1976	16
Arizona:			
Coconino	Mormon Lake	Oct 1977	7
Coconino	Happy Jack	Oct 1977	8
Coconino	Miller Ridge	Oct 1977	15
Coconino	1W Baker Butte	Oct 1977	5
Coconino	Woods Canyon Lake Jct.	Oct 1977	14
Gila	Colcorn Summit (Young)	Oct 1977	6
Utah:			
Iron	E. Cedar City	Jul 1976	10
Kane	Strawberry Peak	Jul 1976	4
Salt Lake	Big Cottonwood Canyon: Storm Mt.	Dec 1977	6
Salt Lake	Little Cottonwood Cyn: Snow Bird	Dec 1977	6
Salt Lake	Big Cottonwood Cyn: 6200 ft	Dec 1977	5
Salt Lake	Little Cottonwood Cyn: Lisa Falls	Dec 1977	6

TABLE 3. CONTINUED.

County	Locality	Date	Sample size
Colorado-New Mexico:			
Rio Grande (Colo.)	S. Girard	Sep 1978	17
Rio Grande (Colo.)	S. Del Norte	Sep 1978	7
Costilla (Colo.)	W. LaVeta Pass	Sep 1978	5
Costilla (Colo.)	E. LaVeta Pass	Sep 1978	5
Conejos (Colo.)	N.E. La Manga Pass	Sep 1978	6
Rio Ariba (N.M.)	9N Chama	Sep 1978	8
Rio Ariba (N.M.)	3N Chama	Sep 1978	7

TABLE 4. MEAN AND STANDARD DEVIATION FOR SEVEN MORPHOLOGICAL TRAITS OF *Abies concolor* IN SEVEN GEOGRAPHICAL REGIONS. 1, northern California; 2, southern California; 3, desert mountains (Nevada-California); 4, Baja California; 5, Arizona; 6, Utah; 7, Colorado-New Mexico. a = scale of 1 to 4 from acute to obtuse to rounded to emarginate; b = scale of 1 to 5 from no twist to twists of 90°, 180°, 270°, and 360°. c = scale of 0 to 4 from no hairs to dense pubescence. Maximum and minimum average values for each trait are underlined.

Geographic area	n	Leaf width (mm)	Leaf thickness (mm)	Leaf length (mm)	Tip shape (a)	Leaf twist (b)	Rows stomata (no.)	Stem pubescence (c)
				Means				
1	101	2.06	0.90	34.24	2.6	2.5	16.3	2.0
2	55	2.05	0.88	26.23	2.1	1.3	17.1	1.2
3	25	2.07	0.82	23.39	2.2	1.0	17.5	2.9
4	16	2.46	1.16	22.48	2.0	1.0	21.4	2.3
5	55	2.12	0.79	32.67	2.1	1.2	20.1	1.5
6	37	2.07	0.79	32.79	2.0	1.1	18.3	2.4
7	54	1.95	0.76	34.59	1.9	1.1	19.9	2.8
Total	343	2.07	0.85	31.26	2.2	1.5	18.1	2.0
				Standard deviations				
1		0.16	0.10	7.31	0.41	0.52	3.06	0.92
2		0.19	0.08	6.32	0.33	0.33	2.84	0.99
3		0.22	0.12	3.75	0.44	0.06	2.54	1.04
4		0.22	0.14	3.67	0.05	0.04	2.52	1.13
5		0.22	0.09	5.52	0.29	0.18	2.47	1.42
6		0.17	0.09	5.88	0.12	0.14	2.35	1.75
7		0.16	0.09	5.20	0.19	0.13	2.34	0.84
Total		0.18	0.10	6.07	0.32	0.33	2.70	1.14

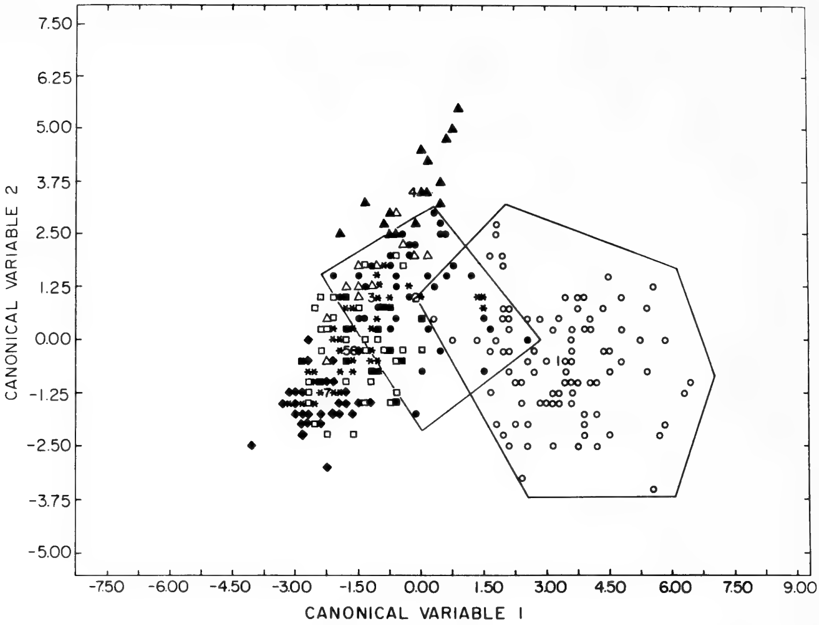


FIG. 1. Distribution of white fir samples relative to two canonical variables. Numbers represent group means; symbols represent individual trees: northern California, 1, ○; southern California, 2, ●; desert mountains, 3, △; Baja California, 4, ▲; Arizona, 5, □; Utah, 6, ■; Colorado-New Mexico, 7, ◆. Asterisks indicate points with occurrence of two or more plants. Distribution of southern California is enclosed by a four-sided figure, northern California by a six-sided figure.

first four characters entered. The remaining characters effected negligible dispersion, although all seven had significant F values. These characters were combined into two canonical variables against which all the individual samples were plotted (Fig. 1) as a formalized description of character distribution. On this scheme, the northern California populations fell out to the right and are completely distinct from all other populations except for a very slight overlap with southern California. The remaining populations fall in a line between the Baja California populations and the Colorado-New Mexico populations. The southern California populations are slightly off line toward the right but clearly overlap strongly with populations from Arizona, Utah, and especially the desert mountains.

DISCUSSION

Variation in white fir has now been studied from several viewpoints. On the basis of seedling morphology, Hamrick and Libby (1972) proposed several groups of white fir: *Abies concolor* var.

lowiana in northern California, *A. concolor* var. *concolor* in the Rocky Mountains, and another form of *A. concolor* var. *concolor* in southern California-Arizona. Examination of their data indicates that some groups, especially Group IV, Utah-Nevada, are markedly heterogeneous. Simple clustering, based on interpopulation difference indexes, places the Utah populations in an expanded Group III with those from Arizona and southern California. The expanded Group III is more similar to Group II, northern California, than to the Nevada populations residual in Group IV. The reorganized Group III indicates a stronger relationship among populations from southern California, Arizona, and Utah than Hamrick and Libby (1972) had proposed.

On the basis of terpenoid chemistry, Zavarin et al. (1975) demonstrate three chemical races. The extreme variation in chemical composition makes difficult an unambiguous interpretation of the relationship among the three chemical races. Nevertheless, Zavarin et al. (1975) suggest a somewhat greater overall similarity of the southern California populations to those in Arizona and the Rocky Mountains than to those in northern California.

On the basis of mature tree leaf morphology, the present study shows two groups of populations, the northern California (mostly Sierra Nevada) populations, corresponding to *A. concolor* var. *lowiana*; and all the other populations being definitely referred to *A. concolor* var. *concolor.* Populations of the latter variety are distributed along a line (Fig. 1) from Colorado-New Mexico to Baja California, a pattern that approximates a latitudinal gradient. (Inversion and reversal of Fig. 1 emphasizes the geographical correlation.) The southern California populations fall slightly off line toward the northern California populations. A slightly higher incidence of leaves with a basal twist (Table 4) may account for the difference. Furthermore, the individual trees within the overlap area with northern California all have a leaf twist and all occur on Palomar Mountain. Their occurrence there may suggest some ancient introgression at a time when Sierran forests extended southward (early Quaternary?) and met Rocky Mountain forests that had extended southwest across the southern Great Basin (Miocene to late Pliocene?) (Axelrod 1976).

The rather close relationship between southern California and Arizona populations, as proposed by Hamrick (1966) and Hamrick and Libby (1972), and confirmed in the present study, is rather surprising in view of the long separation of the two areas by the intervening Sonoran Desert and the current climatic differences (Axelrod 1976). Nevertheless, several plants evidence phytogeographic relationships between the two areas. For example, *Rhus ovata* occurs in chaparral, and *Arctostaphylos pringlei* occurs in montane forests or woodlands, of the two areas (Kearney and Peebles 1960, Munz 1959). In addition, *Acer grandidentatum brachypterum,* known from early Pleistocene fossils in the San Jacinto Mountains (Axelrod 1966), presently occurs in the mountains near Prescott in west-central Arizona. Among herbaceous plants, *Clarkia rhomboidea* occurs in montane forests of both the Rocky Mountain region and the Californian region (Mosquin 1964). Analysis of translocation heterozygosity in interpopulational hybrids of *C. rhomdoidea* indicates disjunct distribution of a "southern type" in Arizona and southern California and a skewed horseshoe-shaped distribution of a "northern type" in mountains around the Great Basin. Mosquin (1964) interprets that late Wisconsin distributions in broad, shallow horseshoe-shaped bands across the Great Basin region, and subsequent retreat from the Great Basin upon increase in aridity, would account for the present distribution and disjunctions.

Since the montane forests of central Arizona and southern California have long been separate (Axelrod 1976), the similarity of white fir trees of the two regions may derive from a distribution similar to that proposed by Mosquin (1964) for *Clarkia* in Late Pleistocene. In the case of white fir, links across the present desert may have occurred prior to the Late Pleistocene, as implied by Wells and Berger (1967) and Mehringer and Ferguson (1969), and may extend clear back to the Miocene, when conifer forests were widespread in the Great Basin (Axelrod 1976). A forested region is also indicated by late Pliocene–early Pleistocene pollen floras from the Coso Mountains, Panamint Valley, Little Lake, and other stations in the northern Mojave Desert (Axelrod and Ting, 1960, 1961). Rocky Mountain forest vegetation most probably ranged to southern California well before the Pleistocene and left populations of white fir that clearly are referable to *Abies concolor* var. *concolor.*

ACKNOWLEDGMENTS

I wish to thank the following for their aid and encouragement: C. Huszar for statistical aid; S. James, J. Lippert, and N. Smith-Huerta for technical assistance; A. Wyckoff, A. Sanders, M. Vasek, L. LaPré, P. Rowlands, and O. Clarke for collecting some of the samples; J. R. Haller, E. Zavarin, and R. Scora for helpful discussion; and B. Bickler for typing the manuscript.

LITERATURE CITED

AXELROD, D. I. 1966. The Pleistocene Soboba flora of southern California. Univ. Calif. Publ. Geol. Sci. 60:1–79.

———. 1976. History of the coniferous forests, California and Nevada. Univ. Calif. Publ. Bot. 70:1–62.

FOWELLS, H. A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Agric. Handb. 271, Washington, D.C.

GRIFFIN, J. R. and W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S. For. Serv. Res. Paper PSW-82.

HAMRICK, J. L. 1966. Geographic variation in white fir. M.S. thesis, Univ. Calif., Berkeley.

——— and W. J. LIBBY. 1972. Variation and selection in western U.S. montane species. I. White fir. Silvae Genet. 21:29–35.

HENRICKSON, J. and B. PRIGGE. 1975. White fir in the mountains of Eastern Mojave Desert of California. Madroño 23:164–168.

KEARNEY, T. H. and R. H. PEEBLES. 1960. Arizona flora. Univ. Calif. Press, Berkeley.

LAMB, W. M. 1914. A conspectus of North American firs (exclusive of Mexico). Soc. Amer. Foresters Proc. 9:528–538.

LIU, T. 1971. A monograph of the genus *Abies.* Dept. of Forestry, College of Agriculture, National Taiwan Univ., Taipai.

MARKSTROM, D. C. and J. R. JONES. 1975. White fir—an American wood. USDA For. Serv. Bull. 237.

MEHRINGER, P. J. and C. W. FERGUSON. 1969. Pluvial occurrence of bristlecone pine (*Pinus aristata*) in a Mohave Desert mountain range. J. Arizona Acad. Sci. 5:284–292.

MILLER, A. H. 1940. A transition island in the Mohave Desert. Condor 42:161–163.

MOSQUIN, T. 1964. Chromosomal repatterning in *Clarkia rhomboidea* as evidence for post-Pleistocene changes in distribution. Evolution 18:12–25.

MUNZ, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.

SMEDMAN, L. A., K. SNAJBERK, E. ZAVARIN, and T. R. MON. 1969. Oxygenated monoterpenoids and sesquiterpenoid hydrocarbons of the cortical turpentine from different *Abies* species. Phytochemistry 8:1471–1479.

SUDWORTH, G. B. 1908. Forest trees of the Pacific slope. USDA For. Serv. U.S. Govt. Printing Office, Washington, D.C.

———. 1916. The spruce and balsam fir trees of the Rocky Mountain region. USDA Bull. 327.

VASEK, F. C. and R. F. THORNE. 1977. Transmontane coniferous vegetation. *In* J. Major and M. G. Barbour, eds., Terrestrial vegetation of California, Chap. 23. Wiley-Interscience, NY.

WELLS, P. V. and R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science 155:1640–1647.

ZAVARIN, E. 1975. The nature, variability and biological significance of volatile secondary metabolites from Pinaceae. Phytochem. Bull. 8:6–15.

———, K. SNAJBERK, and J. FISHER. 1975. Geographic variability of monoterpenes from *Abies concolor.* Biochem. Syst. Ecol. 3:191–203.

———, K. SNAJBERK, T. REICHERT, and E. TSIEN. 1970. On the geographic variability of the monoterpenes from the cortical blister oleoresin of *Abies lasiocarpa.* Phytochemistry 9:377–395.

(Received 15 March 1984; accepted 29 July 1984.)

SOME FLORAL NECTAR-SUGAR COMPOSITIONS OF SPECIES FROM SOUTHEASTERN ARIZONA AND SOUTHWESTERN NEW MEXICO

C. Edward Freeman and Richard D. Worthington
Department of Biological Sciences, University of Texas,
El Paso 79968-0519

Abstract

The floral nectar-sugar compositions of 34 species from southeastern Arizona and southwestern New Mexico were determined by high-performance liquid chromatography (HPLC). Of these, 26 species have not been reported previously. Among the species surveyed were hummingbird flowers (18 species), hawkmoth flowers (seven species), bee flowers of various kinds (five species), butterfly flowers (two species), and those whose pollinators were not known (two species). Both the hummingbird and hawkmoth nectars were high in sucrose, averaging 71% and 81% respectively. The nectars of the purportedly butterfly flowers were very different at 76% and 46% sucrose. Bee nectars from large-flowered species with large corolla tube openings were high in sucrose (average = 76%) whereas small-flowered bee species with small corolla tube openings were lower in sucrose (average = 35%).

It is clear from the work of Baker (1978) and Baker and Baker (1975, 1979, 1983) that the sugar composition of floral nectars is worthy of careful examination in regard to its differential attractiveness to various groups of potential pollinators. It has been found that the most common sugars in nectars are the hexoses, glucose and fructose, and the disaccharide sucrose. These are the so-called "big three" sugars of nectars (Baker and Baker 1983). Other sugars are occasionally present in very small amounts.

We present here the floral nectar-sugar compositions of a series of species from southeastern Arizona and southwestern New Mexico. The pollinators of many of these species have been studied but their sugar compositions have not been reported.

Methods and Materials

Sugar compositions by mass were quantified using HPLC. The methods employed are described in earlier publications (Freeman et al. 1983, Freeman et al. 1984). HPLC was used because the analysis is direct, eliminating the derivatization steps of other techniques that add to the error term. This makes HPLC much more accurate. In addition, HPLC is much more rapid. Sugar compositions were calculated to the nearest 0.1%. Voucher specimens are deposited at UTEP. Nomenclature follows Lehr (1978) and Lehr and Pinkava (1980).

Madroño, Vol. 32, No. 2, pp. 78–86, 26 April 1985

RESULTS AND DISCUSSION

The nectar-sugar compositions of 34 species are presented in Table 1. Freeman et al. (1984) have previously reported on seven species (*Bouvardia glaberrima, Epilobium canum* subsp. *latifolia* [as *Zauschneria latifolia*], *Fouquieria splendens, Mimulus cardinalis, Penstemon barbatus, P. pseudospectabilis,* and *Silene laciniata*). Sherbrooke and Schereens (1979) have reported on *Erythrina flabelliformis.* About half of the species surveyed in this study are known or suspected to be hummingbird-pollinated. These include *Anisacanthus thurberi, Aquiliegia triternata, Bouvardia glaberrima, Castilleja patriotica, Erythrina flabelliformis, Fouquieria splendens, Lonicera arizonica, Lobelia cardinalis, Mimulus cardinalis, Penstemon barbatus, P. pinifolius, P. pseudospectabilis, Ribes pinetorum, Salvia lemmoni, Silene laciniata,* and *Epilobium canum* subsp. *latifolium.* These nectars ranges in sucrose composition from 55% (*Mimulus cardinalis*) to 93% (*Ribes pinetorum*).

The mean value of 71% sucrose is very similar to the means of other groups of hummingbird flowers (Freeman et al. 1984, Freeman, unpubl. data). In addition, many of these species also have a hexose imbalance; i.e., fructose is present in much larger quantities than glucose. A reversed imbalance is found in *Aquilegia triternata,* which has about twice as much glucose as fructose. In this species hexoses are present in very low quantities. The sugar composition of the floral nectar of *Erythrina flabelliformis* collected in this study from the Dragoon Mountains of Arizona is virtually identical with a sample collected and analyzed earlier from the same mountain range (Sherbrooke and Schereens 1979) also using HPLC as the analysis technique. Several species previously reported by Freeman et al. (1984) from other localities had very similar sugar compositions in the study area, including *Bouvardia glaberrima, Penstemon barbatus,* and *P. pseudospectabilis.* Others varied somewhat. The sucrose composition of *Silene laciniata* in the Chiricahua Mountains averaged about 10% higher than a sample of the same species from the White Mountains, also in eastern Arizona. *Mimulus cardinalis* and *Epilobium canum* subsp. *latifolium* nectars, however, were lower in sucrose in southeastern Arizona (Freeman et al. 1984). *Lonicera arizonica* was very similar in sugar composition to a sample of *L. involucrata,* also hummingbird-pollinated, reported previously (Freeman et al. 1984).

Brown and Kodrick-Brown (1979) report a population of *Lobelia cardinalis* in the White Mountains of eastern Arizona that did not produce nectar. They suggested that this population was mimetic to several common hummingbird-pollinated species in the area. Other populations of that species in the Chiricahua Mountains in southeastern Arizona and near Montezuma Wells National Monument

TABLE 1. NECTAR SUGAR COMPOSITIONS FOR SPECIES FROM SOUTHEASTERN ARIZONA AND SOUTHWESTERN NEW MEXICO. N = number of determinations.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
HUMMINGBIRD				
Anisacanthus thurberi (Torr.) Gray				
AZ, Santa Cruz Co., Pajarito Mtns.	2	17.7 ± 0.06	19.4 ± 1.6	63.0 ± 2.3
AZ, Santa Cruz Co., Pena Blanca Lake	3	12.1 ± 3.6	15.0 ± 2.9	72.9 ± 6.5
AZ, Cochise Co., Dragoon Mtns.	6	15.7 ± 2.3	15.1 ± 3.7	69.2 ± 5.7
Total =	11	15.1 ± 3.1	15.8 ± 3.4	69.1 ± 6.1
Aquilegia triternata Payson				
AZ, Cochise Co., Chiricahua Mtns.	2	3.1 ± 0.7	8.4 ± 5.6	88.6 ± 6.3
Bouvardia glaberrima Engelm.				
AZ, Cochise Co., Chiricahua Mtns.	6	33.4 ± 1.6	10.0 ± 1.8	56.7 ± 2.8
Castilleja integra Gray				
NM, Luna Co., Florida Mtns.	3	19.1 ± 4.2	5.8 ± 1.1	75.1 ± 4.0
Castilleja patriotica Fern.				
AZ, Cochise Co., Chiricahua Mtns.	1	15.2	3.3	81.5
Epilobium canum (Greene) subsp. *latifolia* (Hook.) Raven				
AZ, Cohcise Co., Chiricahua Mtns.	3	19.2 ± 3.2	18.6 ± 4.0	62.3 ± 7.0
Erythrina flabelliformis Kearney				
AZ, Cochise Co., Dragoon Mtns.	7	20.2 ± 3.6	19.5 ± 5.1	60.3 ± 6.1

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
Fouquieria splendens Engelm.				
NM, Hidalgo Co., Peloncillo Mtns.	1	18.4	16.6	65.0
Lobelia cardinalis L.				
AZ, Cochise Co., Huachuca Mtns.	6	28.8 ± 1.6	13.8 ± 1.0	57.2 ± 1.9
Lonicera arizonica Rehd.				
NM, Grant Co., Pinos Altos Mtns.	4	10.7 ± 5.9	14.6 ± 14.6	74.7 ± 13.1
Mimulus cardinalis Dougl.				
AZ, Cochise Co., Chiricahua Mtns.	1	34.6	10.1	55.3
Penstemon barbatus (Cav.) Roth.				
AZ, Cochise Co., Chiricahua Mtns.	37	12.1 ± 5.0	13.4 ± 5.4	74.5 ± 10.3
Penstemon pinifolius Greene				
AZ, Cochise Co., Chiricahua Mtns.	5	16.9 ± 2.6	19.2 ± 3.3	68.8 ± 5.7
Penstemon pseudospectabilis Jones				
AZ, Cochise Co., Chiricahua Mtns.	32	15.0 ± 4.3	19.0 ± 5.0	66.1 ± 9.2
Penstemon ramosus Crosswhite				
NM, Hidalgo Co., Peloncillo Mtns.	7	19.2 ± 3.9	22.4 ± 3.6	58.4 ± 7.5
Ribes pinetorum Greene				
AZ, Cochise Co., Chiricahua Mtns.	4	5.8 ± 0.9	0.7 ± 0.3	93.5 ± 1.1
Salvia lemmoni Gray				
AZ, Cochise Co., Chiricahua Mtns.	5	7.9 ± 1.6	4.0 ± 1.2	88.3 ± 2.4

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
Silene laciniata Cav.				
AZ, Cochise Co., Chiricahua Mtns.	3	14.1 ± 0.9	4.1 ± 0.7	81.8 ± 0.5
Mean		17.2 ± 8.5	12.1 ± 6.7	71.0 ± 12.0
HAWKMOTH				
Aquilegia chrysantha Gray				
AZ, Cochise Co., Chiricahua Mtns.	1	4.2	9.0	86.8
AZ, Apache Co., White Mtns.	1	2.0	3.0	95.0
Calylophus hartwegii (Benth.) Raven				
NM, Hidalgo Co., Peloncillo Mtns.	1	5.5	4.1	90.4
Castilleja sessiliflora Pursh				
AZ, Santa Cruz Co., Mustang Mtns.	3	17.3 ± 1.5	7.0 ± 0.4	75.7 ± 1.9
Datura meteloides DC.				
AZ, Cochise Co., Huachuca Mtns.	1	11.1	9.6	79.3
Ipomopsis longiflora (Torr.) V. Grant				
AZ, Cochise Co., W. Jct. Hwys 82–90	1	11.5	11.4	77.2
Ipomopsis thurberi (Torr.) V. Grant				
AZ, Cochise Co., Huachuca Mtns.	7	16.0 ± 2.2	13.5 ± 2.9	70.6 ± 5.0
Oenothera caespitosa Nutt.				
NM, Luna Co., Florida Mtns.	1	6.0	4.1	89.9
Mean		10.1 ± 5.3	8.0 ± 3.6	82.0 ± 8.3

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
BEE				
Agave parviflora Torr.				
AZ, Santa Cruz Co., Pena Blanca Lake	2	30.4 ± 0.1	29.1 ± 0.5	40.6 ± 0.6
Penstemon dasyphyllus Gray				
AZ, Cochise Co., Chiricahua Mtns.	7	30.0 ± 4.9	33.1 ± 6.6	38.3 ± 11.4
AZ, Santa Cruz Co., Mustang Mtns.	4	13.1 ± 3.8	16.3 ± 4.0	70.6 ± 7.7
Penstemon linarioides Gray				
NM, Grant Co., Silver City	2	32.7 ± 0.7	35.5 ± 0.4	31.7 ± 1.1
Penstemon stenophyllus Gray				
AZ, Cochise Co., Huachuca Mtns.	1	27.0	12.1	60.9
Swertia radiata (Kell.) Kuntze				
NM, Grant Co., Pinos Altos Mtns.	1	38.3	31.6	30.1
Mean		28.6 ± 8.5	26.3 ± 9.7	45.4 ± 16.6
BUTTERFLY				
Nyctaginea capitata Choisy				
NM, Grant Co., Apache Mtns.	2	12.8 ± 2.3	11.2 ± 6.1	76.0 ± 8.4
Ipomopsis macombii (Torr.) V. Grant				
AZ, Cochise Co., Chiricahua Mtns.	3	26.1 ± 4.0	27.4 ± 4.5	46.4 ± 8.4
UNKNOWN				
Hedeoma hyssopifolium Gray				
AZ, Cochise Co., Chiricahua Mtns.	1	10.7	12.9	76.4
Mertensia franciscana Heller				
NM, Grant Co., Pinos Altos Mtns.	1	54.5	43.2	2.3

in central Arizona do produce nectar. We found a population of *L. cardinalis* in the Guadalupe Mountains of trans-Pecos Texas that also did not produce nectar, even when the plants were removed from the field and grown in a greenhouse. We found ample production of nectar in a population sampled in the Huachuca Mountains in this study, although the nectar was rather low in sucrose for a hummingbird flower (57%).

The hawkmoth-pollinated taxa sampled in this study include *Ipomopsis longiflora, I. thurberi* (Grant and Grant 1968), *Castilleja sessiliflora* (Cruden et al. 1983), *Datura meteloides* (Grant 1983, Grant and Grant 1983), *Aquilegia chrysantha* (Miller 1982), *Oenothera caespitosa* (Grant 1983), and presumably *Calylophus hartwegii* because of its great similarity to the other hawkmoth-pollinated *Oenothera* species (Cruden et al. 1983). All have the high-sucrose nectars described by Baker and Baker (1983) for this pollinator syndrome, averaging 81%. *Ipomopsis thurberi* has the lowest sucrose composition among this group and its overall composition is very similar to that of the closely related hummingbird taxon *I. aggregata* (Freeman et al. 1984, Freeman, unpubl. data), from which it differs only in color. *Castilleja sessiliflora* has a nectar-sugar composition like the other hummingbird-pollinated *Castilleja* species studied to date (Freeman et al., 1984, Freeman, unpubl. data).

Two of the three populations for which floral morphology suggests large-bee pollination had high-sucrose nectars. *Penstemon stenophyllus* and one population of a similar species, *P. dasyphyllus,* had 71% and 61% sucrose, respectively. In contrast, another population of *P. dasyphyllus* averaged only 38% sucrose. The reason for this difference in populations separated by only about 130 km and at the same latitude is not known. The smaller flowered *P. linarioides,* however, produces a nectar much lower in sucrose, and is perhaps pollinated by short-tongued bees, as its size and nectar-sugar composition suggest (Baker and Baker 1983). Schaffer and Schaffer (1977) studied nectar secretion and pollinators of four species of *Agave* from Arizona, of which three (*A. schottii, A. toumeyana,* and *A. parviflora*) are in subgenus *Littaea* and are probably closely related. While the three species vary in time of daily nectar secretion and sugar concentrations, all are pollinated by large bees (*Bombus sonorus* and *Xylocopa arizonensis*). *Agave parviflora,* reported here, has a nectar-sugar composition like those of *A. schottii* and *A. toumeyana,* which are atypical of the agaves surveyed to date (Freeman et al. 1983). The pollinators of *Swertia radiata* (or *Frasera speciosa*) have been studied in detail by Beattie et al. (1973). A wide variety of insects, primarily hymenopterans, dipterans, and lepidopterans, visited flowers of this species in Colorado. The nectar-sugar composition is very similar to the majority of the bee-pollinated taxa in this study.

Two purportedly butterfly-pollinated species, *Nyctaginea capitata* (Cruden et al. 1983) and *Ipomopsis macombii* (Grant and Grant 1965), were sampled. Baker and Baker (1983) have described butterfly nectars as being predominately either sucrose-rich or -dominated. *Nyctaginea capitata,* at 76% sucrose, fits that description. However, *I. macombii,* at an average of 46% sucrose, is considerably more hexose-rich. A study of butterfly and skipper nectars, utilizing more sensitive analytical techniques, is needed in order to more adequately define them statistically. Only then will it be possible to determine if either of these nectars is anomalous.

Hedeoma hyssopifolium, and *Mertensia franciscana* are coniferous forest species with unknown pollinators. *Hedeoma hyssopifolium* has the typical high-sucrose nectar of the family Lamiaceae (Baker and Baker 1983). The nectar of *Mertensia* is low in sucrose, which, along with open flowers, suggests pollination by short-tongued bees or flies.

ACKNOWLEDGMENTS

We wish to thank the Research Ranch Foundation of Elgin, Arizona, for a summer fellowship grant to CEF during 1983 when the nectar samples were collected. We also thank M. Murray for collecting nectar samples from the Dragoon Mountains of Arizona.

LITERATURE CITED

BAKER, H. G. 1978. Chemical aspects of the pollination biology of woody plants in the tropics. *In* P. B. Tomlinson and M. H. Zimmerman, eds., Tropical trees as living systems, p. 57–82. Cambridge Univ. Press, Cambridge.

——— and I. BAKER. 1975. Nectar constitution and pollinator-plant coevolution. *In* L. E. Gilbert and P. H. Raven, eds., Animal and plant coevolution, p. 100–140. Univ. of Texas Press, Austin.

——— and ———. 1979. Sugar ratios in nectars. Phytochem. Bull. 12:43–45.

——— and ———. 1982. Chemical constituents of nectar in relation to pollinator mechanisms and phylogeny. *In* M. N. Nitecki, ed., Biochemical aspects of evolutionary biology, p. 131–171. Univ. of Chicago Press, Chicago.

——— and ———. 1983. Floral nectar sugar constituents in relation to pollinators. *In* C. E. Jones and R. J. Little, eds., Handbook of experimental pollination biology, p. 117–141. Van Nostrand-Reinhold Co., NY.

BEATTIE, A. J., D. E. BREEDLOVE, and P. H. RAVEN. 1973. The ecology of the pollinators and predators of *Frasera speciosa.* Ecology 54:81–91.

BROWN, J. H. and A. KODRICK-BROWN. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60: 1022–1035.

———, ———, T. G. WHITHAM, and H. W. BOND. 1981. Competition between hummingbirds and insects for the nectar of two species of shrubs. Southw. Naturalist 26:133–145.

CRUDEN, R. W., S. M. HERMANN, and S. PETERSON. 1983. Patterns of nectar production and plant-pollinator coevolution. *In* B. Bentley and T. Elias, eds., The biology of nectaries, p. 80–125. Columbia Univ. Press, NY.

FREEMAN, C. E., W. H. REID, and J. E. BECVAR. 1983. Nectar sugar composition in some species of *Agave* (Agavaceae). Madroño 30:153–158.

———, ———, ———, and R. SCOGIN. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. 145:132–135.

GRANT, K. A. and V. GRANT. 1965. Flower pollination in the Phlox family. Columbia Univ. Press, NY.

——— and ———. 1968. Hummingbirds and their flowers. Columbia Univ. Press, NY.

GRANT, V. 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. Bot. Gaz. 144:439–449.

——— and K. A. GRANT. 1983. Behavior of hawkmoths on flowers of *Datura meteloides*. Bot. Gaz. 144:439–449.

LEHR, J. H. 1978. A catalog of the flora of Arizona. Northland Press, Flagstaff, AZ.

——— and D. J. PINKAVA. 1980. A catalog of the flora of Arizona, Supplement I. J. Arizona-Nevada Acad. Sci. 15:19–32.

MILLER, R. B. 1982. Hawkmoth pollination of *Aquilegia chrysantha* in southern Arizona. Bot. Soc. Amer. Misc. Publ. No. 162, p. 39.

SCHAFFER, W. M. and M. V. SCHAFFER. 1977. The reproductive biology of Agavaceae: I. Pollen and nectar production in four Arizona agaves. Southw. Naturalist 22:157–168.

SHERBROOKE, W. C. and J. C. SCHEREENS. 1979. Ant-visited extrafloral (calyx and foliar) nectaries and nectar sugars of *Erythrina flabelliformis* Kearney in Arizona. Ann. Missouri Bot. Gard. 66:472–481.

(Received 6 April 1984; accepted 21 August 1984.)

PARONYCHIA AHARTII (CARYOPHYLLACEAE), A NEW SPECIES FROM CALIFORNIA

BARBARA ERTTER
Plant Resources Center, University of Texas,
Austin 78712

ABSTRACT

A tiny annual *Paronychia* that has been known from the Sacramento Valley of California for 46 years is described as **Paronychia ahartii**. Its affinities appear to be with the Mediterranean *P. arabica,* from which it is nevertheless clearly differentiated by the erect, scarious, bilobed apices of its sepals.

In the course of studying a new variety of dwarf rush from the Peter Ahart ranch in Butte County, California, the following inconspicuous *Paronychia* was brought to my attention with the request that I provide a name and description for it. The request is herewith fulfilled.

Paronychia ahartii Ertter, sp. nov.

Herbae annuae minutae glomerulum argenteum ca. 1 cm diam. efformantes. Sepala elliptico-lanceolata basi pilis uncinatis induta, costa in aristum ca. 1 mm longa exeunti, marginibus latis hyalinis ultra costam productis et inter se in limbum erectum bilobum ca. 1 mm longum coadunatis (Fig. 1).

Inconspicuous annual plants 0.5–1.2 cm tall, 0.5–1.8 cm across, consisting of a tight silvery glomerule dominated by stipules, bracts, and sepals, arising from a slender taproot; *leaves* linear to oblanceolate, drying reddish-stramineous, 2.5–7.5 mm long, 0.5–1.2 mm wide, often inconspicuously ciliate, tipped with a colorless awn to 0.8 mm long; *stipules* and *bracts* similar, conspicuous, concealing flowers, scarious, broadly ovate, 3–6 mm long, 2–4 mm wide, acute to acuminate; *flowers* few, sessile, 4.2–5 mm long; *hypanthium* 0.5–1 mm long, often dark red-brown resinous-papillate below the free portion of the sepals; *sepals* 5, lanceolate to elliptic, 3.5–4.5 mm long, 1.5–2.5 mm wide, the herbaceous midrib linear, 2.5–3 mm long, 0.2–0.5 mm wide, green to stramineous, sometimes red-flecked proximally, terminated by a spreading colorless awn 1–1.5 mm long, the edges of the midrib thickened, covered with upwardly spreading hairs with tightly coiled tips, the conspicuous scarious margins 0.5–1 mm wide on each side of the midrib, united beyond the midrib

MADROÑO, Vol. 32, No. 2, pp. 87–90, 26 April 1985

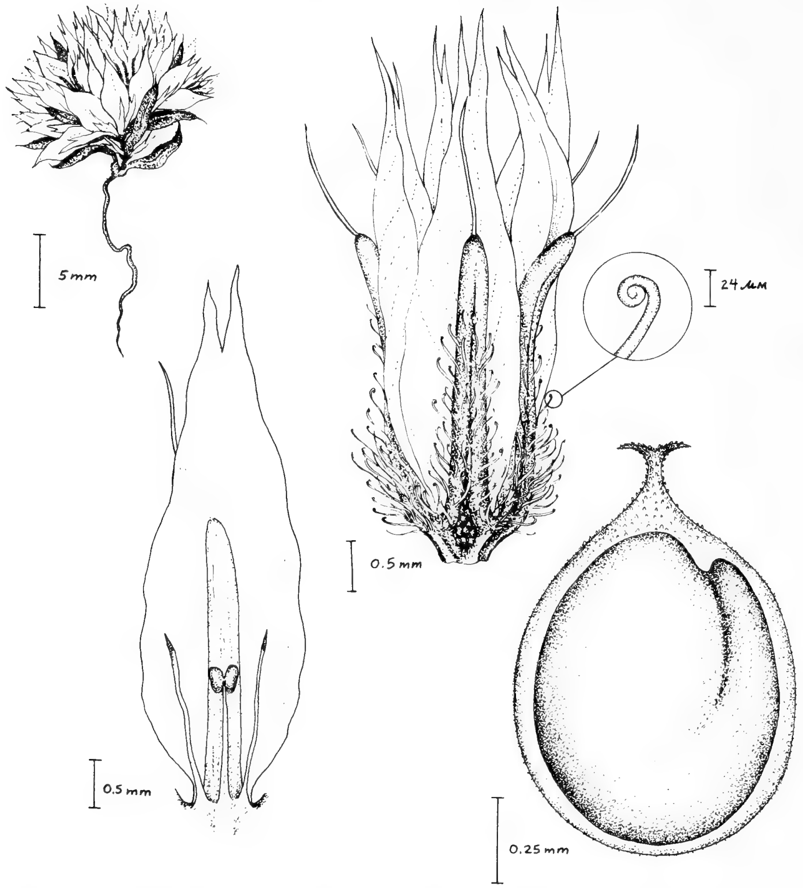


FIG. 1. *Paronychia ahartii.* A. Habit. B. Flower, with enlargement of crozier-tipped hair. C. Inside of sepal, showing stamen and staminodia. D. Utricle with seed.

to form an erect scarious tip 1–1.5 mm long, the apical 0.5 mm bilobed; *staminodia* (petals?) filiform, ca. 1 mm long, equaling or exceeding the stamens; *filaments* flattened, 0.5–1 mm long; *anthers* ovoid, 0.2 mm long, orange; *styles* (including stigmatic portion) ca. 0.5 mm long, bilobed, persistent; *fruit* a thin-walled utricle with a compressed ovoid body 1.3 mm long and beak ca. 0.5 mm long, the apex papillose; *seed* lenticular, ca. 1 mm long, brown, borne on a flattened curved funiculus ca. 1.5 mm long.

TYPE: CALIFORNIA. Tehama Co., 8.5 mi s. of Corning, rolling plains, 12 Jun 1955, *J. T. Howell 30307*. (Holotype: CAS; isotypes: B, GH, K, NY, RM, TEX, U, US.)

PARATYPES: CALIFORNIA. Butte Co., Ahart Ranch, Honcut, 5

May 1974, *Ahart s.n.* (CAS); same, 8 May 1980, *Ertter et al. 3326* (NY); 3 mi n. of Chico, 24 Apr 1938, *Hoover 3242* (CAS); Hwy 99 between Williams and Oroville, 19 Apr 1958, *Langenheim 4480* (JEPS). Shasta Co., Hwy 44 ca. 11 mi se. of Millville, 23 Apr 1958, *Bacigalupi et al. 6318* (JEPS, TEX). Tehama Co., ca. 7 mi s. of Corning, 22–23 Apr 1958, *Bacigalupi et al. 6290* (JEPS, TEX); Jelley's Ferry, 20 May 1942, *Hoover 5879* (CAS).

Very rare on poor clay of swales and higher ground around vernal pools in the northern Sacramento Valley of Butte, Shasta, and Tehama Counties, California, from 30 to 500 m elevation. Flowering from April to June.

Although this diminutive species has been collected several times since R. F. Hoover first discovered it in 1938, these collections remained unidentified beyond tentative placement in *Paronychia.* Rimo Bacigalupi and Alice Howard worked with the specimens, but no publications resulted from their studies. Although it was suspected of being another example of a Mediterranean annual established in California, with the appearance of Chaudhri's (1968) worldwide monograph of the genus it became evident that the collections did indeed represent a distinctive new species.

In Chaudhri's monograph, *Paronychia ahartii* would be associated with *P. arabica* (L.) Del. subsp. *annua* (Del.) Maire & Weiller var. *annua* of the Middle East and north Africa. According to Chaudhri, *P. arabica* "is the most variable species of this genus, and, for that matter, of the entire subtribe, and exhibits marked variability in duration, leaf form, length of stipules, size and form of the glomerules, bracts, flower-size, and the form of the tepals as well as the structure of their awns and the anthers." Nevertheless, *P. ahartii* is easily distinguished from *P. arabica* and appears to be unique in the genus by virtue of the prominent, erect, bilobed apices of the sepals formed by the prolongation of the broad scarious margins beyond the awned herbaceous midrib. Its extremely reduced size is also unusual.

It might at first seem curious that a rare Californian endemic could have a Mediterranean progenitor. Nevertheless a comparable situation involving North American derivatives of a basically Mediterranean genus can be found in *Loeflingia,* as summarized by Barneby and Twisselmann (1971).

Paronychia franciscana Eastwood, the only other species of *Paronychia* in California, is considered to be introduced from Chile (Munz 1959). This species is a coastal, mat-forming perennial to 4 dm across, with herbaceous sepals lacking scarious margins. Confusion with *P. ahartii* is therefore not likely.

If *Paronychia ahartii* is indeed as rare as it appears to be, its continued existence is precarious. Not only is it restricted to the highly developed Sacramento Valley, but a reproduction rate of less than ten seeds per individual does not bode well under any circumstances.

It is in response to Lowell Ahart's plea for a name to place in his checklist of the flora of his ranch that this species is finally being described. The epithet honors Ahart (b. 1938) not only for his persistence and interest in this inconspicuous plant, but also in recognition of his careful collections of the flora of the Sacramento Valley and Sierran foothills.

ACKNOWLEDGMENTS

The cooperation, encouragement, and advice of John Thomas Howell, Rupert Barneby (who helped with the Latin), James Hickman, and Lowell Ahart are all greatly appreciated. I am especially appreciative of the drawings done by Julia Larke.

LITERATURE CITED

BARNEBY, R. C. and E. C. TWISSELMANN. 1971. Notes on *Loeflingia* (Caryophyllaceae). Madroño 20:398–408.

CHAUDHRI, M. N. 1968. A revision of the Paronychiinae. Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 285:1–440.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley, CA.

(Received 5 March 1984; accepted 19 July 1984.)

CHROMOSOME COUNTS IN SECTION *SIMIOLUS* OF THE GENUS *MIMULUS* (SCROPHULARIACEAE). X. THE *M. GLABRATUS* COMPLEX

ROBERT K. VICKERY, JR., STEVEN A. WERNER, DENNIS R. PHILLIPS,
and STEVEN R. PACK
Department of Biology, University of Utah,
Salt Lake City 84112

ABSTRACT

Chromosome numbers were ascertained from aceto-carmine squash preparations for members of the *Mimulus glabratus* complex that had been little studied previously. Representative populations of *M. glabratus* var. *fremontii* from Chihuahua, Durango, and Baja California Sur were found to have $n = 15$ chromosomes. Populations from Colombia, the disjunct South American range of *M. glabratus* var. *glabratus*, have $n = 31$ chromosomes. Populations from Peru of *M. andicolus* and *M. pilosiusculus* have $n = 46$. An intergrading population between *M. glabratus* var. *glabratus* ($n = 31$) and *M. andicolus* ($n = 46$) was found at Pasto on the southern border of Colombia.

This cytological study is an integral part of our long-range, experimental studies on the evolution of species in *Mimulus* (Vickery 1950, 1964, 1978). The chromosome counts here reported are for populations of the *M. glabratus* complex of related species—*M. glabratus* H.B.K. (and its varieties), *M. andicolus* H.B.K., and *M. pilosiusculus* H.B.K. Not only do these counts help provide baseline data for the larger project, but they are of intrinsic interest for a better understanding of this highly polymorphic and plastic complex.

MATERIALS AND METHODS

The study populations sampled areas of the Western Hemisphere range of the complex that had been little studied previously (McArthur et al. 1972, Vickery 1978), although they represent some of the main taxa comprising the complex (Table 1). Cultures of 20 to 30 plants of each population were grown in the University of Utah greenhouse.

The chromosome counts were obtained from aceto-carmine squash preparations of pollen mother cells as before (Mia et al. 1964, McArthur et al. 1972). Twenty or more cells were studied from five or more plants of the culture of each population. Representative cells were recorded with sketches, camera lucida drawings or photographs (Fig. 1).

MADROÑO, Vol. 32, No. 2, pp. 91–94, 26 April 1985

TABLE 1. CHROMOSOME COUNTS IN THE *Mimulus glabratus* COMPLEX OF RELATED SPECIES AND VARIETIES. All populations, except as noted, were collected by R. K. Vickery, Jr. and grown under his culture numbers. Vouchers are in the Garrett Herbarium of the University of Utah (UT).

Mimulus glabratus var. *fremontii* (Bentham) Grant. $n = 15$

Cuauhetemoc, Chihuahua, Mexico, 2060 m, culture no. 12183; Aldama, Chihuahua, Mexico, 1150 m, culture 12185; Durango, Durango, Mexico, 1677 m, culture 12215; San Bertola Oasis, Baja California Sur, Mexico, 75 m, culture 12223.

Mimulus glabratus H.B.K. var. *glabratus*. $n = 31$

Sierra de Toluca, Toluca, Mexico, 2830 m, culture 7306; Duitama, Dept. Boyaca, Colombia, 2760 m, culture 13021; Aquitania, Dept. Boyaca, Colombia, 2975 m, culture 13026; Lago Tota, Dept. Boyaca, Colombia, 3010 m, culture 13029.

Mimulus andicolus H.B.K. $n = 46$

Río Grande, Dept. Ancash, Peru, 3000 m, culture 13066 (*Emma Cerrate de Ferreya #6547*); Anta, Dept. Cuzco, Peru, 3468 m, culture 13096 (Leonardo Flórez 3/7/81).

Mimulus andicolus H.B.K. × *M. glabratus* H.B.K. var. *glabratus*. $n = 40–48$

Pasto, Dept. Nariño, Colombia, 2750 m, culture 13033 has $n = 40–48$ typically, but ranges from $n = 31$ to $n = 55$ chromosomes (the median is between $n = 44$ and $n = 45$).

Mimulus pilosiusculus H.B.K. $n = 46$

Thermas Baños de Yura, Dept. Arequipa, Peru, 2475 m, culture 13069; Bolneario Tingo, Dept. Arequipa, Peru, 2250 m, culture 13070; Chilina, Dept. Arequipa, Peru, 2350 m, culture 13071.

RESULTS AND DISCUSSION

Mimulus glabratus var. *fremontii* (Benth.) Grant has the diploid $n = 15$ chromosome number (see Table 1 and Vickery 1978) throughout its range from eastern Canada to western Mexico, except for a single questionable $2n = 28$ count from Manitoba (Löve and

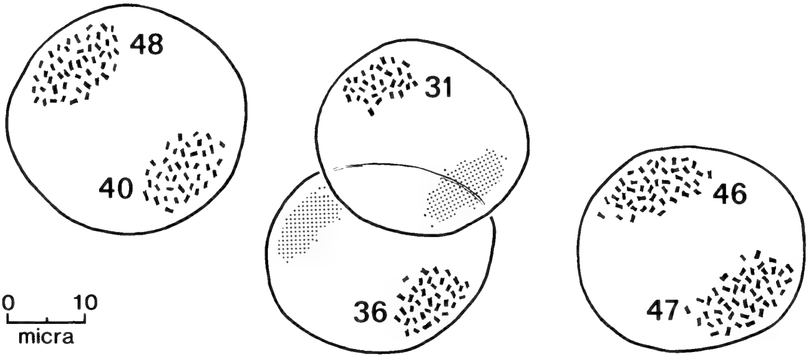


FIG. 1. Anaphase I configurations of pollen mother cells from plants of the intergrading population from Pasto, Colombia (culture 13033).

TABLE 2. CHROMOSOME COUNTS OBSERVED IN POLLEN MOTHER CELLS OF THE PASTO, COLOMBIA, POPULATION (13033) OF *M. andicolus* H.B.K. × *M. glabratus* H.B.K. var. *glabratus*.

Chromosome number, n =	Number of cells observed	
31	1	
35	1	
36	2	
37	1	
39	1	
40	8	
41	4	
42	3	
44	7	median
45	5	
46	10	
47	6	
48	4	
51	1	
53	1	
55	1	
	56	

Löve 1982) and except for populations in the Rio Grande drainage, where *M. glabratus* var. *fremontii* has the tetraploid $n = 30$ chromosome number (McArthur et al. 1972). The present study shows that the pervasive $n = 15$ chromosome number occurs also in the populations of the geographic races of the Chihuahuan desert of northern Mexico (Table 1, e.g., culture numbers 12183, 12185) and of the Mexican Mesa Central (e.g., culture number 12215) as well as in the distinctive erect, delicate but wiry form from a palm oasis (San Bertola) of southern Baja California (culture number 12223). The last mentioned is suggestive of the typically erect and branched form of the tetraploid, $n = 30$ populations of *M. glabratus* var. *fremontii* from Texas. Except for the erect, more or less wiry forms that probably represent separate taxa, the rest of the *M. glabratus* var. *fremontii* group constitutes a diploid, polymorphic complex of geographic races and sibling species separated by an intricate network of partial to complete barriers to gene exchange (Vickery 1978).

Mimulus glabratus var. *glabratus* has the aneuploid tetraploid chromosome number, $n = 31$, both in its Meso-American range in Mexico and Guatemala (e.g., culture 7306 and see Vickery 1978) and in its South American range in Colombia (e.g., culture numbers 13021, 13026, 13029). *Mimulus glabratus* var. *glabratus* appears to intergrade morphologically and chromosomally with the Ecuadorian and Peruvian *M. andicolus* ($n = 46$) in the southern Colombia population (culture 13033) near Pasto. The chromosome numbers we observed in microsporocytes of this population ranged from $n = 31$

to $n = 55$ (Table 2). The median number of chromosomes fell between $n = 44$ and $n = 45$. This suggests to us that the chromosome number is truly lower and variable, as well as showing aberrant segregations, such as 45/47, 44/48, etc., from the normal hexaploid $n = 46$ chromosome number of *M. andicolus.* The Pasto population appears to be closer to *M. andicolus* than to *M. glabratus* var. *glabratus* both chromosomally and morphologically. We found, as expected from earlier work (Vickery 1978), that our two populations of *M. andicolus* (cultures 13066 and 13096) from central Peru were $n = 46$.

Lastly, we found three populations (cultures 13069, 13070, 13071) of *M. pilosiusculus* from southern Peru to have $n = 46$ chromosomes. These counts agree with our earlier reports (McArthur et al. 1972, Vickery 1978) for related forms from farther south in Argentina and Chile.

Thus, this study fills in several important geographic lacunae—Chihuahua, Baja California, Colombia, Peru—in the north-to-south series of polyploid and aneuploid adaptive radiations of the *Mimulus glabratus* complex (Vickery 1978).

ACKNOWLEDGMENTS

We thank the Biomedical Research Support Program, grant S07-RR07092, and the National Science Foundation, grant DEB 79-11554, for their support of this project.

LITERATURE CITED

LÖVE, A. and D. LÖVE. 1982. *In* A. Löve, ed., IOPB chromosome number reports LXXV. Taxon 31:324–368.

MCARTHUR, E. D., M. T. ALAM, F. A. ELDREDGE II, W. TAI, and R. K. VICKERY, JR. 1972. Chromosome counts in section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). IX. Polyploid and aneuploid patterns of evolution. Madroño 21: 417–420.

MIA, M. M., B. B. MUKHERJEE, and R. K. VICKERY, JR. 1964. Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). VI. New numbers in *M. guttatus, M. tigrinus* and *M. glabratus.* Madroño 17:156–160.

VICKERY, R. K., JR. 1950. An experimental study of the races of the *Mimulus guttatus* complex. Proc. 7th Int. Bot. Cong. Stockholm, p. 272.

———. 1964. Barriers to gene exchange between members of the *Mimulus guttatus* complex (Scrophulariaceae). Evolution 18:52–69.

———. 1978. Case studies in the evolution of species complexes in *Mimulus.* Evol. Biol. 11:405–507.

(Received 20 July 1984; accepted 30 October 1984.)

THE IDENTITY OF *CRACCA* BENTHAM (FABACEAE, ROBINIEAE) IN THE UNITED STATES

MATT LAVIN
Department of Botany, University of Texas,
Austin 78712

ABSTRACT

The identity and circumscription of species of *Cracca* Bentham in the United States are confused in the literature. As clarified herein, two species of *Cracca*, **C. glabella** (Gray), comb. et stat. nov. and *C. sericea* (Gray) Gray, occur in the United States, where they are restricted to oak woodlands and associated grasslands of southeastern Arizona.

Cracca Bentham is composed of approximately 27 species found from sea level to high elevations along the Andean cordillera of northern Argentina to Colombia, in Central America, and through Mexico to the United States in southeastern Arizona. The genus includes large shrubs, subshrubs and herbaceous forms, and is closely allied to *Coursetia* DC.

The genus *Cracca* Bentham has been beset by much taxonomic and nomenclatural confusion since its erection by Bentham in 1854 (see Wood 1949 and White 1980). Unknown to Bentham, Linnaeus (1753) had also proposed a genus *Cracca,* comprising six species now included in *Tephrosia.* The work of Alefeld (1862) and subsequent work of Kuntze (1891) established *Cracca* Bentham as a later homonym. *Benthamantha* Alefeld was erected to include those species of *Cracca* Bentham, and *Cracca* L. was used to incorporate the species of *Tephrosia* Persoon. This latter arrangement was followed by botanists such as Rydberg (1924) during the early 1900s. Eventually, *Cracca* Bentham was conserved over *Cracca* L. (Taxon 8:293, 1959), and *Tephrosia* was reinstated to include Linnaeus's species of *Cracca.*

Compounding the nomenclatural problems is the fact that the species of *Tephrosia* Persoon and *Cracca* Bentham are superficially very similar, belonging to two closely related tribes, the Tephrosieae and Robinieae, respectively. Many species of *Cracca* Bentham are filed in herbaria under "barbistyled" *Tephrosia,* and various species of *Tephrosia* are filed under *Cracca.* Important morphological features that distinguish the two genera are summarized as follows:

Inflorescences of axillary racemes with 1 flower per node, never

MADROÑO, Vol. 32, No. 2, pp. 95–101, 26 April 1985

terminal; wing petals free from the keel; mature pod partitioned; leaflets stipellate, venation reticulate . . *Cracca* Bentham

Inflorescences of terminal and/or axillary pseudoracemes with 2–3 flowers per node; wing petals lightly adherent to the keel; mature pod not partitioned; leaflets not stipellate, venation penniparallel . . . . *Tephrosia* Persoon

The two most important features distinguishing the two genera are the position of the inflorescence and the number of flowers per node. These are two important systematic characters that distinguish the tribe Tephrosieae from Robinieae.

The circumscription and nomenclature of the two species in the United States have also been unsettled since Gray (1853) described *Cracca edwardsii* from a plant collected "Near Monterey [sic], Mexico, Dr. Edwards, in herb. Torr." and from plants collected by Charles Wright in Arizona. The one species of *Cracca* that occurs naturally in the Monterrey area is identical to the lectotype (NY!, designated by Rydberg 1924) of *C. edwardsii* and belongs to a species complex confined to northeastern Mexico (Coahuila, San Luis Potosi, Tamaulipas, Veracruz and Hidalgo). It is quite distinct from the two species that occur in southern Arizona and northwestern Mexico. Gray, however, reported *C. edwardsii* from southern Arizona and northern Sonora, having confused Charles Wright's collection *963* (number assigned by Gray) with *C. edwardsii.* A further complication arose when Gray distributed Wright's collections because *Wright 963* actually consisted of two taxa of *Cracca,* neither of them *C. edwardsii.* Later, Gray (1882) rectified this oversight by describing the vars. *sericea* and *glabella* of *C. edwardsii,* but he lacked sufficient material to distinguish between the species of Arizona and Monterrey. As a result, the majority of the specimens of the genus *Cracca* from Arizona have the wrong name applied to them.

Rydberg (1924) treated the genus *Cracca* Bentham as *Benthamantha* Alefeld, a later synonym, and listed *Benthamantha wrightii, B. edwardsii,* and *B. glabella* from the United States. He treated *Cracca sericea* as a synonym of *C. edwardsii.*

Kearney and Peebles (1960) omitted *Cracca sericea* from their treatment. They listed *Cracca edwardsii* from Arizona and treated *C. glabella* as a variety of *C. edwardsii.* They also state that the two Arizona taxa intergrade with each other. Based on personal preliminary field and herbarium studies, this condition is not known to occur, and I am unaware of any definite references to intergradation between these taxa other than the vague one in Kearney and Peebles.

Wiggins (in Shreve and Wiggins 1964) also treated the genus *Cracca* Bentham as *Benthamantha* Alefeld. He did not mention *Cracca sericea* in the text but listed *B. edwardsii* and treated *B. glabella* as a variety of *B. edwardsii.*

More recently, Kartesz and Kartesz (1980) listed only *Cracca caribaea* from the United States; *C. glabella* and *C. sericea* were omitted from their work altogether. *Cracca caribaea,* a widespread weed, is not known from the United States but gets as close as southern Tamaulipas and southern Baja California.

Actually, only *Cracca sericea* and *C. glabella* occur in the United States, where they are restricted to the pine-oak woodlands and associated grasslands of southeastern Arizona (Santa Rita Mts. to the Chiricahua Mts.). They are distinct species that do not intergrade and belong to two separate phyletic lines within the genus. *Cracca sericea* is closely allied to the widespread, lowland *C. caribaea* and belongs to a group of *Cracca* that has an erect habit, tap roots, and relatively few, large, elliptic leaflets. In fact, if it were not for the tannin deposits on the leaflets and racemes congested above the leafy portions of the plant, *C. sericea* would be almost indistinguishable from *C. caribaea.*

Cracca glabella, on the other hand, belongs to the *C. pumila* complex, which is centered at high elevations in the Transverse Volcanic Axis and the Sierra Madre Occidental of Mexico. This species complex is characterized by plants with a prostrate habit, fusiform tuberous roots, and many, small, oval leaflets. *Cracca glabella* is distinguished from *C. pumila* only by its larger, yellowish flower, sericeous ovary and different pattern of tannin deposits on the lower surface of the leaflets.

Cracca glabella is remarkable in that it is one of the few herbaceous species of the genus in Mexico that has developed showy corollas, a feature more characteristic of South American craccas. The species has large, yellow flowers, and a deep reddish, relatively long-tubed calyx. It has thickenings or protuberances at the base of the banner that appear to act as nectar-guides. The filament of the vexillary stamen is thickened and clasped by the well developed auricles of the basal portion of the staminal tube. *Cracca glabella* is thus quite distinctive compared to most other Mexican species of *Cracca,* which are predominantly self-fertile and have flowers that are inconspicuous and/or predominantly cleistogamous.

In essence, to regard these two taxa as synomymous, or as mere varieties, obscures or ignores phylogenetically important characters of the genus.

Cracca edwardsii, in contrast, is a small, erect subshrub with fusiform tuberous roots and leaves lacking tanning deposits. The inflorescences are reduced and do not overtop the leafy portion of the plant. Additionally, the flowers are very small, inconspicuous and cleistogamous. It inhabits dry, limestone foothills of the Sierra Madre Oriental.

Key to species of *Cracca* Bentham in the United States

Stems prostrate, decumbent; roots fusiform tuberous; leaflets ovate-elliptic, rounded at both ends, (9–)11–21 per leaf, largest leaflets 7–15 × 4–7 mm, adaxial surface glabrate, rarely lightly sericeous, abaxial surface sericeous but with hairs restricted to leaf margins and main veins; abaxial calyx lobes at least 4 mm long; all petals yellow, banner commonly with a reddish mid-vein; ovary sericeous; leaflet tannin deposits (evident upon aging or drying) restricted to veins of abaxial surface; stipels minute, rarely to 1 mm .... *C. glabella*

Stems erect, from a taproot, roots not tuberous; leaflets elliptic, acute at both ends, 7–13 per leaf, largest leaflet 14–28 × 6–14 mm, adaxial surface evenly sericeous, occasionally glabrate in older leaves, abaxial surface evenly to densely sericeous; abaxial calyx lobe to 3.5 mm long; banner reddish-pink, whitish at base, wings and keel whitish; ovary glabrous, granuliferous; leaflet tannin deposits (evident upon aging or drying) restricted to the center of the leaflet on the abaxial surface; stipels 0.5–1.5 mm long, rarely minute .... *C. sericea*

Cracca glabella (Gray) Lavin, comb. et stat. nov.—*Cracca edwardsii* Gray var. *glabella* Gray, Proc. Am. Acad. Arts 17:201, 1882.—*Benthamatha grayi* Alefeld var. *glabella* (Gray) Britton & Baker, J. Bot. 38:19, 1900.—*Benthamantha glabella* (Gray) Rydb., North American Flora 24:247, 1924.—*Benthamantha edwardsii* (Gray) Rose var. *glabella* (Gray) Wiggins, Veg. and Flora Sonoran Desert. Vol. 1:690, 1964.—TYPE: hills between the Barbocomori and Santa Cruz [the Huachuca Mts., Arizona], 23 Sep, 1851. *C. Wright 963* p.p. Lectotype (designated by Rydberg 1924): US!; isotypes: MO! NY! UC! US!.

Cracca glabella is restricted to pine and pine-oak forests at high elevations (2000–2200 m) in the Huachuca (Lanner and Garden Canyons), Chiricahua (Rucker Valley) and Patagonia Mountains of southeastern Arizona and the Sierra Madre of west-central Chihuahua. It flowers from July through September. Only five collections of *Cracca glabella* are known from Arizona; the most recent collection is from 1928. It may have been eliminated from the Arizona flora by overgrazing. Based on preliminary investigations, the genus is very sensitive to the pressures of grazing.

Gray (1853), in his original description of *Cracca edwardsii,* stated that the collections made by Wright were from "Valleys in the mountains between the San Pedro and the Sonoita, Sonora (in flower and with young fruit); and on hills between the Barbocomori and Santa Cruz (with ripe pods): Sept. (963)." The collection "in flower and with young fruit" is of *Cracca sericea,* whereas the collection "with ripe pods" is of *C. glabella.* Wright's collection numbers, for what were obviously two separate collections, were discarded by Gray, who distributed both collections under a new number, *963.* This practice has been documented by McKelvey (1955) and Johnston (1940):

> Not only did Gray ignore Wright's field-numbers but he also frequently united and distributed under a single distribution number, two or even more collections which Wright had collected under different field-numbers, frequently at distant stations and at different seasons. If Gray thought two or more of Wright's collections represented the same species and if there was any advantage in uniting them, he did so regularly without scruples.

Cracca glabella was first collected in September, 1851 by Charles Wright (no. *963*) in southeastern Arizona. Gray (1882), in his original description, cited one additional collection by Lemmon in 1881. Although Wright's collection consists of both *C. glabella* and *C. sericea,* Rydberg (1924) indicated the collections of Wright as type for *C. glabella* when he stated the type locality to be "hills between the Barbocomori [Arizona] and Santa Cruz, Sonora." This is the same locality that Gray (1853) indicated the plants to have ripe pods, and these plants correspond precisely with *C. glabella* in the mixed Wright collection *963.*

The exact locality at which Wright first collected *C. glabella* can be deduced from the protologue combined with Wright's field notes. It was most likely collected on 23 September 1851, as Wright went around the north end of the Huachuca Mountains, leaving the Barbocomori River drainage and starting down into that of the Santa Cruz River. Johnston (1940) says that Wright's collections dated September 23 were probably all collected before he reached Santa Cruz and probably all from within present day Santa Cruz County, Arizona. This is supported by the herbarium record, which documents *C. glabella* as occurring only at relatively high elevations in southeast Arizona and west-central Chihuahua. Suitable habitats are missing in Sonora near Santa Cruz.

Cracca sericea (Gray) Gray, Proc. Am. Acad. Arts 19:74 (1883) 1884. —*Cracca edwardsii* Gray var. *sericea* Gray, Proc. Am. Acad. Arts 17:201, 1882.—*Brittonamra sericea* (Gray) Kearney, Trans. N.Y. Acad. Sci. 14:32, 1894.—*Benthamantha sericea* (Gray) Britton & Baker, J. Bot. 38:19, 1900.—TYPE: Santa Rita Mts., Arizona, 6 May, 1881. *C. G. Pringle 292.* Lectotype (here designated): GH!; isotypes: F! NY!.

Benthamantha wrightii Rydberg, North American Flora 24:246, 1924. TYPE: between San Pedro River and the Sonoita [River, east side of the Huachuca Mts., Arizona]. *C. Wright 963* p.p. Holotype NY!; isotypes: UC! US!.

Cracca sericea inhabits moderate elevations (1300–1900 m) in southeastern Arizona, northeastern Sonora, central and western Chihuahua, and northern Sinaloa and Durango. It flowers from July to September and occasionally in the spring (March through May) during wet years. One of the more abundant species of *Cracca, C. sericea* is a conspicuous understory member of oak woodlands and associated grasslands of this area and, in typical form, has conspicuous reddish-flowered racemes that overtop the leaves. Tannins, which are evident on the older leaflets and dried herbarium specimens, are deposited centrally in each leaflet, a pattern unique to this species.

Cracca sericea was first collected, along with *C. glabella,* by Charles Wright (no. *963*) in September, 1851, in southeastern Arizona. Gray included these combined collections as syntypes of *C. edwardsii* in his original description of that species. Thirty years later, Gray (1882) recognized that some of the Arizona collections were different from the type of *C. edwardsii* and named these var. *sericea* and var. *glabella.* Later, Gray (1884) raised var. *sericea* to the species rank as more collections became available for comparison.

Gray (1882) based var. *sericea* on *Pringle 292* from the Santa Rita Mts. and *Lemmon "136 & 588"* from Spring Creek Canyon of the Santa Catalina Mts. The latter collection consists of a single sheet and although Rydberg designated (on the herbarium sheet) *Lemmon "136 & 588"* as type of *C. edwardsii* var. *sericea,* an account was never so published. The sheets of *Pringle 292* are a bit more numerous and the specimen at GH is annotated by Gray. This collection is, therefore, designated as the type.

Rydberg (1924) also based *Benthamantha* (=*Cracca* Bentham) *wrightii* on *Wright 963.* The collection, as mentioned earlier, contains two distinct species. Rydberg expressly distinguished between the two on the pertinent sheets and his intention, therefore, is obvious. His designation of the type locality is that given by Gray (1853), but one qualification is needed here. Gray understood this locality to be between the "San Pedro" and the "Sonoita" in Sonora. The "Sonoita" Wright referred to is a river that drains the east slope of the Huachuca Mts. (Johnson 1940). If Wright's path is retraced, the locale between the San Pedro River and the Sonoita River lies roughly near the northeast end of the Huachuca Mts. in Arizona. It is possible to narrow the collections down to three of Wright's collection numbers, but as with *Cracca glabella,* the real collection number may never be known.

ACKNOWLEDGMENTS

I thank Dr. R. C. Barneby and my colleagues at TEX for helpful suggestions and the curators of the following herbaria for loans: ARIZ, ASU, CAS, CHAPA, COLO, F, ISC, GH, LL, MEXU, MICH, MO, NMC, NY, TEX, UCB, UNM, and US.

LITERATURE CITED

ALEFELD, F. 1862. Namensanderung zweier Leguminosen-Gattung. Bonplandia 10: 264.

Bentham, G. 1854. *In* G. Bentham and A. Oersted. Leguminosae Centroamericanae. Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn. 1853 (Nr. 1–2): 1–19.

Gray, A. 1853. Plantae Wrightianae. Texano-Neo-Mexicanae. Part II. Smithsonian Contr. Knowl. V, Art. 6. Oct. 1952.

———. 1882. Contributions to North American botany. Proc. Am. Acad. Arts 17: 199–230.

———. 1884. Contributions to North American botany. Proc. Am. Acad. Arts 19: 1–96.

Johnston, I. M. 1940. Field notes of Charles Wright for 1849 and 1851–1852, relating to collections from Texas, New Mexico, Arizona and adjacent Sonora and Chihuahua. A copy with commentary by I. M. Johnston, Feb., 1940 (Unpubl. manuscript at TEX).

Kartesz, J. and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Vol. 2. Univ. North Carolina Press, Chapel Hill.

Kearney, T. H. and R. H. Peebles. 1960. Arizona flora (2nd ed.) with supplement. Univ. California Press, Berkeley.

Kuntze, O. 1891. Rev. Gen. 1:164–165.

Linnaeus, C. 1753. *Cracca. In* Species Plantarum 2:752.

McKelvey, S. D. 1955. Botanical exploration of the Trans-Mississippi West, 1790–1850. The Arnold Arboretum of Harvard University, MA.

Rydberg, P. A. 1924. Robinianae. North American Flora 24:220–249.

Shreve, F. and I. L. Wiggins. 1964. Vegetation and flora of the Sonoran Desert. Vol. 1. Stanford Univ. Press, Stanford, CA.

White, P. S. 1980. Flora of Panama—Fabaceae: *Cracca.* Ann. Missouri Bot. Gard. 67:596–599.

Wood, C. E. 1949. The American barbistyled species of *Tephrosia* (Leguminosae). Contr. Gray Herb. 170:193–384.

(Received 27 July 1984; accepted 30 November 1984.)

A NEW SUBSPECIES OF PERENNIAL *LINANTHUS* (POLEMONIACEAE) FROM THE KLAMATH MOUNTAINS, CALIFORNIA

T. W. Nelson
P.O. Box 6435, Eureka, CA 95501

R. Patterson
Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Abstract

Linanthus nuttallii subsp. **howellii** Nelson & Patterson is described from the serpentine soil of the southern Klamath Mountains of California. It is near *L. nuttallii* subsp. *nuttallii* and subsp. *pubescens* morphologically, differing by its smaller leaf lobes as well as dense pubescence.

During a recent expedition by the first author to the southernmost portion of the Klamath Mountains in Tehama County, California, an unusual population of perennial *Linanthus* was noticed. Further field investigation and examination of herbarium material support the taxonomic distinctness of this population, and it is herein proposed as a new subspecies.

Linanthus nuttallii Milliken subsp. **howellii** Nelson & Patterson, subsp. nov.

Caules, folia et calyces dense brevisetosi; folia divergens ad levitor arcuata, 5–7 partita, segmenta 3.5–7 mm longa; pollinis grana 34–36 μm; chromosomatum numerus $2n = 18$ (Fig. 1).

Herbaceous perennial from woody root crown; stems reclining to slightly ascending at tips, forming a compact mat 7–19 cm in diameter, 4–8 cm high, densely gray pubescent, the trichomes short-bristly; internodes 3–9(–12) mm long; leaves opposite, divergent to slightly arcuate, palmately partite into 5–7 narrowly oblanceolate divisions, 3.5–7 mm long, the trichomes short-bristly, mostly spreading at right angles to the leaf surface; flowers sessile to subsessile in dense subcapitate clusters; calyx narrow-campanulate, trichomes short-bristly, the lobes lanceolate-subulate, pungent, 7–11 mm long; corolla funnelform, white with yellow throat, 8–11 mm long, densely white villous on exterior, the tube included in the calyx; stamens inserted at base of the throat, included to barely exserted;

Madroño, Vol. 32, No. 2, pp. 102–105, 26 April 1985

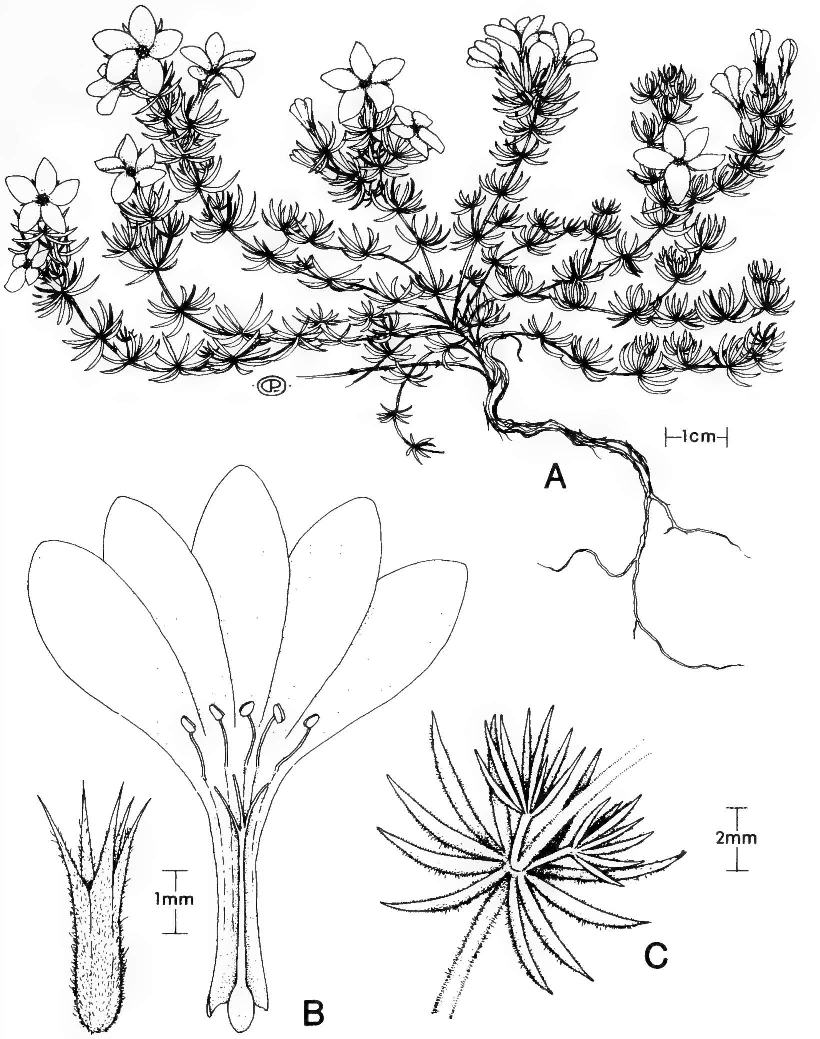


FIG. 1. *Linanthus nuttallii* Milliken subsp. *howellii* Nelson & Patterson. A. Habit. B. Perianth with corolla opened. C. Node showing leaf detail. From *Nelson and Nelson 5847*.

pollen grains 34–36 μm in diameter, yellow; chromosome number $2n = 18$. Flowering period is from June to early July.

TYPE: USA. California. Tehama Co., w. side of Mt. Tedoc along NF road 45, ca. 1.5 miles n. of Tedoc Gap, Yolla Bolly Quad. T28N, R9W, Sec. 28, 1500 m, 22 Jun 1980, *Nelson and Nelson 5847* (Holotype: CAS; isotypes: GH, HSC, MO, NY, OSC, SFSU, WTU).

PARATYPES: USA. California. Tehama Co., nw. side of Tedoc, 16

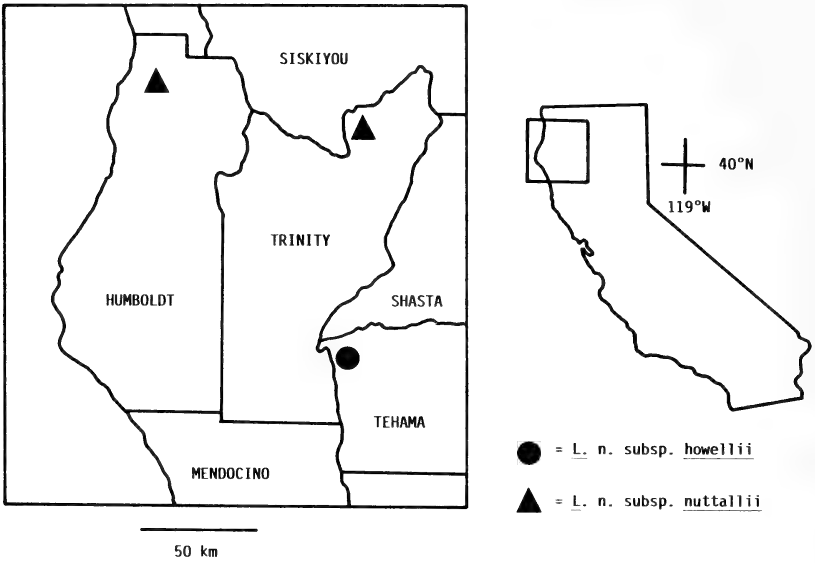


FIG. 2. Map showing distribution of *Linanthus nuttallii* subsp. *howellii* and *L. nuttallii* subsp. *nuttallii* in northwestern California.

Jun 1972, *Stebbins s.n.* (JEPS); slopes of Tedoc Mtn., Tedoc Gap road, 30 Jun 1974, *Lester 338* (HSC); along Tedoc road ca. 10 mi from junction with State route 36, 21 Jul 1978, *Nelson and Nelson 4441* (HSC); along forest road 45 at milepost 11, 25 Jun 1975, *Nelson and Nelson 4930* (JEPS); along forest road 27N13 2.5 mi s. of Tedoc Gap, 1 Jul 1983, *Nelson and Nelson 7436* (CAS); along forest road 27N13 0.7 mi s. of junction with forest road 27N12, 1 Jul 1983, *Nelson and Nelson 7437* (BYU, JEPS, NY, MO); along forest road 27N12 0.3 mi from junction with forest road 27N13, 1 Jul 1983, *Nelson and Nelson 7438* (DAV, RSA).

Distribution. Linanthus nuttallii subsp. *howellii* is apparently very rare. It is limited in distribution to Mt. Tedoc and immediate vicinity in the southernmost Klamath Mountains of western Tehama County, California, at elevations of 1500–1800 m (Fig. 2). It represents the southernmost extension of perennial *Linanthus* in the North Coast Ranges. It is disjunct from the nearest population of subsp. *nuttallii* by 90 km. It is found on serpentine soil in association with Jeffrey pine woodlands where it is often a common understory species.

Linanthus nuttallii subsp. *howellii,* although similar in most features to the other perennial taxa in the genus, is easily distinguished by its low-growing habit, short leaf lobes and dense short-bristly indumentum on stems, leaves and calyces. Typical subsp. *nuttallii* is usually less hairy overall and possesses longer ((6–)10–32 mm) leaf lobes; subsp. *pubescens,* which is considerably disjunct, generally possesses longer leaf lobes. The newly described species, as are most narrow endemics, is noteworthy for being much less variable morphologically than the other subspecies of *L. nuttallii.*

Pollen grain diameter in subsp. *howellii* presents an additional intriguing problem. The grains of diploid perennial taxa have diameters ranging from 23–28 μm, whereas those of related tetraploid taxa measure 33–38 μm (Patterson 1977). Pollen grains of subsp. *howellii* measure 34–36 μm, well within the range of tetraploid perennials; however, subsp. *howellii* is diploid. This seeming discrepancy cannot be explained readily, and it points out the difficulty in relying on pollen grain diameter measurements in determining polyploid level.

The discovery of the disjunct Tedoc Mountain populations of subsp. *howellii* and the apparent restriction to serpentine soil may be important in interpreting the nature of the entire perennial species complex. Throughout its range, this complex (Sect. *Siphonella*) occurs as a series of disjunct populations, sometimes separated from the nearest population by only a few kilometers. This pattern is suggestive of a formerly more continuous range that has subsequently fragmented. There is no evidence supporting great vagility in perennial *Linanthus* species; hence it is unlikely that the Tedoc populations result from "long" distance dispersal. A possible explanation for the distribution seen is that populations of perennial *Linanthus* represent relict stands that persist due to special features of a given region. Perhaps near Tedoc the ability to survive on serpentine soil allows *Linanthus nuttallii* to persist in this part of its range, some distance south of its nearest population. While this hypothesis is highly speculative it may be worth future study in this group.

The new subsp. of *Linanthus nuttallii* is named for John Thomas Howell, long a student of the California flora and worker with plants of the Tedoc region

ACKNOWLEDGMENTS

Appreciation is extended to Jane Nelson, Chris Bern, and Barbara Williams for their assistance in the field, and to the curators of CAS, DS, JEPS, and UC for facilitating access to herbarium material.

LITERATURE CITED

PATTERSON, R. 1977. A revision of *Linanthus* sect. *Siphonella* (Polemoniaceae). Madroño 24:36–48.

(Received 3 October 1984; accepted 3 December 1984)

THE MISSING FRÉMONT CANNON—AN ECOLOGICAL SOLUTION?

Jack L. Reveal
RBR & Associates, Suite 904, Centre City Bldg.,
233 A St., San Diego, CA 92107

James L. Reveal
Department of Botany, University of Maryland,
College Park 20742

Abstract

Donald Jackson and Mary Lee Spence (1970) proposed that the cannon John Charles Frémont abandoned on 29 January 1844 is to be sought in the Mill Creek Canyon area of the Sierra Nevada, while Ernest Allen Lewis (1981) suggests the site was on an unnamed peak ("Mt. 8422") above West Walker River in the Sweetwater Mountains of northern Mono Co., California. Both suggestions fail to account fully for the descriptive details given in Frémont's 1845 report, especially as they relate to geological, ecological, topographic and vegetational features. We propose that Frémont's men abandoned his twelve-pound howtizer in a cache near the base of a steep hill a short distance north of Cottonwood Meadow along Cottonwood Creek in northwest quarter of Sec. 23, T.7N., R.23E. This site is on the western edge of the Sweetwater Mountains in the Toiyabe National Forest.

On 29 January 1844, John Charles Frémont and his men abandoned a small cannon on the western edge of the Sweetwater Mountains in northern Mono County, California. The fate of this twelve-pound mountain howitzer[1] has been the subject of several local legends, sought after for years, had geographical place-names assigned to areas where the cannon was believed to have been left, and has been discussed in numerous articles (e.g., Jackson 1967, Russell 1957) and two recent books (Jackson and Spence 1970, Lewis 1981). Lewis tells an appealing story of the Frémont cannon and of certain other cannons that were not Frémont's but proclaimed by museums and assorted charlatans to be the very one that he transported to California. In our opinion, both books fail to present a realistic view of the probable route of the Frémont (1845) expedition on the critical days of 26–29 January, when the howitzer was abandoned. We propose an alternative route and suggest a probable site where it was left.

On 26 January, Frémont and Kit Carson made a reconnaissance of the country that lay ahead of the party. The expedition was camped just downstream from the junction of the East Walker River and Swauger Creek, about four miles north of the present-day town of

---

Madroño, Vol. 32, No. 2, pp. 106–117, 26 April 1985

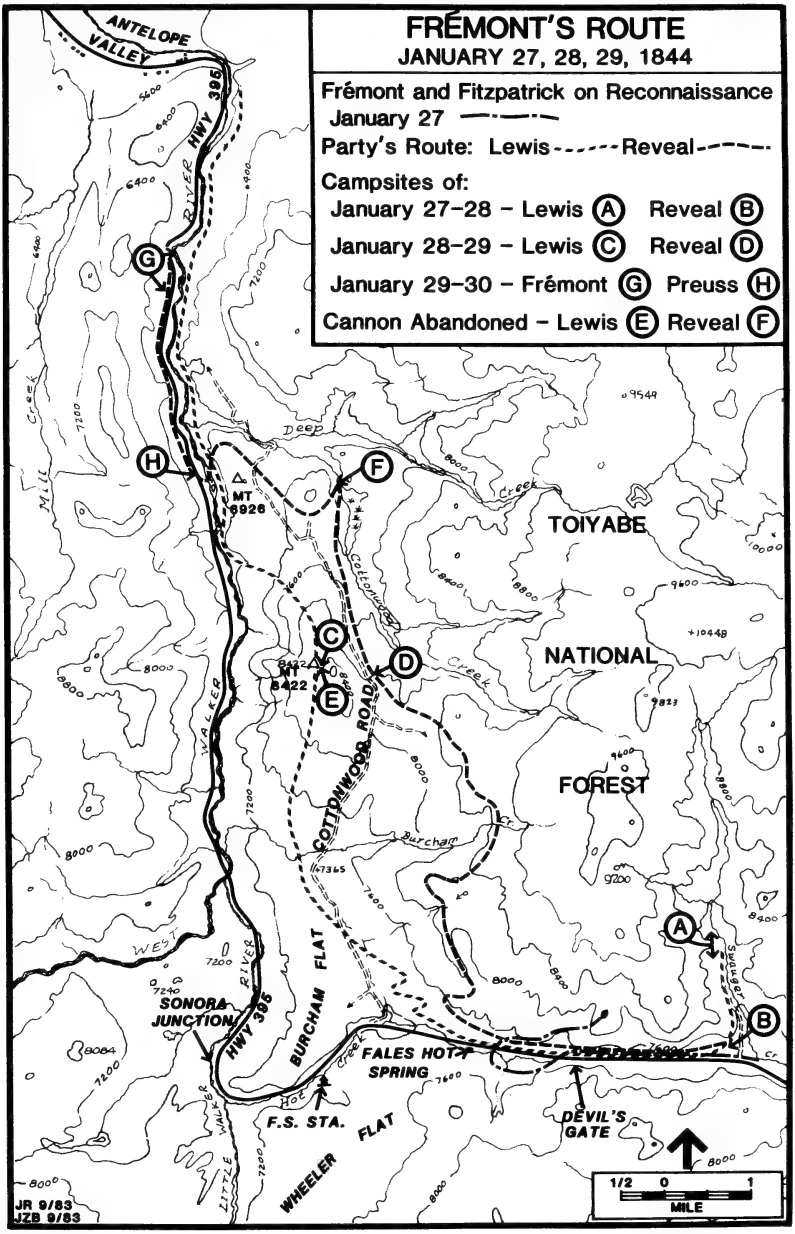


FIG. 1. Frémont's route, 27–29 January 1844.

Bridgeport.[2] Frémont wrote that "one of its branches [East Walker River]" was "coming directly from the south," and the other branch [Swauger Creek], "issued from a nearer pass, in a direction S. 75° W., forking [into Robinson and Buckeye Creeks] at the foot of the mountain, and receiving part of its water from a little lake."[3] Frémont and Carson went up Swauger Creek and entered Huntoon Valley probably on the north side of the creek just northwest of the former Bridgeport Ranger Station. Frémont states that they went in a "northwesterly direction up the valley [Huntoon], which here [at Huntoon Campground] bent to the right . . . . The little stream grew rapidly smaller, and in about twelve miles we had reached its head,[4] the last water coming immediately out of the mountain on the right [south flank of the Sweetwater Mountains]; and this spot we selected for our next encampment [Fig. 1]." Later, Frémont wrote: "To the left, the open valley [Pimentel Meadows] continued . . . forming a beautiful pass [Devil's Gate] . . . which we deferred until the next day . . . ."

On 27 January, Frémont and Thomas Fitzpatrick went quickly ahead leaving Carson to follow with the camp. The two men traveled rapidly up Huntoon Valley and "Arriving at the head of the stream, we began to enter the pass—passing occasionally through open groves of large pine trees [*Pinus jeffreyi*], on the warm side of the defile [north side of Pimentel Meadow, or the south-facing slope] . . . . Continuing along a narrow meadow [Pimentel], we reached in a few [two] miles the gate of the pass [Devil's Gate], where there was a narrow strip of prairie, about fifty yards wide."

Frémont and Fitzpatrick passed through Devil's Gate and onto the headwaters of Hot Creek in the West Walker River drainage. "On either side [of Devil's Gate] rose the mountains, forming on the left [Bush Mountain] a rugged mass, or nucleus, wholly covered with deep snow, presenting a glittering and icy surface. At this time, we supposed this [Devil's Gate, the Sweetwater Mountains to the north and crest of the Sierra Nevada extending southward] to be the point into which they [the mountains] were gathered between the two great rivers [San Joaquin and Sacramento], and from which the waters flowed off to the [San Francisco] bay. This was the icy and cold side of the pass [they were on the west side] . . . . On the left, the mountains [Mahogany Ridge] rose into peaks; but they were lower and secondary, and the country had a somewhat more open and lighter character. On the right were several hot springs [Fales Hot Springs]."

As Frémont and Fitzpatrick moved into the area where the hot springs would have been seen on the right, they were almost a mile west of Devil's Gate and three-tenths of a mile east of Fales Hot Springs. In going through Devil's Gate, which is a massive granodiorite outcrop, Frémont was impressed "by the majesty of the mountain, along the huge wall of which we were riding." Frémont next states: "Here there was no snow [we believe "here" means the hot springs area]; but immediately beyond was a deep bank [into the meadow below the north edge of Wheeler Flat], through which we dragged our horses with considerable effort. We then immediately struck upon a stream [Hot Creek], which gathered itself rapidly, and descended quick; and the valley [of Hot Creek] did not preserve the open character of the other side [e.g., Huntoon Valley on the east or "other" side of Devil's Gate], appearing below to form a cañon."

Frémont then writes that they "climbed one of the peaks on the right, leaving our horses below; but we were so much shut up, that we did not obtain an extensive view." We believe the men climbed the steep ridge north of the present U.S. Highway 395 on the northwestern edge of Devil's Gate (Fig. 1). Here they would not have had an "extensive view." Frémont wrote that the "valley of the stream [Hot Creek] pursued a northwesterly direction, appearing below to turn sharply to the right, beyond which further view was cut off." From their likely vantage, the rim of Burcham Flat would have cut off the Sonora Junction area and the West Walker River as it flows from Pickle Meadows to the west. Frémont would have seen Hot Creek flowing westerly, then making a sharp turn to the right and going north into West Walker Canyon.

Jackson and Spence suggest the men climbed a peak called Mt. 8422 some three miles north of Burcham Flat (Fig. 1), and some five airline miles north-northeast of Sonora Junction. This is exceedingly unlikely since Mt. 8422 provides an excellent vista of much of the region. Lewis is of the opinion the men climbed "the steep escarpment up to Burcham Flat." Looking at Lewis's map, we believe he places their climb at a point above the gauging station some 1.2 mi north-northeast of Sonora Junction. Had this been the case, Frémont would have seen the West Walker River coming down from the Sierra Nevada. As no mention is made of this river (nor is it shown on Preuss's maps of the region made for Frémont's report), it is unlikely they were ever aware of this important branch of the Walker River.

Frémont states that after viewing the countryside from his vantage point he "resolved to continue our road the next day down this valley, which we trusted still would prove that of the middle stream between the two great rivers [San Joaquin and Sacramento]." It was clear to any observer that the crest of the Sierra Nevada to the west would not have allowed a river to flow through to the Pacific. Frémont was looking for the fabled Buenaventura River, and he hoped the small stream he was on was one of its headwaters and that by following this stream to the north he would find his way through the Sierra Nevada. From Frémont's view of the territory beyond Devil's Gate, the valley of Hot Creek and its "right" turn, West

Walker Canyon, would certainly have been an attractive route. By cutting across the eastern edge of Burcham Flat, as he would the following day, Frémont could avoid deep snow and the impassability of Walker River Canyon.

Frémont completes his report of the day by saying that toward "the summit of this peak, the fields of snow were four or five feet deep on the northern side . . . ." At that time of the year, these conditions would surely apply to the summits above Devil's Gate, and equally be true of Burcham Flat and Mt. 8422.

The camp that evening was established on the north side of Pimentel Meadow at the point where Swauger Creek enters Huntoon Valley (Fig. 1). The slopes on both sides of Swauger Creek are south-facing and essentially devoid of conifers. The sagebrush (*Artemisia tridentata*) covered slopes were nearly snow-free and likely harbored some grass for the animals. Lewis is of the opinion Frémont established his camp "one or two miles up the canyon [of Swauger Creek] from U.S. 395." The aspen (*Populus tremuloides*) dominated canyon floor with conifers interfingering onto the bottom-lands would have been heavily choked with snow. Passage up and into such a canyon would have been difficult. The north–south trending exposures would not have afforded pasture for the party's horses and mules.

The events of 28 January are only briefly described by Frémont. The camp went through Devil's Gate and traveled twelve miles, making camp "on a high point where the snow had been blown off, and the exposed grass afforded a scanty pasture for the animals." During the day, the "snow and broken country together made our travelling difficult: we were often compelled to make large circuits, and ascend the highest and most exposed ridges, in order to avoid snow, which in other places was banked up to a great depth." Jackson and Spence are of the opinion that Frémont crossed the West Walker River and climbed up onto an 8600-foot peak in the Sierra Nevada south of Grouse Meadow on the west side of West Walker Canyon and south of Mill Creek. Frémont does not report crossing any river, nor is such a crossing shown on Preuss's maps.

In graphic terms, Lewis (p. 99) describes the party's journey of 28 January. He tells how Frémont and his men nearly exhausted themselves climbing steep embankments and criss-crossing exposed ridges to reach the south end of Burcham Flat by early afternoon. The actual topography along this route, however, belies his description. Burcham Flat is only about 150 feet higher in elevation than Hot Creek at Wheeler Guard Station, and just east of this Forest Service post there is a shallow draw where the party could easily have ascended onto the flat. Above that point, the elevation between the stream's edge and that of the flat is even less. Lewis's map shows the Frémont route as turning northwestwardly at Fales Hot Springs (where access to the flat is not difficult and thus contradictory of his text), crossing the middle of Burcham Flat, and climbing the south slope of Mt. 8422, where a camp was established "in the saddle near the top of the mountain."[5]

We agree that Frémont, to avoid deep snow, had to ascend the highest and most exposed ridges. Our proposed route (Fig. 1) accepts Frémont at his word. Our experience with Burcham Flat in the winter indicates that the snow on the flat would have been deep and the area difficult to traverse. The terrain over which Frémont would have passed as suggested by Lewis is shown in two photographs on page 92 of his book. They depict a fairly moderate slope over a distance of two miles. The average gradient is only ten percent between Burcham Creek (7400 ft) and the saddle of Mt. 8422. The topography to the east and north of the flat, where we believe the expedition traveled, is one of "exposed ridges" and "steep ascents" compelling "large circuits" which fits Frémont's characterization of his travel that day.

Lewis places Frémont's camp in a small saddle on his Mt. 8422 above West Walker River. We believe Frémont came around toward "Mt. 8422" from the southeast, following the ridges, and camped in the saddle east of the mountain at Cottonwood Pass.

The Cottonwood Pass camp for the night of 28–29 January might have been in the pass itself, where the prevailing winds would have exposed some grass for the animals, or in a somewhat more protected site less than half a mile to the east. At the latter place, the snow might have been deeper, but the camp would have had some protection from the wind. There was ample firewood in both sites consisting mainly of aspen and Rocky Mountain juniper [*Juniperus scopulorum*]. Frémont speaks of the camp having "scanty pasture" for his animals, and this leads us to suggest the camp was in the pass.[6]

The campsite suggested by Lewis is exposed and without tree cover, an unlikely camp for Frémont to have selected given the protection and cover provided at Cottonwood Pass. The rocky saddle proposed by Lewis does harbor some grass, but the swale, in our opinion, would have been covered with deep snow and thus what grass might have been present would have been buried. The pass could have been seen by Frémont even if he had traveled northward across Burcham Flat as suggested by Lewis. Looking at "Mt. 8422" from the south, Cottonwood Pass is clearly observable. The small saddle on the western slope can be seen as well, but Cottonwood Pass, at 8066 ft elevation, is certainly a more inviting campsite than the western saddle on "Mt. 8422," nearly 250 ft higher.

Frémont reports that they "did not succeed in getting the howitzer into camp" the evening of the 28th, and thus a party was sent back on the 29th to get it. Some time was required to "bring up the gun . . . ." While this was being done, Frémont, Fitzpatrick "and a few men" left the camp and "followed a trail down a hollow where the Indians had descended, the snow being so deep we never reached the ground . . . when we reached a little affluent to the river at the bottom, we suddenly found ourselves in presence of eight or ten Indians."

If Frémont was on the Sierra Nevada above Grouse Meadows as proposed by Jackson and Spence, he would have had to cross the meadows before descending Mill Creek and encountering the Indians. Frémont makes no mention of this large expanse of several hundred acres. The campsite suggested by Jackson and Spence is some twelve miles from the Swauger Creek campsite on a straight line path down Hot Creek, across West Walker River and up to the saddle above Grouse Meadows. Because Frémont states his route was circuitous, the Jackson and Spence route seems unlikely. The route we propose from the Swauger Creek camp to the Cottonwood Pass camp measures closer to ten miles than twelve, which suggests Frémont's actual route was even more circuitous than we have indicated.

Lewis states that Frémont and his men "rode down the north face of the mountain along a gradual trail to the [West Walker] river." No such route is described by Frémont.

It is unlikely that the local Indians would have established a trail along the north slope and ridge of "Mt. 8422" as proposed by Lewis. It is more likely the trail was through the pass and down the hollow to Cottonwood Creek, the approximate route of today's Cottonwood Road, and that this was the trail followed by Frémont in the belief that it would lead to Indian villages in the valley [Antelope Valley] he had seen from the vicinity of his encampment.[7] While it is true one can see more of Antelope Valley to the north from the upper reaches of "Mt. 8422," the western slopes of the valley can still be seen from Cottonwood Pass. Likewise, a walk from the pass toward the summit of "Mt. 8422" would not have been too difficult. From there Frémont would have had an excellent view of Antelope Valley, as suggested by Lewis.

We believe the "little affluent" Frémont mentions is Cottonwood Creek. Lewis believes the "little affluent" is an unnamed spring and runoff channel found on the northwest side of Mt. 8422. Lewis's map shows Frémont's route as along the western edge of "Mt. 8422" and the ridge (not on the crest of the ridge, as given in the text) going toward an unnamed mountain peak illustrated as similar in size to "Mt. 8422." Because no such mountain is to be found, we suspect Lewis's unnamed peak is Mt. 6926, a point south of Deep Creek on the ridge north of Mt. 8422. On the western slope between elevations 8422 and 6926 is an intermittent stream that reaches the West Walker River at Toll House Campground. This is on the route suggested by Lewis and we believe is what he illustrates as the "little affluent."

Frémont presented gifts to the several Indians he found "on the hill side above our heads." Such a locality description is possible for our proposed Cottonwood Creek route, and would place this incident where the canyon narrows a short distance down stream from Cottonwood Meadows at an elevation of about 7100 ft. Lewis states correctly that the upper end of his spring-fed draw is "twenty foot wide and ten foot deep." It is hardly likely that Frémont would have elected to enter such a narrow draw, especially with snow on the ground. Furthermore, it is not a place where the Indians could wait "above our heads" as stated by Frémont. The Cottonwood Creek route is much wider, with elevated slopes along both sides of the stream. If Frémont met the Indians in the canyon below Cottonwood Meadow as we suggest, where the timbered slopes are high and steep, and where the distance between the two slopes is more than one hundred feet, the Indians would have been "out of reach" and would have "thought themselves safe" as he describes.

At this point Frémont makes a critical statement regarding the fate of his howitzer: "The principal stream [Cottonwood and Deep Creeks] still running through an impracticable cañon, we ascended a very steep hill, which proved afterwards the last and fatal obstacle to our little howitzer, which was finally abandoned at this place."

Jackson and Spence are of the opinion the cannon was left on Mill Creek. An examination of the Mill Creek area provides places where Frémont could have had Indians above him and out of reach, but no steep hills that would have to be ascended on 29 January. Also, Frémont would not have found in Mill Creek an "impracticable cañon" which would have forced him to leave the drainage. Likewise, Jackson and Spence (p. 623) state that Frémont's expedition departed the mountains in Antelope Valley "which it entered from the mouth of West Walker Canyon." To accomplish this, the party would have had to climb over the high ridge separating Mill Creek and the West Walker River, an unnecessary passage and much more difficult than simply continuing down Mill Creek.

Lewis says that Frémont followed his "little affluent" down to the West Walker River. Frémont clearly does not say this. Upon seeing or perhaps learning from the Indians of the difficulties of taking animals farther down Cottonwood Creek and into Deep Creek, he "ascended a very steep hill" to get out of the "little affluent." If our route is correct then Frémont and his men turned westward where the canyon narrows below Cottonwood Meadows, and ascended the southeast-facing slope. That steep slope is covered with single-leaf pinyon (*Pinus monophylla*). There are no signs of fire and the trees are of an age estimated to be in excess of 250 years. The sideling ground and undulations in the snow would have made pulling the wheeled cannon difficult. Likewise, the descent into the Walker River Canyon along a timbered slope with a mixed stand of pinyon and Jeffrey pine (which also show signs of considerable age and no fire), would have made getting the cannon down to the river difficult. By climbing out of Cottonwood Canyon, Frémont would avoid Deep Creek Canyon, and by crossing over the ridge of his "steep hill" he could get onto a southwest-facing slope and thus avoid deep snow.

Frémont never saw the howitzer's last resting place, nor does he state in what condition it was left. Lewis speculates the cannon was left unattended at the campsite on "Mt. 8422," and that it "was a jubilant group that rode away from the little howitzer, sitting atop its carriage in a small meadow . . . ." Frémont's own words clearly refute this statement.

Frémont says that the howitzer was "left by Mr. Preuss in obedience to my orders." Lewis suggests that Carson was sent "back to the camp" with instructions to leave the cannon, but most likely Carson was put in charge of the camp party and was moving ahead of Preuss and the cannon party who were, as Frémont reports, bringing the cannon up from where it had been left the day before. We speculate that Frémont's orders, if any were actually given at the time, were to attempt to get the cannon beyond "this place," but if impossible, his men were to abandon it.[8] Perhaps a written message was left on the trail, a common practice among wilderness travelers.

Lewis recounts Preuss's dislike for the howitzer, but Frémont, if not Preuss, had a military man's attachment to the cannon (see Note 1). It is unlikely they would have abandoned such a weapon to an unknown fate. With the party were mountain-men skilled at concealing bales of fur, traps and other equipment. Because Frémont states "I reluctantly determined to leave it [the howitzer] there *for the time* [our emphasis]," it is reasonable to speculate that the howitzer was disassembled and, along with its ammunition, safely cached.

We believe the site of the cache for the cannon and its ammunition was situated near the bottom of the steep side-slopes below Cottonwood Meadow at the point Frémont abandoned Cottonwood Creek. The "very steep hill" is the one in the northwest quarter of Sec. 23, T.7N., R.23E. (Mt. Diablo Base and Meridian). It has a gradient of 30 to 35 percent, which could be considered "very steep," especially in the winter and with laden horses and mules. The soil in this area is of decomposed granite and, on the south-facing slope, it would have been easy to dig rapidly a suitable cache for the disassembled howitzer. If the cannon and ammunition had been left exposed, certainly some remains would have been discovered. Cattlemen, sheepherders and hunters could have traveled in the area unaware of a hidden cache, but if it were unburied some evidence of the cannon would have been found. We believe that downslope slough-ing of weathering rock and soil have continued to cover the cache and that this accounts for the lack of physical evidence of the cannon at this site.

After describing his ascent from Cottonwood Creek, Frémont states that "We passed through a small meadow a few miles below, crossing the river . . . and, after a few more miles of very difficult trail, issued into a larger prairie bottom, at the farther end of which we encamped, in a position rendered strong by rocks and trees. The lower parts of the mountain were covered with nut pine [*Pinus monophylla*]." He indicates that camp was established in the afternoon and in his table of distances states the party traveled seven miles this day.

The presence of single-leaf pinyon, as nut pine is now called, and the description of a "larger prairie bottom," leads us to believe that Frémont and his small party camped at China Garden, today a sagebrush flat with scattered conifers. Given the heavy grazing and other disturbances that have happened in this area since the 1890s, the grasses Frémont saw have been replaced with sagebrush and other shrubs, thus changing the vegetational characteristics of the area. We suspect that Frémont came down to the West Walker River and crossed it in the vicinity of Shingle Mill Flat.[9] This we take to be Frémont's "small meadow."

Preuss and his group did not advance as far as China Garden, "but encamped in the upper meadow," which we believe to be Shingle Mill Flat. If our route is correct, the distance from Cottonwood Pass down Cottonwood Creek, across the West Walker River, and then down the river to China Garden is seven miles as noted by Frémont. The Lewis route is only five miles, whereas that suggested by Jackson and Spence is a minimum of ten airline miles.

The events of the 29th were trying for Frémont and his men. The cannon was left not in the Sierra Nevada but on the western edge of the Sweetwater Mountains, geologically and floristically a part of the Great Basin (Cronquist et al. 1972, Harper and Reveal 1978, Reveal 1980). Lewis believes the cannon is yet to be discovered. He is probably correct. We suggest that the route proposed here (Fig. 1) best fits Frémont's own description and that the routes indicated by Jackson and Spence and by Lewis fail to account for all the factors described by him. We also suggest Frémont and his men cached the cannon and its ammunition. Perhaps the howitzer was found by Indians who moved it elsewhere or even destroyed it as local legend tells. However, some of the five hundred pounds of ammunition ought to be in the area of the original cache and likely might be discovered by a careful, and we must add, *legal* search.[10]

ACKNOWLEDGMENTS

The research reported here has been made possible in part by funds from contracts with the Toiyabe Natl. Forest for studies by the senior author on range-trend plots on the western slope of the Sweetwater Mountains in the 1980s, and by National Science Foundation grants GB-22645 and BMS75-13063 to the junior author for ongoing studies on the flora of the Intermountain West. Our initial investigations began in 1958 (the subject of a "term paper" at Sonora Union High School, California) and continued in 1960 when working for the U.S. Forest Service at Lee Vining (*pater*) and Wheeler Guard Station (*filius*). We wish to thank Joan Bonin of RECON, Inc., San Diego, California, for providing valuable assistance in preparing the map, and the Bridgeport Ranger District for use of aerial photographs. This is Scientific Article A3840, Contribution No. 6820 of the Maryland Agricultural Experiment Station.

NOTES

[1] Frémont obtained the field piece "from the United States arsenal at St. Louis, agreeably to the orders of Col. S.W. Kearney." This acquisition was deemed unnecessary by Col. J. J. Abert, head of the Bureau of Topographic Engineers, and a letter was sent to Frémont asking him to justify his actions (see Jackson and Spence 1970, for its text). According to Frémont's wife, Jessie, the daughter of Missouri Senator Thomas Hart Benton, she intercepted the letter and in a dramatic note urged her husband to depart immediately. Jackson (1967) questions that this event ever happened. Frémont clearly had no authority to request or take a field piece into Spanish California, an action that could have been considered an act of war. The howitzer was placed "under the charge of Louis Zindel, a native of Germany, who had been 19 years a non-commissioned officer of artillery in the Prussian army . . . ."

[2] The junction of the two streams (and others) is now covered by the waters of Bridgeport Reservoir.

[3] Although Frémont used the singular, we believe he is referring to Twin Lakes. Robinson Creek arises from these lakes. We are not certain how he learned of any lake, but it is possible Indians told him. The maps of the expedition do not show such a lake. Meadow irrigation in Bridgeport Valley has changed greatly the configuration of the four streams. See USGS 1911 Bridgeport Quadrangle.

[4] Lewis's map shows that Frémont and Carson rode to the little spring tributary to Swauger Creek in Sec. 8, T.6N., R.24E. This spring is at 9200 ft, 1800 ft in elevation above Pimentel Meadow. Had the men made such a difficult climb, certainly it would have been reported.

[5] Mt. 8422 as defined by Lewis (and maintained here for purposes of consistency) often refers to the entire elevated area north of Burcham Flat and west of Cottonwood Pass. USGS point 8422 on the Fales Hot Springs Quadrangle is actually a small nob above West Walker River and west of an unnamed, higher, north–south trending ridge that is approximately 8560 ft in elevation. Evidently, this higher ridge is Lewis's Mt. 8422, thereby causing some confusion in his book. When we refer only to the higher ridge and not the entire mountain top, we use "Mt. 8422." Lewis's camp was in a saddle between 8422 and 8560.

[6] An examination of our proposed campsites for this night indicates there was a much better stand of aspen/juniper in Cottonwood Pass when Frémont was there. The reduction of tree cover in the area probably has been due to livestock use and sheep trailing through the pass.

[7] Frémont describes "yellow spots" in Antelope Valley to the north. Such spots are still visible today. They are the grassy western slopes above the valley floor and west of U.S. Highway 395.

[8] Lewis suggests Frémont sent Carson back to the morning camp with his orders and that the "courier probably arrived in camp at about the same time as the cannon party returned with the cannon." There is a small basin or flat on top between Mt. 8422 and the higher ridge to the east. This was both Lewis's camp and where he suggests the howitzer was left.

[9] Preuss's maps have been criticized for their lack of details concerning the critical days of 26–30 January 1844. We disagree. Preuss's maps (see maps 3 and 5 in Jackson

and Spence) clearly show Bridgeport Valley and the route up Huntoon Valley, where the party turned westward toward Devil's Gate. Swauger Creek is shown to continue northward onto the southern flank of the Sweetwater Mountains. The mapped route shows the expedition going through the pass down to the Little Walker River, which arises from the south. West Walker River, which comes from the Sierra Nevada to the west, is not shown. The route then follows the edge of the mountains east of West Walker River, not in the mountains west of the river as suggested by Jackson and Spence. The two maps differ slightly in this respect. The 1845 map shows the route along the immediate bank of the river, making three crossings, and with two campsites shown in the canyon. On a later map released in 1848, no camps are shown, and the route is east of the river, seemingly—in part—to be in the mountains. Both maps indicate Frémont crossed the river at the mouth of the canyon, but we believe he crossed only once and then in the vicinity of Shingle Mill Flat. Lewis's map also shows a route down the east side of the river, and although his location can be supported by the Preuss maps, Frémont states he crossed the river upon reaching it. The east bank of the river defies passage today and it was probably an impossible route also in Frémont's day.

It should be noted that on 1 February, Frémont, then on the East Carson River in Carson Valley, gave his latitude as 38°37′38″. This is an error or a misprint: it should be 47′, as indicated by Preuss's maps. No doubt the confusion reported by Jackson and Spence regarding the placement of Frémont's camp this night is due to this error.

[10] Any search activity for the Frémont cannon that would involve surface disturbance, excavation or disturbance of artifacts must be authorized by an archaeological permit issued by the U.S. Forest Service, the land managing agency, via U.S. Department of Interior under the provisions of the National Antiquities Act of 1906 and the Archaeological Resources Protection Act of 1979 [16 U.S.C., Sec. 470aa, et seq.].

Literature Cited

Cronquist, A., A. H. Holmgren, N. H. Holmgren, and J. L. Reveal. 1972. Intermountain flora. Vascular plants of the Intermountain West, U.S.A., Volume one. Hafner Publ. Co., NY.

Frémont, J. C. 1845. Report of the exploring expedition to the Rocky Mountains in the year 1842, and to Oregon and North California in the year 1843–1844. Gales and Seaton, Washington, D.C. 693 pp.

Harper, K. T. and James L. Reveal, eds. 1978. Intermountain biogeography: a symposium. Great Basin Naturalist Mem. 2:1–268.

Jackson, D. 1967. The myth of the Frémont howitzer. Bull. Missouri Hist. Soc. 23:205–214.

——— and M. L. Spence. 1970. The expeditions of John Charles Frémont. Volume 1. Travels from 1838 to 1844. Univ. Illinois Press, Urbana.

Lewis, E. A. 1981. The Frémont cannon high up and far back. Arthur H. Clark Co., Glendale, CA.

Reveal, J. L. 1980. Intermountain biogeography—a speculative appraisal. Mentzelia 4:1–92.

Russell, C. P. 1957. Frémont's cannon. California Hist. Quart. 36:359–363.

NOTES AND NEWS

INHIBITION OF *Abies concolor* RADICLE GROWTH BY EXTRACTS OF *Ceanothus velutinus*.—*Ceanothus velutinus* Dougl. ex Hook is a major shrub species that invades recently burned areas and clearcuts at middle elevations in the Sierra Nevada, California, where it competes strongly with natural and planted conifer seedlings (Conard and Radosevich, Forest Sci. 28:243–304, 1982; Zavitkovski et al., J. For. 67:242–245, 1969). Establishment of natural *Abies concolor* (Gord. & Glend.) Lindl. seedlings in brush fields with a high cover of *Ceanothus velutinus* is frequently spotty, and many established seedlings appear somewhat unhealthy for several years. The earlier study by Conard and Radosevich was concerned primarily with competitive interactions. Chemical (allelopathic) effects, however, are also a possible partial explanation for reduced growth of conifers in the presence of *Ceanothus velutinus.* To investigate this possibility, I conducted a series of laboratory and growth chamber experiments.

Methods. The first two experiments compared germination and growth of *Abies concolor* seedlings under *Ceanothus velutinus* canopies and without *Ceanothus* canopies. Seeds were germinated in 1.4-liter pots containing either a 20- to 25-cm tall *Ceanothus* seedling or no seedling (control). Pots were filled with potting mix (1:1:: peat:sand plus balanced fertilizer). Twenty *Abies* seeds were placed in each pot, with two pots per treatment. Seeds were watered regularly with distilled water. Seeds in the *Ceanothus* treatment were watered through the shrub canopy. To minimize potential moisture competition, the soil was kept near field capacity at all times in both treatments. Both experiments were conducted in a controlled environment chamber (23°C day, 10°C night, 16-h photoperiod). Average daytime light intensity was 0.6 mmol m^{-2} sec^{-1}.

In the first experiment, germination was recorded after 1 month, and a random sample of eight seedlings selected from each treatment was measured for root and shoot length. In the second experiment, the treatments were the same as those described, except that the seedlings were grown for 7 weeks, at the end of which germination and survival were recorded. This experiment was repeated three times, with two pots per treatment each time.

On the basis of the results of these first two experiments, and of a series of extremely inconclusive experiments that had been designed to look at possible effects of *Ceanothus* root exudates on *A. concolor* seedlings (S. Conard, unpubl. data), I hypothesized that the *Ceanothus* foliage was the most likely source of allelopathic compounds. To test this hypothesis, I conducted two additional experiments to examine more closely the effects of *Ceanothus velutinus* foliage extracts on radicle growth of germinating *Abies concolor* seeds. Leaf extracts were prepared by soaking crushed, fresh-frozen *Ceanothus* foliage for 1 h in enough distilled water to cover the leaves. Leaves and water were placed in a Waring blender (trade names are used for information only; no endorsement by the U.S. Department of Agriculture is implied) for 3 min. The resulting mixture was strained through cheesecloth and vacuum-filtered through Whatman No. 1 filter paper to remove suspended solids. The osmolality of these extracts was measured with a vapor pressure osmometer (Wescor, Model 5130) to determine if observed effects could be attributed to osmotic potential of the extracts. Extracts were stored in the refrigerator for up to 2 weeks until use.

In one experiment, standard glass-chromatography plates were covered with chromatography filter paper that had been moistened and rolled to remove air bubbles. Plates were set on an angle in covered plastic trays with their bottom edges in 250 ml of either *Ceanothus* extract or distilled water. A row of five *Abies concolor* seeds was placed 2.5 cm from the top edge of each plate. On half of the plates, seeds were

---

MADROÑO, Vol. 32, No. 2, pp. 118–121, 26 April 1985

covered with a 2.5-cm wide strip of chromatography paper moistened with distilled water. Each of the four treatment combinations was replicated twice. Radicle growth and germination were recorded 10 and 22 days after the beginning of the experiment, which was conducted at room temperature (20° to 25°C) in indirect sunlight in the laboratory.

In a second similar experiment, seeds were germinated in 1-pint plastic freezer containers. A 1-cm thick pad of open-cell foam placed in the bottom of each container was covered with a square of chromatography paper cut so it could be folded over the edges of the foam to contact the bottom of the container and act as a wick for treatment solutions. Nine seeds of *Abies concolor* were placed in a square grid in each container. The same two treatment solutions were used in this experiment as in the previous one. To minimize fungal attack, 10 mg captan was added per 450 cc of each treatment solution. Twenty ml of the appropriate treatment solution was added along the edges of each freezer container after the foam pad and seeds were in place. Containers were covered with plastic wrap and placed on a windowsill in the laboratory. Each treatment was replicated three times. Germination, radicle growth, emergence of cotyledons, and evidence of fungal attack or root dieback were recorded 21 days after the start of the experiment.

Results of all experiments were analyzed by analysis of variance. In experiments with more than two treatments, the least significant difference (LSD) was used to compare treatments. Arcsine square-root transformations were applied to percentage data where appropriate.

Germination. Germination of seeds grown with *Ceanothus* and watered through their canopies averaged 47%. This germination was not significantly different (paired $t = 0.1727$, $df = 3$) from germination in control pots (45%). I also observed no significant differences in germination among treatments in either the chromatography plate bioassay or the foam pad bioassay, where germination averaged across treatments was the same (78% ± 4 SD) for both experiments. Germination percentages observed in the two bioassay experiments ranged from 60 to 89%. Because treatments appeared not to affect germination, seeds that did not germinate were omitted from calculations of growth parameters.

Survival. Although treatments did not affect germination, they substantially affected survival after 7 weeks. The survival rate of *Abies* seedlings grown in pots with *Ceanothus* (0.20 ± 0.02 SE) was significantly lower ($p < 0.005$) than survival of seedlings grown in the same soil without *Ceanothus* (0.81 ± 0.06 SE).

Radicle growth. The germinated *Abies* seedlings that were harvested in the first experiment showed dramatically different patterns of root growth, despite nearly identical shoot growth (Table 1). I also observed that the roots of seedlings that had been germinated in pots with *Ceanothus velutinus* were withered and broke off readily, whereas roots of the controls were healthy. With chromatography plate and foam pad bioassays I more closely evaluated the possible effects of *Ceanothus* foliage extracts on root growth of germinating *Abies* seedlings in the absence of potentially confounding variables such as moisture competition, shading, and root exudates. In the chromatography plate bioassay, radicle growth of germinated *Abies* seeds averaged 126.8 ± 3.6 mm for the control and 71.2 ± 1.2 mm for the control with filter paper strips. Values for the comparable treatments with *Ceanothus* extract were 45.4 ± 0.1 mm for the control and 55.6 ± 11.8 mm for the control with filter paper strips. All differences, except between the two extract treatments, were statistically significant at the 0.1 level or greater.

The foam pad bioassay produced similar results, with average radicle growth of 5.3 ± 0.6 mm for seeds exposed to the *Ceanothus* treatment and 41.9 ± 3.8 mm for seeds exposed to the distilled water treatment. The extract treatments showed highly significant decreases ($p < 0.001$) in radicle growth compared with those of the control. No differences were observed among treatments in the degree of fungus attack (range = 3–16%) or the number of radicles with tip dieback (16–25%). Significantly more of

TABLE 1. STEM AND ROOT GROWTH OF *Abies concolor* SEEDLINGS GROWN FOR 1 MONTH IN POTS WITH OR WITHOUT *Ceanothus velutinus* (±ONE STANDARD ERROR).

Treatment	Stem length (cm)	Root length (cm)
Ceanothus	3.3 ± 0.3	2.4 ± 0.2
Control	3.5 ± 0.3	11.4 ± 0.4

the seedlings in control treatments, however, had cotyledons emerged at the end of the experiment (44%) than those in the *Ceanothus* extract treatment (0%). The osmolality of *Ceanothus* extract used in these experiments was 77 ± 1 mOS/kg (about -1.8×10^{-3} MPa). It is unlikely, therefore, that osmotic potential of the solutions affected the results to any great degree.

Discussion. The results of these experiments suggest the possibility of an allelopathic inhibition of radicle growth of *Abies concolor* seedlings by *Ceanothus velutinus.* At least one compound (cinnamic acid), found by Craig et al. (Phytochemistry 10:908, 1971) in the leaves of *C. velutinus* has been implicated as inhibiting seedling growth in some species (Rice, E. L., 1974, Allelopathy, Acad. Press, NY, p. 256). Further experiments are required to isolate the causes of the responses described here and to determine whether extracts of foliage and litter produced under field situations are sufficiently concentrated and persistent to have measurable effects. If responses similar to those described here are observed in the field, *Ceanothus velutinus* may be expected to affect adversely the natural regeneration of *Abies concolor*—especially in dry years or in other situations where rapid root growth could be critical to seedling survival.—SUSAN G. CONARD, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S.D.A., 4955 Canyon Crest Dr., Riverside, CA 92507. (Received 16 Feb 1984; accepted 30 Oct 1984.)

PITFALLS IN IDENTIFYING *Ventenata dubia* (Poaceae).—The annual Eurasian grass species *Ventenata dubia* (Leers) Coss. & Dur. appears to be expanding its range in the Pacific Northwest, and botanists who may encounter it need to be aware of some pitfalls in making a correct identification of this potential weed. Its occurrence as an adventive species in Idaho and Washington was first reported by Baker (Leafl. Western Bot. 10:108–109. 1964), and it was subsequently described and illustrated by Hitchcock et al. (Vasc. Pl. Pac. N.W. 1:724. 1969). A recent collection from Polk County (*Halse 2857,* 21 Jun 1984, OSC) documents its invasion of the Willamette Valley in western Oregon. The spread of *V. dubia* by human agency may accelerate if it becomes a contaminant of the various crop grasses grown for seed in the Pacific Northwest.

Ventenata is generally considered to be taxonomically allied with *Trisetum* and *Avena* (Hackel, The true grasses, Henry Holt and Co., 1890, p. 121; Bews, The world's grasses, Longmans, Green and Co., 1929, p. 174). The two upper florets of its 3-flowered spikelets are fertile; as commonly occurs in members of tribe Aveneae, these lemmas bear a conspicuous dorsal, geniculate awn. The lowest floret, however, is usually staminate, and its lemma has a straight terminal awn, as is found in various members of tribes Poeae, Brachyeltreae, Stipeae, etc. This floret is incorrectly described as awnless by Gould and Shaw (Grass systematics, Texas A&M Univ. Press, 1983, p. 179) and Hackel (op. cit.). Both glumes are shorter than the first lemma, and disarticulation occurs in the rachilla above the lowest floret.

Because the dorsally-awned florets are shed at maturity and the terminally-awned one is retained within the glumes, this grass is deceptive when presented for identification in post-mature condition. It convincingly mimics a 1-flowered member of tribes like Stipeae or Eragrosteae, whose genera may have terminally awned lemmas and relatively short glumes. The deception is increased when, as sometimes happens, a caryopsis is formed in the lowest floret. Distinctive features of the species are its conspicuously 7-nerved glumes and smooth, obconical pedicels. Probably the best protection against being fooled by this grass, when it has shed its dorsally-awned fertile florets, is simply to be aware of the problems described here. I hope that this note will save others the several hours I wasted trying to identify this species before serendipitously discovering the cause of the difficulty.—KENTON L. CHAMBERS, Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331. (Received 31 October 1984; accepted 3 December 1984.)

NOTEWORTHY COLLECTIONS

ARIZONA

ANTENNARIA MICROPHYLLA Rydb. (ASTERACEAE).—Coconino Co., San Francisco Mt., ridge between Agassiz and Humphreys Pks., fellfield, 3658 m, 28 Jul 1983, *J. D. Morefield 1563 and C. G. Schaack* (DHA); *Schaack 1182 and J. D. Morefield* (DHA, NY). (Verified by A. Cronquist.)

Significance. New addition to the Arizona alpine. A depauperate specimen of *A. microphylla* may have been the source of McDougall's *A. rosulata* Rydb. report for the Arizona tundra (*Seed plants of Northern Arizona,* Museum of Northern Arizona, Flagstaff, 1973). The presence of *A. rosulata* in the alpine could not be confirmed in the field or herbarium (MNA) and this species should be deleted from Schaack's alpine list (Madroño 30:Suppl., p. 79–88, 1983).

AQUILEGIA CHRYSANTHA Gray (RANUNCULACEAE).—Coconino Co., San Francisco Mt., nne.-facing slope below the knob designated 3685 m (12,089 ft) on the ridge between Agassiz and Humphreys Pks., melt-water channel and alpine meadow, 3612–3627 m, 27 Aug 1983, *C. G. and B. J. Schaack 1167 and J. D. Morefield* (DHA).

Significance. New addition to the Arizona alpine. Though identified here as *A. chrysantha,* "yellow" columbine at highest elevation, ca. 3048 m or above, often has spurs and sepals tinged blue or purple and an overall habit that differs from more typical specimens below.

CAREX HAYDENIANA Olney (CYPERACEAE).—Same site as the *A. chrysantha* collection (above), melt-water channel, ca. 3642 m, 16 Jul 1983, *J. D. Morefield 1580 and C. G. Schaack*; *C. G. and B. J. Schaack 1173 and J. D. Morefield* (DHA).

Significance. New addition to the Arizona alpine.

PINUS FLEXILIS James (PINACEAE).—Coconino Co., San Francisco Mt., ridge between Agassiz and Humphreys Pks., sw.-facing slope, ca. 3627 m, 16 Jul 1983, *C. G. & B. J. Schaack 1175 and J. D. Morefield* (DHA).

Significance. New addition to the Arizona alpine. Only a single depauperate (ca. 30 cm), individual is presently known from this area, growing with rock protection at the upper end of an open extended krummholz. Though protected, the condition of the plant suggests that prolonged survival in this rigorous environment is unlikely. Clark's Nutcracker is known for the area and periodic introduction of Limber Pine seed into the alpine is expected.

MADROÑO, Vol. 32, No. 2, pp. 121–128, 26 April 1985

Potentilla nivea L. (Rosaceae).—Coconino Co., San Francisco Mt., nw. projecting ridge of Agassiz Pk., fellfield, 3688 m, 12 Jul 1983, *C. G. Schaack 1153 and J. D. Morefield* (DHA); 0.4 mi n. of Agassiz Pk. summit on an exposed andesitic ridgetop, 3667 m, 16 Jul 1983, *J. D. Morefield 1568 and C. G. Schaack 1163* (DHA); ridge leading to the summit of Humphreys Pk., fellfield, 3780–3795 m, 27 Aug 1983, *C. G. Schaack 1194 and J. D. Morefield* (ASU, DHA, NY). (Verified by N. Holmgren.)

Significance. First AZ record. *Cannon and Lloyd s.n.* (Aug 1904) (NY) were apparently the first to collect and recognize *P. nivea* from the San Francisco Mountain (N. Holmgren, pers. comm.). This specimen was unknown to Kearney and Peebles (Arizona flora, Univ. of Calif. Press, Berkeley, 1960) and subsequent authors, and collectors using these keys identified the trifoliolate *P. nivea* with the digitate *P. concinna* Richards. *Potentilla nivea* is primarily restricted to the ridgetops within the Arizona tundra. This habitat is subject to increasing foot traffic, particularly on Humphreys Peak, where the greatest number of plants were observed. Since this species is poorly represented in the alpine, and apparently finds its southernmost North American station and only Arizona occurrence on the San Francisco Mountain, protection seems warranted.—C. G. Schaack and J. D. Morefield, Deaver Herbarium, Dept. of Biol. Sciences, Northern Arizona University, Flagstaff 86011.

Cowania subintegra Kearney (Rosaceae).—Yavapai Co., n. end of Dead Horse Ranch St. Park near Cottonwood, low calcareous mesa top on Verde Formation with *Krameria, Guttierrezia, Canotia* and *Parthenium,* ca. 1050 m: flowering and producing abundant fruit, 10 May 1984, *N. B. Herkenham s.n.* (DHA); 16 Mar 1984, *J. Anderson 84-2* (ASU). Yavapai Co., Coconino Natl. Forest, 0.5 km ne. of Bridgeport on U.S. Hwy 89A on calcareous Verde Formation, 1020 m, 23 Sep 1984, *Schaack and Schaack 1365* (DHA); 1 km n. of Bridgeport along Rocking Chair Rd., 1005 m, 23 Sep 1984, *Schaack and Schaack 1363* (DHA).

Significance. First reports for Yavapai Co., extensions of 130 km e. from the type locality in Mohave Co., and 200 km nw. from nw. Graham Co. These are the only known localities for this species, and Federal Endangered status has recently been granted. Many of the state park plants appeared to have been heavily grazed. A complex series of putative hybrids involving *C. mexicana* D. Don var. *stansburiana* (Torr.) Jeps. occurs in the Bridgeport area, and is currently under investigation by Schaack and Morefield.—Clark G. Schaack, James D. Morefield, James M. Rominger, Deaver Herbarium, Dept. Biol. Sci., Northern Arizona Univ., Flagstaff 86011; and John Anderson, Dept. Botany and Microbiol., Arizona St. Univ., Tempe 85287.

CALIFORNIA

Dedeckera eurekensis Reveal & Howell (Polygonaceae).—Mono Co., Inyo Natl. For., w. flank of White Mts. ca. 5.5 km up Coldwater Canyon on s.-sloping talus above stream with *Atriplex, Artemisia* and *Mirabilis,* 2070 m (observed to 2200 m), 19 Jun 1984, *Morefield 2126* (DHA, MICH, Morefield, NY, RSA, US); BLM land ca. 0.8 km up Coldwater Canyon on n.-sloping talus with *Petalonyx, Hecastocleis, Eriogonum* and *Pericome,* 1570 m, 19 Jun 1984, *Morefield 2132* (DHA, MICH, Morefield, NY, RENO, RSA); Inyo Co. and Inyo Natl. For., 1.9 km S45°E of Southern Belle Mine in Gunter Cr. Canyon, crevices in n.-sloping calcareous rock with *Hecastocleis, Brickellia* and *Psorothamnus,* 1570 m, 18 Jun 1984, *Morefield 2124* (DHA, KANU, MICH, MNA, Morefield, NY, RENO, RSA, UNLV, VDB), all collections in bloom. Specimens to be distributed.

Previous knowledge. Ca. 10 generally small, disjunct stands known from the Last Chance, Inyo, Panamint and White Mts., all in Inyo Co., mostly on steep, unstable carbonate cliffs and talus from 1220–2070 m (Mary DeDecker, pers. comm., 1984; Novak and Strohm, Madroño 28:86–87, 1981; Reveal and Howell, Brittonia 28:245–251, 1976).

Significance. The Coldwater Canyon specimens represent the largest continuous stand known for the species (ca. 2.5 km²), the first records for Mono Co., and an extension 12 km n. from the one small stand previously reported for the White Mts. Along with the Gunter Cr. stand (ca. 0.3 km²), the known species population is approximately tripled. *Dedeckera* remains rare throughout its range, but does not appear endangered at this time.

OPUNTIA PULCHELLA Engelm. (CACTACEAE).—Inyo Co., White Mts., BLM land 5.3 km N70°E of Antelope Spgs. along trail between Beer and Birch Cks. in Deep Springs Valley, plants in bloom on disturbed sandy flats dominated by *Hilaria jamesii,* 1560 m, 30 May 1984, *Morefield 1982* (DHA, Morefield, NY, RSA); Deep Springs Valley, 30 May 1982 (flowering), *A. C. Sanders 2464* (RSA); also observed in CA just n. of Deep Springs College (Inyo Co.) and at the mouth of McAfee Cr., e. side of the White Mts. (Mono Co.), both on disturbed sandy flats.

Significance. First records for CA, confirming Munz's (1959, p. 313) prediction, and an extension 53 km s. from the nearest known locality in NV. The species should be considered rare and endangered in CA, because all the sites found are subject to trampling during heavy grazing.—JAMES D. MOREFIELD, Deaver Herbarium, Dept. Biol. Sci., Northern Arizona Univ., Flagstaff 86011.

DALEA ORNATA (Dougl.) Eat. & Wright (FABACEAE).—Lassen Co., flats on nw. side of Shaffer Mt., 12 km nnw. of Litchfield, growing in areas of churning vertisol clay soil (T30N R14E S5), 1670 m, 7 Jun 1984, *Tiehm, Evans and Young 8592* (CAS, NY, RSA, UTC).

Significance. First record for CA and a nnw. range extension of over 110 km from the Reno, NV area. Previously known from e. WA, e. OR, sw. ID and w. NV.

IVESIA BAILEYI S. Wats. (ROSACEAE).—Lassen Co., Skedaddle Mts., Wendel Canyon, ca. 13 km e. of Wendel, growing in rock crevices along canyon walls (T29N R16E S22), 1600 m, 21 Jun 1979, *Schoolcraft 87* (NY); #2 canyon of Amedee Mt., growing in moist shade of rock crevices, 28 Jun 1983, *Schoolcraft 1032* (NY).

Significance. First record for CA and a range extension of about 50 km nw. from the Virginia Mts., Washoe Co., NV. Previously known from se. OR, sw. ID, and n. NV. We here consider var. *setosa* S. Wats. to be worthy of specific rank as *I. setosa* (S. Wats.) Rydb.—SCHOOLCRAFT and TIEHM, see note below.

NEVADA

CRYPTANTHA CELOSIOIDES (Eastw.) Pays. (BORAGINACEAE).—Washoe Co., s. side of Mahogany Mt., 1.1 km ese. of Denio Camp on n. side of Little High Rock Cr., growing on whitish ash deposits (T39N R22E S23), 1610 m, 30 Jun 1983, *Tiehm 8041* (CAS, NY, RSA, UTC).

Significance. First record for NV and a se. range extension of over 150 km from southern OR. Previously known from ND to ID and se. OR. The corollas are unusually small, being at most 6 mm broad.

ERIOGONUM CROSBYAE Reveal (POLYGONACEAE).—All from whitish ash deposits in Washoe Co., and all determined by J. L. Reveal. East of Butcher Flat (T42N R23E S36), 1700 m, 28 Jun 1983 *Lisa Ganio 95* (MARY); e. of Grassy Ranch (T41N R22E S18), 1790 m, 22 Jun 1983 *Lisa Ganio 96* (MARY); s. side of Mahogany Mt., 1.1 km ese. of Denio Camp, n. of Little High Rock Creek (T39N R22E S23), 1610 m, 30 Jun 1983, *Tiehm 8040* (CAS, MARY, NY, RSA, UTC); Granite Range, e. side of Grass Valley Cr., 3.2 km nnw. of Grass Valley Ranch (T38N R22E S32), 30 Jun 1983, *Tiehm 8043* (CAS, MARY, NY, RSA, UTC).

Significance. First records for Nevada and a sse. range extension of about 90 km. Previously known only from the type area in Lake Co., OR (Brittonia 33:442, 1981).

ERIOGONUM PROCIDUUM Reveal (POLYGONACEAE).— Washoe Co., Hays Canyon Range, near upper end of Hays Canyon, ca. 18 km e. of Eagleville, CA, growing with *Artemisia* on a small gravelly, rather barren knob (T39N, R19E, S2), 2180 m, 14 Jun 1979, *Schoolcraft 62* (MARY) (verified by J. L. Reveal); 13 Jul 1982, *Schoolcraft 781* (NY); 5 Jul 1983, *Tiehm 8056* (CAS, MARY, NY, RSA, UTC).

Significance. First records for NV and a range extension of about 30 km ese. from Modoc Co., CA. Previously known from Lassen and Modoc Cos., CA and Lake Co., OR.

IVESIA RHYPARA Ertter & Reveal (ROSACEAE).—Washoe Co., Yellow Rock Canyon area, ca. 8 km n. of Mahogany Mt., growing on steep yellowish ash deposits along canyon walls, in two separate populations (T40N R22E S1), 1640 m, 14 Jun 1983, *Schoolcraft 995* (TEX) (verified by B. Ertter); 7 Jul 1983, *Tiehm 8100* (NY).

Significance. Previously known from two areas, one in ne. Malheur Co., OR, and one in w. Elko Co., NV. This is a w. range extension of about 290 km from the Elko Co. site.

MENTZELIA PACKARDIAE Glad (LOASACEAE).—Elko Co., near the IL Ranch, growing on barren tuffaceous clay hills (T42N R50E S6), 1600 m, 15 Jun 1982, *Williams and Tiehm 82-133-1* (CAS, RENO) (verified by H. J. Thompson).

Significance. First record for Nevada and a se. range extension of about 190 km from the type area in Leslie Gulch, Malheur Co., OR.

PHACELIA THERMALIS Greene (HYDROPHYLLACEAE).—Washoe Co., 9.8 km w. of Buffalo Meadows road on Buckhorn Rd. to Ravendale, growing along a small rocky wash (T35N R19E), 1800 m, 25 Jun 1984, *Tiehm, Nachlinger and Schoolcraft 8818* (CAS, NY, RSA, UTC).

Significance. First record for NV and a short range extension w. from adjacent Lassen Co., CA. Previously known from ne. CA, se. OR, sw. ID and MT.

SCUTELLARIA HOLMGRENIORUM Cronq. (LAMIACEAE).—Washoe Co., nw. of Norton Place, growing on a rocky vertisol with *Chrysothamnus* (T34N R19E S29), 1740 m, 16 May 1984, *Schoolcraft 1167* (NY); Washoe Co., 3 km w. of Buffalo Meadows road on Buckhorn Rd. to Ravendale, plants growing in clay soil with vertisols (T35N R19E), 1550 m, 25 Jun 1984, *Tiehm, Nachlinger and Schoolcraft 8808* (CAS, NY, RSA, UTC).

Significance. First record for NV and a ne. range extension of about 24 km. Previously known only from e. Lassen Co., CA.—GARY SCHOOLCRAFT, Bureau of Land Management, 2545 Riverside Dr., Susanville, CA 96130 and ARNOLD TIEHM, New York Botanical Garden, Bronx, NY 10458.

OREGON

AMSINCKIA CARINATA Nelson & Macbride (BORAGINACEAE).—Malheur Co., ca. 7 km sw. of Harper via Hwy. 20, n. of Malheur River on low, rocky hills with outcrops of welded tuff (T20S R41E S22/23), 850–925 m, 15 Jun 1984, *Joyal 496* (OSC, NY, ORE, US); ca. 8 km sw. of Harper (T20S R41E S 22/27), 900–925 m, 16 Jun 1984, *Joyal 510* (OSC, NY, UTC, DS). Plants numerous in rocky soil of upper slopes, with *Atriplex spinosa* and *Hordeum jubatum*; *Amsinckia tessellata* occurs on lower slopes and in disturbed sites on hilltops.

Previous knowledge. Known only from the type collection, *J. B. Leiberg 2234* (isotype, OSC!), cited by Nelson and Macbride as from "Oregon: rocky soil, Malheur Valley, near Harper Ranch, alt. 1100 ft., June 10, 1896." Leiberg's specimen label, as well as his field notes (consulted courtesy of the Smithsonian Institution archives), give the elevation as "1100 m." Mentioned by Suksdorf (Werdenda 1:112, 1931), Ray and Chisaki (Amer. J. Bot. 44:530, 1957), and Cronquist (Vascular plants of the

Pacific Northwest 4:183, 1959; Intermountain flora 4:478, 1984) without citation of additional collections.

Significance. This represents the rediscovery of a species that was thought to be extinct. The species was omitted from the standard floras for the Pacific states prior to the mention by Cronquist; however, Ray and Chisaki suggested that it "appears to be a distinct and interesting species . . . not known to exist in nature today." The U.S. Fish and Wildlife Service (Federal Register 48:53643, 1983) listed *Amsinckia carinata* as a possibly extinct taxon for which more information was needed to support a proposal for endangered or threatened status. The rediscovery of populations near the type locality should make it possible to clarify the species' status under the Endangered Species Act.—ELAINE JOYAL, Dept. Botany Pl. Pathol., Oregon St. Univ., Corvallis 97331.

UTAH

ASTER SIBIRICUS L. (ASTERACEAE).—Summit Co., Uinta Mts., 19 km nw. of Kings Pk. (T2N R13E S18 sw.¼), 3140 m, with scattered Engelmann spruce, 31 Aug 1981, *Goodrich 16211* (BRY, NY). (NY collection verified by A. Cronquist.)

Significance. First record of this species for UT and a range extension of ca. 240 km s. of the nearest locale in nw. WY.

GNAPHALIUM VISCOSCUM H.B.K. (ASTERACEAE).—Uintah Co. (T1S R23E S10 se.¼), e. side of Cow Cr., 2350 m, 17 Aug 1983, *Neese 14964* (BRY).

Significance. First record of this species for UT and a range extension of ca. 280 km w. of the nearest locale in nc. CO.

DRABA DOUGLASII Gray (BRASSICACEAE).—Box Elder Co., Grouse Creek Mts., 29 km 263 degrees sw. of Rosette (T12N R17W S2 s.¼), windswept rocky ridge, 2438 m, 23 Jun 1982, *Goodrich and Atwood 17127* (BRY, GH, SSLP). (GH specimen verified by R. C. Rollins.)

Significance. First record of this species for UT and a range extension of ca. 50 km s. of the nearest locale in Twin Falls Co., ID.

ASTRAGALUS ROBBINSII (Oakes) Gray (FABACEAE).—Summit Co., Wasatch Natl. Forest, Whitney Guard Station, 38 km 52 degrees ne. of Kamas (T1N R9E S3 nw.¼), 2730 m, 15 Aug 1983, *Goodrich 19670* (BRY, NY).

Significance. First record of this species for UT and a range extension s. and w. from the Rocky Mountains of WY and CO.

RIBES LAXIFLORUM Pursh (GROSSULARIACEAE).—Juab Co., Deep Creek Mts., Thomas Cr., waterfall area, 2895 m, 20 Jun 1959, *D. W. Lindsay 279* (UT); Toms Cr., 15 km 260 degrees w. of Callao (T11S R18W S16 NW ¼), 2615 m, wet area with boulders and downed timber, Engelmann spruce-aspen community, 13 Jul 1983, *Goodrich 19052* (BRY, ID, NY, SSLP).

Significance. These specimens represent a disjunction of ca. 800 km e. from the Pacific Coast. The UT specimens seem closer to *R. l.* var. *laxiflorum* than to *R. l.* var. *coloradense* (Cov.) Jancz.—SHEREL GOODRICH, USDA For. Serv. Intermt. For. and Range Exp. Sta., Ogden, UT, stationed at Shrub Sciences Laboratory, Provo, UT 84601, DUANE ATWOOD, USDA For. Serv. Uinta Natl. For., Provo, UT 84601, and ELIZABETH NEESE, Monte L. Bean Life Science Museum, Brigham Young Univ., Provo, UT 84602.

WYOMING

ARISTIDA OLIGANTHA Michx. (POACEAE).—Weston Co., 5.6 km se. of Upton, abundant in gray shale soil in semibarren pine-prairie (T47N R64W), 1280 m, 5 Aug 1973, *Stephens 70098* (KANU).

Significance. Reported for Weston Co., WY (Barkley, T. M. 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press), but without location. A range extension of 200 km nw. from Sheridan Co., NE.

BOISDUVALIA GLABELLA (Nutt.) Walp. (ONAGRACEAE).—Campbell Co., along tributary of East Fork of S Bar Creek, ca. 13.7 air km w. of Gillette on Montgomery Rd., common in loamy clay in vernal pool (T50N R73W S29 nw.¼), 1433 m, 18 Sep 1978, *Nelson 1994* (RM); Crook Co., ca. 4.8 air km n. of Oshoto, muddy pond margin (T54N R67W S32), 1250 m, 26 Jul 1978, *Dueholm 4897* (RM).

Significance. First records for WY, a range extension of ca. 80 km w. from Butte Co., SD.

CELTIS OCCIDENTALIS L. var. OCCIDENTALIS (ULMACEAE).—Sheridan Co., Big Horn Mts., Tongue River Canyon, ca. 8 air km wsw. of Dayton, woodland with *Acer* and *Populus* (T56N R87W S10), 1371 m, 6 Sep 1933, *Stell S-1* (USFS); woodland with *Prunus* and *Rhus* (T56N R87W S8 and 9), 1463 m, 23 Sep 1935, *Dickson 401* (USFS); Tongue River Canyon Trail, population of 1–2 ha on calcareous substrate, from canyon wall to river, containing all age classes (T56N R87W S4 se.¼), 1341 m, 30 Oct 1983, *Hamann 456* (RM).

Significance. Second report of an apparently native population in WY; the other stand is in Goshen Co., ca. 410 km to the sw.

CLAYTONIA LANCEOLATA Pursh var. FLAVA (A. Nels.) C. L. Hitchc. (PORTULACACEAE).—Fremont Co., Waynes Cr., occasional at edge of meadow (T43N R105W S11), ca. 2834 m, 21 Jun 1956, *Gierisch 1877* (USFS).

Significance. First record for WY, a range extension of 185 km se. from Henry's Lake, Fremont Co., ID, the type locality. The only other known location is Anaconda, Deer Lodge Co., MT (*Blankinship 768*, RM; Henderson, D. M. 1981. *In* Vasc. Plt. Spp. of Concern in Idaho. Univ. Idaho, For. Wldlf. and Range Expt. Sta. Bull. 34).

ERAGROSTIS TRICHODES (Nutt.) Wood var. TRICHODES (POACEAE).—Goshen Co., ca. 11.2 air km nne. of Lingle, common in sandy soil on roadside (T26N R62W S10 se.¼), 1341 m, 27 Sep 1978, *Nelson 2435* (RM).

Significance. Listed as "reported" for Goshen and Laramie Cos., WY (Beetle, A. A. 1977. Grasses of Wyoming. Univ. Wyoming Agric. Expt. Sta. Res. J. 39R), but without locations. A range extension of ca. 100 km w. from Box Butte and Morrill Cos., NE.

EUPHORBIA SERPENS H.B.K. (EUPHORBIACEAE).—Crook Co., ca. 9.7 air km se. of Moorcroft, wet ditch (T49N R67W S34 and 35), 1310 m, 24 Jul 1978, *Dueholm 4696* (RM).

Significance. First record for WY, a range extension of ca. 100 km sw. from Butte Co., SD.

LARIX OCCIDENTALIS Nutt. (PINACEAE).—Teton Co., Teton Range, Darby Creek Canyon, ca. 9.7 air km sse. of Alta, in forest of *Picea* and *Pinus* (T43N R118W S22), ca. 2286 m, 4 Jul 1983, *Hartman 15720* (RM).

Significance. First record for WY, a range extension of ca. 370 km ese. from Valley Co., ID, and se. from Granite Co., MT. An apparently native stand of 14 or more trees (14–16 m in height with a DBH of 25–30 cm), extending along creek bottom for 2–3 km.

LEPTODACTYLON WATSONII (A. Gray) Rydb. (POLEMONIACEAE).—Fremont Co., Wind River Indian Reservation, vicinity of Boysen Dam, limestone rock crevices with *Lesquerella* and *Petrophytum* (T5N R6E S8), 1767 m, 23 Jun 1980, *Dorn 3458* (COLO, RM). (Determined by W. A. Weber, COLO; verified by D. Wilken, CS.)

Significance. First record for WY and a range extension ne. of ca. 275 km from Bear Lake Co., UT.

LOEFLINGIA SQUARROSA Nutt. subsp. TEXANA (Hook.) Barneby & Twisselmann (CARYOPHYLLACEAE).—Weston Co., Cambria Canyon, n. of Newcastle (T45, 46N R61W), 1300–1525 m, 29 Jul 1896, *A. Nelson 2534* (COLO, RM). (Distributed as *Gilia pungens caespitosa*; the annotation as *Leptodactylon pungens* [Torr.] Nutt. by C. L. Porter, 1968, questioned and brought to our attention by W. A. Weber, COLO.)
Significance. First record for WY, a range extension of 200 km nw. from Dawes Co., NE. Subspecies *artemisiarum* Barneby & Twisselmann is known from n.-cent. Sweetwater Co. (Barneby and Twisselmann. 1970. Madroño 20:398–408).

LINARIA CANADENSIS (L.) Dum. Cours. var. TEXANA (Scheele) Penn. (SCROPHULARIACEAE).—Campbell Co., ca. 54.4 km n. of Gillette, sandy prairie pasture, 30 Jun 1968, *Stephens and Brooks 23858* (KANU); ca. 30.6 air km nne. of Gillette, eroded slopes and drainage (T53N R71W S25), 1190 m, 21 Jun 1978, *Hartman, Dueholm and Sanguinetti 6830* (RM); ca. 18.5 air km nne. of Weston, open slopes and drainage (T55N R70W S14), 1190 m, 22 Jun 1978, *Hartman, Dueholm and Sanguinetti 6925* (RM); Cow Cr., ca. 10.5 air km s. of Weston, plains with *Artemisia* (T53N R71W S26), 1190 m, 21 Jun 1978, *Dueholm, Hartman and Sanguinetti 2394* (RM); Horse Cr. Ranch, ca. 14.5 air km nw. of Weston, plains with *Artemisia* (T55N R72W S26), 1220 m, 8 Jul 1978, *Dueholm and Sanguinetti 3544* (RM); Crook Co., ca. 27 km nw. of Belle Fourche, SD, few plants in alkaline soil in moist prairie (T56N R60W), 975 m, 8 Jul 1973, *Stephens 66672* (KANU); ca. 12.9 air km nne. of New Haven, shaley ridge with *Quercus* and *Pinus* (T56N R66W S7 and 8), 1160 m, 26 Jul 1978, *Dueholm 4991* (RM).
Significance. Reported from Campbell and Crook Cos., WY (Barkley 1977), but without location. A range extension of ca. 60 km sw. from Harding Co., SD.

MONARDELLA ODORATISSIMA Benth. subsp. GLAUCA (Greene) Epling (LAMIACEAE).—Lincoln Co., Salt River Range, head of Strawberry Cr., on w. side of pass, abundant on grassy s. exposure (T33N R117W), 2895 m, 20 Aug 1927, *McDonald 719* (USFS); ca. 9.6 air km e. of Etna, rocky se. exposure with *Balsamorhiza, Apocynum, Cirsium,* and *Pseudotsuga,* 2500 m, 27 Jul 1979, *Shultz 621* (USFS).
Significance. First records for WY, a short range extension e. from adjacent ID.

OPUNTIA MACRORHIZA Engelm. var. MACRORHIZA (CACTACEAE).—Goshen Co., 11.2 km w. of Ft. Laramie, common in valley in prairie hills (T26N R65W), 1310 m, 11 Aug 1973, *Stephens 70884* (KANU); ca. 6.4 km n. of Torrington, roadside with *Kochia, Salsola,* and *Artemisia* (T25N R61W), 1280 m, 20 Aug 1977, *Dorn 3010* (RM); along the North Platte River, ca. 1.6–2.4 air km sw. of Torrington, sandy soil in disturbed bottomland with *Tribulus* (T24N R61W S17 ne.¼), 1250 m, 26 Sep 1978, *Nelson 2379* (RM); along the North Platte Ditch, ca. 3.7 air km nw. of Torrington, common in sandy soil in upland grassland with *Andropogon* and *Panicum* (T24N R61W S5 ne.¼), 1250 m, 29 Sep 1978, *Nelson 2570* (RM); ca. 6.4 air mi nw. of Ft. Laramie, frequent on sandy gravel roadcut (T26N R64W S7 ne.¼), 1325 m, 29 Sep 1978, *Nelson 2571* (RM).
Significance. Reported from Goshen Co., WY (Barkley 1977), but without location. A short range extension w. from adjacent NE.

PECTIS ANGUSTIFOLIA Torr. var. ANGUSTIFOLIA (ASTERACEAE).—Goshen Co., on gravel hills on North Platte, ca. 19 km below Ft. Laramie, 1280 m, 30 Jul 1858, *Engelmann s.n.* (MO) (determined by D. J. Keil, OBI); Converse Co., top of prominent red clinker hill ca. 25 air km nnw. of Bill, common in coarse gravel (T40N R71W S12 e.½ of ne.¼), 1458 m, 30 Jul 1978, *Guidinger 324* (RM); ca. 25 air km

n. of Bill, scoria slopes with *Artemisia* and *Eriogonum* (T40N R70W S6 sw.¼ and S7 nw.¼), 1463 m, 3 Sep 1980, *Dorn 3673* (RM).

Significance. First records for WY, a range extension of ca. 150 km n. from Weld Co., CO.

PHYSALIS HEDERAEFOLIA A. Gray var. COMATA (Rydb.) Waterfall (Solanaceae).—Goshen Co., 6.4 km n. of Lingle, few plants in coarse gravel soil on prairie hillside (T26N R62W), 1371 m, 10 Jul 1974, *Stephens 77428* (KANU).

Significance. Reported from Goshen and Sheridan Cos., WY (Barkley 1977), but without location. A short range extension w. from adjacent NE. The record for Sheridan Co. was based on a specimen (*Stephens 69841,* KANU) of *P. heterophylla* Nees.

POTENTILLA HOOKERIANA Lehm. (ROSACEAE).—Albany Co., alpine summits, Telephone Mines (T16N R79W), 3048–3353 m, 31 Jul 1900, *A. Nelson 7877* (RM); Johnson Co., Big Horn Mts., ca. 4 km e. of Cloud Pk., alpine tundra (T51N R85W S17 and 18), 3108 m, 9 Jul 1979, *Odasz 1647a* (RM); Park Co., Beartooth Range, ridge above US 212 at MT border, alpine tundra (T58N R104W S15), ca. 3100 m, 5 Jul 1958, *Johnson 18* (RM); Teton Co., vicinity of Hoback Canyon, rocky moist hillside (T38N R115W), 2133 m, 24 Jun 1932, *Williams and Pierson 704* (RM); Hoback Canyon, s. exposure (T38N R115W), 2286 m, 24 Jun 1933, *Williams and Pierson 1164* (RM). (All except *Odasz 1647a* determined by B. C. Johnston, COLO.)

Significance. First records for WY, a range extension of ca. 300 km se. from Deer Lodge Co., MT.

RORIPPA TRUNCATA (Jeps.) R. Stuckey (BRASSICACEAE).—Goshen Co., Springer Reservoir, ca. 2.4 air km s. of Yoder, frequent in dry sandy clay on margin of reservoir with *Chenopodium, Leptochloa,* and *Spergularia* (T22N R62W S10 se.¼), ca. 1310 m, 28 Sep 1978, *Nelson 2492* (RM); Hawk Springs Reservoir, ca. 10.5 air km se. of Hawk Springs, common in dry sandy clay on margin of reservoir with *Cyperus, Eragrostis,* and *Gnaphalium* (T20N R61W S9 se.¼), ca. 1360 m, 28 Sep 1978, *Nelson 2515* (RM). (Verified by R. L. Stuckey, OS.)

Significance. Reported from Laramie Co., WY (Barkley 1977), but without location. A short range extension w. from adjacent NE.

SCIRPUS HETEROCHAETUS Chase (CYPERACEAE).—Sheridan Co., ca. 21 km e. of Leiter, abundant around prairie farm pond (T54N R76W), 1158 m, 2 Aug 1973, *Stephens 69820* (KANU).

Significance. Reported from Sheridan Co., WY (Barkley 1977), but without location. A range extension of ca. 380 km wnw. from Jackson Co., SD.

THELLUNGIELLA SALSUGINEA (Pall.) O. E. Schulz (BRASSICACEAE).—Carbon Co., ca. 38 air km sse. of Wamsutter (T16N R92W S19), 2011 m, 21 Jun 1979, *Colony Oil III A–E8* (COLO). (Determined by W. A. Weber, COLO.)

Significance. First record for WY, a range extension of ca. 300 km nw. from Park Co., CO.

VERATRUM TENUIPETALUM Heller (LILIACEAE).—Carbon Co., Sierra Madre, Hog Park Reservoir, ca. 21 air km sw. of Encampment, frequent in clay in a grassy park with *Erigeron* (T12N R84W S6 sw.¼), 2560 m, 3 Jul 1977, *Nelson and Nelson 1479* (RM); ca. 26.5 air km sw. of Encampment, springy slope (T12N R86W S1), ca. 2530 m, 18 Jul 1979, *Nelson and Blunt 4034* (RM).

Significance. First records for WY, a short range extension n. from adjacent Routt Co., CO.—RONALD L. HARTMAN, B. E. NELSON, and KEITH H. DUEHOLM, Rocky Mountain Herbarium, Dept. of Botany, University of Wyoming, 3165 University Station, Laramie 82071.

ANNOUNCEMENT

Eight Dollar Mountain, Josephine County, Oregon, USA. Eight Dollar Mountain, composed of ultramafic parent material and laterite soils, is a significant natural landmark in the Illinois River Valley of sw. Oregon. The mountain has become a source of conflict among land use planners because the soils support populations of rare plants and contain nickel and other heavy metals. Botanists want to protect the plants, miners want to surface mine, the timber industry wants to log, and ranchers want to graze cattle. The major property owners, the United States Forest Service, the Bureau of Land Management, the State of Oregon, and Josephine County, are presently attempting to develop a management plan for the area that will satisfy these diverse interests.

The mountain is the type locality for two taxa, *Hastingia bracteosa* Wats. and *Aster paludicola* Piper, and possibly a third, *Senecio hesperius* Greene. In addition, many Illinois Valley and sw. Oregon endemics (*Calochortus howellii* Wats., *Lewisia oppositifolia* (Wats.) Robins., and *Gentiana bisetacea* Howell, among others) grow on the drier slopes of the mountain or in the many fine interior-valley *Darlingtonia* bogs around its base. Eight Dollar is a botanical treasure.

To ensure that Eight Dollar Mountain remains a botanical rather than a mineral treasure, a strong case must be made for its botanical importance to the scientific community. To accomplish this I need some information. If you knew of Eight Dollar Mountain before reading this note: 1) How did you learn about the mountain? 2) Have you ever visited the mountain? If so, what was the purpose and number of your visits? This information will be summarized and passed on to the government agencies.

At least 51 taxa of plants have been described from the relatively small Illinois Valley area. Most of the species were collected by Thomas Howell between 1884 and 1887. Are there other places with that concentration of type localities, or is the Illinois Valley unique?

Please send your responses to FRANK A. LANG, Department of Biology, Southern Oregon State College, Ashland, OR 97520, USA.

ANNOUNCEMENT

INTERNATIONAL ORGANIZATION OF PLANT BIOSYSTEMATISTS

The Executive and Council of the International Organization of Plant Biosystematists (IOPB) will meet during the Third International Congress of Systematics and Evolutionary Biology, University of Sussex, Brighton, U.K., 4–10 July 1985. Anyone wishing to place an item on the agenda for discussion should write to Dr. Liv Borgen, Secretary, IOPB, Botanical Garden and Museum, Trondheimsveien 23B, N-Oslo 5, Norway.

IOPB is holding a Symposium "Differentiation Patterns in Higher Plants," Zurich, Switzerland, July 13–18, 1986. Information on participation may be obtained from the Chairperson, Dr. Krystyna Urbanska, Geobotanisches Institut, ETH, Stiftung Rubel, Zurichbergstrasse 38, CH-8044 Zurich, Switzerland.

IOPB publishes the IOPB Newsletter. Information for the IOPB Newsletter may be sent to the Editor, Dr. Krystyna Urbanska.

MADROÑO, Vol. 32, No. 2, pp. 129–130, 26 April 1985

Application forms for membership in IOPB may be obtained from the President of IOPB, Dr. William F. Grant, Department of Plant Science, P.O. Box 282, Macdonald College of McGill University, Ste. Anne de Bellevue, Quebec, Canada H9X 1C0, or by sending US $25 (for the period 1983–1987) directly to the Secretary-Treasurer of IOPB, Dr. L. Borgen.

ANNOUNCEMENT

The Shrub Research Consortium is sponsoring the fourth wildland shrub symposium August 7–9, 1985, at Snowbird Resort, near Salt Lake City, Utah. The symposium, "Plant/Herbivore Interactions," will feature invited and contributed papers on aspects of plant-animal interactions, emphasizing but not limited to vertebrate herbivores and shrub ecosystems. Contributed presentations will be 20 minutes long. The proceedings will be published. If you would like to present a paper, send a title and abstract by 15 May 1985, to: Dr. F. D. Provenza, Department of Range Science, College of Natural Resources, UMC 52, Utah State University, Logan, UT 84322. For further information about the symposium and facilities, please contact: Theresa A. Bigbie, Conferences and Workshops, Brigham Young University, 297 CONF, Provo, UT 84602, (801) 378-4903.

ERRATUM

The name *Polygonum douglasii* E. Greene subsp. *austiniae* (E. Greene) E. Murray (Kalmia 12:23. 1982) has precedence over the identical combination proposed by Hickman (Madroño 31:250. 1984).

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

VOLUME 32, NUMBER 3 JULY 1985

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES AND NEWS

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Science, San Francisco, CA 94118.

Editor—CHRISTOPHER DAVIDSON
Idaho Botanical Garden
P.O. Box 2140
Boise, Idaho 83701

Board of Editors
Class of:

1985—STERLING C. KEELEY, Whittier College, Whittier, CA
    ARTHUR C. GIBSON, University of California, Los Angeles
1986—AMY JEAN GILMARTIN, Washington State University, Pullman
    ROBERT A. SCHLISING, California State University, Chico
1987—J. RZEDOWSKI, Instituto Politecnico Nacional, Mexico
    DOROTHY DOUGLAS, Boise State University, Boise, ID
1988—SUSAN G. CONARD, USDA Forest Service, Riverside, CA
    WILLIAM B. CRITCHFIELD, USDA Forest Service, Berkeley, CA
1989—FRANK VASEK, University of California, Riverside
    BARBARA ERTTER, University of Texas, Austin

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928

First Vice President: RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

Second Vice President: DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403

Recording Secretary: VIRGIL THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: WAYNE SAVAGE, Department of Biological Sciences, San Jose State University, San Jose, CA 95192

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542; the *Editor* of MADROÑO; three elected *Council Members:* JAMES C. HICKMAN, Department of Botany, University of California, Berkeley, CA 94720; THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

THE SPECIFIC STATUS OF *LASTHENIA MARITIMA* (ASTERACEAE), AN ENDEMIC OF SEABIRD-BREEDING HABITATS

MICHAEL C. VASEY
Department of Biological Sciences, San Francisco State University,
San Francisco, CA 94132

ABSTRACT

The taxonomic status of *Lasthenia maritima* has been a subject of some disagreement largely because of the poor representation of this taxon in herbaria. The present study, based on field observation and morphological analyses of numerous additional collections, supports specific status. The closely related, self-incompatible *L. minor* occurs on mainland central California whereas the autogamous *L. maritima* primarily occupies off-shore rocks and islands inhabited by breeding and roosting seabirds from central California to northern British Columbia. Morphological comparison indicates that the two taxa differ significantly in nine out of the 12 quantitative characters that were investigated. Although the two taxa can produce relatively fertile hybrids under greenhouse conditions, they maintain a high level of reproductive isolation under natural conditions.

Lasthenia (Asteraceae: Heliantheae) is a genus of predominantly annual herbs confined largely to western North America (Ornduff 1966). It has received the benefit of a comprehensive biosystematic study (Ornduff 1966, 1976, Ornduff et al. 1974, Bohm et al. 1974, Altosaar et al. 1974) and relationships within the genus are generally well defined. One member of this genus, originally described as a species, has been relegated to subspecific status as *Lasthenia minor* (DC) Ornduff subsp. *maritima* (Gray) Ornduff. This taxon has been collected rarely and was poorly understood as a consequence of a lack of adequate material for comparative analysis. This paper presents new evidence that this taxon should be recognized at the specific level as *Lasthenia maritima* (Gray) M. Vasey.

Lasthenia maritima was originally described at the specific level by Gray (1868) and was accepted as a species by Greene (1894) and Jepson (1925). In a discussion concerning the biota of the Farallon Islands, however, Blankenship (Blankenship and Keeler 1892) observed that "Only one plant—*Baeria maritima* [=*L. maritima*]—has been long enough isolated to show variation for which specific rank has been claimed, and it is seriously questioned whether it has departed far enough from *B. uliginosa* [=*L. minor*] to be considered even a variety." These doubts concerning the status of this taxon foreshadowed its later relegation by Ferris (1955) to subspecific sta-

MADROÑO, Vol. 32, No. 3, pp. 131–142, 19 August 1985

tus, a status accepted in the most recent revision of the genus by Ornduff (1966).

Ornduff (1965, 1966), using field and experimental evidence, concluded that *L. maritima* (as subsp. *maritima*) is apparently confined to seabird-breeding habitats in California and, presumably, elsewhere throughout its distribution. At that time, *L. maritima* was known from only twelve localities over a distance of ca. 2400 km, ranging from the Farallon Islands, California (37°41′53″N, 123°00′05″W) to Triangle Island (50°52′00″N, 129°05′00″W) near the northwestern tip of Vancouver Island, British Columbia; whereas *L. minor* was known from numerous collections from both the interior and coast of mainland central California (Fig. 1). Ornduff determined that *L. minor* and *L. maritima* have $n = 4$ and are interfertile after artificial hybridization. *Lasthenia minor* is self-incompatible; *L. maritima* is predominantly autogamous. One of the primary morphological distinctions between the two taxa, reduced length of ray floret ligules in *L. maritima,* was believed to be associated with its autogamous breeding system. Ornduff (1966) hypothesized that *L. maritima* represents a relatively recent derivative of *L. minor* and speculated further that *L. maritima* has achieved its much more extensive geographical distribution via dispersal by seabirds.

The present study was motivated by the findings and hypotheses raised by Ornduff (1966). The relationship of *L. maritima* to seabird-breeding habitats was examined and these habitats were explored throughout the potential range of *L. maritima* in order to survey its actual distribution. As a consequence, the number of known populations of *L. maritima* has increased to seventy-four. Material of *L. minor* was collected in order to provide an adequate basis for comparing the two taxa. These collections and other available material were used to analyze several key morphological characters. The results of this survey and other lines of evidence support the recognition of *L. maritima* at the specific level.

METHODS

Nine field trips were made to Southeast Farallon Island at different times of the year in order to gather life history data for *Lasthenia maritima* and its relationship to the seabird-breeding habitat. Potential seabird-breeding habitats were explored between Santa Barbara Island in Southern California and Barkley Sound on the west coast of Vancouver Island, resulting in the collection and/or observation of *L. maritima* at 43 sites. Collections of *L. minor* were made at 21 coastal and eight interior localities. Where possible, collections were made of up to ten or more individuals per population and voucher specimens were deposited at CAS, UC, and SFSU. Field

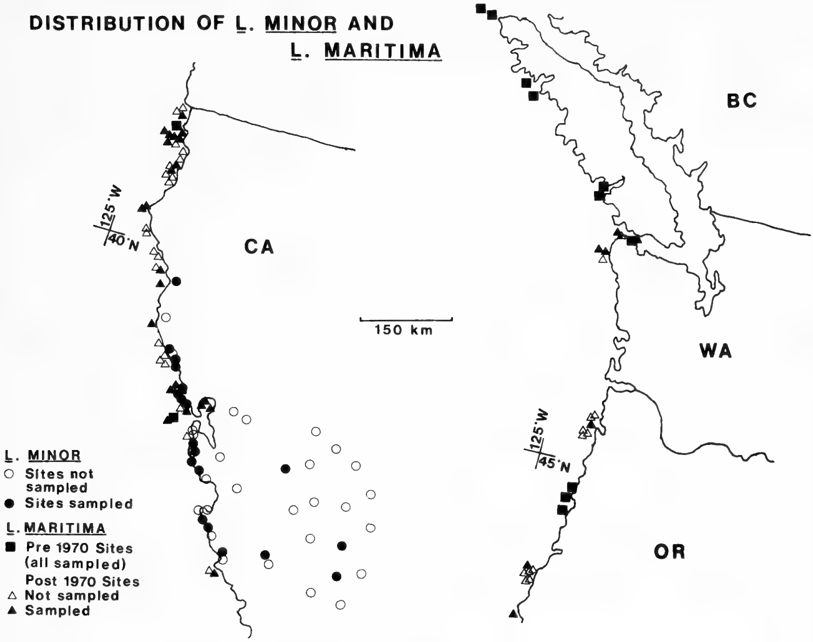


FIG. 1. Distribution of *Lasthenia minor* and *L. maritima.* Symbols indicate the sites sampled in the morphological analysis as well as the sites known for *L. maritima* prior to 1970 as contrasted to those that have been discovered since 1970.

information recorded included features of the habitat, associated vegetation, and, in the case of *L. maritima,* associated seabirds and their breeding or roosting activity. Loans of both taxa from 22 herbaria were also examined, providing supplemental material for morphological analysis. An analysis of 25 morphological characters and nine derived ratios was used to survey 10 individuals per population in six populations of *L. minor* and 12 populations of *L. maritima.* These characters encompassed vegetative as well as ray floret, pappus, and achene traits. Twelve basic and eight ratio characters were then selected and the analysis was expanded to include 19 populations of *L. minor* (n = 5–10), totaling 165 individuals, and 41 populations of *L. maritima* (n = 1–10), totaling 249 individuals. Mean values were computed for these characters in each population and submitted to discriminant function analysis and cluster analysis using Statistical Analysis System programs. The discriminant function analysis provided mean and variance data for each of these taxa and the 20 characters used in the survey. Standard error determinations were computed and the character means were compared by multiple group-comparison "*t*"-tests (Schefler 1980).

The genetic basis of these quantitative characters was evaluated by planting achenes from 7 *L. minor* populations and 26 *L. maritima* populations under uniform conditions at the San Francisco State University greenhouse during winter, 1981. Progenies (n = 1–10) were obtained from 21 populations of *L. maritima* and phenetic data concerning growth habit and flowering and fruiting times were recorded. Progenies were later scored for the same characters as the parent populations. The mean values for the progeny and parent populations were then compared by correlation analysis (Schefler 1980).

RESULTS AND DISCUSSION

Seabird-breeding habitats include islands, offshore rocks, and isolated coastal headlands that annually host colonies of breeding and/or roosting coastal and oceanic seabirds. Such habitats are characterized by trampling, burrowing, and plant predation for nest materials as a result of the activities of these birds, by stringent edaphic conditions resulting in part from guano deposition, and by exposure to persistent wind and salt spray. *Lasthenia maritima* is currently known to inhabit 74 localities (Fig. 1). Forty five of these sites occur along the California coast, where the most intensive exploratory efforts have been concentrated. It is possible that many undiscovered localities exist along the coasts of Oregon, Washington, and British Columbia. Although *L. maritima* is listed as rare and endangered in California (Smith et al. 1980), it is now recognized that this status represents an artifact of the collection record and, as a result of this study, *L. maritima* will be removed from this list. Of the 74 populations that have been identified, 70 are found on islands or offshore rocks and only four occur on coastal headlands. All of these sites demonstrated differing degrees of activity by breeding and/or roosting seabirds. The most common avian associates of *L. maritima* are the Western Gull (*Larus occidentalis*) and, north of northwestern Washington, also the Glaucous-winged Gull (*Larus glaucescens*), which collectively were noted to be breeding at 55 of the 69 *L. maritima* sites for which data and/or observations were available. Other seabirds often associated with *L. maritima* sites include Pelagic Cormorants (*Phalacrocorax pelagicus*), Pigeon Guillemots (*Cepphus columba*), and Brandt's Cormorants (*Phalacrocorax penicillatus*).

Over two-thirds of the 43 observed populations of *L. maritima* were estimated to be small in numbers of individual plants (fewer than 1000) and yet in 34 of these 43 sites, *L. maritima* either dominated or locally dominated the vegetation occupying these habitats (Vasey, unpubl. data). This underscores the observation that few plant species appear to be capable of tolerating seabird-breeding habitats and, of those that can, these habitats are often so limited in size that only small populations occur. By contrast, when large areas of habitat are available (e.g., Southeast Farallon Island), *L. maritima* occurs in dense colonies containing hundreds of thousands of individuals. The few mainland localities for *L. maritima* include the only known mainland site for this species in California (on a granite ledge at the tip of Tomales Point, Point Reyes Peninsula, Marin County), and three headland populations along the central Oregon coast (Seal Rock State Park, Yaquina Head, and Otter Crest) in Lincoln County. All of these populations were included in the morphological analysis.

The range of habitats for *L. minor* is much more varied than for *L. maritima,* but these do not include seabird-breeding sites. *Lasthenia minor* occurs along canyon bottoms in the Sierra Nevada foothills that border the San Joaquin Valley, along pond margins, disturbed areas, and in openings in the alkali scrub and grassland in the San Joaquin Valley, in arid valley flats in the Inner South Coast Ranges, and along the immediate coast from San Luis Obispo through Mendocino County. The most extensive populations were observed in the halophytic communities of the southern San Joaquin Valley and San Luis Obispo County. South of San Francisco Bay, *L. minor* occurs sporadically at the margins of coastal terraces, bluffs, and disturbed sites near the ocean. North of San Francisco Bay, *L. minor* additionally occupies stabilized dunes as well as coastal bluffs and disturbed areas near the ocean.

Nine out of the twelve quantitative morphological characters surveyed differ significantly between *L. minor* and *L. maritima,* one at the $p < 0.05$ level and eight at the $p < 0.001$ level (Table 1). All eight ratio characters also differ significantly. This analysis helps to identify a number of characters that, in combination, consistently distinguish these two taxa. As recognized by Ornduff (1966), ligules of the ray florets for *L. maritima* are usually short, ca. 2 mm long, whereas in *L. minor* rays are significantly larger, averaging close to 5 mm long. This distinction is even more consistently expressed as the ratio between ray floret/phyllary length, which is less than 0.7 in *L. maritima* and greater than 0.7 in *L. minor.* Pappus characters are also particularly helpful in distinguishing these two species. *Lasthenia maritima* frequently has ca. 4–12 awns and short, narrow scales each with a deeply laciniate superior margin. *Lasthenia minor* generally possesses ca. 2–3 awns and long, wide scales with a shallowly fimbriate margin. Differences in achene size and pubescence pattern also characterize *L. minor* and *L. maritima.* Although *L. minor* achenes are usually 1.9–2.6 mm long and pubescent along achene margins, the majority of *L. maritima* populations have larger achenes (2.6–3.3 mm) that are densely pubescent throughout; however, occasional populations of *L. maritima* have much shorter achenes (2.1–2.4 mm) and certain populations have achenes that are

TABLE 1. MORPHOLOGICAL CHARACTER COMPARISON BETWEEN *Lasthenia minor* (N = 19) AND *L. maritima* (N = 41). n = number of population means per each morphological character. Data analyzed by group-comparison "*t*"-tests; * = $p < 0.05$; ** = $p < 0.001$. (A table indicating populations sampled, sample sizes, and population means for each character will be made available upon request from the author.)

	L. minor			*L. maritima*			
Morphological characters	$\bar{x}$	S.E.	Range	$\bar{x}$	S.E.	Range	*t*-values
1. Percent peduncle pubescence	80.6	±3.00	(50.0–98.0)	57.4	±3.60	(10.0–89.0)	4.032**
2. Phyllary length (mm)	5.15	±0.119	(4.41–6.24)	5.24	±0.155	(3.88–7.21)	0.384
3. Ray ligule length (mm)	4.88	±0.201	(3.76–6.24)	2.02	±0.104	(1.30–4.76)	14.739**
4. Achene length (mm)	2.31	±0.051	(1.92–2.62)	2.64	±0.048	(2.10–3.34)	4.260**
5. Number of mid-achene hairs	7.5	±0.585	(4.50–12.0)	11.7	±0.576	(5.0–19.8)	4.563**
6. Number of marginal achene hairs	12.3	±0.468	(8.4–15.6)	12.0	±0.388	(6.7–19.0)	0.495
7. Number of awns	2.41	±0.088	(1.6–3.0)	6.27	±0.268	(2.9–9.2)	6.276**
8. Awn length (mm)	1.67	±0.039	(1.41–1.87)	1.58	±0.038	(1.21–2.12)	1.527
9. Scale length (mm)	0.714	±0.023	(0.518–0.903)	0.453	±0.014	(0.367–0.671)	10.034**
10. Scale width (mm)	0.357	±0.011	(0.250–0.456)	0.184	±0.009	(0.080–0.345)	11.215**
11. Number of scale divisions	9.27	±0.545	(5.0–15.6)	2.75	±0.206	(1.0–6.5)	13.670**
12. Length of scale division (mm)	0.153	±0.009	(0.068–0.242)	0.192	±0.008	(0.100–0.306)	2.959*
13. Ray ligule/phyllary length	0.944	±0.032	(0.700–1.23)	0.382	±0.012	(0.250–0.696)	7.315**
14. Awn/achene length	0.728	±0.016	(0.590–0.792)	0.617	±0.013	(0.464–0.762)	5.035**
15. Achene/ray ligule length	0.486	±0.018	(0.363–0.644)	1.40	±0.049	(0.634–1.96)	12.406**
16. Scale/awn length	0.436	±0.010	(0.367–0.562)	0.286	±0.005	(0.224–0.361)	14.028
17. Scale/achene length	0.311	±0.011	(0.253–0.405)	0.172	±0.004	(0.121–0.235)	14.496**
18. Scale division/scale length	0.220	±0.017	(0.092–0.467)	0.432	±0.019	(0.250–0.725)	7.081**
19. Mid/marginal achene hairs	0.600	±0.037	(0.318–0.908)	1.03	±0.045	(0.625–1.92)	6.013**
20. Total achene hairs	20.3	±0.998	(11.0–26.7)	23.8	±0.098	(13.0–35.8)	2.327*

TABLE 2. CORRELATION BETWEEN *L. maritima* POPULATION MEAN VALUES AND POPULATION PROGENY MEAN VALUES FOR MORPHOLOGICAL CHARACTERS. n = number of populations and population progeny compared. Significance test ("*t*"-value) for correlation coefficient ("*r*"-value) according to Schefler (1980). * = $p < 0.05$; ** $p < 0.001$. (A table indicating populations sampled, sample sizes, and means for populations and population progeny will be provided on request by the author.)

Morphological characters	n	"*r*"-value	"*t*"-value
1. Percent peduncle pubescence	21	0.890	8.508**
2. Phyllary length (mm)	21	0.841	6.776**
3. Ray ligule length (mm)	21	0.838	6.683**
4. Achene length (mm)	21	0.638	3.611*
5. Number of mid-achene hairs	21	0.619	3.435*
6. Number marginal achene hairs	21	0.596	3.239*
7. Number of awns	21	0.910	9.526**
8. Awn length (mm)	21	0.602	3.015*
9. Scale length (mm)	18	0.44	1.919
10. Scale width (mm)	17	0.678	4.025**
11. Number of scale divisions	16	0.619	2.946*
12. Length of scale division (mm)	16	0.376	1.520
13. Ray ligule/phyllary length	21	0.736	4.739**
14. Awn/achene length	21	0.546	2.840*
15. Achene/ray ligule length	21	0.686	4.110**
16. Scale/awn length	18	0.205	0.842
17. Scale/achene length	18	0.428	1.890
18. Scale division/scale length	16	−0.204	0.780
19. Mid/marginal achene hairs	21	0.072	0.314
20. Total achene hairs	21	0.552	2.893

sparsely pubescent. Similarly, while *L. minor* has densely pubescent peduncles (as well as other vegetative features), *L. maritima* populations are highly variable with respect to vegetative pubescence, ranging from subglabrous to highly pubescent. Other morphological differences reported by Ornduff (1966) include reduced, obtuse anther tips and reduced stigmatic hairs in *L. maritima* as opposed to *L. minor.*

The cluster analysis supported the placement of the Tomales Point and Oregon coast populations in *L. maritima.* Tomales Point is the only sympatric site known for these two species since one of the largest coastal populations of *L. minor* occurs on the uplifted dunes that border abruptly the lower granite ledge that hosts *L. maritima.* The Tomales Point *L. maritima* population does show some intermediate characteristics, but both taxa retain their identity to a great extent despite this proximity. Furthermore, parapatric populations at three other localities (Bird Rock and nearby bluffs, Pt. Reyes Peninsula; stack near Chimney Rock and nearby bluffs, Pt. Reyes Peninsula; and San Pedro Rock and Point San Pedro, San Mateo Co.) maintain a high level of morphological distinctness.

The parent-progeny correlation analysis was limited to 21 populations of *L. maritima* ranging from Southeast Farallon Island, California to Triangle Island, British Columbia (Table 2). Because of the high level of morphological inter-population variation in *L. maritima,* these results are particularly useful for providing insight into the heritability of these quantitative characters. Two of the key characters separating *L. minor* and *L. maritima* (ray ligule length and awn number) were found to be highly correlated when population means were compared to first generation progeny means. This suggests a strong genetic component to these two characters and attests to their reliability in distinguishing *L. maritima* from *L. minor.* Although there also appears to be a significant genetic component to vegetative and achene characters surveyed, these are not as useful in separating the two species because of the amount of inter-population variation in *L. maritima* and the consequent degree of overlap between *L. minor* and *L. maritima* in these characters. Pappus scale characters are also highly variable within individuals and populations and presented some of the lowest correlation coefficients. Nevertheless, the scales of *L. maritima* are generally so qualitatively different from those of *L. minor* that they are still quite useful in separating the two taxa.

The combination of multiple awns, reduced laciniate scales, and densely pubescent achenes in *L. maritima* may represent an adaptive shift towards enhanced dispersability by seabirds. Achenes of *L. maritima* were found embedded in the feather matrix of ten out of 15 recently dead Western Gulls examined on Southeast Farallon Island during late summer, 1979 (Vasey 1984). Gulls use large amounts of achene-laden *L. maritima* during the breeding season on Southeast Farallon Island and, at summer's end, thousands of these birds disperse rapidly from the island to favorite "vacation spots" as far north as the Washington coast (Spear 1982). Ornduff's (1966) seabird dispersal hypothesis for *L. maritima* thus seems highly plausible on the basis of these and other data (Vasey, unpubl. data) and it is bolstered further by the additional distributional information for *L. maritima.* This distributional pattern would be inexplicable except for dispersal by seabirds.

In conjunction with reproductive, ecological, distributional, and morphological differences between *L. minor* and *L. maritima,* there are also certain physiological and biochemical distinctions. Altosaar et al. (1974) found distinctively different albumin and globulin profiles in the dormant achenes of *L. minor* and *L. maritima.* Bohm et al. (1974) determined that the flavonoid profiles of these two species also differ. Whereas greenhouse studies suggest that *L. minor* is not tolerant of guano-modified soils (Vasey, unpubl. data), *L. maritima* thrives under such conditions. Gilham (1956) and Goldsmith (1973) have proposed that the chief limiting factor for most vegetation in guano-modified soils is the water stress that results from the high organic ion concentrations in such soils. Ornduff (1965) found that *L. maritima* accumulates nitrates in its foliage whereas *L. minor* does not. Possibly *L. maritima* has diverged from *L. minor* in the development of an organic solute (Dainty 1979) that allows *L. maritima* to accumulate nitrate ions within its cell vacuoles and avoid this form of water stress.

Species within *Lasthenia* are generally self-incompatible and the divergence of selfing taxa has occurred with important consequences in three indpendent lines (Ornduff 1966). One line, comprising *L. glaberrima* and *L. kunthii,* is differentiated at the sectional level (sect. *Lasthenia*) with no known close relationship to other sections in the genus (Ornduff 1966). A second line is the putative amphidiploid *L. microglossa* in sect. *Burrielia.* The third line is *L. maritima* in sect. *Ptilomeris.* A common denominator between all three lines is that *L. glaberrima, L. kunthii, L. microglossa,* and *L. maritima* represent four of the most geographically widespread species in the genus, especially compared to known progenitors in the cases of *L. microglossa* and *L. maritima.* Each has been highly successful at colonizing unusual habitats requiring specialized adaptations. They also share in common reduced ray floret ligules and relatively large, trichomed achenes with an awned or awn-like pappus.

The present study has demonstrated that there is a high level of reproductive isolation between natural populations of *L. minor* and *L. maritima.* It is reasonable to expect that this condition will persist through time because of the ecological divergence between these two species and the resultant spatial isolation that is the rule between seabird-breeding habitats and the mainland coast. The potential for cross-pollination between the two taxa is and presumably will continue to be inhibited by this spatial isolation, by a lack of typical pollinator activity on off-shore islands (Moldenke 1971, Vasey, unpubl. data), and by their different breeding systems. As a consequence, *L. minor* and *L. maritima* should continue to diverge until the close relationship between these two taxa eventually becomes obscured. It is, however, the close relationship between this species pair that currently offers the potential for a variety of interesting studies. These include a comparison of the genetic consequences of changes in breeding system, evolution of edaphic endemism, and the biology of colonizing species. Crawford et al. (unpubl. data) recently addressed some of these issues in a survey of allozyme variation within and between these two taxa. Unfortunately, a practical deterrent to such studies is the isolation and inaccessibility of the scattered coastal rocks and islands that harbor the great majority of sites occupied by *Lasthenia maritima.*

TAXONOMIC TREATMENT

Lasthenia maritima (A. Gray) M. Vasey comb. nov.—*Burrielia maritima* A. Gray, Proc. Amer. Acad. Arts 7:358. 1868.—TYPE: USA, California, San Francisco Co., "On the Farallones, rocky islets off San Francisco." *F. Gruber s.n.* 1868. (Holotype: GH!; isotype: US!)

Decumbent or prostrate annual, diffusely branching from a short, thick taproot. Leaves narrow to broadly ligulate, succulent with thick, blunt, occasionally compound lobes and prominent veins on adaxial surface. Variably wooly pubescent at nodes and on peduncles. Phyllaries lance-ovate, 3.8–7.2 mm long, ciliate along margins and mid-rib. Ray flowers 7–12, ligules usually 1–3 mm long and less than 0.7 times as long as phyllaries. Anther tips variable, occasionally oblong and obtuse, about 0.2 mm long; stigmas often lacking apical and subapical hairs. Achenes generally 2.6–3.2 mm long (occasionally shorter), sparsely to densely pubescent with retrorse trichomes. Pappus dimorphic, rarely absent, consisting of multiple, unequal awns (ca. 4–12) and fewer narrow scales (rarely absent) ca. 0.25–0.33 as long as awns, each scale with a deeply laciniate superior margin.

Distribution. Offshore rocks and islands, rarely headland margins, from Lion and Pup Rocks, San Luis Obispo Co., California northward along the California, Oregon, Washington, and western Vancouver Island coasts to Triangle Island near the northwestern tip of Vancouver Island, British Columbia.

Representative specimens. USA: CALIF.: San Luis Obispo Co., Pup Rock, *Vasey 8119*; San Mateo Co., San Pedro Rock, *Vasey 8345*; San Francisco Co., Southeast Farallon Is., *Hovanitz s.n.,* CAS; Contra Costa Co., West Brother Is., *Vasey 809*; Marin Co., Bird Rock, *Vasey 8111*; Mendocino Co., Anchor Rock, *Vasey 8079*; Humboldt Co., Sugarloaf Rock, *Osborne 26469,* HSC; Del Norte Co., Castle Is., *Vasey 8082*; OREGON: Curry Co., Hunter's Is., *Boekelhyde and Vasey 8217*; Coos Co., Table Rock, *Vasey 8086*; Lincoln Co., Yaquina Head, *Kaplan s.n.*; Tillamook Co., Pyramid Rock, *Vasey 8089*; WASH.: Clallam Co., Carroll Is., *Vasey 8090*; Seal Rock, *Vasey 8093*; BR. COL.: Vancouver Is., Baeria Rocks, *Vasey 8096*; Triangle Is., *Foster and Vasey 8095.*

Key to *Lasthenia minor* and *Lasthenia maritima*

Awns usually 2 or 3, scales broad and ⅓ to ½ as long as awns, scale margins shallowly fimbriate; ligules of ray florets about 4–6 mm long, greater than 0.7 times as long as phyllaries. .... *Lasthenia minor*

Awns usually 4–12, scales narrow and ¼ to ⅓ as long as awns, scale margins deeply laciniate; ligules of ray florets about 1.3–3.0 mm long, less than 0.7 times as long as phyllaries. .... *Lasthenia maritima*

ACKNOWLEDGMENTS

I especially thank Dr. R. Ornduff for his seminal ideas and support during this project. Drs. R. Patterson, R. Ornduff, and J. Strother were particularly helpful in the preparation of this manuscript and Drs. V. T. Parker, G. L. Stebbins, S. Jain and J. R. Sweeney provided much useful guidance. G. S. Lester provided invaluable field collections and considerable field support. Additional collections and locality data were provided by M. Sheehan, R. Boekelhyde, B. Foster, B. Henneman, and J. Siddall. Personal collection efforts would not have been possible except for the assistance of M. Nakagawa, M. Harms, J. L. Groulx, L. V. Painter, K. Culligan, L. C. Berner, and E. Ryde. I also thank Dr. T. Duncan for his assistance with the U.C. Berkeley computer and Dr. G. Hunt for cooperation in the California Channel Island survey. Thanks are also due to the following agencies and organizations for their support during this project: U.S. Fish and Wildlife, California Dept. of Fish and Game, and Pt. Reyes Bird Observatory. I also particularly thank California Dept. of Fish and Game for a grant supporting the distribution work and the California Native Plant Society for a mini-grant. Finally, I am thankful to the following herbaria for their generous loans of specimens: UC, JEPS, CAS, WTU, ORE, DSC, MO, ND, NY, OBI, PH, RSA, UCSB, SD, US, V, DAVH, HSC, GH, F, UBC, ND.

LITERATURE CITED

ALTOSAAR, I., B. A. BOHM, and R. ORNDUFF. 1974. Disc-electrophoresis of albumin and globulin fractions from dormant achenes of *Lasthenia.* Biochem. Syst. Ecol. 2:67–72.

BLANKENSHIP, J. W. and C. A. KEELER. 1882. On the natural history of the Farallon Islands. Zoe 3:144–165.

BOHM, B. A., N. A. M. SALEH, and R. ORNDUFF. 1974. The flavonoids of *Lasthenia* (Compositae). Amer. J. Bot. 61:551–561.

CRAWFORD, D. J., R. ORNDUFF, and M. C. VASEY. (In Press). Allozyme variation within and between *Lasthenia minor* and its derivative species *L. maritima* (Asteraceae). Amer. J. Bot.

DAINTY, J. 1979. The ionic and water relations of plants which adjust to a fluctuating saline environment. *In* R. L. Jeffries and A. J. Davy, eds., Ecological processes in coastal environments. Blackwell Sci. Publ., UK.

FERRIS, R. S. 1955. The identity of *Monolopia minor* DC. Contr. Dudley Herb. 4:331–334.

GILHAM, M. E. 1956. Ecology of the Pembrokeshire Islands. V. Manuring by the colonial seabirds and mammals with a note on seed distribution by gulls. J. Ecol. 44:429–454.

GOLDSMITH, F. B. 1973. The vegetation of exposed sea cliffs at South Stack, Anglesey. I. The multivariate approach. J. Ecol. 61:787–818.

GRAY, A. 1868. Characters of new plants of California and elsewhere, principally of those collected by H. N. Bolander in the State Geological Survey. Proc. Amer. Acad. Arts 7:327–401.

GREENE, E. L. 1894. Manual of the botany of the region of San Francisco Bay. Cubery and Co., San Francisco, CA.

JEPSON, W. L. 1925. A manual of the flowering plants of California. University of California, Berkeley.

MOLDENKE, A. R. 1971. Studies on the species diversity of California plant communities. Ph.D. dissertation, Stanford Univ., Stanford, CA.

ORNDUFF, R. 1965. Ornithocoprophilous endemism in Pacific Basin angiosperms. Ecology 46:864–867.

———. 1966. A biosystematic survey of the goldfield genus *Lasthenia* (Compositae: Helenieae). Univ. Calif. Publ. Bot. 40:1–92.

———. 1976. Speciation and oligogenic differentiation in *Lasthenia* (Compositae). Syst. Bot. 1:91–96.

———, B. A. BOHM, and N. A. M. SALEH. 1974. Flavonoid races in *Lasthenia* (Compositae). Brittonia 26:411–420.

SCHEFLER, W. C. 1980. Statistics for the biological sciences. Addison-Wesley, MA.

SMITH, J. P., R. J. COLE, J. O. SAWYER, and W. R. POWELL. 1980. Inventory of rare and endangered vascular plants of California. Spec. Publ. No. 1 (2nd ed.). Calif. Native Pl. Soc.

SPEAR, L. 1982. Dispersal patterns of Farallon Western Gulls. Point Reyes Bird Observatory Newsletter 60:1–11.

VASEY, M. C. 1981. Status report on bird rock goldfields (*Lasthenia minor* ssp. *maritima*). Rare Plants Division, California Dept. of Fish and Game, Sacramento, California.

———. 1984. Vernal pools, seabird rocks, and a remarkable species of *Lasthenia*. *In* S. Jain and P. Moyle, eds., Vernal pools and intermittent streams: a symposium sponsored by the Institute of Ecology, Univ. California, Davis, 9 and 10 May 1981. Institute of Ecology Publ. No. 28.

(Received 17 Jul 1984; accepted 18 Jan 1985.)

ANNOUNCEMENT

Southern California Botanists was established in 1927 and is a non-profit association of professional botanists and interested lay persons. Its past presidents include Mildred Mathias, Peter Raven, and Robert Thorne. It is an active organization of about 500 members. It publishes "Crossosoma," a bi-monthly journal. It conducts 10–15 field trips per year, including at least one trip in Baja California. It presents or co-sponsors one all-day Symposium each year on a subject of botanical interest. Southern California Botanists operates an active book sales activity for its members, providing the opportunity to purchase at a discount botanical books often difficult to locate.

Inquiries may be sent to Southern California Botanists, % Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711.

ANNOUNCEMENT

The International Organization of Plant Biosystematists encourages members and other botanists to send information to the *IOPB Newsletter.* Send changes of address, personal news, promotions, society appointments, publications, projects started, requests for research materials, short articles, controversy, reports on research conferences, etc. Send information to Dr. K. Urbanska, Editor, IOPB Newsletter, Geobotanishes Institut, Stiftung Rubel, Zurichbergstrasse 38, CH-8044 Zurich, Switzerland.

OBSERVATIONS ON *CHAMAESYCE* (EUPHORBIACEAE) IN THE GALÁPAGOS ISLANDS

MICHAEL J. HUFT and HENK VAN DER WERFF
Missouri Botanical Garden, P.O. Box 299,
St. Louis 63166

ABSTRACT

All collections of the endemic species of *Chamaesyce* in the Galápagos Islands were reexamined. Results indicate that hybridization has taken place in several localities, notably on Isla Bartolomé. Plants previously referred to *C. nummularia* and *C. bindloensis* from Bartolomé are considered to be of hybrid origin, and *C. bindloensis* is placed in synonymy under *C. punctulata,* together with two other names that had been overlooked in the treatment of *Chamaesyce* in the Flora of the Galápagos Islands.

The genus *Chamaesyce* has recently been revised for the Galápagos Islands (Burch 1969, 1971). While carrying out ecological studies on the islands, the junior author noticed several aberrant populations that he was unable to identify. We therefore decided to study all available specimens of the native, endemic species in an attempt to place these populations and to clear up some other problems that had become apparent.

Isla Bartolomé is a tiny islet (1.24 km²) that is situated about 200 m from the east coast of San Salvador (572 km²). The island consists of lava flows and a few cinder and tuff cones and supports a sparse vegetation of low shrubs dominated by several species of *Chamaesyce* and *Tiquilia* (=*Coldenia,* Boraginaceae, see Richardson 1976). The island seems unusually rich in species of *Chamaesyce* for its size, and Burch (1971) reports five species from here: *C. amplexicaulis, C. punctulata, C. viminea, C. bindloensis,* and *C. nummularia* var. *nummularia.* Of these, the first three also occur on San Salvador, as does *C. recurva,* which has not yet been reported from Bartolomé. John Thomas Howell collected numerous specimens of *Chamaesyce* on Bartolomé in 1932 (CAS, many duplicates in MO) that had not yet been incorporated into the herbarium at CAS at the time the "Flora of the Galápagos Islands" (Wiggins and Porter 1971) was in preparation and consequently were not seen by Burch. Most of these specimens do not clearly fit into one or the other of the species, but exhibit a full range of intermediate characteristics between the species *C. amplexicaulis, C. punctulata,* and *C. recurva* in leaf shape, pubescence, cyathial appendages, and seed shape and surface. The following note by Howell is attached to each of these sheets: "Part of the hybrid complex involving *EE. amplex-*

MADROÑO, Vol. 32, No. 3, pp. 143–147, 19 August 1985

icaulis, nummularia, and *punctulata* that grew at the northwest point of Bartholomew Island. The plants grew in volcanic ash among lava rocks in a narrow belt less than 100 m long. The individuals varied in habit, vestiture, gland-appendages, and seeds, while the leaves varied in size, shape, margin, and color. *Chamaesyce bindloensis* may have been one of the elements in the complex."

We agree with Howell's note that extensive hybridization occurs on Bartolomé, as is clear from his own collections as well as several others made by Wiggins & Porter and Fagerlind & Wibom. It seems much more likely to us, however, that *C. nummularia* is not involved in the hybrid complex, but that *C. amplexicaulis* is. The collection from Bartolomé that has been identified as *C. nummularia* (*Wiggins and Porter 307,* DS) differs from that species by the sessile leaves and more angular and slender seeds. It is better interpreted as part of the hybrid complex. True *C. nummularia* appears to be confined to the southern islands of Santa Fé, Santa María, San Cristóbal, and Española.

Howell evidently considered *C. nummularia* to be a contributor to the hybrid complex because of the presence of hybrid individuals with hirsutulous indument similar to that of *C. nummularia.* However, although *C. amplexicaulis* is usually completely glabrous, occasional plants from such islands as Marchena (*v.d. Werff 2132,* CAS), Pinta (*Stewart 1847,* CAS), San Salvador (*Stewart 1853,* CAS; *Howell 10013,* CAS, MO), and Bartolomé (*Howell 10063,* CAS; *Wiggins and Porter 308,* CAS) are hirsutulous. Thus, *C. amplexicaulis* occurs near the hybrid zone, as *C. nummularia* does not, and all of the variation in the complex can be explained without involving *C. nummularia.* Furthermore, *C. amplexicaulis* is the only species that can provide the cordate-clasping leaf-bases that are observed in several of the hybrid individuals. *Chamaesyce punctulata* is also represented on San Salvador, just across from Bartolomé, by several hirsutulous collections (*Howell 10054, 10055, 10056,* CAS), although this species is normally glabrous.

Table 1 gives the relevant characters of the three species contributing to the hybrid complex, as well as of *C. nummularia*; the same characters for eight hybrid individuals chosen to illustrate the full range of variability are also given.

The other species that Burch reported from Bartolomé, *Chamaesyce bindloensis,* is problematical. We have examined the type (*Stewart 1868,* GH, lectotype, chosen by Burch 1969; CAS, isolectotype), and it is our opinion that this species, originally described as a wide-leafed variety of what is now called *C. punctulata,* falls within the range of variation exhibited by *C. punctulata.* The prominent gland appendages that are said to characterize *C. bindloensis* are not found on all cyathia. Furthermore, specimens that have the characteristic short, broad leaves and short stipules of *C. bindloensis* but that have the ridged seeds of *C. punctulata* are known from other locations (e.g., east coast of Santa Cruz, *v.d. Werff 2094,* CAS, U; Plaza, *Fagerlind and Wibom 3361, 3386,* S). Because there is no clear-cut distinction between the two concepts, we do not hesitate to place *C. bindloensis* in synonymy under *C. punctulata.* Other specimens that have been identified as *C. bindloensis* are *C. punctulata* (e.g., *A. and H. Adsersen 1144,* C), *C. recurva* (e.g., *M. and O. Hamann 981,* C) and part of the hybrid complex on Bartolomé (e.g., *Fagerlind and Wibom 3482, 3505,* S; *Wiggins and Porter 300,* DS; *304,* CAS, GH and *311,* MO). Thus in addition to the hybrid populations, Bartolomé supports three species of *Chamaesyce, C. amplexicaulis* (e.g., *Howell 10065,* CAS, MO; *Harling 5369,* S), *C. punctulata* (e.g., *Wiggins and Porter 294,* CAS, MO; *Fagerlind and Wibom 3483,* S), and *C. viminea* (e.g., *A. and H. Adsersen 1887,* C).

Reports of *Chamaesyce nummularia* from Isla Wolf in the far northwestern part of the archipelago (*Snodgrass and Heller 11,* DS; *Dawson s.n.,* DS; *Stewart 1855,* CAS; *Fosberg 44967,* MO) are based on specimens that appear morphologically intermediate between *C. amplexicaulis* and *C. nummularia.* These specimens are probably of hybrid origin, but it is doubtful that *C. nummularia* is involved, since that species is known with certainty only from the four southeasternmost islands. Further collections as well as more detailed field observations will be needed in order to elucidate the nature of these puzzling plants.

Another probable hybrid population occurs on Isla Pinzón, represented in herbaria by *Howell 9845* (CAS—4 sheets, MO) and *9846* (CAS), and noted by the collector to be variable in the field. These specimens are similar to *C. punctulata,* but have conspicuous cyathial appendages, and the seeds are, for the most part, smooth, unlike the ridged seeds of typical *C. punctulata.* The leaves exhibit a prominent dimorphy (large on main stems, small on laterals) that is suggestive of *C. recurva,* as are the large stipules. Again, further collections are needed to make a definitive interpretation.

Chamaesyce abdita was known to Burch only from the type collection on Santa Fé. It is now represented by several collections from Santa Cruz (*A. and H. Adsersen 248,* C; *Howell 9128, 9129,* CAS, MO; *v.d. Werff 1121,* CAS), Baltra (*Howell 9955,* CAS, MO), Española (*A. and H. Adsersen 666,* C), and Champion near Santa María (*A. and H. Adsersen 1459,* C; *v.d. Werff 2059,* U). Some of these collections, especially those from Champion, have glabrous capsules and herbage and thus would not key out properly in the Flora. *Howell 9130* (CAS, MO) from Santa Cruz has the pubescence, leaf shape, and leaf size of *C. abdita,* but is perennial. Some of the seeds are typical of *C. abdita,* but a few are ridged like those of *C. recurva,*

TABLE 1. CHARACTERISTICS OF THE SPECIES CONTRIBUTING TO, OR THAT HAVE BEEN THOUGHT TO CONTRIBUTE TO, THE HYBRID COMPLEX ON BARTOLOMÉ (LINES 1–4) AND OF SELECTED HYBRID INDIVIDUALS (LINES 5–12).

Taxon or specimen	Vegetative pubescence	Leaf shape	Leaf base	Cyathial appendages	Capsule pubescence	Seed shape	Seed surface
1. *C. amplexicaulis*	glabrous or hirsutulous	suborbicular	cordate-clasping	conspicuous	glabrous or hirsutulous	plump	smooth
2. *C. recurva*	glabrous	ovate-obovate or lanceolate	obtuse	inconspicuous	glabrous	angular	bluntly ridged
3. *C. punctulata*	glabrous	linear-lanceolate	rounded	inconspicuous	glabrous	angular	prominently ridged
4. *C. nummularia* var. *nummularia*	hirsutulous	orbicular to broadly ovate	rounded to subcordate	inconspicuous	hirsutulous	plump	smooth
5. *Howell 10070* (CAS)	lvs. glabrous stems nearly so	ovate	subcordate	intermediate	glabrous	angular	smooth
6. *Howell 10076* (CAS)	hirsutulous	deltate-orbicular	cordate-clasping	intermediate	glabrous to hirsutulous	plump or slightly angular	smooth
7. *Howell 10077* (CAS)	slightly hirsutulous	deltate-ovate	rounded to cordate-clasping	intermediate	glabrous to hirsutulous	angular	smooth
8. *Howell 10084* (CAS)	hirsutulous	lanceolate-ovate	oblique	lacking	hirsutulous	angular	ridged
9. *Fagerlind & Wibom 3482* (S)	hirsutulous	deltate-ovate	rounded to subcordate				
10. *Wiggins & Porter 300* (DS)	glabrous	ovate	subcordate	inconspicuous	glabrous	angular	ridged
11. *Wiggins & Porter 307* (CAS)	hirsutulous	deltate-ovate	oblique	lacking	glabrous	angular	ridged
12. *Wiggins & Porter 311* (MO)	hirsutulous	ovate	cordate				

and therefore our identification of this specimen as *C. abdita* is with some hesitation.

Following is a list of native species in the Galápagos that we accept, along with synonymy that differs from that given by Burch (1969, 1971), including two published names that were not accounted for by Burch. These are *Euphorbia bisulcata* Howell, Proc. Calif. Acad. Sci., 4th ser., 21:330, 1935; type: *Howell 9880* (CAS, holotype; MO, isotype), which differs from typical *C. punctulata* only in that the back of each carpel on the mature capsule is broadly bisulcate; and *Euphorbia howellii* Wheeler, Contr. Gray Herb. 124:42, 1939, nomen novum for *E. diffusa* Hook. f., non Jacq., a synonym of *E. punctulata.*

CHAMAESYCE ABDITA Burch
C. AMPLEXICAULIS (Hook. f.) Burch
C. GALAPAGEIA (Robins. & Greenm.) Burch
C. NUMMULARIA (Hook. f.) Burch var. NUMMULARIA
C. NUMMULARIA var. GLABRA (Robins. & Greenm.) Burch
C. PUNCTULATA (Anderss.) Burch
  C. bindloensis (Stewart) Burch
  Euphorbia articulata Anderss. var. *bindloensis* Stewart
  E. bisulcata Howell
  E. diffusa Hook. f., non Jacq.
  E. howellii Wheeler
C. RECURVA (Hook f.) Burch
C. VIMINEA (Hook. f.) Burch

One additional adventive species, *Chamaesyce lasiocarpa* (Kl.) Arthur, has been found on the islands since the Flora was published (San Cristóbal, *v.d. Werff 2171,* U, van der Werff, 1977).

ACKNOWLEDGMENTS

We thank the curators of C, CAS, DS, F, GH, K, MO, S, and U for making their collections available to us.

This is contribution no. 373 from the Charles Darwin Foundation.

LITERATURE CITED

BURCH, D. 1969. Notes on the Galápagos Euphorbieae (Euphorbiaceae). Ann. Missouri Bot. Gard. 56:173–178.

———. 1971. *Chamaesyce. In* I. L. Wiggins and D. M. Porter, Flora of the Galápagos Islands, pp. 575–582. Stanford University Press, Stanford, CA.

RICHARDSON, A. 1976. Reinstatement of the genus *Tiquilia* (Boraginaceae: Ehretioideae) and descriptions of four new species. Sida 6:235–240.

VAN DER WERFF, H. 1977. Vascular plants from the Galápagos Islands: new records and taxonomic notes. Bot. Not. 130:89–100.

WIGGINS, I. L. and D. M. PORTER. 1971. Flora of the Galápagos Islands. Stanford University Press, Stanford, CA.

(Received 17 Feb. 1984; 30 Oct. 1984.)

POST-FIRE SEEDLING ESTABLISHMENT OF *ADENOSTOMA FASCICULATUM* AND *CEANOTHUS GREGGII* IN SOUTHERN CALIFORNIA CHAPARRAL

Jochen Kummerow, Barbara A. Ellis, and James N. Mills
Department of Biology, San Diego State University,
San Diego, CA 92182

Abstract

Mortality of *Ceanothus greggii* and *Adenostoma fasciculatum* seedlings during the first growing season after a burn in the southern California chaparral was 92 and 90%, respectively. Survival of these shrub seedlings was not affected by the presence of stump sprouts, which grew at a rate of 2 cm in height per week, or by herbaceous plants (65% cover). However, the presence of annuals reduced the growth of the shrub seedlings significantly. Watering increased seedling growth, but additional fertilizer had no significant effect. Stump sprouting and abundant seedling establishment after fire appear to be main factors that insure maintenance of the shrub species composition of the frequently fire-disturbed chaparral vegetation.

Chaparral in southern California burns at 25- to 40-year intervals, although lower or higher fire frequencies occur (Philpot 1977, Keeley 1982). In spite of these repeated perturbations, the vegetation regenerates rapidly. This phenomenon of fast chaparral re-establishment after fire has been described in detail for a number of different California localities (e.g., Sampson 1944, Horton and Kraebel 1955, Hanes 1971, Keeley and Keeley 1982). From these observations, it can be concluded that the shrub species establishing during the first growing season after a fire are the same ones that composed the pre-fire chaparral community (Hanes 1971). However, the quantitative composition of the shrub cover may change. Assessment of the cover values for *Ceanothus crassifolius* and *Adenostoma fasciculatum* in a 15-year-old stand in the San Gabriel Mountains in 1934 and the re-assessment in 1982, 22 years after a burn, showed that the cover value for the former species had increased by the factor of two while the latter species had declined correspondingly (Jacks 1984).

Although these observations indicate the importance of stump sprout and seedling densities after fire for mature stand composition, little is known about the factors that influence shrub seedling establishment. The importance of the post-fire physical environment has been emphasized (Sauer 1977). Competing seedlings in the early establishment phase can modify the environment, for example through rapid water and nutrient uptake. It is unclear to what degree

---

Madroño, Vol. 32, No. 3, pp. 148–157, 19 August 1985

shrub seedling establishment is influenced by spatially variable factors such as the presence or absence of nearby stump sprouts. The competitive action of the sometimes dense but short-lived herbaceous vegetation on shrub seedling establishment is likewise unclear. Selective herbivory by rabbits on shrub seedlings has recently been documented (Mills 1983).

The objective of the present study was to obtain quantitative information on shrub seedling mortality and establishment. The data may improve our predictive capacity of mature chaparral stand composition.

MATERIALS AND METHODS

Research site. The study site was the Sky Oaks Biological Field Station at 1500 m elevation about 15 km north of Warner Springs, San Diego County, California. The climate of the area is Mediterranean; and the site receives annually about 550 mm of precipitation between November and May. Some thundershowers interrupt the long summer drought. In most winters some snow remains on the ground for a few days. Minimum temperatures of −8°C and summer maxima of 38°C have been observed (Bowman 1984).

The research site was covered by a dense, 54-year-old shrub vegetation (aged by year ring counts, P. Zedler, pers. comm.). Pre-burn analysis showed a density of 1.01 shrubs per m^2; *Adenostoma fasciculatum* and *Ceanothus greggii* were the most important species, with 0.42 and 0.40 individuals per m^2, respectively. We observed the spotty occurrence of *Cercocarpus betuloides* Nutt., and *Quercus dumosa* Nutt. mostly on north-facing slopes and the tree *Quercus agrifolia* Neé. in ravines and washes. The soil is a loamy sand with abundant stones and pebbles. The soil layer, varying between 30 and 50 cm depth, rests on bedrock of a micaceous schist (USDA 1973).

In December 1981, a 2-ha site in this area was burned with the help of the California Department of Forestry and the U.S. Forest Service. The burn was complete and temperatures at the soil surface reached about 350°.

Shrub seedling establishment. Seedling establishment of *A. fasciculatum* and *C. greggii* was assessed post-fire on eight 8 × 2-m plots randomly distributed over the area. In each plot the shrub seedlings of ten 0.25-m^2 subquadrats were counted on 8 May and again on 11 December (i.e., 6 and 13 mo post-fire). Repeated counts from mid-April to the beginning of May indicated no further increases in the number of shrub seedlings; by mid-December the initiation of sustained rainfall made further drought-induced seedling mortality for the current year improbable.

Effect of stump sprouts and annuals on shrub seedling growth. To assess the effect of stump sprouts and annuals on growth of shrub seedlings, twelve 1-m^2 plots, each with a stump-sprouting *A. fasciculatum* in the center were distributed randomly over the 6 mo-old burn area in May 1982. Four replicate plots were established for each of the following treatments: (A) all stump sprouts removed, (B) all stump sprouts and annual herbs removed, and (C) control. Shrub seedlings were counted and their heights recorded biweekly. Stump sprouts and annuals in treatments (A) and (B) were removed with each observation date. The stump sprouts were carefully broken off by hand in order to avoid major wounding of the burls. New sprouts appeared during the entire year after the burn.

Irrigation and fertilizer application. On the burn site, twelve 1-m^2 plots without stump-sprouting shrubs and a minimum of five second-year *C. greggii* and *A. fasciculatum* seedlings each were fenced in the spring of 1983 with 0.5-m tall chicken wire to prevent small-mammal herbivory. Shoots that grew from adjacent stump sprouts into the plots were removed. Three treatments, consisting of four replicates each, were established. (1) Fertilized and watered: 10 liters of full-strength Hoagland's solution, containing 2 g N, 0.3 g P, and the other nutrients in corresponding amounts, were applied to the plots with sprinkler cans. The fertilizer application was repeated four times in two-week intervals between the beginning of June and the end of July. Water and fertilizer application was initiated in early June when soil moisture in the 10–20-cm depth layer had declined to about 3% (g H_2O g^{-1} dry weight; Fig. 1) and herbaceous plants showed symptoms of water stress. From January to June 1983, a total of 650 mm of precipitation fell. Thus, soil moisture remained relatively high until the end of May. Each fertilizer plot received 8 g N and 1.2 g P. (2) Watered only: Irrigation consisted of 10 liters m^{-2} of de-ionized water applied at the same times as the nutrient solution. In addition, the "fertilized and watered" and the "watered only" plots received a total of 80 liters of de-ionized water (20 liters per application) between the end of June and the beginning of September. (3) Unwatered plots.

In September and November 1983 the heights and crown diameters (maximum and minimum lengths between distal branch tips) of five representative seedlings per plot of *A. fasciculatum* and *C. greggii* were recorded. The crown diameter values were more meaningful than height values because branches elongated relatively more than the main leader shoots.

Biweekly gravimetric soil measurements in depth layers of 0–10, 10–20, and 20–30 cm, about one meter distant from the control plots of this experiment, provided basic information on the seasonal fluctuation of soil moisture in the rooting zone of the shrub seedlings.

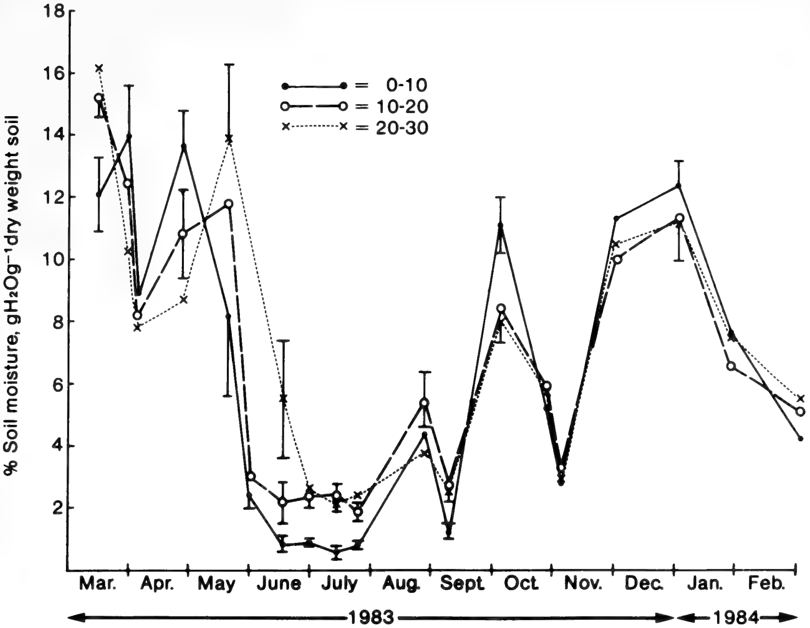


FIG. 1. Soil moisture one meter from the control plots of the irrigation and fertilizer experiment. Each data point is the mean of four samples. Vertical bars indicate standard errors.

Five representative seedlings each of both the species were excavated in bimonthly intervals. Although some root breakage appeared to be unavoidable especially in late summer, we think that the main roots were mostly recovered to their full extension.

RESULTS

Shrub seedling establishment. Abundant rainfall occurred during the first post-fire period (566 mm fell from July 1981–June 1982, Ellis et al. 1983). Thus the conditions for seed germination were favorable. In May 1982, an average of 78 shrub seedlings (34 *A. fasciculatum* and 44 *C. greggii*) per m^2 were counted (Table 1). In December 1982, 9.8% of the *A. fasciculatum* and 7.8% of the *C. greggii* seedlings were still alive. Periodic counts showed that most of the seedlings had died in May and June (Fig. 2).

Effect of stump sprouts and herbaceous plants on shrub seedling growth. Survival of *C. greggii* and *A. fasciculatum* seedlings during the first post-fire growing season was not affected by the presence of stump sprouts or herbaceous plants (the latter with ca. 65% cover). However, seedling growth was reduced by about ⅓ under the influ-

TABLE 1. MEAN NUMBER OF *A. fasciculatum* AND *C. greggii* SEEDLINGS AT BEGINNING AND END OF THE FIRST POST-FIRE GROWING SEASON. Values are means ± standard errors of eighty 0.25-m^2 plots randomly staked on eight 2 × 8-m observation areas.

A. fasciculatum			*C. greggii*		
Mean no. of seedlings m^{-2}		% surv.	Mean no. of seedlings m^{-2}		% surv.
May 8	Dec. 11		May 8	Dec. 11	
33.6 ± 12.96	3.3 ± 1.34	9.8	43.8 ± 7.84	3.4 ± 0.97	7.8

ence of the herbaceous vegetation (Table 2). Removal of stump sprouts did not enhance seedling growth, although these stump sprouts grew vigorously at an elongation rate of about 2 cm per week from May to October (Fig. 3). This indicated an adequate water supply for stump-sprouting *A. fasciculatum* shrubs during the summer of 1982.

Irrigation and fertilizer application. Biweekly gravimetric soil moisture measurements in the vicinity of the experimental plots demonstrated that by mid-June 1983, the soil in the upper layer had already dried out and only the 20- and 30-cm layer was still holding a small moisture reserve (Fig. 1). Our periodic seedling excavations

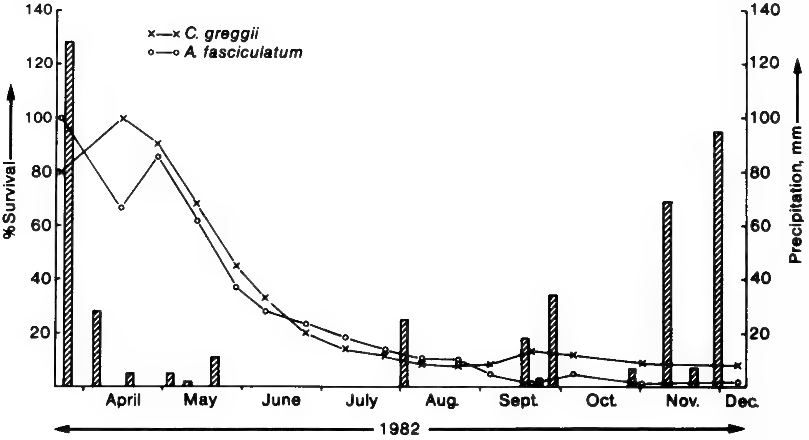


FIG. 2. Survival of *Ceanothus greggii* and *Adenostoma fasciculatum* seedlings which had germinated between February and March 1982, following a burn in December 1981. The highest observed seedling density was considered 100%. Each point is the mean number of seedlings in eight 1-m^2 plots. There was no significant difference in seedling survival between species. The hatched bars indicated rainfall events in mm.

TABLE 2. HEIGHT (mm ± S.E.) OF *C. greggii* AND *A. fasciculatum* SEEDLINGS AT THE INITIATION OF THE OBSERVATIONS (4/28/82) AND AFTER 10 WEEKS UNDER TREATMENTS A (STUMP SPROUTS REMOVED), B (STUMP SPROUTS AND HERBACEOUS PLANTS REMOVED), AND C (UNCHANGED CONTROL). Significance of differences among treatments indicated with different letters. Number of observed seedlings in parentheses. Statistical treatment: Basic statistics, ANOVA on log-transformed data, Newman-Keuls multiple comparison tests. $^1p < 0.01$. $^2p < 0.05$.

	C. greggii		*A. fasciculatum*	
	Initial height 4/28	Final height 7/9	Initial height 4/28	Final height 7/9
A. Stump spr. removed	10.5 ± 0.6a (32)	21.0 ± 1.3a (26)	9.8 ± 0.5a (31)	27.8 ± 2.0a (21)
B. Stump spr. + herbs removed	10.1 ± 0.6a (30)	35.5 ± 5.3b^1 (11)	10.4 ± 0.6a (40)	33.1 ± 3.7b^2 (24)
C. Control	10.4 ± 0.6a (30)	25.7 ± 3.7a (11)	7.6 ± 0.4b^2 (40)	21.9 ± 2.3a (14)

showed that at this time the main roots of these 2nd-year seedlings had reached a length of 20–30 cm. By the end of August and again at the beginning of October 1983, heavy thunderstorms produced enough rain to remoisten the soil profile down to 30 cm (Fig. 1).

On 9 September, the seedlings of both shrub species were larger in both the watered and the watered and fertilized plots. Six weeks later (21 October) this difference was still visible, although not statistically significant in the case of *A. fasciculatum* (Table 3).

DISCUSSION

More than 90% of the seedlings that germinated in March and April 1982 after a fire in December 1981 died during the first growing season. Our biweekly observations had shown that May and June were the months with the highest mortality. These values seem high when compared with others (Musick 1972, Keeley and Zedler 1978, Horton and Kraebel 1955), although exact shrub seedling mortality rates in the spring following a fall fire are poorly quantified (Schlesinger et al. 1982).

We can deduce from precipitation data that drought conditions became severe in May and more so in June (Fig. 1). Excavation of five seedlings each of *A. fasciculatum* and *C. greggii* in July 1982 showed mean tap root lengths of 5 cm and 8 cm, respectively (Ellis 1983). Thus, lack of soil moisture is probably one of the factors causing the high seedling mortality. A second cause for the death of many seedlings was herbivory. By November 1982, 25% of the *A. fasciculatum* and 43% of the *C. greggii* seedlings on this specific research site had been killed by rabbits (Mills 1983).

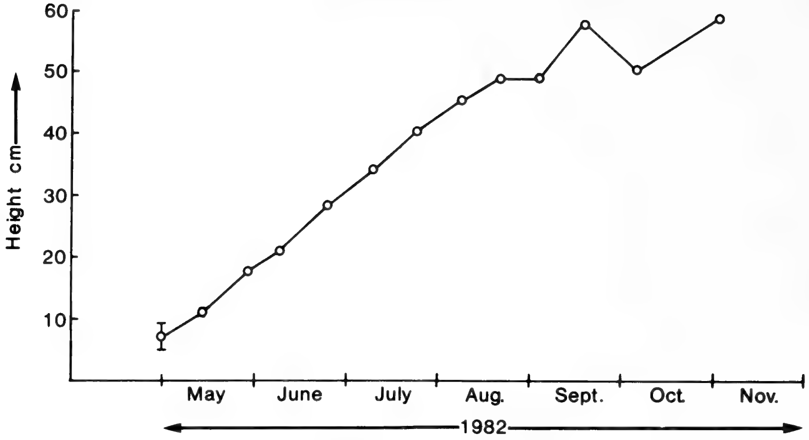


FIG. 3. Growth in height of *Adenostoma fasciculatum* stump sprouts during the 1982 growing season after a burn in December 1981. Ten average-sized shoots of 4 randomly chosen *A. fasciculatum* stumps were measured. A typical standard error is indicated for the first (May) value. Note the linear height increase during the dry summer months.

Very little is known about the effects of the herbaceous post-fire vegetation on shrub seedling establishment. We could not find evidence for increased survival of shrub seedlings when competing stump sprouts and herbaceous plants were eliminated, although roots of the stumps must have remained active. This result contrasts sharply with data shown by Schultz et al. (1955). A grass density of 85% eliminated all shrub seedlings, and a grass density of 18% reduced the number of surviving shrub seedlings by 50%. An explanation for these conflicting results may be that grasses were virtually absent from our research site, whereas the above-mentioned observations were made on a burned and ryegrass re-seeded area. Ryegrass plantings have been shown to inhibit herb establishment and chaparral seedling growth (Corbett and Green 1965). In our site the estimated herbaceous cover was about 65% and consisted mostly of the native fire followers, *Phacelia brachyloba, Streptanthus heterophyllus,* and *Gilia caruifolia,* all with much less aggressive tap root systems than the fibrous root system of ryegrass (Rice and Green 1964).

Although seedling survival was not affected by stump sprouts of *A. fasciculatum* and the herbaceous vegetation, we found that herbs caused a significant growth reduction of the shrub seedlings. The vigorously growing *A. fasciculatum* stump sprouts did not affect shrub seedling growth. These stump sprouts, consisting of clusters with about 150 shoots per burl, grew at a rate of about 2 cm per month from April to October, when they reached a final mean height

TABLE 3. RELATIVE SIZE (HEIGHT OF THE MAIN SHOOT × AVERAGE DIAMETER) OF *C. greggii* AND *A. fasciculatum* SECOND-YEAR SEEDLINGS WHICH WERE NOT WATERED, WATERED, AND WATERED + FERTILIZED, THREE AND FOUR MONTHS AFTER TREATMENT INITIATION. For each treatment n = 19. Statistical treatment: One-way ANOVA on log-transformed data followed by Newman-Keuls multiple range test. Significant differences among treatments for each observation date indicated with different letters ($p < 0.05$). Standard errors given in parentheses.

Observation date	*C. greggii*		*A. fasciculatum*	
	9/9/83	10/21/83	9/9/83	10/21/83
Unwatered	24.3 (3.7)a	30.0 (4.7)a	72.1 (22.0)a	91.1 (12.7)a
Watered	62.1 (11.7)b	71.4 (13.5)b	100.4 (18.8)ab	127.9 (26.1)a
Fertilized + watered	53.0 (9.2)b	61.6 (10.6)b	117.3 (9.6)b	133.4 (13.9)a

of ca. 50 cm (Fig. 3). The fine root density around the burls was several times higher than that around the stems of unburned control shrubs (Kummerow and Lantz 1983). The fine roots of resprouting burls were predominantly located at about 20–30 cm depth, and thus were deeper than the roots of the ½-yr shrub seedlings, which had hardly reached a depth of 10 cm (Ellis 1983). However, roots of annuals and shrub seedlings occupied the same depth zone of the soil and might have competed for the same resources. Continued observations are needed to establish if 2nd- and 3rd-year seedling mortality is higher among seedlings whose growth was retarded by competing annuals and stump sprouts.

The fertilizer and irrigation experiment tested if resources might limit shrub seedling growth in the second post-fire year. The shrub seedlings reacted with a significant growth increase to fertilizer and water addition. The differences between the irrigation only and irrigation + fertilizer treatment in *A. fasciculatum,* although suggestive, were not statistically significant (Table 3). Thus, no clear indication for nutrient deficiency was found.

Overall, the results of this study show that drought is a main factor for shrub seedling mortality in the first year after a burn. During the second year, the seedlings responded with enhanced growth to fertilizer and water addition. The results suggest that the sprouting burls of *A. fasciculatum* plus the abundant seedlings of this species and of *C. greggii* provide more than enough plants to insure perpetuation of these shrubs even after an initial mortality of more than 90% during the first post-fire growing season. Mortality during the second year was insignificant.

ACKNOWLEDGMENTS

This study was supported by NSF-Grant No. DEB-8025977-01. Dr. David Rayle helped in revising a first draft; assistance from Ms. Mildred Johnson and Ms. Robin McQuitty with the manuscript preparation is gratefully acknowledged.

LITERATURE CITED

BOWMAN, W. D. 1984. Seasonal and diurnal changes in water relations parameters in evergreen chaparral shrubs. M.S. thesis, San Diego St. Univ., San Diego, CA.

CORBETT, E. S. and L. R. GREEN. 1965. Emergency revegetation to rehabilitate burned watersheds in southern California. USDA Forest Service, Pac. Southw. For. Range Expt. Sta., Res. Paper PSW-22.

ELLIS, B. A. 1983. Seedling mortality and reestablishment in an early post-fire chaparral community. (Abstract.) Bull. Ecol. Soc. Amer. 64:147.

———, J. R. VERFAILLIE, and J. KUMMEROW. 1983. Nutrient gain from wet and dry atmospheric deposition and rainfall acidity in southern California chaparral. Oecologia 60:118–121.

HANES, T. L. 1971. Succession after fire in the chaparral of southern California. Ecol. Monogr. 41:27–52.

HORTON, J. S. and C. J. KRAEBEL. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology 36:244–262.

JACKS, P. M. 1984. The drought tolerance of *Adenostoma fasciculatum* and *Ceanothus crassifolius* seedlings and vegetation change in the San Gabriel chaparral. M.S. thesis, San Diego St. Univ., San Diego, CA.

KEELEY, J. E. 1982. Distribution of lightning- and man-caused wildfires in California. *In* C. E. Conrad and W. C. Oechel, techn. coord., Dynamics and management of mediterranean-type ecosystems, pp. 431–437. USDA For. Serv., Techn. Rep. No. PSW-58. Pac. Southw. For. Range Expt. Sta., Berkeley, CA.

——— and P. ZEDLER. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seedling strategies. Amer. Midl. Naturalist 99:142–161.

KEELEY, S. C. and J. E. KEELEY. 1982. The role of allelopathy, heat, and charred wood on the germination of chaparral herbs. *In* C. E. Conrad and W. C. Oechel, techn. coord., Dynamics and management of mediterranean-type ecosystems, pp. 128–134. USDA For. Serv., Techn. Rep. No. PSW-58. Pac. Southw. For. Range Expt. Sta., Berkeley, CA.

KUMMEROW, J. and R. K. LANTZ. 1983. Effect of fire on fine root density in redshank (*Adenostoma sparsifolium* Torr.) chaparral. Pl. Soil 70:347–352.

MILLS, J. N. 1983. Herbivory and seedling establishment in post-fire southern California chaparral. Oecologia 60:267–270.

MUSICK, H. B. 1972. Post-fire seedling ecology of two *Ceanothus* species in relation to slope exposure. M.A. thesis, Univ. California, Santa Barbara.

PHILPOT, C. W. 1977. Vegetative features as determinants of fire frequency and intensity. *In* H. A. Mooney and C. E. Conrad, techn. coord., Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems, pp. 12–16. USDA For. Serv., Gen. Techn. Rep. WO-3, Washington, D.C.

RICE, R. M. and L. R. GREEN. 1964. The effect of former plant cover on herbaceous vegetation after fire. J. Forest. (Washington) 62:820–821.

SAMPSON, A. W. 1944. Plant succession of burned chaparral lands in northern California. Calif. Agric. Exp. Sta. Bull. No. 635, 145 pp.

SAUER, J. D. 1977. Fire history, environmental patterns, and species patterns in Santa Monica mountain chaparral. *In* H. A. Mooney and C. E. Conrad, techn. coord., Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems, pp. 383–386. USDA For. Serv., Gen. Techn. Rep. WO-3, Washington, D.C.

SCHLESINGER, W. H., J. T. GRAY, D. S. GILL, and B. E. MAHALL. 1982. *Ceanothus megacarpus* chaparral: a synthesis of ecosystem processes during development and annual growth. Bot. Rev. 48:71–117.

SCHULTZ, A. M., J. L. LAUNCHBAUGH, and H. H. BISWELL. 1955. Relationship between grass density and brush seedling survival. Ecology 36:226–238.

USDA. 1973. Soil survey, San Diego area, California. Part I. USDA, Soil Conserv. Serv., San Diego Co. Planning Dept., San Diego, CA.

(Received 26 Oct 1984; accepted 15 Feb 1985.)

ANNOUNCEMENT

The first segment of a flora for Butte County, California, on the Boraginaceae, initiates the series "Publications from the Herbarium, California State University, Chico." This 35-page pamphlet contains keys to the 31 taxa occurring in Butte County, brief descriptions of the plants, their habitats and (from the literature), their reproductive biology. Thirty detailed range maps are included. For a copy please send $2 to ROB SCHLISING, Department of Biological Sciences, California State University, Chico, CA 95929.

ANNOUNCEMENT

A regional reference herbarium has recently been established at Deep Springs College (located at the south end of the White Mts. in Inyo Co., CA). As curator *in absentia* and a recent alumnus, I am seeking contributions of duplicate specimens from the White Mts., Deep Springs Valley, and the adjacent basins and ranges. A few more exotic species would also be welcomed for teaching purposes. Very common species are already well represented and should be avoided. The collections can be made accessible to outside workers through prior arrangements with the college, and a standard herbarium designation will be obtained when sufficient size is reached. Inquiries or unmounted specimens may be sent to: Professor of Biology, Attn: HERBARIUM, Deep Springs College, CA, *via* Dyer, NV 89010. Specimens received will be acknowledged as tax-deductible contributions; correspondence will, if necessary, be forwarded to me.—JAMES D. MOREFIELD, NAU Box 6201, Northern Arizona Univ., Flagstaff 86011.

SPARTINA (GRAMINEAE) IN NORTHERN CALIFORNIA: DISTRIBUTION AND TAXONOMIC NOTES

DOUGLAS SPICHER and MICHAEL JOSSELYN
Paul F. Romberg Tiburon Center for Environmental Studies,
San Francisco State University, P.O. Box 855,
Tiburon, CA 94920

ABSTRACT

In addition to the native *Spartina foliosa,* four species of *Spartina* have been established in San Francisco Bay by human introduction. One species, *Spartina patens,* has been reported previously and appears to have been introduced accidentally. Three species, *S. alterniflora, S. anglica,* and *S. densiflora,* have been introduced in attempts to establish cordgrass within marsh restoration projects. Only *S. alterniflora* and *S. densiflora* have spread beyond their original sites of introduction. The latter species has been introduced from Humboldt Bay, where it was previously included in the taxon *S. foliosa.* Morphological and ecological data support the conclusion that the species occurring in Humboldt Bay should be referred to as *Spartina densiflora* and was probably introduced to northern California from South America during the mid-nineteenth century.

Mobberley (1956), in his monograph of the genus *Spartina,* cites two species in California: *Spartina foliosa* Trin., found in coastal salt marshes, and *Spartina gracilis* Trin., found along inland alkali lakes and streams. The distribution of *S. foliosa* is given as Baja California to Humboldt and Del Norte Counties by Mobberley (1956), Mason (1957), Munz (1973), and Macdonald and Barbour (1974), whereas Jepson (1925) and Hitchcock (1935) cite San Francisco Bay as being the northern limit. Since these accounts, new information has been gathered on the occurrence of this and several additional *Spartina* species in the salt marshes of northern California.

Coastal SPARTINA *in California. Spartina foliosa* (California cordgrass) is the dominant *Spartina* in southern and central California and San Francisco Bay. Its northern coastal limit occurs north of San Francisco Bay at Bodega Bay. The single patch (ca. 20 m × 30 m) suggests its presence there is recent. *Spartina foliosa* is also present at Bolinas Lagoon and Drakes Estero, but is absent at Tomales Bay even though suitable habitat seems to occur. Macdonald and Barbour (1974) note its "conspicuous absence" here and in several other estuaries and lagoons in California. No *Spartina* occurs north of Bodega Bay until Humboldt Bay and the nearby Eel River delta. In the past, *Spartina* at these two locations was regarded as an ecotype of *S. foliosa* (Mobberley 1956, Gerish 1979, Rogers 1981,

MADROÑO, Vol. 32, No. 3, pp. 158–167, 19 August 1985

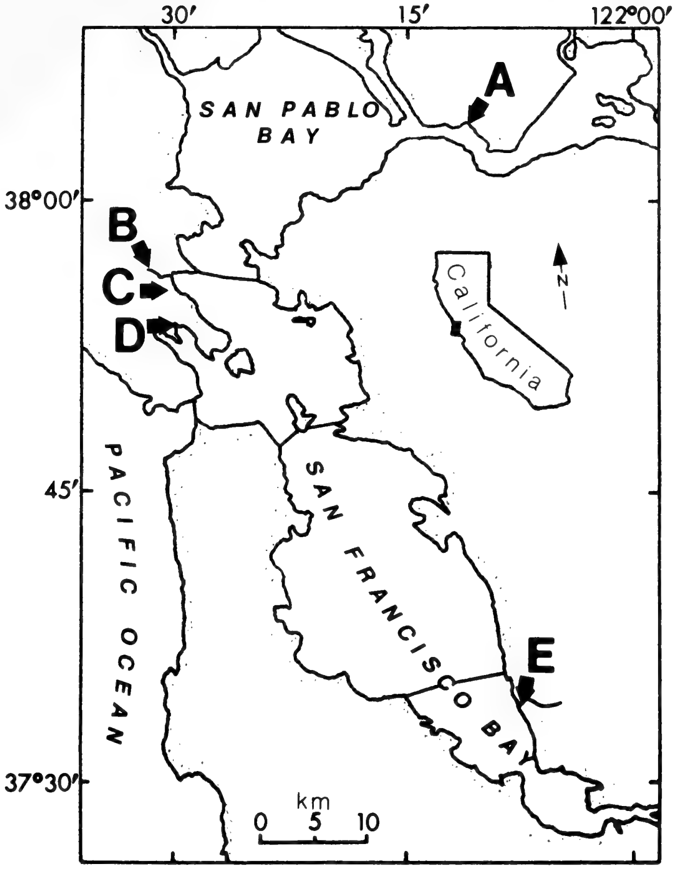


FIG. 1. Locations of introduced *Spartina* spp. in San Francisco Bay. A—Southampton Bay (*S. patens*); B—Creekside Park (*S. densiflora, S. anglica*) and Corte Madera Creek (*S. densiflora*); C—Muzzi Marsh (*S. densiflora*); D—Greenwood Cove (*S. densiflora*); E—Alameda Creek Flood Control Channel (*S. alterniflora*).

Claycomb 1983). However, as discussed in further detail below, ecological and taxonomic investigations have shown it to be a distinct species, *Spartina densiflora* Brong. Despite reports that *Spartina* occurs in Del Norte County (Mason 1957, Munz 1973), we have not seen it north of Humboldt Bay as far as and including Coos Bay, Oregon.

Introduced SPARTINA *in San Francisco Bay.* Until 1973, *Spartina foliosa* was the only *Spartina* described for San Francisco Bay. Since then, four more species have been introduced either accidentally or intentionally: *Spartina patens* (Ait.) Muhl., *Spartina alterniflora* Lois., *Spartina anglica* C. E. Hubbard, and *Spartina densiflora.*

FIG. 2. Introduced *Spartina alterniflora* near the mouth of the Alameda Creek Flood Control Channel. It is taller than *S. foliosa* which is in the foreground.

Munz (1973) reported *Spartina patens* (saltmeadow cordgrass) for Southampton Bay (A—Fig. 1). We found an existing patch, but this species does not appear to have spread from its original location. The second species, *S. alterniflora* (smooth cordgrass), occurs at the mouth of the Alameda Creek Flood Control Channel (E—Fig. 1; Fig. 2) and along the shoreline approximately 3 km to the south. Both of these species are endemic to salt marshes of the eastern United States. The method and precise date of their introduction into San Francisco Bay are unknown.

The third species, *Spartina anglica* (common cordgrass), was introduced at Creekside Park Marsh (B—Fig. 1) from Puget Sound, Washington in 1977 (K. Floyd, pers. comm.). These particular plants have been renamed internationally and misidentified locally in the past, so the use of *S. anglica* requires clarification. Locally in San Francisco Bay, they have been called *Spartina maritima* (K. Floyd, pers. comm., Hedgpeth 1980, Josselyn and Buchholz 1984). Taxonomic descriptions (Mobberley 1956, Hubbard 1968) and herbarium specimens [374220, 466912 (CAS)] clearly indicate these plants are not *S. maritima*; their oversized culms, leaves, and spikelets are among deciding features (Table 1) that place them in *S. anglica.* The name *S. anglica* was coined when two forms of *S. townsendii* (Townsend's cordgrass) were separated nomenclaturally. *Spartina townsendii,* discovered in England in 1870, was regarded as a sterile

TABLE 1. COMPARISON OF MORPHOLOGICAL CHARACTERISTICS BETWEEN *Spartina maritima* AND *S. anglica* AS DESCRIBED BY HUBBARD (1968) AND *S. anglica* FROM CREEKSIDE PARK MARSH, KENTFIELD, CA.

	Species		
Feature	*S. maritima*	*S. anglica*	*S. anglica* (Creekside Park)
Culms	to 50 cm tall	to 130 cm tall	to 126 cm tall
Blades	2–18 cm long to 6 mm wide	10–45 cm long 6–15 mm wide	36–46 cm long 11–13 mm wide
Ligules	0.2–0.6 mm long	2–3 mm long	to 2.5 mm long
Inflorescence	4–10 cm long	12–40 cm long	27–33 cm long
Spikes	1–5 in number	2–12 in number	8–11 in number
Spikelets	11–15 mm long	14–21 mm long	16–20 mm long
Anthers	4–6 mm long	8–13 mm long	8–10 mm long

hybrid resulting from the natural hybridization between the alien *S. alterniflora* from America and the endemic *S. maritima* (Hubbard 1968, Ranwell 1967, 1972). In 1892, a fertile form appeared, apparently a result of natural chromosome doubling (Hubbard 1968, Ranwell 1972). This fertile form remained unnamed until 1968, when Hubbard (1968) gave it the binomial, *Spartina anglica* C. E. Hubbard. The male-sterile hybrid is now *Spartina* × *townsendii* H. and J. Groves (Hubbard 1968).

Because of its aggressive colonization and effective sediment-accreting abilities, *Spartina anglica* (and perhaps *S.* × *townsendii*) ramets were distributed worldwide upon request for creating salt marshes and controlling shoreline erosion (Mobberley 1956, Ranwell 1972, Chung 1983). In 1961 or 1962, as H. M. Austenson noted on a specimen [M155990 (UC)], Washington State University and the U.S. Department of Agriculture introduced *S. townsendii* in Puget Sound, Washington (Snohomish County, Stillaguamish Estuary, near Stanwood). These plants are now known to be *S. anglica* because ramets of these plants introduced at Creekside Park Marsh flowered and produced 20% viable seeds in 1983. No flowering occurred in 1984.

Spartina densiflora (Humboldt cordgrass) is the fourth *Spartina* introduced in San Francisco Bay. As mentioned previously, this species was introduced at Creekside Park Marsh in 1977, and was thought to be an ecotype of *S. foliosa.* Its present distribution in San Francisco Bay is limited to Marin County: at Creekside Park Marsh and Corte Madera Creek, Muzzi Marsh, and Greenwood Cove (Fig. 1).

Taxonomy of the Humboldt Bay SPARTINA. In 1932, the identity of the *Spartina* growing in Humboldt Bay was questioned when Saint-Yves (1932) annotated a specimen identified earlier as *S. fo-*

TABLE 2. COMPARISON OF MORPHOLOGIC, PHENOLOGIC, AND ECOLOGIC CHARACTERISTICS BETWEEN *Spartina foliosa, S. densiflora* AT CREEKSIDE PARK MARSH, AND *S. densiflora* IN SOUTH AMERICA AS DESCRIBED BY MOBBERLEY (1956). Information for *S. foliosa* is from Mobberley (1956), except where noted, and for *S. densiflora* in Creekside Park from Spicher (1984). [a]—Kasapligil (1976), [b]—Spicher (1984).

	Species		
Feature	*S. foliosa*	*S. densiflora* (Creekside Park)	*S. densiflora* (Mobberley 1956)
Culms	to 1.5 m tall (to 2 m)[a]	to 1.4 m tall	to 1.5 m tall
	fleshy	indurate	indurate
	evenly spaced from rhizomes	caespitose from knotty bases	caespitose from knotty bases
Blades	flat to loosely involute	involute	involute
	8–12 mm wide[a]	6–7 mm wide	3–8 mm wide
	adaxial surface glabrous	adaxial surface scabrous	adaxial surface scabrous
	abaxial surface glabrous	abaxial surface glabrous	abaxial surface glabrous
	36–50 blade ridges[a]	9–10 blade ridges	—
Inflorescence	12–25 cm long	8–23 cm long	10–30 cm long
	—	5–10 mm wide	4–8 mm wide
Spikes	4–10[a]	6–20	2–15
	2–8 cm long	1–5.5 cm long	1–11 cm long
Spikelets	8–30	5–27	10–30
	8–25 mm long	9–12 mm long	8–14 mm long
Flowering period	July to November	April to July	—
Seed set	October–November[b]	August	—
Habitat elevation	1.1–2.7 feet (NGVD)[b]	2.0–3.6 feet (NGVD)	—

FIG. 3. Individual tussocks of *Spartina densiflora* at Creekside Park Marsh occupy slightly higher elevations (A) while *Spartina foliosa* forms meadow-like stands nearer channels (B).

liosa by Hitchcock to be *Spartina densiflora* Brong. forma *acuta* St. Y. Mobberley (1956) rejected Saint-Yves' reidentification, stating that Saint-Yves based his decision only on the smaller spikelet lengths of the Humboldt Bay species. However, Saint-Yves (1932) based his opinion on three features: difference in spikelet lengths, difference in foliar structure, and strongly keeled glumes in the Humboldt Bay *Spartina.*

Mobberley (1956) subdivided *Spartina* into three species complexes. The first contains species with numerous short, closely imbricate spikes, hard slender culms, and short (or even lacking) rhizomes (e.g., *S. spartinae*). Complex two is characterized by species with thick, succulent, fleshy culms that grow from solitary bases or in small clumps; spikelets are usually less closely imbricate. These plants rarely show purple coloration (e.g., *S. foliosa*). The third complex contains species with indurate culms, more or less spreading spikes with closely imbricate spikelets, and very often are streaked or tinted with purple color. *Spartina patens* and *S. densiflora* are members of this group.

A comparison of some morphological, phenological, and ecological characters of the Humboldt Bay *Spartina* with those of *S. foliosa* and *S. densiflora* were made from living and herbarium specimens (Table 2). The caespitose habit of the Humboldt *Spartina,* which differs from the solitary, evenly-spaced culms of *S. foliosa,* is the most visible difference between the two species (Fig. 3). The Humboldt Bay *Spartina* possesses all the characteristics of Mobberley's third complex (*S. densiflora*) except for its usually appressed-imbricate spikes. Mobberley (1956) amends his general rule for *S. densiflora,* however, which possesses appressed spikes.

There was speculation that the *Spartina* in Humboldt Bay was *S. spartinae* (Gerish 1979). *Spartina densiflora* does share some characteristics with *S. spartinae,* but Mobberley (1956) distinguished *S. densiflora* and *S. spartinae* in South America as follows:

1) spikelets of *S. densiflora* exceed 8 mm, whereas those of *S. spartinae* do not exceed 7 mm (some N. American specimens to 10 mm)
2) trichomes of *S. densiflora* are short, rigid, and slender; they are about one-half as long as the thicker trichomes of *S. spartinae*
3) the first glume of *S. densiflora* is about one-half as long as the second; rarely is the first shorter by more than 2 mm in any of the other *Spartina* spp., including *S. spartinae*

The differences between herbarium specimens (CAS, UC) (Table 3) of *Spartina spartinae* and *S. densiflora* were found generally to be true. Not all characteristics are necessarily found in every spikelet, but the smaller spikelets and longer, thicker trichomes on the spikelets of the *S. spartinae* inflorescence give it a tighter and more pubescent appearance than in the inflorescence of *S. densiflora.* The spikelets and inflorescences of the Humboldt Bay *Spartina* closely resemble those of *S. densiflora.*

Gerish (1979) found the chromosome number of the Humboldt Bay *Spartina* to be $2n = 60$, the same number counted for *S. foliosa* by Parnell (1976). Gerish inferred that the Humboldt Bay *Spartina* was from *S. foliosa* genetic stock and that any morphological differences were caused by genotypic or phenotypic processes. Although the chromosome numbers match, this single common denominator does not demonstrate conclusively that they are the same species. Many species in the genus have identical chromosome numbers (Moore 1973, Goldblatt 1981).

SPARTINA DENSIFLORA *introduction to North America. Spartina densiflora* is almost certainly not native to Humboldt Bay. Its distribution was reported previously only in South America below the 23rd parallel (Mobberley 1956). If it were a North American native, it would be expected to occur more extensively than in just one location.

Therefore, *Spartina densiflora* was probably introduced into Humboldt Bay, as were many organisms in other estuaries of Cal-

TABLE 3. IDENTIFICATION NUMBERS OF HERBARIUM SPECIMENS STUDIED IN COMPARING THREE *Spartina* SPECIES AT THE UNIVERSITY OF CALIFORNIA HERBARIUM, BERKELEY AND AT THE CALIFORNIA ACADEMY OF SCIENCES, SAN FRANCISCO. Locations where specimens were collected are abbreviated in parentheses [California (CA), Texas (TX), Louisiana (LA), Florida (FL), Mexico (MX), Brazil (BR), Uruguay (UR), Argentina (AR), Costa Rica (CR)].

	Specimen identification number		
Herbarium location	*Spartina foliosa* Trin.	*Spartina densiflora* Brong.	*Spartina spartinae* Trin.
UC Berkeley	M260502 (CA)	298388 (UR)	M153237 (TX)
		MO47062 (BR)	821629 (TX)
		MO27317 (BR)	35760 (MX)
		627472 (AR)	
		627546 (AR)	
		MO25678 (UR)	
California Academy of Sciences	444653 (MX)	101351 (AR)	303562 (CR)
	368772 (CA)		686493 (MX)
	440197 (CA)		382866 (FL)
	386343 (CA)		182083 (LA)
	418931 (CA)		
	274331 (CA)		
	101332 (CA)		

ifornia in modern times. In San Francisco Bay after 1850 for example, organisms were introduced unintentionally by ships from foreign lands. Among these organisms were many marsh plant species, including *Atriplex semibaccata* (L.) Presl. (Australia) and *Cotula coronopifolia* L. (South Africa) (Munz 1973, Atwater et al. 1979).

Similarly, *Spartina densiflora* may have been introduced from Chile. During the 1850s and early 1860s, Chile experienced a period of rapid economic growth that created a demand for processed lumber, much of which was supplied from the northern California coast and Humboldt Bay (Cox 1974, Carranco 1982). Many company-owned lumber ships returned from South America without heavy cargo. For stabilization these ships often took on solid ballast gathered from the shoreline. The Chilean beachhopper, *Orchestia chiliensis,* was introduced to San Francisco Bay in this manner, by the "Discharge of shingle ballast (stones, algae, and debris gathered from beaches) by lumber ships returning from Chile in or before 1900 . . ." (Carlton 1975). Similarly, we propose that seeds of *S. densiflora* were brought to Humboldt Bay from Chile. Spicher (1984) showed that the seeds of this species are tolerant of long periods of storage in either dry or moist conditions. In addition, Mobberley (1956) found *S. densiflora* spikes to shorten in length and increase in number on inflorescences of plants from north to south along the east coast of South America and across to Chile. The greater number and shorter spikes of the Humboldt Bay *Spartina* (Table 2) reflect what might be expected in *S. densiflora* from Chile.

ACKNOWLEDGMENTS

We acknowledge the discovery of *S. foliosa* in Bodega Bay by J. W. Buchholz and *S. alterniflora* at points south of the Alameda Flood Control Channel by T. E. Harvey. We thank M. Barkworth and an anonymous reviewer for their comments on an earlier draft of this paper, and Dr. Stanley Williams and Dr. Robert Patterson for their suggestions. This research was supported in part by a grant from the San Francisco Foundation.

LITERATURE CITED

ATWATER, B. F., S. G. CONRAD, J. N. DOWDEN, C. W. HEDEL, R. L. MACDONALD, and W. SAVAGE. 1979. History, landforms, and vegetation of the estuary's tidal marshes. *In* T. J. Conomos, ed., San Francisco Bay: the urbanized estuary, pp. 347–385. Pacific Division, Amer. Assoc. Advanc. Sci., San Francisco, CA.

CARLTON, J. T. 1975. Introduced intertidal invertebrates. *In* R. I. Smith and J. T. Carlton, eds., Light's manual: intertidal invertebrates of the central California coast, pp. 17–25. Univ. Calif. Press, Berkeley.

CARRANCO, L. 1982. Redwood lumber industry. Golden West Books, San Marino, CA.

CHUNG, CHUNG-HSIN. 1983. Geographical distribution of *Spartina anglica* C. E. Hubbard in China. Bull. Marine Sci. 33:753–758.

CLAYCOMB, D. W. 1983. Vegetational changes in a tidal marsh restoration project at Humboldt Bay, California. M.A. thesis, Humboldt State Univ., Arcata, CA.

COX, T. R. 1974. Mills and markets: a history of the Pacific coast lumber industry to 1900. Univ. Washington Press, Seattle.

GERISH, W. 1979. Chromosomal analysis of a previously unidentified *Spartina* species. M.A. thesis, Long Island Univ., Long Island, NY.

GOLDBLATT, P. 1981. Index to plant chromosome numbers 1975–1978. Missouri Bot. Gard., St. Louis.

HEDGPETH, J. W. 1980. The problem of introduced species in management and mitigation. Helgolander Meeresunters. 33:662–673.

HITCHCOCK, A. S. 1935. Manual of the grasses of the United States. USDA Misc. Publ. No. 200, Washington, D.C.

HUBBARD, C. E. 1968. Grasses: a guide to their structure, identification, uses, and distribution in the British Isles. Penguin Books Ltd., Middlesex, England.

JEPSON, W. L. 1925. Manual of the flowering plants of California. Assoc. Students Bookstore, Univ. Calif., Berkeley.

JOSSELYN, M. N. and J. W. BUCHHOLZ. 1984. Marsh restoration in San Francisco Bay: a guide to design and planning. Techn. Report No. 3. Tiburon Center for Environmental Studies, San Francisco State Univ., Tiburon, CA.

KASAPLIGIL, B. 1976. A synoptic report on the morphology and ecological anatomy of *Spartina foliosa* Trin. Appendix C in U.S. Army Corps of Engineers, Dredge Disposal Study, San Francisco Bay and Estuary, Appendix K. San Francisco, CA.

MACDONALD, K. B. and M. G. BARBOUR. 1974. Beach and salt marsh vegetation of the North American Pacific Coast. *In* R. J. Reimold and W. H. Queen, eds., Ecology of halophytes, pp. 175–233. Academic Press, NY.

MASON, H. L. 1957. A flora of the marshes of California. Univ. Calif. Press, Berkeley.

MOBBERLEY, D. G. 1956. Taxonomy and distribution of the genus *Spartina*. Iowa State J. Sci. 30:71–574.

MOORE, R. J. 1973. Index to plant chromosome numbers 1967–1971. Oosthoek's Uitgeversmaatschappij B. V., Utrecht, Netherlands.

MUNZ, P. A. 1973. A California flora and supplement. Univ. Calif. Press, Berkeley.

PARNELL, D. R. 1976. Chromosome numbers in growth forms of *Spartina foliosa* Trin. Appendix D in U.S. Army Corps of Engineers, Dredge Disposal Study, San Francisco Bay and Estuary, Appendix K. San Francisco, CA.

RANWELL, D. S. 1967. World resources of *Spartina townsendii* (sensu lato) and economic use of *Spartina* marshland. J. Appl. Ecol. 4:239–256.

———. 1972. Ecology of salt marshes and sand dunes. Chapman and Hall, London.

ROGERS, J. D. 1981. Net primary productivity of *Spartina foliosa, Salicornia virginica,* and *Distichlis spicata* in salt marshes at Humboldt Bay, California. M.A. thesis, Humboldt State Univ., Arcata, CA.

SAINT-YVES, A. 1932. Monographia Spartinarem. Candollea 5:19–100.

SPICHER, D. P. 1984. The ecology of a caespitose cordgrass (*Spartina* sp.) introduced to San Francisco Bay. M.A. thesis, San Francisco State Univ., San Francisco, CA.

(Received 24 Oct 1984; accepted 19 Feb 1985.)

ANNOUNCEMENT

The Executive Council of the California Botanical Society is pleased to announce that Mr. Wayne R. Ferren, Jr., has been appointed Editor of Madroño to follow the term served by Dr. Christopher Davidson. Dr. J. Robert Haller has been appointed Associate Editor. All manuscripts to be submitted to Madroño for review, and all inquiries concerning manuscripts submitted previously, should be directed to the Editor or Associate Editor, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

THE SYSTEMATIC RELATIONSHIP OF *ASARINA PROCUMBENS* TO NEW WORLD SPECIES IN TRIBE ANTIRRHINEAE (SCROPHULARIACEAE)

WAYNE J. ELISENS
Department of Botany and Microbiology,
University of Oklahoma, Norman 73019

ABSTRACT

A broad-based examination of *Asarina* s. str. has been undertaken to elucidate its systematic and phytogeographic relationship to New World species in tribe Antirrhineae. *Asarina procumbens* is differentiated from Old World and New World species by a combination of distinctive characters: procumbent stems, opposite leaves, orbiculate to reniform laminas, solitary flowers in leaf axils, large personate corollas, and globose capsules. Although the pollen morphology and seed coat anatomy of *Asarina* s. str. are shared with some taxa in the New World, *A. procumbens* is cross-incompatible with purported congeneric species and differs from native American species by three unique features: opposite leaves with orbiculate to cordiform laminas, a chromosome base number of nine, and a bullate-corrugate seed coat ornamentation. It is hypothesized that *A. procumbens* is more closely related to Old World species, that *Asarina* sensu Pennell delimits an unnatural and heterogeneous assemblage of species, and that *Asarina,* unlike *Antirrhinum,* does not represent a genus with a North American—European Mediterranean disjunction.

Asarina procumbens Mill. is an herbaceous perennial in tribe Antirrhineae confined to calcareous habitats from 300 to 800 m in the Pyrenees Mountains of southern France and northeastern Spain. This species has been recognized in most twentieth century treatments of the Scrophulariaceae (Rothmaler 1943; but not in Melchior 1964) and the European flora (Hartl 1965, Webb 1972) as the sole species constituting the genus *Asarina* Mill. Although many authors (Bentham 1846, Wettstein 1891, Rothmaler 1943) have recognized *Asarina* s. str. as a monotypic taxon, its ranking at the level of genus has not been uniform. *Asarina* has been either accorded generic rank (e.g., Quer y Martinez 1762, Moench 1802) or recognized as a subgenus (Reichenbach 1828, Rouy 1909) or section (Chavannes 1833,Bentham 1846, 1876, Wettstein 1891) in *Antirrhinum* L. *Asarina procumbens* has been segregated from Old World species in *Antirrhinum* and from species in New World *Antirrhinum* sect. *Saerorhinum* A. Gray (sensu Rothmaler 1956) on the basis of several distinctive vegetative, floral, and fruit characters (Rothmaler 1943).

Contrary to most supraspecific concepts in the tribe, *Asarina*'s taxonomic boundaries were greatly expanded when Pennell (1947) transferred 15 North American species into it and did not delineate

MADROÑO, Vol. 32, No. 3, pp. 168–178, 19 August 1985

any infrageneric groups. The species included in Pennell's amplified genus had previously been treated in several supraspecific taxa by other authors. For example, Bentham (1876) and Wettstein (1891) had recognized the species in *Asarina* sensu Pennell in five sections in two genera (*Antirrhinum* sects. *Asarina* and *Maurandella* A. Gray; *Maurandya* Ort. sects. *Eumaurandya* (A. Gray) I. M. Johnst., *Epixiphium* (Engelm. ex A. Gray) A. Gray, and *Lophospermum* (D. Don) A. Gray); Rothmaler (1943) had placed the taxa in six genera (*Asarina, Neogaerrhinum* Rothm., *Maurandella* (A. Gray) Rothm., *Maurandya, Epixiphium* (Engelm. ex A. Gray) Munz, and *Lophospermum* D. Don).

The rationale behind Pennell's mass transfer was "the form of the foliage and also the large flaring corollas . . ." (Pennell 1947, p. 174) supposedly shared by *A. procumbens* and some native American taxa. The floral diversity encompassed in Pennell's expanded *Asarina* was dismissed as adaptation to specific pollinators; polymorphism among other key characters (e.g., capsule shape, seed ornamentation, phyllotaxy, lamina outline and venation, stem type) was not addressed. Although certain authors regarded Pennell's (1947) expanded *Asarina* as unnatural (Johnston 1950, Munz 1959), *Asarina* sensu Pennell has been followed in some recent taxonomic, floristic, and horticultural treatments (DeWolf 1956, Shreve and Wiggins 1968, St. John 1973, Bailey and Bailey 1976, Wiggins 1980).

In order to assess critically the taxonomic and phylogenetic relationships of *Asarina* s. str., an examination of *A. procumbens* has been undertaken that incorporates morphological, geographical, anatomical, chromosomal, palynological, and crossability data. The present study represents the first report of seed coat microsculpturing and anatomical pattern, pollen morphology, and artificial hybridization with New World species for *A. procumbens.* It also presents the first published chromosome count for a species in *Neogaerrhinum.* The primary aims of the investigation have been to gather new systematic information on *A. procumbens,* assess the data to elucidate the tribal affinities of *Asarina* s. str., and evaluate Pennell's (1947) expanded generic concept of *Asarina.* The nomenclature used in the text has followed Rothmaler (1943) or Elisens (1985a).

MATERIALS AND METHODS

Comparative macromorphological studies of *Asarina procumbens* have been based on examination of herbarium specimens from F, MO, NY, PH, TEX-LL, and US as well as material cultivated from seed supplied by the Barcelona, Dijon, and Leipzig botanical gardens. Voucher specimens for all descriptive and experimental studies are on deposit at the University of Texas Herbarium (TEX); collection data are listed in the Appendix.

Mature seeds for morphological and anatomical studies were based on samples supplied by botanical gardens. Each sample was 1) prepared for and examined with scanning electron microscopy (SEM) and 2) paraffin-embedded, stained, sectioned, and observed using light microscopy. Preparative procedures and materials were similar to those reported in Elisens and Tomb (1983) and Elisens (1985b).

Bud material for meiotic chromosome counts was obtained from glasshouse-grown individuals propagated from seed supplied by botanical gardens (*A. procumbens*) or the author's field collections (*Neogaerrhinum*). Buds were fixed in freshly mixed chloroform, absolute ethanol, and glacial acetic acid (4:3:1, v/v/v). Root-tips for mitotic counts were obtained from germinating seeds treated in a saturated 8-hydroxyquinoline solution. Chromosomes were stained with aceto-orcein.

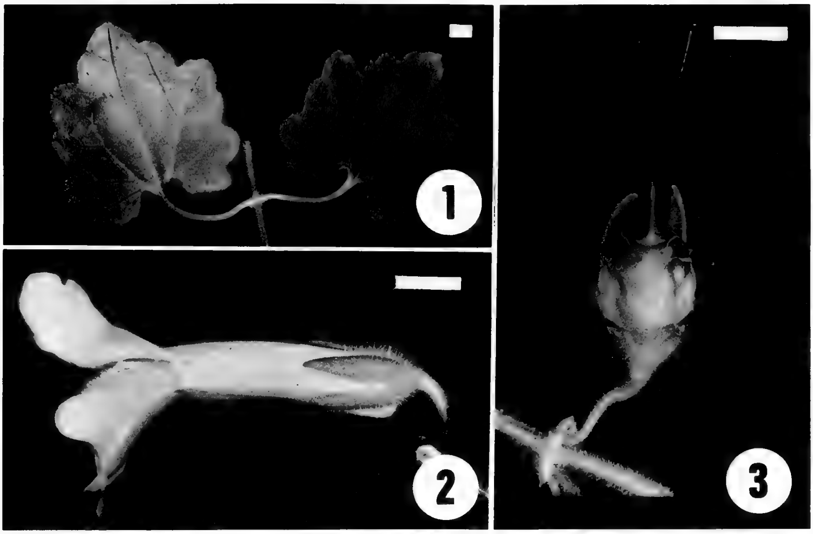
Pollen grains, obtained from fresh anthers, were dehydrated in acetic acid, acetolysed, and prepared using procedures and materials outlined in Elisens (1985a). The glycerin jelly-mounted grains were measured using light microscopy and observed and photographed using the SEM facilities at the Kansas Agricultural Experiment Station. Terminology for the exo- and endomorphology is that of Moore and Webb (1978).

Investigations of reproductive biology were conducted on plants from 13 populations representing 12 species in *Asarina* sensu Pennell that were grown from field-collected seed (North American taxa) or seed supplied by botanical gardens (*Asarina procumbens*) in the glasshouse facilities at the University of Texas and Miami University. Crossability and compatibility studies were undertaken on emasculated flowers with hand pollinations performed with fresh pollen using forceps dipped in 95% ethanol after each pollen transfer. Artificial pollinations that resulted in capsule development and seed set were considered successful crosses. Estimates of pollen fertilities were determined using cotton blue in lactophenol; 300 grains were scored for each flower and 2–3 flowers were examined per individual.

RESULTS

Within tribe Antirrhineae, *Asarina* s. str. is distinctive because of its procumbent stems, opposite leaves, orbiculate to cordiform, glandular-pubescent laminas and palmate venation (Fig. 1); solitary, axillary flowers; lanceolate, apically-distinct calyx segments and large personate corollas (Fig. 2); and globose symmetric capsules (Fig. 3). No other taxon in the Antirrhineae has this combination of macromorphological characters. An opposite leaf arrangement with orbiculate to cordiform laminas is not found among any New World taxon.

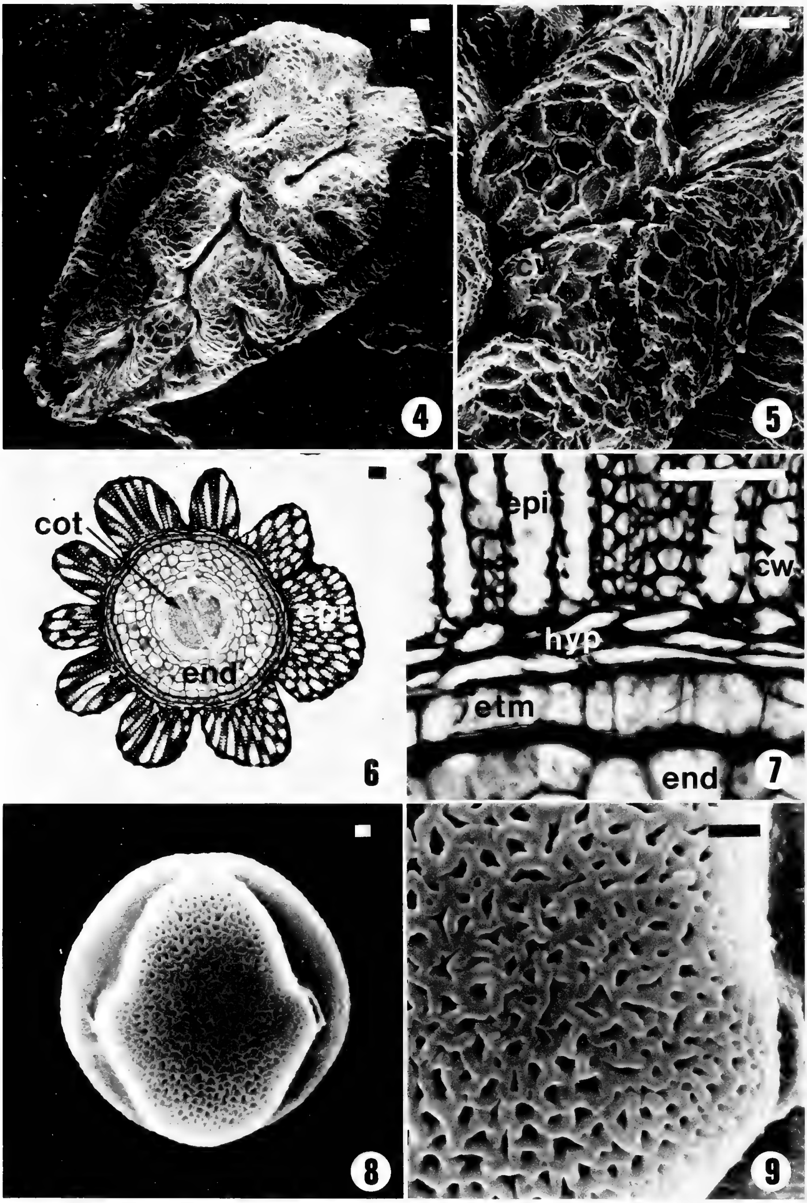
The bullate-corrugate seed coat ornamentation pattern (Fig. 4) of



FIGS. 1–3. Photographs of distinctive morphological features of *Asarina procumbens, Elisens 799.* Scale lines equal 5.0 mm. FIG. 1. Leaf attachment, outline, and vestiture; left leaf abaxial surface, right leaf adaxial surface. FIG. 2. Calyx and corolla. FIG. 3. Mature capsule; three calyx segments removed.

A. procumbens is different from the seed morphology of any New World species in the tribe. The expanded crests on the seed surface form a characteristic reticulated pattern and are covered with interconnected ridges of low relief made up of radial cell walls (Fig. 5). The outer epidermal cell walls lack any protuberances (Fig. 5) similar to those found on expanded crests and tubercles in *Maurandya* and *Lophospermum* (Elisens and Tomb 1983). Mean seed lengths within *A. procumbens* are 1.52 mm long (SD = 0.16 mm, n = 60); the seeds weigh an average 0.20 mg (n = 100). The seed coat anatomical pattern of *A. procumbens* is an epidermis with 90% to 95% of the cells radially elongate (Fig. 6) and a hypodermis of one to three flattened layers (Fig. 7). Reticulated thickenings are present in the epidermal cells (Figs. 6, 7) and are responsible for the ribbed appearance of the radial cell walls visible on the seed surface (Fig. 5). The differentially elongated epidermal cells are solely responsible for the exotestal relief (previously noted by Bachmann 1880).

The pollen morphology of *A. procumbens* was examined from one collection. The grains are subspheroidal, trizonocolporate (Fig. 8), and have a perforate-tectate exine pattern (Fig. 9) with the perforations less than 1 μm in diameter. The mean equatorial diameter



FIGS. 4–9. Photomicrographs of seed and pollen of *Asarina procumbens.* Key to labeling: cot, cotyledon; cw, cell wall; emb, embryo; end, endosperm; epi, epidermis; etm, endothelium; hyp, hypodermis. FIGS. 4–5. Scanning electron micrographs, seed; *Elisens 613.* Scale lines equal 0.05 mm. FIGS. 6–7. Light micrographs, transversely-sectioned seed; *Elisens 613.* Scale lines equal 0.05 mm. FIGS. 8–9. Scanning electron micrographs, pollen; *Elisens 799.* Scale lines equal 1 μm.

of the pollen is 19.81 μm with a polar diameter/equatorial diameter (P/E) ratio of 1.13.

The chromosome base number of *A. procumbens* is $x = 9$. Meiotic chromosome number determinations for *A. procumbens* were obtained from two collections. These counts, as well as Jackson's (1971) unpublished ones from four European botanical garden seed samples, verify the $2n = 18$ reported by Heitz (1927). A mitotic count of $2n = 30$ was also obtained for one population of *Neogaerrhinum filipes* (see Appendix).

Crossability studies have been undertaken between *A. procumbens* and 11 American species in *Asarina* sensu Pennell. Even though pollen fertilities (93%–98%) were uniformly high for all plants, the twenty directional crosses attempted (162 hand pollinations) resulted in no capsule or seed set. In all instances, gynoecia from emasculated flowers of *A. procumbens* aborted within two weeks after anthesis whether they received no pollen or pollen from the other species. Reciprocal crosses also resulted in ovary abortion. Untreated flowers had successful capsule and seed set (25/25) indicating that *A. procumbens* is self-compatible and autogamous. Because unpollinated emasculated flowers or those pollinated from different species did not set capsules, *A. procumbens* exhibited no evidence of apomixis. Purported congeners in Pennell's (1947) expanded *Asarina* are uniformly self-compatible, autogamous (except for *Mabrya geniculata* (Rob. & Fernald) Elisens), and also showed no evidence of apomixis (Elisens 1985a).

DISCUSSION

The systematic information reported in this study supports the taxonomic segregation of *Asarina* s. str. from Old World and New World genera in tribe Antirrhineae. Among the New World taxa, *A. procumbens* can be readily distinguished from each native genus by a combination of distinctive characters. Additionally, *A. procumbens* has several unique characters not found in any native American species: an opposite phyllotaxy with orbiculate to reniform laminas, a bullate-corrugate seed surface sculpturing pattern, and a chromosome base number of nine. The pollen morphology and testal anatomy are shared with some New World taxa.

Among seeds of New World taxa, the bullate-corrugate exotestal ornamentation pattern is most similar to the tumid tuberculate/cristate pattern found on seeds in *Maurandya* subg. *Maurandya* and some *Mabrya* Elisens species (Elisens and Tomb 1983, Elisens 1985a). The seed surfaces of the last two taxa have minute protuberances on the outer tangential and radial epidermal cell walls; similar protuberances are lacking on the seeds of *A. procumbens.* Mean seed lengths and weights are in the range of the nonalate seeds of *Mau-*

randya and *Mabrya* (Elisens and Tomb 1983). The seed coat anatomical pattern of *A. procumbens* is similar to testae of *Maurandya* subg. *Maurandya, Mabrya,* and *Holmgrenanthe* Elisens (Elisens 1985b). The testal anatomy of very few Old World species has been examined (Bachmann 1880). Both the seed coat morphological and anatomical pattern of *Antirrhinum* sect. *Saerorhinum, Neogaerrhinum, Pseudorontium* (A. Gray) Rothm., *Gambelia* Nutt., and other *Antirrhinum* segregates in the New World are different from *Asarina procumbens* (Elisens and Tomb 1983, Elisens 1985b).

The pollen exine pattern of *A. procumbens* is found also in *Maurandya, Mabrya, Lophospermum* (Elisens 1985a), *Neogaerrhinum, Galvezia* Dombey ex Juss., and some Old World and New World *Antirrhinum* species (Elisens, unpubl. data). Similar mean equatorial pollen diameters to *A. procumbens* are found among New World species (15.74 to 25.54 μm). The pollen P/E ratio of *A. procumbens* (1.13) is slightly outside the range of the American species (0.96 to 1.10) except for *Linaria texana* Scheele which has a P/E of 1.34 and some Old World species in *Antirrhinum* and *Chaenarrhinum* Reichb. (Elisens, unpubl. data). Because the pollen exine pattern, dimensions, and shape of *A. procumbens* are widespread in the Antirrhineae, pollen morphology appears to be of limited utility in elucidating the taxonomic or phylogenetic relationships of *Asarina* s. str.

No New World species in tribe Antirrhineae has a base chromosome number of nine, although *Anarrhinum* Desf. and *Kickxia* Dumort. are Old World genera with $x = 9$. Other Old World base numbers are $x = 8$, 7, and 6 (Fedorov 1969). New World tribal base numbers are 15 (*Galvezia, Mohavea* A. Gray, some *Antirrhinum* species, *Neogaerrhinum*), 13 (*Pseudorontium*), 12 (*Maurandya, Mabrya, Lophospermum*), 8 (*Antirrhinum*), and 6 (*Linaria* Mill.) (Günther and Rothmaler 1963, Raven et al. 1965, Jackson and Spellenberg 1973). The New World and Old World base numbers suggest that aneuploidy has been important in trans-specific evolution in the Antirrhineae (Elisens 1985a). If this is the case, the base number of nine for *Asarina* s. str. is clearly anomalous in the New World.

The Old World distribution of *A. procumbens* does not preclude automatically the segregation of *Asarina* s. str. from New World genera. Within the Antirrhineae, *Antirrhinum* and *Linaria* have Old World and New World species, although New World species in these genera usually are placed in different sections. Several North American species in *Antirrhinum* occur in habitats similar to *A. procumbens*; *Antirrhinum* also has a North American–European Mediterranean disjunct pattern (Rothmaler 1956, Raven 1973). The marked morphological and chromosomal differentiation of *A. procumbens* from New World Antirrhineae suggest, however, that *Asarina* s. str. is phylogenetically distant from New World species in *Antirrhinum* and other native American taxa.

The complete cross-incompatibility of *Asarina procumbens* with eleven species from *Neogaerrhinum* (=*Antirrhinum* sect. *Maurandella* p.p.), *Maurandya, Mabrya,* and *Lophospermum* further reinforces the view that *Asarina* s. str. is evolutionarily very distant from New World genera in the Antirrhineae. Species from these four genera were transferred into *Asarina* by Pennell (1947). As noted by Grant (1981), the general interspecific crossability pattern in the Scrophulariaceae (and many perennial herbs with prominent species-to-species differences in floral mechanism) is for congeneric species to be interfertile within wide limits (e.g., Garber and Gorsic 1956, Yeo 1966, Vickery 1978). This pattern occurs within the Antirrhineae in *Antirrhinum* (Baur 1932, Mather 1947), *Linaria* (Viano 1978), and subtribe Maurandyinae (Elisens 1982). Baur (1914, 1932) has previously demonstrated that *Asarina procumbens* is cross-incompatible with several Old World *Antirrhinum* species as well.

Asarina sensu Pennell (1947) is extremely polymorphic and incorporates three chromosome base numbers (15, 12, 9), suggesting that Pennell's expanded genus is an unnatural assemblage of species. The heterogeneity within the amplified *Asarina* is in distinct contrast to the variation pattern characteristic of most generic concepts in the tribe (e.g., Wettstein 1891, Rothmaler 1943, Elisens 1985a, D. Sutton, unpubl. data). Other than solitary flowers in the leaf axils (found in other taxa in the tribe), most potentially unifying characters in *Asarina* sensu Pennell (1947) are those generally used to characterize the tribe or family. Not even *Linaria* or *Antirrhinum,* the largest genera in the Antirrhineae, encompass the morphological diversity of stem, leaf, floral, and fruit characters found in *Asarina* s. lat. Pennell based his expanded genus concept on very few morphological characters: stem type, lamina outline, corolla type, and, to a lesser extent, capsule shape; none of these "key" characters is monomorphic within his boundaries of *Asarina.* The expanded genus can be divided into several chromosomally- and morphologically-coherent segregate taxa, such as the four genera constituting subtribe Maurandyinae (Elisens 1985a) and the genus *Neogaerrhinum* (Rothmaler 1943).

In summary, the findings of the present study indicate that *Asarina procumbens* is morphologically, chromosomally, and geographically different from its purported New World congeners or any New World Antirrhineae species. Furthermore, it is recommended that neither the generic concept of Pennell (1947) nor the purported North American—European Mediterranean disjunction in *Asarina* be recognized. Considering its chromosome base number, shared by other Old World Antirrhineae, and a restricted distribution in the Mediterranean region, where generic diversity among Old World Antirrhineae is the greatest, *A. procumbens* evidently is more closely allied to taxa in the Old World. Even though its relationship among Old

World species in tribe Antirrhineae is obscure, it seems unnecessary and incorrect to look in the southwestern United States and Mexico for its relatives.

ACKNOWLEDGMENTS

The author thanks T. G. Lammers and J. J. Furlow for their comments on an earlier draft of the manuscript. Thanks are also extended to A. S. Tomb for his help in obtaining access to the SEM facilities at the Kansas Agricultural Experiment Station and to G. L. Floyd for use of his darkroom facilities.

LITERATURE CITED

BACHMANN, E. 1880. Die Entwickelungsgeschichte und der Bau der Samenschalen der Scrophularinee. Nova Acta Acad. Caes. Leop.-Carol. German Nat. Cur. 43: 1–179.

BAILEY, L. H. and E. Z. BAILEY (compilers). 1976. Hortus third (revised by the staff of Liberty Hyde Bailey Hortorium). Macmillan, NY.

BAUR, E. 1914. Einführung in die experimentelle Vererbungslehre. Borntraeger, Berlin.

———. 1932. Artumgrenzung und Artbildung in der Gattung *Antirrhinum,* Sektion *Antirrhinastrum.* Z. Indukt. Abstammungs- Vererbungsl. 63:256–302.

BENTHAM, G. 1846. Scrophulariaceae. *In* A. DeCandolle, Prodromus systematis naturalis regni vegetabilis 10:186–586.

———. 1876. Scrophularineae. *In* G. Bentham and J. D. Hooker, Genera plantarum 2:913–980. Reeve and Co., London.

CHAVANNES, E. 1833. Monographie des Antirrhinées. Treuttel and Wurtz, Paris.

DEWOLF, G. P. 1956. Notes on cultivated Scrophulariaceae 2. *Antirrhinum* and *Asarina.* Baileya 4:55–68.

ELISENS, W. J. 1982. A taxonomic monograph of the Maurandyinae. Ph.D. dissertation, Univ. Texas, Austin.

———. 1985a. Monograph of the Maurandyinae (Scrophulariaceae—Antirrhineae). Syst. Bot. Mongr. vol. 5.

———. 1985b. The systematic significance of seed coat anatomy among New World species in tribe Antirrhineae (Scrophulariaceae). Syst. Bot. 10: in press.

——— and A. S. TOMB. 1983. Seed coat morphology in New World Antirrhineae: systematic and phylogenetic implications. Pl. Syst. Evol. 142:23–47.

FEDOROV, A. A., ed. 1969. Chromosome numbers of flowering plants. Acad. Sci. USSR, L. Komarov Bot. Inst., Leningrad.

GARBER, E. D. and J. GORSIC. 1956. The genus *Collinsia* II. Interspecific hybrids involving *C. heterophylla, C. concolor,* and *C. sparsifolia.* Bot. Gaz. (Crawfordsville) 118:73–77.

GRANT, V. 1981. Plant speciation. Columbia Univ. Press, NY.

GRAY, A. 1868. Characters of new plants of California and elsewhere, principally of those collected by H. N. Bolandier in the State's Geological Survey. Proc. Amer. Acad. Arts 7:327–401.

GÜNTHER, E. and W. ROTHMALER. 1963. Chromosomezahlen amerikanischer *Antirrhinum*-Arten. Biol. Zentralbl. 82:95–99.

HARTL, D. 1965. Scrophulariaceae. *In* G. Hegi, ed., Illustrierte Flora von Mittel-Europa. Carl Hanser Verlag, München.

HEITZ, E. 1927. Über multiple und aberrante Chromosomenzahlen. Abh. Naturwiss. Verein. Hamburg 21:47–57.

JACKSON, D. M. 1971. Biosystematics of the *Maurandya erubescens* complex. Master's thesis, Biology Dept., Mankato State Univ., Mankato, MN.

——— and R. SPELLENBERG. 1973. *In* IOBP chromosome number reports XLII. Taxon 22:647–654.

Johnston, I. M. 1950. Noteworthy species from Mexico and adjacent United States, III. J. Arnold Arbor. 31:188–195.

Melchior, H. 1964. Scrophulariaceae. *In* A. Engler, Syllabus der Pflanzenfamilien 2:424–470. Bornträger, Berlin.

Moench, C. 1802. Supplementum ad methodum plantas. Marburgi Cattorum, Marburg.

Moore, P. D. and J. A. Webb. 1978. An illustrated guide to pollen analysis. Hodder and Stoughton, Toronto.

Munz, P. A. 1959. A California flora. Univ. California Press, Los Angeles.

Pennell, F. W. 1947. Some hitherto undescribed Scrophulariaceae of the Pacific states. Proc. Acad. Nat. Sci. Philadelphia 99:155–199.

Quer y Martínez, J. 1762. Flora Española (vol. 3). Joachin Ibarra, Madrid.

Raven, P. H. 1973. The evolution of "Mediterranean" floras. *In* H. Mooney and F. di Castro, eds., Evolution of mediterranean ecosystems, pp. 213–224. Springer-Verlag, NY.

———, D. W. Kyhos, and A. J. Hill. 1965. Chromosome numbers of spermatophytes, mostly Californian. Aliso 6:105–113.

Reichenbach, H. G. L. 1828. Conspectus Regni Vegetabilis. Apud Carolum Cnobloch, Leipzig.

Rothmaler, W. 1943. Zur Gliederung der Antirrhineae. Feddes Repert. Spec. Nov. Regni Veg. 52:16–39.

———. 1956. Taxonomische Monographie der Gattung *Antirrhinum.* Feddes Repert. Beih. 136:1–124.

Rouy, G. 1909. Flore de France. Deyrolle, Paris.

Shreve, F. and I. Wiggins. 1968. Vegetation and flora of the Sonoran Desert. Stanford Univ. Press, Stanford, CA.

St. John, H. 1973. List and summary of the flowering plants in the Hawaiian Islands. Pacific Trop. Bot. Gard. Mem. no. 1. Lawai, Kauai, HI.

Viano, J. 1978. Croisements expérimentaux interspécifiques au sein du genre *Linaria.* Caryologia 31:383–425.

Vickery, R. K. 1978. Case studies in the evolution of species complexes in *Mimulus.* Evol. Biol. 11:405–507.

Webb, D. A. 1972. *Asarina. In* T. G. Tutin, V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, and D. A. Webb, eds., Flora Europaea 3:224. Cambridge Univ. Press, Cambridge.

Wettstein, R. 1891. Scrophulariaceae. *In* A. Engler and K. Prantl, eds., Die natürlichen Pflanzenfamilien IV (3b):39–107.

Wiggins, I. L. 1980. Flora of Baja California. Stanford Univ. Press, Stanford, CA.

Yeo, P. 1966. The breeding relationships of some European Euphrasiae. Watsonia 6:216–245.

(Received 19 Nov 1984; accepted 19 Feb 1985.)

Appendix

Vouchered collections of 1) *Asarina procumbens* used in seed, pollen, and chromosomal studies, 2) *Neogaerrhinum* species whose chromosome numbers were determined, and 3) taxa used in the crossability studies. Voucher specimens are deposited at TEX-LL unless otherwise indicated.

Seed Coat Morphology and Anatomy.
Asarina procumbens. France: Dijon Bot. Gard., 1981; *Elisens 613.*

Pollen Morphology.
Asarina procumbens. Spain: Barcelona Bot. Gard., 1981; *Elisens 799.*

Chromosome Number Determination.

Asarina procumbens, $2n = 18$. France: Dijon Bot. Gard., 1981; *Elisens 613.* Spain: Barcelona Bot. Gard., 1981; *Elisens 799.*

Neogaerrhinum filipes, $2n = 30$. United States: Nevada, *Elisens 617.*

Crossability Studies.

Asarina procumbens. France: Dijon Bot. Gard., 1981; *Elisens 613.* Spain: Barcelona Bot. Gard., 1981; *Elisens 799.*

Neogaerrhinum filipes. United States: Nevada, *Elisens 617.*

Maurandya. M. antirrhiniflora. United States: Texas, Travis Co., *Elisens 528. M. barclaiana.* Mexico: Nuevo Leon, *Turner and Davies A-13. M. scandens.* Mexico: Oaxaca, *Elisens 655. M. wislizeni.* United States: Texas, Ward Co., *Elisens 530.*

Mabrya. M. acerifolia. United States: Arizona, Maricopa Co., *Elisens 584. M. erecta.* Mexico: Coahuila, *Gordon 777. M geniculata.* Mexico: Sonora, *Gordon 763.*

Lophospermum. L. atrosanguineum. Mexico: Oaxaca, *Elisens 665. L. purpusii.* Mexico: Oaxaca, *Elisens 549. L. scandens.* Mexico: Morelos, *Elisens 652.*

ANNOUNCEMENT

On Saturday, 28 September 1985, Huntington Botanical Gardens will host its Second Symposium on Succulent Plants. Featured will be the following speakers and their topics: A. Gibson, Univ. California, Los Angeles, The classification of cacti above the species level; M. Kimnach, Huntington Bot. Gard., The origins of epiphytic cacti; P. Nobel, Univ. California, Los Angeles, Environmental influences on agaves—Implications for establishment, tolerances, and productivity; C. Uhl, Cornell Univ., Polyploidy in *Echeveria* (Crassulaceae); G. Webster, Univ. California, Davis, Evolution and systematics of neotropical *Jatropha* and *Cnidoscolus* (Euphorbiaceae); A. Zimmerman, Univ. Texas, Systematics of the genus *Coryphantha* (Cactaceae).

Included in the day's events will be special tours of the recently opened Desert Garden Conservatory, an auction of rare plants, an optional luncheon and dinner, and an evening panel discussion. For information concerning registration and the schedule of events, please write: Succulent Plant Symposium, Huntington Botanical Gardens, 1151 Oxford Road, San Marino, CA 91108.

MIMULUS NORRISII (SCROPHULARIACEAE), A NEW SPECIES FROM THE SOUTHERN SIERRA NEVADA

LAWRENCE R. HECKARD
Jepson Herbarium, University of California,
Berkeley 94720

JAMES R. SHEVOCK
Department of Botany, California Academy of Sciences,
San Francisco 94118

ABSTRACT

Mimulus norrisii, a new cliff-dwelling species from the Sierra Nevada foothills primarily in Sequoia National Park, Tulare County, California, is described and illustrated. The new species is ecologically similar and morphologically closest to *M. dudleyi* in sect. *Paradanthus* but differs in its moister habitat requirements, leaves with attenuate bases and less serrate margins, and in particular the smaller calyces that develop conspicuous enlarged and rounded ribs.

This attractive new species of *Mimulus* was discovered by the second author and Larry Norris, Naturalist in Sequoia National Park. Review of *Mimulus* specimens in California herbaria (CAS, DS, JEPS, POM, RSA, UC) failed to locate a collection of the new species. That it has been overlooked by botanists remains a mystery, but most plant collections from the Park have been from the coniferous forests and alpine environments during the summer months and the lower elevations within the chaparral and blue oak communities have not been systematically surveyed. Other additions to the Park flora (*Draba cuneifolia, Notholaena jonesii,* and *Parietaria hespera* var. *hespera*) also come from the marble outcrops associated with the new *Mimulus.*

Mimulus norrisii Heckard & Shevock sp. nov.

Planta annua dense glanduloso-villosa, caulibus adscendentibus. Foliorum paginae ovatae leniter repando-denticulatae, palmato-venosae, basibus attenuatis vel cuneatis. Calyx apud florem 3.5–5.0 mm longus campanulatus, dentibus deltatis ca. 1.5 mm longis, apicibus obtusis vel leviter mucronatis. Calyx apud fructus 5–6 mm longus, urceolatus, costis ampliatis, rotundatis. Corolla 15–30 mm longa, infundibuliformis faucis brevi-expansa et limbo quasi rotato (Figs. 1, 2).

MADROÑO, Vol. 32, No. 3, pp. 179–185, 19 August 1985

FIG. 1. *Mimulus norrisii.* Top: Marble outcrop habitat at Comb Rocks, the type locality. Shrubs in foreground are *Toxicodendron.* Bottom: Habit of plants in rock crevice.

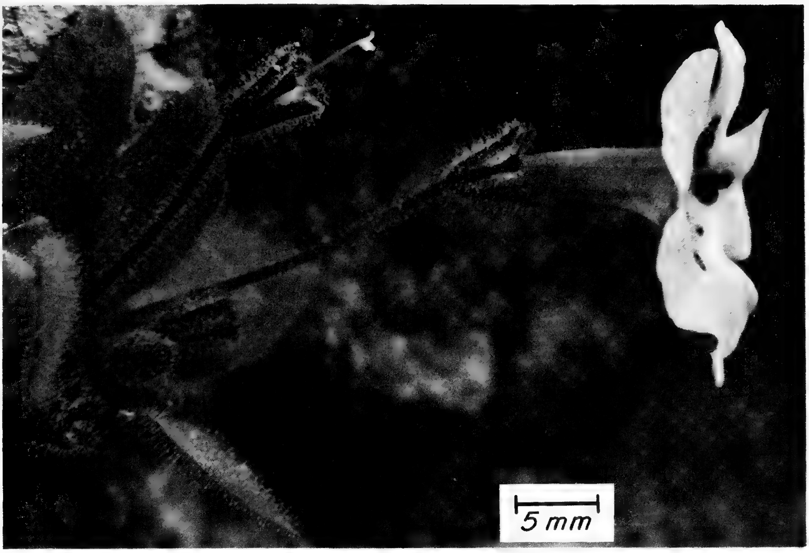


FIG. 2. *Mimulus norrisii.* Lateral view of flower showing pedicel and calyx and their indument, and the widely flaring corolla.

Annual with diffuse roots; stems ascending, 3–15(–25) cm long with internodes reaching 6–7 cm, sometimes branched from lower nodes, often floriferous from near base, the longer stems often geniculate; herbage densely glandular-villous (particularly in nodal regions) with trichomes mostly under 1 mm, occasionally to 2 mm. Leaves usually 2–5 pairs per stem, the blades ovate with attenuate to cuneate bases, mostly 2.0–3.5 cm long and 1–2 cm wide, weakly repand-denticulate with 3–5 pairs of small teeth on upper ⅔ of blade, reduced and often narrowed upwards on stem, palmately 3–5 veined or upper pair (and occasionally 1–2 additional veins) diverging pinnately from parallel unfused veins of midrib, typically the veins running distinct into the petiole; petiole 0.5–1.5 cm long, not sharply delineated from the tapering blade, reduced upwards on stem. Flowers axillary on slender ascending pedicels 2–5 cm long, the pedicels reflexed in fruit and sometimes hooked at the apex; calyx in anthesis 3.5–5.0 mm long, narrow-campanulate, sulcate between rounded ribs, rib region strongly glandular-pilose, usually infused or spotted with purplish red, sulca paler with less spotting and sparser indument; calyx teeth ca. 1.5 mm long, rounded deltate with apices obtuse to slightly mucronulate, inwardly concave; calyx in fruit elongating to 5–6 mm, becoming somewhat urceolate with incurving of lobes and expansion of thinner and paler inter-rib region during capsule enlargement, the ribs enlarged and rounded; corolla caducous, funnelform, 15–30 mm long, the tube gradually widening to about midpoint, expanding to form short, open flaring throat and spreading to almost rotate limb made up of nearly equal lobes (6–10 mm long) that are broader than long, rounded to truncate and often retuse to emarginate, centrally grooved; corolla yellow, marked on throat centrally below each lobe with bilobed to irregular maroon-purple blotches (mostly one per lobe except several smaller ones on central lobe of lower lip), usually with two white spots on throat beneath the two sinuses forming the central lobe, weakly puberulent and sometimes glandular on exterior, the inner surface of lobes with scattered yellow clavate hairs that become smaller and denser on palatal folds of throat and down tube; stamens glabrous, included in lower one-half and attached near tube base, the upper filaments 3.5–4.0 mm long, the lower filaments 5–6 mm long; anthers explanate, longitudinally oriented, ca. 1 mm long; gynoecium ca. 10 mm long, style ca. 6 mm long, the stigma ca. 1.0 mm long, exceeding anthers by ca. 1–3 mm, bilamellate with equal, spreading lobes that are rounded and fimbriolate; capsule narrow-ovoid, 4–6 mm long, about equalling calyx, often unequally developed on opposite sides of style base, the style eventually breaking near the base leaving short, curved apiculation, the placentae adherent to apex, dehiscing full length along both sutures; seeds many (up to 100/capsule), ellipsoid-oblong, longitudinally minutely rugose-striate, tawny-colored, ca. 0.5 mm long. Chromosome number $2n = 32$.

TYPE: USA, CA, Tulare Co.: Comb Rocks above Washburn Cove, 2 mi n. of Three Rivers, T17S R28E S1, 2800 ft. (854 m), 1 May 1983, *L. L. Norris 389.* (Holotype: JEPS; isotypes: CAS, FSC, K, MO, NY, RSA, US.)

PARATYPES: USA, CA, Tulare Co.: West ridge of Blossom Pk., South Fork Kaweah River, Three Rivers, T17S R28E S25, 19 Mar 1984, *Norris 627* (JEPS); Comb Rocks, 2 mi n. of Three Rivers, T17S R28E S1, 1 May 1983, *Shevock 10353* (CAS); Sequoia Nat'l. Park: Divide between Elk Cr. and Marble Fork Kaweah River, T16S R29E S23, *Norris 351* (JEPS) and *Shevock 10165* (CAS); 19 Mar 1983, *Norris 354* (RSA) and *Shevock 10187* (CAS, JEPS); 18 Apr 1983, *Shevock 10330* (CAS, JEPS, RSA); 12 May 1983, *Bacigalupi 9350* (JEPS, OSC, SD); and 24 Apr 1984, *Norris 638* (CAS, FSC, JEPS, MO, RSA); Generals Highway 0.7 mi e. of Ash Mtn., T16S R29E S34, 30 Mar 1983, *Norris 363* (SBBG, UC); and 24 Apr 1984, *Norris 637* (JEPS); Yucca Point just n. of Ash Mtn., T16S R29E S34, 18 Apr 1983, *Norris 372* (JEPS) and *Shevock 10329* (CAS, RSA); 12 May 1983, chromosome voucher, $n = 16$, *Bacigalupi 9344* (CHSC, JEPS, OBI, WTU); Clough Cave, South Fork Kaweah River, T18S R30E S19, 19 Mar 1984, *Norris 626* (JEPS); Above Alder Cr. near Ash Mtn., T16S R29E S34, 23 Mar 1984, *Norris 631* (THRI).

Distribution, habitat and phenology. Marble outcrops in chamise chaparral or blue oak woodland, Kaweah River drainage, 610–1310 m, southern Sierra Nevada within Tulare Co., California; most populations located within Sequoia National Park. Flowers March–May. The plants find rootholds in soil pockets, moss covered ledges, cracks and fractures in the marble outcrops, primarily in areas with concentrations of beige-colored deposits of calcium carbonate. Steep east- or west-facing outcrops have the densest concentrations of plants, although plants do occur sparingly on south-facing cliffs. Light regimes vary during the day from full sun to full shade. The most robust plants occur where dripping water from mossy overhangs keeps the cliff face moist.

Associated species. Asterella californica, Anacolia menziesii var. *baueri, Bryum pseudotriquetrum* var. *bimum, Encalypta vulgaris, Selaginella hanseni, Aspidotis californica, Cheilanthes cooperae, Notholaena jonesii, Pellaea mucronata, Pityrogramma triangularis, Dudleya cymosa* subsp. *cymosa, Eriogonum nudum* subsp. *murinum, Lithophragma bolanderi, Parietaria hespera* var. *hespera, Pterostegia drymarioides, Toxicodendron diversilobum* and *Yucca whipplei* subsp. *caespitosa.*

Populations of *Mimulus norrisii* are fairly common on all marble outcrops investigated in the Kaweah River drainage. The total area of the marble habitat, however, is estimated at only 200 hectares. The number of plants occupying the available habitat can only be grossly estimated because of the inaccessibility of the rugged cliff habitat on which the species occurs. We expect population size to vary markedly from year to year. Following an exceedingly wet winter (1983) for the southern Sierra Nevada, we estimated a total population of 7000 individuals. Essentially all populations are free from disturbances by man.

Mimulus norrisii belongs to the sect. *Paradanthus,* an assemblage of about 70 species that Grant (1924) proposed to accommodate "a collection of groups not necessarily related to one another and in all probability most of them have been derived from members of other sections" (p. 117). The relationship of *M. norrisii* within this poorly understood and possibly polyphyletic section is equivocal. In most features, *M. norrisii* is closest to *M. dudleyi* Grant of the *M. floribundus* Dougl. ex Lindl. alliance, but the smaller, campanulate (to urceolate in fruit) calyx with thickened and rounded ribs is quite unlike that in the *M. floribundus* group. Thickened calyx ribs are found in only two other species of the section—*M. bicolor* Hartw. ex Benth. and *M. filicaulis* Wats. (the latter includes *M. biolettii* Eastw. according to Bacigalupi [1981])—but these species differ from *M. norrisii* in several well-marked features, including size and shape of calyx as well as the type of thickening itself. Thus their calyx is cylindric-oblong with pointed lobes and the "corky ribs," as Grant (1924) and Pennell (1951) described the strongly developed rib angles, are composed of softer tissue than in *M. norrisii*. Based on these differences in the calyx, it seems likely that thickening of the ribs has evolved independently in *M. norrisii* and the *M. bicolor-filicaulis* group.

Our opinion that the nearest relative of *Mimulus norrisii* is *M. dudleyi* is based on their basic similarity in nearly all morphological respects, except the calyx and a few minor traits. The calyx of *M. dudleyi* is narrow-campanulate (with spreading pointed lobes) and ridge-angled in flower, becoming narrowly oblong with erect or spreading lobes in fruit in contrast to the shorter calyx of *M. norrisii,* which changes from campanulate (with rounded lobes) in flower to urceolate with thickened ribs in fruit. Although the plants of both species are petrophilous, their habits differ in that *M. dudleyi* is prostrate-ascending over granitic rocks, while *M. norrisii* is loosely erect or hanging from marble cliffs. Other differences are that the leaves of *M. dudleyi* have obtuse to truncate bases and much more pronounced serrate margins than those of *M. norrisii,* in which the bases are tapered and the margins are sparingly denticulate. Although both species have stems that are geniculate at times, only *M. norrisii* has (fruiting) pedicels that are reflexed and sometimes hooked at the tips, which facilitates very local dispersal of seeds. The corollas of the two species appear remarkably similar in shape and color, as are the short stamens and style-stigma that are included well within the tube. There are slight differences in corolla markings between the two species: *M. dudleyi* lacks the two white spots between the lower lobes and has the maroonish markings at the base of the lobes as flecks that are in less discrete blotches than in *M. norrisii.* The same chromosome number ($2n = 32$) has been found by Dr. T.-I. Chuang in *M. norrisii* (cited above) and *M. dudleyi* (CA, Tulare Co.: 10 mi se. of Porterville, *Heckard and Chuang 4003*).

Although *Mimulus norrisii* and *M. dudleyi* both occur in the foothills of the southern Sierra Nevada, they occupy different habitats and their elevation ranges rarely overlap. Thus plants of *M. norrisii* are in damp and mostly shaded situations on cliffs of metamorphic rock in chamise chaparral (above 600 m). *Mimulus dudleyi,* on the other hand, is mostly at lower elevations in valley grassland or blue oak savanna and occurs on granitic outcrops that are in full sun most of the day and are wet only for short periods following rains. The liverworts, mosses, and ferns typically associated with *M. norrisii* are absent in this latter habitat.

ACKNOWLEDGMENTS

We thank Larry L. Norris for specimens, information, photographs, and field assistance, Rimo Bacigalupi and Robert J. Meinke for sharing their knowledge of

Mimulus, Jim Hickman for critical comment, and T.-I. and Fei-mei Chuang for kindly supplying chromosome counts.

LITERATURE CITED

BACIGALUPI, R. 1981. The identity of *Mimulus filicaulis.* The Changing Seasons 1(3, suppl.):3–5.

GRANT, A. L. 1924 (publ. Jan 1925). A monograph of the genus *Mimulus.* Ann. Missouri Bot. Gard. 11.

PENNELL, F. W. 1951. *Mimulus. In* Abrams, Illustrated flora of the Pacific States 3:688–731. Stanford Univ. Press, Stanford.

(Received 17 Dec 1984; accepted 16 Jan 1985.)

ANNOUNCEMENT

The Graduate Student Meetings, sponsored by the California Botanical Society, will be held this year at the University of California, Santa Barbara, on October 19 and 20, 1985. Graduate students wishing to present papers should prepare abstracts to be submitted when the call for abstracts is announced in August. Please contact Ms. Kathy Rindlaub, Department of Biological Sciences, University of California, Santa Barbara 93106, or Mr. Joseph M. DiTomaso, Department of Botany, University of California, Davis 95616, for information on registration, schedule of events, field trips, and the banquet.

NOTES AND NEWS

NOTES ON THE GENUS *Burroughsia* (VERBENACEAE).—The genus *Burroughsia* was erected by Moldenke (Phytologia 1:411, 1940), based entirely on the presence of filament-like extensions of the connectives of the distal, abaxial pair of stamens (Fig. 1d–f). These appendages have many multicellular glands at the tip and are slightly exserted from the corolla tube throat. Their function is unknown, but their glandular tips may serve to attract insects to the corolla tube.

As erected, the genus consists of two species: *Burroughsia appendiculata* (Robins. & Greenm.) Moldenke (=*Lippia appendiculata* Robins. & Greenm.), of Chihuahua, Coahuila, eastern Durango, and northern San Luis Potosi and *B. fastigiata* (Brandegee) Moldenke (=*L. fastigiata* T. S. Brandegee), of Baja California del Sur. Except for the unique connective extensions the species fit well within the *Lippia–Aloysia* alliance. Both species are strigose, low subshrubs with opposite, small, ovate, lobed, deeply impressed-veined leaves; and both have flowers in short, cylindric, spike-like racemes borne on long axillary peduncles. The flowers have 2-lobed calyces, lavender to white, 5-lobed, zygomorphic corollas with broad, cylindric tubes, and didynamous stamens;

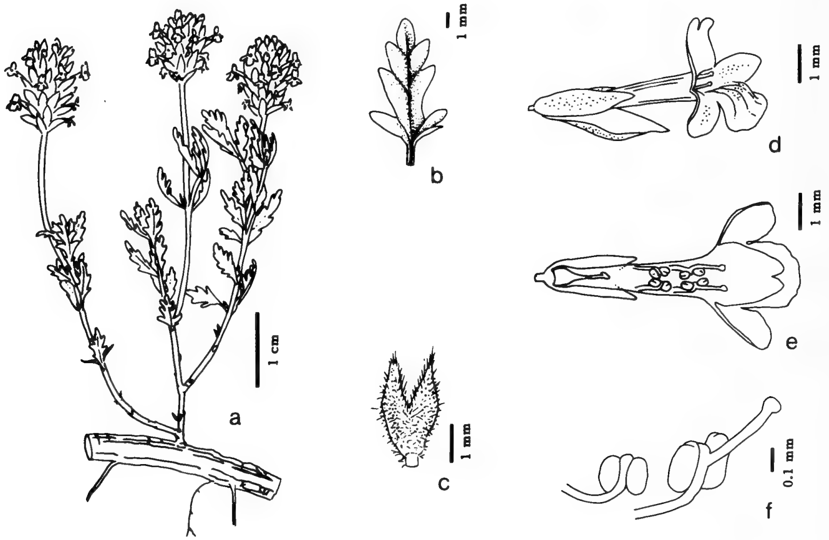


FIG. 1. *Lippia appendiculata* Robins. & Greenm.—a. Habit, showing section of thick, corky basal rhizome and erect ascending stems with long axillary peduncles and spicate inflorescences.—b. Leaf, showing lateral veins that extend to tooth sinuses. Veins are deeply impressed on upper surface.—c. Calyx is two-lobed, hirsute with spreading hairs and has many conspicuous orange glands.—d. Flower, lateral view, showing subtending bract, calyx (without vestiture), and corolla lobe orientation. Note exserted filament-like extensions of the distal anthers.—e. Diagrammatic "transparent" top view of flower, showing position of ovary, stamens, and corolla lobes.—f. Lateral view of stamens of a pre-anthesis flower showing the point of origin of the gland-tipped, filament-like extension of the distal anther connective. All from *D. S. Correll and I. M. Johnston 21557* (LL). Magnifications as indicated. Drawing by Kathleen Cook.

the fruits are obovoid, 2-locular and dry. *Burroughsia appendiculata* is a relatively short plant, 1–1.5 dm tall, with pencil-thick, corky, horizontal rhizomes, rather strongly lobed leaves, uniform, antrorse, strigose stem vestiture accompanied by orange-red glands and a distinct yellow corolla eye (Fig. 1). *Burroughsia fastigiata,* on the other hand, is usually a taller, twiggier plant, with smaller, more crowded, fewer-lobed leaves, and generally denser, more curved vestiture that is retrorse on stems, antrorse on leaves, with light yellowish to colorless glands and corollas that lack a yellow eye (see illustration in Wiggins' *Flora of Baja California,* p. 527, 1980). Several notes on the genus have been published by Moldenke (Phytologia 30:186–189, 1975; 40:423, 1978; 46:402, 1980) and these cite a number of additional references.

Routine study of the two species in connection with the Chihuahuan Desert flora, however, showed that *B. fastigiata* lacks the filament-like extensions on the distal anther connectives—the very character upon which the genus was erected. It is perhaps surprising that this error was not noticed for over 45 years, but the species is restricted to Baja California and is seldom collected. Moldenke (in Shreve and Wiggins, Veget. Flora Sonoran Desert 2:1246–1247, 1964) separated *Burroughsia* in the key on the basis of "anthers appendaged" but did not mention the structures in the species description, though it is noted in the generic description. Wiggins (Fl. Baja California 1980) separates the genus in the key on the basis of the anther appendages, but correctly omits the appendages in his accompanying species illustration.

Clearly *B. fastigiata* must be returned to the genus *Lippia,* as *L. fastigiata* T. S. Brandegee. One can argue phenetically to retain *Burroughsia* as a monotypic genus based on the character of a distinct filament-like connective extension. Cladistically, however, one sees that the genus is based entirely on a single, apomorphic feature and that its generic segregation cannot be supported. Within *Lippia,* the relationship of taxon *appendiculata* is not entirely clear. It shares a number of vegetative and floral characteristics with *Lippia fastigiata* and may indeed be most closely related to that taxon. In the Verbenaceae the presence of anther connective extensions is not restricted to *B. appendiculata*: similar, though less well defined extensions occur on the distal, abaxial filaments in some species of *Glandularia.* This, however, is hardly a synapomorphic character, because the genera differ in many other basic features.

At the present time I can see no reason to retain *Burroughsia* as a distinct genus based on a single apomorphic character and suggest the two species be returned to *Lippia* as *Lippia appendiculata* Robins. & Greenm., of the Chihuahuan Desert region, and *Lippia fastigiata* T. S. Brandegee of Baja California. Perhaps the time has come to look also into the validity of other generic segregates of *Lippia* such as *Aloysia* A. L. Juss., which is based on the presence of elongate inflorescences, and the low-growing *Phyla* Lour.—JAMES HENRICKSON, Department of Biology, California State University, Los Angeles 90032. (Received 19 Nov 1984; accepted 16 Mar 1985.)

NEW COMBINATIONS IN CALIFORNIA *Chamaesyce* (EUPHORBIACEAE).—As an additional installment of nomenclatural changes (Hickman, Madroño 31:249–252. 1984) for a revision of W. L. Jepson's Manual (Jepson, Man. fl. pls. Calif. 1925), four new combinations in the genus *Chamaesyce* are made for California taxa. Attention is also drawn to a nomenclatural change in the taxonomy of the genus from that of Wheeler (Rhodora 43:97–154, 168–286. 1941).

Euphorbia s.l. encompasses a group of plants ranging from small temperate annuals to ten-meter-tall tropical trees. Within this diverse collection, several natural assemblages can be recognized and are variously treated at generic, subgeneric or sectional levels. The generic delimitation of the tribe Euphorbieae to be followed in the new Jepson's Manual will be that of Webster (Taxon 24:593–601. 1975) in which *Chamaesyce* is segregated from *Euphorbia.*

Koutnik (S. African J. Bot. 3:262–264. 1984) recently reviewed the characteristics distinguishing *Chamaesyce* from *Euphorbia.* Of primary importance is the sympodial growth habit of *Chamaesyce,* which is not found in *Euphorbia.* Although the stem anatomy is not fully understood at present (Rosengarten and Hayden, Virginia J. Sci. 34:142. 1983), sympodial growth arises from the abortion of the apical meristem of the main stem after the first true leaves have formed. Subsequent growth is from lateral branches originating in the region of the cotyledonary nodes. Sympodial growth continues throughout the life of the plant: each terminal bud of a branch aborts and is alternately replaced by a bud from either side of the stem apex. The morphology of this pattern is explained in some detail (Verdus, Bull. Soc. Hist. Nat. Toulouse 99:138–156. 1964). There are no other species in the Euphorbiaceae that display this growth form.

Another feature of *Chamaesyce* not found in *Euphorbia* is the occurrence of the C_4 photosynthetic pathway (Downton, Photosynthetica 9:96–105. 1975). Associated with the C_4 photosynthetic pathway is the Kranz anatomy of large chlorenchymatous cells forming a sheath surrounding the vascular bundle, also displayed by *Chamaesyce* species but not by *Euphorbia.* Additional distinguishing characters of *Chamaesyce* are the typically prostrate to ascending plant habit, the alternate arrangement of stem-branches, the opposite leaves, each with a discernibly asymmetric base, the presence of stipules, the frequent presence of white to pink petaloid appendages on the four (rarely five) involucral glands of the cyathium, and the ecarunculate seeds. All of these characters taken collectively should easily place an unknown specimen in the correct genus.

One important departure from the nomenclature of *Chamaesyce* by Wheeler (1941) is the correct application of *C. maculata* (L.) Small (see Burch, Rhodora 68:155–166. 1966). *Chamaesyce maculata* is the correct name for the common garden weed called "spotted spurge." This is a prostrate annual plant that is frequently given the name *E. supina* Raf. (e.g., Munz, Calif. fl. 1959; Fl. S. Calif. 1974). The plant described under *C.* (*E.*) *maculata* by Munz and Wheeler has ascending branches and is properly identified as *C. nutans* (Lag.) Small.

The following four new combinations complete the generic assignment to *Chamaeysce* for all the currently accepted taxa in California. The subspecific rank is used to indicate geographic unity of the taxon and to maintain uniformity within the existing taxonomy for the California members of *Chamaesyce.*

Chamaesyce abramsiana (Wheeler) Koutnik comb. nov.—*Euphorbia abramsiana* Wheeler, Bull. S. Calif. Acad. Sci. 33:109. 1934.—*Euphorbia pediculifera* Engelm. var. *abramsiana* Ewan in Jeps., Fl. Calif. 2:427. 1936.—TYPE: CA, Imperial Co., Heber, Imperial Valley, Jun 1904, *Abrams 4097* (DS).

Chamaesyce hooveri (Wheeler) Koutnik comb. nov.—*Euphorbia hooveri* Wheeler, Proc. Biol. Soc. Wash. 53:9. 1940.—TYPE: CA, Tulare Co., Yettem, 30 Jun 1937, *Hoover 2583* (GH).

Chamaesyce ocellata subsp. **rattanii** (S. Watson) Koutnik comb. nov.—*Euphorbia rattanii* S. Watson, Proc. Amer. Acad. Arts 20:372. 1885.—*Chamaesyce rattanii* Millsp., Publ. Field Columbian Mus. Bot. Ser. 2:411. 1916.—*Euphorbia ocellata* var. *rattanii* Wheeler, Bull. S. Calif. Acad. Sci. 33:107. 1934.—TYPE: CA, Glenn Co., Stony Cr., Jun 1884, *Rattan 57* (GH).

Chamaesyce serpyllifolia subsp. **hirtula** (Engelm. ex S. Watson) Koutnik comb. nov.—*Euphorbia hirtula* Engelm. ex S. Watson, Bot. Calif. 2:74. 1880.—*Chamaesyce hirtula* Millsp., Publ. Field Columbian Mus. Bot. Ser. 2:409. 1916.—*Euphorbia serpyllifolia* var. *hirtula* Wheeler, Proc. Biol. Soc. Wash. 53:11. 1940.—TYPE: CA, San Diego Co., Talley's, Cuyamaca Mts., 1875, *Palmer 451* (GH).

The following is a list of the currently accepted *Chamaesyce* taxa in California:

- *C. abramsiana* (Wheeler) Koutnik
- *C. albomarginata* (Torrey & A. Gray) Small
- *C. arizonica* (Engelm.) Arthur
- *C. fendleri* (Torrey & A. Gray) Small
- *C. glyptosperma* (Engelm.) Small
- *C. hooveri* (Wheeler) Koutnik
- *C. maculata* (L.) Small
- *C. melanadenia* (Torrey) Millsp.
- *C. micromera* (Boiss.) Wooton & Standley
- *C. nutans* (Lag.) Small
- *C. ocellata* (E. M. Durand & Hilgard) Millsp. subsp. *ocellata*
- *C. ocellata* subsp. *arenicola* (Parish) Thorne
- *C. ocellata* subsp. *rattanii* (S. Watson) Koutnik
- *C. parishii* (Greene) Millsp.
- *C. parryi* (Engelm.) Rydb.
- *C. pediculifera* (Engelm.) Rose & Standley
- *C. platysperma* (Engelm. ex S. Watson) Shinners
- *C. polycarpa* (Benth.) Millsp. var. *polycarpa*
- *C. polycarpa* var. *hirtella* (Boiss.) Millsp.
- *C. prostrata* (Aiton) Small
- *C. revoluta* (Engelm.) Small
- *C. serpens* (H.B.K.) Small
- *C. serpyllifolia* (Pers.) Small subsp. *serpyllifolia*
- *C. serpyllifolia* subsp. *hirtula* (Engelm. ex S. Watson) Koutnik
- *C. setiloba* (Engelm. ex Torrey) Millsp.
- *C. vallis-mortae* Millsp.

I thank the two anonymous reviewers and the editor for their helpful suggestions.—Daryl L. Koutnik, Research Assistant, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166. (Received 22 Oct 1984; accepted 19 Apr 1985.)

Rediscovery and Reproductive Biology of *Pleuropogon oregonus* (Poaceae).—*Pleuropogon oregonus* Chase (Oregon semaphore grass) was first collected in 1886 by W. C. Cusick in Hog Valley, probably near Union, in northern Oregon. In 1901, another collection of *P. oregonus* was made by A. B. Leckenby in Union, Oregon; and in 1936 M. E. Peck found it again, but in swampy ground 25.8 km west of Adel, Lake County, Oregon. Because *P. oregonus* has not been collected for nearly half a century and is reported as extinct or endangered (Smithsonian Rept. to Congress, Serial No. 94-A, 1975; Aysenu and DeFilipps, Endang. Threat. Pl. U.S., Smithsonian Inst. and World Wildlife Fund, Wash., D.C., 1978; Siddall, Chambers and Wagner, Rare, Threat. Endang. Vasc. Pl. Oregon, Oregon Nat. Area Preserves Advisory Committee, 1979; U.S. Fish Wildlife Serv., Fed. Reg. 45(242):82480–82569, 1980), its recollection is worthy of note.

Oregon, Lake Co., ca. 25 km w. of Adel on Hwy. 140, T39S, R22E, Sec. 5 nw.¼ and T38S, R22E, Sec. 32 sw.¼. *J. Kagan 60482* (ORE), 4 Jun 1979. Very probably the same locality where Peck made the last previous collection, 47 years ago.

Habitat. Restricted to sluggish water in depressions and sloughs fed by Mud Cr. on both sides of Hwy. 140, on gravelly silt loam or clay. It grows in association with various grasses and sedges, including *Beckmannia syzigachne, Deschampsia danthonioides, Glyceria borealis, Hordeum brachyantherum, Poa nevadensis, Carex anthrostachya, C. nebraskensis,* and *Eleocharis palustris.* The meadow area, including the portion occupied by *P. oregonus,* has been used for years for fall grazing.

Reproductive biology. Oregon semaphore grass blooms from early June to late July and fruits from late July to mid-August. Its inflorescence is a simple, erect raceme, 13–20 cm long, bearing 6–7 spikelets. Pedicels are 2–5(–12) mm long. Spikelets spread toward one side of the raceme, 2–4(–5) cm long, each bearing 7–14 florets. Bentham and Hooker f. (1883, Genera Plantarum) described the florets of the genus *Pleuropogon* as "hermaphroditis v. summo masculo." However, the uppermost floret of *P. oregonus* is usually reduced.The upper florets are pistillate, whereas the lower ones are perfect. Anthesis within each gynomonoecious spikelet is protogynous, starting with the upper pistillate flowers and then progressing to the lowest protandrous, hermaphroditic flowers, then upward. Gynomonoecy and overall protogyny in spikelets but protandry in hermaphroditic florets found in *P. oregonus* are also observed in *P. californicus* (But, Systematics of *Pleuropogon* R.Br. (Poaceae), Ph.D. diss., U.C. Berkeley, 1977). Connor (1979, Breeding systems in the grasses: a survey. New Zealand J. Bot. 17:547–574) noted that gynomonoecism is uncommon among the Gramineae.

Tests of the pollen, using four enzyme systems (malate dehydrogenase, isocitrate dehydrogenase, succinate dehydrogenase, and monoamine oxidase) showed 87% viability (I. Baker, pers. comm. 1983).

Low fecundity may contribute to its rarity. Of 4645 florets inspected, only 494 bore caryopses. Germinability test of a random sample of 30 caryopses (8 months old) with 0.1% tetrazolium salt solution showed 85% viability.

Although *P. oregonus* should no longer be considered 'extinct,' we suggest that it should remain classified as endangered.

We thank Lincoln Constance and Lawrence Heckard for assistance and encouragement in this study, Irene Baker for the pollen viability tests, and Tammy But and Lawrence But for field assistance.—PAUL P. H. BUT, The Chinese Univ. of Hong Kong, Shatin, N.T. Hong Kong; JIMMY KAGAN, The Nature Conservancy, 1234 Northwest 25th Avenue, Portland, OR 97210; VIRGINIA L. CROSBY, U.S.D.I., Bureau of Land Management, Denver Service Center, Denver Federal Center, Bldg. 50, Denver, CO 80225; and J. STEPHEN SHELLY, Dept. Botany, Oregon State Univ., Corvallis 97331. (Received 25 Oct 1984; accepted 25 Mar 1985.)

NOTEWORTHY COLLECTIONS

ARIZONA

CORCHORUS HIRTUS L. (TILIACEAE).—Cochise Co., San Bernardino Ranch, at T24S R30E S14 sw.¼, 1160 m, grassy w.-facing slope of mesa near inlet to House Pond, deep alluvium; 21, 22 Aug 1981. *Marrs-Smith 855, 945* (ASU).

Significance. First definite record for AZ. Pringle's 1884 collection gives the locality only as sandy plains near the Mexican Boundary.

IBERVILLEA TENUISECTA (Gray) Small (CUCURBITACEAE).—Chochise Co., 0.65 km n. of Geronimo Trail, 7.7 km e. of Douglas, just n. of Douglas Hill at T24S R28E S10 se.¼, 1325 m, ne.-facing slope of rocky limestone hillside, under *Larrea divaricata*; 21 Aug 1981, *T. Van Devender and J. B. Iverson s.n.* (ARIZ). San Bernardino Ranch, 20 m n. of ranch at T24S R30E S12 sw.¼, 1158 m, under *Larrea divaricata* in *Scleropogon brevifolius* grassland, deep alluvium; 26 Oct 1981, *Marrs-Smith 1196* (ASU). (Verified by D. J. Pinkava, ASU.)

Significance. New records for AZ. Seeds show some intermediacy in size and texture toward *I. sonoreae.*—GAYLE MARRS-SMITH, Biological Sciences Center, Desert Research Institute, P.O. Box 60220, Reno, NV 89506.

CALIFORNIA

JUNCUS CYPEROIDES Laharpe (JUNCACEAE).—CA, Butte Co., Forbestown Ridge ca. 18 km e. of Oroville and ca. 5.3 km sw. of Forbestown, e. of and adjacent to Black Bart Rd. ca. 0.8 km sw. of its junction with Oroville-Forbestown Hwy. (T19N, R6E, S18 sw.¼ se.¼). Shaded n.-nw. slope of a low-elevation yellow pine forest. Known from this locality since 1981. Plants produce viable seed and viviparous vegetative shoots occasionally arise in the inflorescence. Several nearby seepages and meadows have been searched but no other populations were found. *Ahart 2925, 3058* and *3527* (CAS, CHSC); *Jokerst and Ahart 1754* (CHSC). Determination confirmed by J. T. Howell.

Significance. First known collection from North America (consulted CAS, MO, NY) representing ca. 5600 km range extension nw. from populations in the Andes of Colombia. It is also known from Argentina, Chile, Equador, and Peru, where elevations range from ca. 2000–4000 km, except in Chile where populations extend down to sea level (Balslev 1982, A monograph of neotropical Juncaceae, Ph.D. diss., City Univ. New York). The method of introduction is unknown and it has not expanded its range or population boundaries since 1981.—JAMES D. JOKERST, Route 7, Box 312C, Oroville, CA 95965.

COLORADO

DRABA APICULATA C. L. Hitchcock (BRASSICACEAE).—Lake Co., Sawatch Mts., Mt. Campion Basin, granitic rock outcropping, 3750 m, 27 Jul 1984, *Hartman & Rottman 6025* (COLO, UC).

Significance. First report for CO. The species is known from mountainous areas of n. WY and the Uintah Mts. of UT. We concur with Rollins (Contr. Gray Herb. 214:6, 1984) in treating *D. apiculata* as distinct from *D. densifolia* Nutt. and *D. daviesiae* (Hitchc.) Rollins.—ROBERT A. PRICE, Botany Dept., Univ. California, Berkeley 94720; MARY LOU ROTTMAN and EMILY HARTMAN, Biology Dept., Univ. Colorado, Denver 80202.

MEXICO

PINUS PATULA var. LONGEPEDUNCULATA Loock (PINACEAE)—Mexico, Oaxaca, Sierra Madre del Sur, 2600 m, near 16°30′N, 97°10′W, 17 Feb 1984, *Perry Mex. 3884* (NCS, Perry herbarium, to be distributed). Forest on 60% ne. slope with *Pinus ayacahuite*

MADROÑO, Vol. 32, No. 3, pp. 191–193, 19 August 1985

Ehrenb., *Pinus pseudostrobus* Lind., *Pinus montezumae* Lamb., *Abies* sp., and *Quercus* spp. Verified by J. P. Perry, Jr., Feb. 1984.

Previous knowledge. Known from mountains near the village of Guajimaloyas, Oaxaca, Mex. 2800 m (near 17°15′N, 96°15′W) and e. and w. of Hwy. 175 near the town of Ixtlán. Also from mountains in area around (10–20 km) the city of San Cristobal de las Casas, Chiapas, Mex. at 2200–2400 m. (Herbaria consulted: MEXU, A, CHIP, NCS; published sources: M. Martinez, Los Pinos Mexicanos, 1948; E. E. M. Loock. The pines of Mexico and British Honduras, 1950; N. T. Mirov, The Genus *Pinus,* 1967; W. H. G. Barrett, Variacion de caracteres morfologicas en poblaciones naturales de *Pinus patula* Schlecht. et Cham. en Mexico, 1972; W. B. Critchfield and E. L. Little, Jr., Geographic distribution of the pines of the world, 1966.)

Significance. First record in the Sierra Madre del Sur, ca. 100 km disjunction from populations found in the mountain ranges north of the city of Oaxaca. Special thanks are expressed here to W. S. Dvorak, Dir. CAMCORE (Central America and Mex. Conifer Resources Coop.) and the field staff J. Donahue and Miguel Muñoz for providing transportation and help in locating this isolated population.—J. P. PERRY, Jr., Assoc. Dir. Agri. Scs. Program, The Rockefeller Foundation (Retired), 306 Front St., Hertford, NC 27944.

NEW MEXICO

GRAYIA BRANDEGEI A. Gray (CHENOPODIACEAE).—San Juan Co., "bad lands" along highway [NM Hwy. 57, formerly 56] w. of Otis Trading Post [T24N R10W, ca. 12 km by air nw. of Nageezi], 29 Aug 1932, *Nelson and Nelson 296* (RM); Kutz Canyon near junction of East and West Forks (T27N R10W S18), uncommon on steep shale slopes with *Atriplex* and *Juniperus,* 1800 m, 23 Jul 1976, *Levin 993* (ARIZ, DAV); Cottonwood Arroyo, 4 km w. of NM Hwy. 170, T30N R14W S24, n. slope of sand/clay badlands, 19 Aug 1984, *Porter 4665* (SD).

Significance. First records for NM. This rarely collected species was previously known from sw. CO, se. UT, and ne. AZ, generally on shale. The long time span between collections probably reflects the relative inaccessibility of the species' habitat and the plant's strong resemblance to the much more abundant *Atriplex canescens,* which the Nelsons had determined their specimen to be. I thank Ken Heil for calling my attention to the Porter specimen.—GEOFFREY A. LEVIN, Botany Dept., San Diego Natural History Museum, San Diego, CA 92112.

RHYNCHELYTRUM REPENS (Willd.) C. E. Hubb. (POACEAE).—Luna Co., Florida Mts., Copper Kettle Spring (T26S R8W S13 ne.¼ se.¼), frequent on gentle sw.-facing gravelly rhyolitic slope, 1450 m, 9 Nov 1984, *McIntosh and Bevacqua 1637* (NMC, NY, RSA).

Significance. First record for New Mexico. Closest known records are in se. Arizona and w. Texas.—LAIRD MCINTOSH, Bureau of Land Management, Las Cruces, NM 88004.

WYOMING

DRABA SPECTABILIS var. OXYLOBA (Greene) Gilg & Schulz (BRASSICACEAE).—Carbon Co., w. slope of Sierra Madre w. of Encampment, spruce-fir forest along Battle Creek, 2560 m, 15 Jul 1966, *C. L. and M. W. Porter 10216* (UC).

Significance. First report for WY. Hitchcock (Univ. Wash. Publ. Biol. 11:44, 1941) cited a collection from the same area (Battle, Carbon Co., *Tweedy 4475*; NY, US), but omitted the name of the state and listed the range of the species as UT and sw. CO. Subsequent collections from WY were misidentified as *D. aurea* M. Vahl and the species was omitted from the recent Flora of Wyoming. The species occurs in the Abajo and La Sal Mts. of e. UT (var. *spectabilis*), the Lukachukai Mts. of ne. AZ and more broadly on the w. slope of the Rocky Mts. in CO. It is apparently quite uncommon in nw. CO (occurring in Routte and Garfield cos.) and reaches the extreme

n. limit of its range in WY.—Robert A. Price, Botany Dept., Univ. Calif., Berkeley 94720.

REVIEWS

Vascular Plants of Montana. By Robert D. Dorn, illustrations by Jane L. Dorn. Mountain West Publishing, P.O. Box 1471, Cheyenne, WY 82003. 1984. $7.95 + $1.00 shipping.

Dorn's is a new and needed flora to satisfy both the herbarium and, particularly, the field botanist. The book (in paper covers) is small and light, well and pertinently, but sparsely, illustrated with nice line drawings, fully indexed to species, families and genera within families (arranged alphabetically), and has a well-illustrated glossary. It has a map of Montana counties and their combination into six areas used to describe plant distributions, and a very valuable map of the scattered distributions of the six kinds of floras found in Montana (Alpine, Rocky Mt., Pacific Northwest, Palouse Prairie, Great Basin, and Great Plains). The latter scheme is more meaningful, but the former is used in the text. Dot maps would offer a unique opportunity to document the latter, floristic classification.

The book is a masterpiece of condensation and composition. Does a word processor do better what a press once did? The book has only 276 pages, with a format of 13.7 × 21.6 × 1.4 cm and a corresponding light weight. Anyone who has carried Munz's California flora or Hulten's Alaska flora for several hundred miles on foot will appreciate Dorn's successful effort. Keys are full and serve as descriptions. They seem excellent. Aquatic and woody plants have their own separate keys, and for the Brassicaceae, Apiaceae, and *Astragalus* there are both flowering and fruiting keys. The characters used are simple, explained, evident, and separable. There are concise morphological descriptions for families and genera so a check can be made before keying to the species level. References in concise form are given for almost all genera. English names are supplied, but invention is not run into the ground. The habitat notes are concise and informative, not schematic. The illustrations are excellent in quality, informative, and helpful.

Again, plants know no political boundaries. The literature on many "North American" plants includes much published outside North America. Numerous Montana plants are also Alaskan, yet Alaska was physically and biologically a part of northeasternmost Asia and separated by vast ice sheets from North America during each glacial. The Soviet botanical literature is a rapidly expanding, very valuable mine of information on many North American plants. Hulten's Alaskan flora has been, and still is, a source of name corrections that are a prerequisite to an improved ecological and taxonomic understanding of Rocky Mountain plants, including several in Montana.

The literature on the distribution, ecology, uses, etc. of several Montana plants is hidden by some of the names Dorn uses (*Kobresia bellardii* for *K. myosuroides, Eriophorum polystachion* for *E. angustifolium, Carex stenophylla* or *C. eleocharis* for *C. duriuscula, Calamagrostis canadensis* for *C. purpures* are examples). However, this is a carping criticism. Dorn has brought the nomenclature and taxonomy of Montana plants up to date for the most part (cf. *Alnus viridus* and *A. incana, Artemisia tridentata* and its relatives, *Sphaeromeria, Triticeae, Leucopoa, Salix,* and *Heracleum,* among others).

A similarly excellent flora of the Black Hills of Wyoming and South Dakota was published earlier by the Dorns (1977) and is a real bargain ($1.50 if ordered with the Montana flora). This "local" flora of 1260 species contains 80% of the flora of South Dakota and 59% of the flora of Wyoming.—JACK MAJOR, Botany Department, University of California, Davis 95616.

Aven Nelson of Wyoming. By ROGER L. WILLIAMS. xii + 407 pp. Colorado Associated University Press, Boulder, CO 80309. 1984. $29.50. ISBN 0-87081-147-9.

This scholarly book is more than a biography of Aven Nelson. It is a brief history of systematic botany from about 1895 to 1945. It describes university life, particularly in the West, for this same period, and it touches on state politics. It also includes abbreviated biographies of many of Nelson's students.

The author, a historian specializing in French history, has taken the time to become familiar with the science of systematic botany to the point of personally collecting and identifying plants. This familiarity is reflected in his writing, yet he frequently provides helpful comments for those who are not taxonomists.

Those who know, or know of, the personalities in systematic botany from Nelson's time will easily relate to the book. Those who do not may find parts somewhat dry reading but should find the author's periodic reflections of interest. One example: "The posture of perfectionism, in academia, usually masks either indolence or fear." Teachers and researchers who read the book will see how well off they really are. Students can discover the qualities for success, qualities that are not taught in the university.

Aven Nelson was one of the first six faculty members at the newly-established University of Wyoming in 1887. His formal training was in English, but the University mistakenly hired two English professors. He had an interest in natural history, so he was appointed Professor of Biology. He founded the Rocky Mountain Herbarium and developed it in his spare time to be the largest in the interior West and one recognized world-wide. Nelson was instrumental in founding the Colorado-Wyoming Academy of Science and the American Society of Plant Taxonomists and served as the first president of each. He was the first interior westerner to be elected president of the Botanical Society of America. He was forced to retire at age 83 when the university instituted a mandatory limited service plan. Nelson was rewarded for his 55 years of service to the school, including 5 years as its president, with a pension of $1500 per year.

The book also gives insight into personalities of other systematic botanists of Nelson's time including E. L. Greene, P. A. Rydberg, B. L. Robinson, M. L. Fernald, N. L. Britton, J. N. Rose, M. E. Jones, J. M. Coulter, L. M. Underwood, W. Trelease, T. S. Brandegee, and A. A. Heller. It provides a basic history of the development of an International Code of Botanical Nomenclature, a valuable asset for students majoring in systematics. The controversies are portrayed better here by Williams than they are, for example, in G. H. M. Lawrence's treatment in *Taxonomy of Vascular Plants.* The battle between the conservatives at the Gray Herbarium and the New York "radicals" frequently surfaces. There is also the struggle of western botanists trying to break free from the dominance of the eastern schools, just as the eastern botanists struggled with Europeans at an earlier date. Once, when M. L. Fernald strongly suggested to Nelson that he should come back East for study before describing new species and offered an invitation, Nelson wrote back, "I wish it were possible for me to accept it at once and to spend much time within the walls of the Gray Herbarium .... One cannot always do as he would, but must do as he can."

In compiling the *New Manual of Botany of the Central Rocky Mountains* (1909), Nelson was forced to rethink the matter of what constitutes a species for all *practical* purposes. He moved toward conservatism by reducing to synonymy 1788 species names. Most botanists were becoming concerned with the excessive splitting of species that was taking place, so Nelson's lead was well received.

The book is concluded with two appendices listing Nelson's proposed new genera, species, and varieties along with their current status and his botanical and horticultural publications.

Biographies of earlier botanists like Thomas Nuttall and Asa Gray help us understand botanical activities of the 19th century. Williams has given us an excellent addition for a succeeding period.—ROBERT D. DORN, P.O. Box 1471, Cheyenne, WY.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren and Keuken, Index Herbariorum, 6th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

VOLUME 32, NUMBER 4 OCTOBER 1985

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Science, San Francisco, CA 94118.

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928

First Vice President: RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

Second Vice President: DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403

Recording Secretary: V. THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: WAYNE SAVAGE, Department of Biological Sciences, San Jose State University, San Jose, CA 95192

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542; the *Editor* of MADROÑO; three elected *Council Members:* JAMES C. HICKMAN, Department of Botany, University of California, Berkeley, CA 94720; THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

SAND DUNE FLORA OF THE GREAT BASIN AND MOJAVE DESERTS OF CALIFORNIA, NEVADA, AND OREGON

BRUCE MICHAEL PAVLIK
Department of Biology, Mills College,
Oakland, CA 94613

ABSTRACT

A floristic survey of 20 stabilized and unstabilized sand dunes in the Great Basin and Mojave deserts was conducted over a 9-year period. Plants were tallied as present only if they were observed growing on deep, windblown accumulations of sand. A total of 166 taxa was documented, representing 88 genera and 27 families of vascular plants. Relative to other desert areas in Nevada and California, the dune flora was enriched with members of Asteraceae, Fabaceae, Chenopodiaceae, and Polemoniaceae and somewhat deficient in Poaceae. Approximately 95% of the taxa were indigenous. In comparison with Death Valley and eastern California, the dunes were overrepresented with annuals and geophytes and underrepresented with hemicryptophytes, chamaephytes, and stem succulents. Only a third of the taxa can be considered as strictly psammophytic and one-sixth as halophytic. Five taxa are endemic to one or a few dunes; 12 are sand-restricted but less limited geographically than the endemics.

Ecological studies on the deserts of North America have concentrated on habitats that are widespread or readily accessible. Specialized habitats, such as limestone outcrops, lava flows, mountainsides, wetlands, and sand dunes, have been largely ignored. These may, in fact, constitute separate ecosystems—islands isolated by their physical and biological properties or by factors related to the evolution of the landscape through geologic time.

Desert sand dunes, defined as windblown accumulations of sand that exist independent of small-scale, fixed-wind obstructions (Bagnold 1933), can be distinguished ecologically from surrounding habitats by a unique set of extreme physical characteristics. These include an intense energy environment (Pavlik 1980), a mobile and abrasive substrate (Bagnold 1941, Evans 1962, Sharp 1966) having coarse texture and high porosity (MacDonald 1970, Dean 1978, Pavlik 1979a) and relatively mesic substrate conditions (Went and Westergaard 1949, Norris and Norris 1961, DeDecker 1976). Plants growing on dunes can maintain a higher internal water status than non-dune plants under the same microclimatic conditions (Pavlik 1980, Toft and Pearcy 1982). Desert dunes are associated invariably with the playas, intermittent water courses, and remnant lakes of arid, lowland basins. These basins and sand dunes are often isolated from one another by high mountain ranges that coalesce and divide

MADROÑO, Vol. 32, No. 4, pp. 197–213, 20 December 1985

in complex physiographic patterns, especially in Nevada and eastern California. The insular nature of dune habitats, as demonstrated by studies of dune-dwelling insects (D. Giuliani, pers. comm.) and mammals (Brown 1973), has yet to be established rigorously from comprehensive floristic data.

Vasek and Barbour (1977) concluded that very few data are available on the floristics and plant ecology of desert sand dunes. The information is confined either to descriptions of single dunes (Rempel 1936, DeDecker 1976, Pavlik 1979a, Thorne et al. 1981) or studies in relation to off-road vehicle impact (Westec 1977, Pavlik 1979b, Bury and Luckenbach 1983). The present study documents the dune flora at 20 locations in the Great Basin and Mojave deserts of California, Nevada, and Oregon as part of an ongoing contribution to the plant ecology and phytogeography of this habitat.

METHODS

Approximately 34 major sand dune systems are known to occur in the desert regions of California, Nevada, and Oregon (Fig. 1). This tally does not include systems dominated by sand sheet, obstacle or shrub-coppice formations (Dean 1978), or small, senescent dunes in advanced stages of stabilization. (Stabilization is indicated by decreasing substrate and dune mobility, high concentrations of silt and clay particles in a saline-alkaline substrate, and uniformity of vegetation between dune and non-dune sites.) Only 20 of the locations shown in Fig. 1 were included in this survey, but many of the others were visited once. Excluded were dunes with a strong floristic affinity to sites in the Colorado and Sonoran deserts (see Johnson 1977, 1982) and several low, semi-stabilized or stabilized dunes found commonly throughout the Great Basin. With respect to regional vegetation, seven of the dunes included in the study are associated with Great Basin, ten with Mojave Desert, and three with transitional community types (Beatley 1976) (Table 1). Twelve dunes may be described as massive and unstabilized, whereas the remainder are relatively small, low, and semi-stabilized. At all sites the dune substrate is a deep, coarse-grained, quartz-dominated, and finely-sorted aeolian sand. The negative impact of off-road vehicles on the native flora is probably significant at three sites, although some undisturbed habitat with plant cover could be found at each of these. Further information on desert sand dunes in California may be found in Dean (1978).

Each site was surveyed intensively on at least three occasions from 1976 to 1984. This period included several years with average or above average amounts of fall and winter precipitation (1975–76, 1977–78, 1979–80, 1982–83) and, consequently, an abundance and diversity of annuals. Only species found growing on dunes sensu

FIG. 1. Locations of major desert sand dune systems in California, Nevada, and Oregon. Dunes included in this study (solid circles) are numbered according to Table 1.

TABLE 1. CHARACTERISTICS OF THE SAND DUNES CHOSEN FOR STUDY. Regional vegetation is indicated as Great Basin (GB), transitional (T), or Mojave (M) desert. Dune stability is indicated as unstabilized (UN) or semi-stabilized (SST). Relative off-road vehicle (ORV) impact is indicated as little or none (0), moderate (+), or heavy (++) at present or in the past.

Dune system	County, state	N latitude & W longitude (°, ′)				Elev. (m)	Region	Stability	ORV impact
1. Alkali Lake	Lake, OR	43	00	120	00	1218	GB	SST	0
2. Silver State	Humboldt, NV	41	11	117	53	1402	GB	UN	+
3. Sand Mountain	Churchill, NV	39	16	118	23	1280	GB	UN	++
4. Teel	Mineral, NV	38	14	118	19	1379	GB	SST	0
5. Crescent	Nye, NV	38	15	117	20	1569	GB	UN	+
6. Mono	Mono, CA	38	08	119	00	1945	GB	SST	0
7. Fish Lake	Esmeralda, NV	37	46	118	04	1448	T	SST	0
8. Clayton	Esmeralda, NV	37	40	117	41	1326	T	UN	0
9. Deep Springs	Inyo, CA	37	35	118	05	1581	GB	SST	0
10. Eureka	Inyo, CA	37	05	117	40	900	M	UN	+
11. Saline	Inyo, CA	36	46	117	50	366	M	UN	0
12. Big Dune	Nye, NV	36	38	116	35	814	M	UN	++
13. Death Valley	Inyo, CA	36	37	117	07	0	M	UN	0
14. Panamint	Inyo, CA	36	27	117	28	732	M	UN	0
15. Ash Meadows	Nye, NV	36	20	116	18	670	M	SST	0
16. Olancha	Inyo, CA	36	18	117	58	1112	T	SST	0
17. Ballarat	Inyo, CA	35	55	117	12	324	M	SST	0
18. Saratoga	San Bern., CA	35	42	116	21	151	M	UN	0
19. Dumont	San Bern., CA	35	41	116	12	229	M	UN	++
20. Kelso	San Bern., CA	34	54	115	42	701	M	UN	+

stricto (in areas having enough accumulated sand to affect local topography) were noted as present and collected. This insured that taxa were related ecologically to dune conditions rather than to ecotonal or non-dune conditions. Voucher specimens were deposited with the Herbarium of the University of California, Davis (DAV), except those of *Gilia* (deposited at CAS). In addition to the field survey, collection data were obtained from searches conducted at CAS, DAV, RSA, UC, UNR, and the private herbarium of M. DeDecker (Independence, California). These records were used to add taxa to the flora only if the label contained sufficient information to establish that the collection was made on a specific dune. Otherwise, the specimen was simply noted and used to describe the substrate fidelity and general distribution of the taxon. Plant lists for individual dune systems may be obtained from the author. Unconfirmed taxa that may occur on the dunes in this study have been listed in Appendix I. These were not included in subsequent analyses of the flora. Nomenclature is based on Kartesz and Kartesz (1980) and the authorities to whom specimens were sent (see Acknowledgments).

Subsequent analyses of the dune flora were made by annotating each taxon with respect to 1) relative occurrence among the twenty dunes (rare = present at 1 or 2 dunes, uncommon = present at 3–5 dunes, common = present at 6 or more dunes); 2) Raunkier life form (annual, Geo = geophyte, Hemi = hemicryptophyte, Cham = chamaephyte, P-shrub = phanerophyte shrub, Succ = stem succulent); 3) fidelity to substrate texture (Ps = sand-restricted psammophyte, Ct = a plant of coarse-textured substrates including rock, gravel, and sand, At = a plant of many substrate textures including rock, gravel, sand, silt, and clay); 4) occurrence on saline or alkaline substrates (indicated by -S following the texture designation, e.g. At-S); and 5) geographic center of distribution among the dunes of this study (GB = dunes of the Great Basin Desert, M = dunes of the Mojave Desert, W = widespread among GB and M dunes, T = dunes that lie in a transition zone between the Great Basin and Mojave deserts). Raunkier life forms are defined in terms of the relationship between perennating buds and the soil surface (Radford et al. (1974) present the criteria used in this study). This relationship is complicated by sand movement in geophytes and hemicryptophytes that produce buds near (usually ±10 cm) the dune surface. For this reason, taxa had to possess a specialized, subterranean organ (e.g. rhizome, creeping rootstock, bulb) in order to be designated as geophytes, and hemicryptophytes were identified by a rosette or tussock growth form. The overlapping categories of substrate fidelity attempt to segregate sand-restricted plants (those Ps taxa that are dependent on the moisture and ionic properties of coarse-textured substrates, yet tolerant of sand movement, intense solar radiation, and low nutrient availability) from the wider ranging Ct plants (dependent on moisture and ionic conditions of coarse substrates but less tolerant of sand movement, intense solar radiation, and low nutrient availability) and At plants (independent of moisture and ionic conditions, and mostly intolerant of the aforementioned characteristics of unstabilized dunes). It should be emphasized that substrate fidelity may vary within the range of widely distributed species, especially those not confined to deserts. The substrate designations were assigned to reflect the principal occurrences of taxa as observed in the Great Basin and Mojave deserts. Similarly, the geographic descriptors (GB, M, W, and T) were used to describe the distribution of species within the study area and do not indicate the entire range. This was done to facilitate the analysis of phytogeographic patterns in subsequent research. All annotations were determined by the concurrence or consensus of many floras, taxonomic monographs, ecological studies, herbarium labels, and field observations.

Discussion

One hundred and sixty-six taxa were found among the 20 dunes included in this study, with 88 genera and 27 families represented. The 159 indigenous taxa were collected within a total area of about 310 km^2, resulting in an index of taxon density that is low (0.51 taxa/km^2) when compared to other plant assemblages in eastern California (0.36–1.56, Thorne et al. 1981). The dune flora was enriched with members of Asteraceae, Fabaceae, Chenopodiaceae, and Polemoniaceae and somewhat deficient in Poaceae (21%, 11%, 8%, 7%, and 7% of the taxa, respectively, Table 2). This is in comparison with larger, more ecologically diverse desert floras, such as that of the Nevada Test Site (17%, 6%, 4%, 4%, and 9%, Beatley 1976), eastern California (16%, 4%, 2%, 5%, and 7%, Thorne et al. 1981) and the entire California Desert Conservation Area (15%, 8%, 3%, 4%, and 9%, BLM unpublished data 1980). The diversity of the Asteraceae was due to a large number of mono- or bi-typic genera, whereas that of the Fabaceae and Polemoniaceae was due to a few genera with large numbers of species and infraspecific taxa (e.g. *Astragalus* and *Gilia*). Although only 7 introduced taxa were observed, these sometimes constituted a significant proportion of the vegetation cover (especially *Salsola*) at any one dune.

The life form spectrum of desert dune plants (Table 3) was very different from other desert spectra in the literature, thus supporting the recognition of a separate psammophytic vegetation type (Thorne et al. 1981). Dunes were overrepresented with annuals and geophytes and underrepresented with hemicryptophytes, chamaephytes, and stem succulents when compared with the desert vegetation of Death Valley (42, 2, 19, 13, and 3% respectively, Raunkier 1934) and

TABLE 2. THE 8 LARGEST FAMILIES AND 9 LARGEST GENERA OF THE SAND DUNE FLORA OF THE GREAT BASIN AND MOJAVE DESERTS.

Family	Taxa	Genus	Taxa
Asteraceae	34	*Astragalus*	10
Fabaceae	19	*Gilia*	8
Chenopodiaceae	13	*Eriogonum*	7
Poaceae	12	*Atriplex*	6
Polemoniaceae	12	*Camissonia*	6
Onagraceae	11	*Cryptantha*	5
Polygonaceae	11	*Chrysothamnus*	4
Boraginaceae	8	*Mentzelia*	4
		Oenothera	4

eastern California (42, 4, 19, 13, and 3% respectively, Thorne et al. 1981). The proportion of dune phanerophytes was the same as in eastern California deserts (17%) but lower than observed in Death Valley (23%). The relative abundance of annuals and geophytes in this flora indicates that these life forms offer an advantage in coping with the extreme conditions found on dunes, particularly with reference to sand movement. The physiological characteristics of annuals, including high rates of carbon assimilation, growth and development, minimize the time that vulnerable vegetative tissues are exposed to burial, deflation, and abrasion (Pavlik 1980, Toft and Pearcy 1982). The resource allocation patterns of annuals emphasize seed production, and seeds can comply with the forces of wind and sand (by moving), unlike rooted plants that must tend to resist those forces. Thus, annuals, either in the form of ephemeral vegetative plants or seeds, are less likely to act as fixed wind obstructions and to be subjected to abrasion or self-induced burial. Although geophytes are perennial, they frequently produce ephemeral shoots and always possess rhizomes or rootstocks that can maintain buds near the dune surface in spite of sand accumulation. The perennating buds of hemicryptophytes and chamaephytes, however, are not formed on an elongate axis capable of extensive subterranean growth. These "stationary" buds, produced at or near the dune surface, would readily be covered by sand, especially on unstable slopes that commonly oscillate by as much as one meter per year (Sharp 1966). The slow growth of stem succulents and phanerophytes further restricts or excludes these species from unstabilized dunes where the rates of sand movement exceed the elongation rates of shoots and roots. Working on coastal beaches and sand dunes, Barbour et al. (1985) also reported that annuals and geophytes were the most abundant life forms and emphasized exposure (wind) and sand movement to explain this pattern in the vegetation.

The dune taxa were divided almost equally among the three classes of substrate fidelity (Table 3). Typical psammophytes, such as *Abronia* spp., *Chaetadelpha wheeleri, Cleome sparsifolia, Dicoria* spp., *Lupinus shockleyi, Psoralea lanceolata* var. *purshii, Tiquilia plicata* and *Tripterocalyx* spp. have such a high fidelity to sand that they accentuate the insular nature of dune vegetation. Additional restrictions on the distribution of these plants also may be imposed by the proximity of many dunes to saline-alkaline playas. Few taxa of well-drained sandy and coarse-textured substrates appear to tolerate salinity (Table 3), although this is complicated by the fact that playa soils are fine-textured in addition to being highly ionic. The implication is that psammophytes lack physiological mechanisms of tolerance to low soil water potentials and, therefore, are dependent on the moisture release characteristics and low ion content of sand accumulations (Pavlik 1980, Toft and Pearcy 1982). The current and historical distributions of such insular taxa would be limited to dunes ("islands") and intermittent patches of sandy habitat ("isles and archipelagos"). In contrast, taxa that could tolerate the moisture and ionic conditions of fine-textured or saline soils would be "oceanic" (to complete the metaphor) and distributed widely between dunes. Clearly, the phytogeographic analysis of dunes will be served only by an examination of the distribution patterns of insular, psammophytic taxa.

Nearly half of the taxa in this flora are associated commonly with dunes of the Mojave Desert and another quarter with those of the Great Basin (Table 3). Geographic transitionals are taxa that occur within a broad area between the two major deserts and are not readily assignable to either region. Included here are the Eureka Dune endemics (see below), several Death Valley endemics, and a few other taxa found in a zone extending from Inyo County, California, through southern Nye and Clark counties, Nevada. Ecologically, however, all of the geographical transitionals are associated with Mojavean vegetation.

It is possible to recognize two categories of endemism in this flora. Dune endemics are those psammophytes found only on deep accumulations of windblown sand. These include *Astragalus lentiginosus* var. *micans, Oenothera avita* subsp. *eurekensis,* and *Swallenia alexandrae* from a single dune complex in Eureka Valley, and *Astragalus pseudiodanthus* and *Psorothamnus kingii* from several dunes of the Lahontan, Columbus-Tonopah, and Mono basins. The fluvial endemics that appear restricted to sandy substrates associated with drainage courses and basins are more widespread geographically than the dune endemics. These fluvial endemics include *Astragalus lentiginosus* var. *borreganus, A. l.* var. *macrolobus, Chaetadelpha wheeleri, Chamaesyce vallis-mortae, Cleome sparsifolia, Eriastrum densifolium* subsp. *mohavense, Eriogonum nummularae, Gilia*

TABLE 3. SAND DUNE FLORA ANALYZED BY LIFE FORM, FIDELITY TO SUBSTRATE TEXTURE, SALT TOLERANCE, AND GEOGRAPHIC DISTRIBUTION. Introduced taxa are included.

	No. of taxa	% of total flora
Raunkier life form		
Annual	83	50.0
Geophyte	30	18.1
Hemicryptophyte	7	4.2
Chamaephyte	16	9.6
Phanerophyte—shrub	28	16.9
Stem succulent	2	1.2
Substrate fidelity—salt tolerance		
Sand restricted		
Ps	49	29.5
Ps-S	3	1.8
Coarse textures		
Ct	56	33.7
Ct-S	4	2.4
All textures		
At	33	19.9
At-S	21	12.6
Geographic distribution		
Great Basin Desert	43	25.9
Mojave Desert	80	48.2
Transitional	7	4.2
Widespread	29	17.5
Introduced	7	4.2

campanulata, Machaeranthera leucanthemifolia, Penstemon acuminatus var. *latebracteatus, Stanleya pinnata* subsp. *inyoensis,* and *Tripterocalyx crux-maltae.* Other dunes (not included in this study) also are known to support endemic, psammophytic taxa, including those in central Nevada (*Astragalus callithrix, Cymopterus ripleyi*), southwestern Utah (*Argemone corymbosa* var. *arenicola, Asclepias welshii, Astragalus striatiflorus,* and the "gigas" form of *Atriplex canescens*), and southeastern California/northern Baja California (*Ammobroma sonorae, Croton wigginsii, Dicoria argentea, Eriogonum deserticola, Helianthus niveus* subsp. *tephrodes,* and *Palafoxia arida* var. *gigantea*). It seems reasonable to conclude that a high degree of plant endemism is often associated with desert sand dunes.

This initial analysis of the flora of sand dunes in the Great Basin and Mojave deserts has presented four lines of evidence to support the insular concept of the dune habitat and its vegetation: 1) the taxonomic composition of the dune flora differs from that of the desert as a whole; 2) dune vegetation has a distinctive life form spectrum that may be related to sand movement; 3) a subset of the flora appears to be edaphically restricted to dunes and patches of sand habitat; and 4) the presence of endemic taxa at several dunes indicates some degree of geographic and ecologic isolation through time. Additional studies will test the insular hypothesis more rigorously and attempt to analyze the patterns of dune plant distribution in relation to the recent geologic history of the Great Basin and Mojave deserts.

SAND DUNE FLORA OF THE GREAT BASIN AND MOJAVE DESERTS

GNETOPHYTA

Ephedraceae

Ephedra nevadensis. Uncommon; P-shrub, At, W.

ANTHOPHYTA—DICOTYLEDONEAE

Amaranthaceae

Tidestromia oblongifolia. Rare; Cham, Ct, M.

Asclepiadaceae

Asclepias erosa. Rare; Geo, At, M.

Asteraceae

Acamptopappus sphaerocephalus. Rare; Cham, At, M.
Ambrosia acanthicarpa. Uncommon; Annual, Ct, W.
Ambrosia dumosa. Uncommon; Cham, At, M.
Artemisia spinescens. Uncommon; Cham, At-S, GB.
Artemisia tridentata var. *tridentata.* Uncommon; P-shrub, At, GB.
Atrichoseris platyphylla. Uncommon; Annual, Ct, M.
Baileya pleniradiata. Uncommon; Annual, Ps, M.
Chaenactis fremontii. Uncommon; Annual, Ct, M.
Chaenactis stevioides var. *stevioides.* Uncommon; Annual, Ct, W.
Chaetadelpha wheeleri. Common; Geo, Ps, GB.
Chrysothamnus nauseosus subsp. *consimilis.* Uncommon; P-shrub, At, GB.
Chrysothamnus nauseosus subsp. *hololeucus.* Uncommon; P-shrub, At, GB.
Chrysothamnus viscidiflorus subsp. *pumilus.* Uncommon; Cham, At, GB.
Chrysothamnus viscidiflorus subsp. *viscidiflorus.* Uncommon; Cham, At, GB.
Dicoria canescens subsp. *canescens.* Common; Annual, Ps, M.
Dicoria canescens subsp. *clarkae.* Common; Annual, Ps, GB.

Glyptopleura marginata. Rare; Annual, Ps, GB.
Haplopappus acradenius. Rare; P-shrub, At-S, M.
Hymenoclea salsola var. *salsola.* Uncommon; P-shrub, Ct-S, M.
Machaeranthera arida. Rare; Annual, Ct, M.
Machaeranthera leucanthemifolia. Rare; Cham, Ps, M.
Malacothrix californica var. *glabrata.* Uncommon; Annual, Ct, W.
Malacothrix sonchoides. Uncommon; Annual, Ct, GB.
Monoptilon bellidiforme. Uncommon; Annual, Ct, M.
Palafoxia arida var. *arida.* Uncommon; Annual, Ps, M.
Pluchea sericea. Uncommon; P-shrub, At-S, M.
Psathyrotes annua. Uncommon; Annual, Ct-S, W.
Rafinesquia californica. Uncommon; Annual, At, M.
Rafinesquia neomexicana. Uncommon; Annual, At, M.
Solidago spectabilis. Rare; Geo, At-S, GB.
Stephanomeria pauciflora. Uncommon; Cham, Ct, M.
Tetradymia tetrameres. Rare; P-shrub, Ct, GB.
Tetradymia glabrata. Uncommon; P-shrub, At, GB.
Tetradymia spinosa. Uncommon; P-shrub, At, GB.

Bignoniaceae

Chilopsis linearis var. *arcuata.* Rare; P-shrub, At, M.

Boraginaceae

Cryptantha angustifolia. Common; Annual, Ct, M.
Cryptantha costata. Rare; Annual, Ct, M.
Cryptantha maritima. Rare; Annual, Ct, M.
Cryptantha micrantha subsp. *micrantha.* Common; Annual, Ps, W.
Cryptantha pterocarya. Rare; Annual, Ct, W.
Heliotropium curassavicum var. *oculatum.* Rare; Geo, At-S, W.
Tiquilia nuttallii. Common; Annual, Ps-S, GB.
Tiquilia plicata. Common; Geo, Ps, M.

Brassicaceae

Descurainia pinnata subsp. *filipes.* Rare; Annual, Ct, GB.
Dithyrea californica. Uncommon; Annual, Ps, M.
Lepidium fremontii. Uncommon; Cham, Ct, M.
Lepidium lasiocarpum. Rare; Annual, Ct, W.
Lepidium perfoliatum. Uncommon and introduced; Annual, At, GB.
Stanleya pinnata subsp. *inyoensis.* Uncommon; P-shrub, Ps, T.
Streptanthella longirostris. Rare; Annual, Ct, W.

Cactaceae

Opuntia echinocarpa var. *echinocarpa.* Uncommon; Succ, Ct, M.
Opuntia pulchella. Rare; Succ, Ct, GB.

Capparaceae

Cleome sparsifolia. Common; Annual, Ps, GB.
Cleomella obtusifolia. Rare; Annual, At-S, M.

Caryophyllaceae

Achyronychia cooperi. Uncommon; Annual, Ct, M.

Chenopodiaceae

Atriplex canescens subsp. *canescens.* Common; P-shrub, At-S, W.
Atriplex confertifolia. Common; P-shrub, At-S, W.
Atriplex hymenelytra. Rare; P-shrub, At-S, M.
Atriplex parryi. Rare; Cham, At-S, M.
Atriplex polycarpa. Uncommon; P-shrub, At-S, M.
Atriplex torreyi. Rare; P-shrub, At-S, M.
Ceratoides lanata. Uncommon; P-shrub, Ct, W.
Corispermum hyssopifolium. Rare and introduced; Annual, Ps, T.
Kochia americana. Rare; Cham, At-S, W.
Nitrophila occidentalis. Rare; Geo, At-S, W.
Salsola spp. (includes both *S. australis* and *S. paulsenii*). Common and introduced; Annual, At-S, W.
Sarcobatus vermiculatus. Common; P-shrub, At-S, GB.
Suaeda torreyana var. *ramosissima.* Uncommon; P-shrub, At-S, W.

Euphorbiaceae

Chamaesyce micromera. Uncommon; Annual, Ps, M.
Chamaesyce ocellata. Uncommon; Annual, Ps, M.
Chamaesyce parryi. Rare; Annual, Ps, M.
Chamaesyce vallis-mortae. Rare; Geo, Ps, M.
Croton californicus var. *mojavensis.* Rare; Cham, Ps, M.

Fabaceae

Acacia greggii. Rare; P-shrub, At, M.
Astragalus didymocarpus var. *dispermus.* Uncommon; Annual, Ps, M.
Astragalus geyeri var. *geyeri.* Uncommon; Annual, Ct, GB.
Astragalus lentiginosus var. *borreganus.* Uncommon; Geo, Ps, M.
Astragalus lentiginosus var. *fremontii.* Rare; Geo, Ct-S, W.

Astragalus lentiginosus var. *kennedyi.* Rare; Geo, Ps-S, GB.
Astragalus lentiginosus var. *macrolobus.* Rare; Geo, Ps, GB.
Astragalus lentiginosus var. *micans.* Rare and endemic to Eureka Valley, Inyo Co., CA; Geo, Ps, T.
Astragalus lentiginosus var. *variabilis.* Uncommon; Geo, Ps-S, M.
Astragalus pseudiodanthus. Rare and endemic to the Mono Basin and the southernmost extensions of the Lahontan Basin; Geo, Ps, GB.
Astragalus sabulonum. Uncommon; Annual, Ps, M.
Lupinus pusillus subsp. *intermontanus.* Common; Annual, Ps, GB.
Lupinus shockleyi. Common; Annual, Ps, M.
Peteria thompsonae. Rare; Geo, Ct, T.
Prosopis glandulosa var. *torreyana.* Uncommon; P-shrub, Ct-S, M.
Prosopis pubescens. Rare; P-shrub, Ct, M.
Psoralea lanceolata var. *purshii.* Uncommon; Geo, Ps, GB.
Psorothamnus kingii. Rare and endemic to the Lahontan Basin; Geo, Ps, GB.
Psorothamnus polydenius var. *polydenius.* Uncommon; P-shrub, At, W.

Geraniaceae

Erodium cicutarium. Uncommon and introduced; Annual, At, W.

Hydrophyllaceae

Nama demissum var. *demissum.* Uncommon; Annual, At, W.
Phacelia bicolor. Rare; Annual, Ps, GB.
Phacelia fremontii. Rare; Annual, At, W.

Loasaceae

Mentzelia albicaulis. Uncommon; Annual, Ct, W.
Mentzelia congesta. Rare; Annual, At, GB.
Mentzelia longiloba. Rare; Hemi, Ps, M.
Mentzelia nitens. Uncommon; Annual, Ct, W.
Pentalonyx thurberi subsp. *gilmanii.* Rare; P-shrub, Ct, T.
Pentalonyx thurberi subsp. *thurberi.* Common; P-shrub, Ct, M.

Malvaceae

Eremalche exilis. Rare; Annual, Ct, M.
Eremalche rotundifolia. Rare; Annual, Ct, M.
Sphaeralcea ambigua subsp. *ambigua.* Common; Cham, At, M.
Sphaeralcea ambigua subsp. *monticola.* Rare; Cham, At, GB.

Nyctaginaceae

Abronia pogonantha. Rare; Annual, Ps, M.
Abronia turbinata. Common; Annual, Ps, GB.
Abronia villosa var. *villosa.* Uncommon; Annual, Ps, M.
Tripterocalyx crux-maltae. Rare; Annual, Ps, GB.
Tripterocalyx micranthus. Rare; Annual, Ps, M.

Onagraceae

Camissonia boothii subsp. *condensata.* Uncommon; Annual, Ct, M.
Camissonia brevipes subsp. *brevipes.* Rare; Annual, At, M.
Camissonia claviformis subsp. *aurantiaca.* Uncommon; Annual, Ct, M.
Camissonia claviformis subsp. *claviformis.* Rare; Annual, Ct, M.
Camissonia claviformis subsp. *funerea.* Uncommon; Annual, Ct, T.
Camissonia claviformis subsp. *integrior.* Common; Annual, Ct, GB.
Oenothera avita subsp. *avita.* Rare; Geo, Ct, GB.
Oenothera avita subsp. *eurekensis.* Rare and endemic to Eureka Valley, Inyo Co., CA; Geo, Ps, T.
Oenothera deltoides subsp. *deltoides.* Uncommon; Annual, Ps, M.
Oenothera deltoides subsp. *piperi.* Uncommon; Annual, Ct, GB.
Oenothera primiveris subsp. *bufonis.* Rare; Annual, At, M.

Papaveraceae

Argemone corymbosa var. *corymbosa.* Uncommon; Hemi, At, M.

Plantaginaceae

Plantago insularis var. *fastigiata.* Uncommon; Annual, Ct, M.

Polemoniaceae

Eriastrum densifolium subsp. *mohavense.* Rare; Cham, Ps, M.
Gilia campanulata. Uncommon; Annual, Ps, GB.
Gilia filiformis. Uncommon; Annual, Ct, M.
Gilia latiflora subsp. *latiflora.* Uncommon; Annual, Ct, M.
Gilia latifolia. Rare; Hemi, At, M.
Gilia leptomeria subsp. "A." Common; Annual, Ps, GB.
Gilia leptomeria subsp. "B." Common; Annual, Ps, GB.
Gilia micromeria. Uncommon; Annual, Ps, GB.
Gilia sinuata. Rare; Annual, Ct, W.
Langloisia matthewsii. Rare; Annual, Ct, M.

Langloisia schottii. Rare; Annual, Ct, M.
Langloisia setosissima. Rare; Annual, Ct, W.

Polygonaceae

Chorizanthe brevicornu subsp. *brevicornu.* Uncommon; Annual, Ct, M.
Chorizanthe rigida. Uncommon; Annual, At, M.
Eriogonum cernuum var. *cernuum.* Rare; Annual, At-S, GB.
Eriogonum deflexum. Rare; Annual, Ct, M.
Eriogonum inflatum var. *inflatum.* Uncommon; Hemi, Ct, M.
Eriogonum insigne. Rare; Annual, Ps, M.
Eriogonum nummularae M. E. Jones (=*E. kearneyi* var. *kearneyi*). Uncommon; Cham, Ps, GB.
Eriogonum reniforme. Uncommon; Annual, Ct, M.
Eriogonum trichopes. Uncommon; Annual, Ct, M.
Rumex hymenosepalus. Uncommon and introduced; Geo, Ct, W.
Rumex venosus. Uncommon; Geo, Ps, GB.

Scrophulariaceae

Penstemon acuminatus var. *latebracteatus.* Rare; Geo, Ps, GB.
Penstemon thurberi. Rare; Cham, Ct, M.

Zygophyllaceae

Larrea tridentata. Common; P-shrub, At, M.

ANTHOPHYTA—MONOCOTYLEDONEAE

Liliaceae

Hesperocallis undulata. Uncommon; Geo, Ps, M.

Poaceae

Bouteloua barbata. Uncommon; Annual, Ct, M.
Bromus tectorum. Common and introduced; Annual, At, W.
Distichlis spicata var. *stricta.* Uncommon; Geo, At-S, W.
Elymus cinereus. Uncommon; Hemi, At, GB.
Hilaria jamesii. Uncommon; Geo, At, GB.
Hilaria rigida. Uncommon; Geo, Ct, M.
Muhlenbergia asperifolia. Uncommon; Geo, At-S, W.
Oryzopsis hymenoides. Common; Hemi, Ct, W.
Panicum urvilleanum. Rare; Geo, Ps, M.
Schismus barbatus. Rare and introduced; Annual, At, M.
Sporobolus airoides. Uncommon; Hemi, At-S, W.
Swallenia alexandrae. Rare and endemic to Eureka Valley, Inyo Co., CA; Geo, Ps, T.

ACKNOWLEDGMENTS

I am very grateful to the following individuals who examined the collections made in this study: R. C. Barneby (*Astragalus*), A. Day (*Gilia*), M. DeDecker (flora of eastern California), P. Raven (*Camissonia*), J. Reveal (*Eriogonum*), and G. Webster (*Chamaesyce*). I am particularly indebted to Mary and Paul DeDecker for their encouragement. Finally, I thank Derham Giuliani and Enid Larson for many hours of discussion on the biology and beauty of desert dunes.

LITERATURE CITED

BAGNOLD, R. A. 1933. A further journey through the Libyan desert. Geog. J. 82: 103–129.

———. 1941. The physics of blown sand and desert dunes. William Morrow and Co., NY.

BARBOUR, M. G., T. DEJONG, and B. PAVLIK. 1985. Marine beach and dune plant communities. *In* B. F. Chabot and H. A. Mooney, eds., Physiological ecology of North American plant communities, pp. 296–322. Chapman and Hall, London.

BEATLEY, J. C. 1976. Vascular plants of the Nevada Test Site and central-southern Nevada: ecologic and geographic distributions. Energy Research and Devel. Adm. Nat. Tech. Inform. Serv., VA.

BUREAU OF LAND MANAGEMENT (BLM). 1980. California Desert Plan. Final environmental impact statement and proposed plan, appendix volume E. California Desert Plan Staff, Riverside, CA.

BROWN, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology 54:775–787.

BURY, R. B. and R. A. LUCKENBACH. 1983. Vehicular recreation in arid land dunes: biotic responses and management alternatives. *In* R. H. Webb and H. G. Wilshire, eds., Environmental effects of off-road vehicles, impacts and management in arid regions, pp. 207–224. Springer-Verlag, NY.

DEAN, L. E. 1978. The California desert sand dunes. BLM—NASA #NSG 7220, California Desert Plan Staff, Riverside, CA.

DEDECKER, M. 1976. The Eureka Dunes. Fremontia 3:17–20.

EVANS, J. R. 1962. Falling and climbing sand dunes in the Cronese ("Cat") Mountain area, San Bernardino Co., California. J. Geol. 70:107–113.

JOHNSON, A. F. 1977. A survey of the strand and dune vegetation along the Pacific and southern Gulf coasts of Baja California, Mexico. J. Biogeogr. 7:83–99.

———. 1982. Dune vegetation along the eastern shore of the Gulf of California. J. Biogeogr. 9:317–330.

KARTESZ, J. T. and R. KARTESZ. 1980. A synonymized checklist of the vascular flora of the United States, Canada and Greenland. Vol. II: the biota of North America. Univ. North Carolina Press, Chapel Hill.

MACDONALD, A. A. 1970. The northern Mojave Desert's little Sahara. Calif. Div. Mines and Geology, Mineral Information Service 23:3–6.

NORRIS, R. M. and K. S. NORRIS. 1961. Algodones Dunes of southeastern California. Geol. Soc. America Bull. 72:605–620.

PAVLIK, B. M. 1979a. A synthetic approach to the plant ecology of desert sand dunes, Eureka Valley, California. M.S. thesis, Univ. California, Davis.

———. 1979b. The biology of endemic psammophytes, Eureka Valley, California, and its relation to off-road vehicle impact. BLM #CA-060-CT8-000049, California Desert Plan Staff, Riverside, CA.

———. 1980. Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. Oecologia 46:147–154.

Radford, A. E., W. C. Dickison, J. R. Massey, and C. R. Bell. 1974. Vascular plant systematics. Harper and Row, NY.

Raunkier, C. 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford.

Rempel, P. J. 1936. The crescentic dunes of the Salton Sea and their relation to the vegetation. Ecology 17:347–358.

Sharp, R. P. 1966. Kelso Dunes, Mojave Desert, California. Geol. Soc. America Bull. 77:1045–1074.

Thorne, R. F., B. A. Prigge, and J. Henrickson. 1981. A flora of the higher ranges and the Kelso Dunes of the eastern Mojave Desert in California. Aliso 10:71–186.

Toft, N. L. and R. W. Pearcy. 1982. Gas exchange characteristics and temperature relations of two desert annuals: a comparison of a winter-active and a summer-active species. Oecologia 55:170–177.

Vasek, F. C. and M. G. Barbour. 1977. Mojave desert scrub vegetation. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, pp. 835–867. Wiley Interscience, NY.

Went, F. W. and W. Westergaard. 1949. Ecology of desert plants III. Development of plants in the Death Valley National Monument, California. Ecology 30: 26–38.

Westec. 1977. Survey of sensitive plants of the Algodones Dunes. Unpublished report, Bureau of Land Management, Riverside, CA.

(Received 20 Dec 1984; accepted 21 Jun 1985.)

Appendix I.

Plants that may occur but could not be confirmed at the dunes included in this study.

Antirrhinum kingii
Baileya pauciradiata
Chamaesyce polycarpa
Cleome lutea
Cryptantha circumscissa
Cycloloma atriplicifolia
Eriastrum eremicum
E. wilcoxii
Eriogonum brachyanthum
E. maculatum
Erioneuron pulchellum
Iva nevadensis
Krameria parvifolia
Nama aretiodes
N. depressum
Oligomeris linifolia
Orobanche cooperi
Pectis papposa
Phacelia ivesiana
Pholisma arenarium
Plagiobothrys kingii
Psoralea castorea
Psorothamnus mollis
Sarcobatus vermiculatus var. *baileyi*
Stephanomeria exigua
Stillingia spinulosa

ADDENDA TO THE VASCULAR FLORA OF SAN LUIS OBISPO COUNTY, CALIFORNIA

DAVID J. KEIL, ROBERT L. ALLEN[1],
JOY H. NISHIDA[2], and ERIC A. WISE[3]
Biological Sciences Department
California Polytechnic State University,
San Luis Obispo, CA 93407

ABSTRACT

Documentation is provided for the occurrence of 76 species of flowering plants not reported previously from San Luis Obispo County, California. Recent collections confirm the presence of three additional species that were reported from San Luis Obispo County but not included in *The Vascular Plants of San Luis Obispo County, California* (Hoover 1970). Of the addenda to the county's flora, 21 are native to California and 58 are introduced. The additions include members of 32 families, four of which were not represented previously in the county's flora: Basellaceae, Haloragaceae, Molluginaceae, and Hydrocharitaceae.

The Vascular Plants of San Luis Obispo County, California (Hoover 1970) has provided a sound foundation for subsequent floristic studies in the county. The thoroughness of Hoover's research on the county flora and his careful scholarship have been demonstrated repeatedly by users of his flora. As can be expected with any flora, subsequent investigations have documented the presence in the county of species not reported by Hoover. In this paper we are adding 76 taxa to the known flora of San Luis Obispo County. Another three species are listed that were reported from San Luis Obispo County in Munz (1968) but overlooked or deliberately omitted in the preparation of the final drafts of Hoover's flora. Recent collections of these species are noted.

The addenda to the San Luis Obispo County flora include members of 32 families. Four of these, Basellaceae, Haloragaceae, Molluginaceae, and Hydrocharitaceae, were not reported previously from the county. Page numbers from Hoover (1970) are indicated for those families already known from San Luis Obispo County.

The following list is based on specimens deposited in OBI. For most taxa we have followed the nomenclature of Munz and Keck (1959) and Munz (1968). For some weedy taxa, particularly those

---

[1] Present address: Museum of Systematic Biology, Univ. of California, Irvine, CA 92717.

[2] Present address: Section of Botany, Carnegie Museum of Natural History, 4400 Forbes Ave., Pittsburgh, PA 15213.

[3] Present address: Biological Sciences Dept., Chabot College, Hayward, CA 94545.

MADROÑO, Vol. 32, No. 4, pp. 214–224, 20 December 1985

of European origin, the names used by Munz and Keck differ from those used by Tutin et al. (1964–1980) and by Kartesz and Kartesz (1980). For these taxa, we have noted in brackets the names used by Munz and Keck. Authorities are from Munz and Keck (1959), Munz (1968), and Kartesz and Kartesz (1980), except as noted.

The additions to the San Luis Obispo County flora represent 21 native and 58 introduced species. Most of the native taxa were probably present when Hoover did his field work but were overlooked. [*Sagittaria latifolia* is native to California but known to have been introduced to San Luis Obispo County.] Some native taxa, such as *Elatine rubella* and *Limosella aquatica,* are very inconspicuous plants. Others occur in very restricted areas that Hoover never visited. Of the introduced taxa, some are well-established and probably were present during Hoover's studies. Others appear to be recent introductions. The documentation of their occurrence at this time will allow later studies to determine whether the taxa have become permanent members of the county's flora. In the species list, introduced taxa are indicated by an asterisk (*).

Some of the additions are a result of intensive floristic surveys. Local areas covered in these floristic studies include the Arroyo de la Cruz region in the northwestern corner of the county, American Canyon in the La Panza Mountains, Black Lake Canyon on the Nipomo Mesa, Laguna Lake Park in San Luis Obispo, and the Huerhuero Creek drainage near Creston. A survey of aquatic habitats throughout the county by Wise (1984) produced several new records.

ADDENDA TO THE VASCULAR FLORA

ANTHOPHYTA—DICOTYLEDONEAE

Anacardiaceae (p. 188)

Rhus integrifolia Benth. & Hook. f. ex Brewer & S. Wats. Between Arroyo Grande and San Luis Obispo along Hwy 227, ca. 3.2 km south of southern jct. with Corbett Canyon Rd., coastal scrub hillside (*Keil 13688*). This population is the northernmost known occurrence for *R. integrifolia.*

Apiaceae (p. 208)

**Apium leptophyllum* (Pers.) F. Muell. ex Benth. & Muell. Common lawn weed on campus of California Polytechnic State Univ., San Luis Obispo (*Keil 13677*).

Perideridia kelloggii (A. Gray) Mathias. Grassy slope in heavy clay soil on south side of Arroyo de la Cruz (*Keil 17394*).

**Torilis arvensis* (Huds.) Link subsp. *purpurea* (Ten.) Hayek. Along channel of Arroyo de la Cruz (*Keil 14881*); lawn weed on campus of California Polytechnic State Univ., San Luis Obispo (*Keil 14931*); Lopez Wilderness Area, abundant along trail in upper Lopez Canyon in open woods (*Keil and Webster 18188*).

Asteraceae (p. 273)

**Chondrilla juncea* L. Reported from the county by Munz (1968). This species was first collected in the county by R. F. Hoover in 1965 from the summit of Cuesta Grade 9.7 km north of San Luis Obispo (*Hoover 9634*) and 1.6 km west of San Luis Obispo along Hwy 1 (*Hoover 9645*). The two infestations were treated chemically by the San Luis Obispo County Agricultural Commissioner's office in 1966 (Fuller 1966) and Hoover did not include the species in his flora. The eradication efforts were apparently unsuccessful and the species was collected at several locations in the San Luis Obispo area in the early 1980s. This species is locally common along the right-of-way of the Southern Pacific Railroad and on roadsides from Santa Margarita to San Luis Obispo, and has been collected from the following sites: Cuesta Summit along unpaved fire road in chaparral area (*Keil s.n.*); San Luis Obispo (*Keil s.n., Burdett and Burdett s.n., Allen A500*). Doug Barbe of the State Department of Food and Agriculture states (pers. comm.) that county personnel are once again attempting to eradicate this invasive weed.

**Eclipta prostrata* (L.) L. [=*E. alba* (L.) Hassk.]. East end of Lopez Lake below confluence of Arroyo Grande Cr. and Phoenix Cr., drying mudflats and sandbars (*Keil 13644*); just south of Creston along Middle Branch of Huerhuero Cr., sandy dry stream bed (*Keil 17976*).

**Erechtites glomerata* (Poir.) DC. [=*E. arguta* (A. Rich.) DC. (Barkley 1981)]. Reported from the county by Munz (1968) but not listed by Hoover (1970); recent collection from lower slopes of Cypress Mountain, in a live oak woodland, roadside on mesic north-facing slope (*Keil et al. 15942*).

**Erechtites minima* (Poir.) DC. [=*E. prenanthoides* (A. Rich.) DC.]. Arroyo de la Cruz in bed of unused dirt road on steep oak-wooded slope (*Keil 17401*).

Lasthenia glabrata Lindl. Baywood Park at Sweet Springs Marsh. Locally common in salt marsh (*Cardwell 238*).

Lasthenia maritima (A. Gray) M. Vasey [=*L. minor* (DC.) Ornduff subsp. *maritima* (A. Gray) Ornduff]. Pup Rock, near Lion Rock, offshore of mouth of Diablo Canyon; in crevices and among loose, guano-soaked rocks in western gull breeding area (*Vasey and Harms 8119*). The Diablo Canyon site is disjunct from the nearest known population in San Mateo County by over 300 km (M. C. Vasey, pers. comm.).

***Leontodon taraxacoides* (Vill.) Merat subsp. *taraxacoides* [=*L. leysseri* (Wallr.) G. Beck]. Along Prefumo Canyon Rd., 1.6 km west of Los Osos Valley Rd. (*Keil 11830*).

Basellaceae

**Anredera cordifolia* (Ten.) Steenis. San Luis Obispo, in shrubs next to San Luis Cr. (*Keil s.n.*).

Brassicaceae (p. 142)

**Coronopus didymus* (L.) Sm. Sand dunes at south end of Morro Bay (*Schwartz and Long 32*); garden weed in Los Osos (*Keil s.n.*); 2.9 km north of Arroyo de la Cruz (*Keil 17387*).

**Erophila verna* (L.) Chev. [=*Draba verna* L.]. Nipomo Mesa along Black Lake Canyon, locally abundant along trail (*Jones and Keil 15812*); American Canyon campground on slight slope in blue oak woodland (*Nishida and Allen 213*).

**Lepidium latifolium* L. Along Hwy 41, 1.6 km northeast of jct. with Hwy 1 in Morro Bay, roadside (*McLeod s.n.*).

**Lepidium oblongum* Small. La Panza Mts., American Canyon in blue oak woodland (*Nishida 231, 287, 551*); Los Osos in cracks of sidewalk (*Keil 15887*); Ridge between Arroyo de la Cruz and Arroyo del Oso (*Keil 16995*).

Caryophyllaceae (p. 129)

**Sagina apetala* Ard. North of Arroyo de la Cruz and west of Hwy 1, locally common in damp soil of dune slack at edge of trail (*Keil 16924*); south end of Santa Lucia Mts., on rd. to Stony Cr. campground, 0.6 km from jct. with Avenales-Agua Escondido Rd. (T31S R16E S27), 700 m elev., very local on moss-covered rocks in shaded ravine with other minuscule herbs and *Anthoceros* (*Keil and Riggins 18211*).

Chenopodiaceae (p. 120)

Chenopodium chenopodioides (L.) Aellen. 4.8 km south of Creston along Hwy 229, along Middle Branch of Huerhuero Cr. (*Keil 14259*).

**Chenopodium multifidum* L. Baywood Park–Los Osos area on roadsides (*Keil 17407, 18301, 18433*).

Elatinaceae (p. 196)

Elatine rubella Rydb. Just south of Creston in damp sand at edge of Creston Lake (*Keil 17996*).

Euphorbiaceae (p. 186)

**Euphorbia serpens* H.B.K. Campus of California Polytechnic State Univ., San Luis Obispo, common weed in ornamental plantings (*Keil 18004*).

Fabaceae (p. 165)

**Lathyrus japonicus* Willd. Intersection of South Bay Blvd. and Turri Rd. in sandy soil just above salt marsh (*Meredith 23*).

Lotus oblongifolius (Benth.) Greene. American Canyon in La Panza Mts., locally common among rocks in stream channel (*Keil et al. 18136*).

**Spartium junceum* L. Well-established and spreading in the sandy channel of Arroyo de la Cruz (*Keil 13992*); occasional on brushy slopes on campus of California Polytechnic State Univ., San Luis Obispo (*Keil 18299*); along Foothill Blvd. ca. 0.4 km from Los Osos Valley Rd., grassy roadside in agricultural area (*Keil 18319*).

**Trifolium campestre* Schreb. [=*T. procumbens* sensu auct. non L.]. 1.4 km north of San Simeon along Hwy 1, locally an aspect dominant growing in dense colonies (*Keil 16950*); ridge south of Arroyo de la Cruz, locally common in grassy areas (*Keil 18123*).

**Trifolium dubium* Sibthorp. Campus of California Polytechnic State Univ., San Luis Obispo, lawn weed (*Keil s.n.*).

**Trifolium fragiferum* L. Campus of California Polytechnic State Univ., San Luis Obispo, weed in lawn (*Keil 17163*); ca. 4.8 km west of Cuesta College along Chorro Cr. near Highway 1 (*Keil 12508*); Laguna Lake Park, San Luis Obispo (*Smeltzer and Turnquist 208*); south of San Luis Obispo, 3.7 km from Johnson Ave. on Orcutt Rd. in rocky streamlet (*Wise 1206*); weed of lawn areas on campus of Los Osos Junior High School (*Keil 18431*).

**Trifolium glomeratum* L. Just south of highway bridge over Arroyo de la Cruz, very local on roadside (*Keil 17072*).

**Trifolium pratense* L. Locally common weed of summer-irrigated lawns and playground areas on campus of Baywood Elementary School, Baywood Park (*Keil 18432*).

**Vicia sativa* L. subsp. *nigra* (L.) Ehrh. [=*V. angustifolia* L.]. Ridge system between Arroyo de la Cruz and Arroyo de los Chinos on grassy slope (*Keil 16962*).

**Vicia villosa* Roth subsp. *varia* (Host.) Corb. [=*V. dasycarpa* Ten.]. Well-established in western half of San Luis Obispo County. Adelaida (*Jackman and Truesdale 11*); 12.3 km northeast of Santa Margarita (*Arnold and Allen 280*); Reservoir Canyon (*Burrows 68*; *Berry and Wilson 55*); Laguna Lake Park, San

Luis Obispo (*Smeltzer and Turnquist 55*); San Luis Obispo (*Dettloff 01*); Indian Knob (*Vanderwier 150*); Black Lake Canyon (*Keil and Wise 16268*); near Rinconada Mine, south of Santa Margarita (*Keil et al. 18224*).

Fumariaceae (p. 142)

**Fumaria parviflora* Lam. San Luis Obispo in cultivated field southwest of Madonna Rd. Shopping Plaza (*Ashley s.n.*).

Haloragaceae

**Myriophyllum spicatum* L. Lopez Lake, locally common in shallow water, particularly around inlets (*Keil 13672* [voucher determined by O. Ceska]; *Wise 1065, 1259*). Smith (1976) listed *Myriophyllum spicatum* subsp. *exalbescens* (Fern.) Jeps. from wetland areas of the Nipomo Dunes. He cited no specimens and did not indicate the source of his information. We have been unable to verify the occurrence of this taxon in San Luis Obispo County.

Hypericaceae (p. 196)

**Hypericum perforatum* L. South of San Luis Obispo on Orcutt Rd. (*Keil 18318*).

Linaceae (p. 186)

**Linum bienne* P. Mill. [=*L. angustifolium* Huds.]. Locally common on grassy roadsides along Hwy 1 from San Carpoforo Cr. (*Brown 2023*) south to Arroyo de la Cruz (*Jones s.n.*; *Keil 16247*).

Malvaceae (p. 193)

**Abutilon theophrasti* Medic. Atascadero, weed in cultivated field (*Dempsey s.n.*); campus of California Polytechnic State Univ., San Luis Obispo, locally common weed in cultivated fields (*Wilgenburg 8*).

**Lavatera arborea* L. Scattered in coastal areas from Morro Bay south into Santa Barbara County. Morro Bay, locally common on sand dunes (*Keil 18309*); Baywood Park on damp roadside near edge of marsh (*Keil 18289*); Arroyo Grande, agricultural area (*Keil 18314*); just north of Santa Maria River on Hwy 1 (*Keil 18315*).

**Modiola caroliniana* (L.) G. Don. Lawn weed at Laguna Lake Park (*Turnquist and Smeltzer 184*); San Luis Obispo (*McLeod 1390*).

Molluginaceae

**Glinus lotoides* L. Reported from the county by Munz (1968) but not listed by Hoover (1970); recent collections from Creston (*Keil 17971, 18015*) and east of Atascadero in Rocky Canyon Cr. (*Keil 18035*).

**Mollugo verticillata* L. Just south of Creston in bed of Middle Fork of Huerhuero Cr. and in adjacent grassy areas (*Keil 17989*); ca. 2.4 km south of Creston at Beck Lake (*Wise 1865*).

Onagraceae (p. 200)

Clarkia rubicunda (Lindl.) Lewis & Lewis subsp. *rubicunda.* On grassy slope above Arroyo de los Chinos east of BM 77 (*Keil 17144*).

Plantaginaceae (p. 266)

**Plantago arenaria* Waldst. & Kit. [=*P. indica* L.]. Nipomo Mesa, locally common along Pomeroy Rd. ca. 1.6 km north of Willow Rd. in area of open dune chaparral (*Wise and Keil 16251*).

Polemoniaceae (p. 224)

Allophyllum divaricatum (Nutt.) A. & V. Grant. Scattered about open disturbed ground and roadside on eastern slope of Pine Mountain in full sun on sandstone soil, 760 m (*Miller 581-44*).

Polygonaceae (p. 109)

**Emex australis* Steinh. In stabilized coastal dunes at south end of Alexander St. in Los Osos (*Keil 15692*); along Pecho Rd. in Montaña de Oro State Park (*Keil et al. s.n.*).

**Polygonum argyrocoleon* Steud. ex Kunze. Occasional lawn weed at Los Osos Junior High School in Baywood Park (*Keil s.n.*).

**Reynoutria sachalinense* (F. S. Petrop.) Nakai in Mori [=*Polygonum sachalinense* F. S. Petrop. (Webb 1964)]. A 27-m^2 infestation was found to the east of El Camino Real, just south of Santa Ysabel Ave. in Atascadero in 1967 (*Fuller 15919*). Because there have been no reports of this infestation since 1967, it is presumed to have been eradicated (Doug Barbe, pers. comm.). Subsequently, the site in Atascadero where this species was collected has been developed commercially.

**Rumex kerneri* Borbas. Black Lake Canyon in *Eucalyptus* grove in partial shade (*Keil and Jones 15811*); San Luis Obispo on roadside in partial shade of *Eucalyptus* (*Keil 18459*).

Rumex occidentalis S. Wats. var. *fenestratus* (Greene) Lepage [=*R.*

fenestratus Greene]. Local in freshwater marsh in lee of dunes just north of Arroyo de la Cruz (*Keil 17068*).

Scrophulariaceae (p. 255)

**Bellardia trixago* (L.) All. In grassland of Laguna Lake Park, San Luis Obispo (*Smeltzer and Turnquist s.n.*; *Keil 13060*); along Turri Rd. (*Walters s.n.*); Arroyo de la Cruz, on flood plain (*Keil 17075*); Poly Canyon, locally abundant on grazed slope on north side of creek (*Riggins 1493*).

**Kickxia elatine* (L.) Dumort. East of Arroyo Grande along rd. to Lopez Lake, ca. 1.6 km east of Orcutt Rd., edge of cultivated field at border of woods (*Keil 13638*); along channel of San Luis Cr. in San Luis Obispo (*Keil 16314*).

Limosella aquatica L. Canyon Ranch south of Shandon on Shell Cr. Rd., Sinton Middle Pond (*Wise 1339, 1493*).

**Linaria vulgaris* P. Mill. Arroyo Grande at corner of Hwy 1 and Grand Ave. in wet area of roadside ditch (*Byrum and Koivisto 9*).

**Veronica persica* Poir. American Canyon, uncommon in small patch along road (*Nishida and Luckow 555*); Shandon, weed in vegetable garden (*Keil 17167*); lawn weed on campus of California Polytechnic State Univ., San Luis Obispo (*Keil 18300*).

Solanaceae (p. 253)

Solanum cornutum Lam. [=*S. rostratum* Dunal]. Atascadero in 3-F Meadows area (*Cunningham s.n.*).

Verbenaceae (p. 246)

**Verbena brasiliensis* Vell. On roadcut just south of highway bridge over Arroyo de la Cruz (*Keil 17967*).

ANTHOPHYTA—MONOCOTYLEDONEAE

Alismataceae (p. 51)

Echinodorus rostratus (Nutt.) Engelm. [=*E. berteroi* (Spreng.) Fassett]. Campus of California Polytechnic State Univ., San Luis Obispo at edge of large pond (*Sparling 1371, 1372, 1373*; *Ashley s.n.*; *Wise 936*); Santa Margarita Lake (*Wise 916, 1712*); east end of Lopez Lake below confluence of Arroyo Grande Cr. and Phoenix Cr. (*Keil 13664*).

**Sagittaria latifolia* Willd. Canyon Ranch on Shell Cr. Rd. south of Shandon where introduced in the 1970s as an ornamental (Norma Sinton, pers. comm.). It has spread locally to nearby reservoirs: Canyon Ranch (*McKei s.n.*); Sinton South Pond (*Wise 1487, 1507*); Sycamore Reservoir (*Wise 1508*).

Araceae (p. 83)

**Peltandra virginica* (L.) Schott. Farm ponds on Canyon Ranch south of Shandon (*Wise 1353, 1496, 1509*). This species was introduced in the 1970s to a small ornamental pool (Norma Sinton, pers. comm.) and has spread subsequently to nearby reservoirs, probably through the activities of waterfowl.

Cyperaceae (p. 76)

**Cyperus esculentus* L. Along Middle Branch of Huerhuero Cr., 4.8 km south of Creston along Hwy 229, damp area in sandy stream channel (*Keil 14247*).

Hydrocharitaceae

**Egeria densa* Planch. Canyon Ranch south of Shandon, Sinton South Pond (*Wise 1317, 1484*).

Iridaceae (p. 98)

**Iris pseudacorus* L. On damp banks of San Luis Cr. (*Wise 2060*) and Meadow Lane (*Wise 1452*).

Juncaceae (p. 84)

Juncus rugulosus Engelm. Pine Canyon at the Cuyama River (*Wise 781*). Hoover (1970) indicated that the occurrence of this taxon [as *J. dubius* Engelm. forma *rugulosus* (Engelm.) Hoover] in San Luis Obispo County was to be expected.

Liliaceae (p. 88)

Calochortus weedii Wood var. *vestus* Purdy. Along road to Hearst Springs on Pine Mountain, 850 m, exposed ocean-facing slope with soil derived from serpentine mixed with rhyolite (*Miller 783-1-A,B*).

Fritillaria ojaiensis Davidson. Reservoir Canyon just north of San Luis Obispo in foothills of Santa Lucia Range (*Hrusa 121, 123*).

**Leucojum aestivum* L. Escaped from cultivation on wet bank at Atascadero Lake (*Wise 1673*) and in San Luis Obispo (*Wainwright 18*).

Poaceae (p. 52)

**Alopecurus pratensis* L. Campus of California Polytechnic State

Univ., San Luis Obispo, at base of railroad overpass on Highland Ave. (*Keil 14048*).

**Arundo donax* L. Occasional to locally abundant along creeks and in ruderal areas: San Luis Cr. (*Wise 1766, 2059*); Cuesta College Rd. (*Wise 2063*); Cambria (*Wise 2064*); along Turri Rd. (*Wise 2061*); observed along Hwy 1 near California Men's Colony, at Atascadero, east of Arroyo Grande, and near Santa Margarita Lake.

**Chloris gayana* Kunth. Weed in flower bed on campus of California Polytechnic State Univ., San Luis Obispo (*Keil 16310*).

**Eleusine tristachya* (Lam.) Lam. Canyon Ranch south of Shandon on wet bank of Sinton South Pond (*Wise 1325*).

**Eragrostis curvula* (Schrad.) Nees. Scattered for several kilometers along Lopez Lake Rd. east of Arroyo Grande (*Keil 14286, 18310*); near San Luis Obispo just north of jct. with Los Osos Valley Rd. on Foothill Blvd., grassy roadside (*Keil 18298*).

**Festuca arundinacea* Schreb. In Los Osos Valley (*Hoover 9023*) and in dry woods near Rocky Butte Lookout (*Hoover 9055*). Misidentified by Hoover (1970) as *F. elatior* L.

**Panicum dichotomiflorum* Michx. Campus of California Polytechnic State Univ., San Luis Obispo, weed at edge of cultivated field (*Ashley s.n.*).

**Panicum hillmanii* Chase. Hwy 166 at jct. with US 101 just north of Santa Maria River (*Brown 2055*).

**Panicum miliaceum* L. Los Osos, weed in residential areas (*Keil 18370*; *18430*).

**Secale cereale* L. Common along old Hwy 101 between Santa Margarita and Atascadero (*Brown 2050*).

Sporobolus contractus A. S. Hitchc. Locally common on grassy roadside along Hwy 101 at San Miguel (*Keil 18434*).

Potamogetonaceae (p. 50)

Potamogeton illinoensis Morong. Santa Margarita Lake (*Wise 908*).

Potamogeton nodosus Poir. Santa Margarita Lake (*Wise 1723*).

Potamogeton pusillus L. Shepperd's Reservoir on the campus of California Polytechnic State Univ., San Luis Obispo (*Wise 1745*); Lopez Treatment Plant near Arroyo Grande (*Wise 626-A*).

ACKNOWLEDGMENTS

We thank the collectors who have provided their personal collection records. We are also indebted to Doug Barbe, plant taxonomist with the State of California Department of Food and Agriculture, for providing information regarding *Reynoutria sachalinense* and *Chondrilla juncea*. We also wish to thank the following individuals for specimen determinations: R. R. Haynes (*Potamogeton*), D. O. Santana (*Fritillaria ojaiensis*), and O. Ceska (*Myriophyllum*).

LITERATURE CITED

BARKLEY, T. M. 1981. *Senecio* and *Erechtites* (Compositae) in the North American Flora: supplementary notes. Brittonia 33:523–527.

FULLER, T. C. 1966. Skeleton Weed: a serious threat to California agriculture. Dept. Ag. Bull. 55(1):20–31.

HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. Univ. Calif. Press, Berkeley.

KARTESZ, J. T. and R. KARTESZ. 1980. A synonymized checklist of the vascular flora of the United States, Canada and Greenland. Univ. North Carolina Press, Chapel Hill.

MUNZ, P. A. 1968. Supplement to a California flora. Univ. Calif. Press, Berkeley.

——— and D. D. KECK. 1959. A California flora. Univ. Calif. Press, Berkeley.

SMITH, K. A. 1976. The natural resources of the Nipomo Dunes and wetlands. Calif. Dept. Fish and Game Coastal Wetlands Series 15.

TUTIN, T. G. et al., eds. 1964–1980. Flora Europaea. Cambridge Univ. Press. 5 vols.

WEBB, D. A. 1964. *Reynoutria. In* T. G. Tutin et al., eds., Flora Europaea. Vol. 1. Lycopodiaceae to Platanaceae, p. 81. Cambridge Univ. Press.

WISE, E. A. 1984. A flora of freshwater vascular plants of San Luis Obispo County, California. M.S. thesis, California Polytechnic State Univ., San Luis Obispo.

(Received 16 Nov 1984; accepted 26 Jan 1985)

ANNOUNCEMENT

The 1985 Jesse M. Greenman Award

The 1985 Jesse M. Greenman Award has been won by George K. Rogers for his publication "*Gleasonia, Henriquezia,* and *Platycarpum* (Rubiaceae)" (Flora Neotropica Monograph No. 39). This monographic study is based on a Ph.D. dissertation from the University of Michigan Herbarium under the direction of William R. Anderson.

The Greenman Award, a cash prize of $250, 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 that was published during the *previous* year. Papers published during *1985* are now being considered for the 18th annual award, which will be presented in the summer of 1986. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1986 award, reprints must be received by 1 July 1986.

A REVISED VASCULAR FLORA OF TUMAMOC HILL, TUCSON, ARIZONA

JANICE E. BOWERS and RAYMOND M. TURNER
U.S. Geological Survey, Research Project Office,
300 West Congress—FB Box 44, Tucson, AZ 85701

ABSTRACT

Tumamoc Hill, a 352-ha preserve near Tucson, Arizona, was the site of the Desert Laboratory of the Carnegie Institution of Washington from 1903 to 1940. The present flora of Tumamoc Hill comprises 346 specific and infraspecific taxa of vascular plants compared with 238 listed in a 1909 flora of the hill. Forty-nine of the new additions to the flora are introduced species, many of which colonized disturbed habitats created on the study area after 1940. Many of the species added may have dispersed to Tumamoc Hill from the nearby Santa Cruz River floodplain as a result of artificial wetland habitats created on the hill in recent years. Two species apparently have become locally extirpated since 1909.

In 1903 the Carnegie Institution of Washington established a Desert Laboratory on Tumamoc Hill two miles west of Tucson, Arizona. The climate, geology, and vegetation of the hill and environs were first described by Spalding (1909); Thornber (1909) prepared the first flora of the hill.

The purpose of this paper is two-fold: first, to update the plant list for a site possessing considerable significance in the history of American plant ecology and, second, to assess changes in the flora over the past 75 years.

Few authors of local floras in Arizona have examined short-term floristic changes in their study areas. Arnberger (1947) listed 151 species for Walnut Canyon, and six years later Spangle (1953) added 82 species to the list. A 1976 study of the vegetation of Walnut Canyon National Monument (Joyce 1976) added another 93 species to the flora but did not speculate on floristic changes that might have occurred since 1947. Similarly, Reeves (1966) listed 687 taxa for Chiricahua National Monument with no discussion of possible losses from or additions to an earlier checklist (Clark 1940). One of the few authors to assess floristic change in local floras in Arizona was Schaack (1983). He noted previous floristic work by Little (1941) and Moore (1965) in the alpine zone of San Francisco Mountain and discussed recent additions to the flora. Another was Bowers (1984), who discussed probable local extirpation between 1909 and 1983 of at least six species in the Rincon Mountains. Her assessment of floristic change was based not on an earlier flora but on collections made in 1909 by J. C. Blumer.

MADROÑO, Vol. 32, No. 4, pp. 225–252, 20 December 1985

STUDY AREA

Environment. Tumamoc Hill, an outlier of the nearby Tucson Mountains, reaches an elevation of 948 m above sea level and rises 245 m above the surrounding plain. The hill is composed of large blocks of dark brown Tertiary basalt that have weathered to a fine clay soil, forming a matrix between the rocks.

Precipitation is biseasonal: from 1907 to 1983, 27.3% of the annual average rainfall (299 mm) fell in the winter months (December–March), and 50.8% fell in the summer (July–September). April, May, and June, called the arid foresummer by Shreve (1911), are the driest months and a time of great moisture stress for all elements of the vegetation. Temperatures frequently exceed 38°C in the summer and occasionally drop below freezing in winter. The lowest temperature recorded on Tumamoc Hill was −9.4°C in 1913 (Turnage and Hinckley 1938), but such low temperatures are rare. Freezing temperatures seldom last longer than 15–20 hours.

Vegetation of Tumamoc Hill fits into Shreve's Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Dominant species on the rocky, basaltic slopes include *Cercidium microphyllum, Carnegiea gigantea, Fouquieria splendens, Hyptis emoryi, Opuntia phaeacantha, Encelia farinosa, Lycium berlandieri,* and *Acacia constricta.* The level or gently rolling plains west of the hill are characterized by *Cercidium microphyllum, Carnegiea gigantea, Larrea divaricata, Ambrosia deltoidea, Opuntia fulgida, O. phaeacantha, O. versicolor, Fouquieria splendens,* and *Calliandra eriophylla.* Broad washes on the plain are dominated by *Cercidium floridum* and *Prosopis velutina* and also support *Acacia greggii, Celtis pallida, Zizyphus obtusifolia,* and other shrubs. A more detailed discussion of the vegetation of Tumamoc Hill and vegetation changes during the first part of this century can be found in Shreve (1929) and Shreve and Hinckley (1937).

History. Spalding (1909) regarded the "Desert Laboratory domain" to be Tumamoc Hill (his Zone I), the fenced plain west of the hill (his Zone II), and the Santa Cruz River floodplain and streambed (his Zones III and IV). Our definition of Tumamoc Hill includes the hill itself and the fenced plain to the west, that is, Spalding's Zones I and II. To the north, west, and south, our study area is bounded by Anklam Road, Greasewood Road, and 22nd Street, respectively; the eastern boundary is irregular. Our total area is 352 ha.

The U.S.D.A. Forest Service took over the laboratory buildings and land when the Desert Laboratory closed in 1940. Under Forest Service management, and later under that of the University of Arizona, various incursions took place on the property, although the area had not been disturbed since the grounds were fenced in 1907. These incursions, which included a clay quarry, a sanitary landfill, electric powerlines, gas pipelines, access roads, and a booster pump for the city water system, have had a significant effect on the flora of Tumamoc Hill, as we will show.

FLORA

Methods. In 1968 and 1969, R. M. Turner collected plants on Tumamoc Hill to document additions and losses to the flora since 1909. Collection of Tumamoc Hill plants was resumed in 1977 and continued through 1984.

Thornber's 1909 flora comprised 429 specific and infraspecific taxa of vascular plants in 68 families and 269 genera. Of these 276 occurred in Spalding's Zones I and II, the areas we examine in this report. Problems that arose in comparing Thornber's list with our own included changes in nomenclature, misapplied names, misidentified specimens, and species listed under two or more names. Not all species listed by Thornber were documented by voucher specimens at ARIZ. We searched for vouchers for the 49 species listed by Thornber that we did not collect between 1968 and 1984, and were able to locate Thornber vouchers collected on Tumamoc Hill, "mesas, Tucson," or "mesas, Tucson Mountains," for 18 species. Of the 429 taxa listed by Thornber for the Desert Laboratory domain, we eliminated those listed only for Zones III or IV (153 in all), those listed for Zones I and II but not documented by herbarium vouchers nor collected during the present study (31 in all), and those listed under two or more names (7 in all). Thus, Thornber's reconstructed flora consists of 238 taxa.

Floristic change. The number of taxa has apparently increased from 238 to 346 over the past 75 years. Although it is difficult to argue from negative evidence (i.e., just because Thornber did not list these "new" species does not mean they did not occur on the study area), we find meaningful patterns that suggest substantial floristic changes have occurred at Tumamoc Hill since 1909.

Many of the recent additions to the Tumamoc Hill flora resulted from changes in habitat, especially from disturbance associated with construction of roads, pipelines, a clay quarry, and a sanitary landfill on the property. Although Thornber listed 52 introduced species in all, most of these were restricted to the Santa Cruz River floodplain. In contrast, 40% of the 126 taxa we added to the flora are not native, and the majority are closely associated with disturbance. Some of the introduced species in the flora—*Lantana horrida, Phacelia parryi, Molucella laevis, Melia azederach, Opuntia lindheimeri* var. *linguiformis, Dimorphotheca aurantiaca, Pennisetum ruppelii, Cyperus* *alternifolius,* and *Cupressus sempervirens*—are common in cultivation in and around Tucson. Recent development of the land surrounding Tumamoc Hill has no doubt facilitated their spread onto our study area. Not all of the introduced species collected on the Desert Laboratory domain have become established. *Bromus tectorum,* a European species common in the Great Basin, was collected on Tumamoc Hill in 1979, but has not been collected since and apparently did not become permanently established.

Changes in habitat have also been responsible for the migration of some species from the Santa Cruz River floodplain (Zones III and IV) to Tumamoc Hill (Table 1). Wetland and riparian species that formerly occupied the seasonally wet bed of the Santa Cruz River now find suitable habitat at several locations on Tumamoc Hill. Spalding (1909) noticed this process occurring with *Cynodon dactylon* as early as 1908. Currently, artificial wetland habitats on Tumamoc Hill include the seasonal ponds at the sanitary landfill and clay quarry; the overflow from a water tank southeast of the laboratory buildings and from the booster pump on Anklam Road; the septic tank installed northwest of the laboratory buildings; and a moist ditch at a broken water main near the eastern boundary of the property. A few of the apparent "migrants," such as *Poa bigelovii* and *Bromus arizonicus,* are annuals characteristic of rocky slopes and gravelly flats and may have been overlooked by Thornber. The majority, however, are recently adventive to our study area, having capitalized upon the availability of new, suitable habitat. Of the 48 species listed in Table 1, 20 are introduced. In addition to species that may have migrated to our study area from the Santa Cruz River floodplain, several other moisture-loving species not listed by Thornber are found in artificial wetland habitats on Tumamoc Hill: *Scirpus maritimus* var. *paludosus, Diplachne fascicularis, Cyperus alternifolius, Tamarix pentandra, Phalaris minor, Molucella laevis, Conyza bonariensis, Typha domingensis,* and *Cupressus sempervirens.*

Certain apparent additions to the flora since 1909 are not easily explained. No doubt Thornber overlooked more than a few species when preparing his flora, and this may account for the recent addition of characteristic desert species such as *Matelea parvifolia, Astragalus wootonii, Eriogonum thurberi, Oenothera primiveris, Thamnosma texana, Yabea microcarpum, Eucrypta micrantha, Euphorbia micromera, Pectocarya recurvata, Ambrosia dumosa, Filago arizonica, Filago depressa,* and *Tillaea erecta.* A few taxa added to the list were probably not overlooked by Thornber but are new to the flora. One of these, *Polanisia dodecandra* subsp. *trachysperma,* was first collected in a wash near Anklam Road in 1980 and apparently occurs nowhere else on the study area.

Table 1. Plants of Tumamoc Hill Listed by Thornber (1909) only for the Santa Cruz River or Its Floodplain. * = introduced.

Amaranthus palmeri
Sarcostemma cynanchoides var. _cynanchoides_
Aster subulatus var. _ligulatus_
Baccharis salicifolia
*_Centaurea melitensis_
Conyza canadensis
Erigeron divergens
Gutierrezia microcephala
Heterotheca psammophila
Hymenothrix wislizenii
*_Matricaria matricarioides_
*_Sonchus oleraceus_
Verbesina encelioides
*_Matthiola bicornis_
Sambucus mexicana
Atriplex canescens
Chenopodium fremontii
*_Chenopodium murale_
*_Medicago polymorpha_ var. _vulgaris_
*_Melilotus indicus_
Corydalis aurea
*_Erodium cicutarium_
Nama hispidum
Koeberlinia spinosa
Teucrium cubense
*_Malva parviflora_
Sphaeralcea coulteri
Boerhaavia coccinea
*_Avena fatua_
Bromus arizonicus
*_Bromus rubens_
*_Bromus willdenowii_
*_Cynodon dactylon_
*_Echinochloa colonum_
*_Eragrostis cilianensis_
Eriochloa lemmonii var. _gracilis_
*_Hordeum murinum_
Hordeum pusillum
Poa bigelovii
*_Polypogon monspeliensis_
Setaria macrostachya
*_Sorghum halepense_
Androsace occidentalis
Clematis drummondii
Maurandya antirrhiniflora
*_Nicotiana glauca_
Physalis acutifolia
*_Tribulus terrestris_

Forty-nine species listed by Thornber for Zones I or II were not collected by us. Eighteen of these are documented by ARIZ voucher specimens collected on Tumamoc Hill, on "mesas, Tucson," or on "mesas, Tucson Mountains." The remaining 31 species were not documented by voucher specimens at ARIZ, and we did not include them in our reconstruction of Thornber's list. It is likely that some of these species still occur on the study area but were overlooked. Two species, *Olneya tesota* and *Simmondsia chinensis,* are of more interest, because they may have been locally extirpated. (*Forestiera shrevei* might be included here, since Thornber collected it on Tumamoc Hill and we did not; however, it still occurs within one-quarter mile of the boundary of our study area.) Although we may have overlooked these species, both are large, woody plants that are not easily missed. Spalding noted that the *Olneya* growing near the east edge of his permanent plot #12 was the only individual known to occur on the Desert Laboratory grounds (Spalding, unpubl. notes, 1906). This individual was shown on maps of permanent plot #12 made by Shreve in 1929 and 1936, but had disappeared by 1948 when the plot was mapped again. *Olneya* is frost-sensitive, and the single individual on Tumamoc Hill may have died following a severe freeze such as the one that occurred in 1937. Alternatively, it may have died after senescence. *Simmondsia chinensis* was collected on Tumamoc Hill in 1905 (*Thornber 2576*), and although it is common in the Tucson Mountains, it has failed to reoccupy the hill. Perhaps individuals of *Simmondsia* were so few that the level of reproduction fell below that necessary to maintain the population. If the few remaining individuals in the population were all of one sex, reproduction would have been impossible, and the population would have died out eventually. Although adults are hardy, seedlings are susceptible to freezing, drought, and predation by rodents (Sherbrooke 1977).

Annotated checklist. The annotated checklist includes 346 specific and infraspecific taxa, in 67 families and 241 genera, known either to occur presently on the Tumamoc Hill property or to have occurred historically and for which vouchers exist. Habitat, local distribution, and relative abundance are noted for most. Species not listed by Thornber for Zones I and II are denoted by an asterisk. Species collected by Thornber and others for which vouchers exist, but which we did not collect, are denoted by a dagger. Names applied by Thornber are listed in brackets where appropriate. Nomenclature follows Lehr (1978) and Lehr and Pinkava (1980, 1982). Nomenclature for cultivated species not listed in Lehr or Lehr and Pinkava follows Bailey and Bailey (1976). A full set of our vouchers has been deposited at ARIZ. Additional vouchers have been deposited at ASU, BRI, ENCB, HUF, LIL, MEXU, MICH and MNA.

VASCULAR PLANTS OF TUMAMOC HILL[1]

PTEROPHYTA

Adiantaceae

Cheilanthes wootonii Maxon. Rocky slopes; under trees; rare.

Cheilanthes wrightii Hook. Rocky, north-facing slopes; rare.

Notholaena cochisensis Goodding. Rocky, north-facing slopes; occasional.

Notholaena standleyi Maxon. Rocky slopes; occasional to common.

Pellaea truncata Goodding [*Pellaea wrightiana* Hook.]. Rocky, north-facing slopes; occasional.

---

[1] See text for explanation of symbols.

CONIFEROPHYTA

Cupressaceae

**Cupressus sempervirens* L. Local, along moist ditch; tree commonly cultivated in Tucson, probably spreading onto our area from nearby housing developments.

Ephedraceae

Ephedra trifurca Torr. Gravelly flats and along washes; occasional to common.

ANTHOPHYTA—DICOTYLEDONEAE

Acanthaceae

Anisacanthus thurberi (Torr.) Gray. Along washes; common; usually flowering in the spring.

Carlowrightia arizonica Gray. Rocky slopes; occasional.

Ruellia nudiflora (Engelm. & Gray) Urban. Banks of washes, in shade of trees; locally common.

Siphonoglossa longiflora (Torr.) Gray. Rocky slopes, often in shade of trees; common.

Aizoaceae

Trianthema portulacastrum L. Disturbed sites, abundant on sanitary landfill; introduced.

Amaranthaceae

Amaranthus fimbriatus (Torr.) Benth. Washes and sandy flats; occasional summer annual.

**Amaranthus palmeri* Wats. Washes and roadsides; common summer annual.

Tidestromia lanuginosa (Nutt.) Standl. Gravelly slopes; locally common summer annual.

Anacardiaceae

**Rhus lancea* L. f. Moist soil, local, ditch at broken water main; an ornamental common in cultivation in Tucson; probably spreading to our area from nearby housing developments.

Apiaceae

Bowlesia incana Ruiz & Pav. Rocky slopes and gravelly flats, often under shrubs, trees or rocks; common spring annual.

Daucus pusillus Michx. Rocky slopes or gravelly flats, often under shrubs, trees, or rocks; common spring annual.

Spermolepis echinata (Nutt.) Heller. Rocky slopes and gravelly flats; common spring annual.

**Yabea microcarpum* (Hook. & Arn.) K.-Pol. Rocky slopes; common spring annual.

Apocynaceae

Haplophyton crooksii L. Rocky slopes, flowering in spring; common.

Aristolochiaceae

Aristolochia watsonii Woot. & Standl. Disturbed sites on flats; apparently uncommon.

Asclepiadaceae

**Asclepias nyctaginifolia* Gray. Along washes; apparently uncommon.

†*Cynanchum arizonicum* (Gray) Shinners. *Thornber 4855, 8989.*

**Matelea parvifolia* (Torr.) Woods. Climbing on cacti, trees, and shrubs; gravelly flats; rare.

**Sarcostemma cynanchoides* Decne. var. *cynanchoides.* Along washes; climbing on shrubs; apparently rare.

**Sarcostemma cynanchoides* Decne. var. *hartwegii* (Vail) Shinners. Along washes; climbing on trees and shrubs; common.

Asteraceae

Acourtia nana (Gray) Reveal & King. Gravelly flats, often under shrubs; flowering in spring.

Acourtia wrightii (Gray) Reveal & King. Banks of washes and rocky slopes; common.

Ambrosia confertiflora DC. Washes and dirt roads, often in disturbed areas; locally common.

Ambrosia deltoidea (Torr.) Payne. Rocky slopes and gravelly flats; a common dominant.

**Ambrosia dumosa* (Gray) Payne. Gravelly flats and rocky slopes; near clay quarry and on south slopes of hill; locally common; probably overlooked by Thornber.

**Aster subulatus* Michx. var. *ligulatus* Shinners. Moist soil; local, near pond at sanitary landfill and along ditch below water tank; apparently recently adventive to our study area.

Baccharis brachyphylla Gray [*Baccharis wrightii* Gray]. Gravelly flats; local; occasional.

**Baccharis salicifolia* (Ruiz & Pav.) Pers. Low-lying, disturbed sites; apparently recently adventive to our study area.

Baccharis sarothroides Gray [*Baccharis emoryi* Gray]. Washes and disturbed sites; locally common.

Bahia absinthifolia Benth. Rocky slopes and gravelly flats; common on edges of old roadways and on soils containing caliche.

Baileya multiradiata Harv. & Gray. Along washes and on sandy flats; common; flowering sporadically throughout the year.

Bebbia juncea (Benth.) Greene. Gravelly flats, often along washes; occasional.

**Brickellia californica* (Torr. & Gray) Gray. Rocky flats, in shade of trees; rare.

Brickellia coulteri Gray. Along washes and on rocky slopes, often under trees; common; flowering sporadically throughout the year.

Calycoseris wrightii Gray. Gravelly flats and rocky slopes; a common and showy spring annual.

**Centaurea melitensis* L. Disturbed sites; common on sanitary landfill; introduced; apparently recently adventive to our study area.

Chaenactis stevioides Hook. & Arn. Gravelly flats and rocky slopes, often under shrubs and trees; a common and showy spring annual.

**Cirsium neomexicanum* Gray. Rocky slopes; rare.

**Conyza bonariensis* (L.) Cronq. Moist soil; local, along moist ditch at broken water main.

**Conyza canadensis* (L.) Cronq. Disturbed sites; local along moist ditches and other damp spots; perhaps recently adventive to our study area.

Conyza coulteri Gray. Moist soil; local, near pond in sanitary landfill and at moist ditch at broken water main.

**Dimorphotheca aurantiaca* DC. Gravelly flats and along washes; occasional; apparently adventive from nearby housing developments; an introduced ornamental common in cultivation in and around Tucson.

Dyssodia pentachaeta (DC.) Robins. Rocky flats; common on soils containing caliche and on disturbed sites such as dirt roads and scraped ground.

Dyssodia porophylloides Gray. Rocky slopes and gravelly flats; uncommon.

Encelia farinosa Gray. Rocky slopes; a common dominant; flowering in late winter and early spring.

Ericameria laricifolia (Gray) Shinners. Rocky slopes; rare; only a few individuals known from the study area; a marginal population at the lower limit of its range.

***Erigeron divergens* Torr. & Gray. Rocky slopes and gravelly flats; common; flowering sporadically throughout the year.

Eriophyllum lanosum Gray. Rocky slopes and gravelly or rocky flats; common spring annual.

Evax multicaulis DC. Gravelly or rocky flats; locally common spring annual.

**Filago arizonica* Gray. Rocky slopes and gravelly or rocky flats; common spring annual.

Filago californica Nutt. Rocky slopes; common spring annual.

**Filago depressa* Gray. Gravelly flats, often under shrubs; rare.

Gaillardia arizonica Gray. Sandy flats and washes; locally common; flowering in late spring.

Gutierrezia arizonica (Gray) Lane. Gravelly flats; rare; flowering in late spring.

**Gutierrezia microcephala* (DC.) Gray. Rocky slopes; rare; perhaps recently adventive to our study area.

**Heterotheca psammophila* Wagenkn. Disturbed sites and low-lying areas; locally common; perhaps recently adventive to our study area.

**Hymenothrix wislizenii* Gray. Often on disturbed sites, common along roads; perhaps recently adventive to our study area.

Isocoma tenuisecta Greene. Gravelly flats, often on disturbed sites; common on scraped ground and along roads.

**Lactuca serriola* L. Along washes; usually under shrubs; occasional; introduced.

†*Lasthenia californica* DC. ex Lindl. *Thornber 5307.*

†*Machaeranthera gracilis* (Nutt.) Shinners. *Thornber 2028.*

Machaeranthera pinnatifida (Hook.) Shinners. Gravelly flats, often on disturbed sites; common.

**Machaeranthera tagetina* Greene. Disturbed sites; along roads and near buildings; locally common.

Malacothrix californica DC. var. *glabrata* Eaton. Gravelly flats; apparently rare; showy spring annual.

Malacothrix clevelandii Gray. Rocky slopes, under trees and shrubs; rare spring annual.

†*Malacothrix coulteri* Gray. *Thornber 387, 4621.*

**Matricaria matricarioides* (Less.) Porter. Disturbed sites; introduced; perhaps recently adventive to our study area; *Schoenwetter T-28.*

Microseris linearifolia (DC.) Schultz-Bip. Rocky slopes; common spring-flowering annual.

Monoptilon bellioides (Gray) H. M. Hall. Rocky or gravelly flats; common spring annual.

Parthenium incanum H.B.K. Rocky slopes and gravelly flats; locally common.

Pectis papposa Harv. & Gray. Gravelly flats, often in low-lying areas; locally common summer annual.

Porophyllum gracile Benth. Rocky slopes and gravelly flats; locally common.

Psilostrophe cooperi (Gray) Greene. Gravelly flats; abundant; flowering after winter and summer rains.

Rafinesquia neomexicana Gray. Rocky slopes; a common and showy spring annual.

**Senecio douglasii* DC. var. *douglasii.* Often along washes; common spring-flowering annual.

Senecio lemmonii Gray. Rocky slopes; common spring annual, rarely flowering in late fall.

**Sonchus oleraceus* L. Rocky slopes and gravelly flats; locally common in moist areas; introduced. Apparently recently adventive to our study area.

Stephanomeria pauciflora (Torr.) A. Nels. Along washes, also on rocky slopes; occasional.

**Stylocline gnaphaloides* Nutt. Gravelly flats, perhaps rare, but easily overlooked.

Stylocline micropoides Gray. Rocky slopes and gravelly or rocky flats; common spring annual.

Trixis californica Kellogg. Rocky slopes; common.

**Verbesina encelioides* (Cav.) Benth. & Hook. Locally common in low-lying areas; perhaps recently adventive to our study area.

Zinnia acerosa (DC.) Gray [*Zinnia grandiflora* Nutt.]. Gravelly flats; locally common; often on soils containing caliche.

Boraginaceae

Amsinckia intermedia Fisch. & Mey. Rocky slopes and gravelly flats; a common spring annual.

Amsinckia tessellata Gray. Disturbed sites; apparently only locally common.

Cryptantha angustifolia (Torr.) Greene. Gravelly or sandy flats; an uncommon spring annual.

Cryptantha barbigera (Gray) Greene. Rocky slopes and sandy or gravelly flats; a common spring annual.

Cryptantha micrantha (Torr.) Johnst. Sandy washes; apparently rare.

Cryptantha nevadensis Nels. & Kenn. [*Cryptantha intermedia* (Gray) Greene]. Rocky slopes; common spring annual.

Cryptantha pterocarya (Torr.) Greene. Rocky and gravelly slopes and flats, often under shrubs; a common spring annual.

Harpagonella palmeri Gray. Rocky slopes and flats; typically sprawling over and between rocks; a common spring annual.

Lappula redowskii (Hornem.) Greene var. *redowskii.* Gravelly flats, often in disturbed areas; common spring annual.

Lappula redowskii (Hornem.) Greene var. *cupulatum* (Gray) Jones. Gravelly flats; rare.

Pectocarya heterocarpa Johnst. Gravelly flats; often growing with the next two species; common.

Pectocarya platycarpa Munz & Johnst. Gravelly flats; occasional.

**Pectocarya recurvata* Johnst. Rocky and gravelly flats; locally abundant.

Plagiobothrys arizonicus (Gray) Greene. Gravelly flats; an uncommon spring annual.

†*Plagiobothrys pringlei* Greene. *Thornber 533, 2206.*

Tiquilia canescens (DC.) A. Richardson. Gravelly flats and dirt roads; especially common on soils containing caliche.

Brassicaceae

Arabis perennans Wats. Rocky, north-facing slopes; local and uncommon.

**Brassica tournefortii* Gouan. Disturbed ground; locally common along roads; introduced.

Caulanthus lasiophyllus (Hook. & Arn.) Payson. Rocky slopes and gravelly flats, often under shrubs and trees; common spring annual.

Descurainia pinnata (Walt.) Britt. Rocky slopes and gravelly flats; common spring annual.

Draba cuneifolia Nutt. Gravelly and rocky flats, often under trees; common; flowering early in the spring.

**Dryopetalon runcinatum* Gray. Rocky, north-facing slopes; uncommon.

Lepidium lasiocarpum Nutt. Rocky slopes and gravelly flats; common spring annual.

**Lepidium oblongum* Small. Disturbed sites; common on sanitary landfill; introduced.

Lesquerella gordoni (Gray) Wats. Rocky slopes and gravelly or rocky flats; common spring annual.

**Matthiola bicornis* (Sibth. & Smith) DC. Disturbed sites; common on and near sanitary landfill; introduced; perhaps recently adventive to our study area.

**Sisymbrium altissimum* L. Along washes; apparently uncommon; introduced. *Turner 78-11* is unusual in its soft pubescence and rather wide leaf segments.

**Sisymbrium irio* L. Rocky slopes and gravelly flats, often on disturbed sites; introduced.

Streptanthus arizonicus Wats. Rocky slopes and gravelly or rocky flats; common spring annual.

Thysanocarpus curvipes Hook. Rocky slopes, often under shrubs and trees; common spring annual.

Cactaceae

Carnegiea gigantea (Engelm.) Britt. & Rose. Rocky slopes and gravelly flats; a common dominant.

**Echinocereus fasciculatus* (Engelm.) L. Benson. Gravelly flats; occasional.

Echinocereus fendleri Engelm. Gravelly flats; common.

Ferocactus wislizenii (Engelm.) Britt. & Rose. Rocky slopes and gravelly flats; occasional; flowering in August.

Mammillaria microcarpa Engelm. [*Cactus grahamii* (Engelm.) Kuntze]. Gravelly flats, often under trees, shrubs, and large cacti; common.

**Opuntia ficus-indica* (L.) Mill. Gravelly flats; common in cultivation in and around Tucson; apparently spreading to our study area from nearby housing developments.

Opuntia fulgida Engelm. Gravelly flats west of hill; locally abundant.

**Opuntia kleiniae* DC. var. *tetracantha* (Toumey) Marshall. Rocky flats; widely scattered; locally common. Possibly of hybrid origin between *O. leptocaulis* and *O. versicolor.*

Opuntia leptocaulis DC. Rocky slopes and gravelly flats; sometimes forming impenetrable thickets.

**Opuntia lindheimeri* Engelm. var. *linguiformis* (Griffiths) L. Benson. Gravelly flats; common in cultivation in and around Tucson; apparently spreading to our area from nearby housing developments.

Opuntia phaeacantha Engelm. var. *discata* (Griffiths) Benson & Walkington. Rocky slopes and gravelly flats; common; intergrading with *O. p.* var. *major.*

Opuntia phaeacantha Engelm. var. *major* Engelm. Rocky slopes and gravelly flats; common; intergrading with *O. p.* var. *discata.*

Opuntia spinosior (Engelm.) Toumey. Gravelly flats; uncommon.

Opuntia versicolor Engelm. Rocky slopes and gravelly flats; common.

Peniocereus greggii (Engelm.) Britt. & Rose. Gravelly flats, usually under trees; occasional.

Campanulaceae

Nemacladus glanduliferus Jeps. var. *orientalis* McVaugh [*Nemacladus ramosissimus* Nutt.]. Rocky slopes and gravelly flats; uncommon spring annual.

Caprifoliaceae

**Sambucus mexicana* Presl. Local, wet area by septic system near laboratory buildings; apparently recently adventive to our study area.

Caryophyllaceae

**Herniaria cinerea* DC. Gravelly flats; rare; introduced.

Loeflingia squarrosa Nutt. Gravelly flats; an uncommon spring annual.

Silene antirrhina L. Rocky slopes and gravelly and rocky flats; common spring annual.

Chenopodiaceae

**Atriplex canescens* (Pursh) Nutt. Along washes and on rocky slopes; occasional.

Atriplex elegans (Moq.) D. Dietr. Disturbed sites; common on sanitary landfill.

**Chenopodium fremontii* Wats. Gravelly flats and rocky slopes; often under trees; common spring annual.

**Chenopodium murale* L. Disturbed site near laboratory buildings; introduced.

†*Monolepis nuttalliana* (Schult.) Greene. Gravelly flats and washes; occasional spring annual; *P. S. Martin 1053.*

**Salsola iberica* Sennen & Pau. Disturbed sites; abundant on sanitary landfill; introduced.

Cleomaceae

**Polanisia dodecandra* (L.) DC. var. *trachysperma* (Torr. & Gray) Iltis. Washes and roadsides; localized in somewhat disturbed sites; apparently recently adventive to our study area.

Convolvulaceae

**Ipomoea barbatisepala* Gray. Climbing on shrubs and trees in rocky slopes, often in shallow ravines.

Crassulaceae

**Tillaea erecta* Hook. & Arn. Gravelly flats; perhaps local, but easily overlooked.

Cucurbitaceae

†*Apodanthera undulata* Gray. *Thornber 5259.*

Cucurbita digitata Gray. Gravelly flats and low-lying spots; uncommon.

Tumamoca madougalii Rose [*Maximowiczia tripartita* Cogn. var. *tenuisecta* Wats.]. Gravelly flats, climbing on shrubs and trees; occasional on our study area, but rare in Arizona. Described in 1912 from specimens collected on Tumamoc Hill.

Euphorbiaceae

Argythamnia neomexicana Muell.-Arg. Rocky slopes and gravelly flats; occasional; flowering after summer rains.

Euphorbia capitellata Engelm. Rocky slopes; common; flowering sporadically throughout the year.

Euphorbia florida Engelm. Gravelly flats and shallow, sandy washes; common summer annual.

**Euphorbia heterophylla* L. Along washes and in low-lying areas; locally common summer annual.

**Euphorbia hyssopifolia* L. Gravelly flats and shallow, sandy washes; common summer annual.

**Euphorbia micromera* Boiss. Gravelly flats and sandy washes; common summer annual.

Euphorbia pediculifera Engelm. Gravelly flats and sandy washes; common; flowering in summer.

Euphorbia setiloba Engelm. Gravelly and rocky flats; flowering after winter and summer rains; occasional.

†*Euphorbia serrula* Engelm. *Thornber 47, 8948.*

Jatropha cardiophylla (Torr.) Muell.-Arg. Rocky slopes; occasional.

**Tragia nepetaefolia* Cav. Rocky slopes; uncommon.

Fabaceae

Acacia constricta Benth. Gravelly flats, rocky slopes, and along washes; common.

Acacia greggii Gray var. *arizonica* Isely. Washes, gravelly flats, and rocky slopes; common.

Astragalus nuttallianus DC. Rocky slopes and gravelly flats; common spring annual.

**Astragalus wootonii* Sheldon. Gravelly flats; occasional.

Calliandra eriophylla Benth. Gravelly flats and rocky slopes; common.

Cercidium floridum Benth. Along the larger washes; a common dominant.

Cercidium microphyllum (Torr.) Rose & Johnst. Gravelly flats and rocky slopes; a common dominant.

†*Hoffmanseggia glauca* (Ort.) Eifort. *Thornber s.n.* (1904).

Lotus humistratus Greene. Gravelly flats; common spring annual.

Lotus tomentellus Greene [*Hosackia humilis* Greene]. Gravelly flats; occasional spring annual.

Lupinus concinnus Agardh. Along washes and on gravelly flats; occasional spring annual.

Lupinus sparsiflorus Benth. Rocky slopes; common spring annual.

Marina parryi (Torr. & Gray) Barn. Rocky slopes, often along paved roads; locally common.

**Medicago polymorpha* L. var. *vulgaris* (Benth.) Shinners. Local, moist site near buildings; introduced; apparently recently adventive to our study area.

**Melilotus indicus* (L.) All. Pond at sanitary landfill; locally common; introduced; apparently recently adventive to our study area.

Nissolia schottii (Torr.) Gray. Rocky slopes; climbing on trees and shrubs; occasional.

†*Olneya tesota* Gray. *Spalding* (1909).

**Parkinsonia aculeata* L. Disturbed sites; along roads and on sanitary landfill; an introduced ornamental common in cultivation in and around Tucson.

Prosopis velutina Woot. Gravelly flats and along washes; a common dominant.

†*Senna bauhinioides* (Gray) Irwin & Barneby. *Thornber s.n.* (1903).

Senna covesii (Gray) Irwin & Barneby. Gravelly flats and rocky slopes; common; flowering after summer rains.

**Sphinctospermum constrictum* (Wats.) Rose. Rocky slopes; rare summer annual; not listed by Thornber, although collected by him (*Thornber 4851*) on Tumamoc Hill in August 1906.

Vicia ludoviciana Nutt. Rocky slopes, climbing on shrubs and annuals; common spring annual.

Fouquieriaceae

Fouquieria splendens Engelm. Gravelly flats and rocky slopes; a common dominant.

Fumariaceae

**Corydalis aurea* Willd. Along washes; rare spring annual.

Geraniaceae

**Erodium cicutarium* (L.) L'Her. Rocky slopes and gravelly flats; locally common spring annual; introduced. Listed by Thornber only for the Santa Cruz River floodplain, but occurring on Tumamoc Hill according to Spalding (1909).

Erodium texanum Gray. Gravelly and rocky flats; locally common spring annual.

Hydrophyllaceae

Eucrypta chrysanthemifolia (Benth.) Greene. Rocky slopes, often under trees; occasional spring annual.

**Eucrypta micrantha* (Torr.) Heller. Rocky slopes and gravelly flats, often under trees and shrubs; common spring annual.

**Nama hispidum* Gray. Along washes; occasional spring annual.

**Phacelia affinis* Gray. Along washes; rare spring annual.

†*Phacelia arizonica* Gray. *Thornber 4013.*

Phacelia crenulata Torr. Rocky slopes and gravelly flats; common spring annual.

Phacelia distans Benth. Rocky slopes and gravelly flats; often reclining on shrubs and other annuals; common spring annual.

**Phacelia parryi* Torr. Gravelly flats; local. An exotic species in Arizona, native to California, cultivated nearby at St. Mary's Hospital and adventive to our study area.

Koeberliniaceae

**Koeberlinia spinosa* Zucc. Gravelly flats and banks of washes; locally common.

Krameriaceae

Krameria grayi Rose & Painter. Gravelly flats and rocky slopes; occasional.

Krameria parvifolia Benth. Gravelly flats and rocky slopes; occasional.

Lamiaceae

Hyptis emoryi Torr. Rocky slopes; common.

**Molucella laevis* L. Disturbed sites, low-lying areas; locally common; an introduced ornamental cultivated in and around Tucson.

Salvia columbariae Benth. Gravelly flats and along washes; occasional spring annual.

**Teucrium cubense* Jacq. Along washes; locally common; perhaps recently adventive to our study area.

Linaceae

Linum lewisii Pursh. Rocky slopes and gravelly flats; uncommon. Although *L. lewisii* is described by Kearney and Peebles (1960) as a perennial herb, it is an annual on Tumamoc Hill and on other desert mountain ranges in southern Arizona. It can be distinguished from *L. usitatissimum* (cultivated flax), which is also an annual, by its capitate stigmas and ovate sepals. *L. usitatissimum* has longitudinal stigmas and acuminate, ciliate sepals.

Loasaceae

Mentzelia albicaulis Dougl. Rocky slopes and gravelly flats; occasional spring annual.
Mentzelia multiflora (Nutt.) Gray. Rocky slopes; occasional.

Loranthaceae

Phoradendron californicum Nutt. Gravelly flats and along washes; parasitic on a variety of trees and shrubs; common.

Malpighiaceae

Janusia gracilis Gray. Rocky slopes and gravelly flats; common.

Malvaceae

Abutilon incanum (Link.) Sweet subsp. *pringlei* (Hochr.) Felger & Lowe. Rocky slopes; occasional.
Anoda pentaschista Gray. Rocky slopes; rare; flowering in the summer.
†*Eremalche exilis* (Gray) Greene. *Thornber 4884, 5326.*
Herissantia crispa (L.) Brizicky. Rocky slopes; common.
Hibiscus coulteri Harv. Rocky slopes; often among shrubs; occasional.
Hibiscus denudatus Benth. Rocky slopes and gravelly flats; locally common.
**Malva parviflora* L. Disturbed sites, low-lying areas; locally common; introduced; apparently recently adventive to our study area.
Rhynchosida physocalyx (Gray) Fryxell. Disturbed sites and on banks of washes; locally common.
Sida procumbens Swartz. Sandy or gravelly flats; occasional summer-flowering perennial herb.
Sphaeralcea angustifolia (Cav.) G. Don. var. *cuspidata* Gray. Disturbed sites and along washes; local and uncommon.
**Sphaeralcea coulteri* (Wats.) Gray. Gravelly flats; uncommon spring annual.
**Sphaeralcea emoryi* Torr. var. *californica* (Parish) Shinners. Rocky, north-facing slopes; rare and local.
Sphaeralcea laxa Woot. & Standl. [*Sphaeralcea pedata* Torr.]. Rocky slopes and gravelly flats; common.

Martyniaceae

Proboscidea altheaefolia (Benth.) Decne. Gravelly flats and sandy washes; occasional; flowering in summer.

**Proboscidea parviflora* (Woot.) Woot. & Standl. Disturbed sites; apparently local, near sanitary landfill.

Meliaceae

**Melia azedarach* L. Disturbed sites; local, at sanitary landfill; an ornamental commonly cultivated in and around Tucson.

Nyctaginaceae

Allionia incarnata L. Gravelly flats, rocky slopes and along washes; common; flowering sporadically throughout the year.

**Boerhaavia coccinea* Mill. Banks of washes; locally common.

Boerhaavia coulteri (Hook. f.) Wats. Sandy flats; occasional summer annual.

Boerhaavia intermedia Jones. Rocky slopes, low-lying areas, often on disturbed sites; common.

†*Boerhaavia megaptera* Standl. *Thornber 161, 4863.*

†*Boerhaavia spicata* Choisy. Rocky slopes and washes; uncommon summer annual; *B. Fink s.n.*

**Boerhaavia wrightii* Gray. Disturbed sites; locally common on roadbanks; not listed by Thornber, although collected by him (*Thornber 2617*) on Tumamoc Hill in September 1903.

Commicarpus scandens L. Along washes, scandent on trees and shrubs; occasional.

Oleaceae

†*Forestiera shrevei* Standl. *Thornber s.n.* (1906).

Menodora scabra Gray. Rocky slopes and gravelly flats; common; flowering after spring and summer rains.

Onagraceae

Camissonia californica (Nutt. ex Torr. & Gray) Raven. Rocky slopes and flats; common spring annual.

Camissonia chamaenerioides (Gray) Raven. Gravelly flats; occasional spring annual.

Camissonia clavaeformis (Torr. & Frem.) Raven. Gravelly or sandy flats; locally common spring annual.

†*Oenothera caespitosa* Nutt. *Shreve s.n.* (1931).

**Oenothera primiveris* Gray. Gravelly flats and rocky slopes; occasional spring annual.

Orobanchaceae

**Orobanche cooperi* (Gray) Heller. Rocky slopes and disturbed sites, particularly favoring berms along dirt roads; uncommon.

Papaveraceae

Argemone pleicantha Greene subsp. *pleicantha.* Gravelly flats, often in disturbed areas; occasional.

Eschscholzia californica Cham. subsp. *mexicana* (Greene) C. Clark. Rocky slopes; locally common spring annual.

Plantaginaceae

Plantago insularis Eastw. Gravelly flats and rocky slopes; common; flowering early in spring.

Plantago patagonica Jacq. Rocky slopes and gravelly flats; common spring annual.

Plantago rhodosperma Decne. [*Plantago virginica* L.]. Moist soil on rocky slopes; local.

Polemoniaceae

Eriastrum diffusum (Gray) Mason [*Gilia floccosa* Gray]. Rocky slopes and gravelly flats; common spring annual.

Gilia stellata Heller [*Gilia glutinosa* Benth.; *Gilia inconspicua* (Small) Dougl. var. *sinuata* Gray]. Rocky slopes and gravelly flats; occasional spring annual.

†*Ipomopsis longiflora* (Torr.) V. Grant. *Thornber 4439, 4988.*

Linanthus bigelovii (Gray) Greene. Rocky slopes; occasional spring annual.

Polygalaceae

Polygala macradenia Gray. Rocky slopes and gravelly flats, often on soil containing caliche; occasional.

Polygonaceae

Chorizanthe brevicornu Torr. Gravelly flats; common spring annual.

Chorizanthe rigida (Torr.) Torr. & Gray. Gravelly flats; locally common spring annual.

Eriogonum abertianum Torr. Gravelly flats, disturbed sites; locally common.

Eriogonum deflexum Torr. Along washes; common summer annual.

Eriogonum maculatum Heller. Gravelly flats; occasional spring annual.

**Eriogonum polycladon* Benth. Along washes; locally common.
**Eriogonum thurberi* Torr. Gravelly flats; occasional.
Eriogonum trichopes Torr. Gravelly flats and sandy washes; common.

Portulacaceae

Calyptridium monandrum Nutt. Sandy flats; locally common.

Primulaceae

**Androsace occidentalis* Pursh. Rocky, north-facing slopes; uncommon spring annual.

Ranunculaceae

Anemone tuberosa Rydb. Rocky slopes; common; flowering in spring.
**Clematis drummondii* Torr. & Gray [*Clematis ligusticifolia* Nutt.]. Along washes, climbing on trees and shrubs; occasional.
Delphinium scaposum Greene. Rocky slopes and gravelly flats; common.

Resedaceae

Oligomeris linifolia (Vahl) Macbr. Gravelly flats, often in dirt roads; locally common.

Rhamnaceae

Condalia warnockii M. C. Johnst. var. *kearneyana* M. C. Johnst. Gravelly flats and borders of washes; occasional.
Zizyphus obtusifolia (Hook. ex Torr. & Gray) Gray var. *canescens* (Gray) M. C. Johnst. Gravelly flats and along washes; occasional.

Rubiaceae

Galium proliferum Gray. Rocky slopes; locally common spring annual.
Galium stellatum Kellogg. Rocky slopes; rare.

Rutaceae

**Thamnosma texana* (Gray) Torr. Gravelly flats, often on banks of washes and under trees; locally common.

Scrophulariaceae

**Maurandya antirrhiniflora* Humb. & Bonpl. Along washes, climbing on trees; occasional to common.

Orthocarpus purpurascens Benth. Rocky slopes; locally abundant spring annual.

Penstemon parryi Gray [*Penstemon wrightii* Hook.]. Gravelly flats, rocky slopes and along washes; occasional; flowering in spring.

Simmondsiaceae

†*Simmondsia chinensis* (Link.) Schneid. *Thornber 2576.*

Solanaceae

**Datura discolor* Bernh. Sandy flats, disturbed sites; locally common.

Lycium berlandieri Dunal. Rocky slopes; common dominant.

Lycium exsertum Gray. Rocky slopes and along washes; occasional.

**Nicotiana glauca* Graham. Rocky slopes and along moist ditch; locally common; introduced; apparently recently adventive to our study area.

Nicotiana trigonophylla Dunal. Rocky slopes; occasional.

**Physalis acutifolia* (Miers) Sandw. Rocky slopes, moist soil; rare; perhaps recently adventive to our study area.

Physalis crassifolia Benth. Gravelly flats and rocky slopes; uncommon; flowering mostly in summer.

Quincula lobata (Torr.) Raf. Gravelly and sandy flats, occasionally in washes; locally common; flowering after spring and summer rains.

Solanum elaeagnifolium Cav. Disturbed sites, near buildings and along roads; occasional.

Sterculiaceae

**Ayenia compacta* L. Rocky slopes and flats, often under shrubs and trees; locally common. Not listed by Thornber although collected by him (*Thornber 2561*) on Tumamoc Hill in March 1905.

Ayenia microphylla Gray. Rocky slopes and gravelly flats, often under trees; occasional.

†*Hermannia pauciflora* Wats. *Thornber 2281.*

Tamaricaceae

**Tamarix pentandra* Pall. Disturbed sites, moist soil; common near ponds at sanitary landfill and clay quarry; introduced.

Ulmaceae

Celtis pallida Torr. Rocky slopes and along washes; common.

Urticaceae

Parietaria hespera Hinton [*Parietaria debilis* Forst. f.]. Rocky slopes, usually in recesses under rocks and boulders; common spring annual.

Verbenaceae

Aloysia wrightii (Gray) Heller. Rocky, north-facing slopes and along washes; locally common.

Glandularia gooddingii (Briq.) Solbrig [*Verbena ciliata* Benth.]. Rocky slopes; common; flowering sporadically throughout the year.

**Lantana horrida* H.B.K. Disturbed sites; occasional; an ornamental commonly cultivated in and around Tucson.

Tetraclea coulteri Gray. Disturbed sites, often in low-lying areas; locally common.

Zygophyllaceae

Kallstroemia grandiflora Torr. Rocky and gravelly flats and along washes; occasional summer annual.

**Kallstroemia hirsutissima* Vail. Disturbed sites and along roads; occasional.

Larrea divaricata Cav. subsp. *tridentata* (Sesse & Moc. ex DC.) Felger & Lowe. Gravelly flats and rocky slopes; common dominant; flowering sporadically throughout the year.

**Tribulus terrestris* L. Disturbed sites; occasional; introduced; apparently recently adventive to our study area.

ANTHOPHYTA—MONOCOTYLEDONEAE

Agavaceae

**Agave americana* L. Perhaps local; under tree along wash; an ornamental commonly cultivated in and around Tucson, probably spreading onto our area from nearby housing developments.

Yucca elata Engelm. Gravelly flats; rare; only one individual known from the study area. Spalding (1909) also found only one plant; this was not the same individual currently found on the study area.

Cyperaceae

**Cyperus alternifolius* L. Moist soil; local; along ditch near broken water main; an ornamental commonly cultivated in and around Tucson.

**Scirpus maritimus* L. var. *paludosus* (A. Nels.) Kukenthal. Moist soil; local; in pond at sanitary landfill.

Liliaceae

Allium macropetalum Rydb. Gravelly flats; not uncommon locally; flowering in the spring.

Calochortus kennedyi Porter. Rocky slopes; occasional; flowering in the spring.

Dichelostemma pulchellum (Salisb.) Heller. Rocky slopes and gravelly flats; common; flowering in the spring.

Poaceae

Aristida adscensionis L. Rocky slopes; common along roads; flowering in spring and summer.

**Aristida parishii* Hitchc. Rocky slopes; occasional.

Aristida purpurea Nutt. var. *glauca* (Nees) A. Holmgren & N. Holmgren. Rocky slopes; common along paved road.

Aristida ternipes Cav. [*Aristida scheidiana* Trin. & Rupr.]. Rocky slopes and gravelly flats; common.

**Avena fatua* L. Along washes, in shade of trees; occasional; introduced; probably recently adventive to our study area.

Bothriochloa barbinodis (Lag.) Herter. Rocky slopes and gravelly flats; locally common; flowering after summer rains.

Bouteloua aristidoides (H.B.K.) Griseb. Gravelly flats and shallow, sandy washes; locally abundant summer annual.

Bouteloua barbata Lag. var. *barbata*. Gravelly flats; common on disturbed sites; summer-flowering annual.

Bouteloua barbata Lag. var. *rothrockii* (Vasey) Gould. Gravelly flats; rare; flowering after summer rains.

Bouteloua curtipendula (Michx.) Torr. Rocky slopes; locally common; flowering after summer rains.

Bouteloua repens (H.B.K.) Scribn. & Merr. [*Bouteloua bromoides* (H.B.K.) Lag.]. Rocky slopes; common along paved road.

Bouteloua trifida Thurb. Gravelly flats; probably occasional.

**Bromus arizonicus* (Shear) Stebbins. Rocky slopes and gravelly flats, also banks of washes, usually under trees and shrubs; common spring annual.

**Bromus rubens* L. Rocky slopes and gravelly flats, often on disturbed sites; common; introduced; apparently recently adventive to our study area.

**Bromus willdenowii* Kunth. Disturbed sites; local and rare; introduced; probably recently adventive to our study area.

Chloris virgata Swartz. Gravelly flats; occasional summer annual.

**Cortaderia selloana* (Schult. & Schult.) Asch. & Graebn. Moist soil; local; ditch near broken water main; an ornamental common in cultivation in Tucson; recently adventive to our study area.

Cottea pappophoroides Kunth. Rocky slopes; locally common; flowering after summer rains.

**Cynodon dactylon* L. Banks of washes; occasional; introduced. Listed by Thornber only for the Santa Cruz River floodplain, but noted by Spalding (1909) to occur near buildings on the hill.

**Diplachne fascicularis* (Lam.) Beauv. Moist soil; local, around ponds at clay quarry and sanitary landfill.

**Echinochloa colonum* (L.) Link. Disturbed sites; local, moist soil below water tank; introduced; probably recently adventive to our study area.

Enneapogon desvauxii Beauv. Gravelly flats and rocky slopes; occasional; flowering after summer rains.

**Eragrostis barrelieri* Daveau. Disturbed sites; local and uncommon; introduced; summer annual.

**Eragrostis cilianensis* (All.) Mosher. Disturbed sites and sandy flats; locally common summer annual; introduced; probably recently adventive to our study area.

**Eragrostis echinochloidea* Stapf. Moist soil; local, below water tank; introduced.

**Eragrostis lehmanniana* Nees. Gravelly flats and disturbed sites; locally common; introduced.

**Eragrostis pectinacea* (Michx.) Nees. Along washes and in moist soil; occasional; summer annual.

**Eriochloa lemmonii* Vasey & Scribn. var. *gracilis* (Fourn.) Gould. Moist soil; rare; apparently recently adventive to our study area.

Erioneuron pulchellum (H.B.K.) Tateoka. Gravelly flats and rocky slopes; common.

Heteropogon contortus (L.) Beauv. Rocky slopes, ravines and roadways; common.

Hilaria belangeri (Steud.) Nash. Rocky, north-facing slopes and gravelly flats; occasional.

Hilaria mutica (Buckl.) Benth. Sandy flats and rocky slopes; locally common.

**Hordeum murinum* L. Disturbed sites, gravelly flats, and rocky slopes; common; introduced. Listed by Thornber only for the Santa Cruz River floodplain, but noted by Spalding (1909) to occur on Tumamoc Hill.

***Hordeum pusillum* Nutt. Gravelly flats, low-lying areas; locally common.

Leptochloa filiformis (Lam.) Beauv. Along washes, on rocky slopes and in moist soil at disturbed sites; common summer annual.

Muhlenbergia microsperma (DC.) Kunth. Rocky slopes and along washes; locally common spring annual.

Muhlenbergia porteri Scribn. Gravelly flats, typically growing among shrubs; common.

Panicum arizonicum Scribn. & Merr. Sandy flats and shallow washes; occasional; flowering in the summer.

Panicum hirticaule Presl. Disturbed sites; along roads and near buildings.

Pappophorum vaginatum Buckl. Along washes and on gravelly flats; locally common.

**Pennisetum ciliare* (L.) Link. Rocky slopes and disturbed sites, along roads and on sanitary landfill; locally common; introduced.

**Pennisetum setaceum* (Forssk.) Chiov. Disturbed sites, near buildings; an introduced ornamental common in cultivation in and around Tucson.

**Phalaris minor* Retz. Moist soil; local, at pond in sanitary landfill; introduced.

**Phragmites australis* (Cav.) Trin. ex Steud. Moist soil; rare; local, near booster pump on Anklam Road; apparently recently adventive to our study area.

**Poa bigelovii* Vasey & Scribn. Rocky slopes and gravelly flats; common spring annual.

**Polypogon monspeliensis* (L.) Desf. Moist soil; local, at pond in sanitary landfill; introduced; apparently recently adventive to our study area.

**Schismus arabicus* Nees. Rocky slopes and gravelly flats; common spring annual; introduced.

**Schismus barbatus* (L.) Thell. Rocky slopes and gravelly flats; common spring annual; introduced.

**Setaria liebmannii* Fourn. Rocky slopes; occasional; summer-flowering annual.

**Setaria macrostachya* H.B.K. Rocky slopes; occasional.

**Sitanion hystrix* (Nutt.) J. G. Smith. Rocky slopes; occasional.

**Sorghum halepense* (L.) Pers. Disturbed sites, moist soil; locally common; introduced; apparently recently adventive to our study area.

**Sporobolus airoides* Torr. var. *wrightii* (Munro ex Scribn.) Gould. Along washes; locally common; listed by Thornber only for the Santa Cruz River floodplain, but collected by F. Shreve in 1908 "near wash northwest of Desert Laboratory."

***Sporobolus contractus* Hitchc. Gravelly or sandy flats and rocky slopes; occasional.

Sporobolus cryptandrus (Torr.) Gray. Gravelly flats, low-lying areas; occasional.

Trichachne californica (Benth.) Chase. Rocky slopes and gravelly flats; common; flowering after summer rains.

Tridens muticus (Torr.) Nash. Rocky slopes; occasional.

**Trisetum interruptum* Buckl. Moist soil and at roadsides; uncommon.

Vulpia octoflora (Walt.) Rydb. Rocky slopes and gravelly flats; common spring annual.

Typhaceae

**Typha domingensis* Pers. Moist soil; locally common along wet ditch, pond at clay quarry and below water tank.

ACKNOWLEDGMENTS

We thank T. L. Burgess, C. T. Mason, Jr., and S. P. McLaughlin for reviewing the manuscript; J. R. Reeder and L. J. Toolin for identifying several grasses; and O. M. Grosz for compiling the rainfall data.

LITERATURE CITED

ARNBERGER, L. P. 1947. Flowering plants and ferns of Walnut Canyon. Plateau 20: 29–36.

BAILEY, L. H. and E. Z. BAILEY. 1976. Hortus Third. Macmillan Publishing Co., Inc., New York.

BENSON, L. 1982. The cacti of the United States and Canada. Stanford Univ. Press, Stanford, CA.

BOWERS, J. E. 1984. Woodland and forest flora and vegetation of Saguaro National Monument. Unpublished report on file at Saguaro National Monument, Route 8, Box 695, Tucson, AZ.

CLARK, O. M. 1940. Checklist of the flora of Chiricahua National Monument. Southwestern Monuments Monthly Reports (Sept.):201–215.

JOYCE, J. F. 1976. Vegetational analysis of Walnut Canyon, Arizona. J. Arizona-Nevada Acad. Sci. 11:127–135.

KEARNEY, T. H. and R. H. PEEBLES. 1960. Arizona flora, 2nd ed. Univ. Calif. Press, Berkeley.

LEHR, J. H. 1978. A catalogue of the flora of Arizona. Desert Botanical Garden, Phoenix, AZ.

——— and D. J. PINKAVA. 1980. A catalogue of the flora of Arizona: supplement I. J. Arizona-Nevada Acad. Sci. 15:17–32.

——— and ———. 1982. A catalogue of the flora of Arizona: supplement II. J. Arizona-Nevada Acad. Sci. 17:19–26.

LITTLE, E. L., JR. 1941. Alpine flora of San Francisco Mountain, Arizona. Madroño 6:65–81.

MCGINNIES, W. G. 1981. Discovering the desert. Univ. Arizona Press, Tucson.

MOORE, T. C. 1965. Origin and disjunction of the alpine tundra on San Francisco Mountain, Arizona. Ecology 46:860–864.

REEVES, T. 1976. Vegetation and flora of Chiricahua National Monument, Cochise County, Arizona. M.S. thesis, Arizona State Univ., Tempe.

SCHAACK, C. G. 1983. The alpine vascular flora of Arizona. Madroño 14 (supplement):79–88.

SHERBROOKE, W. C. 1977. First year seedling survival of jojoba (*Simmondsia chinensis*) in the Tucson Mountains, Arizona. Southw. Naturalist 22:225–234.

SHREVE, F. 1911. Establishment behavior of the palo verde. Pl. World 14:289–296.

———. 1929. Changes in desert vegetation. Ecology 10:364–373.

———. 1951. Vegetation of the Sonoran Desert. Publ. Carnegie Inst. Wash., no. 591.

——— and A. L. HINCKLEY. 1937. Thirty years of change in desert vegetation. Ecology 18:463–478.

SPALDING, V. M. 1909. Distribution and movements of desert plants. Publ. Carnegie Inst. Wash., no. 113.

SPANGLE, P. F. 1953. A revised checklist of the flora of Walnut Canyon National Monument. Plateau 26:86–88.

THORNBER, J. J. 1909. Vegetation groups of the Desert Laboratory domain. *In* V. M. Spalding, Distribution and movements of desert plants, pp. 103–112. Publ. Carnegie Inst. Wash., no. 113.

TURNAGE, W. V. and A. L. HINCKLEY. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. 8:530–550.

(Received 23 Jul 1984; accepted 16 Jan 1985)

ANNOUNCEMENT

Additional authors are sought for the revision of JEPSON'S MANUAL OF CALIFORNIA PLANTS. If you have expertise or particular interest in any of the groups listed below and are willing to contribute to this project, or know of those we might invite to participate, or would like more information, please write or call James C. Hickman, Botany Dept., Univ. of California, Berkeley, CA 94720, (415)642-2465.

Groups available: Apocynaceae; Aristolochiaceae; Asclepiadaceae; Asteraceae (some genera); Betulaceae; Boraginaceae (esp. *Cryptantha, Hackelia, Plagiobothrys*); Cactaceae; Callitrichaceae; Capparidaceae; Caprifoliaceae; Convolvulaceae; Crassulaceae (esp. *Sedum*); Elatinaceae; Garryaceae; Gentianaceae; Haloragaceae; Hydrophyllaceae (esp. *Phacelia*); Hypericaceae; Lamiaceae (esp. *Monardella, Scutellaria, Stachys*); Polygalaceae; Portulacaceae (esp. *Calyptridium, Lewisia*); Resedaceae; Rhamnaceae (esp. *Ceanothus, Rhamnus*); Salicaceae (*Populus*); Sterculiaceae; Urticaceae; Verbenaceae; Violaceae; Vitaceae; Liliaceae (esp. *Brodiaea* [+*Dichelostemma, Triteleia*], *Erythronium, Fritillaria, Lilium, Yucca, Zigadenus*); Poaceae (some genera).

THE ALPINE VASCULAR FLORA OF THREE CIRQUE BASINS IN THE SAN JUAN MOUNTAINS, COLORADO

EMILY L. HARTMAN and MARY LOU ROTTMAN
Department of Biology, University of Colorado at Denver,
Denver 80202

ABSTRACT

The San Juan Mountains are located along the Continental Divide in southwestern Colorado. The only previous floristic study of this range was done in the Needle Mountains of the San Juan Range by Michener (1964). Three cirque basins, representative of the San Juan tundra, were analyzed floristically. A vascular flora of 197 species in 92 genera and 31 families is reported. Eight species are Colorado endemics. The phytogeographic distribution of the flora is primarily alpine and western North American.

The San Juan Mountains are a discontinuous section of the southern Rocky Mountains situated along the Continental Divide in southwestern Colorado. These mountains are considered to be a quadrilateral block with dimensions of 77.5 km from east to west and 65.1 km from north to south (Larsen and Cross 1956), resulting in an area of approximately 20,000 km^2, 2000 km^2 of which are in the alpine zone (Carrara et al. 1984). The relief of the area varies from sharp pinnacles, rounded crests, serrate ridges, and broad upland surfaces of the alpine to the foothills, plateaus, and canyons of the lowlands. The elevation ranges from 1524 m in the southwest corner to 4358 m at the summit of Uncompahgre Peak.

The San Juan Mountains, a youthful part of the southern Rocky Mountains, are composed largely of Tertiary volcanic tuffs and lavas that lie unconformably over metamorphic, sedimentary, and volcanic intrusive rocks of Precambrian age, as well as sediments of Paleozoic, Mesozoic, and early Cenozoic age (Casadwall and Ohmoto 1977). During the Pleistocene, the San Juan Mountains were glaciated by broad regional ice fields and transection glaciers. Glacial effects are evident in the present alpine landscape as cirques, basins, tarns, hanging valleys, and broad U-shaped valleys. Palynological investigations suggest that the San Juan Mountains were free of glaciers prior to 10,000 B.P. (Andrews et al. 1975).

The climate of the San Juan Mountains is montane continental. Winters are long and severe; the first snowfall usually occurs by mid- to late September and snowstorms continue to late May or early June. Maximum snow depth at higher elevations (over 3680 m) has been estimated to reach 11.6 m. Summers are cool and short with

MADROÑO, Vol. 32, No. 4, pp. 253–272, 20 December 1985

an estimated maximum of 75 frost-free days in the alpine tundra. Periglacial features such as active patterned ground and active rock glaciers indicate the occurrence of sporadic or discontinuous permafrost (Ives and Fahey 1971, Barsch 1978). Previous investigations in the San Juan Mountains include one floristic study by Michener (unpubl. thesis 1964) and an ecological study of snowpack augmentation by Webber et al. (1976).

Collections were made in the San Juan Mountains during the summers 1981–1983. Nomenclature in the checklist follows Kartesz and Kartesz (1980). Partial voucher sets are deposited in COLO, CS, and CU-Denver. Phytogeographic abbreviations used in the annotated checklist of vascular species are identified in the discussion section.

Description of Study Basins

Three alpine cirque basins, representative of the San Juan Mountain tundra, were selected for floristic analysis. The basins are within a 10 km radius of each other. American Basin, 15 km southwest of Lake City, contains the headwaters of the Lake Fork of the Gunnison River. It is separated from Burns Basin, 8 km north of Silverton, by Jones Mountain. Stony Basin is located 4.5 km northeast of Silverton. The drainage of Burns and Stony basins is the Animas River.

American Basin. American Basin, T42N R6W, Hinsdale County, is characterized by a well-developed, moist, turf mantle interrupted by areas of bedrock outcrops, talus deposits, a tongue-shaped rock glacier, and patterned ground features. The elevational range of the basin is 3536–3962 m.

The vegetation in this basin reflects a more moist climatic regime than in the other two basins. This mesic environment is attributable to several factors: a north–south orientation, massive headwall on the south, windward pass on the southwest and high peaks on the east and west sides of the basin. These features contribute collectively to a heavy accumulation and retention of snow in the winter months and adequate substrate moisture in the summer months. The moist meadow is the predominant community type in the basin.

The moist ledges on the north side of the basin yield a high representation of two families, Caryophyllaceae and Saxifragaceae. This habitat seems to be favorable for members of these families, which normally are not too successful in the highly competitive moist meadow turf. The plant species on the top surface of the rock glacier, although representative of a modified fellfield community, consist of several mesophytic species, e.g., *Chionophila jamesii,* which is overwhelmingly dominant.

Dry habitats are poorly represented in the basin. There are no dry meadows, and fellfield communities are restricted to two high-elevation sites. The vegetation on dry ledges as well as on the unstable slopes of the rock glacier, although not limited to xerophytic species, provides the best example of this type of vegetation in the basin.

The high diversity of species represented in the krummholz community reflects the expected blending of the subalpine and alpine vegetation in an ecotone. Most of the subalpine species present in this community are not found higher in the basin.

Burns Basin. Burns Basin, T42N R6W, San Juan County, has a northwest–southeast orientation. The elevational range is 3634–3932 m. The convex slopes forming the perimeter of the main basin present an interesting contrast of moisture regimes. The southeast-facing slope is characterized by a dry meadow, dominated by *Carex elynoides, Geum rossii* var. *turbinatum,* and *Hymenoxys grandiflora,* alternating with fellfields and unvegetated talus. The communities on this slope are adapted to high solar insolation, steep slope, and relatively poor soil development.

The northwest-facing slope consists of a series of tiers of massive, moist and wet ledges with adjacent moist meadows. The ledge community is dominated by *Salix reticulata* subsp. *nivalis.* A number of rare species occur within the ledge complex. An isolated solitary meadow, dominated by *Kobresia myosuroides,* is present on the lower part of the slope below the ledges.

Another indication of the effects of slope aspect and differing moisture regimes on vegetation is reflected by the discrete occurrence of a community dominated by *Salix brachycarpa* on the southeast-facing slope and a community dominated by *Salix planifolia* on the northwest-facing slope. Both communities show a segregation of dominants and associated species along a moisture gradient.

The openness of the mid-section of the basin, created by the lack of headwall protection, promotes the occurrence of strong winds, as shown by the uniform upslope shearing of the krummholz conifers and the presence of many typical fellfield communities in this part of the basin.

Burns Basin also contains a rock glacier complex composed of tongue and lobate units. Well-defined communities are present in limited areas of fines on the unstable slopes. A highly-localized moist meadow occurs on the top surface of the rock glacier.

Stony Basin. Stony Basin, T41N R6W, San Juan County, is formed of three broad turf-mantled steps, each separated by a bedrock escarpment. The elevational range of the basin is 3764–3926 m. This northwest-facing basin is continually buffeted by strong wind, resulting in a more severe climatic regime than is found in the other two basins. Islands of dry meadow and fellfield interrupt the moist meadow of the upper two steps of the basin. The latter have an abundance of frost-associated features including frost boils, subnival boulder pavement, ephemeral ponds, and rock debris islands. The lower step is characterized by a shallow lake and hummocky wet meadow.

Moist meadows are the most extensive type of vegetation in the basin; the dominant and some of the associated species, however, vary according to aspect and elevation.

The dry meadow dominated by *Carex elynoides* matures earlier than do adjacent moist meadow communities. The subnival boulder pavement, a periglacially-related habitat, supports a community of high diversity including several rare species. The ridgetop vegetation is exposed to the most severe environmental extremes found in the Basin. However, the species in these communities show no reduction in stature as contrasted with the many dwarfed species found in moist meadows dominated by *Salix reticulata* subsp. *nivalis* and located in more protected sites than the dry meadows.

Discussion

The alpine flora of the basins selected as representative of the San Juan Mountains consists of 191 species representing 86 genera of angiosperms, three genera and three species of gymnosperms, and three genera and three species of pteridophytes.

Twenty-eight taxa included in this study were unreported by Michener (1964) and Webber et al. (1976). These taxa are:

Arabis divaricarpa
Artemisia campestris ssp. *borealis*
Botrychium lunaria
Carex incurviformis
Carex norvegica
Draba cana
Draba nivalis
Draba spectabilis var. *spectabilis*
Erigeron compositus var. *glabratus*
Erigeron grandiflorus
Erigeron vagus
Erysimum capitatum var. *amoenum*
Hierochloe hirta ssp. *arctica*
Kobresia sibirica
Minuartia rossii
Moehringia lateriflora
Oxytropis podocarpa
Poa leptocoma
Potentilla hookeriana
Potentilla subjuga var. *minutifolia*
Salix glauca var. *villosa*
Saxifraga chrysantha
Senecio porteri
Silene kingii
Silene uralensis
Taraxacum lyratum
Townsendia rothrockii
Vaccinium scoparium.

Habitats and Communities. The moist meadow is the predominant habitat in the study basins. This contrasts with the predominant dry meadows of the Front Range and correlates generally with the higher moisture regime characteristic of the San Juan Mountains. The moist meadow may be regarded as a complex of several communities, each with a distinct spatial occurrence within the complex. A *Deschampsia caespitosa–Geum rossii* var. *turbinatum* element is found in lower sites on basin slopes and in concavities; a *Carex nigricans–Sibbaldia procumbens* element is located in flat areas at mid-slope; and a *Salix reticulata* ssp. *nivalis* element is present on the highest sites of this complex.

The dry meadow community is virtually absent in American Basin and is of minor importance in Burns and Stony basins. *Carex elynoides* is the most frequent dominant in the dry meadow community. Throughout all three basins only two, small, isolated meadows dominated by *Kobresia myosuroides* occur. This is of interest when compared to the Front Range where *Kobresia* has long been recognized as the climatic climax community (Cox 1933, Bamberg 1961, Marr 1961, and Eddleman and Ward 1984). The highly restricted occurrence of *Kobresia myosuroides* in this study contrasts sharply with the *Kobresia* meadows in the Eldorado Lake and Williams Lakes basins of the San Juan Mountains as reported by Webber et al. (1976), who extrapolate that *Kobresia* meadows are one of the two community types that account for perhaps 50 percent of the alpine vegetation in the San Juan Mountains. Michener (1964), on the other hand, reports only one occurrence of *Kobresia* in the Needle Mountains in a soil-filled depression site near timberline. *Dryas octopetala* subsp. *hookeriana,* a dominant species in dry meadows and mat shrub communities in the Front Range (Cooper 1908, Cox 1933, and Eddleman and Ward 1984), is conspicuously absent or rare in occurrence in the San Juan Mountains. This species was found by Michener (1964) only on north-facing ledges on the ridge and also to the east of Ruby Pass, outside our study areas, and was reported as very rare by Webber et al. (1976).

Habitats dominated by rocks are varied and common in occurrence in all three basins. Some of these, such as moist and wet ledges, fellfields, ridgetops, and surfaces on rock glaciers support communities where dominants can be recognized. Others, such as rock crevices, subnival boulder pavement, blockfield, and certain patterned ground forms show a lack of dominants. In general, diversity or species richness of a community increases as the amount of rock material in a habitat increases. Rare species also may increase in predominantly rock habitats, especially on ledges, subnival boulder pavement, and on unstable slopes of the rock glacier. Major and Bamberg (1968) and Komarkova (1976) have discussed the occurrence of rare species and conclude that they are most likely to occur where competition is low or where the development of a climax vegetation is continuously disrupted.

Fellfield and ridgetop habitats reflect a higher degradation of rock material and greater amount of mineralized soil than the other rock-predominating habitats. Some of the rare species such as *Artemisia campestris* ssp. *borealis, Erigeron compositus* var. *glabratus, E. vagus, Townsendia rothrockii, Poa epilis,* and *Anemone multifida* var. *globosa* are found only on the ridgetop sites. The typical fellfield cushion plant community, dominated by *Paronychia pulvinata* and *Phlox caespitosa* ssp. *condensata,* which is frequently found on windswept sites of the Front Range (Cox 1933, and Eddleman and Ward 1984), is absent in the San Juan Mountains (Michener 1964, Webber et al. 1976, and Rottman 1984).

Although we have emphasized some of the major differences in community structure and dominants between this study and other studies in the San Juan Mountains and Front Range, much similarity is evident in the floristic inventories from the respective areas. For example, there is a 76.5 percent similarity in the vascular plant species found in this study and those of the Williams Lakes and Eldorado Lake basins as reported by Webber et al. (1976). They report a greater diversity of grasses, including *Calamagrostis purpurascens, Danthonia intermedia, Poa pattersonii,* and *P. fendleriana,* and shrub species, including *Actaea rubra, Arctostaphylos uva-ursi,* and *Gaultheria humifusa.* They also found two *Carex* species that were not observed during this study: *Carex scopulorum,* a wet meadow species, and *C. rupestris* var. *drummondiana,* a dry meadow species. There is a 73.6 percent similarity between species found in this study and those reported by Michener (1964) for the Needle Mountains of the San Juan Range. This lesser degree of similarity may be due, in part, to substrate differences. The Needle Mountains are a discrete metamorphic unit within the larger volcanic San Juan Range. Michener (1964) found *Pinus flexilis* and *Populus tremuloides* at a timberline elevation of 3749 m, both of which were absent in this study. She also reports some grasses not found during this study, including *Agrostis filicumis, Poa interior, P. longiligula, Danthonia intermedia,* and *Koeleria cristata,* and shrubs, including *Actaea rubra, Gaultheria humifusa, Lonicera involucrata, Ribes lacustre,* and *R. wolfii.* In comparing the vascular plant inventories of this study and that of the Indian Peaks area of the Front Range, a still lower (70.0%) similarity results. This reflects differences in the phytogeographic distributions of species from the northern and southern Colorado alpine tundra.

Phytogeography. Table 1 shows the phytogeographic distribution of the flora. Four elements are recognized, each of which may be

TABLE 1. AFFINITIES OF THE FLORA ELEMENTS IN THREE HIGH BASINS OF THE NORTHERN SAN JUAN MOUNTAINS, COLORADO. Abbreviations following each unit are cited in the annotated checklist.

Element	Abbreviation	Percent of taxa
ELEMENT		
Boreal montane	BM	19.8
Montane	M	6.0
Arctic alpine	AA	31.5
Alpine	A	42.6
GEOGRAPHIC SUBELEMENT		
Circumpolar	C	22.8
North American	NA	10.2
Western North American	WNA	25.8
Rocky Mountains	RM	13.7
Southern Rocky Mountains	SRM	11.6
Colorado	CO	4.0
North American—Asiatic	NAA	9.6
North American—European	NAE	2.0

combined with more specific geographic subelements (Komarkova, 1976).

As may be seen from the percentages given, the largest part of the vascular flora is made up of alpine species (42.6%) and Western North American species (25.0%). The circumpolar subelement (22.8%), which is largely identified with the arctic-alpine element, is a second important component of the flora. The higher percentage of North American–Asiatic species (9.6%) in relation to North American–European species (2.0%) indicates a stronger affinity of the San Juan alpine flora to the Asiatic alpine flora than to the European alpine flora.

A comparison of phytogeographical analyses of the San Juan Mountains shows a lower boreal-montane and montane representation and a concomitantly higher alpine and arctic-alpine representation in this study than in that of Webber et al. (1976). This reflects the higher base elevations of the basins in this study and the greater distance from treeline. There is close agreement between the two studies in the percentages of North American–Asiatic, Colorado, western North American, and Rocky Mountains subelements. In comparing the phytogeographic analysis of this study with that of the vascular flora of the Indian Peaks area, northern Colorado (Komarkova 1976), a decrease in circumpolar and North American–Asiatic subelements and an increase in Rocky Mountain, southern Rocky Mountain, and Colorado subelements is evident. A similar north to south trend is reported by Webber et al. (1976). The number of Colorado endemics in the San Juan Mountains is greater than the number reported for the Indian Peaks area. This agrees with Major and Bamberg (1967), who state that endemism increases in a southerly direction. The endemic species found in this study include: *Besseya ritteriana, Draba streptobrachia, Minuartia macrantha, Penstemon harbourii, Potentilla subjuga* var. *subjuga, P. subjuga* var. *minutifolia, Senecio soldanella,* and *Townsendia rothrockii.*

ANNOTATED CHECKLIST OF VASCULAR PLANT SPECIES

PTEROPHYTA

Selaginellaceae

Selaginella densa Rydb. Common; dry and moist meadows, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Ophioglossaceae

Botrychium lunaria (L.) Sw. Very rare; fellfield. BM/NA.

Aspleniaceae

Cystopteris fragilis (L.) Bernh. Infrequent; shrub tundra, rock ledge, and rock debris habitats. AA/C.

CONIFEROPHYTA

Pinaceae

Abies lasiocarpa (Hook.) Nutt. Very rare; krummholz. BM/WNA.
Juniperus communis L. Very rare; krummholz. BM/C.
Picea engelmannii Parry ex Engelm. Rare; krummholz. BM/WNA.

ANTHOPHYTA—DICOTYLEDONEAE

Adoxaceae

Adoxa moschatellina L. Very rare; rock crevice. BM/C.

Apiaceae

Angelica grayi Coult. & Rose. Infrequent; moist meadow, rock ledge, rock crevice, and rock debris habitats. A/SRM.
Oreoxis bakeri Coult. & Rose. Ubiquitous; dry, moist and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.
Oxypolis fendleri (Gray) Heller. Very rare; wet meadow and rock ledge. M/SRM.

Pseudocymopterus montanus (Gray) Coult. & Rose. Very rare; krummholz. M/SRM.

Asteraceae

Achillea millefolium L. var. *lanulosa* (Nutt.) Piper. Very rare; krummholz. A/WNA.

Agoseris aurantiaca (Hook.) Greene. Very rare; wet meadow. BM/NA.

Agoseris glauca (Pursh) Raf. Very rare; krummholz. BM/NA.

Antennaria alpina (L.) Gaertn. Infrequent; moist meadow, shrub tundra, krummholz, and rock debris habitats. AA/NAE.

Arnica cordifolia Hook. Very rare; wet meadow and krummholz. BM/WNA.

Arnica mollis Hook. Very rare; krummholz. BM/NA.

Artemisia campestris L. subsp. *borealis* (Pallas) Hall & Clements. Rare; moist meadow and fellfield. AA/C.

Artemisia scopulorum Gray. Ubiquitous; dry, moist and wet meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/RM.

Cirsium scopulorum (Greene) Cockerell. Infrequent; moist meadow, krummholz, and rock ledge. A/RM.

Dugaldia hoopesii (Gray) Rydb. Very rare; krummholz. M/RM.

Erigeron compositus Pursh var. *glabratus* Macoun. Very rare; rock ledge. AA/NA.

Erigeron grandiflorus Hook. Very rare; dry meadow and rock ledge. AA/WNA.

Erigeron melanocephalus A. Nels. Common; moist and wet meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.

Erigeron pinnatisectus (Gray) A. Nels. Infrequent; dry meadow, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.

Erigeron simplex Greene. Ubiquitous; dry, moist and wet meadows, shrub tundra, krummholz, fellfield, rock crevice, and rock debris habitats. A/WNA.

Erigeron vagus Payson. Rare; rock ledge and rock debris habitats. A/WNA.

Haplopappus pygmaeus (Torr. & Gray) Gray. Rare; dry meadow and fellfield. A/RM.

Hymenoxys grandiflora (Torr. & Gray ex Gray) Parker. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, and rock crevice. A/RM.

Senecio amplectens Gray var. *amplectens.* Infrequent; moist meadow, fellfield, and rock debris habitats. M/RM.

Senecio amplectens Gray var. *holmii* (Greene) Harrington. Infrequent; moist meadow, fellfield, rock ledge, and rock debris habitats. A/WNA.

Senecio atratus Greene. Very rare; krummholz. A/SRM.

Senecio dimorphophyllus Greene. Infrequent; moist and wet meadows, shrub tundra, rock ledge, and rock crevice. M/RM.

Senecio porteri Greene. Very rare; rock debris habitats. A/RM.

Senecio soldanella Gray. Infrequent; moist meadow, shrub tundra, fellfield, rock crevice, and rock debris habitats. A/CO.

Senecio triangularis Hook. Very rare; rock ledge. BM/WNA.

Senecio werneriifolius Gray. Infrequent; dry and moist meadows, shrub tundra, rock crevice, and rock debris habitats. M/RM.

Taraxacum ceratophorum (Ledeb.) DC. Infrequent; moist meadow and fellfield. AA/C.

Taraxacum lyratum (Ledeb.) DC. Rare; fellfield and rock debris habitats. AA/NAA.

Townsendia rothrockii Gray ex Rothrock. Very rare; fellfield. A/CO.

Boraginaceae

Mertensia bakeri Greene. Infrequent; moist meadow, shrub tundra, krummholz, fellfield, rock ledge, rock crevice and rock debris habitats. A/SRM.

Mertensia ciliata (James ex Torr.) G. Don. Very rare; moist meadow and krummholz. BM/WNA.

Brassicaceae

Arabis divaricarpa A. Nels. Infrequent; moist meadow, rock ledge and rock debris habitats. BM/NA.

Arabis drummondii Gray. Very rare; krummholz. BM/NA.

Arabis lemmonii S. Wats. Rare; fellfield and rock debris habitats. A/WNA.

Cardamine cordifolia Gray. Infrequent; moist and wet meadows and rock ledge. BM/WNA.

Draba aurea Vahl. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, and rock ledge. AA/C.

Draba cana Rydb. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, and rock ledge. AA/C.

Draba crassa Rydb. Common; dry, moist and wet meadows, fellfield, rock ledge, rock crevice, and rock debris habitats. A/RM.

Draba crassifolia Graham. Ubiquitous; moist and wet meadows, krummholz, fellfield, rock crevice, and rock debris habitats. AA/NAE.

Draba fladnizensis Wulfen. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, and rock debris habitats. AA/C.

Draba nivalis Lilj. Rare; fellfield and rock ledge. AA/C.

Draba spectabilis Greene var. *spectabilis.* Very rare; rock ledge. M/RM.

Draba streptobrachia Price. Rare; fellfield, rock ledge and rock debris habitats. A/CO.

Erysimum capitatum (Dougl.) Greene var. *amoenum* (Greene) R. J. Davis. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, and rock debris habitats. A/SRM.

Rorippa curvipes Greene var. *alpina* (S. Wats.) R. Stuckey. Very rare; wet meadow. A/RM.

Smelowskia calycina (Steph.) C. A. Mey. ex Ledeb. Common; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Thlaspi montanum L. Common; dry, moist and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/C.

Campanulaceae

Campanula uniflora L. Rare; dry and moist meadows, rock ledge, and rock debris habitats. AA/C.

Caryophyllaceae

Cerastium earlei Rydb. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/RM.

Minuartia macrantha (Rydb.) House. Rare; fellfield. A/CO.

Minuartia obtusiloba (Rydb.) House. Common; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Minuartia rossii (R. Br.) Graebn. Infrequent; dry and moist meadows, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NA.

Minuartia rubella (Wahlenb.) Hiern. Common; dry, moist and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

Moehringia lateriflora (L.) Fenzl. Infrequent; dry meadow, shrub tundra, krummholz, fellfield, and rock ledge. AA/C.

Sagina saginoides (L.) Karst. Infrequent; moist meadow, shrub tundra, fellfield, rock ledge, and rock debris habitats. AA/C.

Silene acaulis (L.) Jacq. var. *subacaulis* (F. N. Williams) Fern. & St. John. Ubiquitous; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Silene drummondii Hook. Very rare; wet meadow and krummholz. BM/NA.

Silene kingii (S. Wats.) Bocquet. Rare; shrub tundra and rock ledge. A/SRM.

Silene uralensis (Rupr.) Bocquet subsp. *uralensis.* Infrequent; rock ledge, rock crevice, and rock debris habitats. AA/C.

Stellaria irrigua Bunge. Very rare; rock debris habitats. A/NAA.

Stellaria umbellata Turcz. ex Kar. & Kir. Common; moist and wet meadows, shrub tundra, fellfield, rock ledge, and rock debris habitats. A/NAA.

Crassulaceae

Sedum integrifolium (Raf.) A. Nels. ex Coult. & A. Nels. Common; moist and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Sedum lanceolatum Torr. Infrequent; dry and moist meadows, shrub tundra, krummholz, fellfield, and rock ledge. A/WNA.

Sedum rhodanthum Gray. Rare; moist meadow and rock ledge. A/RM.

Ericaceae

Vaccinium caespitosum Michx. Rare; moist and wet meadows, shrub tundra, and fellfield. BM/NA.

Vaccinium myrtillus L. subsp. *oreophilum* (Rydb.) Love, Love & Kapoor. Very rare; krummholz. BM/C.

Vaccinium scoparium Leib. Rare; moist meadow and fellfield. BM/WNA.

Fabaceae

Astragalus alpinus L. Rare; moist meadow and rock ledge. AA/C.

Oxytropis podocarpa Gray. Very rare; dry meadow. AA/C.

Trifolium attenuatum Greene. Infrequent; dry and moist meadows, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.

Trifolium dasyphyllum Torr. & Gray. Very rare; rock ledge. A/RM.

Trifolium nanum Torr. Common; dry and moist meadows, shrub tundra, krummholz, fellfield, rock ledge, and rock debris habitats. A/RM.

Trifolium parryi Gray. Ubiquitous; moist and wet meadows, shrub tundra, fellfield, rock ledge, and rock debris habitats. A/RM.

Gentianaceae

Gentiana algida Pallas. Rare; dry and moist meadows. AA/NAA.

Gentiana prostrata Haenke ex Jacq. Infrequent; dry and moist meadows, fellfield and rock ledge. AA/NAA.

Gentianella amarella (L.) Borner. Rare; dry meadow and rock ledge. BM/C.

Gentianella tenella (Rottb.) Borner. Rare; dry and moist meadows and rock ledge. AA/C.

Swertia perennis L. Very rare; rock ledge. A/C.

Hydrophyllaceae

Phacelia sericea Hook. Infrequent; dry meadow, shrub tundra, krummholz, fellfield, rock crevice, and rock debris habitats. A/WNA.

Onagraceae

Epilobium anagallidifolium Lam. Rare; wet meadow, shrub tundra, and rock ledge. AA/C.

Epilobium angustifolium L. Very rare; rock ledge. BM/C.

Epilobium latifolium L. Very rare; rock debris habitats. A/C.

Polemoniaceae

Polemonium delicatum Rydb. Rare; krummholz and rock ledge. M/SRM.

Polemonium viscosum Nutt. Common; dry and moist meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Polygonaceae

Oxyria digyna (L.) Hill. Common; moist and wet meadows, rock ledge, rock crevice, and rock debris habitats. AA/C.

Polygonum bistortoides Pursh. Ubiquitous; dry, moist and wet meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Polygonum viviparum L. Infrequent; dry, moist and wet meadows, krummholz, rock ledge, rock crevice, and rock debris habitats. AA/C.

Portulacaceae

Claytonia megarhiza (Gray) Parry ex S. Wats. Common; moist meadow, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/RM.

Lewisia pygmaea (Gray) B. L. Robins. Rare; moist meadow and rock ledge. A/WNA.

Primulaceae

Androsace septentrionalis L. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

Primula parryi Gray. Infrequent; moist and wet meadows. A/RM.

Ranunculaceae

Anemone multifida Poir. var. *globosa* (Nutt.) Torr. & Gray ex Pritz. Very rare; fellfield. BM/NA.

Aquilegia coerulea James. Infrequent; wet meadow, shrub tundra, krummholz, fellfield, rock crevice, and rock debris habitats. M/RM.

Caltha leptosepala DC. Common; moist and wet meadows, shrub tundra, krummholz, and rock ledge. A/WNA.

Delphinium barbeyi (Huth) Huth. Very rare; moist meadow. M/SRM.

Ranunculus eschscholtzii Schlecht. Infrequent; dry and moist meadows, krummholz, and rock ledge. AA/NAA.

Ranunculus macauleyi Gray. Infrequent; moist meadow, fellfield, rock ledge, and rock debris habitats. A/SRM.

Thalictrum alpinum L. Infrequent; dry and moist meadows, fellfield, rock ledge, and rock debris habitats. A/SRM.

Thalictrum fendleri Engelm. ex Gray. Rare; fellfield and rock ledge. BM/WNA.

Trollius laxus Salisb. subsp. *albiflorus* (Gray) Love, Love & Kapoor. Very rare; shrub tundra. BM/WNA.

Rosaceae

Geum rossii (R. Br.) Ser. var. *turbinatum* (Rydb.) C. L. Hitch. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Potentilla diversifolia Lehm. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAA.

Potentilla gracilis Dougl. ex Hook. var. *pulcherrima* (Lehm.) Fern. Very rare; krummholz. BM/WNA.

Potentilla hookeriana Lehm. Very rare; fellfield. AA/NAA.

Potentilla nivea L. Infrequent; dry and moist meadows, shrub tundra, fellfield, rock ledge, and rock debris habitats. AA/C.

Potentilla rubricaulis Lehm. Infrequent; dry meadow, shrub tundra, fellfield, and rock ledge. AA/NA.

Potentilla subjuga Rydb. var. *minutifolia* Rydb. Infrequent; dry and moist meadows, shrub tundra, and fellfield. A/CO.

Potentilla subjuga Rydb. var. *subjuga.* Infrequent; dry and moist meadows, shrub tundra, fellfield, and rock ledge. A/CO.

Potentilla uniflora Ledeb. Very rare; rock ledge. AA/NAA.

Sibbaldia procumbens L. Ubiquitous; moist and wet meadows, shrub tundra, krummholz, fellfield, and rock crevice. AA/C.

Salicaceae

Salix arctica Pallas. Common; dry, moist, and wet meadows, shrub tundra, and rock ledge. A/WNA.

Salix brachyphylla Nutt. Rare; shrub tundra and rock ledge. BM/NA.

Salix glauca L. var. *villosa* (Hook.) Anderss. Very rare; shrub tundra. BM/WNA.

Salix planifolia Pursh. Infrequent; wet meadow, shrub tundra, and rock ledge. BM/NA.

Salix reticulata Hook. subsp. *nivalis* (Hook.) Love, Love & Kapoor. Common; moist meadow, shrub tundra, fellfield, and rock ledge. A/WNA.

Saxifragaceae

Heuchera parvifolia Nutt. ex Torr. & Gray. Rare; krummholz, fellfield, and rock ledge. A/SRM.

Parnassia fimbriata Koenig. Very rare; rock ledge. BM/WNA.

Parnassia kotzebuei Cham. & Schlecht. Very rare; rock ledge. AA/NAA.

Ribes montigenum McClatchie. Rare; krummholz, fellfield and rock ledge. BM/WNA.

Saxifraga adscendens L. subsp. *oregonensis* (Raf.) Bacig. Infrequent; dry and moist meadows, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/NAE.

Saxifraga bronchialis L. subsp. *austromontana* (Wieg.) Piper. Infrequent; moist meadow, fellfield, rock ledge, and rock crevice. A/WNA.

Saxifraga cernua L. Infrequent; dry and moist meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

Saxifraga cespitosa L. subsp. *delicatula* (Small) Porsild. Infrequent; dry and moist meadows, rock ledge, and rock debris habitats. AA/C.

Saxifraga cespitosa L. subsp. *monticola* (Small) Porsild. Very rare; rock ledge and rock crevice. A/C.

Saxifraga chrysantha Gray. Rare; moist meadow, rock ledge and rock debris habitats. AA/NAA.

Saxifraga debilis Engelm. ex Gray. Common; moist and wet meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/RM.

Saxifraga flagellaris (Sternb.) Willd. subsp. *platysepala* (Trautv.) Porsild. Infrequent; dry and moist meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.

Saxifraga odontoloma Piper. Rare; wet meadow and rock ledge. BM/WNA.

Saxifraga rhomboidea Greene. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Saxifraga rivularis Greene. Rare; moist meadow and rock ledge. AA/C.

Scrophulariaceae

Besseya alpina (Gray) Rydb. Common; dry, moist, and wet meadows, shrub tundra, fellfield, rock ledge, rock crevice, and rock debris habitats. A/SRM.

Besseya ritteriana (Eastw.) Rydb. Very rare; rock ledge. A/CO.

Castilleja haydenii (Gray) Cockerell. Infrequent; dry and moist meadows, fellfield, and rock ledge. A/SRM.

Castilleja miniata Dougl. ex Hook. Very rare; shrub tundra. BM/WNA.

Castilleja occidentalis Torr. Infrequent; moist and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, and rock debris habitats. A/RM.

Castilleja rhexifolia Rydb. Rare; moist meadow and rock ledge. BM/WNA.

Chionophila jamesii Benth. Infrequent; moist and wet meadows, fellfield, rock ledge, and rock debris habitats. A/SRM.

Mimulus guttatus DC. Very rare; rock ledge. BM/NA.

Pedicularis groenlandica Retz. Infrequent; moist and wet meadows. AA/NA.

Pedicularis sudetica Willd. subsp. *scopulorum* (Gray) Hulten. Very rare; shrub tundra. A/RM.

Penstemon harbourii Gray. Rare; rock debris habitats. A/CO.

Penstemon whippleanus Gray. Infrequent; krummholz, fellfield and rock ledge. M/RM.

Veronica wormskjoldii Roemer & Schultes. Infrequent; dry, moist, and wet meadows, shrub tundra, fellfield, and rock ledge. AA/NA.

Violaceae

Viola adunca Sm. subsp. *bellidifolia* (Greene) Harrington. Rare; moist meadow and rock ledge. BM/NA.

ANTHOPHYTA—MONOCOTYLEDONEAE

Cyperaceae

Carex albonigra Mackenzie. Infrequent; dry, moist, and wet meadows, krummholz, fellfield, rock ledge, and rock debris habitats. AA/WNA.

Carex aquatilis Wahlenb. Rare; wet meadow. AA/C.

Carex arapahoensis Clokey. Infrequent; dry and moist meadows, krummholz, fellfield, rock ledge, and rock debris habitats. A/SRM.

Carex bella Bailey. Very rare; krummholz. M/RM.

Carex capillaris L. Very rare; moist meadow. AA/C.

Carex ebenea Rydb. Infrequent; dry, moist, and wet meadows, shrub tundra, fellfield, rock crevice, and rock debris habitats. A/RM.

Carex elynoides Holm. Infrequent; dry and moist meadows, shrub tundra, fellfield, and rock debris habitats. A/WNA.

Carex hallii Olney. Very rare; moist meadow. BM/NA.

Carex haydeniana Olney. Infrequent; moist meadow, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Carex heteroneura W. Boott var. *chalciolepis* (Holm) F. J. Herm. Common; moist meadow, shrub tundra, krummholz, fellfield, rock ledge, and rock debris habitats. A/WNA.

Carex incurviformis Mackenzie. Infrequent; dry and moist meadows and fellfield. A/WNA.

Carex misandra R. Br. Rare; moist meadow and rock ledge. AA/C.

Carex nardina Fries var. *hepburnii* (Boott) Kukenth. Rare; moist meadow and rock debris habitats. AA/NAA.

Carex nelsonii Mackenzie. Infrequent; moist meadow. A/SRM.

Carex nigricans C. A. Mey. Infrequent; moist and wet meadows, shrub tundra, krummholz, and fellfield. A/NAA.

Carex norvegica Retz. subsp. *norvegica.* Rare; dry and moist meadows and shrub tundra. AA/NAE.

Carex nova Mackenzie. Infrequent; dry and moist meadows, fellfield, rock ledge, and rock crevice. BM/WNA.

Carex perglobosa Mackenzie. Infrequent; dry and moist meadows, fellfield, rock ledge, and rock debris habitats. A/SRM.

Carex phaeocephala Piper. Infrequent; dry meadow, fellfield, and rock debris habitats. A/WNA.

Carex pseudoscirpoidea Rydb. Infrequent; dry, moist and wet meadows, shrub tundra, krummholz, fellfield, and rock debris habitats. A/WNA.

Carex pyrenaica Wahlenb. Rare; moist and wet meadows and rock debris habitats. A/C.

Carex vernacula Bailey. Infrequent; moist and wet meadows and shrub tundra. A/WNA.

Kobresia myosuroides (Vill.) Fiori & Paol. Infrequent; dry meadow, fellfield and rock debris habitats. AA/C.

Kobresia sibirica Turcz. Very rare; moist meadow and rock debris habitats. AA/NAA.

Juncaceae

Juncus drummondii E. Mey. Infrequent; moist and wet meadows, fellfield, and rock ledge. A/WNA.

Juncus mertensianus Bong. Very rare; wet meadow. A/NAA.

Luzula parviflora (Ehrh.) Desv. Very rare; shrub tundra. BM/C.

Luzula spicata (L.) DC. Common; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, and rock debris habitats. A/RM.

Liliaceae

Lloydia serotina (L.) Salis. ex Reichenb. Infrequent; dry and moist meadows, shrub tundra, fellfield, rock ledge, and rock debris habitats. AA/C.

Veratrum tenuipetalum Heller. Very rare; krummholz. A/SRM.

Poaceae

Agropyron scribneri Vasey. Infrequent; moist meadow, krummholz, fellfield, rock ledge, and rock debris habitats. A/WNA.

Agropyron trachycaulum (Link) Malte ex H. F. Lewis var. *latiglume* (Scribn. & Smith) Beetle. Infrequent; dry meadow, fellfield, and rock ledge. AA/NA.

Deschampsia caespitosa (L.) Beauv. Common; dry, moist, and wet meadows, fellfield, and rock ledge. BM/C.

Festuca brachyphylla Schultes. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

Hierochloe hirta (Schrank) Borbas subsp. *arctica* (Presl.) G. Weismarck. Very rare; krummholz. AA/C.

Phleum alpinum L. Infrequent; moist and wet meadows and krummholz. AA/C.

Poa alpina L. Ubiquitous; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

Poa epilis Scribn. Very rare; fellfield. BM/WNA.

Poa leptocoma Trin. Very rare; dry meadow and rock ledge. A/WNA.

Poa reflexa Vasey & Scribn. ex Vasey. Very rare; moist meadow. A/WNA.

Poa rupicola Nash ex Rydb. Common; dry, moist, and wet meadows, shrub tundra, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. A/WNA.

Trisetum spicatum (L.) Richter. Ubiquitous; dry, moist, and wet meadows, krummholz, fellfield, rock ledge, rock crevice, and rock debris habitats. AA/C.

LITERATURE CITED

ANDREWS, J. T., P. E. CARRARA, F. B. KING, and R. STUCKENRATH. 1975. Holocene environmental changes in the alpine zone, northern San Juan Mountains, Colorado: evidence from bog stratigraphy and palynology. Quaternary Res. 5:173–197.

BAMBERG, S. A. 1961. Plant ecology of alpine tundra areas in Montana and adjacent Wyoming. M.A. thesis, Univ. Colorado, Boulder.

BARSCH, D. 1978. Rock glaciers as indicators for discontinuous alpine permafrost: an example from the Swiss Alps. *In* Proceedings of the Third International Conference on Permafrost, pp. 349–352. National Research Council of Canada, Ottawa.

CARRARA, P. E., W. N. MODE, M. RUBIN, and S. W. ROBINSON. 1984. Deglaciation and post-glacial timberline in the San Juan Mountains, Colorado. Quaternary Res. 21:42–55.

CASADWALL, T. and H. OHMOTO. 1977. Sunnyside Mine, Eureka Mining District, San Juan County, Colorado: geochemistry of gold and base metal ore deposition in a volcanic environment. Econ. Geol. 72:1285–1320.

COOPER, W. S. 1908. Alpine vegetation in the vicinity of Long's Peak. Bot. Gaz. 45:319–337.

COX, C. F. 1933. Alpine plant succession on James Peak, Colorado. Ecol. Monog. 3:299–372.

EDDLEMAN, L. F. and R. T. WARD. 1984. Phytoedaphic relationships in alpine tundra, north-central Colorado, U.S.A. Arctic and Alpine Research 16:343–359.

IVES, J. D. and B. D. FAHEY. 1971. Permafrost occurrence in the Front Range, Colorado Rocky Mountains, United States of America. J. Glaciology 10:105–111.

KARTESZ, J. T. and R. KARTESZ. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Vol. II: the biota of North America. Univ. North Carolina Press, Chapel Hill.

KOMARKOVA, V. 1976. Alpine vegetation of the Indian Peaks area, Colorado Rocky Mountains. Ph.D. dissertation, Univ. Colorado, Boulder.

LARSEN, E. S., JR. and C. W. CROSS. 1956. Geology and petrology of the San Juan region, southwestern Colorado. U.S.G.S. Prof. Paper 258.

MAJOR, J. and S. A. BAMBERG. 1967. A comparison of some North American and Eurasian alpine ecosystems. *In* H. E. Wright, Jr. and W. H. Osburn, eds., Arctic and Alpine environments, pp. 89–118. Indiana Univ. Press, Bloomington.

MARR, J. W. 1961. Ecosystems of the East Slope of the Front Range in Colorado. Univ. Colorado Stud., Series in Biology 8:1–134.

MICHENER, M. J. 1964. The high altitude vegetation of the Needle Mountains of southwestern Colorado. M.A. thesis, Univ. Colorado, Boulder.

ROTTMAN, M. L. 1984. A floristic analysis of three alpine basins in the northern San Juan Mountains, Colorado. Ph.D. dissertation, Univ. Colorado, Boulder.

WEBBER, P. J., J. C. EMERICK, D. C. E. MAY, and V. KOMARKOVA. 1976. The impact of increased snowfall on alpine vegetation. *In* H. W. Steinhoff, and J. D. Ives, eds., Ecological impacts of snowpack augmentation in the San Juan Mountains, Colorado, pp. 201–254. Final Report, San Juan Ecology Project, Colorado State Univ., Fort Collins.

(Received 7 Jun 1984; accepted 16 Jan 1985)

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY AWARD FOR GRADUATE STUDENT RESEARCH

An award of $250 will be given annually to the student member of the California Botanical Society submitting the winning proposal for thesis or dissertation research. The award is intended to help defray costs of research travel, field work, or laboratory supplies for which no other source of support exists. Each year's competition will be announced in MADROÑO and at the CBS Graduate Student Meeting.

Each applicant must be a student member of the California Botanical Society both in the year of submittal and during the year in which the funds are used. During the year of the award the student must be enrolled in a graduate program leading to the preparation of a thesis.

Proposals are to include a brief description of the project, including an assessment of its importance; the need for funds; and a summary of current support. They should not exceed six double-spaced typewritten pages. Proposals should be accompanied by an evaluative cover letter from the major adviser for the project. Five copies are to be sent to the Past President of the Society.

Proposals will be reviewed by a Committee consisting of the three elected Council members, the Second Vice President, and, as *ex officio* convener, the Past President. They will be evaluated on criteria of scientific merit and appropriateness for publication in MADROÑO upon completion (no contract is assumed on either side). The Committee will present a small number (usually 2–3) of the best proposals to the Council with a recommendation of one as winner. The final decision will rest with the Council.

NOTES AND NEWS

NOTES ON THE *Salvia leucophylla* COMPLEX (LAMIACEAE) OF CALIFORNIA AND BAJA CALIFORNIA NORTE.—The *Salvia leucophylla* complex includes two species, *S. leucophylla* Greene and *S. chionopeplica* Epling. *Salvia leucophylla* is a member of the Southern California coastal sage scrub formation in the Coast Range foothills of California, from Monterey County southward to the Santa Ana Mountains of eastern Orange County. *Salvia chionopeplica,* a little-known Baja California endemic closely related to *S. leucophylla,* is differentiated by distinct floral and leaf features. Both species share a dendritic pubescence virtually unique to the *Salvia* section in which they belong, and have almost identical inflorescence structure, calyx morphology, and volatile oil components (Neisess, K. R., 1983, Evolution, systematics, and terpene relationships of *Salvia* Section *Audibertia,* Ph.D. diss., Univ. California, Riverside). *Salvia leucophylla* has a uniformly rose-lavender corolla (sometimes very pale) with pollen ranging in color from dusky-yellow to olive-drab, whereas *S. chionopeplica* has a distinctly blue-lavender corolla with bright yellow pollen. Vegetatively, the leaf blades of *S. leucophylla* are usually 3 or more times longer than wide, whereas those of *S. chionopeplica* are usually less than 2.5 times as long as wide. The range of *S. chionopeplica* has been stated to encompass the "western slopes of (the) Sierra San Pedro Martir from the vicinity of San Telmo south to San Fernando" (Wiggins, I. L., 1980, Flora of Baja California, Stanford Univ. Press). An extensive review of collected material deposited in western herbaria (SD, LAM, RSA, PC, OBI, DAV, UNLV, MACF, OSC, ASUC, TUC, UCR, MO, WTU, UTC, CIC, TEX, LL, BRY) indicates, and uniform garden studies confirm, nomenclatural confusion and distortion of the distributional range of both species.

The focal point of this confusion involves a population occurring on Mesa el Barrial, along the road from San Telmo to Meling Ranch in the western foothills of the Sierra San Pedro Martir of Baja California. On-site investigations conducted in August, 1980, established that the leaves of the Barrial plants more closely resembled those of *S. leucophylla,* although somewhat smaller in size. To examine the exact degree of this relationship, seed was collected at the Barrial locality and 24 seedlings were grown under uniform garden conditions at the University of California, Riverside, with like samples of *S. chionopeplica* from the type locality (about 56 km east of El Rosario, near Rancho El Arenoso) and *S. leucophylla* from San Luis Obispo, Los Angeles, and Orange counties. Under these conditions, leaves of the Barrial plants clearly approximated the leaf shape characterizing *S. leucophylla* (Fig. 1). The flowers of these plants matched those of the *S. leucophylla* populations, although they came into bloom about two months earlier.

Hand pollinations, conducted in greenhouse facilities at UC Riverside, proved both species interfertile and self-compatible. Plant association for *S. chionopeplica,* given by Wiggins as creosote bush scrub, is somewhat misleading. Although the area in which *S. chionopeplica* occurs is predominantly creosote bush scrub, the species is usually found in localized, relatively mesic areas (north-facing slopes and summits of hills and small peaks) associated with typical coastal sage scrub species, such as *Eriogonum fasciculatum* Benth., *Lotus scoparius* Ottley, and *Viguiera laciniata* Gray.

Evidently, the Mesa el Barrial population represents a southeastward disjunction of approximately 350 km for *S. leucophylla,* and is not *S. chionopeplica* as assumed previously (Fig. 2). It appears likely that the Mesa el Barriel population of *S. leucophylla* and the closely related *S. chionopeplica* are both remnants of Pleistocene assemblages of coastal sage scrub vegetation.—KURT R. NEISESS, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711. (Received 3 May 1984; accepted 7 Aug 1985.)

MADROÑO, Vol. 32, No. 4, pp. 273–275, 20 December 1985

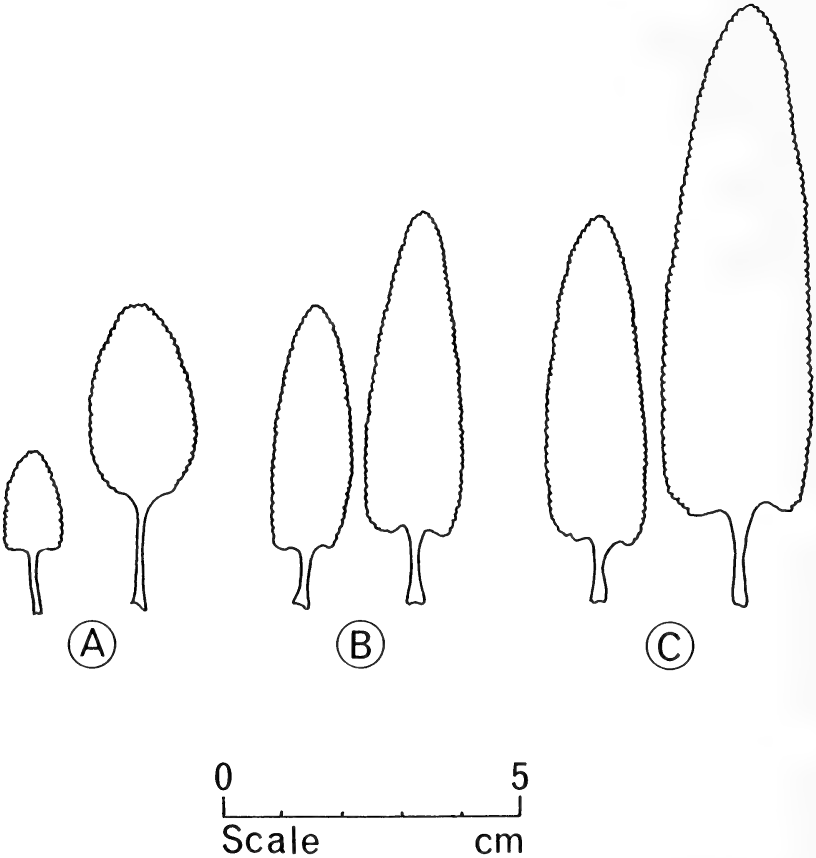


FIG. 1. Leaf variation in *Salvia leucophylla* and *S. chionopeplica.* Pairs represent the range of largest leaf size from each of three representative population samples in the uniform garden study conducted at the University of California, Riverside. A. El Arenoso, Baja California Norte (type locality of *S. chionopeplica*). B. Mesa el Barrial, Baja California Norte (*S. leucophylla*). C. Santiago Canyon, Orange County, California (*S. leucophylla*).

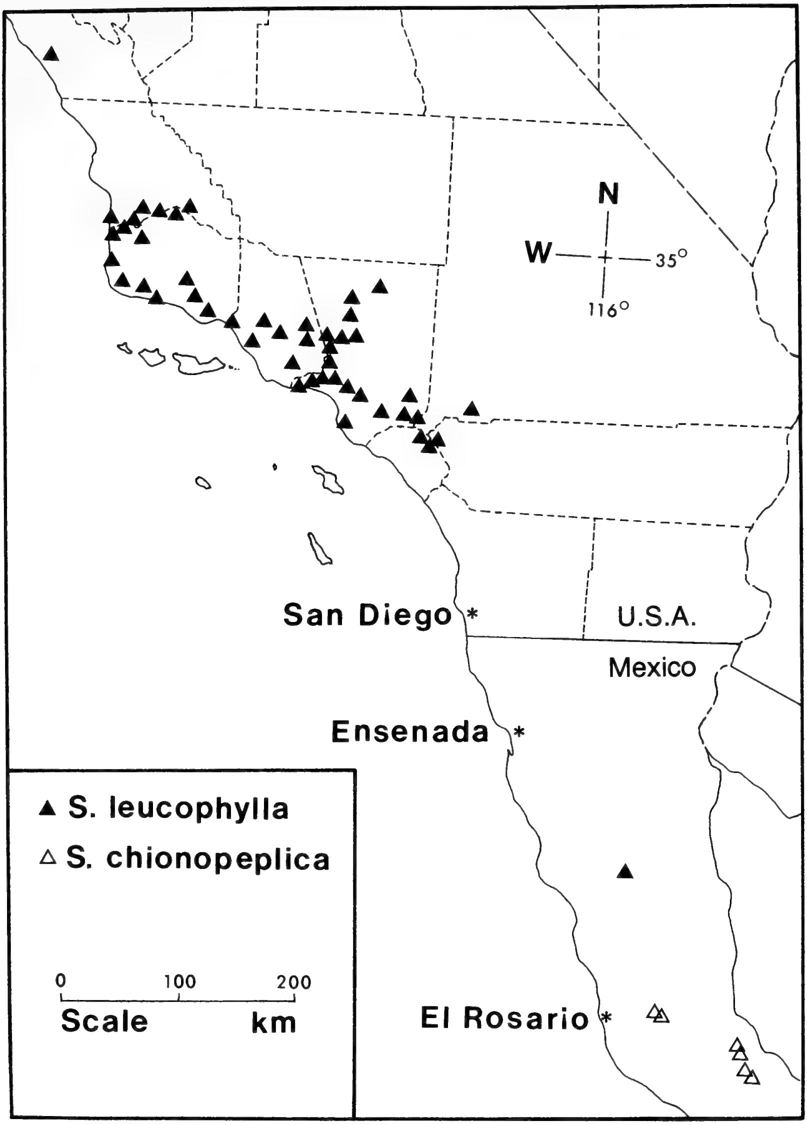


FIG. 2. Distribution of the *Salvia leucophylla* complex.

REVIEWS

Bibliographies on Chaparral and the Fire Ecology of Other Mediterranean Systems. By Jon E. Keeley. California Water Resources Center. University of California, Davis. Report No. 58. 1984. ISSN 0575-4968.

This volume is a collection of separate and non-overlapping bibliographies on ten topics: 1) Chaparral—Evolution and Systematics, 2) Chaparral—Community Structure, 3) Chaparral—Fire and Demography, 4) Chaparral—Morphology and Physiology, 5) Chaparral—Soils and Management, 6) Chaparral—Animals, 7) Seed Germination [California species], 8) California Grasslands, 9) California Forests—Fire and Demography, and 10) Mediterranean Systems—Fire and Demography. Within each bibliography, citations are arranged alphabetically by authors' names.

The first five of the six bibliographies that focus on chaparral contain an impressively comprehensive compilation of the literature. Several major references, however, are missing from the animal bibliography. The inclusion of allelopathy references in the bibliography on seed germination is confusing, especially since the review of allelopathy literature is probably more comprehensive than that on germination (for example, only two of the articles in Seeds of Woody Plants of the United States are cited specifically). Particularly as regards non-chaparral species, there is a wealth of germination literature that is not reflected in this bibliography. The grasslands bibliography also appears reasonably complete, except for the curious omission of any literature on vernal pools. By far the least thorough of the bibliographies is the one on California forests, whose coverage of the literature is spotty at best. This section seems to contain leftovers from the other bibliographies rather than representing a thorough search of its own. It was difficult to decide just what segment of the literature it was intended to represent. I found it particularly annoying that the literature on tree form oaks was apparently randomly split between this section and the chaparral bibliographies. The final section, which contains references for publications on Mediterranean ecosystems outside of western North America, should provide easy access to the international literature, much of which might otherwise be ignored.

The division of this volume into ten separate bibliographies with no cross-referencing is sometimes more of a hindrance than a help. Because there is no overlap between the citation listings, most searches will require paging through a minimum of three or four of the bibliographies to be sure relevant papers are not missed. Although I recognize the effort it would have required, the usefulness of this set of bibliographies would have been enhanced substantially by the addition of a comprehensive subject index.

Despite their weaknesses, these bibliographies should prove an excellent resource for those interested in chaparral. Proofing errors are generally minimal—with the exception that my name is misspelled throughout! The compiler is to be lauded for his attention to frequently ignored early papers and to easily missed master's theses. This completeness should make the bibliographies especially useful—to researchers and to graduate and undergraduate students—as an introduction to a wide body of literature.—Susan G. Conard, USDA Forest Service Forest Fire Laboratory, Riverside, CA.

Insects and Flowers: The Biology of a Partnership. By Friedrich G. Barth. Translated by M. A. Biederman-Thorson. ix + 297 pp. Princeton University Press, NJ. 1985. $35. ISBN 0-691-08368-1.

New pollination books and reviews abound. One's first impression of this lively book, *Insects and Flowers,* is that it is a twin to another beautiful book published recently by Bastiaan Meeuse and Sean Morris called (unfortunately) *The Sex Life of*

Madroño, Vol. 32, No. 4, pp. 276–280, 20 December 1985

Flowers. But this is not an identical twin by any means; the greater emphasis in Barth's book is on the insects although the flowers are given a good deal of attention. The illustrations in both books are magnificent (in color and black and white plates and appropriate line drawings) and the texts are accurate and readable in both books. They are synergistic.

Insects and Flowers was first published (in 1982) in German by Friedrich Barth, who is Professor of Zoology in Frankfurt. He was a graduate student at UCLA after gaining his first degree at the University of Munich. The book was translated by M. Biederman-Thorson, who is also a biologist as well as a professional translator of scientific works. The result is a book that reads as if it were written originally in English. There is an introductory chapter, followed by 6 chapters on pollination mechanisms and pollinators, followed, in turn, by 4 chapters on the collecting of pollen and nectar. Then there are 18 chapters on the senses and behaviors of insects (with most space, naturally, being devoted to bees). A concluding chapter explores the co-evolution that has produced the efficient "orthodox" pollination systems as well as the bizarre stories of the aroids and Orchidaceae and their relations with insects. Barth shows that he means business by *starting* with the complicated interaction between figs and fig-wasps, but the going gets easier later on. His book will be useful to professional and amateur biologists for it is simply written, factually convincing, and well-backed by references. These references include German works that are not usually considered in books written in English. His explanation of the structure of insect mouth-parts is a marvel of clarity, which will be appreciated by non-entomologists.

In his evolutionary considerations, Barth is an unashamed Darwinian "phyletic gradualist" (as opposed to being a "punctuated equilibrium" supporter), and he has the advantage of material that fits the gradualist view of insect/plant co-evolution. His discussion of the evolution of the social habit among bees, and the almost incredible senses and communication patterns that these insects show, is considered in relation to the flowers and their phenology, thus making this book appropriate reading for botanists!

There are very few misstatements of botanical fact even though the author is a zoologist. Thus, reference is made to "nectar guides" in some taxa that do not produce this liquid, but these are scarcely visible blemishes on a text that is well-informed and most informative. Princeton University Press has brought us a book that will be a leader in its field.—H. G. BAKER, University of California, Berkeley.

California Riparian Systems: Ecology, Conservation, and Productive Management. Edited by RICHARD E. WARNER and KATHLEEN M. HENDRIX. University of California Press, Berkeley. 1984. xxix + 1035 pp. $57.50, $19.95 paper. ISBN-529-05034-7 and -05035-5 (pbk.).

This massive, catholic, inclusive, wide-ranging book is the record of, and a monument to, the California Riparian Systems Conference held at the University of California, Davis, 17–19 Sep 1981. The more than 250 authors are outstandingly expert, dedicated, responsible, involved. One hundred twenty-eight papers are printed in 22 sections: Biogeography and change; Structure, status and trends; Hydrology related to structure, function and protection; Aquatic riparian interactions; Riparian/upland interactions; Economic and social values; legal framework; Classification, inventory, and monitoring; National and regional trends in use; Restoration; Water diversion project conflicts; Levees; Bird populations; Coastal zone; Desert systems; Sustained yield production; Cultural, recreational and aesthetic values; Integrated approaches to management—protection; State versus local control; The Rivers and Harbors Act of 1899 and conservation; Non-avian wildlife; and Private ownership. This sectional classification is far from absolute. Very many papers burst their bounds to become even more interesting. However, a 39 page, double column index will facilitate reference. Notably it does not include authors' names.

The book is obviously more than a mine of information for California's botanists. Even on the subject of riparian ecosystems it ranges not only throughout California but from Oregon to the Great Basin and the desert Southwest, from the mountains to the sea coast. This vast area is mostly arid, but riparian ecosystems are obviously uniquely mesic in the summer-dry, lowland landscapes of the American West. Judging from the productivity studies available from Soviet work on similar riparian systems in central Asia (tugai), our western riparian plant communities may have been the most productive natural vegetation in the West.

Several papers, quite arbitrarily selected, supply intelligible botanical data, contain traces of the field work on which they are based, use more or less standard methods, compare their results with similar studies, produce an inductive rather than a deductive classification, and employ few or no "*Salix* spp." (Strahan, Whitlow, and Bahre; McBride and Strahan; Laymon, Shanfield, Warner; etc.). Others, which are simply intensely interesting, on the Carmel River, structure of vegetation, Mono Lake, and *Prosopis glandulosa* productivity, deserve mention (Kondolf and Curry; Stone, Cavallaro, and Stromberg; Stine, Gaines, and Vorster; Nilsen, Rundel, and Shariff; etc.). Holstein's biogeographical paper is a model, with adequate paleobotanical and ecological data, including good distribution maps. Other readers will certainly have their own highlights.

An only slightly slimmer European book is an interesting supplement and contrast to the Californian volume (Gehu, J.-M., ed., 1984, *La vegetation des forests alluviales,* Colloques Phytosociologiques 9 in Strasbourg, 1980. J. Cramer, Vaduz. xiv + 744 pp., tables). Riparian vegetation from Austria, Hungary, Rumania, and Czechoslovakia to Spain, and from Italy to W. Germany was discussed by 94 attendees in 46 papers. There were field trips in addition to the presentations. Languages are French, German, English, and Italian. About ⅕ of the book's thickness is tables of the stands of vegetation studied, the data manipulated and discussed. Braun-Blanquet's methods of studying vegetation and its ecology were used. A classification of riparian vegetation has resulted and is generally agreed upon. Where numerical methods of analysis were employed, the results are also often illustrated by tables of stands. The numerical data can thus be tested by the reader's ecological experience with the species in the field, greenhouse, or laboratory.

A stand's position in an ordination or in a classification of vegetation is due to its species composition. Which species? The unique value of Braun-Blanquet's method of studying vegetation is that the result is a table of individual species occurrences in particular stands. Much can be done with such data; no interpretation of vegetation and particularly no interpretation of the ecology of vegetation is of value without such data.

If the reader can tear himself away from this volume, including a paper that used good topographic maps of riparian areas of the upper Rhine from 1838, 1852, 1872, and the present or from another that from a population of 1420 stands containing 1223 species made a selection of 328 riparian stands containing 331 species, then a volume by B. M. Mirkin et al. (1980) (*Riparian vegetation of the Mongolian Peoples' Republic,* Biological resources and natural conditions of the MPR, vol. 13. 284 pp. Nauka, Leningrad) should be of interest. It covers in considerable detail the vegetation of a dozen Mongolian rivers from their origins in the high mountains to their disappearance in the Gobi deserts or across the Soviet border. This group took data on 3500 stands and made 5000 plant collections, so we evidently still have some purely botanical work to do on California's riparian ecosystems!—JACK MAJOR, Botany Department, University of California, Davis.

Forest Succession and Stand Development Research in the Northwest. Proceedings of the Symposium held 26 March 1981, at Corvallis, Oregon. Edited by JOSEPH E. MEANS. Forest Research Laboratory, Oregon State University, Corvallis 97331. 1982. $6.00.

In creating his revised tolerance table for American forest trees, Baker (1949) made a significant observation. Noting that a number of the "outstanding men in the field of silviculture" submitted a minority view on the place of a species in the tolerance hierarchy he commented: "We are at a loss to account for this, but the disturbing suggestion has been made that most of us accept the things we learned in school as the gospel truth; only a few of the best learn to observe and think for themselves." It is apparent from some of the papers of this symposium that many of the participants were among the outstanding men in the field. Although the study of succession is considered by many to be responsible for the birth of ecology in the United States and has been a major focus of an inordinate number of ecological studies and publications, there is still a great deal to be learned about whatever we want to include under the heading of succession.

The symposium proceedings cover a broad range of topics including studies of trees growing in computers, observations of real world situations where old dogmas were not verified, and a discussion of stratification of the sites as a means of understanding the processes of succession.

The papers are arranged by subject matter into two parts. Part I is devoted to the larger topic of forest succession. The introductory paper by D. M. Smith sets a fine stage for the papers that follow. He raises a number of interesting points about some of the differences that have developed in ecological thought and warns us against trying to force observed patterns into the few classes already described. A trap that he does not mention is letting our preconceived patterns influence the results of our observations. Hopefully none of us are subject to that mistake.

The next four papers describe computer simulations. The first of these papers, by D. C. West and others, aptly introduces these, giving examples of how simulations may help us compress time into a comprehensible vector and make some predictions about long-term effects of management actions or natural variations of the environment.

Six papers are devoted to reporting observations of real world situations from northern California to southeast Alaska and inland to western Montana. For some reason Canada was not represented in the symposium. Papers by R. D. Pfister and S. F. Arno demonstrated the reason for using some form of habitat type classification for stratification of successional observations.

Part II consists of papers on stand development. The introductory paper of this section by C. D. Oliver gives an overview of the growth, development, and importance of this newly-budded aspect of succession. Papers by B. C. Larsen and S. D. Viers give examples of why careful observations are better than conventional wisdom in trying to understand natural processes. Larsen demonstrated that much of a stand's growth may be concentrated in the dominant trees and that thinning does not always release the smaller trees. Viers demonstrated that redwoods would reproduce with or without fire in certain environments.

In the summary paper, J. F. Franklin pointed out a lack of papers dealing with permanent plot studies. This results from a lack of research using that method. Also evident in most of the papers is our continued dependence on the eastern deciduous forest for successional concepts. These concepts are undoubtedly useful for a great number of areas in the west, but there is still a great deal to learn about succession where shade tolerance is not the driving force behind the patterns of succession we see, especially in many of the drier interior forests.

The body of the text is reduced to the point where it is difficult to read. Some of the figures have lettering that is almost too small, but I didn't find any that were unreadable. Also, don't plan to read it more than a few times. My copy is now held together with a paper clip.

All things considered, this is a valuable volume for those studying succession in the Pacific Northwest. The summary paper by Franklin is especially valuable. Many suggestions for further studies are made that, if followed, would certainly improve our understanding of succession. It was emphasized that more permanent plot studies should be started now to help validate the models and hypotheses that have evolved from comparing different-aged stands. — DON G. DESPAIN, Yellowstone National Park, Wyoming.

ANNOUNCEMENT

A New Section for MADROÑO

Beginning with Volume 33, each issue of MADROÑO will contain an editorial page on which comments by the editor, invited contributions, unsolicited letters, and other remarks will be featured. This editorial page will serve as a vehicle for communication among our members and could include, for example, opinions of authorities on current trends in botany, rebuttals or comments on papers published in MADROÑO, letters from the President of our society, and other noteworthy communications. The editors invite all members to participate in this forum; however, all editorials will be published at the discretion of the editors.

ANNOUNCEMENT

Attention Contributors of Floras

New conventions for the publication of floras have been adopted by the editors of MADROÑO. All annotated catalogues and lengthy checklists will be printed in 8 point type and will appear in the body of papers after the discussion section and before acknowledgments. The catalogue should include latin names and authors, references to habitats and plant communities in which the plants are found, standardized estimates of the frequency and abundance of each taxon, and citation of a limited number of voucher specimens. The annotated catalogue also should include or be preceded by an explanation of categories and abbreviations. Nomenclature should be current and synonyms should follow names that do not appear in standard regional floras. Other sections of floras, including introduction, study area, methods, vegetation, analysis of the flora, etc., will be printed in 10 point type. We encourage the use of a limited number of high quality photographs of plant communities or topographic setting, but such photographs are not required. Standardization of the basic format of floras will improve the quality of such papers published in MADROÑO and should reduce the amount of revision that may be required. We look forward to working with authors and welcome suggestions regarding conventions of format and style adopted for MADROÑO.

ANNOUNCEMENT

The Tenth Annual Graduate Student Meeting, sponsored by the California Botanical Society, was held at the University of California, Santa Barbara on 19 October 1985. More than 50 people attended the twenty presentations by students from 8 institutions. The following individuals received awards for their presentations:

Completed Research

Best Paper	Jeffrey P. Hill Department of Botany and Plant Sciences University of California, Riverside
Second Place	William Bond Department of Biology University of California, Los Angeles
Third Place	Niall F. McCarten Department of Biological Sciences San Francisco State University

Research in Progress

Best Paper	Alan L. Koller Department of Botany University of California, Davis
Second Place	Richard W. Kerrigan Department of Biological Sciences University of California, Santa Barbara
Third Place	Kirk E. Apt Department of Biological Sciences University of California, Santa Barbara

Proposed Research

Best Paper	Edith A. Reed Department of Ecology and Evolutionary Biology University of California, Irvine
Second Place	Christine Schierenbeck Department of Biological Sciences San Francisco State University

The Society also would like to recognize and thank Kathy Rindlaub, Chairperson of the Organizing Committee, and the many committee members for providing a well organized and successful meeting; John Bleck for hosting a social hour and tour of the UCSB greenhouses; and Walter H. Muller for giving an entertaining and informative keynote address at the banquet. Next year, the meeting will be held at the University of California, Davis.

REVIEWERS OF MANUSCRIPTS

The editors thank all reviewers listed below for their assistance with papers published in volume 32. We are grateful for their generous contributions of time and effort toward maintaining the quality of papers published in MADROÑO.

Wayne Armstrong
Daniel I. Axelrod
H. G. Baker
Mary E. Barkworth
James Bartel
Derek Burch
Judith M. Canne
Kenton L. Chambers
Susan G. Conard
Lincoln Constance
William B. Critchfield
Robert W. Cruden
Alva G. Day
W. J. Ferlatte
Amy Jean Gilmartin
James R. Griffin
Lawrence R. Heckard
Douglass Henderson
James Henrickson
James Hickman
John T. Howell
Duncan Isely
Dale Johnson
Jon E. Keeley
Sterling Keeley
Robert W. Lichvar
John Little
Jack Maze
Elizabeth McClintock
Steven P. McLaughlin
John McNeill
Robert J. Meinke
Richard A. Minnich
Reid Moran
Arthur M. Phillips
Donald J. Pinkava
Duncan M. Porter
Barry A. Prigge
J. Rzedowski
Clark Schaack
Rob Schlesing
James R. Shevock
James P. Smith
Richard Spellenberg
John L. Strother
Ronald J. Taylor
Robert F. Thorne
Frank C. Vasek
William A. Weber
Grady L. Webster
Dieter H. Wilken

EDITORS' REPORT FOR VOLUME 32

This annual report provides an opportunity for the editors to communicate the status of manuscripts received for publication in MADROÑO and to comment on other aspects of the journal. Between 1 Jul 1984 and 30 Jun 1985, 86 manuscripts were received (34 articles, 12 notes, and 40 individual noteworthy collections). This total includes manuscripts received by the previous editor and the new editors. The current status of all unpublished manuscripts, including those received after 30 Jun 1985, is 33 in review (7, 3, 23), 7 in revision (7, 0, 0), 14 awaiting decision by the editors (9, 3, 2), and 19 accepted (8, 1, 10). There are three unpublished book reviews. Volume 32 included 83 published manuscripts (22, 7, 54) and 7 reviews, totaling 283 pages plus an index. The period between submittal and publication has averaged about one year.

The past year has included the transition between editors, and hence also has been a period of readjustment of review and publication schedules. The new editors apologize for the lateness of some communications with authors and for the slowness of the review process during the past few months. We expect the editorial process to improve with volume 33 and look forward to working with the present and future contributors. We thank the authors for their patience during this early period of our editorships and are grateful for the guidance provided by the Executive Council.

We give special thanks to the former editor, Dr. Christopher Davidson, Director of the Idaho Botanical Garden, for his kind and helpful assistance during the transition period. On behalf of the Society, we express sincere appreciation for the professional guidance of the journal during his 4½ years as editor. The many important papers and notes published during his editorship illustrate the strength of MADROÑO and the contribution Chris has made. We shall strive to continue this record of excellence and to expand the coverage and readership of MADROÑO.

We also take this opportunity to encourage members of the Society to submit well-written manuscripts for review and for potential publication in MADROÑO. The strength of our journal depends on the quality and quantity of papers submitted by members. In addition to the various papers published traditionally in MADROÑO, the editors welcome manuscripts on other topics such as marine phycology and bryology. We also welcome all suggestions from authors and other members to help us maintain or improve the status of MADROÑO as an important botanical journal.

W.R.F. and J.R.H. 30 Oct 1985

Dates of publication of MADROÑO, volume 32

No. 1, pp. 1–63: 15 Feb 1985
No. 2, pp. 65–130: 26 Apr 1985
No. 3, pp. 131–195: 19 Aug 1985
No. 4, pp. 197–289: 20 Dec 1985

INDEX TO VOLUME 32

Classified entries: major subjects, key words, and results; botanical names and plant families (new names are in **boldface**); geographical areas; reviews. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, state, or country. Authors and titles are listed alphabetically in the Table of Contents.

Madroño, Vol. 32, No. 4, pp. 284–288, 20 December 1985

CALIFORNIA BOTANICAL SOCIETY

MEETING PROGRAM FOR 1985–1986

8:00 PM University of California, Berkeley LSB 4093

DATE	SPEAKER & TOPIC
SEP 19	Deborah LeTourneau, University of California, Santa Cruz Mutualism in a tropical rainforest.
OCT 17	Don Santana, Gavilan College Studies in North American *Fritillaria.*
NOV 21	Pam Matson, NASA, Ames Disturbance effects on nutrient cycling in forest ecosystems.
JAN 16	Howard Wilshire, USGS, Menlo Park Residual impacts of World War II armored maneuvers in California's deserts.
*FEB 22	Prof. Joseph Ewan, Tulane University What happened beside the Golden Gate? Was it imitation or innovation? * ANNUAL BANQUET—Location to be announced.
MAR 20	Steve Botti, NPS, Yosemite Rare and endangered flora of Yosemite.
APR 17	Thomas Fuller, Sacramento, CA Plants and livestock poisoning.
MAY 15	Paul Zinke, University of California, Berkeley Analytical variation of foliage in relation to soils.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XXXII
1985

Published quarterly by the
California Botanical Society, Inc.
Life Sciences Building, University of California, Berkeley 94720

Printed by Allen Press, Inc., Lawrence, KS 66044

To Rimo Bacigalupi, "Ba[t]ch," first Curator of the Jepson Herbarium and Library (1950–1968) for his lifelong devotion to Nature and The Arts, for his extraordinary knowledge of the California flora that he generously shared with colleagues and successive generations of students, for his helpfulness as a linguist and botanical Latinist, for his warm personality, and for his civilizing influence, volume 32 is affectionately dedicated. Photo taken in 1959 by Marion Cave.

TABLE OF CONTENTS

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

ME 33, NUMBER 1 JANUARY 1986

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Science, San Francisco, CA 94118.

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928

First Vice President: RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

Second Vice President: DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403

Recording Secretary: V. THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: CHERIE L. R. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542; the *Editor* of MADROÑO; three elected *Council Members:* JAMES C. HICKMAN, Department of Botany, University of California, Berkeley, CA 94720; THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

MONTANE MEADOW PLANT ASSOCIATIONS OF SEQUOIA NATIONAL PARK, CALIFORNIA

CHARLES B. HALPERN
Department of Botany and Plant Pathology,
Oregon State University, Corvallis 97331

ABSTRACT

Twelve plant associations are recognized and described for montane meadows of Sequoia National Park based on 81 relevés. Three major groups are defined by growth-form dominants: mixed forb and grass associations, *Carex* and *Scirpus* associations, and *Eleocharis* associations. Major environmental factors influencing vegetation distribution include: 1) a complex moisture gradient incorporating water depth and movement, and 2) site exposure and shading. Monitoring of water wells indicates that seasonal fluctuations of the water table are important in structuring the vegetation.

Montane meadows, a common feature of Sequoia National Park in the southern Sierra Nevada of California, punctuate a landscape dominated by mixed conifer forest. Scenic vistas, a rich and colorful flora, proximity to Giant Sequoia groves, and accessibility result in disproportionate public visitation to these sites. Nevertheless, montane meadows in the Park and in the southern Sierra Nevada in general have been poorly described.

Studies of montane meadows and their environmental controls were initiated as part of a comprehensive study of riparian ecosystems and the interactions between terrestrial (forest and meadow) and stream systems in Sequoia National Park. As hydric sites, these montane meadows may be grouped functionally with forest riparian systems. Stream channels, overland flows, and pooled water are common. Plant community physiognomy, composition, and distribution reflect strong seasonal and spatial hydrologic patterns.

Disturbance history and microenvironmental characteristics also influence vegetation composition and structure. It is difficult to assess the degree to which montane meadows in Sequoia National Park are recovering from a history of human and livestock use. Although disturbance currently appears minimal, present-day meadow vegetation may reflect the burning activities of aboriginal man as well as the widespread grazing of sheep and cattle during the late 1800s and early 1900s. The sites studied, however, do not exhibit the characteristics of habitat deterioration (trampling, surface erosion, hummock formation, gullying, and obvious reduction in vegetation cover) reported from many subalpine meadows in the southern Sierra Nevada (Armstrong 1942, Sumner 1941, 1948, Sharsmith 1959, Hubbard et al. 1965, 1966, Harkin and Schultz 1967, Leonard

MADROÑO, Vol. 33, No. 1, pp. 1–23, 27 March 1986

et al. 1967, 1968, Giffen et al. 1969). Whereas these studies are qualitative, subsequent studies by Bennett (1965) and Strand (1972) provide a more quantitative basis for the evaluation of disturbance and subsequent plant succession. DeBenedetti and Parsons (1979a) reviewed the history of human and domestic livestock use of meadows in the southern Sierra Nevada, providing examples of subsequent resource problems and evaluating the effectiveness of management actions.

Natural disturbance in the form of lightning fire may play an infrequent yet important role in subalpine meadows of the southern Sierra Nevada, particularly along the forest-meadow ecotone (DeBenedetti and Parsons 1979b, 1984). Natural fire in montane meadows of Sequoia National Park has not been reported in the literature and its historical role is unknown.

The focus of this paper is the composition and distribution of montane meadow plant communities and their relationship to major environmental features in Sequoia National Park. It provides basic information for managers as well as a baseline for future research. The classification presented complements studies of subalpine meadows in the southern Sierra Nevada and in Sequoia National Park in particular (Sumner 1941, Sharsmith 1959, Bennett 1965, Harkin and Schultz 1967, Strand 1972, Ratliff 1979, 1982, Benedict and Major 1982, Benedict 1981, 1983).

STUDY AREA

Meadows examined were located in the mixed conifer forest zone of Sequoia National Park (Rundel et al. 1977) between 1493 and 2390 m elevation (Fig. 1). Sample plots were concentrated in the Giant Forest area and included Log, Crescent, Circle, Huckleberry, and Round Meadows and Vasey's Paradise; Long, Cahoon, Cabin, and Halstead Meadows were sampled outside the *Sequoiadendron* groves. Ten unnamed meadows were sampled and two additional sites were included from Kings Canyon National Park.

Forest composition surrounding meadow sites varies. *Pinus ponderosa, P. lambertiana, Abies concolor, A. magnifica* var. *shastensis, Calocedrus decurrens,* and *Sequoiadendron giganteum* are the most common tree species within the closed canopy forests. Understory dominants include *Chrysolepis sempervirens, Ceanothus cordulatus,* and *Pteridium aquilinum.* A variety of herbs comprise only minimal cover in the ground layer. Forest-meadow ecotones are abrupt both in vegetation and environment; tree encroachment is minimal.

Long-term climatic records are available for the Giant Forest (elevation 1966 m) (Parsons and DeBenedetti 1979). The regional climate is Mediterranean with warm, relatively dry summers and cool wet winters. Hydric montane meadows, however, are less in-

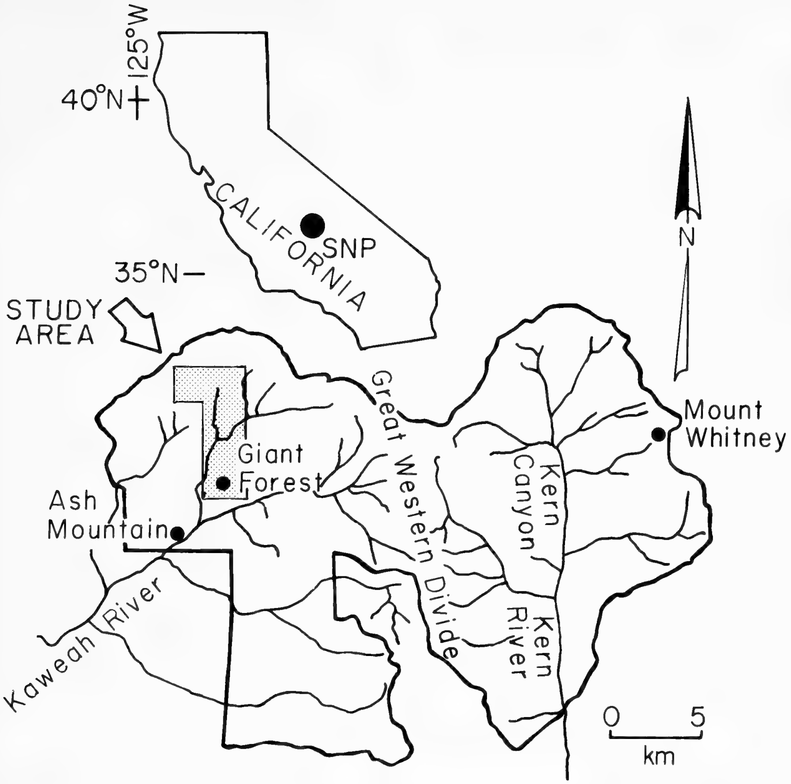


FIG. 1. Location of the study area in Sequoia National Park, California.

fluenced by regional climate than are surrounding forests, as they receive surface as well as sub-surface water throughout the growing season. Although average annual precipitation is 113 cm, June through September averages less than 3 cm (Rundel 1972); most precipitation occurs from December to March as snow. Mean annual snowfall at the Giant Forest exceeds 500 cm and depths of greater than 2 m are common in mid-winter. The average date when mountain basins are free of snow is May 20 (Wood 1975). Average minimum temperatures range from −6.7°C in February to 11.8°C in August. Average maximum temperatures range from 3.4°C in December and January to 27.4°C in August (Parsons and DeBenedetti 1979).

METHODS

Vegetation sampling. Field sampling was conducted during September 1982 using a modification of the reconnaissance method of

Franklin et al. (1970). A total of 81 plots in 20 meadows was sampled. Each plot was located subjectively in an area of visually homogeneous vegetation and habitat. Although the shape varied to accommodate vegetation patterns, plots were most often circular and located within larger areas of similar vegetation to minimize edge effects. Sample plot areas were 250–500 m^2; homogeneous units smaller than this were not sampled. Areas of recent natural or man-caused disturbance as well as areas that lacked visually uniform topographic or hydrologic features also were avoided. For each plot visual estimates of projected crown cover were recorded for each vascular plant species. Cover estimates also were made of the various substrate types (bedrock, loose rock, mineral soil, coarse and fine litter, and moss). Environmental features such as elevation, slope, aspect, landform, topography, and hydrologic characteristics also were recorded. Field notes included descriptions of the following: 1) sample plot species composition and physiognomy, 2) hydrologic regime, 3) neighboring vegetation, 4) surrounding forest vegetation, and 5) apparent forest-meadow ecotone changes (seedling and sapling encroachment, meadow expansion, or forest to meadow treefall). Voucher specimens of unidentified species were collected for identification and incorporation into the Oregon State University Herbarium (OSC). Nomenclature of vascular plants follows Munz (1959, 1968). Nomenclature of mosses follows Lawton (1971).

Vegetation analysis. Vegetation data were analyzed using two complementary approaches: cluster analysis and ordination analysis. Cluster analysis utilized indicator species analysis (Hill et al. 1975) using the computer program TWINSPAN (Hill 1979a) and manual table sorting techniques (Mueller-Dombois and Ellenberg 1974, Westhoff and van der Maarel 1978). Ordination analysis utilized correspondence analysis (Hill 1973, 1974) as implemented by the program DECORANA (Hill 1979b, Hill and Gauch 1980). Both TWINSPAN and DECORANA are part of the Cornell Ecology Program Series; other programs were developed at Oregon State University (B. G. Smith, unpublished programs).

TWINSPAN is a hierarchical, polythetic, divisive classification technique that uses reciprocal averaging (RA) to produce a classification of samples and species based on differential species. DECORANA is an eigenvector ordination technique derived from reciprocal averaging that attempts to correct two problems of RA—an arch distortion effect and a compression of the axis ends relative to the axis middle (Gauch 1982). An octave transformation of species cover values was performed to compress the range of abundance. The octave scale is logarithmic (base 2) and the transformation prevents the few very abundant species from dominating the analysis.

Montane meadow plant associations were delineated based upon the correspondence of TWINSPAN clusters with manual table sorting results. Ten of the initial 81 samples were ecotonal or outlier stands and could not be assigned successfully to a recognizable association. Because only one sample was available for each, designation at the association level was not justified. Subsequently, the ecotonal and outlier samples were excluded from DECORANA ordination analysis. Associations were plotted on ordination axes and a final classification was developed based upon subjective consideration of group homogeneity with field observations.

Water table sampling. To assess seasonal water table fluctuations in a variety of vegetation types, 16 permanent perforated PVC pipe water wells (15 cm diameter) were established along a transect line perpendicular to the long axes of Log and Crescent Meadows, Giant Forest. Wells were placed subjectively in homogeneous vegetation representing selected plant associations. A meter stick was lowered to the water surface to establish depth from ground level. Biweekly measurements of water table depth were taken from 6 July through 8 November 1983.

RESULTS AND DISCUSSION

Floristic Analysis

A total of 116 vascular plant species and 6 bryophyte genera were identified within the montane meadow sample plots of Sequoia National Park. The vascular flora included 38 families and 77 genera. The 10 families with the greatest number of species are presented in Table 1. The Gramineae had the largest number of genera (14) and species (18). The Cyperaceae was represented by 3 genera and 17 species, and the Compositae by 9 genera and 12 species. Canopy cover of the Cyperaceae, however, dominates these meadows due to the prominence of *Carex, Scirpus,* and *Eleocharis* species. Species with the greatest frequency of occurrence in the samples (constancy) are listed in Table 2. *Oxypolis occidentalis* (Umbelliferae) is nearly ubiquitous, with 78% constancy and 25% characteristic cover (average cover for only those plots in which the species occurs) (Pakarinen 1984). Other important species include *Scirpus microcarpus, Glyceria elata, Eleocharis montevidensis,* and *Carex rostrata,* with constancies of 47 to 60% and characteristic covers of 13 to 20%. Species such as *Athyrium filix-femina, Carex amplifolia,* and *Vaccinium occidentale* are relatively uncommon, but are diagnostic of particular plant associations, and often dominate cover therein.

Vegetation Analysis

Twelve plant associations and one phase are recognized from the montane meadows of Sequoia National Park. These are grouped

TABLE 1. TEN VASCULAR PLANT FAMILIES WITH THE GREATEST NUMBER OF SPECIES.

Family	Genera	Species
Gramineae	14	18
Cyperaceae	3	17
Compositae	9	12
Scrophulariaceae	4	6
Juncaceae	2	5
Liliaceae	4	4
Salicaceae	1	4
Orchidaceae	3	3
Umbelliferae	3	3
Polygonaceae	2	3

into three broad types based on growth-form dominants (Table 3): mixed forb and grass associations, *Carex* and *Scirpus* associations, and *Eleocharis* associations. The association concept used herein refers to a recurring assemblage of plant species with visually homogeneous composition and physiognomy representing a modal position in the pattern of vegetation, and, possibly, environment. Association names reflect the diagnostic and often dominant species. Phase names represent recognizable variation in an association attributed to the presence of one or more species.

Species constancy and characteristic cover are compared between plant associations in Tables 4–6. Only species exceeding 49% constancy in at least one association have been included for ease in interpretation. Stand tables containing constancy and characteristic cover statistics for all sample plots within an association are available from the author. Within the following descriptions of associations, "channeled flows" refers to perennial stream courses, "overland flows" refers to unrestricted, generally seasonal runoff across meadow surfaces, "pooled and standing water" refers to relatively still water above the soil surface, and "stagnant water" refers to water not subject to movement at or above the soil surface.

A. MIXED FORB AND GRASS TYPES. Six plant associations comprise the Mixed Forb and Grass Types. A mixture of herbaceous perennials or grass species, or both, dominate these sites, although *Scirpus microcarpus* is occasionally abundant (Table 4). Typically, the Mixed Forb and Grass Types occur in the drier portions of montane meadows.

1. *Glyceria elata–Lotus oblongifolius* Association. This is an herb-rich association with a mosaic appearance. Local dominance of individual species within the mosaic is not accompanied by observable differences in microenvironment; the patterning is likely the result

TABLE 2. TWENTY MOST COMMON MONTANE MEADOW SPECIES, RANKED BY CONSTANCY. [1]Growth-form key: K = herb, G = grass, and S = sedge or rush. [2]Characteristic cover represents the average cover for only those samples in which the species occurs.

Species	Growth-form[1]	Constancy (%)	Characteristic cover (%)[2]
Oxypolis occidentalis	H	77.8	25.2
Glyceria elata	G	60.5	7.3
Scirpus microcarpus	S	55.6	20.0
Lotus oblongifolius	H	55.6	3.5
Eleocharis montevidensis	S	53.1	16.5
Veratrum californicum	H	50.6	21.7
Carex rostrata	S	46.9	13.7
Dodecatheon jeffreyi	H	45.7	5.2
Epilobium exaltatum	H	44.4	0.5
Stachys albens	H	44.4	4.7
Polygonum bistortoides	H	42.0	1.3
Carex nebrascensis	S	38.3	7.9
Juncus oxymeris	S	34.6	2.9
Senecio triangularis	H	32.1	3.3
Habenaria dilatata	H	32.1	0.2
Deschampsia caespitosa	G	29.6	2.6
Perideridia parishii	H	29.6	1.7
Cinna latifolia	G	29.6	0.8
Agrostis scabra	G	27.2	1.9
Castilleja miniata	H	27.2	0.7

TABLE 3. MONTANE MEADOW PLANT ASSOCIATIONS OF SEQUOIA NATIONAL PARK. Association acronyms are indicated in parentheses.

Mixed Forb and Grass Types

1. *Glyceria elata–Lotus oblongifolius* Association (GLEL–LOOB)
2. *Elymus glaucus–Heracleum lanatum* Association (ELGL–HELA)
3. *Agrostis scabra* Association (AGSC)
4. *Glyceria elata–Scirpus microcarpus* Association (GLEL–SCMI)
5. *Calamagrostis canadensis–Scirpus microcarpus* Association (CACA–SCMI)
6. *Athyrium filix-femina* Association (ATFI)

Carex and *Scirpus* Types

7. *Scirpus microcarpus–Oxypolis occidentalis* Association (SCMI–OXOC)
8. *Carex amplifolia–Oxypolis occidentalis* Association (CAAM–OXOC)
9. *Carex nebrascensis–Oxypolis occidentalis* Association (CANE–OXOC)
10. *Carex rostrata* Association (CARO2)

Eleocharis Types

11a. *Eleocharis montevidensis–Oxypolis occidentalis* Association,
Eleocharis montevidensis Phase (ELMO–OXOC–ELMO Phase)
11b. *Eleocharis montevidensis–Oxypolis occidentalis* Association,
Carex rostrata Phase (ELMO–OXOC–CARO2 Phase)
12. *Eleocharis montevidensis*–Moss Association (ELMO–MOSS)

TABLE 4. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE MIXED FORB AND GRASS TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%), [3]COV = average cover (%) based only on those samples in which species occurs.

Plant association[1]:	GLEL–LOOB		ELGL–HELA		AGSC		GLEL–SCMI		CACA–SCMI		ATFI	
Number of plots per type:	4		5		3		6		4		5	
Mean number of species per plot (s.d.):	25.0 (6.4)		13.4 (5.3)		20.7 (2.9)		14.0 (2.7)		10.5 (5.7)		19.6 (2.2)	
	CON[2]	COV[3]	CON	COV	CON	COV	CON	COV	CON	COV	CON	COV
Herb species												
Pteridium aquilinum	75	3	—	—	—	—	—	—	—	—	20	T
Botrychium multifidum	75	1	—	—	—	—	—	—	—	—	20	2
Senecio clarkianus	100	5	40	2	67	1	67	5	50	6	—	—
Solidago canadensis	75	31	100	13	67	14	50	23	75	3	—	—
Castilleja miniata	100	4	40	2	33	1	17	2	—	—	60	1
Lotus oblongifolius	100	12	20	2	67	9	33	1	—	—	60	2
Sidalcea ranunculacea	75	12	20	1	100	4	17	1	25	2	40	1
Heracleum lanatum	—	—	100	19	—	—	50	2	25	T	20	T
Veratrum californicum	100	6	40	1	100	1	67	11	75	14	60	3
Stachys albens	75	8	100	10	100	13	100	19	50	23	80	5
Senecio triangularis	75	10	80	26	33	1	50	6	—	—	100	22
Epilobium exaltatum	50	2	60	2	100	1	83	1	50	1	60	1
Viola glabella	75	1	—	—	—	—	33	1	25	2	60	9
Lupinus latifolius	50	3	40	2	33	2	—	—	25	T	80	4
Oxypolis occidentalis	75	2	—	—	67	5	17	8	50	3	100	13
Habenaria dilatata	75	1	—	—	—	—	17	1	25	T	100	2
Mimulus guttatus	—	—	20	3	33	T	50	7	—	—	60	1
Athyrium filix-femina	25	T	20	1	—	—	17	1	—	—	100	72
Grass species												
Elymus glaucus subsp. *jepsonii*	100	3	—	—	67	T	—	—	—	—	—	—
Elymus glaucus subsp. *glaucus*	75	2	100	47	33	5	67	3	50	1	—	—
Phleum pratense	75	3	—	—	100	20	50	1	25	1	—	—

TABLE 4. CONTINUED.

Plant association[1]:	GLEL–LOOB		ELGL–HELA		AGSC		GLEL–SCMI		CACA–SCMI		ATFI	
Number of plots per type:	4		5		3		6		4		5	
Mean number of species per plot (s.d.):	25.0 (6.4)		13.4 (5.3)		20.7 (2.9)		14.0 (2.7)		10.5 (5.7)		19.6 (2.2)	
	CON[2]	COV[3]	CON	COV	CON	COV	CON	COV	CON	COV	CON	COV
Agrostis scabra	50	3	40	1	100	43	67	2	25	7	—	—
Poa pratensis	—	—	—	—	67	2	17	1	—	—	—	—
Calamagrostis canadensis	25	T	60	27	—	—	—	—	100	55	—	—
Glyceria elata	100	5	80	5	100	2	100	49	100	15	100	16
Cinna latifolia	25	5	40	2	—	—	50	1	—	—	100	5
Sedge and rush species												
Juncus oxymeris	50	9	—	—	67	1	17	10	—	—	—	—
Carex leporinella	25	7	20	3	67	46	17	1	—	—	60	2
Scirpus microcarpus	25	2	60	7	100	2	83	66	100	51	60	26
Carex feta	—	—	—	—	67	1	17	T	—	—	20	T

of initial establishment and vegetative spread of rhizomatous perennial forbs. Species of greatest constancy and cover include *Lotus oblongifolius, Senecio clarkianus, Castilleja miniata, Solidago canadensis,* and *Glyceria elata.* Species of Cyperaceae occur occasionally, but are more common on wetter sites. This association is common along meadow edges and on elevated flats in the driest portions of montane meadows.

2. *Elymus glaucus–Heracleum lanatum* Association. This association is characterized by a dominance of *Elymus glaucus* and a host of perennial forbs, including *Heracleum lanatum, Solidago canadensis, Stachys albens,* and *Senecio triangularis.* Floristic composition is similar to the *Glyceria elata–Lotus oblongifolius* Association, but dominance has shifted to grasses. This association occurs along montane meadow edges and on elevated flats where the water table falls well below the soil surface throughout the growing season.

3. *Agrostis scabra* Association. This association is limited to small areas in several montane meadows. It resembles the two mixed forb and grass associations described previously, but also has abundant *Agrostis scabra. Phleum pratense* is a common grass associate, whereas *Stachys albens, Solidago canadensis,* and *Lotus oblongifolius* are common herbs. This association is restricted to drier, convex landforms that have a relatively deep water table. The abundance of *Agrostis scabra* and *Phleum pratense* suggest previous disturbance on these sites.

4. *Glyceria elata–Scirpus microcarpus* Association. *Glyceria elata* reaches its peak abundance within this association, and *Scirpus microcarpus* is a codominant. *Stachys albens* is a consistent associate and *Solidago canadensis* and *Veratrum californicum* are locally common. These sites typically exhibit channeled or overland water flows.

5. *Calamagrostis canadensis–Scirpus microcarpus* Association. *Calamagrostis canadensis* and *Scirpus microcarpus* exceed 100% total canopy cover in this species-poor association. *Glyceria elata* is the only other species with 100% constancy. This association commonly occurs near meadow edges on moist to saturated sites adjacent to channeled or overland flows.

6. *Athyrium filix-femina* Association. A nearly complete upper canopy of the fern *Athyrium filix-femina* characterizes this association. *Senecio triangularis* and *Oxypolis occidentalis* are common, as are the grasses *Glyceria elata* and *Cinna latifolia.* This association is restricted to narrow, cool, and shaded meadows that are commonly the smaller basin swales in which forest canopy shading is important. It also can occur in modified form as streamside vegetation where forest canopies are relatively dense. These sites typically have saturated soils, and seeps are common.

B. *CAREX* AND *SCIRPUS* TYPES. Four plant associations comprise the *Carex* and *Scirpus* Types. Sites are typically dominated by *Scirpus microcarpus,* or coarse-leaved species of *Carex,* or both (Table 5). Species richness is generally low. These associations occupy areas with pooled, channeled, or overland flows.

7. *Scirpus microcarpus–Oxypolis occidentalis* Association. Height and density of the vegetation suggest that this type has the highest standing crop of any montane meadow type. *Scirpus microcarpus* reaches greatest abundance in this association; *Oxypolis occidentalis* is an important codominant; and *Athyrium filix-femina, Stachys albens, Mimulus guttatus,* and *Equisetum arvense* are frequent associates. This vegetation type is widespread, usually occurring along stream channels and within areas of overland flow where the water table remains at or above the soil surface throughout the growing season.

8. *Carex amplifolia–Oxypolis occidentalis* Association. This association is restricted to small, shaded, swale meadows similar to those supporting the *Athyrium filix-femina* Association. *Carex amplifolia* dominates these sites and *Oxypolis occidentalis* is of secondary importance. Common associates include *Glyceria elata, Cinna latifolia, Athyrium filix-femina, Mimulus guttatus,* and *Cardamine breweri.* Soils typically are saturated throughout the growing season.

9. *Carex nebrascensis–Oxypolis occidentalis* Association. *Carex nebrascensis* reaches peak abundance in this association, whereas *Oxypolis occidentalis, Carex rostrata,* and *Eleocharis montevidensis* are codominant species. This vegetation type is related compositionally and structurally to the *Eleocharis montevidensis–Oxypolis occidentalis* type. Habitats typically are flat to gently sloping; pooled to slightly-flowing water is present throughout the growing season.

10. *Carex rostrata* Association. This association occurs under a variety of topographic and hydrologic regimes. Under deeply-pooled water, pure stands of *Carex rostrata* develop. On sloping sites or under conditions of decreased water tables, *C. rostrata* abundance and vigor decrease and species diversity increases. The common associated herbs include *Dodecatheon jeffreyi, Polygonum bistortoides, Oxypolis occidentalis,* and *Perideridia parishii.* Moss can be locally abundant.

C. *ELEOCHARIS* TYPES. Two plant associations and one phase comprise the *Eleocharis* Types. Typically, sites are dominated by the fine-stemmed spike-rush, *Eleocharis montevidensis* (Table 6). Standing or nearly stagnant water at or above the soil surface is characteristic of these communities.

11a. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Eleocharis montevidensis* Phase. This association resembles the *Carex nebrascensis–Oxypolis occidentalis* Association; however, *Carex*

TABLE 5. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE *Carex* AND *Scirpus* TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%). [3]COV = average cover (%) based only on those samples in which species occurs.

Plant association[1]:	SCMI–OXOC		CAAM–OXOC		CANE–OXOC		CARO2	
Number of plots per type:	7		2		10		5	
Mean number of species per plot (s.d.):	17.6 (4.7)		15.0 (1.4)		11.6 (4.9)		10.6 (6.5)	
	CON[2]	COV[3]	CON	COV	CON	COV	CON	COV
Herb species								
Lupinus latifolius	71	2	—	—	—	—	—	—
Senecio triangularis	71	1	50	T	—	—	—	—
Mimulus guttatus	71	4	100	9	—	—	—	—
Cardamine breweri	43	1	100	3	—	—	—	—
Athyrium filix-femina	86	5	100	5	10	T	—	—
Stachys albens	71	16	100	2	10	T	—	—
Viola glabella	57	1	—	—	—	—	20	5
Lilium kelleyanum	57	T	—	—	20	T	20	T
Veratrum californicum	57	3	50	15	40	4	20	1
Epilobium exaltatum	57	1	100	2	20	1	40	3
Lotus oblongifolius	71	2	50	3	40	2	40	9
Equisetum arvense	57	17	—	—	70	3	—	—
Oxypolis occidentalis	100	47	100	33	90	66	60	7
Polygonum bistortoides	14	T	—	—	70	2	60	10
Dodecatheon jeffreyi	14	3	—	—	40	4	60	22
Perideridia parishii	—	—	—	—	10	T	60	7
Grass species								
Cinna latifolia	86	3	100	2	10	1	—	—
Glyceria elata	100	7	100	7	40	4	20	T
Deschampsia caespitosa	14	1	—	—	30	T	60	6

TABLE 5. CONTINUED.

Plant association[1]:	SCMI–OXOC		CAAM–OXOC		CANE–OXOC		CARO2	
Number of plots per type:	7		2		10		5	
Mean number of species per plot (s.d.):	17.6 (4.7)		15.0 (1.4)		11.6 (4.9)		10.6 (6.5)	
	CON[2]	COV[3]	CON	COV	CON	COV	CON	COV
Sedge and rush species								
Carex amplifolia	14	7	100	83	—	—	—	—
Scirpus microcarpus	100	79	—	—	50	30	40	5
Eleocharis montevidensis	29	2	100	4	90	20	60	6
Carex nebrascensis	14	2	—	—	100	42	40	9
Carex rostrata	29	3	—	—	90	25	100	79

TABLE 6. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE *Eleocharis* TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%). [3]COV = average cover (%) based only on those samples in which species occurs.

Plant association[1]:	ELMO–OXOC CARO2 PHASE		ELMO–OXOC ELMO PHASE		ELMO–MOSS	
Number of plots per type:	2		5		13	
Mean number of species per plot (s.d.):	16.0 (11.3)		16.6 (6.8)		19.1 (4.8)	
	CON[2]	COV[3]	CON	COV	CON	COV
Shrub species						
Vaccinium occidentale	—	—	—	—	54	15
Herb species						
Habenaria dilatata	—	—	60	1	15	T
Veratrum californicum	50	1	60	1	15	T
Lotus oblongifolius	100	13	60	5	69	3
Oxypolis occidentalis	100	41	100	62	100	17
Dodecatheon jeffreyi	100	15	60	7	100	15
Camassia leichtlinii	50	3	60	T	69	1
Perideridia parishii	50	T	40	3	92	8
Polygonum bistortoides	—	—	60	T	69	3
Hypericum anagalloides	—	—	20	7	54	9
Spiranthes romanzoffiana	—	—	20	T	62	1
Mimulus primuloides	—	—	—	—	69	21
Aster alpigenus	—	—	—	—	85	5
Grass species						
Glyceria elata	50	1	60	2	8	T
Deschampsia caespitosa	50	1	—	—	62	8
Muhlenbergia filiformis	—	—	—	—	69	8
Sedge and rush species						
Scirpus microcarpus	100	8	60	19	15	23
Carex rostrata	100	45	60	2	69	15
Juncus oxymeris	100	5	80	2	77	17
Eleocharis montevidensis	100	63	100	66	100	46
Carex nebrascensis	—	—	60	5	62	15
Carex ormantha	—	—	—	—	69	9
Bryophyte species						
Sphagnum/Philonotis/Aulacomnium	50	4	60	13	92	64

is less important and *Eleocharis* assumes dominance. Although species richness can be high, few species have constancies greater than 60%. The physiognomy is two-layered, having a tall *Oxypolis* overstory and an open *Eleocharis* understory. Water remains at or slightly above the soil surface throughout the growing season.

11b. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Carex rostrata* Phase. This uncommon phase occurs on habitats with slightly higher standing or flowing water regimes than the typical community. The physiognomy is similarly two-layered, but the understory is denser due to the abundance of *Carex rostrata. Eleocharis montevidensis* and *Oxypolis occidentalis* are dominant, and *Dodecatheon jeffreyi* and *Lotus oblongifolius* are common herbs.

12. *Eleocharis montevidensis*–Moss Association. This association is characterized by 1) a moss mat composed primarily of *Sphagnum, Philonotis,* and *Aulacomnium,* occurring singly or in combination; 2) an abundance of *Eleocharis*; and 3) a characteristic mosaic of mat-forming vascular species such as *Aster alpigenus, Hypericum anagalloides, Mimulus primuloides,* and *Muhlenbergia filiformis. Juncus oxymeris* and *Perideridia parishii* are taller diagnostic associates. The average cover of moss is 60%. Standing to stagnant surface water typifies level sites whereas surface seeps typify sloping sites.

Relation to Other Sierra Nevada and Cascade Meadows

Several meadow associations of Sequoia National Park are similar structurally and, in certain instances, floristically to montane meadows found elsewhere in the Sierra Nevada and in the Cascade Range of Oregon.

The physiognomy and floristic character of the *Eleocharis montevidensis*–Moss Association tie it to many montane mire systems throughout the Sierra Nevada and the Oregon Cascade Range. The complex of matted-boggy species with a taller, open *Eleocharis* layer is characteristic. *Eleocharis pauciflora* is the diagnostic counterpart in the montane zone of the Cascade Range and in the subalpine zone of the southern Sierra Nevada. Within the Sierra, Benedict (1981, 1983) describes an *Eleocharis pauciflora* Association and an *Eleocharis pauciflora–Mimulus primuloides* variant from the Rock Creek and Whitney Creek drainages of Sequoia National Park. Similarly, Ratliff (1979, 1982) defines an *Eleocharis pauciflora* type (few-flowered spike-rush/Site Class H) within the subalpine zone of Yosemite, Sequoia, and Kings Canyon National Parks, and the Stanislaus, Sierra, and Sequoia National Forests. In the Western Cascades of Oregon, Hickman (1976) alludes to a phase of his Bog Association that may have a similar assemblage of low-growing herbs. Halpern et al. (1984) describe similar vegetation, defined as the *Eleocharis pauciflora* community type, within the Three Sisters Wilderness Area, Oregon. An *Eleocharis pauciflora*/bryophyte community at Sphagnum Bog, Crater Lake National Park, Oregon (very similar in composition and physiognomy to that in Sequoia National Park), is described by Seyer (1979). At Multorpor Fen, Mt. Hood National

Forest, Oregon, Seyer (1983) also describes an *Eleocharis*/herbs/*Aulacomnium–Sphagnum* community, which is a similar low stature, moss-mat community with permanently saturated soils. Campbell (1973) describes an *Eleocharis–Aulacomnium* community at Hunts Cove, Mt. Jefferson, Oregon, within a larger *Carex scopulorum* meadow complex.

The *Carex nebrascensis–Oxypolis occidentalis* and the *Carex rostrata* Associations, typical of standing to slightly flowing water regimes in montane meadows of Sequoia National Park, have analogues elsewhere. Ratliff (1979, 1982) describes a Nebraska sedge class (Site Class G) common on nearly level, imperfectly to moderately well-drained, subalpine sites in the southern Sierra Nevada. *Carex nebrascensis*- and *Carex rostrata*-dominated vegetation is described from Grass Lake, California, by Beguin and Major (1975). Benedict (1981, 1983) describes a subalpine *Carex rostrata–Mimulus primuloides* Association from the Whitney and Rock Creek drainages of Sequoia National Park. It appears similar to the herb-rich variant of the montane *Carex rostrata* association of the Park, occurring on sites with depressed water tables. Ratliff (1979, 1982) describes a *Carex rostrata* type (beaked sedge/Site Class A) occupying poorly and imperfectly drained sites. *Carex rostrata* assemblages are also important in many hydric montane meadows throughout the Oregon Cascade Range. Campbell (1973) describes a *Carex rostrata–Sphagnum* community at Hunts Cove, Mt. Jefferson, Oregon. *Carex rostrata*-dominated reedswamps at Sphagnum Bog, Crater Lake National Park, and Gold Lake Bog near Willamette Pass, Oregon, have been described by Seyer (1979). A *Carex rostrata* community with *C. sitchensis* has been reported for Big Springs near Nash Crater, Oregon (Roach 1958). Frenkel (pers. comm.) identifies similar reedswamp vegetation at Torrey Lake Mire, Oregon. Comparable assemblages are scattered throughout the Three Sisters Wilderness Area, Oregon, under standing to slightly flowing water conditions.

Several associations of the Mixed Forb and Grass Types within the montane meadows of Sequoia National Park contain herb species common to meadows of the Sierra Nevada and Oregon Cascade Range. The particular compositions and physiognomies of these assemblages, however, may be specific to the Park. This uncertainty reflects the paucity of reports of similar associations in the montane and subalpine meadow literature. Similarly, basin swale communities dominated by *Athyrium filix-femina* may represent a rather unique aspect of montane meadows in Sequoia National Park. Although the fern is common in coastal forested swamps in Oregon and Washington (Franklin and Dyrness 1973) and along mountain streams in the Cascade Range and Sierra Nevada, extensive meadow swards have not been described outside of Sequoia National Park.

The prominence of *Oxypolis occidentalis* is perhaps the most unique floristic aspect of the montane meadows of Sequoia National Park. A tall, leafy umbel of marshy meadows and shallow water, *Oxypolis* ranges from Tulare Co. to Eldorado Co. in the Sierra Nevada, and north to Crater Lake in Oregon (Jepson 1936). It has been reported as a fairly common component of only two geographically limited hydric communities in the subalpine of the southern Sierra Nevada and at Crater Lake National Park (Ratliff 1979, Seyer 1979). In contrast, in montane meadows of Sequoia National Park, *Oxypolis* occurs in 11 of 12 associations and dominates in nearly half of these. In most cordilleran wet meadows, graminoids are the sole dominants, but in similar communities in Sequoia National Park, *Oxypolis occidentalis* plays a significant role as a codominant.

Detrended Correspondence Analysis

The results of the detrended correspondence analysis are useful in describing vegetation patterns and inferring complex environmental gradients (Fig. 2). The overlay of TWINSPAN groups on the ordination reveals the spatial relationship between associations within the two dimensional compositional space portrayed. Interpretation of these axes as environmental gradients is possible if we consider stand compositions, species autecology, and environmental information.

DCA ordination yielded the four eigenvalues of 0.63, 0.31, 0.19, and 0.16, which suggest that only the first two axes are important. The first eigenvector, or axis of the ordination, is 4.6 standard deviation units long, representing a moderate turnover in species composition within samples along that gradient (Gauch 1982). Field observations suggest this axis represents a complex moisture gradient that incorporates water table depth and water movement. The driest representatives of this gradient (toward the left end of Axis 1) are the *Elymus glaucus–Heracleum lanatum, Glyceria elata–Lotus oblongifolius,* and *Agrostis scabra* Associations. They typify sites with seasonal lowering of the sub-surface water table. Located more centrally along Axis 1 is vegetation that typifies channeled or flowing water sites—the *Scirpus microcarpus–Oxypolis occidentalis* Association is a representative. To the right of these are associations that exhibit shallow to deep and standing to slightly flowing water throughout the growing season. Included are both phases of the *Eleocharis montevidensis–Oxypolis occidentalis* Association, the *Carex rostrata* Association, and the *Carex nebrascensis–Oxypolis occidentalis* Association. To the extreme right lies the *Eleocharis montevidensis*–Moss Association typical of sites with persistent, standing to stagnant, surface water.

The second DCA axis is not as easily interpreted as the first. The

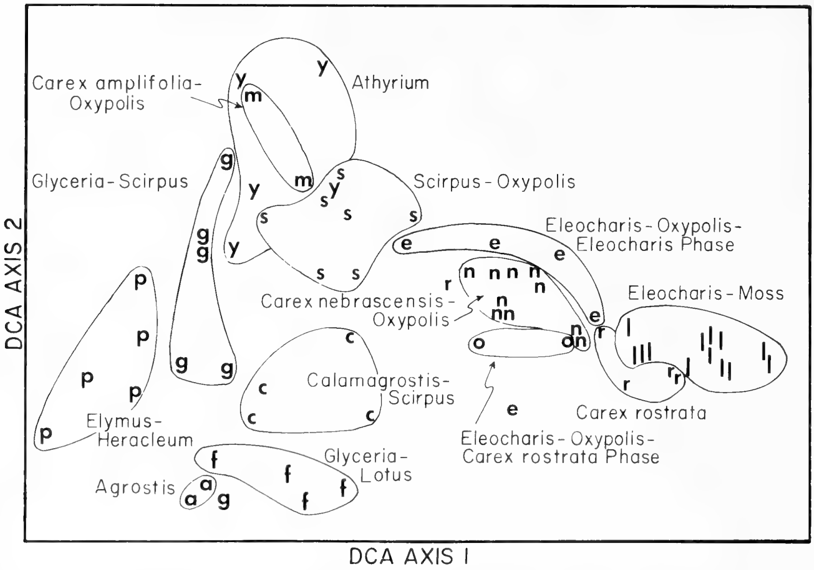


FIG. 2. Detrended correspondence analysis ordination of samples. Letters indicate samples representing the same association, as defined in Table 3.

axis is 2.8 standard deviation units long, representing a significantly smaller turnover in species composition than along Axis 1. The forb–grass associations in the left portion of the ordination space have a better separation than the *Carex* and *Eleocharis* Associations to the right. Field observations suggest that at its ends, the axis seems to describe extremes in meadow exposure and shading, reflecting site location in one of two broad landform classes: 1) within small concave openings or swales in mixed conifer forest or in *Sequoiadendron* groves, where bordering trees provide much shade; or 2) in large, broad basins of greater area and minimal shading.

Typical swale vegetation occurs highest on Axis 2 and is represented by the *Carex amplifolia–Oxypolis occidentalis* and *Athyrium filix-femina* Associations. At the other extreme, open basin vegetation (represented by the *Agrostis scabra* and *Glyceria elata–Lotus oblongifolius* Associations) occurs lowest on Axis 2. Those types with intermediate positions along Axis 2 (the *Glyceria elata–Scirpus microcarpus* and *Scirpus microcarpus–Oxypolis occidentalis* Associations) occur over a wider range of habitats. They are found within more shaded sites in swale, stringer, or streamside meadows, as well as within large, open meadow basins. The *Calamagrostis canadensis–Scirpus microcarpus* Association has affinities to the *Glyceria elata–Lotus oblongifolius* Association as it is restricted to open basins. The former usually occurs farther from drier edges and closer to drainage channels and areas of overland flow than the latter.

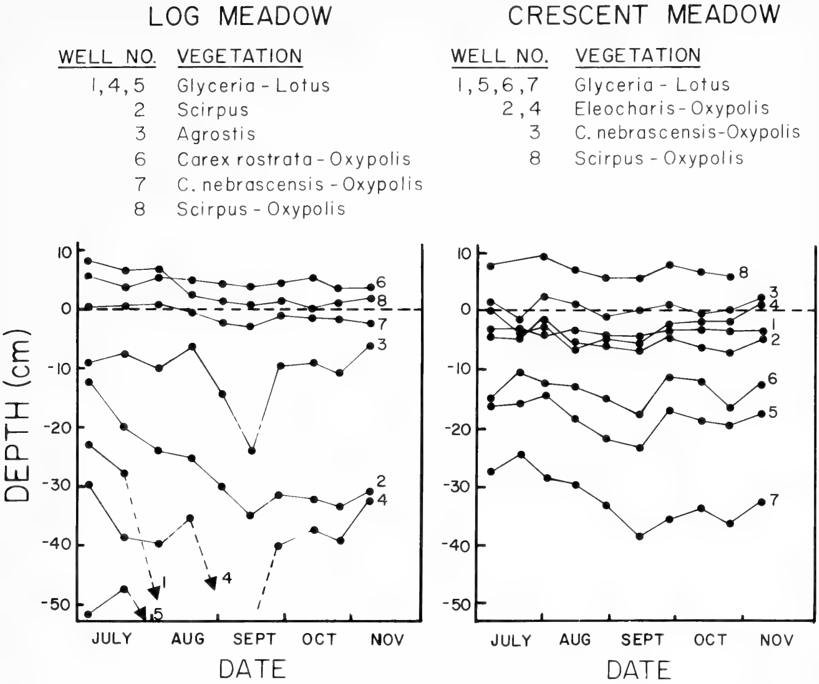


FIG. 3. Water table depths for Log and Crescent Meadows, Giant Forest, for 6 Jul to 8 Nov 1983.

Water Table Dynamics

Species distributions and vegetation composition largely reflect meadow hydrology. Detrended correspondence analysis ordination indicates that plant associations segregate along a complex moisture gradient reflecting water table depth and movement. Results from seasonal water table measurements reinforce this interpretation (Fig. 3). Although the water table patterns represent only two meadow sites for a single growing season during a year with an unusually high snow-pack and greater than average summer rains, the distribution of vegetation nevertheless reflects spatial differences in meadow hydrology.

Several general trends are evident from the water well transects in Log and Crescent Meadows. Water was progressively drawn down from 6 July through 12 September in those communities that experienced a fluctuating water regime (see Fig. 3, *Glyceria elata–Lotus oblongifolius* Association, Wells 1, 4, 5, Log Meadow; *Glyceria elata–Lotus oblongifolius* Association, Wells 5, 6, 7, Crescent Meadow; and *Agrostis scabra* Association, Well 3, Log Meadow). In several instances, the water table fell below well bottoms (see arrows, Fig.

3). Small but distinct increases in the water table during the period of decline may correspond to summer rains (8–10 August, 1.5 cm; 15–19 August, 4.0 cm). From 12 September through final sampling on 8 November, the water table progressively increased to levels that were near initial sampling heights in most areas even though fall rains had been minimal (approximately 7.1 cm from 22 September to 8 November). Apparently enough water remains within side-slopes to restore the water table to early summer levels when evapotranspiration is reduced during senescence of late summer vegetation. Wood (1975) described similar patterns in a subalpine meadow at the Central Sierra Snow Laboratory.

Rates of decline and increase in the water table were variable across meadow transects; maximum rates of change appeared in the *Agrostis scabra* community of Log Meadow. Here, levels dropped an average of 0.21 cm per day through mid-September and rose an average of 0.25 cm per day through early November. Wood (1975) reported a stronger water table rise, 1.2 cm per day, in his subalpine meadow.

Water wells located more centrally in the meadows (in vegetation dominated by *Scirpus microcarpus–Oxypolis occidentalis, Carex rostrata–Oxypolis occidentalis, Carex nebrascensis–Oxypolis occidentalis,* and *Eleocharis montevidensis–Oxypolis occidentalis*) showed minor fluctuations in growing season water depths. These were communities with water essentially at or above the soil surface throughout the sampling period. *Eleocharis montevidensis–Oxypolis occidentalis* sites (Wells 2, 4, Crescent Meadow) showed minor water table fluctuations of 1 to 2 cm. The *Carex nebrascensis*-dominated sites (Well 7, Log Meadow, and Well 3, Crescent Meadow) maintained water levels between −0.5 and +2.0 cm. *Scirpus microcarpus*-dominated sites exhibited standing water tables as great as 9 cm, but levels slowly declined to 0.5 and 5.0 cm by September (Well 8, Log Meadow, and Well 8, Crescent Meadow, respectively). The *Carex rostrata* site maintained a stable, standing water table at 2.0–3.0 cm (Well 6, Log Meadow).

A *Scirpus microcarpus* site near a stream channel in Log Meadow (Well 2) appeared anomalous in that water table fluctuations resembled those more characteristic of *Glyceria elata–Lotus oblongifolius* meadow edge communities. Its occurrence on elevated coarse sand deposits may explain the rather large 17 cm depression of the water table from 6 July through 12 September. Patterns within a *Glyceria elata–Lotus oblongifolius* site in Crescent Meadow (Well 1) also appeared anomalous as the water table remained stable beneath the soil surface through the growing season. Unusually high winter snowpack and August rainfall may be masking more distinct water table patterns in these meadows, particularly in communities with permanently saturated soils. Typically, the water table in these sites may drop both differentially, and more quickly to lower mid-summer depths. Nevertheless, seasonal measurements, field observations, and ordination results suggest the importance of water depth and movement in montane meadow vegetation patterns.

CONCLUSION

The analysis of montane meadow vegetation in Sequoia National Park complements similar research within subalpine meadows of the southern Sierra Nevada and provides baseline data for future research and management. Twelve plant associations and one phase are segregated floristically, reflecting environmental variation in 1) water table depth and water movement, and 2) site exposure and shading. Vegetation similar floristically and physiognomically to that described herein exists elsewhere in the Sierra Nevada and in the western Cascade Range of Oregon. Although spatial and seasonal patterns of water depth and movement influence the composition and distribution of plant communities, future research is necessary to address the relative importance of microenvironmental parameters and disturbance.

ACKNOWLEDGMENTS

I thank Teresa Magee for assistance with vegetation sampling and Annie Esperanza, Patti Haggerty, Sara Molden, and Tom Stohlgren for help with water table measurements. Larry Norris aided in location of many of the sites and Bradley Smith provided much guidance with computer analyses. Joseph Antos, Jerry Franklin, Robert Frenkel, Arthur McKee, Annette Olson, and Dean Taylor provided useful criticism of the manuscript. Finally, I thank Jerry Franklin and David Parsons for the opportunity to pursue this research as part of the PULSE studies of 1982 and 1983. The study was supported in part by the National Park Service, under an Interagency Agreement Grant IA-9088-82-01 with the Pacific Northwest Forest and Range Experiment Station, USDA, Forest Service.

LITERATURE CITED

ARMSTRONG, J. E. 1942. A study of grazing conditions in the Roaring River District, Kings Canyon National Park, with recommendations. National Park Service Report.

BEGUIN, C. and J. MAJOR. 1975. Contribution a l'etude phytosociologique et ecologique des marais de la Sierra Nevada (Californie). Phytocoenologia 2:349–367.

BENEDICT, N. B. 1981. The vegetation and ecology of subalpine meadows of the southern Sierra Nevada, California. Ph.D. dissertation, Univ. California, Davis.

———. 1983. Plant associations of subalpine meadows, Sequoia National Park, California. Arctic and Alpine Research 15:383–396.

——— and J. MAJOR. 1982. A physiographic classification of subalpine meadows of the Sierra Nevada, California. Madroño 29:1–12.

BENNETT, P. 1965. An investigation of grazing impact of 10 meadows in Sequoia-Kings Canyon National Park. M.A. thesis, San Jose State College, California.

CAMPBELL, A. G. 1973. Vegetative ecology of Hunts Cove, Mt. Jefferson, Oregon. M.S. thesis, Oregon State Univ., Corvallis.

DEBENEDETTI, S. and D. J. PARSONS. 1979a. Mountain meadow management and research in Sequoia and Kings Canyon National Parks: a review and update. *In* R. L. Linn, ed., Proceedings of the First Conference on Scientific Research in the National Parks. U.S.D.I. Nat. Park Serv. Trans. and Proc. Series No. 5. Washington, DC 2:1305–1311.

——— and ———. 1979b. Natural fire in subalpine meadows: a case description from the Sierra Nevada. J. Forest. (Washington) 77:477–479.

——— and ———. 1984. Post-fire succession in a Sierran subalpine meadow. Amer. Midl. Naturalist 111:118–125.

FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Serv. Gen. Techn. Rept. PNW-8.

———, ———, and W. H. MOIR. 1970. A reconnaissance method for forest site classification. Shinrin Richi (Tokyo) 12:1–14.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.

GIFFEN, A., C. M. JOHNSON, and P. ZINKE. 1969. Ecological study of meadows in Lower Rock Creek, Sequoia National Park (unpubl.).

HALPERN, C. B., B. G. SMITH, and J. F. FRANKLIN. 1984. Composition, structure, and distribution of the ecosystems of the Three Sisters Biosphere Reserve/Wilderness Area. Report to the U.S.D.A.

HARKIN, D. W. and A. M. SCHULTZ. 1967. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1966 (unpubl.).

HICKMAN, J. C. 1976. Non-forest vegetation of the central western Cascade Mountains of Oregon. Northw. Sci. 50:145–155.

HILL, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237–249.

———. 1974. Correspondence analysis: a neglected multivariate method. Applied Statistics 23:340–354.

———. 1979a. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell Univ., Ithaca, NY.

———. 1979b. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell Univ., Ithaca, NY.

———, R. G. H. BUNCE, and M. W. SHAW. 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. J. Ecol. 63:597–613.

——— and H. G. GAUCH. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

HUBBARD, R. L., C. E. CONRAD, A. W. MAGILL, and D. L. NEAL. 1966. The Sequoia National Park and Pacific Southwest Forest Range Exp. Sta. cooperative mountain meadow study. Part II: An ecological study of Lower Funston Meadow (unpubl.).

———, R. RIEGELHUTH, H. R. SANDERSON, A. W. MAGILL, D. L. NEAL, R. H. TWISS, and C. E. CONRAD. 1965. A cooperative study of mountain meadows. Part I: Extensive survey and recommendations for further research (unpubl.).

JEPSON, W. L. 1936. A flora of California. Vol. 2. California School Book Depository, San Francisco.

LAWTON, E. 1971. Moss flora of the Pacific Northwest. The Hattori Botanical Laboratory, Nichinan, Japan.

LEONARD, R., D. HARKIN, and P. ZINKE. 1967. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1967 (unpubl.).

———, C. M. JOHNSON, P. ZINKE, and A. SCHULTZ. 1968. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1968 (unpubl.).

MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, NY.

Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.

———. 1968. Supplement to a California flora. Univ. California Press, Berkeley.

Pakarinen, P. 1984. Cover estimation and sampling of boreal vegetation in northern Europe. *In* R. Knapp, ed., Handbook of vegetation sampling: methods and taxon analysis in vegetation science, p. 35–44. W. Junk, The Hague, Netherlands.

Parsons, D. J. and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed conifer forest. Forest Ecol. Manage. 2:21–33.

Ratliff, R. D. 1979. Meadow sites of the Sierra Nevada, California. Classification and species relationships. Ph.D. dissertation, New Mexico State Univ., Las Cruces.

———. 1982. A meadow site classification for the Sierra Nevada, California. U.S.D.A. Forest Serv. Pacific Southw. Forest Range Exp. Sta., Gen. Techn. Rept. PSW-60.

Roach, A. W. 1958. Phytosociology of the Nash Crater lava flows, Linn County, Oregon. Ecol. Monogr. 22:169–193.

Rundel, P. W. 1972. Habitat restriction in Giant Sequoia: the environmental control of grove boundaries. Amer. Midl. Naturalist 87:81–95.

———, D. J. Parsons, and D. T. Gordon. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 559–599. Wiley-Interscience, NY.

Seyer, S. C. 1979. Vegetation ecology of a mountain mire, Crater Lake National Park, Oregon. M.S. thesis, Oregon State Univ., Corvallis.

———. 1983. Ecological analysis of Multorpor Fen Preserve, Oregon. Report to the The Nature Conservancy.

Sharsmith, C. W. 1959. A report on the status, changes and ecology of back country meadows in Sequoia and Kings Canyon National Parks (unpubl.).

Strand, S. 1972. An investigation of the relationship of pack stock to some aspects of meadow ecology for seven meadows in Kings Canyon National Park. M.S. thesis, California State Univ., San Jose.

Sumner, E. L. 1941. Special report on range management and wildlife protection in Kings Canyon National Park (unpubl.).

———. 1948. Tourist damage to mountain meadows in Sequoia-Kings Canyon National Park 1935–1948. A review with recommendations (unpubl.).

Westhoff, V. and E. van der Maarel. 1978. The Braun-Blanquet approach. W. Junk, The Hague, Netherlands.

Wood, S. H. 1975. Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. Ph.D. dissertation, California Institute of Technology, Pasadena.

(Received 7 Jan 1985; revision accepted 17 Oct 1985.)

VEGETATION OF TORREY LAKE MIRE, CENTRAL CASCADE RANGE, OREGON

ROBERT E. FRENKEL
Department of Geography, Oregon State University,
Corvallis 97331

WILLIAM H. MOIR
U.S. Forest Service Region 3, 517 Gold Avenue SW,
Albuquerque, NM 87102

JOHN A. CHRISTY
Botany Section, Milwaukee Public Museum,
800 West Wells Street, Milwaukee, WI 53233

ABSTRACT

Torrey Lake Mire is typical of many small isolated wetlands in the predominantly forested central Oregon Cascade Range. Four mire communities, identified by floristic similarity analysis, exhibit distinct zonation with respect to a complex moisture gradient observed in the field and shown by detrended correspondence analysis ordination. In order of increasing moisture and soil saturation they are: *Kalmia microphylla/Sphagnum* Bog, *Vaccinium occidentale/Trifolium longipes* Thicket, *Carex sitchensis* Fen, and *Carex rostrata* Reedswamp. Montane mires are often regarded as having higher species diversity than surrounding forest because mire communities are packed into small areas in response to a fairly sharp environmental gradient. Forest communities, occupying more uniform environments, extend over broad areas. Because of a sharp hydrological gradient, Torrey Lake Mire embraces several closely packed plant communities. Based on the jackknife procedure, individual mire communities are shown to have similar species diversity to that of the surrounding *Tsuga mertensiana* forest community.

Mires and wet meadows are small scattered features within the predominantly forested Cascade Range. These dispersed wetlands are seldom studied although they are important faunal habitat, attractive recreational features, often rich in plant taxa, and valuable sites for research on vegetational history.

The term 'mire' is used in this paper in preference to 'bog.' Until recently 'bog' has been applied loosely, and often improperly in North America, to wetland types ranging from convex ombrotrophic wetlands with peat (true bogs) to seasonally flooded minerotrophic wetlands without peat. International wetland classifications now employ the neutral term 'mire' to encompass bogs, fens, and a number of other wetland types (Gore 1983). Proper classification of a mire requires detailed knowledge of its topographical, hydrological, chem-

MADROÑO, Vol. 33, No. 1, pp. 24–39, 27 March 1986

ical, and biological characteristics, information generally unavailable for wetlands in the Cascade Range. 'Mire' is, therefore, broadly applied here to denote a minerotrophic, peat-based wetland in which sedges and mosses, including *Sphagnum,* dominate the ground layer.

There is relatively little published research on mires and wet montane meadows in the Oregon Cascade Range; most studies are reports or theses and consider only the vascular flora. Hansen (1947) studied pollen profiles from several mires in the Western and High Cascades, but provided incomplete descriptions of contemporary vegetation. Aller (1956) identified a "bog-marsh" community at 1220 m elevation on Monument Peak in the Western Cascades and furnished a brief description and species list. Hickman (1968, 1976) surveyed the vascular flora of a number of non-forested communities in the Western Cascades among which were three very generalized wetland types including a "bog association" for which he provided a partial floristic list. In the Three Sisters Wilderness, in the central Cascades, Halpern et al. (1984) surveyed montane and subalpine meadows including 11 hydric and 8 mesic community types. Seyer (1983) assessed the vegetation of Multorpor Fen, near Mt. Hood, recognizing aquatic, low sedge, moss mound, *Carex sitchensis,* low shrub, and carr (shrubby mire) communities. A brief description of the Big Spring Mire assemblage appears in a study by Roach (1952) of the Nash Crater lava flow vegetation near Santiam Pass.

The most complete study, which considered both ecological relationships and the bryophyte flora of an Oregon Cascade mire, is by Seyer (1979) who identified 11 communities at Sphagnum Bog, Crater Lake National Park, and related these to nutrient status, hydrology, and microtopography. In another detailed investigation in Hunts Cove, Mt. Jefferson Wilderness, Campbell (1973) described 11 meadow associations embracing four hydric communities. These communities correlated strongly with snow persistence and, to a lesser extent, with soil moisture and nutrient status.

Because of the lack of published studies, the primary purpose of our paper is to describe the main floristic and structural features of Torrey Lake Mire, a typical wetland of the central Cascades in Oregon, and to relate the communities to those identified in published and unpublished regional research. Because there are only fragmentary accounts of the bryophyte composition of Cascade mires, a secondary objective is to describe the bryophyte flora of the mire and associated mire communities. A third objective is to relate mire communities to microtopography, associated hydrological conditions, and surrounding forest vegetation. There is also a need to document the resources of Torrey Lake Mire because it is a distinctive element in the proposed Torrey-Charlton Research Natural Area, a 1075 ha tract in the Willamette and Deschutes National Forests.

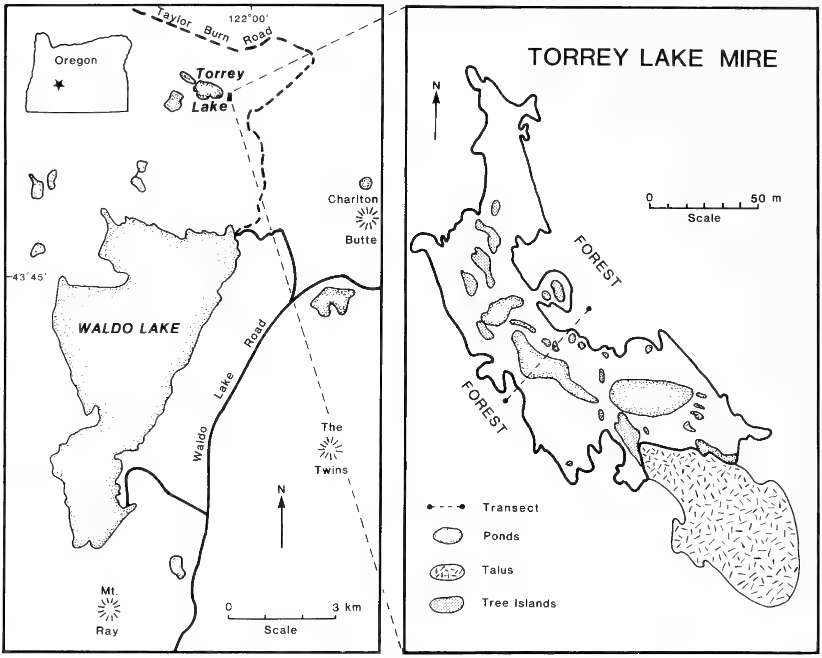


FIG. 1. Location of Torrey Lake Mire.

LOCATION AND SITE

Torrey Lake Mire lies at 1650 m elevation, 4 km north of Waldo Lake in the Willamette National Forest and approximately 200 m southeast of Torrey Lake into which it drains (Fig. 1). The 0.9 ha mire is the largest of more than 10 small wetlands in the 380 ha Torrey Lake Unit of the proposed research natural area (RNA). The RNA is being established to protect old-growth *Tsuga mertensiana* forest and associated wet meadows, ponds, lakes, and rock outcrops (McKee and Franklin 1977).

Located within the High Cascades geological province, the mire is situated on a gently undulating plateau formed by a series of composite volcanoes that deposited scoriaceous materials, andesites, and basalts during the Pliocene and Pleistocene Epochs (Baldwin 1981). The area was subsequently glaciated and more recently covered by Mount Mazama ash and pumice. A soil pit shows that Torrey Lake Mire developed directly on Mount Mazama ash (ca. 40 cm below the present surface); the present mire is, therefore, at least 6700 years old (Sarna-Wojcicki et al. 1983).

The area has a cool, wet climate. Annual precipitation ranges from 1600 to 2000 mm, more than three-fourths of which occurs as snow.

Snow depths often exceed 5 m and snow packs may persist from six to eight months. Mean January and July temperatures are −3.5°C and 13.5°C respectively, whereas the mean January minimum is −8.5°C and the mean July maximum is 21.5°C. Frosts can occur in any month (McKee and Franklin 1977).

Torrey Lake Mire is an inclusion within a broad expanse of *Tsuga mertensiana* forest that mantles the crest of the central Cascades. The forest is included within the *Tsuga mertensiana* Zone (Franklin and Dyrness 1973, Schuller 1978, Hemstrom et al. 1982). The major vegetation community surrounding the mire community is the *Tsuga mertensiana/Vaccinium scoparium* association.

METHODS

A single 60 m transect was established at right angles to the long axis of the mire between permanently marked endposts in the fringing upland forest, 2–3 m in elevation above the mire. The transect extends into the forest about 7 m on both sides of the mire (Fig. 1). Sixty-four 20 × 50 cm microplots were placed at 50 to 100 cm intervals along the transect and species canopy cover was estimated by Daubenmire (1959) cover classes. Substrate pH at 5 cm depth was measured colorimetrically at several locations within a community. Adjacent forest was sampled with two 500 m^2 circular reconnaissance plots centered 20 m from the mire edge in line with the transect. Additionally, the regional *Tsuga mertensiana* forest was sampled with 46 reconnaissance plots, each 500 m^2. Forest plot placement followed landscape stratification based on aerial photography and field survey and was aimed at typifying the general vegetation of the proposed Torrey-Charlton RNA. Reconnaissance plot methods followed Franklin et al. (1970). A nearly complete species list was compiled by observations beyond plots for the mire and adjacent forest. Vascular plant nomenclature follows Hitchcock and Cronquist (1973) and bryophyte nomenclature follows Crum et al. (1973) and Crum (1984). Voucher specimens are deposited at OSC.

Mire microplot and forest macroplot data were analyzed using the program TABORD, which structures phytosociological data in the form of an association table based on sample similarity (Maarel et al. 1978). Microplot data were also ordinated by detrended correspondence analysis, an eigenvector ordination technique derived from reciprocal averaging using the Cornell University ecology program DECORANA (Gauch 1982, Hill 1979). From the latter analysis, major environmental controls were inferred, floristic changes across environmental gradients were quantified, and plant associations based on TABORD were displayed with respect to environmental gradients.

Mire and forest diversity were analyzed by PRHILL, an unpublished computer program developed by B. G. Smith that was designed to calculate jackknife estimates of M. O. Hill's diversity numbers (Hill 1973, Heltsche and Forrester 1983) for each community type. By simulation, Heltsche and Forrester (1983) have shown that jackknife estimates of diversity permit community comparisons under a wide variation in sample size. Details of the forest segment of the study are to be published separately.

RESULTS AND DISCUSSION

The flora of Torrey Lake Mire and the adjacent forest include 6 trees, 15 shrubs, 58 herbs, and 28 bryophytes (Table 1). The vascular plant families represented by the greatest number of species include the Cyperaceae (10), Gramineae (8), Rosaceae, Ranunculaceae, and Pinaceae (6), and Asteraceae and Ericaceae (5). A species list for the forest plots is available from the senior author.

Plant communities. Two terrestrial and four mire communities are identified by TABORD similarity analysis and are summarized in Table 2 with respect to mean percent cover and percent constancy of dominant vascular plant species in microplots. Communities also are depicted by profile of dominant species cover as it occurs across the mire (Fig. 2).

TABLE 1. FLORA OF TORREY LAKE MIRE AND ADJACENT FOREST. Forest species occur in the *Tsuga mertensiana/Vaccinium scoparium* Association and *Xerophyllum tenax* mire fringe; mire species occur in four mire communities.

Mire	Forest
Trees	
Picea engelmannii	*Abies amabilis*
Pinus contorta var. *latifolia*	*A. lasiocarpa*
	Pinus monticola
	Tsuga mertensiana
Shrubs	
Kalmia microphylla var. *microphylla*	*Arctostaphylos nevadensis*
Lonicera caerulea	*Vaccinium caespitosum*
Ribes lacustre	*V. membranaceum*
Salix geyeriana	*V. ovalifolium*
S. myrtillifolia	*V. scoparium*
Spiraea densiflora	
S. douglasii var. *menziesii*	
Sorbus sitchensis	
Vaccinium caespitosum	
V. occidentale	
Herbs	
Agrostis idahoensis	*Achlys triphylla*
A. thurberiana	*Anemone deltoidea*
Apargidium boreale	*A. lyallii*
Arnica mollis	*Berberis nervosa*
Aster occidentalis	*Carex pensylvanica*

TABLE 1. CONTINUED.

Mire	Forest
Calamagrostis canadensis var. *scabra*	*C. rossii*
Caltha biflora var. *rotundifolia*	*Chimaphila umbellata* var. *occidentalis*
Carex buxbaumii	*Clintonia uniflora*
C. limosa	*Cornus canadensis*
C. muricata	*Fragaria virginiana* var. *platypetala*
C. rostrata	*Gaultheria humifusa*
C. simulata	*Hypopitys monotropa*
C. sitchensis	*Juncus parryi*
Danthonia intermedia	*Pyrola secunda*
Deschampsia atropurpurea	*Rubus lasiococcus*
D. cespitosa	*Smilacina stellata*
Dodecatheon jeffreyi	*Viola glabella*
Eleocharis pauciflora	*V. orbiculata*
Elymus glaucus	*Xerophyllum tenax*
Epilobium alpinum var. *gracillimum*	
Hypericum anagalloides	
Juncus balticus var. *balticus*	
Juncus bolanderi	
Mimulus primuloides	
Muhlenbergia filiformis	
Nuphar polysepalum	
Pedicularis attolens	
Potentilla drummondii	
Ranunculus alismaefolius var. *davisii*	
R. flammula	
R. gormanii	
Scirpus congdonii	
Senecio cymbalarioides	
S. triangularis	
Tofieldia glutinosa	
Trifolium longipes var. *shastense*	
Utricularia vulgaris	
Veronica wormskjoldii	
Viola macloskeyi	
Bryophytes	
Aulacomnium palustre	*Andreaea blyttii*
Bryum pseudotriquetrum	*Brachythecium leibergii*
Calliergon stramineum	*B. collinum*
Cephalozia sp.	*Ceratodon purpureus*
Cephaloziella sp.	*Claopodium bolanderi*
Drepanocladus exannulatus	*Dicranoweisia crispula* var. *contermina*
Philonotis fontana	*Dicranum fuscescens*
Pohlia nutans	*D. pallidisetum*
Rhizomnium magnifolium	*Dryptodon patens*
Scapania irrigua	*Kiaeria starkei*
Sphagnum capillifolium	*Marsupella* sp.
S. squarrosum	*Pohlia cruda*
S. subsecundum	*P. nutans*
	Polytrichum piliferum
	Rhacomitrium heterostichum var. *sudeticum*

TABLE 2. MEAN PERCENT COVER AND PERCENT CONSTANCY FOR SELECTED VASCULAR PLANTS AND ASSOCIATED BRYOPHYTES IN PLANT COMMUNITIES ALONG A TRANSECT OF TORREY LAKE MIRE. Key: selected vascular plants had 50% constancy in 20 × 50 cm microplots; number to left of "/" is mean % cover and number to right is % constancy in community microplots; T = trace (≤1% cover); X = present in community; Tsme/Vasc = *Tsuga mertensiana/Vaccinium scoparium*; Xete = *Xerophyllum tenax*; Kami/Sphg = *Kalmia microphylla/Sphagnum*; Caro = *Carex rostrata*; Casi = *Carex sitchensis*; and Vaoc/Trlo = *Vaccinium occidentale/Trifolium longipes*.

	Plant community						
Community name	Tsme/Vasc forest	Xete fringe	Kami/Sphg bog	Caro reedswamp	Casi fen	Vaoc/Trlo thicket	
Number of microplots	13	10	8	12	9	6	Substrate
Vascular taxa							
Vaccinium scoparium	28/100	2/20					
Xerophyllum tenax	3/15	87/100	T			T	
Gaultheria humifusa		17/80	2/25			T	
Rubus lasiococcus		3/80					
Kalmia microphylla		5/60	12/100		T	T	
Vaccinium caespitosum	1/15	4/40	4/50				
Vaccinium occidentale		6/30	11/88			60/100	
Trifolium longipes		8/20			13/33	26/100	
Spiraea densiflora		4/20	5/63		2/22	7/50	
Apargidium boreale		2/20	23/100		8/22	3/50	
Viola macloskeyi		T/10			3/78	1/50	
Tofieldia glutinosa		1/10	2/50		4/33		
Agrostis thurberiana			6/63		16/78	13/50	
Dodecatheon jeffreyi			1/38	1/20	23/78	3/50	
Scirpus congdonii			T	1/8	26/67		
Carex muricata			T		21/89		
Carex rostrata				54/100			
Carex sitchensis				13/67	15/100		
Utricularia vulgaris				1/58	T/33		
Carex buxbaumii					14/67		
Ranunculus gormanii					5/56		
Potentilla drummondii						6/83	

Table 2. Continued.

	Plant community						
Community name	Tsme/Vasc forest	Xete fringe	Kami/Sphg bog	Caro reedswamp	Casi fen	Vaoc/Trlo thicket	
Number of microplots	13	10	8	12	9	6	Substrate
Bryophyte taxa							
Dicranum fuscescens	X						rotten wood
Kiaeria starkei	X						shaded rocks
Andreaea blyttii	X						shaded rocks
Ceratodon purpureus	X						duff
Dicranum pallidisetum	X	X					duff
Pohlia nutans	X	X					duff, peat
Polytrichum piliferum	X						duff
Rhacomitrium heterostichum var. *sudeticum*	X						rock outcrop
Brachythecium leibergii	X						rock outcrop
Brachythecium collinum	X						rock outcrop
Claopodium bolanderi	X						rock outcrop
Dicranoweisia crispula var. *contermina*	X						rock outcrop
Dryptodon patens	X						rock outcrop
Marsupella sp.	X						rock outcrop
Pohlia cruda	X						rock outcrop
Sphagnum capillifolium		X	X			X	peat
Sphagnum subsecundum			X	X	X	X	peat
Drepanocladus exannulatus				X	X		peat
Aulacomnium palustre						X	peat
Bryum pseudotriquetrum						X	peat
Cephalozia sp.						X	peat
Philonotis fontana						X	peat
Scapania irrigua						X	peat

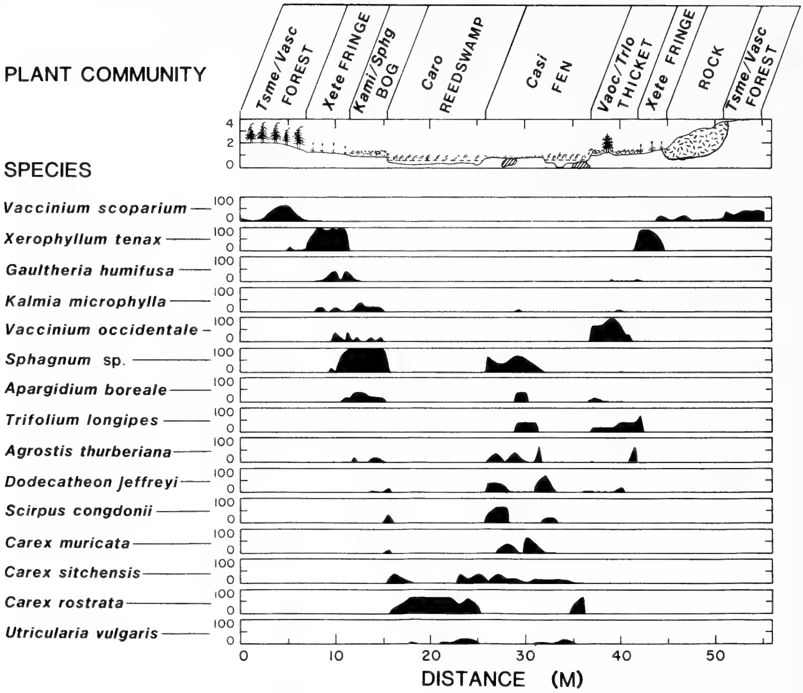


FIG. 2. Percent cover of characteristic species in microplots along a transect across Torrey Lake Mire. Community species abbreviations given in Table 2.

The principal community surrounding the mire, a closed canopy forest with approximately 80 percent tree cover, is comparable to the *Tsuga mertensiana/Vaccinium scoparium* Association of Hemstrom et al. (1982) and Schuller (1978). The shrub layer is comprised of about 40 percent *V. scoparium* cover, and occasional *V. membranaceum* and *V. caespitosum.* Scattered herbs include *Xerophyllum tenax, Hypopitys monotropa,* and *Carex pensylvanica.* Because substrate varies from andesitic basalt to duff and decayed wood, many bryophytes are associated with the forest community (Table 2). Soils are seldom saturated except after heavy precipitation or snowmelt.

The second terrestrial community, the *Xerophyllum tenax* Fringe, is more open (less than 50 percent tree cover), and occupies a band 3–5 m wide encircling the mire except for the southeast margin where talus abuts the wetland. *Xerophyllum tenax* and *Gaultheria humifusa* are prominent understory species. Characteristic bryophytes associated with the lower edge of the *Xerophyllum* Fringe are *Dicranum pallidisetum, Pohlia nutans,* and *Sphagnum capillifolium,* the latter extending upwards from the mire. Substrate, which is seldom saturated, consists of thick duff developed on sandy loam derived from underlying tephra. Floristically, this ecotonal community grades abruptly into the forest and shares a large number of species with the mire (Table 2 and Fig. 2).

The four mire communities are distinctly zoned, largely in response to increased inundation toward the center of the wetland (Fig. 2). The *Kalmia microphylla/Sphagnum* Bog occupies the immediate mire margin and in places is still under partial shade of the open *Tsuga* forest. It is marked by a band of dwarf shrubs including *Kalmia, Spiraea densiflora,* and *Vaccinium occidentale,* and the herb *Apargidium boreale.* Associated with this border is a thick mat of *Sphagnum capillifolium* and occasional *S. subsecundum.* Peat, 15–25 cm thick, grades directly into the mantle of Mt. Mazama pumice. Substrate is saturated throughout the summer, but inundation is confined to late spring after snowmelt. Because of convex topography, dominance by *Sphagnum,* and acidity, this community is best called a bog. This mire-margin community is repeated on slightly elevated natural levees along the main creek draining the wetland.

A distinct 5–25 cm topographic and hydrologic break marks the edge of the *Carex rostrata* Reedswamp and *Carex sitchensis* Fen where they border the *Kalmia* Bog and *Vaccinium* Thicket (Fig. 2). Of the mire communities, the reedswamp is wettest, occupying shallow depressions in which water depth varies from 5–35 cm from mid-June after snowmelt to early September before autumn precipitation. *Carex rostrata* is dominant and *C. sitchensis* is an occasional species, the latter growing in slightly shallower areas than *C. rostrata.* Bryophytes are sparse in this community but are occasionally represented by *Drepanocladus exannulatus* and *Sphagnum subsecundum.*

Broad areas of the mire, less inundated than the *Carex rostrata* Reedswamp, remain saturated throughout the year and are aggregated here under the name *Carex sitchensis* Fen. Prominent species include *C. sitchensis, C. muricata, C. buxbaumii, Scirpus congdonii, Agrostis thurberiana,* and *Dodecatheon jeffreyi* and such bryophytes as *Drepanocladus exannulatus* and *Sphagnum subsecundum* (Table 2).

Shrubby patches of the mire are placed in the *Vaccinium occidentale/Trifolium longipes* Thicket community, which is dominated by *V. occidentale* but includes a dense herbaceous understory characterized by *Trifolium longipes, Agrostis thurberiana,* and *Apargidium boreale* (Table 2). Common bryophytes include *Aulacomnium palustre, Bryum pseudotriquetrum, Philonotis fontana,* and *Sphagnum capillifolium.* This community is vernally wet but dries out in late summer. Frequently, the thicket occupies slightly elevated areas

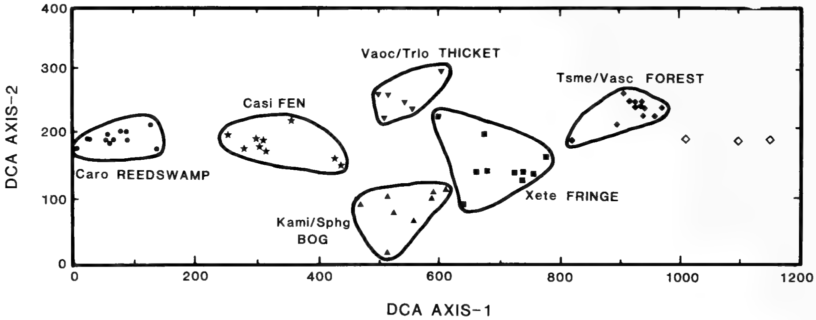


FIG. 3. Detrended correspondence analysis ordination of Torrey Lake Mire microplots. Community species abbreviations given in Table 2. Open diamonds (◇) are unclassified forest plots; units are standard deviations × 100.

associated with fallen and decayed logs. Because of the slight elevation above the water table, these mire patches occasionally include both *Pinus contorta* and *Picea engelmannii* and are rich in herbaceous species.

Floristic data from 64 mire and terrestrial microplots were ordinated by detrended correspondence analysis (DCA) and displayed in Fig. 3. Plant communities identified by TABORD similarity analysis are superimposed upon the ordination. DCA ordination yielded four eigenvalues (0.91, 0.31, 0.16, and 0.13) the first two of which represent most of the compositional variation along the transect and are interpretable. The principal eigenvector, DCA axis-1, is 11.5 standard deviation units long and indicates an exceptionally sharp environmental gradient. Field observations suggest that this axis represents a complex moisture gradient.

The two terrestrial communities displayed on the right side of the ordination are driest (Fig. 3). The outlying plots to the right are unclassified forest microplots. At the wet end of the gradient, the *Carex rostrata* Reedswamp is clearly separated from the other mire communities. The *Kalmia microphylla/Sphagnum* Bog and *Vaccinium occidentale/Trifolium longipes* Thicket have intermediate positions with respect to DCA axis-1 and share a number of species with intermediate moisture status; therefore, these communities are not well separated along DCA axis-1. They form the extremes of DCA axis-2, however, which is interpreted as a nutrient axis where the *Kalmia/Sphagnum* Bog represents the most nutrient poor of the communities. This interpretation is consistent with the nutrient status of *Sphagnum*-dominated communities reported in the literature (Gore 1983). Further support for this interpretation is derived from pH measurements; the most acidic community is the *Kalmia microphylla/Sphagnum* Bog (mean substrate pH = 4.0, 0.08 s.d.) and the least acidic is the *Vaccinium occidentale/Trifolium longipes* Thicket (mean substrate pH = 5.0, 0.29 s.d.).

Floristic diversity. It is commonly intuited that montane mires and wet meadows have greater floristic diversity than surrounding forest. To evaluate this perception, mire and adjacent forest vegetation were analyzed with respect to two species diversity components (Whittaker 1960): *alpha* diversity measuring richness of a particular community, and *beta* diversity measuring change in species composition across an environmental gradient. Alpha diversity is expressed by number of species per plot, jackknife (Heltsche and Forrester 1983) estimates of total number of species per community, and the inverse of Simpson's index of diversity, which accounts for abundance in addition to richness and is most sensitive to dominant species (Hill 1973, Peet 1974). Bryophyte taxa are excluded from diversity measurements because of the difficulty in determining moss abundance.

Alpha diversity of the surrounding forest is based on reconnaissance plots, each 500 m^2 in area. *Tsuga mertensiana* forests are typically poor in species as illustrated by an average of 9.5 taxa in the two plots adjacent to the mire. This floristic impoverishment is comparable to an average of 6.3 taxa for the *Tsuga mertensiana/Vaccinium scoparium* Association based on 19 samples in the general mire area, an average of 7.9 taxa in all 46 plots of *T. mertensiana* in the region around Waldo Lake (Table 3), and an average of 5.2 taxa for 51 forest plots of *T. mertensiana* in the drier eastern central Oregon Cascades reported by Schuller (1978). For the *Tsuga mertensiana* forest, 58 species were tallied in 46 plots. Based on this sample, jackknife estimates of the total number of species is 75 (s.e. = 5.7) for the forest and 32 (s.e. = 4.8) for the *Tsuga/Vaccinium scoparium* association (Table 3). The high standard error, in part, is related to a limited sample over an area of many square kilometers.

In contrast to the forest, mire communities are extremely fine-grained and occupy areas of a few square meters in extent. Because of small areal extent, microplot size was confined to 0.1 m^2. Of four wetland communities, the *Carex rostrata* Reedswamp, the wettest of mire associations, exhibits the lowest richness, averaging 2.6 taxa per microplot and a total of 6 species (Table 3). The jackknife estimate of the expected total number of species of 8 (s.e. = 1.2) is also low. A very modest value for the inverse of Simpson's index of diversity (N_2) reflects strong dominance by *C. rostrata.* The shrubby *Vaccinium occidentale* Thicket and *Carex sitchensis* Fen display the greatest richness, averaging 9.3 and 8.7 taxa per microplot respectively. Higher N_2 values (10.9 and 8.9 respectively) indicate more equitability among species. Excluding data for the "total forest" and the inundated *Carex rostrata* Reedswamp, alpha diversity

TABLE 3. DIVERSITY MEASURES FOR TORREY LAKE MIRE COMMUNITY TYPES AND SURROUNDING *Tsuga mertensiana* FOREST. Key: N_2 = inverse of Simpson's index of diversity; s.e. = standard error; community abbreviations are given in Table 2.

	Vegetation type and plant community						
	Forest			Mire			
	Total forest	Tsme/ Vasc Assoc.	Xete Fringe	Kami/ Sphg Bog	Caro reed-Swamp	Casi Fen	Vaoc/ Trlo Thicket
No. plots	46	19	10	8	12	9	6
Average no. species/ plot	7.9	6.3	5.7	7.0	2.6	8.7	9.3
Total no. species observed	58	23	17	15	6	18	20
Estimated no. species	75	32	22	19	8	20	24
s.e.	5.7	4.8	3.6	2.7	1.2	1.0	2.0
N_2	14.6	5.8	4.9	8.2	2.5	8.9	10.9

measures for the mire communities are similar to those for the forest communities (Table 3). The commonly intuited richness of a mire with respect to a species-poor forest follows from the small size of fairly distinct wetland communities packed into a limited area. The mire is often regarded a single "community," but in actuality it is frequently comprised of many small communities. Forest communities, with a large areal extent, are perceived to have less alpha diversity than mire communities but may often have similar, or even higher alpha diversities (Table 3).

Change in species composition across an environmental gradient, or beta diversity, is displayed by detrended correspondence analysis (DCA). The first DCA axis (Fig. 3) is 11.5 standard deviation units long, indicating a marked turnover in species composition between samples along a complex environmental gradient involving variation in inundation, water movement, and water table depth. Although floristic changes are great between forest and mire, very strong compositional shifts also exist within the mire as expressed by the relative positions in the ordination of the *Carex rostrata* Reedswamp, *Carex sitchensis* Fen, *Vaccinium* Thicket, and *Kalmia* Bog (Fig. 3).

Relation to other Oregon montane mires. Of the four Torrey Lake Mire communities, the shallowly-flooded *Carex rostrata* Reedswamp is most distinctive and has been identified by a number of researchers. Seyer (1979) described a *C. rostrata* Reedswamp at Crater Lake National Park and Gold Lake Bog near Willamette Pass. Communities dominated by *C. rostrata* and lesser amounts of *C. sitchensis* were reported by Roach (1952) and Campbell (1973).

Another widespread and frequently reported mire community in the Oregon Cascades is the *Carex sitchensis* Fen with its characteristic species, *C. sitchensis, C. muricata,* and *Dodecatheon jeffreyi.* This compares with Campbell's (1973) hydric *C. sitchensis* community, which is related to early snowmelt and persistent summer moisture, and to Seyer's (1979) *C. sitchensis* Tall Sedge Fen at Crater Lake. Seyer also recorded this fen community at four localities elsewhere in the Oregon Cascades. North of Torrey Lake in the Three Sisters Wilderness, Halpern et al. (1984) identified three *C. sitchensis* community types within a Hydric Series, one of which was dominated by *C. sitchensis* and was most common at the high water table extreme of montane meadow types.

Vaccinium occidentale is common in mires throughout the Cascades, and *V. occidentale* thicket communities have occasionally been reported. Among these are the *Carexeto–Vaccinetum occidentale* Association at Big Spring (Roach 1952) and the *V. occidentale/Aulacomnium palustre* and *V. occidentale/Carex sitchensis* communities at Crater Lake and six other localities in the Oregon Cascades (Seyer 1979). This creek channel community was not specifically identified, although Halpern et al. (1984) recorded *V. occidentale* as important in four of the most hydric montane meadow community types.

The *Kalmia microphylla/Sphagnum* Bog occurring along levees and mire margins at Torrey Lake has seldom been reported in the literature. It is marked by *Kalmia, Vaccinium occidentale,* and *Sphagnum capillifolium.* Seyer (1979) reported a *Vaccinium occidentale/Sphagnum capillaceum* (=*S. capillifolium*) community at Thousand Springs Bog in Douglas County, a community with floristic and positional resemblance to that at Torrey Lake Mire.

CONCLUSION

Although less than one hectare in expanse, Torrey Lake Mire encompasses three montane hydric plant communities that are common in the Oregon Cascade Range. In order of increasing moisture gradient, these are: *Vaccinium occidentale/Trifolium longipes* Thicket, *Carex sitchensis* Fen, and *Carex rostrata* Reedswamp. A fourth distinct mire community at Torrey Lake is the *Kalmia microphylla/Sphagnum* Bog characterizing mire margin and creek levees.

Mire species composition changes rapidly in relation to a complex moisture gradient as shown by community arrangement along the principal axis of detrended correspondence analysis ordination. A second environmental gradient displayed in the ordination relates to nutrient status and separates the oligotrophic *Kalmia/Sphagnum* Bog from the more nutrient-rich *Vaccinium/Trifolium* Thicket.

The mire is a floristically complex inclusion within an otherwise species-poor *Tsuga mertensiana* forest. The fine-grained character of the mire is a response to a sharp environmental gradient. Each mire community occupies an area of a few tens of square meters. Forest communities, on the other hand, extend over many hectares and occupy a more uniform habitat. The floristic richness of individual mire communities, expressed by jackknife estimates of total number of species per community, is similar to the richness of the adjoining forest community.

Because of the contrast with the surrounding *Tsuga mertensiana* forest and the representation in the mire of a number of common Cascade wetland types, Torrey Lake Mire is an important component of the proposed Torrey-Charlton Research Natural Area.

ACKNOWLEDGMENTS

Field work on Torrey Lake Mire was conducted as part of the U.S. Forest Service, Forest and Range Experiment Station "Waldo Lake Pulse," an interdisciplinary research effort started in September 1976 under the direction of Jerry Franklin (Mathews 1983). Appreciation is extended to Dr. Franklin and to the Oregon State Natural Area Preserves Advisory Committee, which provided transportation assistance. We thank two anonymous reviewers and the editors for their helpful suggestions on an earlier version of this paper, Bradley G. Smith for computer assistance and useful discussions, Charles Halpern for carefully reviewing the paper, and Stephen Frenkel for drawing the figures.

LITERATURE CITED

ALLER, E. R. 1956. A taxonomic and ecologic study of the flora of Monument Peak, Oregon. Amer. Midl. Naturalist 56:454–472.

BALDWIN, E. M. 1981. Geology of Oregon. 3rd. ed. Kendall/Hunt Publ. Co., Dubuque, IA.

CAMPBELL, A. G. 1973. Vegetative ecology of Hunts Cove, Mt. Jefferson, Oregon. M.S. thesis, Oregon State Univ., Corvallis.

CRUM, H. A. 1984. Sphagnopsida, Sphagnaceae. N. Amer. Flora, Ser. II, 11:1–180.

———, W. C. STEERE, and L. E. ANDERSON. 1973. A new list of mosses of North America north of Mexico. Bryologist 76:85–130.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetational analysis. Northw. Sci. 33:43–64.

FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington, U.S.D.A. Forest Serv., Pac. Northw. Forest and Range Exp. Sta. Gen. Techn. Rep. PNW-8, Portland, OR.

———, ———, and W. H. MOIR. 1970. A reconnaissance method for forest site classification. Shinrin Richi (Tokyo) 12:1–14.

GAUCH, H. G., JR. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.

——— and R. H. WHITTAKER. 1972. Comparison of ordination techniques. Ecology 53:868–875.

GORE, A. J. P. 1983. Introduction. *In* A. J. P. Gore, ed., Ecosystems of the World, 4A. Mires: swamp, bog, fen and moor, general studies, p. 1–34. Elsevier Scientific Publishing Co., Amsterdam.

HALPERN, C. B., B. G. SMITH, and J. F. FRANKLIN. 1984. Composition, structure, and distribution of the ecosystems of the Three Sisters Biosphere Reserve/Wilderness Area. U.S.D.A. Forest Serv. Pac. Northw. Forest and Range Expt. Sta. Forest. Sciences Lab., Corvallis, OR.

HANSEN, H. P. 1947. Postglacial forest succession, climate, chronology in the Pacific Northwest. Trans. Amer. Philos. Soc. New Ser., vol. 37, part 1.

HELTSCHE, J. F. and N. E. FORRESTER. 1983. Estimating species richness using the jackknife procedure. Biometrics 39:1–11.

HEMSTROM, M. A., W. H. EMMINGHAM, N. M. HALVERSON, S. E. LOGAN, and C. TOPIK. 1982. Plant association and management guide for the Pacific silver fir zone, Mt. Hood and Willamette National Forests. U.S.D.A. Forest Serv. Pac. Northw. Region R6-Ecol 100-1982a, Portland, OR.

HICKMAN, J. C. 1968. Disjunction and endemism in the flora of the central Western Cascades of Oregon: an historical and ecological approach to plant distribution. Ph.D. dissertation, Univ. of Oregon, Eugene.

———. 1976. Non-forest vegetation of the central western Cascade mountains of Oregon. Northw. Sci. 50:145–155.

HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432.

———. 1979. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell Univ., Ithaca, NY.

HITCHCOCK, C. L. and A. CRONQUIST. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle.

MAAREL, E. VAN DER, J. G. M. JANSSEN, and J. M. W. LOUPPEN. 1978. TABORD, a program for structuring phytosociological tables. Vegetatio 38:143–156.

MATTHEWS, J. 1983. Cross disciplinary approach to complex park problems supplied by 'pulse studies.' Park Science 4:3–5.

MCKEE, A. and J. F. FRANKLIN. 1977. Draft establishment report for Torrey-Charlton Research Natural Area, Willamette and Deschutes National Forests. U.S.D.A. Forest Serv. Pac. Northw. Forest and Range Expt. Sta. Forest. Sciences Lab., Corvallis, OR.

PEET, R. K. 1974. The measurement of species diversity. Annual Rev. Ecol. and Syst. 5:285–307.

ROACH, A. W. 1952. Phytosociology of the Nash Crater lava flows, Linn County, Oregon. Ecol. Monogr. 22:169–193.

SARNA-WOJCICKI, A. M., D. E. CHAMPION, and J. O. DAVIS. 1983. Holocene volcanism in the conterminous United States and the role of silicic volcanic ash layers in correlation of latest-Pleistocene and Holocene deposits. *In* H. E. Wright, Jr., ed., Late-quaternary environments of the United States, volume 2. The Holocene, p. 52–77. Univ. Minnesota Press, Minneapolis.

SCHULLER, S. R. 1978. Vegetation ecology of selected mountain hemlock (*Tsuga mertensiana*) communities along the eastern high Cascades, Oregon. M.S. thesis, Oregon St. Univ., Corvallis.

SEYER, S. C. 1979. Vegetative ecology of a montane mire, Crater Lake National Park, Oregon. M.S. thesis, Oregon State Univ., Corvallis.

———. 1983. Ecological analysis of Multorpor Fen Preserve, Oregon. The Nature Conservancy, Oregon Field Office, Portland.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279–338.

(Received 26 Aug 1984; revision accepted 16 Oct 1985.)

GRASSLANDS AS COMPARED TO ADJACENT *QUERCUS GARRYANA* WOODLAND UNDERSTORIES EXPOSED TO DIFFERENT GRAZING REGIMES

LORETTA SAENZ and J. O. SAWYER, JR.
Department of Biological Sciences,
Humboldt State University, Arcata, CA 95521

ABSTRACT

The grasslands in northwestern California show striking differences in species composition when compared to understories of adjacent woodlands. In addition, sites that differ in the length of time during which cattle graze are distinct. Native grasses, although present, are not important in any of the areas studied. Greater perennial grass cover occurs only in the grassland grazed for a partial season. Perennial forbs are well represented in the sites grazed for a partial season. A greater cover of introduced annual grasses and reduced species richness are found in sites grazed for a full season.

Many of the extensive woodlands in California support grassy ground layers. These understories are similar structurally to adjacent grasslands lacking trees, but the two differ in species composition. This difference has been referred to as "the canopy effect," and has been shown to occur under *Quercus douglasii* (Holland 1973) and *Q. agrifolia* (Parker and Muller 1982). We are interested in whether a similar effect occurs under *Q. garryana* in the northwestern part of the state. We are interested further in whether grazing practices also result in changes in species composition. Some of these woodlands are grazed by cattle for about four months, only late in the season after a toxic larkspur, *Delphinium trolliifolium,* has died back for the year (Rehling 1979). These sites will be referred to as being grazed for a partial season. Areas lacking larkspur are grazed for as much of the year as weather permits, typically about eight months. These sites will be referred to as being grazed for a full season.

Location. Woodlands and grasslands form an extensive mosaic in northwestern California. The woodlands represent the Bald Hill phase of the northern woodland (Griffin 1977); the grasslands are described by Heady et al. (1977) as coastal prairie. Two sites based on the length of grazing season were chosen in an area near Schoolhouse Peak, Humboldt County, California. One, grazed for a partial season, was located in Redwood National Park; the other, grazed for a full season, was on adjacent private land. Each site had both a woodland and a grassland component. The areas were chosen to minimize variation in soils, slope, and aspect. The average elevation was 850 m.

MADROÑO, Vol. 33, No. 1, pp. 40–46, 27 March 1986

METHODS

Quercus garryana was the only canopy tree in the woodlands chosen for study. Sampling was limited to the herbaceous layer, and was done in early May and again in late June 1982. The area was divided into four homogeneous vegetation units: 1) grassland grazed for a partial season, 2) woodland grazed for a partial season, 3) grassland grazed for a full season, and 4) woodland grazed for a full season. Transitional areas, obvious springs, and drainage courses were not sampled. Woodland was distinguished from grassland by woodland having oak canopy overhead. Areas outside the canopy of oaks were designated as grassland.

After testing three plot sizes, a 0.125 m^2 circular plot was chosen as most efficient (Cochran 1977). Ten 10 m transects were located randomly within each vegetation unit. After locating the transects, five plots were sampled randomly along each transect. Advance estimates of means and variances for the species with the largest cover value in each unit were obtained from the early data. They were used to judge sampling adequacy. A sample size of 50 plots per vegetation unit produced the desired $<10\%$ standard error.

The percentages of ground covered by live plants, thatch, and bare ground were estimated and recorded for each plot. These estimates were made using the Domin scale (Mueller-Dombois and Ellenberg 1974). Absolute and relative cover were calculated by first transforming Domin scale intervals to midpoint values. These values were then multiplied by the number of plots in which a species occurred to calculate the absolute cover of a species. Relative cover values for each species were then expressed as percentages of this total. The sum of all species values represents ground covered by live plants. Thatch and bare ground were calculated in the same manner. Thatch was considered to be any dead organic material above the surface of the ground. Thatch cover was estimated regardless of overlying live plants.

RESULTS

Considering only the June data, important species in the grasslands have lower cover or are absent from under the oaks. Similarly, species typical of woodland understories vary markedly in cover or are absent from the grasslands (Table 1). The average number of species per plot in the areas grazed for a partial season is significantly greater than the number in the areas grazed for a full season ($\bar{x}$ per plot: 10 vs. 8; t-test, Sokal and Rohlf 1969). The number of exclusive species is greatest in the woodlands grazed for a full season. Similar patterns are seen in the May data (Saenz 1983).

Only in the grassland grazed for a partial season are perennial grasses common (Table 2). In the other sites, both woodlands and

TABLE 1. SPECIES COVER CALCULATED RELATIVE TO THE COVER OF ALL LIVING PLANTS (TABLE 2) USING JUNE 1983 DATA. Species organized by life form and place of origin. Introduced plants indicated by an asterisk (*), others are considered native to the area. Nomenclature follows Kartesz and Kartesz (1980).

	Grasslands		Woodlands	
Site grazed a partial season	XXXXX		XXXXX	
Site grazed a full season		XXXXX		XXXXX
Perennial grasses and sedges				
*Agrostis stolonifera**	11.3	—	1.3	2.1
*Arrhenatherum elatius**	10.7	—	0.2	—
Bromus orcuttianus	—	—	1.0	0.4
Carex tumicola	9.3	—	<0.1	—
*Dactylis glomerata**	1.1	—	6.9	—
Elymus glaucus	1.7	0.3	0.2	2.1
Festuca viridula	11.8	—	1.6	—
*Holcus lanatus**	1.7	0.1	0.5	0.7
*Lolium perenne**	0.2	—	0.8	—
Luzula multiflora	0.3	—	3.3	0.4
Melica subulata	0.1	—	0.1	0.2
Poa canbyi	—	0.1	—	3.0
*Poa pratensis**	7.2	—	1.0	0.3
Annual grasses				
*Aira caryophyllea**	1.0	4.2	—	0.6
*Avena barbata**	—	1.3	—	0.2
Bromus carinatus	<0.1	—	—	0.2
*Bromus diandrus**	—	0.5	—	0.1
*Bromus hordeaceus**	5.7	6.2	0.1	0.4
*Bromus sterilis**	<0.1	—	14.5	0.5
*Cynosurus echinatus**	5.4	41.9	16.4	64.6
*Taeniatherum caput-medusae**	—	3.0	—	—
*Vulpia bromoides**	0.2	1.1	—	0.4
Perennial forbs				
Achillea millefolium	3.0	—	1.0	0.5
Agoseris grandiflora	—	0.1	—	0.2
*Bellis perennis**	2.6	3.0	0.2	0.2
Cardamine californica	1.1	—	1.4	—
Delphinium trolliifolium	1.6	—	9.0	—
Dichelostemma pulchellum	1.2	—	0.2	0.3
Fragaria vesca	—	—	1.8	—
Galium mexicanum	<0.1	0.1	4.1	1.3
*Hypochoeris radicata**	<0.1	1.4	0.2	—
Lithophragma affine	—	—	0.1	—
Marah oreganus	<0.1	—	—	—
Osmorhiza chilensis	—	—	8.2	1.3
*Plantago lanceolata**	5.3	—	0.2	—
Pteridium aquilinum	0.3	0.9	—	—
Ranunculus occidentalis	0.6	0.3	1.3	6.7
*Rumex acetosella**	6.0	13.1	6.4	3.7
Sanicula crassicaulis	—	—	3.0	2.1
*Taraxacum officinale**	0.8	0.3	<0.1	0.2
*Trifolium repens**	—	—	<0.1	—
*Vicia benghalensis**	0.4	0.4	1.2	2.5
Viola praemosa	4.0	—	—	—

TABLE 1. CONTINUED.

	Grasslands		Woodlands	
Site grazed a partial season	XXXXX		XXXXX	
Site grazed a full season		XXXXX		XXXXX
	Annual forbs			
Cardamine oligosperma	—	—	0.3	—
*Cerastium glomerata**	0.3	0.1	—	—
Claytonia perfoliata	0.1	—	5.6	1.6
Epilobium minutum	1.5	3.8	0.1	0.1
*Erodium cicutarium**	—	0.6	0.2	—
*Linum bienne**	—	—	—	0.5
Lotus subpinnatus	0.7	7.1	0.2	1.4
Lupinus bicolor	—	0.1	—	—
Madia gracilis	0.5	6.2	—	—
Micropus californicus	—	0.4	—	—
Microseris gracilis	—	0.6	—	—
Microsteris gracilis	—	—	<0.1	0.5
Nemophila parviflora	—	—	2.9	—
Plectritis congesta	—	—	—	1.3
*Sherardia arvensis**	1.3	0.9	—	—
*Stellaria media**	—	—	2.0	0.3
*Torilis arvensis**	1.0	1.1	2.5	0.2
Trifolium albopurpureum	—	0.7	—	0.5
Trifolium tridentatum	—	—	—	0.2

the grassland grazed for a full season, the cover by annual grasses is significantly greater than that of the perennial grasslands (t-test). *Cynosurus echinatus* is the major annual at these sites (Table 1).

Introduced grasses contribute more to the flora than do the perennial ones, and they have more cover (Table 2). These differences are significant (t-test) in all but the grassland grazed for a partial season.

As with the grasses, forb species tend to be perennial, but unlike the grasses they tend to be native (Table 2). The cover of perennial and annual forbs varies more among the sites than it does for the grasses. Forb cover differences are not significant. Introduced forb cover in the grasslands is similar to that of the native forbs. In the woodlands, native forb cover is greater than that of introduced forbs.

Thatch covers much of the ground (Table 2). The areas grazed for a full season have more thatch than those grazed for a partial season. The differences in thatch between the two woodlands is insignificant, but the differences between the grasslands is significant (t-test). Most thatch, especially in areas grazed for a full season, is dead *Cynosurus echinatus*.

More bare ground exists in areas grazed for a full season than in areas grazed for a partial season. Additionally, there is more bare ground under woodland canopies than in the grasslands. These differences are significant (Table 2).

TABLE 2. SUMMARY OF FLORISTIC AND STRUCTURAL CHARACTERISTICS ORGANIZED BY VEGETATION TYPES AND GRAZING REGIMES.

	Grasslands		Woodlands	
Grazed a partial season	XXXXX		XXXXX	
Grazed a full season		XXXXX		XXXXX
No. species sampled	39	30	42	37
Mean species/plot	10.7	8.0	10.0	8.0
Number of grass and sedge species				
Perennial species	11	3	12	8
Annual species	6	7	3	8
Native species	6	2	6	6
Introduced species	10	8	9	10
Number of forb species				
Perennial species	15	9	17	11
Annual species	7	11	9	10
Native species	4	8	6	7
Introduced species	3	4	3	3
Relative cover of species (%)				
Perennial grasses	55.4	0.5	16.9	9.1
Annual grasses	12.3	58.2	31.0	66.0
Native grasses	23.2	0.4	6.1	6.1
Introduced grasses	44.5	58.4	41.5	68.9
Perennial forbs	26.9	19.6	38.3	18.3
Annual forbs	5.4	21.7	13.8	6.6
Native forbs	14.6	20.3	37.1	17.5
Introduced forbs	17.7	20.9	15.3	7.5
Ground covered by living plants	41.6	14.5	34.6	20.7
Ground covered by thatch	56.4	79.6	61.6	71.9
Bare ground	2.0	5.9	3.8	7.4

DISCUSSION

Dissimilarities found in the species composition of grasslands and woodlands in northern California are consistent with the canopy effect hypothesis. Certain species are restricted to grasslands, others to woodlands; those found in both vegetation types vary in importance. These differences suggest that the environment found under the *Quercus garryana* canopy is unlike that of the surrounding grassland. The presence or absence of a canopy is constant between the vegetation units, so differences between the grazing regimes can be sought in Tables 1 and 2. It is evident that perennial grass and forb cover is greater in areas grazed for a partial season as compared to areas grazed for a full season. We hypothesize that cropping of leaves over an extended period depletes the storage capacity of the plants, and can result in loss of perennials from the vegetation. After years of season-long grazing, seeds of annuals can become established in areas left by the declining populations of perennial plants.

In a region where perennial grasses dominated the grassland and woodland understories historically (Heady et al. 1977), annual grasses are now more important than perennial grasses in all but the grassland grazed for a partial season. If grazing favors annuals it is expected that the areas grazed for a full season would be dominated by annual grasses. In addition, if cattle prefer woodlands, then the grasslands may receive less grazing over the year. Such differential grazing may explain the perennial grass abundance in the grassland grazed for a partial season, but it does not explain the annual grass dominance in the woodland grazed in the same way. In other woodland studies, researchers have noted that the herbaceous cover consists of mainly annual grass species, even without grazing (Davy 1902, Duncan and Clawson 1979). According to local ranchers, however, cattle stay under the oak canopy at the study site for a greater portion of the season than in the open grassland.

In areas grazed for a full season, the number of plant species is lower than in areas grazed for a partial season. Grazing appears in this case to lower species richness by reducing the number of kinds of perennials. Surprisingly, the amount of thatch is greater in areas grazed for a full season. Apparently, cattle graze preferentially on plants other than the annual *Cynosurus.* Heady (1956) has pointed out that accumulation of thatch not only reduces seed sites, but smothers living plants and even reduces seed stalk formation. The lower species richness and plant cover in the areas grazed for a full season suggest that thatch is inhibiting the annuals as well. The smothering by thatch, combined with the selective grazing by cattle and response of the plants, favors annuals in sites grazed for a full season.

ACKNOWLEDGMENTS

We thank Mary Hektner, Redwood National Park; and Michael Mesler, HSU, for their assistance. Funds were provided by the Biology Graduate Student Association of Humboldt State University.

LITERATURE CITED

COCHRAN, W. G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, NY.

DAVY, J. B. 1902. Stock ranges of northwestern California: notes on the grasses and forage plants and range conditions. U.S.D.A. Bureau Pl. Industr. Bull. 12:1–81.

DUNCAN, D. A. and W. J. CLAWSON. 1979. Livestock utilization of California's oak woodlands. *In* T. R. Plumb, ed., Proceedings of the symposium on the ecology, management, and utilization of California oaks, p. 306–313. U.S.D.A., Forest Serv., Pacific Southw. Forest Range Exp. Sta., Gen. Techn. Rep. PSW-44. Berkeley, CA.

GRIFFIN, J. R. 1977. Oak woodland. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 383–415. Wiley-Interscience, NY.

HEADY, H. F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37:798–812.

———, T. C. FOIN, M. M. HEKTNER, D. W. TAYLOR, M. G. BARBOUR, and W. J. BARRY. 1977. Coastal prairie and northern coastal scrub. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 733–762. Wiley-Interscience, NY.

HOLLAND, V. L. 1973. A study of soil and vegetation under *Quercus douglasii* compared to open grassland. Ph.D. dissertation, Univ. California, Berkeley.

KARTESZ, J. T. and R. KARTESZ. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Vol. II. The biota of North America. Univ. North Carolina Press, Chapel Hill.

MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, NY.

PARKER, V. T. and C. H. MULLER. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. Amer. Midl. Naturalist 107:69–81.

REHLING, J. C. 1979. A survey of the anatomy of the poisonous plants of northwestern California. M.A. thesis, Humboldt State Univ., Arcata, CA.

SAENZ, L. 1983. *Quercus garryana* woodland/grassland mosaic dynamics in northern California. M.A. thesis, Humboldt State Univ., Arcata, CA.

SOKAL, R. R. and F. J. ROHLF. 1969. Biometry. W. H. Freeman & Co., San Francisco, CA.

(Received 23 Jan 1984; revision accepted 9 Sep 1985.)

ANNOUNCEMENT

A NEW SECTION FOR MADROÑO

Beginning with Volume 33, each issue of MADROÑO will contain an editorial page on which comments by the editor, invited contributions, unsolicited letters, and other remarks will be featured. This editorial page will serve as a vehicle for communication among our members and could include, for example, opinions of authorities on current trends in botany, rebuttals or comments on papers published in MADROÑO, letters from the President of our society, and other noteworthy communications. The editors invite all members to participate in this forum; however, all editorials will be published at the discretion of the editors.

FUNCTION OF OLFACTORY AND VISUAL STIMULI IN POLLINATION OF *LYSICHITON AMERICANUM* (ARACEAE) BY A STAPHYLINID BEETLE

Olle Pellmyr
Department of Entomology, Uppsala University,
Box 561, S-751 22 Uppsala, Sweden

Joseph M. Patt
Department of Botany (KB-15), University of Washington,
Seattle 98195

Abstract

Lysichiton americanum Hultén & St. John (Araceae) is pollinated by *Pelecomalius testaceum* Mann. (Staphylinidae), a rove beetle, which utilizes the inflorescences as a mating site and food source. The fragrance produced by the inflorescences is the first cue in the attraction of the beetles. It elicits in the beetles a search behavior for the yellow color typical of the spathe.

The pollination biology of Araceae, a family of over 2000 species, has been documented only in a few dozen cases. Many species are apparently pollinated by large scarabaeid beetles, which utilize them as food sources, mating sites, and hideouts during the day (Schrottky 1910, van der Pijl 1937, Beach 1982, Pellmyr in press). Others have trap inflorescences, where pollinators such as flies and beetles enter during the female phase of the flowers and depart after pollen has been shed on them (Knoll 1926, Vogel 1978). In a few cases, secondary adaptations to pollination by euglossine bees have been recorded (Williams and Dressler 1976, Meeuse and Morris 1984).

Most members of the family grow in tropical or subtropical regions; however, about 10 species are known from temperate parts of North America. Early in the spring, the bright yellow spathe of *Lysichiton americanum* Hultén & St. John is a prominent feature in swampy places in the Pacific Northwest. The yellow color is unusual in the family; it could be expected therefore to be of major significance in the pollination system of *L. americanum.* There are, however, no reported studies of this species. Raven et al. (1981) stated that "... small, actively flying [staphylinid] beetles ..." pollinate the flowers, but did not present further evidence. In the present study, we describe the pollination system of *L. americanum.*

Materials and Methods

Floral morphology, phenology, and pollination. Observations were made from 1 to 22 April 1984 at three localities in the Seattle area

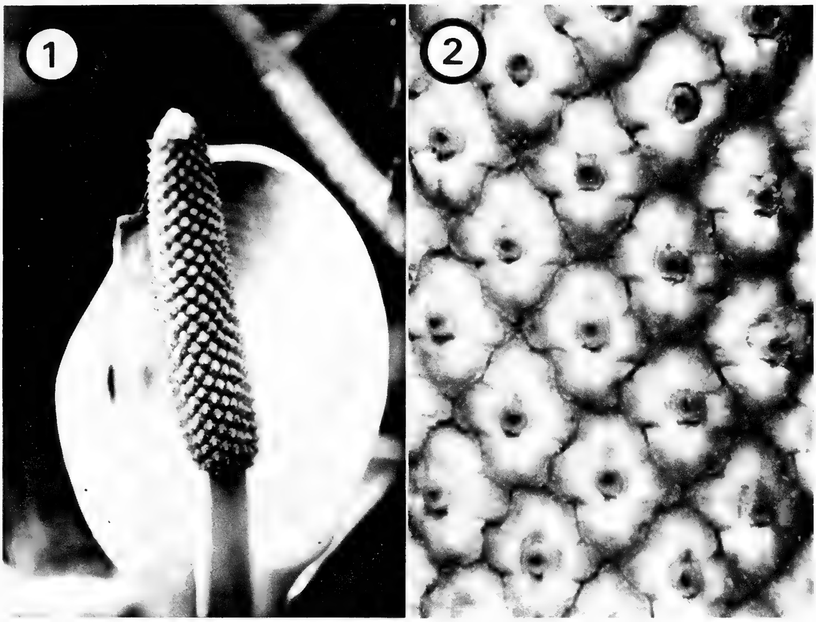
Madroño, Vol. 33, No. 1, pp. 47–54, 27 March 1986

(Kirkland; Issaquah; Ravenna Park, Seattle) and near Soleduck River on the Olympic Peninsula. Population sizes ranged between 50 and ca. 500 ramets. The study included observations of floral phenology, visitor diversity, and pollinator behavior. The pollen/ovule (P/O) ratio and spectral composition of reflected light from the spathe were determined. Three ramets were put under net cages (1 mm mesh) slightly before anthesis to test for self-compatibility. Six individuals were hand-pollinated to determine whether complete fruit-set could be accomplished. In the largest population examined, three 15 × 15 cm plastic plates, covered with glycerin jelly, were put on stalks at inflorescence height to trap possible wind-carried pollen. The traps were recovered after 48 hours and checked (under a microscope) for pollen.

Flower visitors and their behavior. The identity and frequency of insect visitors was determined by observation of flowering populations for a total of ca. 30 hours. The effect of floral odor and spathe color in attraction of the primary pollinator, *Pelecomalius testaceum* Mann., was studied. A series of experiments were performed inside of a net cage (3 × 1.5 × 1 m) inside a greenhouse. Beetles were collected from inflorescences in the field in the late afternoon, starved overnight in a refrigerator at about 10°C, and released in the cage the following morning. Fifty cm from the point of release, plant parts of *Lysichiton* were presented in experiments of choice to the beetles in the following combinations: 1) two sealed petri dishes (diam. 15 cm), the first containing green leaves only, and the second a yellow spathe; 2) two sealed petri dishes, both containing green leaves but one also including a spadix concealed between the leaves and 100 small perforations in the dish, allowing passage of fragrance; 3) similar dishes as in 1, plus a visible spathe in a vase; 4) two spathes, one bearing a male-phase spadix, and the other a female-phase spadix. In each experiment 40 beetles were used, and the number of approaches and alightings to the different samples were recorded for 30 minute intervals. The glass in the petri dishes may have affected the beetles attraction to the materials kept inside because it would prevent passage of UV light; however, because reflectance off of the spathe surface was very low in the UV region, any filtering of light by the glass was deemed unimportant.

RESULTS

Floral morphology and phenology. The inflorescence of *L. americanum* consists of an elongate spadix of small hermaphroditic flowers (Fig. 1). The 6–15 cm long spadix has 350–1350 ($\bar{x} = 690$, s.d. 236; $n = 14$) flowers. Each unicarpellate flower contains one or rarely two ovules ($\bar{x} = 1.01$; $n = 163$). Four stamens arise from the base of each flower (Fig. 2). Flowering within the inflorescence is syn-



FIGS. 1, 2. Photographs of *Lysichiton americanum.* FIG. 1. Inflorescence in female phase, 0.4× magnification. FIG. 2. Female-phase flowers at 4.6× magnification; the lower stamen of some flowers are ready to dehisce.

chronous or weakly acropetalous. The spadix is partly surrounded by a 15–25 cm long spathe. During the last two to four days before anthesis, xanthophyll accumulates in the spathe, which causes it to become bright yellow at maturity. When the spathe opens up, the flowers inside are in female phase. The stigmas remain receptive for 5–6 days. Two lateral stamens appear and dehisce on day five or six of stigmatic receptivity, and the two other stamens dehisce about two days later. Wilting occurs 5–8 days after start of the male phase. The inflorescence produces a distinctive fragrance from the first day of anthesis. It gradually ceases by the end of the male phase. This odor is noticeably different from the "skunk" odor of the vegetative parts.

The P/O ratio of *Lysichiton* was 76,912:1 (s.e. 2689; n = 10). Raphides were found in several pollen samples.

Breeding system experiments. Of the three inflorescences that were caged in the field and left untouched, two were recovered. Fruit-set was 100%. This suggests that *Lysichiton* is self-compatible and capable of self-pollination due to partial temporal overlap between male and female function in the inflorescences. Of the six hand-pollinated individuals, four were lost to a landfill operation, but the remaining two set 100% fruit. Conifer grains on the wind pollen traps were abundant, but no *Lysichiton* pollen was found, suggesting an absence of wind-pollination in this species.

Flower visitors. The only regular flower visitors were the beetles *Pelecomalius testaceus* (Staphylinidae) and *Plateumaris emarginata* (Donaciinae, Chrysomelidae). Individuals of a few other species of beetles and flies were found on inflorescences on single occasions, but they appeared to use them only as resting sites.

Pelecomalius testaceum was found exclusively on *L. americanum.* Individuals of this beetle species were 4–6 mm long, slender, brown and black in color, and carried considerable amounts of pollen on most body parts. They were undoubtedly efficient pollinators. Near flowering peak, about half the mature inflorescences had at least one beetle visiting when checked (Table 1). Beetles of both sexes fed on pollen—five individuals of each gender were dissected and the intestines contained pure *Lysichiton* pollen in every case. Visitors to female-phase inflorescences, which lack food reward, ran rapidly over the spadix. Slightly fewer beetles were found on pure female-phase inflorescences than on those in male phase. The inflorescences also serve as mating sites for the beetles. Males flew between inflorescences and ran over them, searching for females. When a female was found, the male always mounted her, stroked her tergites by lateral abdominal movements, and tried to copulate. Female refusal led to chases over the flowers, and if the male was too persistent the female flew to another inflorescence. When copulation occurred, the couple usually moved to a position between flowers on a part of the spadix appressed against the spathe. Covered with pollen, the beetles are hardly discerned. Alternative resting sites were in the slightly incurved apex of the spathe, or located as far as possible down the stem of the spathe. Beetles were found throughout the duration of anthesis of *L. americanum,* and beetle mating activity peaked simultaneously with flowering. One mutant genet with green fragrant spathes was never observed to be visited by *Pelecomalius.*

Individuals of *Plateumaris emarginata* were found sitting on various flower parts, often *in copula.* Their intestines were empty of pollen, and the beetles only became common by the end of the flowering season. They are poor pollen vectors because of the low rate of movement between inflorescences, combined with the small amount of pollen that adhered to their bodies. There is reason to believe, however, that *L. americanum* is its host plant, because all donaciine beetles utilize species of Nymphaeaceae or aquatic monocotyledons as larval development sites (Crowson 1981).

Experiments testing visual and olfactory stimuli on beetle attraction. The results of the experiments are shown in Table 2. In experiment one, sealed petri dishes received only occasional alightings,

TABLE 1. PERCENT ATTRACTIVE INFLORESCENCES OF *Lysichiton americanum* AT THE STUDY SITES THAT HAD AT LEAST ONE VISITING *Pelecomalius testaceum*.

Locality	n	Percent
Ravenna Park, Seattle (2 April)	86	64
(4 April)	52	42
Kirkland (16 April) (after peak)	100	15
Issaquah (16 April) (after peak)	12	25

independent of color of the content. Most beetles flew around in the cage, but almost completely ignored both dishes. When presented the green dishes in experiment two, beetle alighting frequency on the fragrant dish was significantly higher than on the non-fragrant one. Beetles typically alighted on the fragrant dish and ran over it, in some cases for about 15 minutes, looking for a place to enter. Some beetles managed to force their way into the dish, despite the fact that a green leaf was pressed tightly against the holes from the inside. When presented a fragrant, exposed spathe and the two dishes in the third experiment, visit frequency was more than two and a half times as high on the exposed spadix as it was on the green, fragrant dish ($G = 10.321$; $df = 1$; $p < 0.005$). When given a choice between inflorescences exhibiting spadices in female and male phase in experiment four, no significant preference was shown.

DISCUSSION

Our data strongly suggest that *L. americanum* is adapted for pollination by the staphylinid beetle, *Pelecomalius testaceum.* In *Arum nigrum,* staphylinids constituted a minority of all visitors, and were believed to effect some pollination (Knoll 1926). Whigham (1974) suggested that staphylinids pollinate *Uvularia perfoliata* (Liliaceae), but did not present convincing evidence. Staphylinids are common visitors in many flowers (Knuth 1898–1904, Hatch 1957), but appear to pollinate them only rarely.

The P/O ratio in *L. americanum* is about 100 times higher than for the average self-compatible species (Cruden 1977), and may be interpreted as an indication of wind-pollination. It is equally possible, however, that this ratio is the result of the function of pollen as the pollinator reward, together with the relative inefficiency of beetles as pollinators compared, for example, to bees (Pellmyr 1985). Camazine and Niklas (1984) suggested that the closely related *Symplocarpus foetidus* may be wind-pollinated, rather than insect-pollinated. This conclusion was based on the scarcity of insects, documented by the authors as well as earlier investigators (e.g., Trelease 1879), aerodynamic properties of the spathe, poor synchronization of flowering within populations (Niklas, pers. comm.),

TABLE 2. RESULTS FROM EXPERIMENTS ON FUNCTION OF COLOR AND FRAGRANCE IN ATTRACTION OF *Pelecomalius testaceum.* Numbers represent individual beetles observed during 30 minute intervals.

Experiment	No. of approaches only	No. of alightings	G-test
1.			
Spathe in sealed dish	4	1	G = 1.386
Leaf in sealed dish	0	0	df = 1; n.s.
2.			
Leaf in sealed dish	1	1	G = 14.699 df = 1; $p < 0.001$
Spathe hidden between leaves in perforated dish	2	15	
3.			
Spathe in sealed dish	1	3	G = 68.002 df = 2; $p < 0.001$
Leaf in sealed dish	0	0	
Spathe in vase	0	38	
4.			
Inflorescence with female-stage spadix	1	13	G = 1.202
Inflorescence with male-stage spadix	2	8	df = 1; n.s.

and considerable flexibility in flowering time between years. Although the aerodynamic properties of the open spathe of *L. americanum* are unknown, potential pollinators are present and flowering time is relatively constant between years (Meeuse, pers. comm.) and highly synchronized within populations. These characteristics together with the absence of *Lysichiton* pollen on the pollen traps suggest insect pollination rather than wind-pollination in *L. americanum.*

Successful attraction to female-phase flowers, where rewards are lacking, may be a case of "pollination by deceit" (sensu Baker 1976). The inflorescence, however, still serves the function of a mating site, a crucial resource to the beetles, and thus the system cannot be considered entirely deceptive.

The behavior experiments indicate a sequential function of stimuli in attraction of beetles. Odor alone induced search behavior, whereas non-odorous yellow dishes did not. When the entire spathe was exposed, the number of alightings increased with a factor of about 2.5. This suggests that the fragrance elicits search behavior in *P. testaceum* for yellow objects. A few similar cases are known from nocturnal as well as diurnal moths—the fragrance of *Melandrium album* (Caryophyllaceae) induces search for white objects in *Hadena* (Noctuidae) (Brantjes 1976), and several plusiine moths behave similarly when exposed to fragrance of *Platanthera* spp. (Orchidaceae)

(Nilsson 1978) and other flowers (Schremmer 1941). Although strong fragrance is typical of most beetle-pollinated flowers (Faegri and van der Pijl 1979), the sensory steps in pollinator attraction are usually not known. It is important to point out that these experiments did not allow the conclusion that the beetles possess color vision. Because we could not match green leaves and yellow spathes for brightness, it is possible that the insects only detected differences in brightness. Knoll (1926) used purple and white glass models to study the effects of odor on the pollinators of the purple-spathed *Arum nigrum.* Presence of the carrion-like odor resulted in as many visits to each of the models as to the natural flowers. The results demonstrate that the odor could attract the visitors, but his experiments are inconclusive as to whether visual stimuli are important in pollinator attraction.

Pelecomalius testaceum is apparently heavily specialized on *Lysichiton americanum* during its adult life. The inflorescence is a focal spot for mating activities, it provides some degree of shelter during mating, and it is a cornucopia of food. The life-cycle of the genus *Pelecomalius* may be closely tied to *Lysichiton.* A number of species were described by Casey (1886, 1893) from small numbers of individuals collected on or around *L. americanum* in California. Several were not recognized by Schwarz (1892), and Hatch (1957) listed only two species, both with distributions well matching that of *Lysichiton americanum.*

In Japan and the northern Pacific parts of Asia, *Lysichiton camtschatkense* grows in much the same habitats as its North American vicariant (Ohwi 1984). The only obvious difference from *L. americanum* is its bright white spathe. Studies of the pollination biology of *L. camtschatkense* could provide data for a better understanding of the evolution of interaction between *Pelecomalius* and *Lysichiton.*

ACKNOWLEDGMENTS

We thank Bastiaan J. D. Meeuse for sharing his knowledge of the Araceae, for showing us several populations of *L. americanum,* and for having the 1984 pollination class perform thin-layer chromatography of spathe pigment extractions for us; Douglas Ewing for access to the greenhouse cage; the Remote Sensing Lab at the University of Washington for help with reflectance analyses; and B. J. D. Meeuse, Angela M. Brown, Robert A. Schlising, and two anonymous reviewers for comments on the manuscript.

LITERATURE CITED

BAKER, H. G. 1976. "Mistake" pollination as a reproductive system with special reference to the Caricaceae. *In* J. Burley and B. T. Styles, eds., Tropical trees: variation, breeding, and conservation, p. 161–169. Academic Press, New York.

BEACH, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Amer. J. Bot. 69:1074–1081.

BRANTJES, N. B. M. 1976. Riddles around the pollination of *Melandrium album*

(Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae, Lepidoptera), I + II. Proc. Konikl. Ned. Akad. Wetensch., Ser. C, Biol. Med. Sci. 79:1–12, 127–141.

CAMAZINE, S. and K. J. NIKLAS. 1984. Aerobiology of *Symplocarpus foetidus*: interactions between the spathe and spadix. Amer. J. Bot. 71:843–850.

CASEY, T. L. 1886. Descriptive notices of North American Coleoptera. I. Bull. Calif. Acad. Sci. 2:157–264.

———. 1893. Coleopterological notices. V. Ann. New York Acad. Sci. 7:281–606.

CROWSON, R. A. 1981. The biology of the Coleoptera. Academic Press, London.

CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31:32–46.

FAEGRI, K. and L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd ed. Pergamon Press, Oxford.

HATCH, M. H. 1957. The beetles of the Pacific Northwest, part II. Univ. Washington Press, Seattle.

KNOLL, F. 1926. Insekten und Blumen. IV. Die Arum-Blütenstande und Ihre Besucher. Abh. K. K. Zool.-Bot. Ges. Wien 12:383–481 + 1 plate.

KNUTH, P. 1898–1904. Handbuch der Blütenbiologie I–III. Engelmann, Leipzig.

MEEUSE, B. and S. MORRIS. 1984. The sex life of flowers. Facts on File Publ., New York.

NILSSON, L. A. 1978. Pollination ecology and adaptation in *Platanthera chlorantha* (Orchidaceae). Bot. Not. 131:35–51.

OHWI, J. 1984. Flora of Japan, 2nd ed. Smithsonian Press, Washington, DC.

PELLMYR, O. 1985. Pollination biology of *Cimicifuga arizonica* (Ranunculaceae). Bot. Gaz. (Chicago) 146:404–412.

———. In press. *Cyclocephala*: visitor and probable pollinator of *Caladium bicolor* (Araceae). Acta Amaz.

RAVEN, P. H., H. EVERT, and H. CURTIS. 1981. The biology of plants, 3rd ed. Worth Publishers, New York.

SCHREMMER, F. 1941. Sinnesphysiologie und Blumenbesuch des Falters von *Plusia gamma* L. Zool. Jahrb. 74:375–434.

SCHROTTKY, C. 1910. Die Befruchtung von *Philodendron* und *Caladium* durch einen Kafer (*Erioscelis emarginata* Mann.). Zeitschr. Wiss. Insektenbiol. 6:67–68.

SCHWARZ, E. A. 1892. In protocol from meetings. Proc. Entomol. Soc. Wash. 2: 396.

TRELEASE, W. 1879. On the fertilization of *Symplocarpus foetidus*. Amer. Naturalist 13:580–581.

VAN DER PIJL, L. 1937. Biological and physiological observations on the inflorescence of *Amorphophallus*. Rev. Trav. Bot. Neerl. 34:157–167.

VOGEL, S. 1978. Pilzmückenblumen als Pilzmimeten. Flora 167:367–398.

WHIGHAM, D. 1974. An ecological life history study of *Uvularia perfoliata* L. Am. Midl. Naturalist 91:343–359.

WILLIAMS, N. H. and R. L. DRESSLER. 1976. Euglossine pollination of *Spathiphyllum* (Araceae). Selbyana 1:349–356.

(Received 28 Jan 1985; revision accepted 17 Oct 1985.)

AN APPARENT CASE OF INTROGRESSION BETWEEN PINYON PINES OF THE NEW YORK MOUNTAINS, EASTERN MOJAVE DESERT

JAMES DES LAURIERS
Department of Biology, Chaffey Community College,
Alta Loma, CA 91701

MARK IKEDA
Department of Biological Sciences,
California State Polytechnic University, Pomona 91768

ABSTRACT

The pinyon pines in the New York Mountains of the Mojave Desert are polymorphic along an altitudinal gradient. The possibility that this gradient is the result of hybridization between *Pinus monophylla* and *P. edulis* is the subject of this study. Counts of needle number per fascicle, resin canal number per needle, and cone width were made over the entire altitudinal range of distribution of the pine community. We conclude that there are two species present and that an extensive altitudinal zone of introgression exists at intermediate elevations.

The characterization of the pinyon pines in the New York Mountains, San Bernardino County, California, has been addressed by several authors (Lanner 1974, Vasek and Thorne 1977, Trombulak and Cody 1980, Thorne et al. 1981). The slopes of the New York Mountains are described as containing the westernmost sympatric distribution of *Pinus edulis* and *P. monophylla* (Griffin and Critchfield 1972). Lanner (1974), however, concluded that *P. monophylla* is the only species present and that the two-needle form represents a mutant to the ancestral two-needle condition. His argument was based on the resemblance of other morphological characters to those of *P. monophylla.* Trombulak and Cody (1980) found that the proportion of two-needle fascicles on individual trees showed a nearly disjunct distribution with practically no trees displaying intermediate proportions, and concluded that both *P. monophylla* and *P. edulis* were present with the latter species limited to higher elevations. Their transects were near Prospect Canyon on the north side of New York Peak.

Reported here are the results of a new study carried out in a south-facing drainage on the same mountain. We describe an altitudinal zone of intergradation between the one- and two-needle forms and speculate on its significance.

MADROÑO, Vol. 33, No. 1, pp. 55–62, 27 March 1986

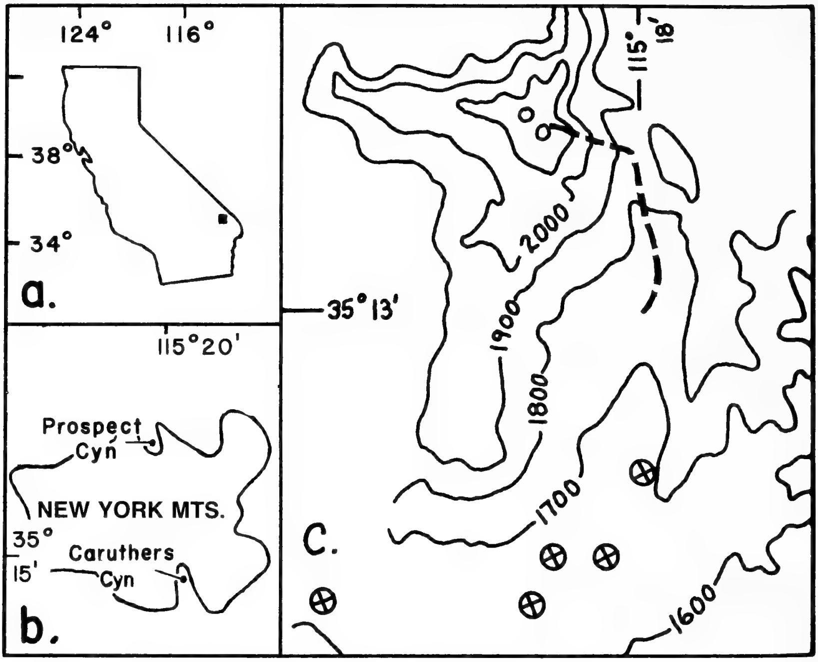


FIG. 1. Location of the transect. a. Map of California. Dark square shows location of New York Mountains. b. New York Mountain range showing both Prospect and Caruthers Canyons. c. Topographic map with 100 m contour intervals showing transect location (dashed line) in Caruthers Canyon. The 5 isolated stations (⊗) are on outcrops at the lower limit of pinyon distribution.

STUDY SITE AND METHODS

Data were collected during the month of May in the years 1981–1985. A transect was placed in the Caruthers Canyon drainage (Fig. 1). The transect followed the jeep road north from the lower limit of pinyons at an elevation of 1620 m to the Giant Ledge Mine, then up an east-facing slope to the peak. The sampling stations along the transect tended to occupy the more mesic situations in the drainage. Elevations and positions were determined using a Thommen temperature compensated altimeter and by triangulation using a Brunton Pocket Transit and USGS topographic maps (Ivanpah, CA, and Midhills, CA, quadrangles).

At 5–60 m increments in elevation, 8–25 trees were sampled. The terminal 15–20 cm segment of a twig was taken at about chest height from the side of the tree most exposed to illumination. From the cut end of the twig the first 20 fascicles were classified as bearing one or two needles. Three-needle fascicles were reported as two-needle ones. The mean number of two-needle fascicles was computed for each collecting station.

Resin canal numbers were determined from an additional 11–15 twigs (one twig per tree), obtained at each station in a manner similar to that described above. Trees were selected for sampling without regard to which had been sampled previously for fascicle ratio. Five needles were selected at random from near the cut end of each twig. Counts of resin canals in razor-sectioned needles were made under a 10× hand lens. When two-needle fascicles were sampled only one of the two needles was counted.

Sampling was repeated at all but the highest two stations, where measurements of fascicle ratio and resin canal numbers were taken from one twig from each of ten trees at each station. Each twig yielded 20 fascicle counts and five resin canal counts.

Thirty intact seed cones were collected haphazardly from the ground at each station. Vernier calipers were used to obtain the greatest diameter of each cone, to the nearest 0.1 mm.

RESULTS

The frequency of one- and two-needle fascicles on individual trees is shown in Fig. 2B. Of the 388 trees sampled, 122 (31%) showed a range between 20–80 percent two-needle fascicles. A strong altitudinal shift occurred in the proportion of two-needle fascicles.

The proportion of two-needle fascicles (Y) plotted against elevation (X) is illustrated in Fig. 3. The proportion of two-needle fascicles rises sharply between 1700–1900 m and then changes more slowly to the peak. The data are best described by the sigmoid equation

$$Y = \frac{20}{1 + 1.21 \times 10^{49} X^{-14.93}} \quad r^2 = 0.89, \quad p \ll 0.01. \qquad \text{(eq. 1)}$$

The elevation at which 50 percent of the sampled fascicles contain two needles ($X_{0.5}$, the turnover elevation) is computed from the regression equation to be 1940 m.

The average number of resin canals per needle (Y) is plotted against elevation (X) (Fig. 3). The average number of resin canals per needle declines sharply between 1620–1860 m. From that elevation to the peak, the number of resin canals changes only slightly (Fig. 3). The data are described best by the sigmoid equation

$$Y = \frac{9}{1 + 7.50 \times 10^{-25} X^{7.38}} \quad r^2 = 0.87, \quad p \ll 0.01. \qquad \text{(eq. 2)}$$

The mean number of resin canals for all needles sampled below 1900 m equals 5.5 ± 0.9, n = 950 ($\bar{X} \pm$ 95% confidence interval). This

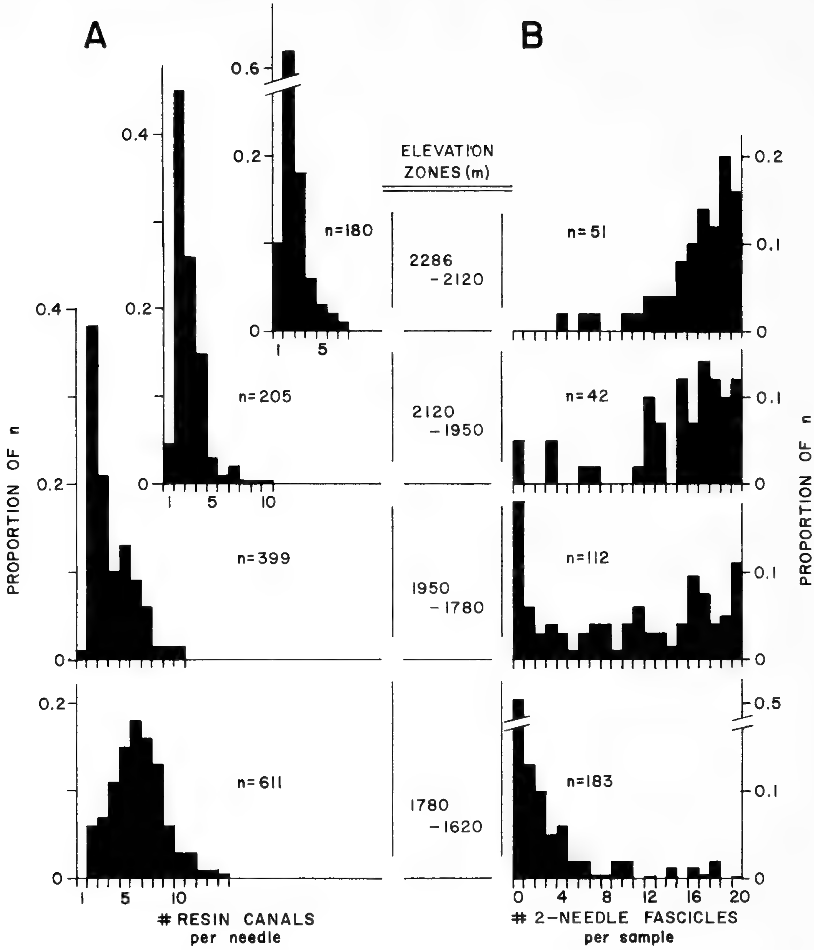


FIG. 2. A. Frequency distribution of the proportion of the sample of needles (n) against resin canal number per needle in four elevation zones. B. The proportion of individual tree samples (n) is plotted against the number of two-needle fascicles per 20 needle sample in four elevation zones.

value does not differ significantly from that reported for *P. monophylla* (4.9 ± 1.1) by Lanner (1974). For the trees above 1900 m the number of resin canals equals 2.7 ± 0.2, n = 445. Lanner's value for *P. edulis* (2.0 ± 0.1) is smaller than that we obtained. The mean resin canal number above 1900 m is significantly lower ($t = 4.12$; $p < 0.001$) than it is at lower elevations.

There is a highly significant correlation ($t = 8.23$, $p \ll 0.01$) between the mean number of two-needle fascicles and the mean number of resin canals per needle (Fig. 4). The values near the x-axis are

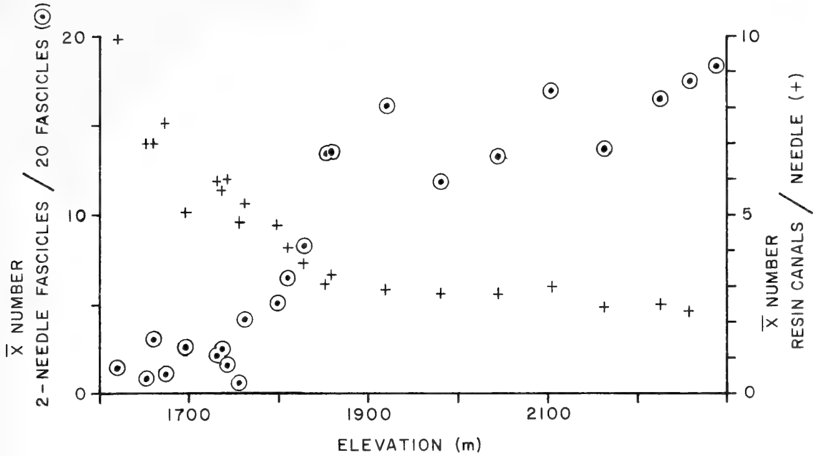


FIG. 3. Change in the mean number of two-needle fascicles per 20 fascicle sample over elevation (circles) and the change in mean number of resin canals per needle over elevation (crosses). Needle number is plotted to the left and resin canal number is at the right.

from sites at the highest elevations and are typical of *P. edulis.* The values near the y-axis are from low elevation sites and resemble *P. monophylla.* The intermediate points are from stations at intermediate elevations.

Seed cone diameter varies independently of elevation. The mean maximum cone diameter for the entire sample equals 54.8 ± 2.5, n = 660. This value is not significantly different from Lanner's (1974) value for widely dispersed hybrid populations in the western U.S. (53.2 ± 5.9, range 30–87 mm). Lanner also reports cone diameters for *P. edulis* and *P. monophylla* as 42.5 ± 4.6, range 20–68 mm and 64.6 ± 4.8, range 39–80 mm, respectively.

DISCUSSION

Lanner (1974) concluded that the ratio of one-needled to two-needled fascicles is heritable. Experimental *P. monophylla* × *P. edulis* hybrids exhibited a 0.5 ratio. In comparing mesic and xeric sites, he also concluded that for *P. monophylla* the ratio is stable and insensitive to site differences.

The transition of trees with one-needle fascicles and several resin canals at lower elevations and on arid slopes toward two-needle, two-resin-canal plants in higher, presumably moister locations is compatible with expectations about *P. monophylla* and *P. edulis.* Trombulak and Cody (1980) present a scenario of progressive replacement of *P. edulis* by *P. monophylla* upward on the slopes in-

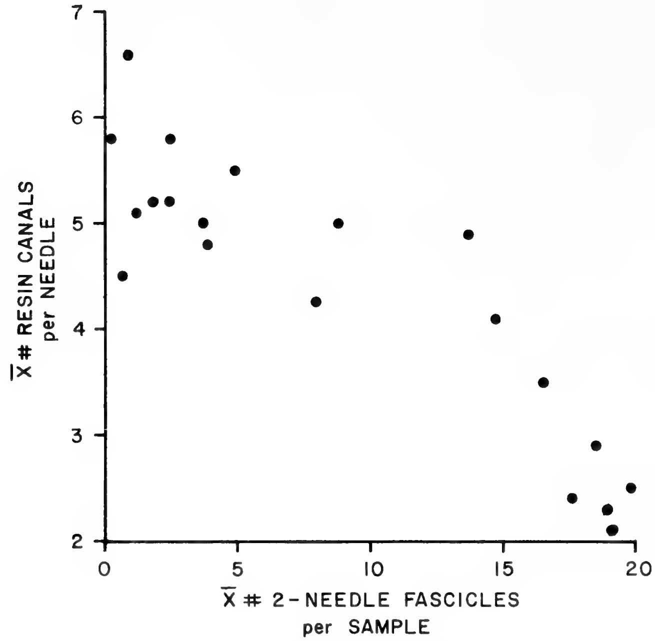


FIG. 4. Relationship between the mean number of two-needle fascicles per 20 fascicle sample and the mean number of resin canals per needle per 50 needle sample. Each point represents one sample station containing 10 trees.

duced by generally more arid conditions since pluvial times. The $X_{0.5}$ needle ratio values they obtained (1680 m and 1834 m) are lower on north-facing slopes than is the value we obtained (1940 m, computed from equation 1) on the south side of the range (Fig. 3). We would add that frost hardiness, especially in seedlings, may be greater in *P. edulis* (R. M. Beeks, pers. comm.), thus making it a superior competitor only at greater elevation and on north-facing slopes. Together these results are consistent with the Trombulak and Cody interpretation of an interaction between the two taxa that is mediated by moisture and temperature (see also Wells 1979, 1983).

The decline in resin canal number that occurs over the same altitudinal range (Figs. 2A, 3) supports the evidence that a zone of intergradation exists between the two taxa. This trait, however, is highly sensitive to site differences. Lanner (1974) showed a 40 percent increase in the number of resin canals in *P. monophylla* when the samples from arid sites ($\bar{X}$ = 5.06 canals) were compared to mesic ones ($\bar{X}$ = 3.62 canals) in the Raft River Mountains, Utah. The impact of this moisture response in our study is minimized by our deliberate choice of mesic sites to sample. This shifting relationship of needle number to resin canal number (Fig. 4) is a pattern found elsewhere in hybrid swarms of *P. monophylla* × *P. edulis* (Lanner 1974). Alternatively, but less parsimoniously, the pattern of intergradation might be produced by primary differentiation of altitudinal races or species.

Finally, seed cone size variation is chaotic. The population mean, however, is the same as that obtained for hybrid populations elsewhere in the southwestern U.S. (Lanner 1974). Because this trait overlaps broadly in the two species, it is of little value here in attempting to characterize hybrids.

Endler (1982) defined the width of contact zones between hybridizing species as the region having hybrid index values between 0.2 and 0.8. A substantial number (31%) of the individuals in our sample have those intermediate proportions of two-needle fascicles at middle elevations (Fig. 2B). The distribution shown in Fig. 2B differs significantly ($\chi^2 = 202$; $p < 0.001$) from that obtained by Trombulak and Cody (1980, p. 64). They found practically no trees having intermediate proportions of two-needle fascicles in Prospect Canyon on the north side of New York Peak. They interpret their result as distinguishing clearly between *P. monophylla* and *P. edulis* in the New York Mountains. The distinction fails in Caruthers Canyon, on the south side. In fact, the pattern demonstrated (Fig. 3) shows a zone of intergradation and suggests introgression between about 1700 and 1900 m elevation.

In conclusion, the trees near the peak appear to be a remnant stand of *P. edulis* whose distinctiveness is reduced by hybridization with the regionally abundant *P. monophylla.* The fact that populations in Caruthers and Prospect Canyons show different patterns is particularly interesting. Any explanation for the difference awaits further study.

ACKNOWLEDGMENTS

The students in the Chaffey College Population Biology course during 1981–1985 sweated up hot mountainsides and braved grumpy rattlesnakes. Their eager cooperation is greatly appreciated. Various drafts of this paper were commented on by Drs. Richard M. Beeks, Curtis Clark, Ronald M. Lanner, and David Moriarty. Dr. Moriarty also provided statistical advice.

LITERATURE CITED

ENDLER, J. 1982. Problems in distinguishing historical from ecological factors in biogeography. Amer. Zool. 22:441–452.

GRIFFIN, J. R. and W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S.D.A. Forest Serv. Res. Pap. PSW-82.

LANNER, R. M. 1974. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American southwest. Silvae Genet. 23:108–116.

THORNE, R. F., B. A. PRIGGE, and J. HENDRICKSON. 1981. A flora of the higher ranges and the Kelso dunes of the eastern Mojave desert in California. Aliso 10: 71–186.

TROMBULAK, S. C. and M. L. CODY. 1980. Elevational distribution of *Pinus edulis* and *P. monophylla* (Pinaceae) in the New York Mountains, eastern Mojave Desert. Madroño 27:61–67.

VASEK, F. C. and R. F. THORNE. 1977. Transmontane coniferous vegetation. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 797–834. J. Wiley-Interscience, New York.

WELLS, P. V. 1979. An equable glaciopluvial in the West: pleniglacial evidence of increased precipitation on a gradient from the Great Basin to the Sonoran and Chihuahuan Deserts. Quaternary Research 12:31–325.

———. 1983. Paleobiogeography of the montane islands in the Great Basin since the last glaciopluvial. Ecol. Monogr. 53:341–382.

(Received 9 Jan 1985; revision accepted 18 Oct 1985.)

ANNOUNCEMENT

SYMPOSIUM TO HONOR G. LEDYARD STEBBINS

An International Symposium will be held in Davis, California, on 12–14 September 1986, to honor Professor G. Ledyard Stebbins in the year of his 80th birthday. Invited talks by leading plant biologists will include topics in population and ecological genetics, organelle and nuclear molecular genetics, morphogenesis and plant development, and evolution and systematics. For further information please contact: Dr. L. D. Gottlieb, Department of Genetics, or Dr. S. K. Jain, Department of Agronomy and Range Science, University of California, Davis, CA 95616.

SYSTEMATICS OF *COLLINSIA PARVIFLORA* AND *C. GRANDIFLORA* (SCROPHULARIACEAE)

FRED R. GANDERS
Department of Botany, University of British Columbia,
Vancouver, B.C. V6T 2B1, Canada

GERDA R. KRAUSE
Department of Biology, Langara Campus
Vancouver Community College,
Vancouver, B.C. V5Y 2Z6, Canada

ABSTRACT

Collinsia parviflora and *C. grandiflora* are distinguished primarily on the basis of flower size, but intermediate populations are more numerous than either small- or large-flowered populations in coastal British Columbia. Experimental hybridizations demonstrated that populations of all flower sizes are completely interfertile, and all are tetraploid with $2n = 28$. Flower size in F_1 hybrids was intermediate between the parents, and the F_2 generation showed a greater range than the F_1, indicating segregation at several loci. We consider the two taxa to be intergrading varieties of one species, *C. parviflora* Dougl. ex Lindl. var. *parviflora* and **C. parviflora** var. **grandiflora** (Dougl. ex Lindl.) Ganders & Krause.

Collinsia parviflora Dougl. ex Lindl. and *C. grandiflora* Dougl. ex Lindl. are the only species of this predominantly Californian genus that are found in western Washington and British Columbia. They are very similar, being distinguished primarily on the basis of flower size. In their extreme forms, the flowers are very different in appearance. *Collinsia parviflora* has corollas 4–5 mm in length and the flowers are highly to completely autogamous. *Collinsia grandiflora* has corollas 10–17 mm in length and sets few seeds if pollinators are excluded, although it is completely self-compatible. West of the Cascade Mountains in British Columbia and Washington State most populations of *Collinsia* have flowers intermediate in size (Fig. 1). These intermediate populations have been named as varieties of one species or the other or even treated as a separate species, although recent floristic treatments do not accept the intermediate taxa (Hitchcock et al. 1959, Taylor and MacBryde 1977). In her monograph of the genus, Newsom (1929) noted, "In studying these two closely allied species, one finds a continuous series of intergradation from the largest-flowered *grandiflora* var. *typica* through *grandiflora* var. *pusilla* to the smallest-flowered *parviflora,* and yet the two extremes differ greatly." Nevertheless, all authors have maintained the two as specifically distinct. The dividing line between *C. parviflora* and *C. grandiflora,* however, has been drawn arbitrarily at different flow-

---

MADROÑO, Vol. 33, No. 1, pp. 63–70, 27 March 1986

er sizes by different authors. Only St. John (1956) and Peck (1961) formally recognized any overlap in flower size between the two species. Some authors, notably Gilkey and Dennis (1980), make the two species appear to be quite distinct.

Garber (1956, 1958, 1974) reported both *C. parviflora* and *C. grandiflora* to be diploids with $n = 7$. Unfortunately Garber cited neither voucher specimens nor localities for the plants on which the counts were based, although the plants were probably from California because the seeds from which he grew the plants were sent to him by people living in California. Taylor and Mulligan (1968) reported *C. parviflora* from Haida Point, Graham Island, in the Queen Charlotte Islands, British Columbia, to be tetraploid with $n = 14$.

The distribution of flower sizes among populations in British Columbia suggests that the two species recognized traditionally may just represent the extremes of a single variable species. Flower sizes are not correlated with other morphological characters (Krause 1978). The reports of both diploid and tetraploid chromosome numbers suggest, however, the possibility that ploidy level may be correlated with flower size. We analyzed experimental intra- and interpopulational hybridizations and counted chromosome numbers to determine the taxonomic relationship of the two species and their intermediate populations.

MATERIALS AND METHODS

Seeds were collected from the localities shown in Fig. 1, all in British Columbia except one population from Anacortes, WA, USA. Plants were grown from seed in growth chambers under a long-day regime of 16 hr light at 20°C and 8 hr dark at 10°C. Total corolla length was measured on these plants.

Interpopulational hybridizations were made in growth chambers. Seed parents were emasculated in bud by removing anthers with fine forceps, and were pollinated several days later. Crosses involving small-flowered plants were difficult to make because emasculation of small buds was difficult and small flowers produced few pollen grains. Hybrids involving the Lindeman Lake population were obtained using this population as the male parent only, because the small buds were destroyed by our attempts to emasculate them.

Inheritance of flower size was investigated in five interpopulational crosses. In the genetic studies of corolla size, corolla length was measured from the tip of the lips to the bend in the corolla tube, in order to compensate for differences in the total corolla length caused solely by differences in the angle of the bend in the corolla tube. Therefore, the lengths reported in the inheritance studies are less than the total corolla lengths shown in Fig. 1.

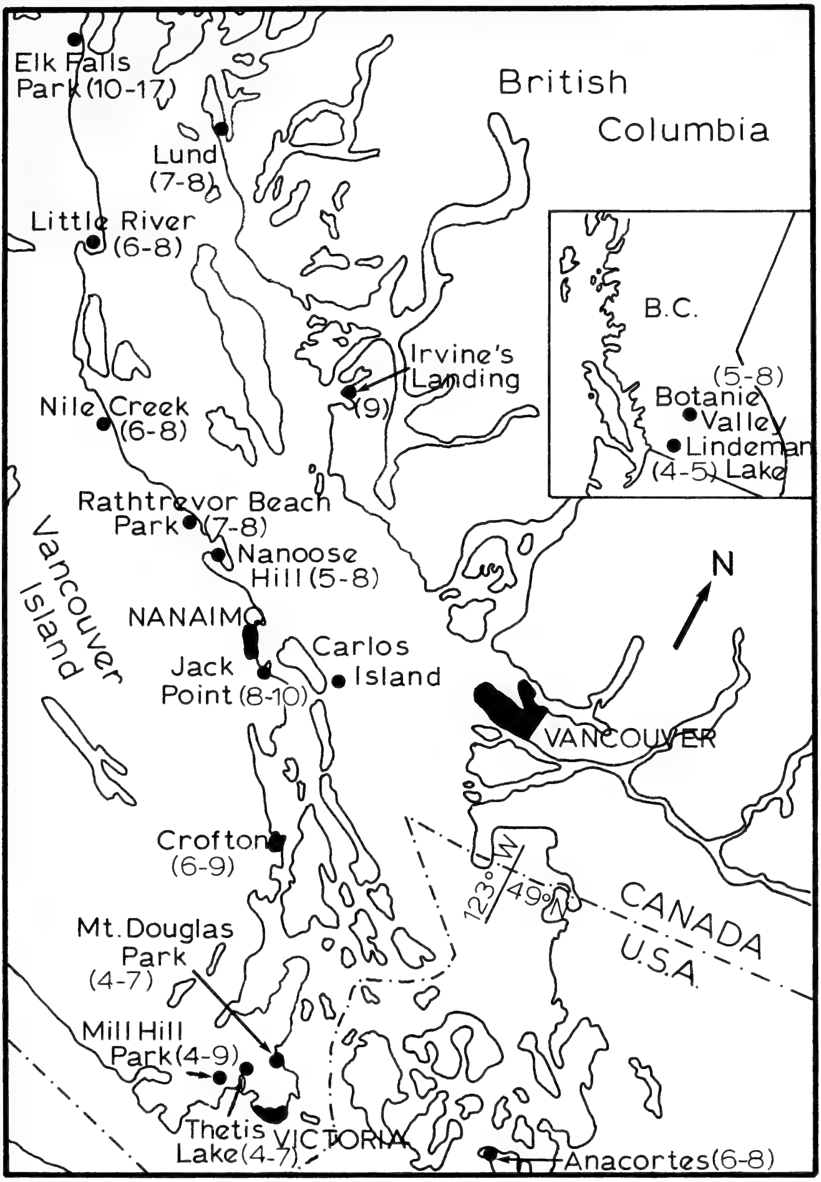


FIG. 1. Range of corolla lengths in mm in populations of *Collinsia* in southwestern British Columbia and northwestern Washington State and the localities of the populations studied. The numbers following the locality are the range of corolla lengths in each population.

TABLE 1. NUMBERS OF HYBRIDS OBTAINED IN INTER- AND INTRAPOPULATIONAL CROSSES IN *Collinsia*. All crosses attempted were successful and all hybrids completely fertile.

Parent populations	F_1 progeny (including reciprocals)	F_2 progeny
Carlos Island × Carlos Island	40	1395
Carlos Island × Jack Point	27	2529
Elk Falls × Elk Falls	14	13
Elk Falls × Botanie Valley	47	337
Elk Falls × Mt. Douglas Park	165	749
Jack Point × Jack Point	70	1401
Jack Point × Botanie Valley	67	410
Jack Point × Lindeman Lake	2	31
Jack Point × Mt. Douglas Park	42	94
Jack Point × Nanoose Hill	58	1161
Nanoose Hill × Botanie Valley	83	984
Nanoose Hill × Lindeman Lake	1	0
Nanoose Hill × Mt. Douglas Park	16	30

For chromosome counts buds were fixed in a 6:3:2 solution of ethanol, chloroform, and propionic acid and stained in alcoholic hydrochloric acid-carmine (Snow 1963). Vouchers are at UBC.

RESULTS

Chromosome counts of $2n = 28$ ($2n = 14$ pairs) were obtained from six populations: Botanie Valley, Carlos Island, Elk Falls, Jack Point, Lindeman Lake, and Nanoose Hill. These populations cover a range of flower sizes, including the populations with the largest and smallest flowers studied. The counts confirm the tetraploid status of *Collinsia* in British Columbia.

All intra- and interpopulational crosses produced vigorous, fertile hybrids; F_2 generation plants were also vigorous and fully fertile. More than 600 F_1 hybrid plants and more than 6000 F_2 hybrids were grown (Table 1). There are no intrinsic isolating mechanisms between *C. parviflora* and *C. grandiflora* or intermediate populations. Interpopulation F_1 hybrids were confirmed by intermediacy in flower size or by the use of single gene markers for flower color or leaf pigmentation (Griffiths et al. 1977, Krause 1978). A few progeny from accidental self-pollinations were detected in this way in crosses involving small-flowered plants as seed parents.

Plants from self-pollinations and intrapopulational crosses showed the same narrow range of flower sizes found in the parental populations (Krause 1978). This suggests that plants within natural populations are homozygous at most loci determining flower size. Av-

TABLE 2. SUMMARY OF CROSSES TO INVESTIGATE INHERITANCE OF FLOWER SIZES.

Parental, F_1, and F_2 populations	Flower size (mm)			Sample size	
	Range	Mean	s.d.	Flowers	Plants
Botanie Valley	3–6	4.5	0.64	27	9
Nanoose Hill	5–7	6.1	0.58	15	5
F_1	4–6	4.6	0.68	53	18
F_2	4–7	5.2	0.73	380	160
Lindeman Lake	3–4	3.7	0.49	15	5
Jack Point	6–8	6.7	0.57	18	6
(F_1 not measured)					
F_2	4–8	5.8	0.98	21	10
Botanie Valley	3–6	4.5	0.64	27	9
Jack Point	6–8	6.7	0.57	18	6
F_1	4–7	5.4	0.78	49	18
F_2	4–9	6.5	1.01	290	120
Mt. Douglas Park	3–5	4.4	0.53	47	18
Elk Falls Park	8–13	10.6	1.19	53	18
F_1	6–10	8.6	0.90	70	20
F_2	4–11	7.5	1.22	388	154
Botanie Valley	3–6	4.5	0.64	27	9
Elk Falls Park	8–13	10.6	1.19	53	18
F_1	6–9	7.5	0.82	33	11
F_2	4–11	7.3	1.39	187	107

erage flower size in interpopulation hybrids was intermediate between the parental averages, except in crosses between the Botanie Valley and Nanoose Hill populations. Both of these populations have small flowers and flower size of F_1 hybrids was not significantly different from the Botanie Valley parental population. Mean flower sizes of the F_2 generations from these interpopulation crosses also were intermediate between the parental populations, except that the F_2 from the cross between the Botanie Valley and Jack Point populations was not significantly different from the Jack Point parental population. The ranges and standard deviations of flower size in the F_2 generations were all greater than in the F_1 hybrids (Table 2). This indicates segregation at several loci controlling flower size. It was impractical to attempt to determine the number of loci because flower size is also affected by environmental and developmental factors (even in growth chambers) that tend to obscure discrete size classes and smooth out the size frequency distributions. In particular, flower size on a given plant tends to decrease with age of the plant, so that the first formed flowers are largest. Developmental differences in flower size were most prominent in plants with relatively large flowers; those with very small flowers were quite uniform in flower size throughout their life cycle.

DISCUSSION

Populations of *Collinsia* in British Columbia are uniformly tetraploid and are completely interfertile. Different populations exhibit a range of flower sizes from the smallest reported for *C. parviflora* to the largest *C. grandiflora,* but most populations in coastal British Columbia are intermediate in flower size. Although it is possible that diploid populations may exist in California (Garber 1974), chromosome number is not correlated with flower size.

We do not believe that there is any biological basis for regarding *C. parviflora* and *C. grandiflora* as separate species. Most genera of Pacific Coast annuals that have been studied biosystematically have well developed prezygotic or post-zygotic interspecific isolating mechanisms. Most recognized species of *Collinsia* will not form fertile interspecific hybrids (Garber 1974). All reported attempts to cross *C. parviflora* and *C. grandiflora* with other species of *Collinsia* have failed (Ahloowalia and Garber 1961, Garber 1974). We think that the species of *Collinsia* that form fertile hybrids should be regarded as conspecific varieties (or subspecies) rather than as separate species.

The extremes in flower size are conspicuously different and probably represent adaptations for outcrossing in large flowers and self pollination in small flowers. Seed set in unpollinated large flowers isolated from insects was low, but small flowers set full capsules and often self-pollinated before the corolla opened. Populations with flowers of intermediate size probably experience some outcrossing in nature but also are capable of full seed set by automatic selfing. Individual populations, especially those with smaller flowers, are quite uniform in flower size, indicating fixation of alleles at most loci controlling flower size. But, different populations show every degree of intermediacy in the range of flower size in the species. These populations are probably fixed for alleles for large flowers or small flowers at different numbers of loci. No other morphological character is correlated with flower size, and it is clear that all populations belong to a single species that is variable in flower size.

Large-flowered populations are restricted to the Pacific Coast from British Columbia to California west of the Cascades and Sierra Nevada (Newsom 1929). Small-flowered populations extend eastward to Manitoba, Michigan, Colorado, and Arizona, as well as occurring along the Pacific Coast. The small-flowered plants have a geographical range much larger than that of the large-flowered plants, and the ranges are largely but not completely allopatric. Therefore, it is useful taxonomically to recognize the widespread small-flowered plants as distinct from the large-flowered plants. A new combination for the large-flowered variety is herein proposed.

Collinsia parviflora Dougl. ex. Lindl. var. **grandiflora** (Dougl. ex Lindl.) Ganders & Krause, comb. nov.—*Collinsia grandiflora* Dougl. ex Lindl. Bot. Reg. 13:pl. 1107. 1827.—Type: Garden specimens from seed collected by Douglas on the banks of the Columbia a hundred miles or more from the ocean; the plate fixes application of the name.

Collinsia grandiflora Dougl. ex Lindl. var. *nana* A. Gray, Proc. Amer. Acad. Arts 8:394. 1872.—Type: Oregon, *Hall 366* (Holotype: GH!).

These rather weak varieties intergrade completely on the west coast, however, and the division between them is arbitrary. Intermediate populations are common west of the Cascade-Sierra axis, and some intermediates also occur in eastern Washington and northern Idaho. The two varieties can be separated as follows:

1A. Corollas 4–7 mm long; corolla tube saccate or gibbous, usually declined less than 45° or even almost erect .... *C. parviflora* var. *parviflora*

1B. Corollas 7–19 mm long; corolla tube usually saccate, usually declined about 45–90° .... *C. parviflora* var. *grandiflora*

Acknowledgments

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the University of British Columbia. We thank Dr. Ken Carey, Dr. A. J. F. Griffiths, Dr. Katherine Beamish, and Dr. Wilfred Schofield for some of the seed samples.

Literature Cited

Ahloowalia, B. S. and E. D. Garber. 1961. The genus *Collinsia.* XIII. Cytogenetic studies of interspecific hybrids involving species with pedicelled flowers. Bot. Gaz. (Chicago) 122:219–228.

Garber, E. D. 1956. The genus *Collinsia* I. Chromosome number and chiasma frequency of species in the two sections. Bot. Gaz. (Chicago) 118:71–73.

———. 1958. The genus *Collinsia* VII. Additional chromosome numbers and chiasmata frequencies. Bot. Gaz. (Chicago) 120:55–56.

———. 1974. *Collinsia. In* R. C. King, ed., Handbook of genetics, vol. 2, p. 333–361. Plenum Press, New York.

Gilkey, H. M. and L. R. J. Dennis. 1980. Handbook of northwestern plants. Oregon State Univ. Bookstores, Inc., Corvallis, OR.

Griffiths, A. J. F., G. Krause, and F. R. Ganders. 1977. A leaf spot polymorphism in *Collinsia grandiflora* (Scrophulariaceae). Canad. J. Bot. 55:645–661.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1959. Vascular plants of the Pacific Northwest. Part 4. Ericaceae to Campanulaceae. Univ. Washington Press, Seattle.

Krause, G. R. 1978. Genetic studies in populations of *Collinsia parviflora* Dougl. ex Lindl. (Scrophulariaceae). M.S. thesis, Univ. British Columbia, Vancouver.

Newsom, V. M. 1929. A revision of the genus *Collinsia.* Bot. Gaz. (Chicago) 87: 260–301.

Peck, M. E. 1961. A manual of the higher plants of Oregon. Binfords and Mort, Portland, OR.

SNOW, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol. 38:9–13.

ST. JOHN, H. 1956. Flora of southeastern Washington and adjacent Idaho. State Coll. Washington Press, Pullman.

TAYLOR, R. L. and B. MACBRYDE. 1977. Vascular plants of British Columbia, a descriptive resource inventory. Techn. Bull. No. 4. Univ. British Columbia Bot. Gard., Univ. British Columbia Press, Vancouver.

——— and G. A. MULLIGAN. 1968. Flora of the Queen Charlotte Islands. Part 2. Research Branch, Canada Dept. Agriculture Monograph No. 4, Ottawa.

(Received 8 Aug 1983; revision accepted 10 Sep 1985.)

ANNOUNCEMENT

ASH VALLEY RESEARCH NATURAL AREA

The Susanville District of the Bureau of Land Management has recently designated 1120 acres of public land in Lassen County, California, as a Research Natural Area. The notification designating the area as the Ash Valley RNA was published in the *Federal Register,* Vol. 49, No. 236, Thursday, 6 December 1984. The designation was made to provide protection for a unique assemblage of sensitive plants. The area is to be preserved for research and education purposes and the continued existence of the sensitive plants and their habitat. Present are three plants listed by the U.S. Fish and Wildlife Service as "candidates for listing as threatened or endangered" (*Astragalus tegetarioides, Eriogonum prociduum,* and *Ivesia paniculata*) and three plants listed by the California Native Plant Society (*Dimeresia howellii, Draba douglasii* var. *douglasii,* and *Erigeron elegantulus*).

A Habitat Management Plan (HMP) was recently completed by the Bureau of Land Management to establish guidelines for the management and protection of this unique botanical area. The objectives of this plan were to ensure that the sensitive plants and their habitats are protected, to ensure that the area is preserved in its natural state for research and educational purposes, and to generate interest into the scientific research of the area. The Bureau hopes that any knowledge gained from scientific research will aid in the understanding and successful management of this area. Anyone desiring a copy of the Ash Valley Research Natural Area HMP or wishing to use the area for research purposes should contact the District Manager, Bureau of Land Management, 705 Hall Street, Susanville, California 96130.

A NEW SPECIES OF *LOMATIUM* (APIACEAE) FROM SOUTHWESTERN OREGON

JAMES S. KAGAN
The Nature Conservancy, 1234 NW 25th Ave.,
Portland, OR 97210

ABSTRACT

Lomatium cookii, a new species from vernal pools in the Agate Desert area near Medford, Oregon, is described and illustrated. The species appears to be local and rare. It is morphologically most similar to another rare Oregon endemic, *Lomatium bradshawii,* of the southern Willamette Valley, and to a northern California endemic, *Lomatium humile.*

The Agate Desert region, an approximately 10,000 ha area of the Rogue River Valley north of Medford, Oregon, has long been known for its botanical diversity (Detling 1968). In 1981, during a search for populations of *Limnanthes floccosa* subsp. *grandiflora* in the Agate Desert, a new species of *Lomatium* was discovered.

Lomatium cookii J. S. Kagan, sp. nov.

Planta perennis, glabris, acaulis vel subacaulis, 1.5–5 dm alta; radice elongata, angusta, 1.5–3 dm longa aut incrassata ob caudicem 2–8 ramosum plantam multicaulem formantem. Foliis radicalibus oblongis 8–17 cm longis petiolo excluso, 2.5–10 cm latis, ternatis deinde tripinnatisectis, segmentis ultimis linearibus, acutis, nonnunquam apiculatis, distinctis, 6–12 mm longis, minus quam 1 mm latis; petiolis vaginatis, 5–22 cm longis. Pedunculis foliis longioribus, 1.5–4 dm longis; umbellis 6–12 radiatis, radiis fertilibus 2–9 cm longis, inaequaliter elongatis, radiis sterilibus 1–2 cm longis; involucro nullo; bracteis involucelliorum 8–12, 6–10 mm longis, linearibus, viridibus, marginibus scariosis; pedicellis fruitificantibus 1–3 mm longis; floribus flavis. Fructibus oblongis, 8–13 mm longis, 4–6 mm latis, alis lateralibus suberosis, crassis, alis dorsalibus ternis, filiformibus, elevatis; vittis plerumque obsoletis (Fig. 1).

Plant perennial, glabrous, acaulescent or subacaulescent, 1.5–5 dm tall; root elongate, narrow, 1.5–3 dm long, simple, occasionally surmounted by a thickened 2–8-branched caudex. Leaves oblong, 8–17 cm long excluding petiole, 2.5–10 cm broad, ternate then tripinnatisect, ultimate segments linear, acute, or sometimes apiculate, 6–12 mm long, less than 1 mm broad; petioles vaginate, 5–22 cm long. Peduncles exceeding leaves, 1.5–4 dm long; umbels 6–12-radiate, fertile rays 2–9 cm long, unequally elongate, sterile rays 1–2 cm long;

MADROÑO, Vol. 33, No. 1, pp. 71–75, 27 March 1986

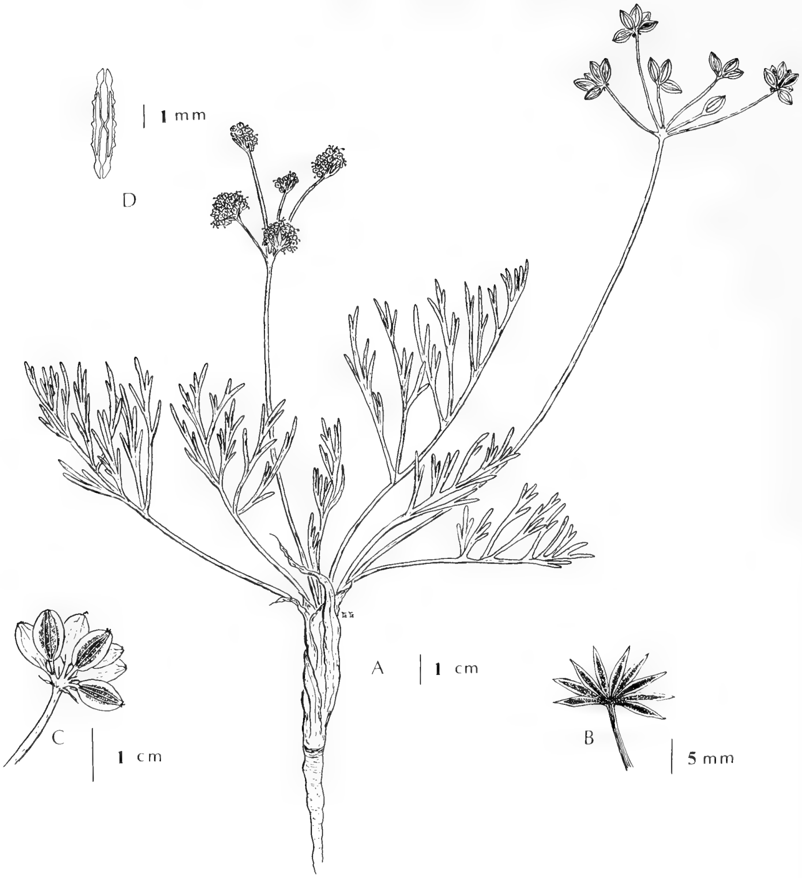


FIG. 1. *Lomatium cookii.* A. Habit. B. Bractlets of involucel. C. Fruits. D. Fruit cross section.

involucre none; involucel bracklets 8–12, 6–10 mm long, linear, green, margins scarious; fruiting pedicels 1–3 mm long; flowers yellow. Fruits oblong, 8–13 mm long, 4–6 mm wide, lateral wings corky, thick, dorsal ribs three, filiform, elevated; oil tubes obsolete.

TYPE: USA, Oregon, Jackson Co., Agate Desert vernal pools, just nw. of junction of Antelope and Table Rock Roads (T36S R2W S24 nw. ¼); 380 m elev.; 1 Jun 1983, *J. S. Kagan 6018301* (Holotype: ORE; isotypes: UC, OSC).

PARATYPES. USA, Oregon, Jackson Co., Agate Desert vernal pool margins, off road to Jackson Co. Sports Park (T36S R1W S22 se. ¼), 12 May 1983, *J. S. Kagan 5128303, 04, 05* (ORE, OSC); Agate Desert vernal pool margins, just south of Hwy. 140, 4 mi e. of Hwy.

64 (T36S R1W S23 sw. ¼), 13 Apr 1983, *J. S. Kagan 4138301* (ORE).

Ecology and phenology. Lomatium cookii is found on margins and bottoms of vernal ponds in an area having "patterned ground" topography. The flat landscape is composed of a continuous series of shallow vernal pools surrounded by low mounds. The pools have stony, pebbly bottoms, whereas the mounds are composed of relatively rock-free light clay of volcanic origin. The area is an ancient alluvial outwash plain adjacent to the Rogue River. The vernal pools have standing water only in the winter and early spring, from December to April or May, and appear somewhat dry and barren from July to October. Common species (nomenclature follows Munz 1959) of the vernal pools include *Deschampsia danthonioides, Alopecurus geniculatus, Plagiobothrys austinae, P. bracteatus, P. nothofulvus, Juncus uncialis, Navarretia leucocephala, N. tagetina,* and *Limnanthes floccosa.* The mounds are usually dominated by non-native grasses including *Bromus mollis, B. commutatus, Cynosurus echinatus, Elymus caput-medusae,* and *Poa bulbosa,* but also can have a significant component of native forbs such as *Saxifraga integrifolia, Viola douglasii, Brodiaea pulchella, B. hyacinthina,* and *Lupinus bicolor.*

This species blooms from mid-March through mid-May, depending on the season. Many plants bloom while in standing water. The plants usually have 2–5 flowering umbels. The earliest inflorescences are largely male, with most of the flowers having undeveloped ovaries. The later umbels have perfect flowers and produce almost all of the fruits. The only floral visitor observed was a small black moth, as yet unidentified. *Lomatium cookii* is protogynous, having stigmas that are exposed and receptive to pollen prior to anther dehiscence in the same flower. Mature fruit is present from late May through July.

Relationship to other species. There are 2 other species of *Lomatium* occurring in the Agate Desert area. *Lomatium utriculatum* (Nutt.) Coult. and Rose commonly occurs on the mounds, and is easily distinguishable from *L. cookii* by its obovate involucel bracklets, cauline habit, and thin winged fruits. *Lomatium macrocarpum* (Nutt.) Coult. and Rose occurs on vernal pool margins, as well as on hillsides at the edges of mounded prairie areas. In the Rogue Valley, it is distinguishable from *L. cookii* by its pubescent herbage, pale white to tan flowers, and narrow, thin winged fruits.

Lomatium cookii is very similar to *L. bradshawii* (Rose) Math. and Const., a species indigenous to wet prairies of the southern Willamette Valley, Oregon. It is most easily differentiated by the narrow, linear involucel bracklets, as opposed to the wider, ternately or biternately divided bractlets of *L. bradshawii.* In cross section, the fruit of *L. cookii* has dorsal ribs that are clearly raised and are 80–120 μm in diameter, whereas *L. bradshawii* has ribs that are less distinct, 35–50 μm in diameter, and are imbedded in the thick, stratified cortex. The endocarp of the fruit of *L. cookii* is three layers thick, whereas in *L. bradshawii* it is 5–6 layers thick. Plants of *L. cookii* tend to be shorter but more robust, having more umbels and stems per plant than plants of *L. bradshawii.* In ungrazed populations, *L. cookii* has a mean pedicel height of 24 cm in fruit, and averages 4 fruiting umbels per plant (n = 34); whereas *L. bradshawii* has a mean pedicel height of 31 cm, and averages less than 2 fruiting umbels per plant (n = 100). Both species grow from a long, slender taproot. Plants of *L. cookii* appear more robust because, in about half of the plants observed, the taproot is surmounted by a multiple caudex (2, 4, and 6 are the most common stem numbers). Of the more than 500 plants of *L. bradshawii* observed, only 6 plants had multiple caudices (Kagan 1980).

Lomatium cookii also is similar to *Lomatium humile* (Coult. & Rose) Hoover. This taxon also is described as *Lomatium caruifolium* (H. & A.) C. & R. var. *denticulatum* (Jepson) Jepson (Jepson 1936). *Lomatium cookii* and *L. humile* both occur in plains with vernal ponds and have similar fruits and bractlets. *Lomatium humile* has 4 to 6 dorsal ribs on the fruit, whereas *L. cookii* has only 2. Also, the fruit of *L. humile* is inflated in the commissure, whereas *L. cookii* has fruit that is not inflated. Although the bractlets of these taxa are fairly similar in appearance, those of *L. cookii* are linear and 6–10 mm long, whereas those of *L. humile* are orbicular to lanceolate, and usually shorter, 3–5 mm long. The two taxa are most easily distinguished by the leaves, which in *L. humile* have ultimate segments ranging from 2–60 mm long (Abrams 1951), and averaging about 15–20 mm. The ultimate segments of the leaves of *L. cookii* are much smaller, usually between 6–10 mm long.

Distribution and status. Lomatium cookii is both rare and threatened (Oregon Natural Heritage Data Base 1985). In thorough searches of the Agate Desert area in 1982 and 1983, only 3 small populations of the species were identified. Fewer than 2000 plants have been observed, and 90% of these were at the type locality. Plants are readily eaten by cattle. Most available habitat has been very heavily grazed, and in these areas plants of this species are not present. In addition, large portions of the Agate Desert, including the type locality, are in the process of being developed for heavy industry, causing additional habitat destruction. Thus, it appears that *L. cookii* may be a good candidate for the Endangered Species List of the U.S. Fish and Wildlife Service.

ACKNOWLEDGMENTS

I have the honor to name the species after Stanton A. Cook, Professor of Plant Ecology at the University of Oregon. I would like to thank Dr. Kenton Chambers, Dr. David Wagner, Dr. Lincoln Constance, and Julie Kierstead as well as the Madroño reviewers for their help with this work, and Gaylee Goodrich for the illustration.

LITERATURE CITED

ABRAMS, L. 1951. Illustrated flora of the Pacific states, Vol. III. Stanford Univ. Press, Stanford, CA.

DETLING, L. E. 1968. Historical background of the flora of the Pacific Northwest. Museum Nat. Hist., Univ. Oregon, Eugene, Bull. No. 13.

JEPSON, W. L. 1936. A flora of California, Vol. II. California School Book Depository, San Francisco, CA.

KAGAN, J. S. 1980. The biology of *Lomatium bradshawii* (Apiaceae), a rare plant of Oregon. M.S. thesis, Univ. Oregon, Eugene.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

OREGON NATURAL HERITAGE DATA BASE. 1985. Rare, threatened, and endangered plants and animals of Oregon. Oregon Natural Heritage Data Base, Portland.

(Received 23 Nov 1984; revision accepted 10 Sep 1985.)

ANNOUNCEMENT

Phytologia Memoir VI, *A Preliminary, Verified List of Plant Collectors in Mexico,* is a 179 page booklet containing the names of over 4000 plant collectors of Mexico with some 800 references to their collecting activities. The work should prove of interest to all who have or intend to collect in Mexico. It can be ordered from the compiler, Dr. Irving W. Knobloch, 438 Tulip Tree, E. Lansing, MI 48823, for $16.00 domestic, $17.00 foreign surface mail, and $19.00 foreign air mail (identification number 479-22-0904 A).

NOTES

Spineless Petioles in *Washingtonia filifera* (Arecaceae).—The flattened petioles of the desert fan palm, *Washingtonia filifera* (Lindl.) Wendl. are described as being more or less spiniferous (Munz, A flora of Southern California, Univ. California Press, 1974) or as having spines along either edge (Shreve and Wiggins, Vegetation and flora of the Sonoran Desert, Stanford Univ. Press, 1964). Spines are usually assumed to aid in the protection of plant tissue from herbivore attacks (Louw and Seely, Ecology of desert organisms, Longman Group, 1982). In *W. filifera,* spine density is greatest around the apical meristem where the emergent, spine-covered petioles are in closest proximity to each other.

I have examined over 300 specimens of *W. filifera* and found that petiole spines are absent or nearly so in individuals exceeding 14 m in height (Fig. 1). The spines also are absent on distal ends of petioles in trees exceeding 8 m in height and cover a decreasing percentage of the petiole in taller trees (Table 1). These tendencies persist regardless of whether the trees are growing under cultivated or natural conditions.

If the spines function to deter herbivores from consuming vital plant tissues, then it can be assumed that petiole spines in small to intermediate individuals of *W. filifera* have evolved as a result of the protection afforded the apical meristem. (Extensive damage to this portion results in death of the tree because *Washingtonia* does not produce vegetative offshoots as do some palms.) It appears, however, that the utility of this protection decreases or is lost as *W. filifera* exceeds 14 m in height. Palms that develop spines only when small to intermediate may be at a selective advantage if energy for spine development is utilized for a more beneficial trait as the trees become taller and the utility of armament decreases.

Other than the infrequent nibbling of seedlings by desert cottontails (*Sylvilagus audubonii*) and the browsing of leaf tips by domestic cattle (in the three locations where livestock and native palms occur together), no known herbivores consume the foliage of *W. filifera* today. During past geological epochs, numerous mammals existed within the present range of *W. filifera,* and some probably browsed upon palms. No known species, however, could have browsed upon palms exceeding 12 m in height. The giant camel, *Titanotylopus,* occurred throughout southern California during the Pliocene and Pleistocene epochs, but had a vertical reach of just 5 m (D. Whistler, pers. comm.). Ground sloths were widespread in western North America during the Pliocene and Pleistocene (Anderson, *In* Martin and Klein, eds., Quaternary extinctions, Univ. Arizona Press, 1984). The largest sloth known from the southern half of California is the big-tongued sloth, *Glossotherium* (Stock, Rancho La Brea, Los Angeles Co. Mus. Nat. Hist., 1956). When erect, this sloth could not reach more than 5 m (G. Jefferson, pers. comm.). Mastodons (*Mammut*) appeared in the Miocene and persisted into the early Holocene in southern California. Some stood 3 m at the shoulder and had a vertical reach of about 6 m (Anderson 1984). Mammoths (*Mammuthus*) were the largest terrestrial herbivores to occur in western North America from the Pliocene forward. Their fossils are abundant and widespread throughout the West (Agenbroad, *In* Martin and Klein 1984). They are believed to have fed upon a tremendous variety of plant material, including palms, but did not have a vertical reach of more than 9 m (G. Jefferson, pers. comm.).

Whether or not these herbivores were sympatric with *Washingtonia,* and thus able to provide the selective pressure behind the development of spined petioles in young palms, is conjecture. No fossils attributable to *Washingtonia* have been identified. Natural populations of *W. filifera* are presently confined to the Sonoran Desert of southeastern California, Baja California, and western Arizona (Vogl and McHargue,

---

Madroño, Vol. 33, No. 1, pp. 76–78, 27 March 1986

FIG. 1. Leaves of *Washingtonia filifera*: left, spines on a petiole from a 4 m palm; right, a spineless petiole from a 12 m palm.

Ecology 47:532–540, 1966; Brown et al., J. Ariz. Acad. Sci. 11:37–41, 1976). Axelrod (*In* Barbour and Major, eds., Terrestrial vegetation of California, Wiley and Sons, 1977) implies that *Washingtonia* had a broader range in past epochs than at present. In addition, palm fossils of Pliocene age, assigned to the genus *Sabal,* occur over much of the southern half of California including what is now the Mojave Desert (Axelrod, Evolution 2:127–144, 1948). These fossils may be misidentified. The taxonomic affinity of fossil palm leaves from California is based (in part) upon the presence or absence of spines on the petioles (Axelrod, pers. comm.). As I have shown, however, the petioles of *Washingtonia* may lack spines and therefore could be assigned erroneously to the genus *Sabal.*

TABLE 1. PERCENT OF SAMPLED TREES OF *Washingtonia filifera* (BY HEIGHT CATEGORY) WITH SPINES ON ALL OR PART OF PETIOLES. n = number of trees in each catergory.

Palm height categories (meters)	n	Percent of petiole length covered with spines										
		100	90	80	70	60	50	40	30	20	10	0
0–4	20	100										
4–6	18	72	11	6		6			6			
6–8	33	55	6	6	3	3	12		9	3	3	
8–10	24	4		8	8		13	8	4	29	25	
10–12	43			2	2	2	4	4	2	12	58	12
12–14	34								3	21	50	26
14–16	45									4	42	53
16–18	59										25	75
18–20	29										10	90

Financial support for this research was provided by the Richard King Mellon Foundation of Pittsburgh, Pennsylvania.—JAMES W. CORNETT, Natural Science Department, Palm Springs Desert Museum, Palm Springs, CA 92263. (Received 18 Feb 1985; revision accepted 16 Oct 1985.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

CORYPHANTHA VIVIPARA (Nutt.) Britt. & Rose var. DESERTII (Engelm.) W. T. Marsh. (CACTACEAE).—Inyo Co., Funeral Mts., eastern end of Echo Canyon, calcareous flats and slopes, 1300–1600 m, T27N R3E, 18 Jan 1984, *Peterson and Annable 1054, 1056* (UNLV).

Significance. First record for Inyo Co. and Death Valley National Monument. A range extension of 56 km sw. of Shoshone Mt., Nye Co., NV (Beatley, Vascular plants of the Nevada Test Site and Central Southern Nevada, Technical Information Center, VA, 1976).

STIPA SCRIBNERI Vasey (POACEAE).—Inyo Co., Cottonwood Mts., near White Top Mt. and w. of Tin Mt., calcareous talus slopes and rock outcrops, 1900–2100 m, T12–13S R41–42E, 20 Jun 1981, *Peterson 345* (UNLV, UTC), 27 Jun 1982, *Peterson 629* (UNLV, UTC), 21 Jul 1982, *Peterson 659, 662* (UNLV, UTC). (Verified by M. E. Barkworth.)

Significance. First record for CA and a range extension of ca. 200 km w. of the Sheep Range, Clark Co., NV.

LINANTHUS NUDATUS Greene (POLEMONIACEAE).—Inyo Co., Cottonwood Mts., Hunter Mt., granitic sandy clay loam slopes, 2050 m, T16S R41E, 2 Jun 1981, *Peterson 228* (UCSB, UNLV), 25 May 1982, *Dunn, Annable and Peterson 530* (UCSB, UNLV). (Verified by D. M. Smith.)

Significance. First record for Inyo Co. and Death Valley National Monument. A range extension of 86 km ne. of the southern Sierra Nevada, Tulare Co., CA.—PAUL M. PETERSON and CAROL R. ANNABLE, see notes below.

NEVADA

CAREX OCCIDENTALIS Bailey (CYPERACEAE).—Clark Co., Spring Mts., 6 km s. of Charleston Peak, sandy clay loam ridges, 3292 m, T20S R56E S1 sw.¼, 19 May 1984, *Charlton, Wisura, Annable and Peterson 2460* (DES, UNLV). (Determined by J. H. Lehr.)

Significance. First record for Clark Co. extending the range approximately 122 km s. of Pahute Mesa, Nye Co., NV, and 214 km w. of Shivwits Plateau, Mojave Co., AZ.

PHACELIA BARNEBYANA J. T. Howell (HYDROPHYLACEAE).—Clark Co., Spring Mts., near Lucky Strike Tunnels, calcareous rocky slopes, 1950 m, T19S R57E S1 ne.¼, 14 May 1983, *Lathrop and Peterson 952* (UNLV).

Significance. First record for the Spring Mts. between known locations 54 km s. in the Clark Mts., San Bernardino Co., CA (Thorne, Prigge and Henrickson, Aliso 10: 71–186, 1981) and 35 km ne. in the Sheep Range, Clark Co., NV (Ackerman, pers. comm.).

MIMULUS MONTIOIDES Gray (SCROPHULARIACEAE).—Clark Co., Spring Mts., ne. of Grassy Spring, calcareous rock outcrops, 1585 m, T18S R58E S32 se.¼, 14 May 1983, *Lathrop and Peterson 960* (UNLV).

Significance. First record for the Spring Mts. between known locations 140 km nw. in the Panamint Range, Inyo Co., CA, and 51 km n. in the Spotted Range, Clark Co., NV.—PAUL M. PETERSON and CAROL R. ANNABLE, Dept. Biol. Sci., Univ. Nevada, Las Vegas 89154.

MADROÑO, Vol. 33, No. 1, pp. 79–80, 27 March 1986

OREGON

DOWNINGIA INSIGNIS Greene (CAMPANULACEAE).—Malheur Co., Barren Valley, s. of Dickinson Ranch, T27S R38–39E, black adobe soil along edge of playa, 1030 m, 17 Jun 1984, *E. Joyal 517* (CAS, NY, OSC).

Significance. Second report for OR, the first by Cusick in 1885, also from "Barren Valley." This central CA taxon was thought to be extirpated in OR.—ELAINE JOYAL, see note below.

WASHINGTON

ASTRAGALUS GEYERI Gray (FABACEAE).—Grant Co., Lower Crab Creek n. of Saddle Mt., Columbia River Natl. Wildlife Refuge, T16N R24E S32, 175 m, stabilized sand dunes, 13 Jun 1984, *E. Joyal 488* (BLM—Spokane, NY, OSC, WSU). (Verified by R. Barneby, NY.)

Significance. Second report for WA, an extension of ca. 110 km nw. from Wallula Gap, WA-OR, otherwise a Great Basin taxon.

CLAYTONIA EXIGUA T. & G. (=MONTIA SPATHULATA (Dougl.) Howell) (PORTULACACEAE).—Grant Co., Saddle Mt., above lower Crab Creek, T15N R24E S½, 300–400 m, steep basalt talus on n. slope, 15 May 1984, *E. Joyal 473* (BLM—Spokane, OSC). (Verified by K. Chambers, OSC.)

Significance. Extension ne. of ca. 100 km from the Columbia River Gorge, David Douglas' type collection is from "the vallies of the Rocky Mtns.," an ambiguous locale, possibly in WA or BC. All subsequent reports from WA e. of the Cascades have been in the immediate vicinity of the C.R.G.—ELAINE JOYAL, Dept. Botany, Oregon State Univ., Corvallis, OR 97331.

UTRICULARIA INFLATA Walt. (LENTIBULARIACEAE).—Kitsap Co. Horseshoe Lk., 15 km s. from Port Orchard, in water near the public fishing area, w. side of the lake, 90 m, 26 Oct 1980, *A. and O. Ceska 4913* (K, V, WTU). Sterile specimens, but with typical coiled winter buds. Verified by P. Taylor (K).

Significance. The first report from Washington and from w. USA. Previously known from NJ and FL, westward to e. TX. Most probably introduced, but the mechanism of introduction is not known.—ADOLF CESKA and OLDRISKA CESKA, P.O. Box 1761, Victoria, B.C. V8W 2Y1, Canada.

REVIEWS

California Serpentines: Flora, Vegetation, Geology, Soils, and Management Problems. By ARTHUR R. KRUCKEBERG. University of California Publications in Botany, Vol. 78. 1985. $10.95. ISBN 0-520-09701-7 (pbk).

Was there field botany in California before "serpentine"? Yes—but as this volume eloquently explains, attempts to understand serpentine-plant relationships have prompted a great deal of important fieldwork and have enriched our systematic, ecological, and evolutionary literature. Arthur Kruckeberg worked on serpentine problems in California during the height of serpentine enthusiasm in the 1950s. His professional interest in serpentine continues, and he is well versed in the international literature on ultramafic research. I can think of no one better qualified to assemble this sort of comprehensive review.

Kruckeberg first discusses the slowness of California botanists to appreciate the nature of serpentine habitats. These collectors were attracted to the sterile, rocky slopes that harbored so many endemics, disjuncts, and puzzling distributions. But they didn't say much about the rocks and soils involved. Discussion of calcium-magnesium imbalances and the host of related physiological problems in serpentine soils did not surface in California botanical or agricultural literature until the 1930s.

The sections on geology, soil and mineral nutrition, and physiological and morphological responses are well developed with more than enough detail for most readers. After discussing ultramafic, serpentinite, peridotite, and other rock and mineral terms, Kruckeberg reverts to the common and convenient usage of "serpentine" for rock, soil, or vegetation of ultramafic affinity. One uncited reference that is relevant to the physiological response section is J. L. Jenkinson's work on *Pinus ponderosa* seedlings from serpentine and non-serpentine sources grown on serpentine and non-serpentine soils (U.S. Forest Service Resarch Paper PSW-127/1977).

Some botanical readers may pass over the above sections quickly and settle down to see if their favorite serpentine taxa are dealt with properly in the serpentine vegetation and flora sections (with related appendices). A great deal of information is summarized in helpful ways in this material. One value of such summaries is to prod constructive critics into new fieldwork to check on apparent inconsistencies and omissions.

The highlight of this volume may be the *Streptanthus* case history in the evolutionary ecology section. After review of established principles of ecotypic adaptation to serpentine, the principles are applied to *Streptanthus,* a genus on which Kruckeberg speaks with great authority. This is a most interesting discussion.

The volume concludes with sections on exploitation threats and conservation needs. Although California serpentines have been mined for well over a century for mercury and chromium, massive geothermal developments and open-pit mining operations for trace amounts of gold and nickel pose new threats. Not mentioned is a serpentine mineral use that is declining—asbestos. Only two asbestos mines currently operate in the United States, and one is within the New Idria serpentine mass. A defunct asbestos mine nearby is considered one of the greatest "toxic waste" problems in California.—JAMES R. GRIFFIN, Hastings Natural History Reservation, Carmel Valley, CA 93924.

Vascular Plants of the Channel Islands of Southern California and Guadalupe Island, Baja California, Mexico. By GARY D. WALLACE. Contributions in Science, No. 365, Natural History Museum of Los Angeles County. 1985. 136 pp., $18.00 + $1.80 shipping. (Available from the bookstore, Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007.)

MADROÑO, Vol. 33, No. 1, pp. 81–82, 27 March 1986

A century ago E. L. Greene published his catalog of the flowering plants and ferns of Guadalupe Island, providing the first in a series of studies by California botanists of the interesting floras of the Channel Islands of southern California and of Guadalupe Island, Baja California. Despite the relative closeness of some of these islands to the mainland, they support distinctive floras (and faunas) that exhibit many features of truly oceanic islands. Woodiness occurs in groups that are otherwise commonly herbaceous (as in *Eriogonum*). Endemics include relic genera (such as *Lyonothamnus* and *Baeriopsis*) as well as taxa that appear to have evolved in situ from ancestral immigrants (as in some taxa of *Malacothrix, Camissonia*). The total vascular flora consists of 758 native taxa (one-fifth of them endemic) and 227 introduced taxa; the abstract is worded to indicate only 621 native taxa.

In this volume, Wallace's objectives are to "provide a current guide to the floras . . . which clearly distinguishes between those records based on available herbarium specimens and those based on reports from the literature," to "present a picture of floristic relationships," and to "draw attention . . . to the insular distributions of native taxa and to the numerous misidentifications and synonymous treatments of those taxa." The flora is presented in tabular fashion, with occurrences of each taxon (exotics included) noted on individual islands. No descriptions of the taxa are given. Where a literature report is in some question, reference to a literature citation is given (as, for example, Eastwood's 1941 undocumented list of species). However, the insular occurrences of rather few taxa (such as *Calyptridium monandrum, Centaurium muhlenbergii*) appear to be based on such questionable reports; rather it is the insular distribution of these taxa that is involved. Appendices list "selected" exsiccatae and their location and present an index to the disposition of synonyms, misidentifications, etc. In the latter index, the nature of the disposition is not clear. *Baeria chrysostoma* F. & M. = *Lasthenia californica* DC. ex Lindl., but *Baeria macrantha* (Gray) Gray, listed in identical format does not. This latter species does not occur on these islands, and its record there represents a misidentification of *L. californica.*

Wallace's phytogeographic analysis is of particular interest to insular biogeographers (and should be read in conjunction with Johnson et al., American Nat. 102:297–306, 1968). The islands of the northern group (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) bear more floristic similarity to each other than do the islands of the southern group, which is not surprising in view of the greater distances separating the latter. Interestingly, tiny Santa Barbara Island, with an area of 3 sq. km, has three endemic taxa; the largest number of endemics (51) is on Guadalupe Island, which is also the largest and most isolated of the group. The total number of native taxa on that island, however, is the same as that on Anacapa Island, which is 1 percent of its size. Despite its isolation, the flora of Guadalupe Island bears affinity with that of the Channel Islands and floristically it must be considered a member of this group.

Like all taxonomic and floristic treatments, Wallace's paper must be viewed as a progress report subject to modification. He intends this publication to be a working document, and my copy is already copiously annotated. It represents a welcome and important contribution to the floristics of California and to the phytogeography of its islands.—ROBERT ORNDUFF, Department of Botany, University of California, Berkeley 94720.

EDITORIAL

Nomenclature is a precise and essential element of communication among biologists. Systematic, floristic, and ecological botanists, including the majority of authors who publish in Madroño and most of the members of the California Botanical Society, are particularly dependent upon nomenclature to convey the results of their research to fellow botanists and other interested persons. Thus, it is important that scientific names are used without introducing unnecessary ambiguity or inaccuracy.

A few years ago two compilers, J. T. and R. Kartesz, with the help of many specialists, produced a synonymized checklist of the vascular plants of much of North America (A synonymized checklist of the vascular flora of the United States, Canada and Greenland, Vol. II, The biota of North America, Univ. North Carolina Press, Chapel Hill, 1980). Other checklists of plants for portions of North America also have been published with synonyms (e.g., U.S.D.A. Soil Conservation Service, National list of scientific names, Vol. 1, List of names; Vol. 2, Synonymy, SCS-TP-159, 1982). We believe these checklists are commendable efforts to incorporate the large amount of current botanical nomenclature into convenient references for much of North America. During the six years since its publication, however, the volume by Kartesz and Kartesz has been used to standardize nomenclature in publications and reports. It has been used even to organize herbaria. This checklist generally includes current nomenclature and corresponding synonyms for taxa recognized by participating researchers; but it also contains many errors and ambiguous applications of names, rendering it an unacceptable resource for these important uses.

Because of such errors and ambiguities, we are alarmed by the casual acceptance and citation of Kartesz and Kartesz or other recent checklists as the primary sources of nomenclature and taxonomic treatments in some of the manuscripts submitted to Madroño. In this regard, we are in agreement with many reviewers who have expressed concern about manuscripts in which the authors rely solely on synonymized checklists for nomenclature. A principal concern is the unavoidable transmission of errors; another is the use of plant names not present in regional floras or manuals. We see no reason to encourage a perpetuation of misapplied names or other errors from either recent checklists or regional works. We also think that because many of our members are not taxonomists and may not have synonymized checklists or convenient access to recent treatments, the use of nomenclature from checklists, without reference to synonyms present in widely-used regional manuals, can detract from the information provided by authors.

We suggest, therefore, that contributors to Madroño attempt to achieve a satisfactory compromise by 1) citing only widely-used regional references as their basic source of nomenclature, 2) providing current nomenclature and corrections when necessary or desirable, and 3) including appropriate synonyms from regional works for the substitutions. As new or anticipated manuals or floras are published, the need to incorporate changes from recent contributions will be reduced. Because taxonomy is not a static science, however, and because nomenclature will continue to require refinement, no single reference will ever be sufficient for all plants. Thus, each of us should strive to achieve the best method to communicate to our colleagues with a minimum of ambiguity. We anticipate that members of our Society and other readers of Madroño will be most appreciative and that scientific communication will be enhanced. W.R.F. and J.R.H.

MADROÑO, Vol. 33, No. 1, p. 83, 27 March 1986

ANNOUNCEMENT

INTERNATIONAL ORGANIZATION OF PLANT BIOSYSTEMATISTS

The Executive Council of the International Organization of Plant Biosystematists (IOPB) will meet during the IOPB 1986 Symposium, "Differentiation Patterns in Higher Plants," Zurich, Switzerland, 13–18 July 1986. Anyone wishing to place an item on the agenda for discussion should write to Dr. Liv Borgen, Secretary, IOPB, Botanical Garden and Museum, Trondheimsveien 23B, N-OSLO 5, NORWAY.

Information on participation may be obtained from the Chairperson, Dr. Krystyna Urbanska, Geobotanisches Institut, ETH, Stiftung Rubel, Zurichbergstrasse 38, CH-8044, ZURICH, SWITZERLAND.

IOPB publishes the IOPB NEWSLETTER. Information for the IOPB NEWSLETTER may be sent to the Editor, Dr. Krystyna Urbanska.

Application forms for membership in IOPB may be obtained from the Secretary by sending US $25 (for the period 1983–1987) directly to the Secretary-Treasurer of IOPB, Dr. L. Borgen at the above address.

ANNOUNCEMENT AND CALL FOR PAPERS

ENDANGERED PLANT CONFERENCE

The California Native Plant Society (CNPS) will serve as lead sponsor, assisted by the California Botanical Society and other groups, for a conference on the conservation and management of rare and endangered plants scheduled for 5–8 November 1986. The conference will be held in Sacramento, California. Persons wishing to present papers are invited to submit an abstract.

The purpose of the conference is to provide a forum for exchange of information on rare and endangered plants. The conference will include formal presentations in concurrent sessions, open forum discussions, a poster session, and workshops. Proceedings will be published by CNPS.

Papers describing research on endangered plants are requested. Taxonomic and ecological studies are of interest although emphasis will be placed on management-related topics including specialized field techniques for evaluating, monitoring, and mitigating adverse effects on endangered plants. Experience from regions other than western United States are welcome. This conference will be of interest to persons involved with endangered species management for public agencies, private industry, educational institutions, or through conservation organizations.

Early submittal by authors is requested. Abstracts are due no later than 1 June 1986. Abstracts and requests for information should be directed to Jim Nelson, Conference Coordinator, California Native Plant Society, 909 Twelfth Street, Suite 116, Sacramento, CA 95814.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

(Required by Title 39, U.S.C. 3685)

MADROÑO, A West American Journal of Botany, is published quarterly at Berkeley, California. Annual subscription price is $25.00.

The Publisher is the California Botanical Society, Inc., Life Sciences Building, University of California, Berkeley, CA 94720.

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

The owner is the California Botanical Society, Inc., Life Sciences Building, University of California, Berkeley, CA 94720. There are no bondholders, mortgagees, or other security holders.

The average number of copies distributed of each issue during the preceding 12 months is 1081; the number of copies of the single issue closest to the filing date is 1081. The net press run is 1250 copies.

I certify that the statements made by me above are correct and complete.

January 31, 1986 WAYNE R. FERREN, JR., *Editor*

VOLUME 33, NUMBER 2 APRIL 1986

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928

First Vice President: RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95114

Second Vice President: DAVID H. WAGNER, Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403

Recording Secretary: V. THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: CHERIE L. R. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* ROLF W. BENSELER, Department of Biological Sciences, California State University, Hayward, CA 94542; the *Editor* of MADROÑO; three elected *Council Members:* JAMES C. HICKMAN, Department of Botany, University of California, Berkeley, CA 94720; THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; and a *Graduate Student Representative,* JOSEPH M. DITOMASO, Department of Botany, University of California, Davis, CA 95616.

FOSSIL MISTLETOES IN PACKRAT MIDDENS FROM THE SOUTHWESTERN UNITED STATES

THOMAS R. VAN DEVENDER
Arizona-Sonora Desert Museum, Route 9, Box 900,
Tucson, AZ 85743

FRANK G. HAWKSWORTH
U.S.D.A. Forest Service,
Rocky Mountain Forest and Range Experiment Station,
Fort Collins, CO 80526

ABSTRACT

Mistletoe remains from eight species in the genera *Arceuthobium* and *Phoradendron* (Viscaceae) have been identified from 53 fossil packrat middens from various areas in the Southwest. Radiocarbon dates on the samples range from 32,000 to 610 yr B.P. Major changes in the ranges of mistletoes occurred at the end of the Late Wisconsin glacial and in the Early Holocene as woodland trees withdrew from the lowlands and desert trees and shrubs expanded. In two cases, Late Wisconsin mistletoes parasitized tree species that are not hosts today.

Analyses of the well-preserved plant remains in ancient packrat (*Neotoma*) middens have provided a wealth of information on the history of vegetation and climate in the deserts of North America (Van Devender and Spaulding 1979, Spaulding et al. 1983, Wells 1976). In most of the areas studied, Late Wisconsin forest or woodland trees were living in the lowlands now occupied by desertscrub communities prior to about 11,000 years ago. Drier versions of these pluvial forest/woodland communities lingered in many areas for several thousand years into the present interglacial, the Holocene (Van Devender 1977). In the Mojave Desert, which is characterized by winter rainfall, relatively modern creosote bush (*Larrea divaricata* Cav.) desertscrub formed soon after 8000 years ago (King 1976). In the Sonoran and Chihuahuan deserts, characterized by summer rainfall, modern desertscrub communities apparently did not form until the Late Holocene, about 4000 years ago (Van Devender et al. 1984, Van Devender 1986). In this paper, we discuss the mistletoes (Viscaceae) that have been identified from packrat middens from the southwestern United States.

FOSSIL RECORDS

Packrat middens are hard, dark, organic deposits that can be preserved in dry rockshelters indefinitely. The oldest radiocarbon date on packrat midden materials is more than 50,000 yr B.P. (radio-

MADROÑO, Vol. 33, No. 2, pp. 85–99, 30 May 1986

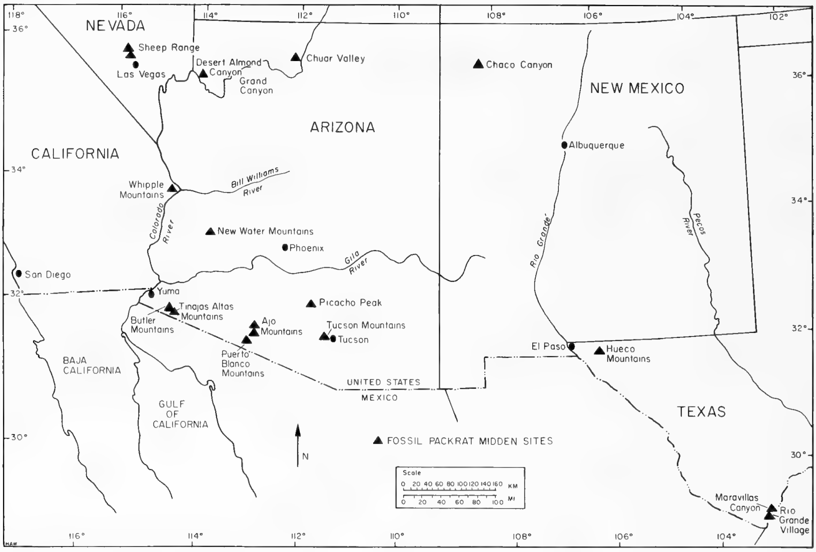


FIG. 1. Map of the southwestern United States showing the localities for fossil mistletoes identified from packrat middens.

carbon years before 1950; Spaulding et al. 1983). Radiocarbon dates for this study were processed by the University of Arizona (A), Geochron (GX), the University of California, Riverside (UCR), and Washington State University (WSU; Table 1). Packrats are excellent plant collectors who bring in samples of most of the plants living within 30–50 m of their dens for food or constructional materials (Finley 1958). The plant fragments that gradually become incorporated into the midden are well-preserved and can usually be identified to species. The plant macrofossil assemblages provide excellent, qualitative samples of the local vegetation. The assemblages contain 15–35(–50) plant taxa including trees, shrubs, succulents, grasses, and perennial and annual herbs. The dry plant remains or packrat fecal pellets are excellent for radiocarbon dating the assemblages. Sequences of packrat middens from one area in chronological order are allowing local vegetational histories to be worked out in detail. Series of packrat midden assemblages often contain over a hundred species of plants including most of the dominants in the local woodland, grassland, and desertscrub communities (Van Devender 1986).

Mistletoes have been found in 53 packrat middens from several regions (Fig. 1) including the Great Basin Desert on the Colorado Plateau in northwestern New Mexico (1 midden), the Mojave Desert in southern Nevada (6) and the Grand Canyon of Arizona (3), the Sonoran Desert in the Lower Colorado River Valley (12) and the

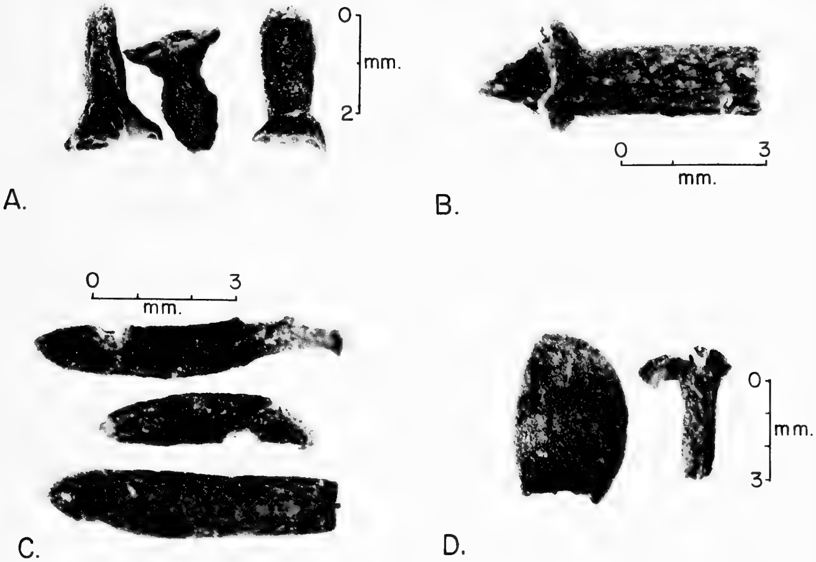


FIG. 2. Late Wisconsin and Early Holocene mistletoes from packrat middens. A. *Arceuthobium divaricatum* twigs from Hueco Mountains #RW4028, El Paso Co., TX. B. *Phoradendron juniperinum* twig from Tinajas Altas #12a, Yuma Co., AZ. C. *Phoradendron bolleanum* subsp. *hawksworthii* leaves from Ernst Tinaja #3B, Brewster Co., TX. D. *Phoradendron coryae* twig and leaf from Alamo Canyon #1B, Pima Co., AZ.

Arizona Upland (13) in Arizona, and the Chihuahuan Desert in Texas (18). Although mistletoes are usually separated using flowers and fruits, most species are readily identified on vegetative structures. For example, *Arceuthobium divaricatum* Engelm. is readily differentiated from species of *Phoradendron* with reduced leaves (*P. californicum* Nutt., *P. juniperinum* Engelm.) by the notched and more cupped leaves and the angular stems (Fig. 2). Most of the fossil mistletoes were identified from leaves and twigs (Fig. 2). The ages of the mistletoe middens range from 32,000 yr B.P. to 610 yr B.P. (Table 1). The temporal distribution of the mistletoes within this time period is: Middle Wisconsin (3; greater than 22,000 yr B.P.), Late Wisconsin (20; 22,000–11,000 yr B.P.), Early Holocene (11; 11,000–8900 yr B.P.), Middle Holocene (8; 8900–4000 yr B.P.) and Late Holocene (11; 4000 yr B.P. to the present). The mistletoes found in the middens include two species of *Arceuthobium* (dwarf mistletoe) and six of *Phoradendron*. Today these genera are repre-

TABLE 1. FOSSIL MISTLETOES FROM PACKRAT MIDDENS FROM THE SOUTHWESTERN UNITED STATES. Explanation of acronyms: ABCO = *Abies concolor*, ACCO = *Acacia constricta*, ACGR = *Acacia greggii*, CEFL = *Cercidium floridum*, CEMI = *Cercidium microphyllum*, CEPA = *Celtis pallida*, CERE = *Celtis reticulata*, JUCO = *Juniperus communis*, JUER = *Juniperus erythrocarpa*, JUMO = *Juniperus monosperma*, JUOS = *Juniperus osteosperma*, JUSP = *Juniperus* sp., OLTE = *Olneya tesota*, PIED = *Pinus edulis*, PIFL = *Pinus flexilis*, PILO = *Pinus longaeva*, PIMO = *Pinus monophylla*, PIPO = *Pinus ponderosa*, PIRE = *Pinus remota*, PRGL = *Prosopis glandulosa*, PRVE = *Prosopis velutina*, PSME = *Pseudotsuga menziesii*, QUAJ = *Quercus ajoensis*, QUHI = *Quercus hinckleyi*, QUPU = *Quercus pungens*, QUSP = *Quercus* sp., SABI = *Sapium biloculare*.

Midden	State: Co.	Elev. (m)	Radiocarbon date (yr B.P.)	Lab. number	Probable host	Other tree associates	References
			Arceuthobium cyanocarpum				
South Crest #1(4)2	NV: Clark	1990	21,500 ± 500	LJ-2840	PIFL/ PILO	ABCO, JUOS, PIMO	Spaulding 1981
Chuar #2	AZ: Coconino	1450	16,165 ± 615	GX-6302	PIFL	ABCO, JUCO, JUcf.OS, PSME	Cole 1981
			Arceuthobium divaricatum				
Basin Canyon #2A	NV: Clark	1630	9365 ± 320	UCR-727		JUOS	Spaulding 1981
Spires #3	NV: Clark	2080	9540 ± 130	A-1670	PIMO	JUOS	Spaulding 1981
Willow Wash #4B	NV: Clark	1585	9820 ± 110	WSU-1861	PIMO	JUOS	Spaulding 1981
Sheep Camp Canyon #2A	NM: San Juan	1975	3030 ± 130	A-2940	PIED	JUMO, PIPO	Betancourt 1984
Hueco Mts. RW#4028	TX: El Paso	1495	13,200 ± 450	A-2142	PIED	JUSP	Lanner & Van Devender 1981
Ernst Tinaja #2B(1)	TX: Brewster	835	17,060 ± 500	A-2981	PIRE	JUSP, QUHI	Van Devender 1986
Maravillas Can. TRV#1	TX: Brewster	610	20,600 ± 1530	A-1860	PIRE	JUSP, QUPU	this report
Maravillas Can. TRV#2	TX: Brewster	610	11,240 ± 160	A-1861	PIRE	JUSP, QUPU	this report
Maravillas Can. TRV#11	TX: Brewster	610	20,950 ± 780	A-4238	PIRE	JUSP, QUPU	this report
			Phoradendron bolleanum subsp. *hawksworthii*				
Maravillas Can. TRV#1	TX: Brewster	610	20,600 ± 1530	A-1860	JUSP	PIRE, QUPU	Lanner & Van Devender 1981
Maravillas Can. TRV#2	TX: Brewster	610	11,240 ± 160	A-1681	JUSP	PIRE, QUPU	Lanner & Van Devender 1981
Maravillas Can. TRV#4	TX: Brewster	610	27,820 ± 1270	A-1847	JUSP	PIRE, QUPU, CERE	Lanner & Van Devender 1981
Maravillas Can. TRV#11	TX: Brewster	610	20,950 ± 780	A-4238	JUSP	PIRE, QUPU	this report

TABLE 1. CONTINUED.

Midden	State: Co.	Elev. (m)	Radiocarbon date (yr B.P.)	Lab. number	Probable host	Other tree associates	References
Baby Vulture Den #5B(1)	TX: Brewster	610	26,430 ± 4600	A-3138	JUSP	PIRE, PRGL	Van Devender 1986
Baby Vulture Den #5B(2)	TX: Brewster	610	19,600 ± 800	A-3133	JUSP	PIRE, PRGL	Van Devender 1986
Ernst Tinaja #2B(1)	TX: Brewster	835	17,060 ± 500	A-2981	JUSP	PIRE, QUHI	Van Devender 1986
Ernst Tinaja #2B(1)	TX: Brewster	835	16,220 ± 400	A-2982	JUSP	PIRE, QUHI	Van Devender 1986
Ernst Tinaja #3B	TX: Brewster	810	15,200 ± 740	A-2963	JUSP	PIRE, QUHI	Van Devender 1986
Tunnel View #15B	TX: Brewster	670	19,800 ± 700	A-4236	JUSP	PIRE, QUHI	this report
Tunnel View #17	TX: Brewster	670	10,500 ± 190	A-4248	JUSP		this report
			Phoradendron californicum				
Redtail Peaks #4A	CA: San Bernardino	510	730 ± 60	A-3648	ACGR		this report
Whipple Mts. #5S2L	CA: San Bernardino	525	6710 ± 160	A-3942	ACGR		this report
Whipple Mts. #6	CA: San Bernardino	525	8540 ± 100	A-3943	ACGR	JUCA	this report
Whipple Mts. #7	CA: San Bernardino	525	8180 ± 130	A-3732	ACGR		this report
Butler Mts. #1	AZ: Yuma	245	8160 ± 250	A-3652	ACGR		this report
Butler Mts. #4	AZ: Yuma	250	3820 ± 70	A-3517	CEFL	OLTE	this report
Butler Mts. #2C	AZ: Yuma	255	750 ± 50	A-3911	ACGR	CEFL, OLTE, PRVE	this report
Butler Mts. #2A	AZ: Yuma	255	610 ± 50	A-3790	ACGR	CEFL, OLTE, PRVE	this report
Tinajas Altas #16A	AZ: Yuma	380	7860 ± 100	A-3521	PRVE	ACGR, CEFL	this report
Alamo Canyon #3	AZ: Pima	890	1150 ± 240	A-2121	ACCO	CEPA, JUER, SABI	this report
Ajo Loop #1A	AZ: Pima	550	5240 ± 90	A-4213	ACGR	CEMI, OLTE, PRVE	Van Devender in press
Ajo Loop #1D	AZ: Pima	550	7970 ± 130	A-3981	PRVE	ACGR, CEFL	Van Devender in press
Ajo Loop #6C	AZ: Pima	550	3400 ± 100	A-4235	CEMI	OLTE	Van Devender in press
Cholla Pass #2	AZ: Pima	590	3440 ± 90	A-4279	CEMI	OLTE	Van Devender in press
Twin Peaks #4	AZ: Pima	550	1910 ± 50	A-3998	CEMI	OLTE	Van Devender in press
Tucson Mts. #2	AZ: Pima	710	2720 ± 100	A-1235	PRVE	ACGR, CEMI	Van Devender 1973

TABLE 1. CONTINUED.

Midden	State: Co.	Elev. (m)	Radiocarbon date (yr B.P.)	Lab. number	Probable host	Other tree associates	References
			Phoradendron coryae				
Alamo Canyon #1B	AZ: Pima	910	14,500 ± 300	A-2120	QUAJ	ACGR, JUSP, PIMO	this report
Montezuma Head #1B	AZ: Pima	975	21,840 ± 650	A-1696	QUAJ	JUSP, PIMO	this report
			Phoradendron juniperinum				
Sawmill Canyon #1	NV: Clark	1755	3530 ± 90	WSU-2045	JUSP	PIMO	Spaulding 1981
Desert View #1(4)	NV: Clark	1810	5210 ± 95	WSU-2044	JUOS	PIMO	Spaulding 1981
Chuar #2	AZ: Coconino	1450	16,165 ± 615	GX-6302	JUcf.OS	ABCO, JUCO, PSME	Cole 1981
Desert Almond #6A	AZ: Mohave	570	10,910 ± 450	A-1427	JUSP	ACGR	Phillips 1977, 1984
New Water Mts. #7B	AZ: La Paz	605	11,000 ± 500	A-1295	JUSP	ACGR, PRVE, QUTU	King & Van Devender 1977
Tinajas Altas #1A	AZ: Yuma	490	9230 ± 140	A-2122	JUCA	ACGR	this report
Tinajas Altas #1B	AZ: Yuma	490	9790 ± 240	A-2494	JUCA	ACGR	this report
Tinajas Altas #12A	AZ: Yuma	565	10,070 ± 110	A-3730	JUCA	ACGR	this report
Alamo Canyon #2C	AZ: Pima	910	32,000 ± 4400	A-2119	JUSP	PIMO, QUAJ	this report
Alamo Canyon #1U	AZ: Pima	910	9910 ± 210	A-2211	JUSP	PIMO, QUAJ	this report
Picacho Peak-AZ #1A	AZ: Pinal	655	13,170 ± 200	A-1827	JUSP	ACGR, PIMO, QUSP	Van Devender & Spaulding 1979
			Phoradendron tomentosum				
Tunnel View #5A	TX: Brewster	680	8820 ± 150	A-2936	PRGL		Van Devender 1986
Tunnel View #5B	TX: Brewster	680	11,000 ± 330	A-2937	PRGL		Van Devender 1986

sented by nine species each in Arizona and New Mexico (Hawksworth and Wiens 1972, Wiens 1964).

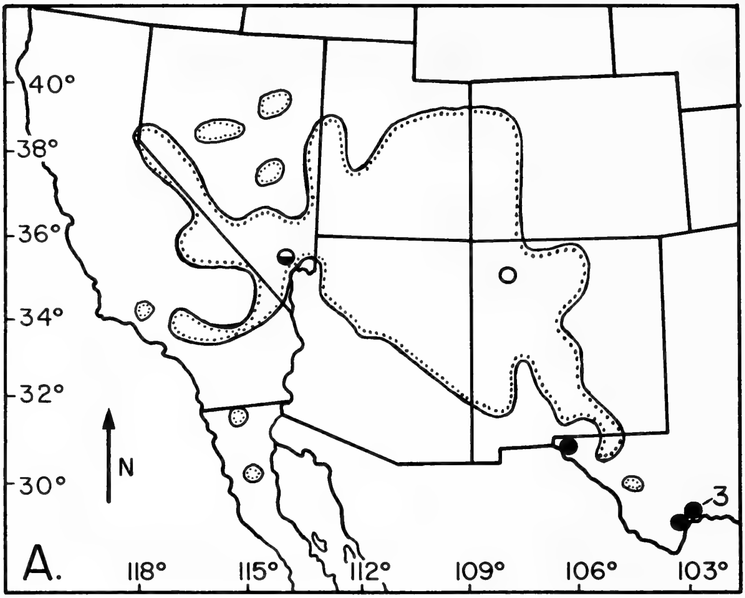
Two middens from southern Nevada and the Grand Canyon contained a dwarf mistletoe (*Arceuthobium cyanocarpum* Coult. & Nels.) that parasitizes mixed-conifer forest conifers. Thirty-one of the fossil mistletoe records are for species that parasitize woodland plants including pinyons (8; *A. divaricatum* in Nevada, New Mexico, and Texas; Fig. 2A), junipers (23; *Phoradendron juniperinum* in Nevada, California, and Arizona, Fig. 2B; *P. bolleanum* (Seem.) Eichler subsp. *hawksworthii* Wiens in Texas; Fig. 2C), and oak (2; *P. coryae* Trel. in Arizona; Fig. 2D). Five samples reported as *P. californicum* in pinyon-juniper or juniper woodland assemblages from 540–585 m elevation in the Grand Canyon of Arizona (Phillips 1977, 1984) have been re-examined and are now referred to as *P. juniperinum* or are not mistletoes. Records of mistletoe from Holocene desertscrub assemblages include *P. californicum* from the Sonoran Desert in Arizona and California (16) and *P. tomentosum* (DC.) Gray from the Chihuahuan Desert in Texas (2).

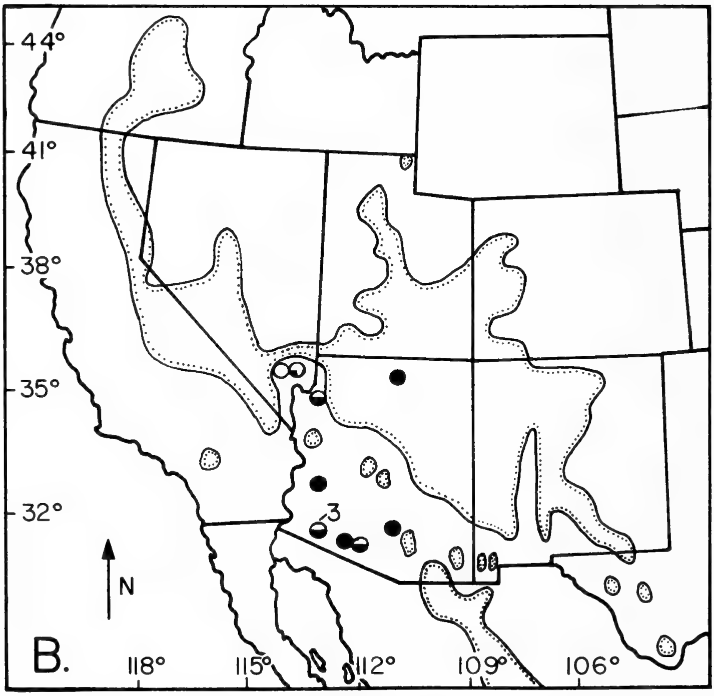
DISCUSSION

Mistletoes have a general host specificity: *Arceuthobium* is found only on conifers and *Phoradendron* on both conifers and angiosperm trees and shrubs. Some species of *Phoradendron* are restricted to junipers (*P. b.* subsp. *hawksworthii, P. juniperinum*), oaks and other sclerophyllous trees and shrubs (*P. coryae*), or riparian trees [*P. macrophyllum* (Engelm.) Cockerell]; others parasitize a broad spectrum of desert legumes and other shrubs (*P. californicum, P. tomentosum*). In general, mistletoes have a smaller geographical range than their host trees because they are more susceptible to catastrophic mortality during freezes or droughts.

The mistletoes in packrat middens are generally in association with trees and shrubs that they parasitize today (Table 1). Because mistletoes are parasites of trees, their responses to major climatic changes strongly reflect the responses of their host trees. In most of the Wisconsin and Early Holocene records, the woodland trees and their mistletoes are extinct at the sites. Today, both occur at elevations from 400–1100 m and at varying distances from the fossil sites. In the following sections, we discuss the fossil mistletoe records that have significant biogeographical interest, and present some general observations on species replacements and paleoclimatic implications.

ARCEUTHOBIUM CYANOCARPUM. This dwarf mistletoe is a parasite of *Pinus flexilis* James (limber pine) and *P. longaeva* D. K. Bailey (Great Basin bristlecone pine), which no longer occurs in Arizona. Hawksworth and Wiens (1972) tentatively listed *A. cyanocarpum*


40°
38°
36°
34°
32°
30°
N
3
A.
118°
115°
112°
109°
106°
103°


44°
41°
38°
35°
32°
3
N
B.
118°
115°
112°
109°
106°

for the San Francisco Mountains near Flagstaff, Arizona, but this mistletoe was later referred to *A. microcarpum* (Engelm.) Hawksworth & Wiens (Mathiasen and Hawksworth 1980). Late Wisconsin midden fossils from southern Nevada and the Grand Canyon dated at 21,500 and 16,165 yr B.P. were associated with *P. flexilis* and *P. longaeva.* The nearest living population to the full-glacial record in the Grand Canyon (Cole 1981) is near Navajo Lake in southwestern Utah, 190 km northwest of the Arizona midden site (Hawksworth and Wiens 1984).

ARCEUTHOBIUM DIVARICATUM. Midden fossils of *A. divaricatum* from the big Bend of Texas are associated with remains of *Pinus remota* (Little) Bailey & Hawksworth (papershell pinyon; Fig. 2). The fossils from the Hueco Mountains east of El Paso, Texas, were in association with *P. edulis* Engelm. (Colorado pinyon). The Late Wisconsin midden records from Texas range in age from 11,240–20,950 yr B.P. Today this mistletoe parasitizes *P. edulis* from New Mexico north into Utah and Colorado and west along the Mogollon Rim into Arizona, and parasitizes *P. monophylla* Torr. & Frem. (singleleaf pinyon) from Nevada south into Arizona and California (Hawksworth and Wiens 1972; Fig. 3). In northern Baja California, it is rare on *P. quadrifolia* Parl. (Parry pinyon; =*P. juarezensis* Lanner, Sierra Juarez pinyon). In Trans-Pecos Texas, it is rare on *P. cembroides* Zucc. (Mexican pinyon) in the Davis Mountains, 190 km north of the Big Bend midden sites. It is also found on the *P. edulis* populations north of the Davis Mountains in the Sierra Diablo and Guadalupe Mountains and on *P. discolor* Bailey & Hawksworth in the Silver City area of New Mexico. *Pinus remota* is an isolated southern derivative of *P. edulis* found on the southern edge of the Edwards Plateau near Del Rio, Texas, and on mountain tops in northeastern Mexico (Bailey and Hawksworth 1979). In the Late Wisconsin, the range of *P. remota* expanded to the north and west to cover the lowlands of the Chihuahuan Desert and was sympatric with *P. edulis* near El Paso (Lanner and Van Devender 1981). *Pinus cembroides* does not have a fossil record. In light of these relationships and distributions it is surprising that *A. divaricatum* does not live on *P. remota* today.

The range of *Pinus edulis* in the Late Wisconsin was probably

←

FIG. 3. Distribution of woodland mistletoes with expanded ranges in the Wisconsin and Early Holocene. A. *Arceuthobium divaricatum* (after Hawksworth and Wiens 1984). B. *Phoradendron juniperinum.* Closed circles = Wisconsin records, half circles = Early Holocene, quarter circles = Middle Holocene, open circles = Late Holocene, dots = ca. present species limits. Number of middens per site indicated if more than one.

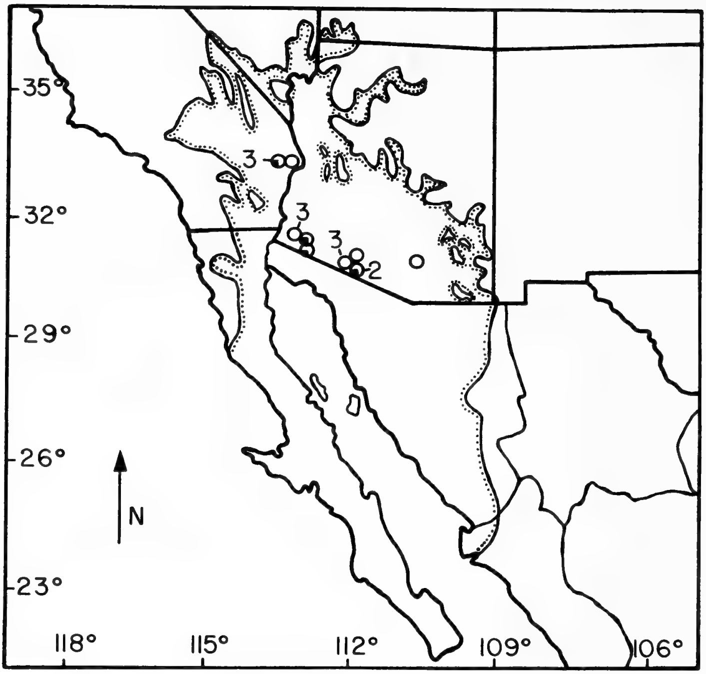


FIG. 4. Distribution of *Phoradendron californicum,* a desert mistletoe that expanded in the Holocene as desertscrub communities formed (after Benson and Darrow 1981). Quarter circles = Middle Holocene records, open circles = Late Holocene, dots = ca. present species limits. Number of middens per site indicated if more than one.

restricted to a small area between 32°–34°W latitude in south-central New Mexico (Van Devender et al. 1984). At that time, the northern ranges of *P. edulis* and *P. monophylla* were widely separated between this area and the northern Mojave Desert in Arizona. The extensive northern ranges of both trees and their hybrid zones in Arizona and Utah are Middle Holocene phenomena (Thompson and Hattori 1983). Relict populations of *P. monophylla* (=*P. edulis* var. *fallax* Little) suggest that the two pinyons may have been sympatric in southwestern New Mexico in the Late Wisconsin. Considering these distributions, the range of *Arceuthobium divaricatum* may have been separated into eastern and western populations. Moreover, *A. divaricatum* has not been found in any of the many Late Wisconsin *P. monophylla* middens from the Sonoran Desert in Arizona and California. During the Wisconsin, *A. divaricatum* may have been restricted to a refugium in the northern Chihuahuan Desert, living on *P. edulis* and *P. remota,* and then spread rapidly during the Holocene with *P. edulis* and *P. monophylla.* Certainly by 9365–

9820 yr B.P. in the Early Holocene, *A. divaricatum* reached the northern Mojave Desert in association with *P. monophylla* (Spaulding 1981).

PHORADENDRON CORYAE. *Phoradendron coryae* was identified from two packrat middens dated at 14,500 and 21,840 yr B.P. from the Ajo Mountains, Arizona (Fig. 2). This mistletoe is a leafy parasite of oaks and occasionally other shrubs, including *Berberis haematocarpa* Woot. (barberry), *Rhamnus crocea* Nutt. (hollyleaf buckbrush), and *Sapindus saponaria* L. (western soapberry). The nearest population to the Ajo Mountains in Organ Pipe Cactus National Monument is in the Baboquivari Mountains (135 km e.). Today it does not parasitize *Quercus ajoensis* C. H. Muell. (Ajo oak), an endemic species also found in the middens. It does live on *Q. turbinella* Greene (shrub live oak), however, a chaparral oak that expanded widely into the lowlands of the present Sonoran Desert in Arizona during the Late Wisconsin and Early Holocene (Van Devender and Spaulding 1979). The Ajo oak has been considered both a subspecies of *Q. turbinella* (Felger and Lowe 1970) and a distinct species with a fossil record back to the Late Miocene of central Washington (Tucker and Muller 1956). It is surprising that *P. coryae* no longer parasitizes *Q. ajoensis.*

PHORADENDRON JUNIPERINUM. In the Late Wisconsin and Early Holocene, *P. juniperinum* was widespread in the Southwest because various junipers [mostly *Juniperus monosperma* (Engelm.) Sarg., *J. californica* Carr.] expanded their lower and southern ranges into lowland deserts (Fig. 3). There are eleven records for *P. juniperinum* south of about 36°N in Nevada and Arizona. The nine records from Arizona are from Late Wisconsin and Early Holocene woodland assemblages dated at 32,000–9230 yr B.P. Although there are no records for *P. juniperinum* from Chihuahuan Desert middens, its present distribution in Trans-Pecos Texas, with isolated populations in the Guadalupe, Davis, and Chisos mountains, suggests that this mistletoe probably also expanded to the south in the eastern part of its range during the Late Wisconsin.

The Tinajas Altas Mountains midden sites for *Phoradendron juniperinum* are from 490 m elevation just east of Yuma, Arizona, and only 7 km north of the Mexican border. Herbarium surveys (ASU, ARIZ) revealed that *P. juniperinum* and *Juniperus californica* (California juniper) no longer occur in Yuma or western Pima counties. Today *P. juniperinum* parasitizes various junipers [*J. deppeana* Steud., *J. erythrocarpa* Cory., *J. monosperma, J. osteosperma* (Torr.) Little, *J. scopulorum* Sarg.], and rarely *Cupressus arizonica* Greene (Arizona cypress) at elevations between 1220 and 2135 m from Utah, Nevada, and northern Arizona, south to the mountain ranges below the Mogollon Rim in Central Arizona. The nearest populations of *P. juniperinum* are on *J. deppeana* (alligator bark juniper) in the Santa Catalina Mountains (335 km e.), on *J. monosperma* near Superior, Pinal Co. (315 km ene.), on an unspecified juniper near Ashdale, Cave Creek, Maricopa Co. (265 km ne.), on *J. deppeana* at Crown King, Yavapai Co. (260 km nne.), on *J. californica* in the Arrastra Mountain area, Mohave Co. (260 km nne.) and on *J. osteosperma* in the Hualapai Mountains, Mohave Co. (270 km n.). The Arrastra Mountain record at 1005 m is the lowest population and possibly the only one parasitizing *J. californica* in Arizona. *Phoradendron juniperinum* also occurs on *J. occidentalis* Hook. near Baldwin Lake, San Bernardino Mountains, San Bernardino Co., California.

The only midden fossils of *Phoradendron juniperinum* from the northern Mojave Desert or the Great Basin are single Middle and Late Holocene records dated at 5210 and 3530 yr B.P. from the Sheep Range of Nevada (Spaulding 1981). Like *Arceuthobium divaricatum, P. juniperinum* probably expanded into the northern portion of its range as *J. monosperma* expanded its range northward into Colorado and Utah, and *J. osteosperma* expanded into Nevada.

Species turnovers. Different mistletoes now live in all of the areas where Wisconsin or Early Holocene woodland mistletoes have been found. In the Sheep Range of Nevada and in the Grand Canyon of Arizona, *Arceuthobium divaricatum* and *Phoradendron juniperinum* of pinyon-juniper woodland replaced *A. cyanocarpum* of the mixed-conifer forest. In the Mojave and Sonoran deserts from the lower Grand Canyon to the Tinajas Altas Mountains, Arizona, *P. juniperinum* retreated with the juniper woodland and *P. californicum* expanded with various Sonoran desertscrub communities (Fig. 4). Moreover, *P. californicum* no longer parasitizes plants growing on rocky slopes near the midden sites but is restricted to nearby riparian wash habitats.

In the Hueco Mountains near El Paso, *Arceuthobium divaricatum* has been replaced by *Phoradendron tomentosum,* the large-leaved mistletoe that parasitizes *Prosopis glandulosa* Torr. (honey mesquite) in desert-grassland and Chihuahuan desertscrub communities. *Phoradendron tomentosum,* however, is presently rare or absent in rocky slope habitats in the limestone portions of the Hueco Mountains near the midden sites. *Phoradendron coryae* and *P. b.* subsp. *hawksworthii* are restricted to the relictual oak and juniper populations on granitic outcrops such as the Hueco Tanks in the predominantly limestone Hueco Mountains (Worthington 1980).

At low elevations in Texas near Rio Grande Village in Big Bend National Park and in Maravillas Canyon in Black Gap Wildlife Refuge, *Arceuthobium divaricatum* and *Phoradendron b.* subsp. *hawksworthii* were replaced by *P. tomentosum* in the Early Holocene. Today, no mistletoes live near the midden rockshelters. *Phoradendron b.* subsp. *hawksworthii* reaches its lower elevational limit at 1280 m near Panther Junction in the Park, where shrubby *Juniperus pinchotii* Sudw. (Pinchot juniper), enters desert-grassland from higher woodlands in the Chisos Mountains. In the same area, *P. tomentosum* is common on legumes down to about 1070 m elevation: i.e., about 385 m above the midden sites. In Maravillas Canyon, *P. tomentosum* presently parasitizes honey mesquite in riparian canyon habitats 75 m below the caves.

The only middens to yield both pinyon (*Arceuthobium divaricatum*) and juniper mistletoes (*Phoradendron b.* subsp. *hawksworthii*) were three Late Wisconsin samples from Maravillas Canyon. After 11,000 yr B.P. in the Early Holocene in most of the warmer desert areas, the climate and woodland vegetation were transitional between those of the last glacial period and today. The woodland and desertscrub mistletoes may have been sympatric until their final separation 9000–8000 yr B.P. In no case are these replacements related to competition for the same host. All of the species turnovers are directly related to changes in the ranges of the host trees as climates shifted from glacial to interglacial regimes.

Paleoclimates. The fossil mistletoes do not reveal much information about paleoclimates. The absence of mistletoes in numerous Late Wisconsin middens containing *Pinus flexilis* and *P. longaeva* from the Great Basin may be due to the reluctance of packrats to forage high in trees, or due to short, cool growing seasons with no summer rainfall (Thompson 1984). The Late Wisconsin records of *Arceuthobium divaricatum* from Texas, its limited occurrence in modern stands of *Pinus edulis* and *P. cembroides,* and its absence from all *P. remota* in Texas, suggest a paleoclimate similar to that occurring presently in areas to the north. The previous paleoclimatic reconstruction for the area is supported: i.e., cool summers, mild winters, and greater annual precipitation with a shift to winter precipitation from Pacific frontal sources at the expense of the summer monsoons (Lanner and Van Devender 1981, Van Devender et al. 1984).

Phoradendron coryae and *P. juniperinum* are absent from the Ajo Mountains today, although *Quercus ajoensis* and *Juniperus erythrocarpa* (redberry juniper) are still there. This suggests that a period of severe climatic stress, probably a drought, in the Middle or Late Holocene, or even in this century, eliminated the mistletoes but not the host trees. Holocene climates and the distances to the nearest populations probably prevented subsequent recolonization.

ACKNOWLEDGMENTS

We thank Tom Daniel, Arizona State Univ. Herbarium, and Rebecca K. Van Devender and Charles T. Mason, Univ. Arizona Herbarium, for distributional records in their care. Kenneth L. Cole, Arthur M. Phillips III, W. Geoffrey Spaulding, and Julio L. Betancourt allowed us to examine their fossil mistletoes. The editors and reviewers provided helpful suggestions. Support was provided by NSF Grants DEB 84-22773, BSR 84-00797 to T. R. Van Devender, DEB 75-13944, DEB 79-23840 to P. S. Martin, and BSR 82-1439 to Martin and Van Devender. Jean Morgan typed the manuscript. Helen Wilson drafted the maps.

LITERATURE CITED

BAILEY, D. K. and F. G. HAWKSWORTH. 1979. Pinyons of the Chihuahuan Desert region. Phytologia 44:129–133.

BENSON, L. and R. A. DARROW. 1981. Trees and shrubs of the southwestern deserts. Univ. Arizona Press, Tucson.

BETANCOURT, J. L. 1984. Fossil packrat middens from Sheep Camp Shelter (29SJ178). *In* A. H. Simons, ed., Archaic prehistory and paleoenvironments in the San Juan Basin, New Mexico: the Chaco Shelters Project. Univ. Kansas Mus. Anthro. Proj. Rept. Ser., No. 53, Lawrence.

COLE, K. L. 1981. Late Quaternary environments in the eastern Grand Canyon: vegetational gradients over the last 25,000 years. Ph.D. dissertation, Univ. Arizona, Tucson.

FELGER, R. S. and C. H. LOWE. 1970. New combinations for plant taxa in northwestern Mexico and southwestern United States. J. Arizona Acad. Sci. 6:82–84.

FINLEY, R. B. 1958. The wood rats of Colorado: distribution and ecology. Univ. Kansas Pub. Mus. Nat. Hist. 10:213–552.

HAWKSWORTH, F. G. and D. WIENS. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). U.S. Forest Serv., Agri. Handb. No. 401, Washington, DC.

——— and ———. 1984. Biology and classification of *Arceuthobium*: an update. *In* F. G. Hawksworth and R. F. Scharpf, eds., Biology of dwarf mistletoes, p. 2–17. U.S. Forest Serv. Gen. Tech. Rept. RM-111, Ft. Collins.

KING, T. J. 1976. Late Pleistocene–Early Holocene history of coniferous woodlands in the Lucerne Valley Region, Mojave Desert, California. Great Basin Nat. 36: 227–238.

LANNER, R. M. and T. R. VAN DEVENDER. 1981. Late Pleistocene piñon pines in the Chihuahuan Desert. Quat. Res. 15:278–290.

MATHIASEN, R. L. and F. G. HAWKSWORTH. 1980. Taxonomy and effects of dwarf mistletoe on bristlecone pine on the San Francisco Peaks, Arizona. U.S. Forest Serv. Res. Pap. RM-224.

PHILLIPS, A. M., III. 1977. Packrats, plants, and the Pleistocene in the lower Grand Canyon. Ph.D. dissertation, Univ. Arizona, Tucson.

———. 1984. Shasta ground sloth extinction: fossil packrat evidence from the western Grand Canyon. *In* P. S. Martin and R. G. Klein, eds., Quaternary extinctions: a prehistoric revolution, p. 148–158. Univ. Arizona Press, Tucson.

SPAULDING, W. G. 1981. The late Quaternary vegetation of a southern Nevada mountain range. Ph.D. dissertation, Univ. Arizona, Tucson.

———, E. B. LEOPOLD and T. R. VAN DEVENDER. 1983. Late Wisconsin paleoecology of the American Southwest. *In* S. C. Porter, ed., The Late Pleistocene, p. 259–293. Univ. Minnesota Press, Minneapolis.

THOMPSON, R. S. 1984. Late Pleistocene and Holocene environments in the Great Basin. Ph.D. dissertation, Univ. Arizona, Tucson.

——— and E. M. HATTORI. 1983. Packrat (*Neotoma*) middens from Gatecliff Shelter and Holocene migrations of woodland plants. *In* D. H. Thomas, ed., The archeology of Monitor Valley 2. Gatecliff Shelter. Anthr. Pap. American Mus. Nat. Hist. 59:157–167.

TUCKER, J. M. and C. H. MULLER. 1956. The geographic history of *Quercus ajoensis*. Evolution 10:157–175.

Van Devender, T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Ph.D. dissertation, Univ. Arizona, Tucson.

———. 1977. Holocene woodlands in the southwestern deserts. Science 198:189–192.

———. 1986. Pleistocene climates and endemism in the Chihuahuan Desert flora. *In* J. C. Barlow, B. N. Timmerman, and A. M. Powell, eds., Proc. Second Chihuahuan Desert Symposium, Chih. Des. Res. Inst., Alpine,TX.

———. In press. Paleoclimatic implications for the monsoonal Sonoran Desert of a packrat midden vegetation sequence form the Puerto Blanco Mountains, southwestern Arizona. Quat. Res.

———, J. L. Betancourt, and M. Wimberly. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. Quat. Res. 22:344–360.

——— and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

Wells, P. V. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quat. Res. 6:223–248.

Wiens, D. 1964. Revision of the acataphyllous species of *Phoradendron*. Brittonia 16:11–54.

Worthington, R. D. 1980. Final report: flora of Hueco Tanks State Historical Park. A report to Texas Parks and Wildlife Dept., Austin.

(Received 25 May 1985; revision accepted 6 Dec 1985.)

POST-FIRE REGENERATION OF KRUMMHOLZ WHITEBARK PINE: A CONSEQUENCE OF NUTCRACKER SEED CACHING

DIANA F. TOMBACK
Department of Biology, University of Colorado,
Denver 80202

ABSTRACT

The potential for post-fire forest regeneration was studied in a 2 ha subalpine burn on Cathedral Peak in Yosemite National Park. The pre-fire forest was a pure stand of krummholz whitebark pine, *Pinus albicaulis.* Data on stand characteristics, seedling density, height, cluster size, and seedling micro-habitats were collected from five 2 × 168 m belt transects. Three additional transects, 2 × 61 m or 2 × 76 m, located in the contiguous, unburned forest provided comparative data. Observations and circumstantial evidence suggest that Clark's Nutcracker, *Nucifraga columbiana,* a bird that buries pine seeds habitually, has initiated the early stages of *P. albicaulis* regeneration on the burn.

In the Sierra Nevada of California, the majority of subalpine fires are caused by lightning strikes, which typically consume less than 0.1 to 0.5 ha of forest (based on records from District Offices or Headquarters of the 8 National Forests and 3 National Parks within the range). Fires that consume larger areas are highly unusual in this range. A lightning strike on 8 August 1975 ignited a fire on Cathedral Peak, Yosemite National Park, and burned approximately 2 ha on the upper west slope. Before the fire, the burned tract was covered by a pure stand of krummholz whitebark pine, *Pinus albicaulis* Engelm., referred to as the elfinwood form (Clausen 1965). In this ecotype, trunks and branches grow close to the ground, forming dense, creeping mats of pine.

Whitebark pine occurs primarily as a climax species in the Sierra Nevada and, consequently, does not depend on fire for regeneration (S. F. Arno, pers. comm.). In the Rocky Mountains of Montana and Wyoming, however, whitebark pine is a climax species on high, exposed sites and successional in more favorable subalpine environments (Lanner 1980, Arno pers. comm.). Seral stands and mixed associations are periodically regenerated by severe fires and surface fires, respectively (Arno pers. comm.).

The question of whitebark pine regeneration in krummholz stands is of particular interest relative to the 1975 fire. The cones of whitebark pine are indehiscent (but not serotinous) and thus do not open when ripe. The seeds are large and wingless. Previous studies (Tomback 1978, 1982, Hutchins and Lanner 1982) have demonstrated that most seed dispersal is effected by Clark's Nutcracker, *Nucifraga*

MADROÑO, Vol. 33, No. 2, pp. 100–110, 30 May 1986

columbiana Wilson, a bird of the family Corvidae. Each fall, one bird may bury as many as 32,000 whitebark pine seeds in caches (i.e., separate clusters) of 1 to 15 seeds, with a mean of 3.7 seeds per cache (Tomback 1982). A common growth form of erect whitebark pine is multi-trunked; a single tree may consist of two or more trunks often partly fused at the base, suggesting that this growth form originates from nutcracker caches. Supporting this hypothesis, the analysis of Linhart and Tomback (1985) indicated that several to all trunks of a multi-trunked tree have distinct genotypes.

Post-fire forest regeneration of the erect form of limber pine, *Pinus flexilis* James, another large-seeded, wingless species, was shown by Lanner and Vander Wall (1980) also to be the consequence of seed storage by Clark's Nutcracker, an important disperser for this species (Tomback and Kramer 1980, Lanner 1980). Because krummholz forms of conifers are noted for low seed productivity and germination potential (Tranquillini 1979), the process of forest regeneration might be slow despite the participation of nutcrackers. It is of interest that the Eurasian Nutcracker, *N. caryocatactes* L., is a disperser of the Japanese stone pine, *P. pumila* Regel, a relative of whitebark pine that occurs only in krummholz form (Mezhenny 1961, 1964). The Cathedral Peak burn provided a unique opportunity to examine 1) the pre-fire composition of the forest community, 2) if and how much forest regeneration had occurred by 1979, 3) the conditions under which regeneration occurred, and 4) whether Clark's Nutcrackers or other sources were responsible for regeneration.

STUDY SITE

The burn occurred near the top of the west slope of Cathedral Peak, Yosemite National Park, elevation 3337 m, approximately 37°55′N and 119°25′W, in Mariposa and Tuolumne Cos., California. A right triangle in shape, the burned tract runs parallel to the ridgetop for 200 m at 3295 m elevation and ends at 3210 m elevation. Slope aspect is nearly due west; the slope angle increases from 25° to 29° near the lower limit of the burn. The substrate is predominantly granitic gravel with occasional patches of duff.

In the center of the burn, on the ridgetop, and on the northern boundary, a few trees escaped fire damage. The southern boundary interfaces with an unburned stand of krummholz *P. albicaulis* that is a maximum of 80 m long in the north–south direction. This stand terminates abruptly above a talus-filled gorge. All burned trees in the study site were killed and defoliated, but the charred skeletons of the krummholz pine generally remained intact. In a few places, however, the fire had burned with such intensity that the trees were reduced to charred pieces.

TABLE 1. DESCRIPTION OF TRANSECTS ON CATHEDRAL PEAK AND DATA COLLECTED.

Transect	Elevation (m)	Length (m)	Data collected
1	3290	168	*In burn:* No. trunks/tree, density of trees, old and new cones, density of seedlings, no. of seedlings per cluster, seedling heights, seedling micro-habitats.
5	3218	122	
2	3274	168	*In burn:* Density of seedlings, no. of seedlings per cluster, seedling heights, seedling micro-habitats.
3	3260	168	
4	3253	168	
6	3290	61	*In live stand:* Density of seedlings, no. seedlings per cluster, seedling heights, seedling micro-habitats, new and old cones.
7	3276	61	
8	3256	76	

Below 3170 m on the west slope of Cathedral Peak, small stands of the typical, erect growth form of whitebark pine occur. The east slope of the peak is forested densely by whitebark pine, the erect growth form giving way to krummholz near the top of the slope.

METHODS

In August and September of 1979, data were gathered from a series of 2 m wide belt transects parallel to the ridgetop in order to describe the pre-fire forest and rate of regeneration. A random numbers table was used to select the starting point elevation for each transect. Transects one and five were completed on 9 and 10 August, transects two to four on 8 and 9 September, and transects six to eight on 9 September. Transects one to five were run through the burned tract with one and five near the upper and lower boundaries, respectively. Transect five is shorter than the others by 46 m to exclude a section where the fire had reduced the trees to charred logs. Transects six, seven, and eight were run through the contiguous, unburned stand. Description of transects and type of data collected are presented in Table 1.

Trunk diameters were measured 0.3 m from the base of the largest trunk on each tree. Whitebark pine seedlings were identified by either number of needles per fascicle (i.e., 5) or the number of cotyledons (7 to 9, Mirov 1967). Seedling heights were measured from the substrate to the tip of the woody stem. All seedlings originating within a circle 5 cm in diameter were defined as one cluster and on one 'site'; diameters of seedling sites (i.e., area containing all seedlings of a cluster) were noted. (No two sites occurred close enough to cause confusion.) Two clusters of seedlings taller than 15 cm were encountered on the transects and probably originated before the fire. Other seedlings were considered to originate post-fire, because whitebark pine, like most arid-site conifers, is likely to be slow-growing

(Fritts 1974). Seedlings were not aged by growth increments, but to test their probable post-fire origin their heights were compared to those of seedlings germinated in August 1975 near Reds Lake on Mammoth Mountain, Inyo National Forest, Mono Co., California at an elevation of 2830 m, and less than 40 km straightline distance southeast from Cathedral Peak (Tomback 1982).

The activities of Clark's Nutcrackers were observed near and on both slopes of Cathedral Peak. In relation to these activities, the numbers and conditions of new and old whitebark pine cones on east and lower west slope trees were censused along base to peak line transects and reported in detail in Tomback (1981).

Non-parametric and parametric tests used for data analysis are from Siegel (1956) and Bailey (1959), respectively. Standard deviations (s.d.) are reported with means.

RESULTS

Pre-fire stand characteristics. As indicated by the tree skeletons on transects one and five, most of the trees had been multi-trunked, with trunks fused at the base with clear lines of demarcation between trunks. Each multi-trunked entity is counted here as a single tree cluster. Between transects one and five there were no significant differences in sample distributions of number of trunks per tree cluster or trunk diameters ($d = 0.0$ and $d = 0.06$, respectively, Normal Distribution Significance test). The overall number of trunks per tree cluster ranged from one to five with a mean and median of 2.2 ± 1.08 and two trunks per tree cluster, respectively. Diameters of trunks ranged from 4 to 43 cm ($\bar{x} = 14.6 \pm 6$ cm, median = 13 cm) (Table 2). Before the fire, the density of krummholz whitebark pine trees was 0.131 trees (each 'tree' may be a cluster or single-trunk form) per m^2 of transect one and 0.168 trees per m^2 of transect five (Table 2).

Seedlings. Data on post-fire seedling establishment were provided by transects one through five for a total survey distance of ca. 790 m (Table 3). Along these transects were a total of 31 seedling sites, represented by 16 solitary seedlings and 15 seedling clusters, with all seedlings below 15 cm in height. It must be emphasized that the stems of the seedlings in a cluster were separate down to the root; thus, each seedling was a distinct individual, and clusters were not produced by branching of a single seedling.

The combined density of solitary seedlings and seedling clusters per transect ranged from $0.015/m^2$ to $0.027/m^2$, with an overall mean density of $0.020/m^2$. The number of seedings per cluster ranged from one to four with an overall mean, s.d., and median of 2.6 ± 0.74 and two seedlings per cluster, respectively. There were no significant differences in the number of seedlings per cluster among the

TABLE 2. PRE-FIRE STAND CHARACTERISTICS AND CONE PRODUCTIVITY OF LIVE TREES IN BURN.

	Transect 1	Transect 5
Burned trees		
No. of trees	36	41
Tree density/m^2	0.131	0.168
No. trunks/tree		
Range	1–5	1–4
Mean	2.2	2.2
s.d.	1.1	1.1
Median	2	2
Trunk diameter (cm)		
Range	4–43	6–30
Mean	15.1	14.2
s.d.	7.6	5.0
Median	14	13
Live trees		
No. of trees	10	3
With new cones	0	0
With old cones	2	0

five transects (t-test) (Table 3). The seedlings in a cluster originated either from nearly the same point (0.0 cm diameter) or within a circle of 5 cm diameter ($\bar{x} = 1.7 \pm 1.7$ cm diameter, median = 1 cm diameter). The overall mean and median number of seedlings in one site were 1.7 ± 0.96 and 1 seedling, respectively (Table 3).

Seedling heights ranged from one to 13 cm ($\bar{x} = 3.9 \pm 2.6$ cm, median = 3.0 cm, n = 54 seedlings). Among the five transects, mean seedling heights ranged from 2.0 cm to 5.3 cm (Table 3). Only between transects three and four were seedling heights significantly different ($t = 3.3$, $df = 22$, $0.002 < P < 0.01$).

Two sites with recently germinated seedlings were encountered during the study. One solitary seedling grew on transect three and has cluster size and micro-habitat data included with other information from transect three. Three seedlings in a cluster (originating within a 0.5 cm diameter circle) were discovered by chance in the study area between transects.

Seedlings in unburned area. Only three solitary seedlings were found on transects six, seven, and eight, for a total transect length of 198 m through the live stand of krummholz whitebark pine. The seedling density ranged from 0.0/m^2 to 0.016/m^2 with a mean of 0.008/m^2 (Table 3). The seedling density was lower in the live stand of whitebark pine than in the burned tract ($P = 0.071$, Mann-Whitney U test) for an overall seedling density of 0.008/m^2. The heights of these seedlings, ranging from 2.5 cm to 11 cm with a mean of

TABLE 3. SEEDLING DENSITY, SEEDLING CLUSTERS, AND SEEDLING HEIGHTS ON TRANSECTS.

	Transects: burn					live stand		
Seedlings	1	2	3	4	5	6	7	8
Sites								
No. sites	7	6	5	9	4	1	2	0
No./m^2	0.021	0.018	0.015	0.027	0.016	0.008	0.016	0
No. solitary	4	2	2	5	3	1	2	0
Cluster sizes	2, 2, 4	2, 3, 2, 2	2, 2, 3	3, 2, 3, 3	4	—	—	—
No./site (singles + clusters)								
Range	1–4	1–3	1–3	1–3	1–4	—	—	—
Mean	1.7	1.8	1.8	1.8	1.8	1	1	—
s.d.	1.1	0.8	0.8	1.0	1.5	—	—	—
Median	1	2	2	1	1	—	—	—
Heights (cm)								
No. seedlings	11	11	9	16	7	1	2	0
Range	1–8.5	1.5–10	1.5–2.5	2–13	2–8	—	2.5–11	—
Mean	3.4	4.2	2.0	5.3	3.6	7	6.8	—
s.d.	2.0	3.1	0.2	2.8	2.1	—	—	—
Median	3	3	2	4.5	3	—	—	—
Cluster area (cm) (diameter of area)								
No. clusters	3	4	3	4	1	—	—	—
Range	0–5	0–3	0–2	0–5	—	—	—	—
Mean	2	1	1	2.9	1	—	—	—

6.8 ± 4.0 cm, were significantly greater than those of the burn area ($t = 1.9$, $df = 55$, $P = 0.05$).

Seedling sites. Transects one through five provided information on the characteristics of those sites in which seeds germinated and survived. In conifers, the heaviest mortality occurs during the early stages of growth (Baker 1950).

For the 31 seedling sites surveyed, substrates were of various combinations of granitic gravel (partly crystalline and coarse), duff, mineral soil, and fine ash. The most common combinations are gravel alone—35%, gravel and duff—19%, and duff alone—16%. Fewer than 10% of all seedling sites contained ash. All of the seedlings were more or less sheltered by large rocks, as opposed to growing in the open: 48% of the seedling sites were 0 to 30 cm from a large rock ($\bar{x} = 8.4 \pm 8.5$ cm, median = 7 cm), 16% were in narrow crevices between large rocks, and about 36% were under rock overhangs. For the three seedlings encountered among live whitebark pine on transects seven and eight, micro-habitat characteristics followed the same trends.

Seedling ages. Cores from five whitebark pine trees in the burned areas, with trunk diameters ranging from 1.3 to 17 cm, had growth rings barely separable under a hand lens, confirming that krummholz whitebark pine, like other arid site conifers, is slow-growing (Fritts 1974). According to growth rings, a seedling 5 cm in height collected in the Cathedral Peak burn in August 1979 was three years old, for a mean height growth rate of ca. 1.7 cm/yr; whereas, a seedling 30 cm in height taken from the less extreme environment of Budd Lake (elevation 3050 m, ca. 1 km straightline distance southeast of Cathedral Peak) was 13 years old for a mean growth rate of ca. 2.3 cm/yr (J. W. van Wagtendonk, pers. comm.).

Fourteen whitebark pine seedlings that germinated in August 1975 on Mammoth Mountain (Tomback 1982) provide additional information for aging seedlings. They ranged in height from 2.5 cm to 5.7 cm with a mean, s.d., and median of 4.2 ± 1.2 cm and 4.0 cm, respectively. Mean growth rates ranged from 0.5 cm/yr to 1.1 cm/yr. In fact, although the mature trees adjacent to the seedlings were of the erect growth form, the local growing conditions are harsh, with deep snow pack, high summer temperatures, and water stress exacerbated by pumice substrate. The mean and median seedling heights recorded in the Cathedral Peak burn (Table 3) fit well within the height range of the Mammoth Mountain seedlings, although of the 54 seedling heights measured in the burn, 12 (22%) fall above the range. These 12 seedling heights are the consequence of either more favorable micro-habitats or pre-fire germination. The former possibility is supported by the 1.7 cm/yr rate reported for the seedling collected on Cathedral Peak in 1979. Thus, it is reasonable to assume in the absence of reliable ages that most of the seedlings surveyed germinated after the 1975 fire.

Seed sources. Few whitebark pine cones were available in or near the study area to provide a direct seed source for reforestation. The scattered patches of live trees in the burned area were non-productive in 1979. Of the 13 trees censused, none had cones of the current crop, and only two had cones of a previous year (Table 2). Although one tree at the top, south end of the burned area bore several whorls of ripe cones, no new cones were observed on any of the live trees on transects six, seven, and eight.

Data gathered on transects of the east- and lower west-facing slopes (Tomback 1981) are summarized here: on the east slope transect from 3050 m to 3250 m, 50% of the 36 trees surveyed bore no cones, 19% bore old cones and a few new cones, and the remainder bore only old cones. On the west slope transect from 3050 m to 3200 m, 43% of the 44 trees surveyed bore no cones, 39% bore old cones and a few new cones, and the rest bore only old cones. Thus, some of the whitebark pine trees on the east and lower west slope were potential seed sources for regeneration in some years.

Nutcracker activities. Nutcrackers occurred on the slopes and forested regions around the base of Cathedral Peak in August and September. Solitary nutcrackers and pairs occasionally flew over the burned study area to the east or west slope. By early August, nutcrackers were harvesting whitebark pine seeds in the Cathedral Peak environs for immediate consumption or for feeding dependent juveniles. Nutcracker-foraged cones are distinct in appearance: they are partly or completely hollowed out from one side. By 10 August, 59% of the new cones observed along the west slope transect had been opened by nutcrackers. In late August, nutcracker seed caching activities begin in the eastern Sierra Nevada (Tomback 1978). By 8 September, 100% of the new cones on the east slope transect had been foraged by nutcrackers (Tomback 1981).

On two separate occasions on 11 September, nutcrackers were observed burying seeds in the study area. The first nutcracker buried two seed caches in the burn and one or more additional caches in the adjacent live stand. The second nutcracker buried two caches in the burn and three in the live stand and then flew upslope and over to the east side of the peak.

DISCUSSION

Data on seedling occurrence indicate that regeneration of the whitebark pine forest in the Cathedral Peak burn is underway. Observations and circumstantial evidence suggest that seed dispersal by Clark's Nutcracker is a primary source of the regeneration, whether or not all the seedlings encountered on the transects originated after the August 1975 fire. Probable sources of whitebark pine seeds for nutcrackers were stands on the east and west slopes of Cathedral Peak and the adjacent forests. Thus, the seedlings in the burned area were probably from parent trees of the erect growth form. Which growth form these seedlings will assume is an interesting question.

It is unlikely that seeds from cones of unburned krummholz whitebark pine were an important source of reforestation. The poor cone productivity in the vicinity of the burn seemed typical of the krummholz form of conifers. The seeds of krummholz conifers, including *P. albicaulis,* also have been found to have less germination capacity than do seeds produced at lower elevations because of differences in seed weight and seed fertility (Tranquillini 1979). With one or two exceptions, those cones produced around the burn were all or partly destroyed by foraging nutcrackers and chipmunks. If a few viable seeds escaped the foragers, however, it is conceivable that the cones might abscise, roll, disintegrate, and establish seedling clusters. Arguments against this possibility have been presented by Tomback (1981, 1982). No debris was evident near seedling sites, especially under rock overhangs where such material might remain undisturbed. The minor role of other vertebrates in the dissemination of whitebark pine has been discussed at length (Tomback 1978, 1981, 1982, Hutchins and Lanner 1982). The low seed productivity of krummholz pine makes significant dispersal by other vertebrates especially doubtful.

At 48% of the seedling sites in the burn, seedlings were in clusters of two to four individuals. Single seedlings and clusters are a logical consequence if one or more seeds of a nutcracker cache germinate. Many such clusters of different ages were evident on the west slope of Mammoth Mountain in 1975, an area used commonly by nutcrackers for seed caching (Tomback 1978, 1982). It is noteworthy that nutcrackers tend to store caches near objects such as rocks, logs, and the base of trees (Tomback 1978) and in fissures in rock faces (Tomback and Kramer 1980). All seedling sites in the burn were in crevices between rocks, next to rocks, or under rock overhangs, and thus concurred with previous observations of nutcracker cache site preferences. These site choices probably increased seedling survivorship rates by providing some shade during the afternoon hours—a critical time in view of the western slope aspect—and perhaps more moisture. High substrate temperatures are a major source of seedling mortality, particularly during the succulent stage when hypocotyl tissue at ground level can be literally ‘cooked.’ The mortality rate from heat injury is notoriously high on dry, sunny slopes (Baker 1950).

Many of the tree skeletons in the burn had more than one trunk, with the multiple trunks fused at the base, clear lines of separation between fused trunks, and distinctive wood grains in each trunk. This growth form resembles the multi-trunked erect form described and analyzed electrophoretically by Linhart and Tomback (1985). Using only two to four gene loci, they discovered that two or more trunks per multi-trunked tree were distinct genotypes, suggesting an origin in nutcracker caches. Until a similar analysis is applied to the 'multi-trunked' krummholz form of *P. albicaulis,* it can only be speculated that this form is also the consequence of seed dispersal by nutcrackers and not of stressful growing conditions. Support for this idea comes from the fact that the krummholz trees had one to five trunks per tree with a mean of 2.2, and seedling cluster sizes ranged from one to four with a mean of 1.7.

If all seedlings surveyed, with the possible exception of two, were established after the fire, then the time required to achieve a pre-fire population density can be estimated. The overall density of mature trees in the pre-fire forest was ca. 0.149 trees/m^2. In 1979, five summers after the burn, the overall density of post-fire seedling sites was ca. 0.020/m^2. If seedling survival rate is 25% (a liberal estimate: see Baker 1950, Tomback 1982), then at the current rate of afforestation, a maximum of about 150 years is required for restocking. It is important to note, however, that many seedling sites are occupied by clusters, and only some of the seedlings within clusters may die. Thus, not all mortality will decrease the rate of 'tree' recruitment. Although this factor decreases actual restocking time, it may be counterbalanced by post-seedling mortality. At some point, the rate of population recruitment may decline. Within the live krummholz pine stand on Cathedral Peak, the seedling density was lower than in the burned area. This may be a consequence of either higher seedling mortality in the forested area or of nutcracker preference for more open sites for seed caching. Regardless, as recruitment progresses, soil conditions and micro-habitats may change and alter regeneration rates.

ACKNOWLEDGMENTS

Funding was provided by the U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, while I was on the faculty of the Department of Biology, University of California at Riverside. The following Experiment Station personnel were generous with their help and time: William Critchfield, Charles Philpot, Timothy Plumb, David Sharpnack, and especially Project Leader Jared Verner. Eldorado, Inyo, Lassen, Plumas, Sequoia, Sierra, Stanislaus, and Tahoe National Forest District Offices and Yosemite, Sequoia, and Kings Canyon National Park Headquarters provided detailed information from fire records. Jan W. van Wagtendonk coordinated my work in Yosemite National Park. Helpful comments on various drafts of this manuscript were provided by Jared Verner, Timothy Plumb, William Critchfield, Frank Vasek, Yan Linhart, and two anonymous reviewers. Translations of the Russian literature were provided by L. Kelso. I am particularly grateful to Kathryn A. Kramer for field assistance and for stoically enduring all, including a hungry, clever bear.

LITERATURE CITED

BAILEY, N. T. J. 1959. Statistical methods in biology. English Universities Press, London.

BAKER, F. S. 1950. Principles of silviculture. McGraw-Hill Book Co., New York.

CLAUSEN, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California high Sierra Nevada. Evolution 19:56–68.

FRITTS, H. C. 1974. Relationships of ring widths in arid-site conifers to variations in monthly temperature and precipitation. Ecol. Monogr. 44:411–440.

HUTCHINS, H. E. and R. M. LANNER. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

LANNER, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Sixth N. Amer. Forest Biol. Workshop Proc., p. 15–48. Univ. Alberta, Edmonton.

——— and S. B. VANDER WALL. 1980. Dispersal of limber pine seed by Clark's Nutcracker. J. Forest. (Washington). 78:637–639.

LINHART, Y. B. and D. F. TOMBACK. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia 67:107–110.

MEZHENNY, A. A. 1961. Food competitors, enemies and diseases. *In* O. V. Egorov, ed., Ecology and economics of the Yakut squirrel. Akademiya Nauk, Moscow.

———. 1964. Biology of the nutcracker (*Nucifraga caryocatactes macrorhynchus*) in south Yakutia. Zoologischeskii Zhurnal 43:1679–1687.

MIROV, N. T. 1967. The genus *Pinus*. Ronald Press, New York.

SIEGEL, S. 1956. Non-parametric statistics. McGraw-Hill Book Co., New York.

TOMBACK, D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16: 123–161.

———. 1981. Notes on cones and vertebrate-mediated seed dispersal in *Pinus albicaulis* (Pinaceae). Madroño 28:91–94.

———. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. J. Anim. Ecol. 51:451–467.

——— and K. A. KRAMER. 1980. Limber pine seed harvest by Clark's Nutcracker in the Sierra Nevada: timing and foraging behavior. Condor 82:467–468.

TRANQUILLINI, W. 1979. Physiological ecology of the alpine timberline. Springer-Verlag, Berlin.

(Received 26 Jun 1985; revision accepted 22 Oct 1985.)

OLD FIELD SUCCESSION IN MOJAVE DESERT SCRUB

DEAN E. CARPENTER
Environmental Science and Engineering, University of California,
Los Angeles 90024

MICHAEL G. BARBOUR[1]
Department of Botany, University of California,
Davis 95616

CONRAD J. BAHRE
Department of Geography, University of California,
Davis 95616

ABSTRACT

Secondary (old field) succession in Mojave Desert scrub vegetation was studied in 20 abandoned homestead fields in the uplands of the eastern Mojave Desert, California. The fields, which were last plowed between 1913 and 1930, were stratified equally in three vegetation types: creosote bush scrub (1100 m elevation), Joshua tree grassland (1280 and 1430 m), and sagebrush/juniper scrub (1615 m). Cattle grazing has been the only widespread disturbance since the fields were abandoned. Our investigation of cover and size of perennial plants indicated that secondary succession in creosote bush scrub is approaching climax (off-field conditions) within approximately 65 years, but that succession in vegetation at higher elevations may require many more years.

Succession in deserts is little understood and little studied. Since the work of Shreve and Hinckley (1937), no studies have been done on long-term succession in the deserts of the American Southwest. This is true especially for the Mojave Desert. Rowlands (1980) reviewed studies of revegetation and disturbance there, and found only a few, all completed since 1961. Those studies involved primarily creosote bush scrub in relation to ghost towns (Wells 1961, Webb and Wilshire 1980), energy corridors (Vasek et al. 1975a), pipeline construction sites (Vasek et al. 1975b), freeways (Vasek 1979), and off-road vehicle impacts (Davidson and Fox 1974). Recently, Prose and Metzger (1985) studied succession on abandoned World War II military training camps in the region.

In the present study, our objective was to document secondary (old field) succession in an array of Mojave Desert vegetation types at several elevations. Abandoned homestead fields in the uplands of the eastern Mojave Desert of California offer an ideal opportunity to accomplish this, because the fields have been relatively undis-

[1] Request reprints from Michael G. Barbour, Department of Botany, University of California, Davis, CA 95616.

MADROÑO, Vol. 33, No. 2, pp. 111–122, 30 May 1986

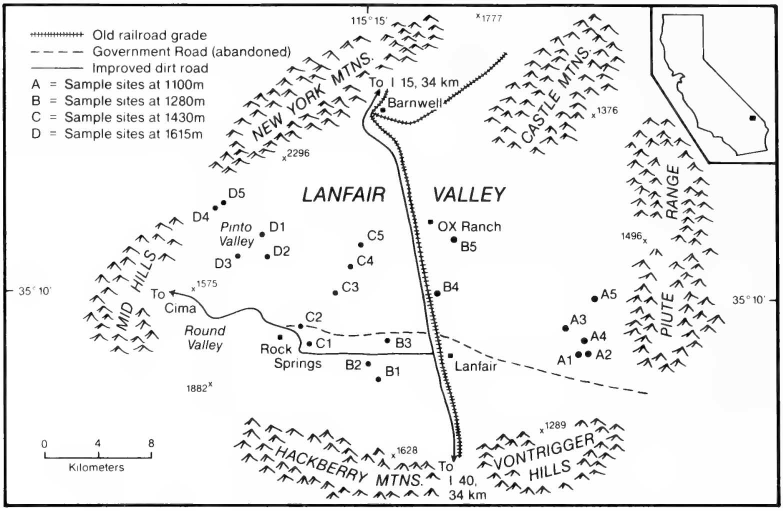


FIG. 1. Map of Lanfair Valley.

turbed since they were abandoned nearly 65 years ago (Carpenter 1983). The fields are located in the Lanfair Valley about 50 km northwest of Needles and range in elevation from 1090 to 1670 m. For the most part, they have similar soils, slope aspects, and slope gradients. Cattle grazing has been the only widespread disturbance since the fields were abandoned. Our hypothesis was that sufficient time had elapsed since these fields were abandoned to permit us to quantify long-term revegetation dynamics by Mojave desert scrub, and to estimate time required to reestablish climax vegetation.

STUDY AREA

Physical setting. Lanfair Valley, which is about 32 km in diameter, is bordered on the west and north by the Mid Hills and the New York Mountains and on the south and east by Hackberry Mountain and the Piute Range (Fig. 1). The valley floor is covered by alluvium and dips in elevation from about 1720 m in the northwestern part near the New York Mountains to 1005 m in the southeastern part.

Bard (1972) estimated that average annual precipitation ranges from 180 mm to 250 mm, with the greatest amounts at the highest elevations. The precipitation pattern is biseasonal: two-thirds falls between December and March, and the remaining third falls between July and September. Daily high temperatures in the summer are typically 32–37°C but occasionally approach 49°C (Bard 1972). Winter temperatures are cool, with occasional minimum temperatures of about −18°C.

The major vegetation types of the valley are (from lowest to highest elevations) creosote bush (*Larrea tridentata*) scrub, Joshua tree (*Yucca brevifolia*) grassland (*sensu* Johnson 1976), and sagebrush (*Artemisia tridentata*)/juniper (*Juniperus osteosperma*) scrub (Munz 1959, Vasek and Barbour 1977). Grasses (C_4 type) are particularly abundant in all these types.

Land-use history. Except for a few hunting-and-gathering Chemehuevi Indians (Miller and Miller 1967, Laird 1976), the Lanfair Valley was largely unsettled until Anglo ranchers moved into the valley in 1880 (Carpenter 1983, Hewett 1956). At that time, now-scarce grama grass (*Bouteloua*) covered the valley "as far as the eye could see" (Foreman 1941, Casebier 1974). The first farmers homesteaded in the valley in 1910 and attempted to dry-farm milo, corn, and beans (Thompson 1929, Gilman 1977). Dry farming failed, however, and new settlers moved into the valley and obtained public land at nominal cost through either the Desert Entry Law or the Homestead Law (U.S. BLM 1971). Those laws required the homesteaders to plow part of their land for crops, even though the fields did not necessarily have to produce a harvest. Most of the homesteads were not "proved up," however, and the claims, with their once-plowed fields, were soon abandoned.

The number of homesteaders was once large; in 1917, 130 registered voters and their families were reported in Lanfair Valley (Thompson 1929, Carpenter 1983). By 1926, however, only nine people lived in the valley (Hewett 1956). Since then, the population has remained low and livestock grazing has been the major economic activity.

METHODS

Seventy-five abandoned homestead fields were identified in large-scale color aerial photographs of Lanfair Valley taken in 1974. Twenty of these fields, divided among four elevation belts (1100 m, 1280 m, 1430 m, and 1615 m) corresponding with vegetational belts, were selected for study and interpolated from the aerial photographs onto 15′ USGS topographic quadrangles. Bureau of Land Management plat records and National Archive documents were used to estimate the years in which the fields were last plowed (Table 1).

Surveys of perennial and dominant plants were conducted in November–December 1982 to quantify differences in plant composition between the abandoned homestead fields and adjacent unplowed areas. For the perennial plant survey, a randomized plot method was used to measure the density, cover, and frequency of each species. A transect line, perpendicular to topograhic lines, was established across the maximum length of each field. Fourteen sample plots, each 4 m^2 in size, were placed randomly along the transect line of the perennial plant survey: 10 plots at least 50 m inside the

TABLE 1. HOMESTEAD FIELD CHARACTERISTICS. Density of dominants is for the surrounding, undisturbed vegetation.

Elevation belt (m) and density of dominants	Site (see Fig. 1)	Elevation (m)	Area (ha)	Year last plowed
1100, *Larrea,* 270 ha^{-1}	A1	1091	22	1921
	A2	1091	9	1921
	A3	1116	15	1921
	A4	1097	7	1930
	A5	1116	13	1913
1280, *Yucca,* 82 ha^{-1}	B1	1274	22	1916
	B2	1311	13	1918
	B3	1292	9	1915
	B4	1274	23	1917
	B5	1268	34	1914
1430, *Yucca,* 67 ha^{-1}	C1	1402	8	1917
	C2	1426	20	1919
	C3	1433	8	1917
	C4	1433	19	1918
	C5	1430	10	1920
1615 *Artemisia,* 750 ha^{-1}	D1	1609	19	1923
Juniperus, 26 ha^{-1}	D2	1561	22	1924
	D3	1585	25	1924
	D4	1670	10	1924
	D5	1664	14	1924

field boundaries (on-field), and four plots at least 50 m outside the field boundaries (off-field). Fewer plots were chosen for off-field vegetation sampling because of the apparent homogeneity in the vegetation, whereas 10 plots were thought necessary to sample gradients in vegetation density from field edges to field centers. Dominant species were not sampled in the plots.

A point-quarter method was chosen for the dominant plant survey (Cottam and Curtis 1956). Because the first transect line placed off-field sampling points too far from the fields, an additional transect line was required to sample adjacent unplowed areas for this survey. This second line was placed either parallel or perpendicular to the transect line of the perennial plant survey (depending on field area); its starting point was 50+ m outside the field boundary. In addition to distance measures along the transects, the maximum diameter of each creosote bush and the height of each Joshua tree were recorded to the nearest 0.5 m in the dominant plant survey.

The Student's t-test was used in the individual-site analysis to compare the on-field and off-field mean cover values of a species. Independent samples and equal variances were assumed for the on-field and off-field populations when using the t-test. The aggregate sample variance was skewed because the numbers of sample plots were unequal (10 on-field and 4 off-field) (Steel and Torrie 1980).

Because cover was a proportional measure and most values were less than 30%, cover data were converted by an angular transformation. This transformation ensured the *t*-test's requirements of normally distributed data. The *t*-test also was used to compare density and width/height means of dominant species at individual sites on-field and off-field.

In order to detect vegetational differences between the plowed and unplowed areas, the five most important off-field perennials and the five most important on-field perennials were selected at each sampled elevation as representative species. A species importance value (I.V., the sum of relative density, cover, and frequency; maximum value of 300) was used to select the representative species and later to compare plowed and unplowed areas.

RESULTS

Distribution of the dominants Larrea and Yucca. Larrea tridentata was the dominant species at off-field 1100 m elevation sites, and *Yucca brevifolia* was the aspect dominant at the intermediate elevations. These two species differed in their ability to invade the abandoned fields. *Juniperus osteosperma* was the potential aspect dominant in the 1615 m elevation belt, but its low density and continuous disturbance (harvesting) in this century made it impossible to compare its behavior on- and off-field.

Larrea density averaged 270 plants ha^{-1} off-field, and those plants had an average diameter of 1.81 m, for an absolute cover of 6.8%. On-field, *Larrea* density averaged 155 plants ha^{-1}, plant diameter was 1.30 m, and absolute cover was 2.0%. Three of the five paired locations showed significant differences in density, and two of the five showed significant differences in shrub diameters.

Yucca density averaged 75 plants ha^{-1} off-field, and those plants had an average height of 2.37 m. In most cases, *Yucca* reestablishment was very slow. On-field, site C-3 exhibited a *Yucca* density ($P < 0.01$) not significant from off-field. On-field, site B-3 had about ⅕ the density of *Yucca* as off-field. No other on-field site showed more than 0.5 *Yucca* plants ha^{-1} and these differed significantly from off-field sites ($P < 0.01$). For the C-3 and B-3 sites, *Yucca* heights on- and off-field were not statistically different.

The fields that showed the least difference in *Larrea* or *Yucca* abundance, compared with the off-field pairs, were those of smallest size and narrowest dimensions (Carpenter 1983).

Distribution of the 10 associated species. Fifty perennial species, in 16 families, were present in the 20 paired sites. Species richness in both on- and off-field sites increased with elevation from 1100 to 1430 m, then fell at 1615 m (Fig. 2). Except at the lowest ele-

TABLE 2. THE 10 MOST IMPORTANT ASSOCIATED PERENNIAL SPECIES AT THE FOUR SAMPLED ELEVATIONS. CR = cover ratio, the ratio of average on-field cover to average off-field cover.

Species	Code	CR
Leucelene ericoides	LEER	12.00
Sphaeralcea ambigua	SPAM	3.27
Acamptopappus sphaerocephalus	ACSP	2.10
Hymenoclea salsola	HYSA	1.69
Gutierrezia microcephala	GUMI	1.51
Lycium andersonii	LYAN	1.17
Haplopappus cooperi	HACO	0.97
Hilaria rigida & H. jamesii	HISP	0.81
Artemisia tridentata	ARTR	0.40
Ephedra nevadensis	EPNE	0.08

TABLE 3. IMPORTANCE VALUES OF THE 10 LEADING ASSOCIATED PERENNIAL SPECIES THAT OCCURRED AT EACH ELEVATION. (Refer to Table 2 for an explanation of species codes.)

Elevation belt (m)	Code	Off-field	On-field
1100	ACSP	41	30
	GUMI	42	7
	HISP	113	92
	HYSA	5	14
	LYAN	23	19
	SPAM	25	87
	Others	51	52
1280	EPNE	14	7
	GUMI	37	43
	HACO	50	59
	HISP	68	50
	HYSA	34	66
	LYAN	9	10
	SPAM	10	23
	Others	78	43
1430	EPNE	11	1
	GUMI	34	53
	HACO	27	23
	HISP	33	38
	HYSA	23	42
	LEER	35	51
	SPAM	10	25
	Others	126	67
1615	ARTR	55	29
	EPNE	18	2
	GUMI	95	92
	HISP	38	19
	LEER	12	62
	SPAM	17	15
	Others	65	83

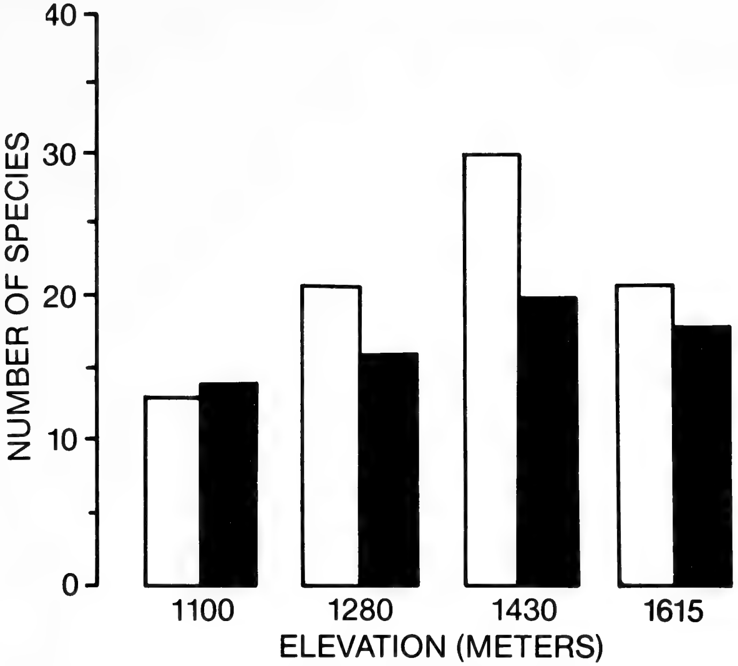


FIG. 2. Off-field (white) and on-field (dark) perennial species richness for stands in the four elevation belts.

vations, off-field sites had about 20% more species per unit area than paired on-field sites. These patterns, however, were not statistically significant.

Perennial cover generally varied between 20 and 30%, and no pattern of increase correlated with elevation. On-field cover was lower than paired off-field cover at all but the lowest elevations where the reverse was true. Cover was significantly different between paired sites, however, only in the 1430 m elevation belt. In general, on-field cover was not significantly different from off-field cover.

Importance values (I.V.s) were calculated for the five leading species from the pooled collection of species found on-field and for the five leading species from the pool of species found off-field. The 10 species (Table 2) included such taxa as *Leucelene ericoides,* which exhibited an overwhelming preference for on-field sites; *Haplopappus cooperi,* which was equally abundant on- and off-field; and others such as *Ephedra nevadensis,* which was skewed to off-field sites. Throughout the range of elevations, the five off-field species accounted for 58–83% of cumulative I.V.s, and the five on-field species accounted for 72–86% of cumulative I.V.s.

At 1100 m, *Hilaria* was the overwhelming plant off-field, with an I.V. twice that of the next most important species (Table 3), whereas on-field it shared importance with *Sphaeralcea. Sphaeralcea* and *Hymenoclea* were three times more important on-field than off-field. *Gutierrezia,* in contrast, dropped in importance from second place off-field to a distant sixth place on-field.

At 1280 m, *Hilaria* was again dominant off-field, but less overwhelmingly so, and it was third in importance on-field (Table 3). *Hymenoclea* and *Sphaeralcea* roughly doubled in importance on-field as compared with off-field. *Haplopappus, Gutierrezia,* and *Lycium* were almost equally important off- and on-field.

At 1430 m, *Leucelene* and *Gutierrezia* had the leading I.V.s both off- and on-field, but dominance was rather closely shared with two or three other species (Table 3). *Hymenoclea* and *Sphaeralcea* again doubled in importance on-field compared with off-field. *Ephedra* dropped in I.V. from 10 off-field to one on-field.

At 1615 m, *Gutierrezia* was the most important plant both off- and on-field (Table 3). The I.V.s of *Artemisia* and *Hilaria* dropped by half on-field compared with off-field, and that of *Ephedra* dropped from 18 to two. In contrast, the I.V. of *Leucelene* increased five-fold on-field compared with off-field. This was the only elevation belt at which "other species" had a collective I.V. greater on-field than off-field, indicating that species richness was greater on the disturbed sites.

In summary, characteristic associated plants that responded positively to past disturbance were *Leucelene, Sphaeralcea, Hymenoclea,* and *Gutierrezia. Acamptopappus, Lycium,* and *Haplopappus* had no strong response. *Hilaria, Artemisia,* and *Ephedra* responded negatively. Absolute cover values for the 10 species paralleled the I.V. patterns (Fig. 3).

DISCUSSION

Undisturbed sites at the 1100 m elevation were dominated by a relatively dense cover of *Larrea,* 2–3 m tall; understory was predominantly *Hilaria,* although *Acamptopappus, Gutierrezia,* and *Lycium* were important understory shrubs. Some 65 years following disturbance, on-field sites showed significant invasion by *Larrea*: in the majority of cases density, cover, and canopy size were statistically equal to those in control, off-field sites. The sub-shrub *Sphaeralcea* and the shrub *Hymenoclea* were the most important associated plants. *Acamptopappus* and *Lycium* were also present, with I.V.s similar to those of off-field sites. In fact, only eight species found on- and off-field showed significant cover differences (Fig. 3), and as a result, field boundaries were sometimes difficult to identify. Species richness differed only 20% between on- and off-field sites.

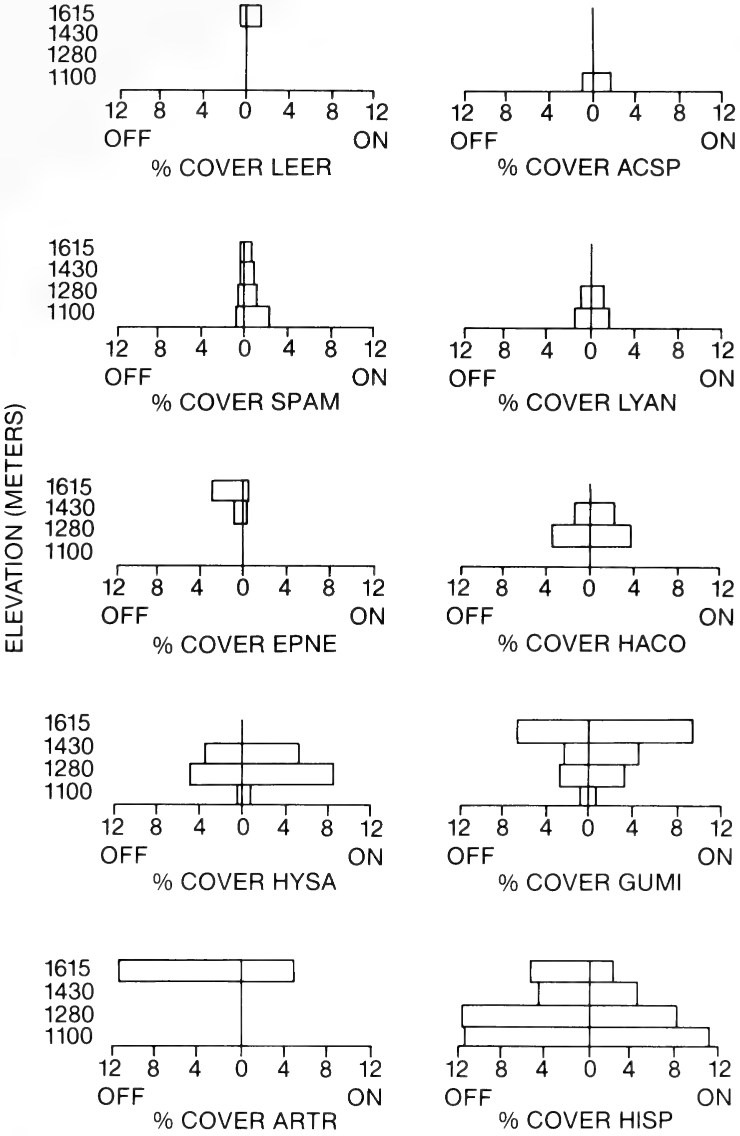


FIG. 3. Off-field (left) and on-field (right) absolute cover for the 10 most important associated perennial species at all four elevations. No LEER or ACSP paired-sites showed significant cover differences (*t*-test) on- or off-field. The other eight taxa showed significant differences in cover on- and off-field for at least some of the sites. (Refer to Table 2 for an explanation of species codes.)

Undisturbed sites at the 1280 and 1430 m elevations were dominated in aspect by *Yucca brevifolia,* 2–4 m tall, sometimes associated with other arboreal species, *Y. schidigera* and *Opuntia acanthocarpa. Hilaria* was among the most important associated plants, as were *Gutierrezia, Haplopappus,* and *Leucelene.* Nearly 70 years following disturbance, on-field sites exhibited virtually no arboreal species. *Hymenoclea* was the dominant, associated with *Sphaeralcea, Gutierrezia,* and *Leucelene.* There was significantly less total cover on-field than off-field, and 23% of all species showed significant differences in cover ($P < 0.05$). Species richness was lower on-field than off-field. In contrast to creosote bush scrub, Joshua tree grassland was far from reaching predisturbance composition.

Undisturbed sites at the 1615 m elevation were dominated in aspect by *Juniperus,* 2–4 m tall, especially near washes. *Opuntia acanthocarpa* was also present in the overstory. *Gutierrezia* and *Artemisia* were the dominant shrubs, and *Ephedra* and *Yucca baccata* were commonly associated. Grasses were less important in the understory than at lower elevations. Nearly 65 years following disturbance, on-field sites had virtually no arboreal species. *Artemisia* was significantly reduced in importance. The dominants were *Gutierrezia* and *Leucelene,* and species richness was lower than on undisturbed, off-field sites. Some 37% of all species showed significant cover difference on-field and off-field (Carpenter 1983). Thus sagebrush/juniper scrub had progressed even less toward regaining predisturbance composition than had Joshua tree grassland.

Secondary succession at the lowest elevations (creosote bush scrub) is apparently approaching climax (the conditions of the off-field grazed vegetation) within a time span of approximately 65 years, but succession at the higher elevations (Joshua tree grassland and sagebrush/juniper scrub) may require twice as many years. The rate of succession is probably confounded by the impact of cattle in this century, and we cannot with certainty estimate what the course or time of secondary succession would have been in its absence.

Although Shreve (1942) stated that succession does not occur in deserts, evidence accumulated since that time suggests that both primary succession (Vasek and Lund 1980) and secondary succession can occur in the Mojave Desert. Prose and Metzger's (1985) very detailed study of tent sites, roads, and parking lots in a tank training area abandoned for 40 years, divided perennial shrubs into three categories: long-lived, long-lived opportunistic (only one species, *Ambrosia dumosa*), and short-lived. On disturbed sites, long-lived perennial cover was significantly less than that of undisturbed controls, but cover by the other two categories of shrubs was greater than that of controls. Long-lived perennials included species of *Atriplex, Encelia, Krameria, Larrea, Opuntia, Dyssodia, Encelia, Hymenoclea, Porophyllum,* and *Stephanomeria.* Recovery of long-lived perennials correlated negatively with the magnitude of soil compaction. Their estimates of time necessary to achieve climax ranged from just less than 50 years to over 550 years.

Wells (1961) also showed that secondary succession proceeds through a seral stage of short-lived perennials. Streets abandoned for 30 years in a mining town were dominated by an open stand of bunchgrass (*Stipa*) and short-lived subshrubs (*Hymenoclea, Salazaria,* and *Thamnosma*)—taxa normally restricted to dry washes. The only substantial densities of long-lived perennials were species of stump-sprouting *Lycium* and *Ephedra.* Adjacent undisturbed sites showed densities of long-lived perennials (*Grayia* and *Larrea)* 20-fold greater than on disturbed sites. Wells gave no estimate of recovery time to climax, but clearly 30 years was far too brief.

Vasek et al. (1975a) examined desert scrub beneath powerlines that were 30 years old and reported an increase in cover by short-lived perennials such that total cover was greater than that of adjacent, undisturbed areas. Pipeline corridors, disturbed 12 years in the past (Vasek et al. 1975b), showed long-lived perennial cover only 0–41% that of controls, and Vasek estimated that the time to reestablished climax there may be 40 years. His observations (Vasek 1979) of an eight year old barrow pit, however, led him to conclude that succession would require "a few centuries." In all of these, a seral stage of short-lived, suffrutescent perennials was apparent.

Our work on old field succession suggests that a similar seral community of short-lived perennials invades and is replaced slowly by increasing populations of long-lived climax shrubs. In our sites, the most prevalent short-lived species were *Leucelene ericoides, Sphaeralcea ambigua, Acamptopappus sphaerocephalus, Hymenoclea salsola,* and *Gutierrezia microcephala,* which had cover values 2–20 times that of undisturbed sites. Our estimate of 65–130 years required for establishment of predisturbance vegetation cover is well within the estimates reported above for other types of disturbance.

LITERATURE CITED

BARD, R. C. 1972. Settlement pattern of the eastern Mojave Desert. Ph.D. dissertation, Univ. California, Los Angeles.

CARPENTER, D. E. 1983. Old-field succession in Mojave Desert scrub. M.S. thesis, Univ. California, Davis.

CASEBIER, D. G. 1974. Fort Pah-Ute, California. Tales of the Mojave Road Publ. Co., Norco, CA.

COTTAM, G. and J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451–460.

DAVIDSON, E. and M. FOX. 1974. Effects of off-road motorcycle activity on Mojave Desert vegetation and soil. Madroño 22:381–412.

FOREMAN, G. 1941. A pathfinder in the southwest—the itinerary of Lieutenant A. W. Whipple during his explorations for a railway route from Fort Smith to Los Angeles in the years 1853 & 1854. Univ. Oklahoma Press, Norman.

GILMAN, H. F. 1977. The origin and persistence of a transit region: eastern Mojave Desert of California. Ph.D. dissertation, Univ. California, Riverside.

HEWETT, D. F. 1956. Geology and mineral resources of the Ivanpah Quadrangle, California and Nevada. U.S.G.S. Prof. Paper No. 275. U.S. Gov. Printing Office, Washington.

JOHNSON, H. B. 1976. Vegetation and plant communities of southern California deserts—a functional view. *In* J. Latting, ed., Symposium proceedings, plant communities of southern California, Spec. Publ. No. 2, p. 125–164. California Native Plant Society, Berkeley.

LAIRD, C. 1976. The Chemehuevis. Malki Museum Press, Banning, CA.

MILLER, R. D. and P. J. MILLER. 1967. The Chemehuevi Indians of southern California. Malki Museum Press, Banning, CA.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

PROSE, D. V. and S. K. METZGER. 1985. Recovery of soils and vegetation in World War II military base camps, Mojave Desert. Open File Report. U.S. Geol. Survey, Menlo Park, CA.

ROWLANDS, P. G. 1980. Recovery, succession, and revegetation in the Mojave Desert. *In* P. G. Rowlands, ed., The effects of disturbance on desert soils, vegetation and community processes with emphasis on off-road vehicles: a critical review, p. 75–118. Spec. Publ., U.S.D.I., Bur. Land Management Desert Plan Staff.

SHREVE, F. 1942. The desert vegetation of North America. Bot. Rev. 8:195–246.

——— and A. L. HINCKLEY. 1937. Thirty years of change in desert vegetation. Ecology 18:463–478.

STEEL, R. G. D. and J. H. TORRIE. 1980. Principles and procedures of statistics, 2nd ed. McGraw-Hill, New York.

THOMPSON, D. G. 1929. The Mojave Desert region, California: a geographic, geologic, and hydrographic reconnaissance. U.S.G.S. Prof. Paper No. 578. U.S. Gov. Printing Office, Washington.

U. S. BUREAU OF LAND MANAGEMENT. 1971. Regulations pertaining to: disposition, occupancy and use—Desert Land Entries. Cir. No. 2291. U.S. Dept. Interior.

VASEK, F. C. 1979. Early successional stages in Mojave Desert scrub vegetation. Israeli J. Bot. 28:133–148.

———, and M. G. BARBOUR. 1977. Mojave Desert scrub vegetation. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 835–867. John Wiley & Sons, New York.

———, H. B. JOHNSON, and G. D. BRUM. 1975a. Effects of power transmission lines on vegetation of the Mojave Desert. Madroño 23:114–130.

———, ———, and D. H. ESLINGER. 1975b. Effects of pipeline construction on creosote bush scrub vegetation of the Mojave Desert. Madroño 23:1–13.

——— and L. J. LUND. 1980. Soil characteristics associated with a primary plant succession on a Mojave Desert dry lake. Ecology 61:1013–1018.

WEBB, R. H. and H. G. WILSHIRE. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town. J. Arid Environ. 3:291–303.

WELLS, P. V. 1961. Succession in desert vegetation on streets of a Nevada ghost town. Science 134:670–671.

(Received 26 Apr 1985; revision accepted 5 Dec 1985.)

BISHOP PINE (*PINUS MURICATA*) OF INLAND MARIN COUNTY, CALIFORNIA

CONSTANCE I. MILLAR
Wildland Resources Center, University of California,
Berkeley 94720

ABSTRACT

The locations and characteristics of five, small, previously undescribed stands of bishop pine (*Pinus muricata*) in central Marin Co., California, are reported. Three stands lie on dry sites in the Kent Lake Drainage north of Mt. Tamalpais: San Geronimo Ridge, a spur ridge above Little Carson Cr., and Oat Hill. These stands are anomalous in occurring 15 km from the ocean and up to 435 m in elevation. The remaining two stands are on rocky, dry sites on the west slope of Bolinas Ridge, near the McCurdy Trail, and south of Wilkins Gulch. Trees of all stands have slower growth, more spindly stems, sparser crowns, and bear more abundant, serotinous cones than trees of other northern California populations. Stomatal traits and number of leaf resin canals, however, resembled coastal bishop pines on Pt. Reyes. Bishop pine once may have grown more widespread in Marin Co., but mesic-adapted stands evolved on Pt. Reyes and xeric, fire-adapted stands evolved in the interior.

This paper describes the location and habit of bishop pine (*Pinus muricata* D. Don) in inland Marin Co., California. Despite a long history of mapping and studying this species, botanists have largely ignored the stands of interior Marin Co. Although the nearby bishop pine population on Inverness Ridge and Point Reyes was described over a hundred years ago (Engelmann 1880), the only subsequent geographic comments have been by Howell (1945, 1949) and Mason (1949).

Western botanists have long been interested in bishop pine because of its complex patterns of variation and crossability among the nine disjunct, maritime (n. California to Baja California) populations, and its affinities to Monterey pine (*P. radiata* D. Don) (Duffield 1951, Critchfield 1967). Bishop pine populations north of Monterey (var. *borealis* Axelrod) are marked by an abrupt transition at Sea Ranch, Sonoma Co., in several traits within continuous pine stands. North of a narrow zone, pines differ qualitatively from those to the south in stomatal anatomy and waxiness (Duffield 1951), monoterpene compositions (Mirov et al. 1966), allozymes, and flowering phenology (Millar 1983).The origin of the sharp contact and the evolution of distinct differences seem related to population biogeographic movements and adaptation to unique soils (Millar 1985).

While studying relationships among northern bishop pine populations, I grew interested in several anomalous features of the inland Marin distribution: the pines grow farther inland, at higher eleva-

---

MADROÑO, Vol. 33, No. 2, pp. 123–129, 30 May 1986

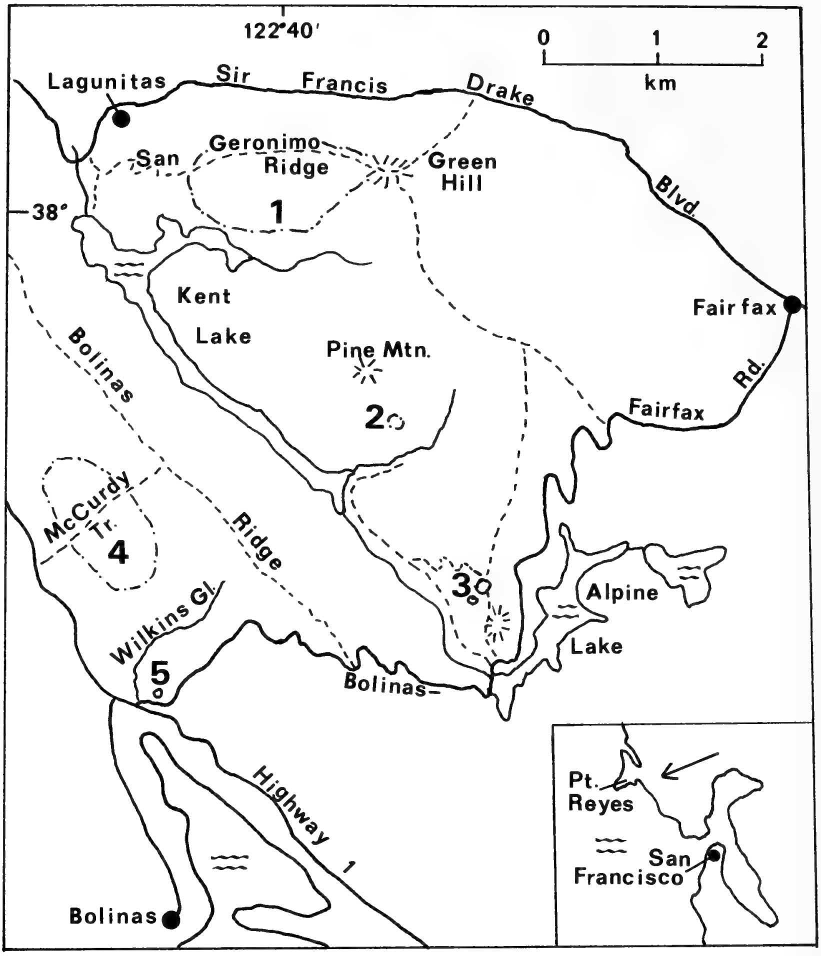


FIG. 1. Map of inland Marin Co. bishop pine stands. 1. San Geronimo Ridge stand; 2. Little Carson Creek stand; 3. Oat Hill stand; 4. McCurdy trail stand; 5. Wilkins Gulch stand. Legend: — — — trail; — · — stand boundaries.

tions, and in drier habitats than most native bishop pines of northern California. They are also the only known bishop pines south of Pt. Arena that grow east of the San Andreas fault. Axelrod (1980) speculated that if the proximity of Pt. Reyes and the Inverness stands to inland Marin Co. is due to northward displacement of the Pacific plate, then the inland Marin Co. stands could be more closely related to the other bishop pine populations east of the fault than to the Pt. Reyes population.

I visited five stands of bishop pine in central Marin Co., at San

Geronimo Ridge, Oat Hill, Little Carson Creek, and Bolinas Ridge (two stands) (Fig. 1). The pines extend 6–15 km from the ocean and 60–435 m in elevation, growing on dry, exposed, and rocky ridges. Four of the stands occur on patches of Maymen gravelly loam soils; the southernmost stand on Bolinas Ridge occurs on Tocaloma-McMullin gravelly loams (Soil Conserv. Ser. 1985). Both soils are shallow, derived from sandstone, and differ considerably from the deep, quartz/diorite-derived Inverness loams underlying the Pt. Reyes population. The pines either form small oases of trees amid large expanses of coastal shrubs, similar to the habit of southern bishop pine populations, or they border forests of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and coast redwood [*Sequoia sempervirens* (D. Don) Endl.]. Although trees vary in age among the stands, middle age classes (15–30 years) dominate in all stands, and few trees are old enough to have survived an extensive burn in 1945.

Specific Stand Descriptions

San Geronimo Ridge. The bishop pines on San Geronimo Ridge grow on the south-facing slope of the ridge above Kent Lake at elevation 155–435 m, and compose the largest stand in central Marin Co. (Fig. 1). Scattered pines grow within the dense manzanita chaparral (*Arctostaphylos* spp.) for about 3.5 km along the ridge as far east as Green Hill, and downslope nearly to Kent Lake. Along the ridge crest, the forest composition changes abruptly, and dense coast redwood, Douglas-fir, and tanbark oak [*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.] forests replace bishop pine on the north-facing slope. Although several large pines along the ridgetop are over 50 years old, most of the trees are younger.

Little Carson Creek. The only other stand noted in the literature is a small grove (less than 100 trees) perched at 430 m on a rocky spur of the south-facing slope of Pine Mountain above Little Carson Creek (Fig. 1). The trees in this stand are young (10–25 years old) and spindly, with sparse foliage and short needles, and are heavily laden with small stem- and branch-cones. No other trees grow in the vicinity; manzanita chaparral surrounds the stand. Although there appear to be no other pines growing on Pine Mountain, other patches of Maymen soil occur in the area, and this small stand may be the sole remnant of a larger population that was decimated by the 1945 fire.

Oat Hill. The Oat Hill stand includes two small groves (Fig. 1). The higher grove, at 395 m, straddles a summit of the ridge that extends northwest from Oat Hill. Although the grove is mostly on the flat ridgetop, a few trees grow on the exposed eastern slope. Most of the trees are young with spindly crowns, short needles, and abundant, small cones; a few trees are large (50 cm DBH) and have more normal form with deeply furrowed bark.

The second grove near Oat Hill is about 0.3 km down a gully on the southwest slope. These trees also are slender with sparse crowns and poor forms. Both Oat Hill groves border on mixed forests of Douglas-fir, tanbark oak, and occasional madrone (*Arbutus menziesii* Pursh) and giant chinquapin [*Chrysolepis chrysophylla* (Dougl. ex Hook.) Helmquist], as well as open slopes of manzanita.

Bolinas Ridge. The three stands described above lie on the eastern slopes of the Kent Lake drainage, removed from the ocean by two major ridges. The remaining stands are on the western slope of Bolinas Ridge. Trees of the larger stand are scattered around the McCurdy Trail between 250 and 370 m (Fig. 1). Occasional Douglas-fir grow near the pines around gullies and at upper elevations, but bishop pine is the only tree growing on exposed slopes, where it is associated with tall, dense manzanita. This stand resembles the San Geronimo Ridge stand in the larger diameters, greater ages, and better bole forms than trees of the other stands. The trees bear abundant closed cones, which are larger than the cones from the three stands in the Kent Lake Drainage.

The second stand on Bolinas Ridge is on a rocky promontory south of Wilkins Gulch (Fig. 1). This small cluster of about 60 trees lies lower (60 m), farther south, and closer to the ocean than any of the other stands. The grove is surrounded by manzanita shrublands. The pines are even-aged (about 25 years old), have fairly good form, and bear abundant branch and stem whorls of asymmetric, heavy-scaled cones. In contrast to the other stands, some old cones on the trees were open, and I observed a few young pine seedlings growing in the bare, rocky soils at the edge of the stand. The greater lushness of the vegetation and proximity to the ocean suggest that the climate may be more mesic at this site than at the more interior locations.

General Observations

Foliage sampled from trees at all five stands had the "green" stomatal characteristic that is typical of bishop pines growing south of the Sea Ranch transition and west of the fault. A sample of 250 needles (5 needles from 10 trees at each of 5 stands) averaged 2.1 resin canals per leaf, which is not significantly different from Inverness (2.1 canals), Sonoma Co. (1.8), or Mendocino Co. (2.3) populations, but is significantly different from population averages south of Inverness (Millar 1985). In general, the central Marin trees grow slowly and have poor bole and crown forms. In these traits, they resemble bishop pines in southern populations, which were shown by common-garden studies to have genetically slow growth, sparse crowns, and poor form.

Cone shape varies among trees within stands, from symmetric and thin-scaled to asymmetric and heavy-scaled. This polymorphism also occurs in most populations from Inverness southward, but not farther north in California. In populations north of Marin Co., cones are mostly asymmetric and heavy-scaled.

Striking features of all the inland Marin stands are the prolific cone production and extreme cone serotiny. Cones not only persist on the trees for many years, but remain closed much longer than the cones of the northern populations. At all five stands, 25–35 whorls of cones occur commonly. Because more than one cone whorl may be produced annually, the exact duration in years of cone serotiny is difficult to assess. Within the south-to-north cline in decreasing cone production and decreasing serotiny that occurs in bishop pine (Duffield 1951), the inland Marin Co. pines resemble southern California and Baja California populations.

DISCUSSION

Although fire undoubtedly has been important in the evolution of all bishop pine populations, fire frequencies differ along the California–Mexico coast, and the extant populations are affected differentially by fire. Fires are least common in the cool, damp parts of the species' range north of Marin Co. Cones in those populations usually open after several years, and seedling regeneration in the absence of fire is common. Although natural and man-related fires have affected bishop pine on Inverness Ridge (Sugnet and Martin 1984), high relative humidities throughout the year lessen the chance for ignition.

With increasing distance from the coast, however, fires become more common (Jacobs et al. 1985). For coast redwood forests near Muir Woods, Jacobs et al. estimate a fire interval of 27 years on the first ridge inland, and an interval of 22 years on a third ridge inland. At the inland site, the distribution of fire intervals was highly skewed toward shorter than average intervals. This indicated a pattern of several short intervals followed by one or a few long intervals. Jacobs et al. also documented a significantly lower averge weekly fog drip during the fire season at the inland site than at the coastal site. Because pine forests are more fire-prone than redwood forests, they undoubtedly burn more often. Fire-charred bark on trees at all pine stands indicates the occurrence of fires. A higher fire frequency in interior Marin Co. compared to Pt. Reyes may, in part, account for the long cone serotiny and prolific cone production of the inland trees.

The origin and relationship of the inland Marin Co. stands to other bishop pine populations remain enigmatic, although the "green" foliage excludes a close affinity to the "blue" race north of Sea Ranch and east of the fault. The general appearance of the trees (form and size, cone serotiny and abundance, and attributes of their location and ecological situation) resembles bishop pine stands of southern California and Mexico, but, due to distance and genetically distinct intervening populations, the inland stands are unlikely to be closely related to those populations. More likely, these pines are remnants of a formerly large bishop pine population in Marin Co. A western group evolved under mesic conditions on Inverness Ridge and Pt. Reyes, and an eastern group evolved under xeric conditions inland. Pleistocene fossils of bishop pine from the east side of Tomales Bay near Millerton, where bishop pine does not grow now (Mason 1934), indicate a formerly more extensive Marin Co. population. The Pt. Reyes population, whose present southernmost extent at Mt. Wittenberg is 13 km from the closest inland stand, may once have extended farther south on Inverness Ridge. Sugnet and Martin (1984) suggest that fire exclusion practices on Pt. Reyes have encouraged Douglas-fir growth on the southern peninsula, and have prevented bishop pines from growing where they otherwise might have flourished. If bishop pine formerly grew farther south on Pt. Reyes, it would have been close to the two Bolinas Ridge stands. The size and extent of the inland population undoubtedly has been restructured often by fire, which may have further obscured links to the Pt. Reyes pines. Additional ecological and genetic studies would clarify the origin and relationship of these trees to other bishop pines.

ACKNOWLEDGEMENTS

I thank F. Sandrock for directing me to the stands, J. Wyneken for field and editorial help, and the editors and reviewers (J. Griffin and J. Sawyer) for critical comments on the manuscript.

LITERATURE CITED

AXELROD, D. I. 1980. History of the maritime closed-cone pines, Alta and Baja California. Univ. Calif. Publ. Geol. Sci. 120:1–143.

CRITCHFIELD, W. B. 1967. Crossability and relationships of the California closed cone pines. Silvae Genet. 16:89–97.

DUFFIELD, J. W. 1951. Interrelationships of the California closed cone pines with special reference to *Pinus muricata* D. Don. Ph.D. dissertation, Univ. California, Berkeley.

ENGELMANN, G. 1880. Abietineae. *In* S. Watson, Botany of California, p. 117–128. John Wilson and Son, Univ. Press, Cambridge, MA.

HOWELL, J. T. 1945. Carbonated landscape. Sierra Club Bull. 31(7):18–23.

———. 1949. Marin flora. Univ. California Press.

JACOBS, D. F., D. W. COLE, and J. R. MCBRIDE. 1985. Fire history and the perpetuation of natural coast redwood ecosystems. Jour. Forest. 83:494–497.

MASON, H. L. 1934. Pleistocene flora of the Tomales formation. Publ. Carnegie Inst. Wash. 415:81–79.

———. 1949. Evidence for the genetic submergence of *Pinus remorata. In* G. L. Jepsen, G. G. Simpson, and E. Mayr, eds., Genetics, paleontology, and evolution, p. 356–362. Princeton Univ. Press.

MILLAR, C. I. 1983. A steep cline in *Pinus muricata.* Evolution 37:311–319.

———. 1985. Genetic studies of dissimilar parapatric populations in northern bishop pine (*Pinus muricata*). Ph.D. dissertation, Univ. California, Berkeley.

MIROV, N. T., E. ZAVARIN, K. SNAJBERK, and K. COSTELLO. 1966. Further studies of *Pinus muricata* in relation to its taxonomy. Phytochemistry 5:343–355.

SOIL CONSERVATION SERVICE. 1985. Soil survey of Marin county. U.S.D.A. National Cooperative Soil Survey.

SUGNET, P. W. and R. E. MARTIN. 1984. Fire history and post-fire stand dynamics of the Inverness bishop pine population with management recommendations for Point Reyes Seashore. A report to U.S. Natl. Pk. Serv., Pt. Reyes.

(Received 30 May 1985; revision accepted 10 Jan 1986.)

FLORAL ULTRAVIOLET IN THE *ENCELIA* ALLIANCE (ASTERACEAE: HELIANTHEAE)

Curtis Clark and Donald L. Sanders
Biological Sciences, California State Polytechnic University,
Pomona 91768

Abstract

The *Encelia* alliance is a monophyletic group comprising *Encelia, Geraea,* and *Enceliopsis.* Disk corollas, usually yellow, but dark brown in some species of *Encelia,* all absorb long-wave ultraviolet radiation. Ray corollas of *Enceliopsis* and *Geraea* are all yellow, and all absorb long-wave ultraviolet. One group of *Encelia* species (including the one white-rayed member) also has ultraviolet-absorbing rays; another group has rays that reflect ultraviolet. Outgroup comparison suggests that ultraviolet reflection is an apomorphy within the alliance that, along with other characters, marks the group of species possessing it as a clade.

Over the last 15 years there has been a resurgence of interest in the role of floral ultraviolet (UV) in the vision of pollinating insects (Clark 1979 provides a brief summary), but comparatively few studies have addressed its usefulness as a taxonomic character. We maintain that ultraviolet is no less important a floral color, especially in insect-pollinated flowers, than those colors visible to humans, and that it is important for taxonomists to characterize floral UV in the groups they study, whether or not they address its importance in pollination.

The genera *Encelia, Geraea,* and *Enceliopsis* form a monophyletic group diagnosed by the presence of caducous paleae coupled with flattened, black achenes having a depigmented ciliate margin. *Encelia,* comprising 20 species of shrubs, is broadly distributed in arid southwestern North America. The five species of *Enceliopsis* are herbaceous rosette perennials, and are found in the region of the Colorado Plateau. *Geraea* consists of two species, a widespread desert annual and an herbaceous perennial of chaparral in eastern San Diego Co., California. As part of our investigations of these genera, we have examined the UV patterns and associated micromorphology of the corolla surfaces of all the species.

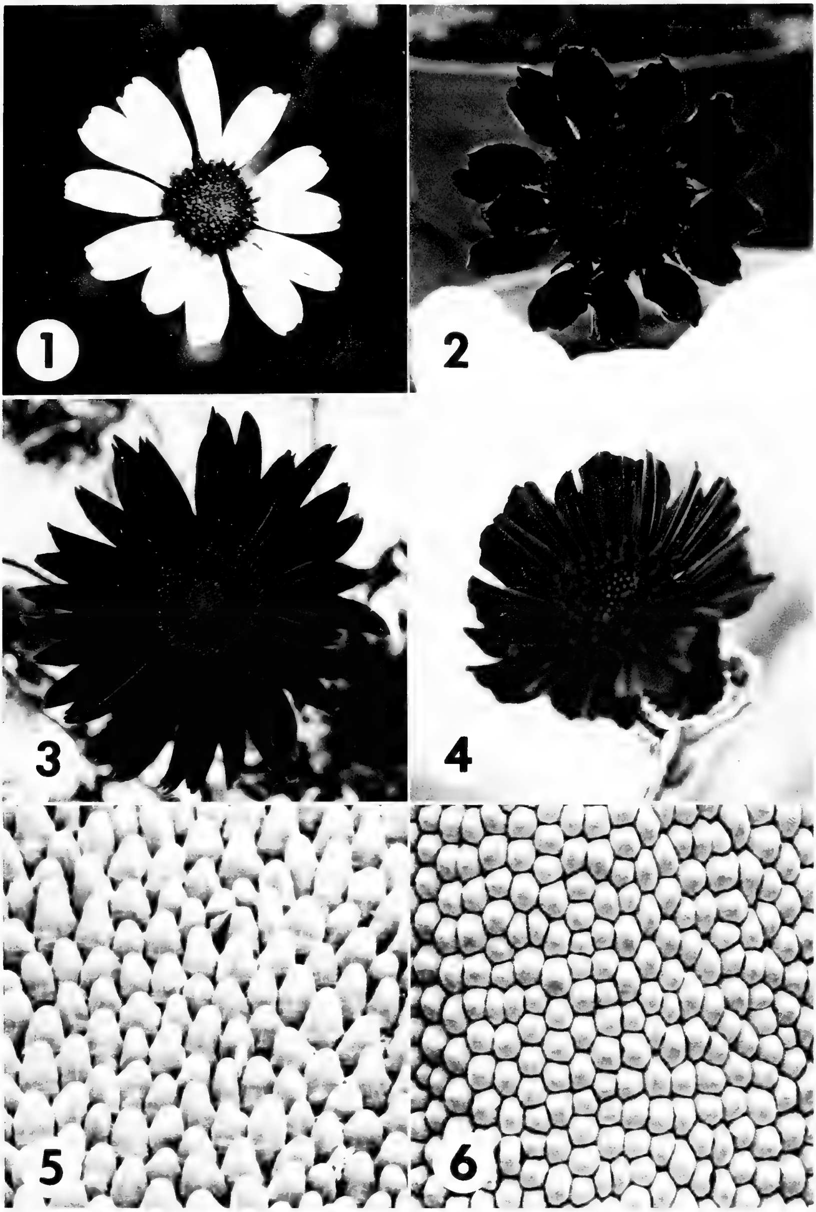
Methods

As part of field and greenhouse studies of the species, we have made UV photographs of flower heads, and have accumulated data from several to many plants from every species.

Heads were photographed with a single-lens reflex camera having

---

Madroño, Vol. 33, No. 2, pp. 130–135, 30 May 1986



FIGS. 1–6. Capitula photographed in long-wave ultraviolet light. 1. *Encelia californica,* south of El Rosario, Baja California. 2. *Encelia virginensis,* greenhouse-grown from cutting taken at St. George, UT. 3. *Enceliopsis argophylla,* near Lake Mead, NV. 4. *Geraea canescens,* near Indio, CA. FIGS. 5, 6. Scanning electron micrographs of adaxial ray corollas, ×200. 5. *Enceliopsis covillei.* 6. *Encelia palmeri.*

TABLE 1. SPECIES WITH UV-ABSORBING RAY COROLLAS.

Geraea canescens T. & G.
Enceliopsis argophylla (D. C. Eaton) A. Nelson
Enceliopsis covillei (A. Nelson) S. F. Blake
Enceliopsis nudicaulis (A. Gray) A. Nelson var. *nudicaulis*
Enceliopsis nudicaulis var. *corrugata* Cronquist
Encelia actoni Elmer
Encelia frutescens (A. Gray) A. Gray var. *resinosa* Jones ex Blake
Encelia ravenii Wiggins
Encelia virginensis A. Nelson

automatic through-the-lens exposure (generally an Olympus OM-2) and a glass lens. UV photographs were taken on Kodak Tri-X film (exposed at ISO 125 in the OM-2 rather than its rated speed of ISO 400, and developed in Kodak Microdol-X diluted 1:3) through a Wratten 18-A filter or a Corning 7-60 filter, both of which transmit only long-wave UV in the neighborhood of 360–370 nm. Visible-light photographs were taken with no filtration.

Corollas were prepared for scanning electron microscopy by the techniques of Clark (1979), Kyhos et al. (1981), or Charest-Clark (1984), which reflect ongoing improvements.

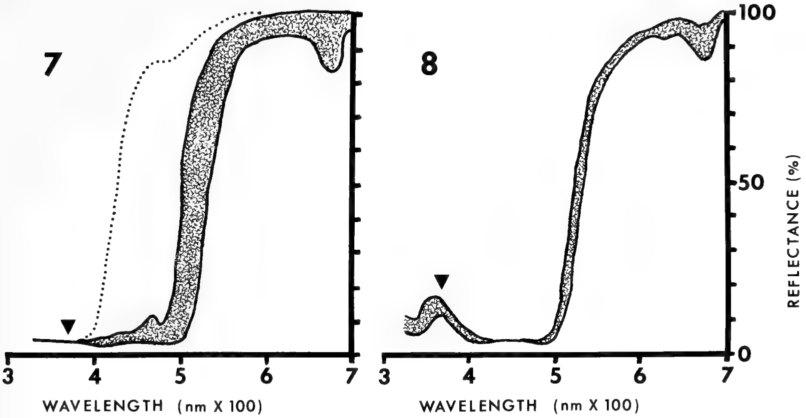
We prepared ray corollas for reflectance spectrophotometry by removing them from the heads, affixing them to cards with double-faced tape, adaxial side up, and placing the cards in the sample slot of a Shimadzu/B&L Spectronic 210 UV recording spectrophotometer. Magnesium oxide was used as a reference.

RESULTS

Disk corollas of all species absorb long-wave UV (e.g., Figs. 1–4). Three species [*Encelia frutescens* (A. Gray) A. Gray var. *frutescens, Enceliopsis nutans* (Eastwood) A. Nelson, and *Geraea viscida* (A. Gray) S. F. Blake] lack rays; the rest fall into two distinct groups,

TABLE 2. SPECIES WITH UV-REFLECTING RAY COROLLAS.

Encelia asperifolia (S. F. Blake) Clark & Kyhos
Encelia californica Nutt.
Encelia canescens Lam.
Encelia conspersa Benth.
Encelia sp. nov.
Encelia farinosa A. Gray var. *farinosa*
Encelia farinosa var. *phenicodonta* (S. F. Blake) I. M. Johnston
Encelia farinosa var. *radians* (T. S. Brandegee) S. F. Blake
Encelia halimifolia Cav.
Encelia palmeri Vasey & Rose
Encelia ventorum T. S. Brandegee



FIGS. 7, 8. Reflectance spectrograms. Shaded portion indicates variation among species, triangle marks 370 nm, the wavelength important in insect vision. 7. UV-absorbing species; dotted line corresponds to the white-rayed *Encelia ravenii.* 8. UV-reflecting species.

those with rays UV-absorbing over their entire length (Table 1, Figs. 2–4) and those with rays UV-reflecting over their entire length (Table 2, Fig. 1).

Because many of the photographs were taken without a gray scale as reference, we were concerned that different densities in the negatives might represent different absolute amounts of absorption or reflection. Reflectance spectrophotometry of the rays of UV-absorbing species showed no differences in the amount of UV absorption between species—all show a reflectance at 370 nm of about 3% of the reference (Fig. 7). UV-reflecting species showed slight differences at 370 nm, varying from 11% to 16% reflection (Fig. 8); however, they show a clear discontinuity from the absorbing species. Reflectance at other wavelengths was markedly uniform among the yellow-rayed species, confirming the visual similarity of their pigmentation.

The adaxial epidermes of both the ray and disk corollas of the species studied show "Helianthoid" papillae (Baagøe 1977). Such papillae have been implicated in UV absorption (Brehm and Krell 1975). Dimorphism has been noted in some species having rays with a "bullseye" pattern (reflecting distally and absorbing proximally), the papillae being taller and more conical in the absorbing region (Baagøe 1977, Scogin and Rogers 1980). In those species studied that have absorptive rays, and in the disk corollas of all species, the papillae are tall and conical (Fig. 5). In the species with reflecting rays, the papillae are generally lower, usually with a flattened or rounded apex (Fig. 6). Because the differences are not always consistent, it is not always possible to identify UV-absorbing species by papilla height. In general, though, this group exhibits the same dimorphism between species as has been reported (Scogin and Rogers 1980) within the UV-bicolored rays of a single species.

DISCUSSION

Ultraviolet-reflecting rays are restricted to a group of species in *Encelia.* The other species of *Encelia,* as well as all the radiate species of *Geraea* and *Enceliopsis,* have absorbing rays. Using the outgroup comparison method (Watrous and Wheeler 1981), we conclude that, within *Encelia,* UV reflection is the apomorphic (derived) state and UV absorption is plesiomorphic (ancestral). This is evidence that the UV-reflecting *Encelia* species constitute a monophyletic group. Another character also supports this hypothesis of monophyly. Proksch and Clark (unpubl.) have found in this same group of *Encelia* species, with one exception, a unique secondary metabolite, a dimer of a benzopyran and a benzofuran. The exception, *E. asperifolia,* is instructive in two regards. First, Clark and Kyhos (1979) have proposed that it originated from hybrids between *E. californica* and a glandular form of *E. frutescens*; this new information is consistent with that hypothesis, because it has the UV reflectance of one parent and the absence of the unique chemical compound of the other. Second, it demonstrates that the chemical compound is not involved with UV reflectance.

It was suggested by an anonymous reviewer that UV absorption of the rays might not be homologous among the three genera, because it has been shown (Harborne and Smith 1978) that at least four different groups of flavonoid pigments provide UV absorption in different genera of the Asteraceae. We find this statement provocative for two reasons. First, although chemical differences among species have been used taxonomically for a number of years, it is still common for taxonomists to address flower color without reference to its chemical basis. This is not to say that the chemical basis should be ignored, just that it often has been. Second, there is more to UV absorption than absorptive pigments. These pigments are accumulated in the vacuoles of the epidermal cells of the corolla (Harborne and Smith 1978, Brehm and Krell 1975, Rieseberg and Schilling 1985), and the adaxial cells are often enlarged (Baagøe 1977). We suggest that, within groups of clearly related species, this syndrome associated with pigment accumulation may be the homology, and that the nature of the pigments themselves may be determined by the general biochemical pathways of the plant. Nevertheless, a preliminary assessment of the ray pigments suggests little variation among the UV-absorbing species, and demonstrates the absence of anthochlors, one of the four classes of pigments.

Although we have not intended specifically to address the function of floral UV in the pollination of this group, it is worth noting that spontaneous natural hybrids are common in areas of sympatry between the UV-absorbing *E. actoni* and the UV-reflecting *E. farinosa,* and between the latter and the rayless *E. frutescens,* suggesting that the differences are not important to the variety of insects that pollinate these species.

ACKNOWLEDGMENTS

This study was supported in part by an Affirmative Action Faculty Development Grant and a Cal Poly Kellogg Unit Foundation Educational Grant to C.C. We thank Lawrence M. Blakely, Nancy Charest-Clark, Donald W. Kyhos, Gregory J. Lee, Wm. C. Thompson, and an anonymous reviewer for their assistance and comments.

LITERATURE CITED

BAAGØE, J. 1977. Microcharacters in the ligules of the Compositae. *In* V. H. Heywood, J. B. Harborne, and B. L. Turner, eds., The biology and chemistry of the Compositae, p. 119–139, Academic Press, London.

BREHM, B. and D. KRELL. 1975. Flavonoid localization in epidermal papillae of flower petals: a specialized adaptation for ultraviolet absorption. Science 190: 1221–1223.

CHAREST-CLARK, N. 1984. Preliminary scanning electron microscopic study of the peduncle, phyllary, and pale trichomes of *Encelia* (Asteraceae: Heliantheae). Crossosoma 10(4):1–7.

CLARK, C. 1979. Ultraviolet absorption by flowers of the Eschscholzioideae (Papaveraceae). Madroño 26:22–25.

——— and D. W. KYHOS. 1979. Origin of species by hybridization in *Encelia* (Compositae: Heliantheae). Bot. Soc. Amer., Misc. Ser., Publ. 157.

HARBORNE, J. B. and D. M. SMITH. 1978. Anthochlors and other flavonoids as honey guides in the Compositae. Biochem. Syst. Ecology 6:287–291.

KYHOS, D. W., C. CLARK, and W. C. THOMPSON. 1981. The hybrid nature of *Encelia laciniata* (Compositae: Heliantheae) and control of population composition by post-dispersal selection. Syst. Bot. 6:399–411.

RIESEBERG, L. H. and E. E. SCHILLING. 1985. Floral flavonoids and ultraviolet patterns in *Viguiera* (Compositae). Amer. J. Bot. 72:999–1004.

SCOGIN, R. and P. ROGERS. 1980. Petal epidermal dimorphism and UV absorption in anthochlor-pigmented flowers. Aliso 9:561–565.

WATROUS, L. E. and Q. D. WHEELER. 1981. The outgroup comparison method of character analysis. Syst. Zool. 30:1–11.

(Received 4 Feb 1985; revision accepted 20 Nov 1985.)

A NEW SPECIES OF *LATHYRUS* (FABACEAE) FROM NORTHWESTERN CALIFORNIA

Steven L. Broich
Department of Crop Science, Oregon State University,
Corvallis 97331

Abstract

Lathyrus glandulosus, a new species from Humboldt and northern Medocino Counties in California, is described and illustrated. Its distinctive features include a winged stem, 14–18 leaflets, relatively small (10–12 mm long) purple flowers and a vestiture of stalked, glandular trichomes on lower leaflet surfaces, stems, calyces and ovaries. **L. glandulosus** has a chromosome number of $2n = 14$.

A systematic study of *Lathyrus* of the Pacific Coast of North America has revealed the existence of a new species, herein described.

Lathyrus glandulosus Broich, sp. nov.

Planta perennis, rhizomatos, dense glandulosa pubescens; caulibus 3–6 dm altis, anguste vel late alatis, erectis vel scandentibus. Foliolis 14–18, inferne dense glandulosis pubescentibus, ovatis ad lanceolatis, 3–5 cm longis, 1–2 cm latis. Racemis (5)7–11(14)-floris, foliis brevioribus. Floribus 10–12(14) mm longis, vexillo purpureo, alis et carina albis; ovariis dense glandulosis pubescentibus; stylo 4–5 mm longis, complanato, non torti. Leguminibus 3–5 cm longis, 6–8 mm latis, parce glandulosis pubescentibus (Fig. 1).

Rhizomatous perennial; stems 3–6 dm long, narrowly to broadly winged, erect to clambering, unbranched or branched at ground level. Leaves paripinnate, 14–18 cm long; stipules semi-hastate, narrowly lanceolate to linear, 10–20 mm long, 1–5 mm wide, usually constricted into two acute lobes, much smaller than leaflets; leaflets 14–18, ovate to lanceolate, 3–5 cm long, 1–2 cm wide, sparsely puberulent and densely glandular pubescent below; tendrils well developed, branched. Racemes 10–16(20) cm long, shorter than the rachis of the subtending leaf, with (5)7–11(14) flowers at 1–2 per cm. Flowers 10–12(14) mm long; calyx obliquely campanulate, tube 3–4 mm long with five unequal teeth, upper ("banner") teeth deltoid, 1–2 mm long, lateral teeth narrowly lanceolate, subequal to or longer than calyx tube, 3–5 mm long, ca. 1 mm wide, lower ("keel") tooth linear, 4–6 mm long; corolla papilionaceous, banner purple, wings and keel lavender to white; banner claw 7–10 mm long, 5–7 mm wide, banner blade 7–10 mm long, 11–14 mm wide, erect in flower;

Madroño, Vol. 33, No. 2, pp. 136–143, 30 May 1986

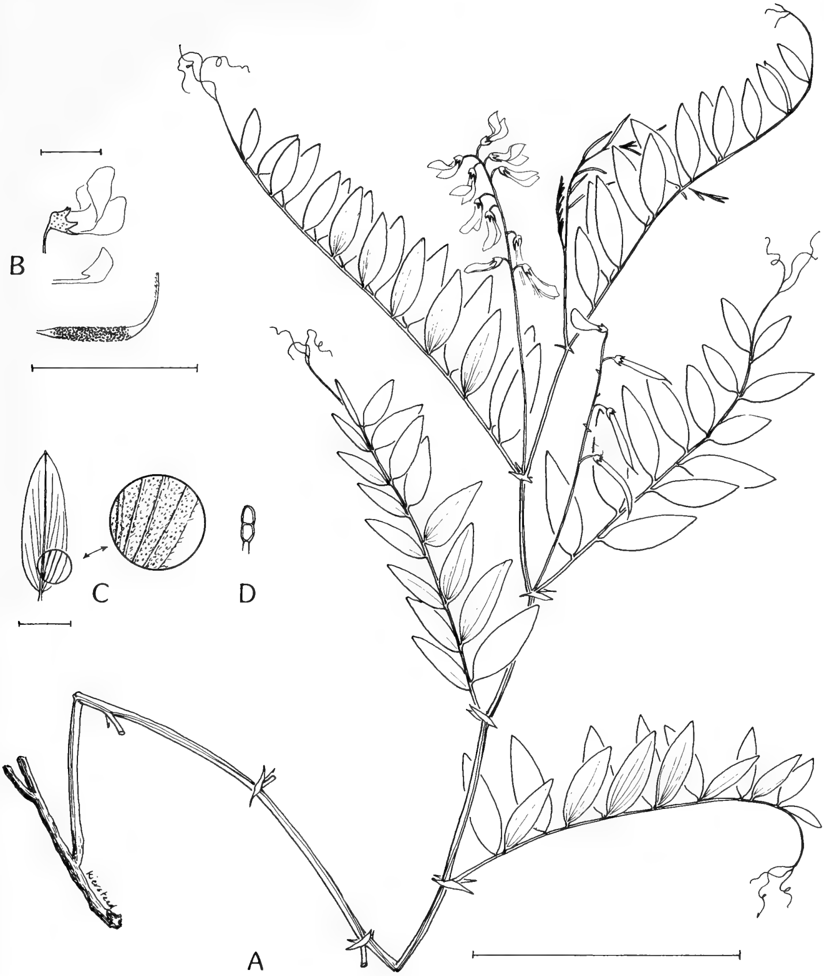


FIG. 1. *Lathyrus glandulosus.* A. Habit of flowering stem. B. Flower: keel, petal, and gynoecium. C. Leaflet pubescence. D. Detail of stalked glandular trichome. Scale equals 10 cm in A, 1 cm elsewhere.

wings 1–3 mm longer than keel, claws 5–7 mm long, blades 7–10 mm long, 4–6 mm wide; keel claws 5–7 mm long, keel blades 4–5 mm long, 6–7 mm high, strongly recurved apically; ovary densely glandular pubescent, 6–10 mm long in flower, containing 10–14 ovules; style 4–5 mm long, flattened, not twisted. Legumes sparsely glandular pubescent, 3–5 cm long, 6–8 mm wide. Seeds mottled green or tan and black, weighing 15–30 mg. Chromosome number $2n = 14$.

TYPE: USA, California, Humboldt Co.: 8.5 km ne. of the Freshwater-Kneeland road on the road to Maple Creek (T4N R2E ca. S2), 9 Jun 1981, *Broich 1146* (Holotype: OSC; isotypes: HSC, ISC, WTU).

PARATYPES: USA, California, Humboldt Co.: along Maple Creek Rd., 0.8 km from junction with Kneeland-Bridgeville rd, 20 May 1980, *Broich 772* (OSC); 42 km n. of Bridgeville on rd to Kneeland, 20 May 1980, *Broich 777* (OSC); 1.9 km se. of Blue Lake on rd to Maple Creek, 9 Jun 1981, *Broich 1141* (OSC); along rd to Maple Creek 11.6 km ne. of junction with the Kneeland-Bridgeville rd, 9 Jun 1981, *Broich 1147* (OSC); along rd to Maple Creek 1.1 km ne. of junction with the Kneeland-Bridgeville rd, 9 Jun 1981, *Broich 1148* (OSC); along rd to Maple Creek 1.6 km ne. of the junction with the Kneeland-Bridgeville rd, 9 Jun 1981, *Broich 1149* (OSC); 1.9 km s. of Kneeland School on rd to Bridgeville, 9 Jun 1981, *Broich 1153* (OSC); 7.9 km s. of the Kneeland School on rd to Bridgeville, 9 Jun 1981, *Broich 1154* (OSC); headwaters of Bear Creek along Cow Creek fire trail, 8 Jun 1934, *Constance 837* (HSC, JEPS); Eureka, Apr 1913, *Hutchinson s.n.* (CAS); Kneeland Prairie, 10 Jun 1906, *Tracy 2474* (UC); Kneeland Prairie, 26 Jun 1912, *Tracy 3855* (UC); Kneeland Prairie, 24 Aug 1930, *Tracy 9170* (UC); valley of South Yager Creek near "Redwood House," 26 Jul 1942, *Tracy 17298* (UC, WTU); Cameron Hill, Kneeland, 19 May 1946, *Tracy 17530* (UC); along "Lord Ellis Rd.," w. of Summit between n. Fork of Mad River and Redwood Creek, 15 Jun 1946, *Tracy 17571* (UC); near the Dan McBride place se. end of Kneeland, 23 Jun 1946, *Tracy 17595* (UC); Fickle Hill, 7 Aug 1948, *Tracy 18085* (UC); Fickle Hill, 20 Jun 1949, *Tracy 19313* (UC); 4.8 km e. of Kneeland on Butter Valley Rd., 29 Jun 1950, *Tracy 18934* (UC); 3.2 km e. of Korbel on Korbel-Maple Creek rd., 23 Apr 1960, *Winter s.n.* (HSC 15267). Medocino Co.: ca. 14.5 km s. of Leggett on rd to coast, 21 May 1980, *Broich 784* (OSC); s. Fork of Eel River opposite Red Mt., 16 km s. of Humboldt Co. line, 28 Apr 1933, *Tracy 12074* (UC).

L. glandulosus is found along roadsides and in the oak woodlands upland from the coastal redwood forests of Humboldt and northern Mendocino Counties in California. It flowers from April to early June and bears seed by mid-July.

Evidence for the existence of *L. glandulosus* surfaced during a taximetric study of *L. vestitus* Nutt. in T. & G. and its allies endemic to the Pacific Coast of North America (Broich 1983). Cluster analyses (hierarchical and non-hierarchical) indicated that three specimens, superficially resembling *L. polyphyllus* Nutt. in T. & G., were, in fact, morphologically unique. Subsequent herbarium and field investigations and additional taximetric studies confirmed the initial observations. Figure 2 displays the results of a discriminant analysis of eight species of Pacific coast *Lathyrus* and demonstrates the dis-

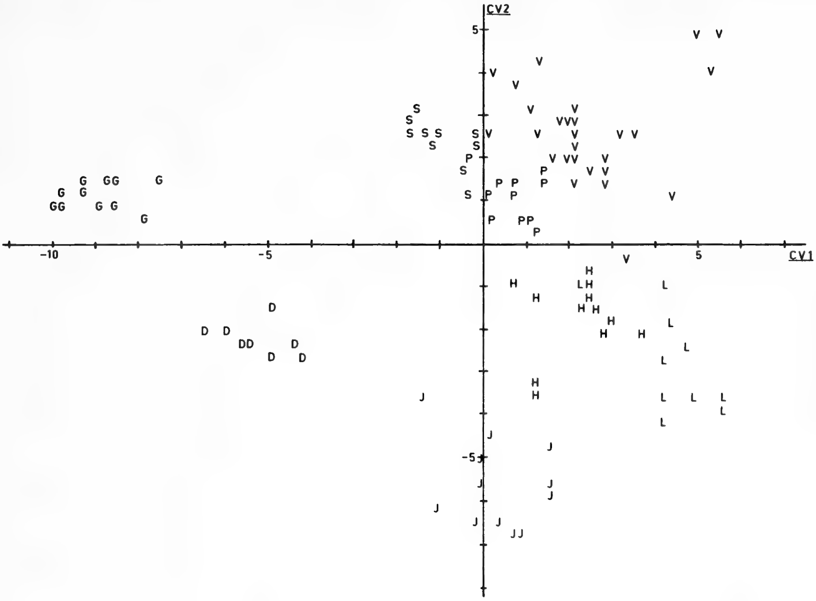


FIG. 2. Ordination of specimens of eight species of *Lathyrus* by scores of the first two canonical variables (CV) resulting from stepwise discriminant analysis of data collected on 36 traits from 112 herbarium specimens (Broich 1983). The computer program used was BMDP7M (Biomedical Computer Programs, P-series, Univ. California, Los Angeles 1979). Species include: G = *L. glandulosus*, D = *L. delnorticus*, H = *L. holochlorus*, J = *L. jepsonii*, L = *L. laetiflorus*, P = *L. polyphyllus*, S = *L. sulphureus* and V = *L. vestitus*. The 14 traits selected by the analysis included: number of lateral branches, presence or absence of stem wings, number of leaflets, adaxial leaflet non-glandular pubescence density, flower density, calyx lateral tooth width, calyx lateral tooth shape, calyx non-glandular pubescence density, calyx glandular pubescence density, keel claw length, keel blade height, keel blade reflex, ovary glandular pubescence density, and style length.

tinctness of *L. glandulosus.* Table 1 lists Mahalanobis distances among these taxa; the morphological divergence of specimens referable to *L. glandulosus* is apparent from these data. Examination of other western North American species of *Lathyrus* not included in taximetric studies (*L. nevadensis* Wats., *L. lanszwertii* Kellogg *sensu* Welsh 1965, *L. pauciflorus* Fernald, *L. tracyi* Bradshaw, *L. torreyi* Gray and *L. biflorus* Nelson and Nelson) also indicated that *L. glandulosus* is distinct.

Vegetatively, *L. glandulosus* most closely resembles *L. polyphyllus* but has winged stems as do *L. delnorticus* C. L. Hitchcock and *L. jepsonii* Greene. In flower shape, *L. glandulosus* most closely resembles *L. pauciflorus* Fernald, but racemes of the latter species bear fewer flowers. A few stalked, glandular trichomes can be found on the epidermal surfaces of almost all Pacific Coast *Lathyrus* species

Table 1. Mahalanobis D^2 Distances among Eight *Lathyrus* Species Native to the Pacific Coast of North America. Data were derived from the stepwise discriminant analysis described in Fig. 2.

	glandulosus	*polyphyllus*	*holochlorus*	*delnorticus*	*sulphureus*	*jepsonii*	*laetiflorus*
vestitus	190.2	57.1	71.3	139.4	84.0	103.1	70.1
laetiflorus	492.9	136.4	126.0	320.9	296.4	109.8	
jepsonii	309.3	156.7	121.8	154.8	225.9		
sulphureus	331.6	146.6	128.2	179.7			
delnorticus	173.6	222.6	193.0				
holochlorus	368.7	122.6					
polyphyllus	270.8						

Table 2. Morphological Comparisons Among the Native Species of *Lathyrus* from the Klamath Mountain Region of Northwestern California and Adjacent Oregon.

	Stem wings	Number of leaflets	Leaflet pubescence	Number of flowers	Flower length (mm)	Flower color	Ovary pubescence
L. glandulosus	present	13–17	puberulent & glandular	7–11	10–12	purple	puberulent & glandular
L. pauciflorus	absent	6–10	glabrous	2–5	12–14	purple	glabrous
L. polyphyllus	absent	12–14	glabrous	8–12	15–17	purple	glabrous
L. vestitus							
subsp. *vestitus*	absent	8–12	puberulent	8–12	14–16	purple	puberulent
subsp. *bolanderi*	absent	8–12	glabrous	8–12	14–16	purple/white	glabrous
L. jepsonii							
subsp. *californicus*	present	8–12	puberulent	6–14	15–17	pink to purple	glabrous
L. sulphureus	absent	8–11	glabrous	9–15	11–13	cream to white	glabrous
L. delnorticus	present	9–12	glabrous	9–11	10–12	cream to white	glabrous
L. nevadensis	absent	4–8	glabrous to puberulent	3–5	12–16	purple	puberulent
L. tracyi	absent	4–6	glabrous	5–8	9–10	white	glabrous
L. lanszwertii							
subsp. *aridus*	absent	6–8	puberulent	2–4	8–12	purple to rose	glabrous
L. torreyi	absent	10–12	villous	1–2	8–10	purple to rose	villous & glandular
L. biflorus	absent	4	villous	2	8–10	greenish white	glabrous

and glandular hairs are common throughout the Vicieae (Kupicha 1977). The relatively dense vestiture of glandular trichomes found on *L. glandulosus,* however, makes this species quite distinctive. Table 2 presents a comparative summary of morphological features of native *Lathyrus* species found in the Klamath Mountains of northern California.

Lathyrus glandulosus has a chromosome number of $2n = 14$, as do the great majority of *Lathyrus* species (Kupicha 1977). I have found that in chromosome number and morphology *L. glandulosus* is not distinguishable from other Pacific Coast *Lathyrus* species.

Hitchcock (1952) cited and annotated several collections of *Lathyrus glandulosus* as possible hybrids between *L. polyphyllus* and *L. jepsonii* subsp. *californicus* (Wats.) C. L. Hitchcock. Neither of the putative parental species, however, is notable for glandular pubescence; the ovaries of both are entirely glabrous and the flowers of *L. glandulosus* are smaller than both.

A number of specimens of *L. glandulosus* in HSC and UC were annotated by J. A. Lackey in 1972 as being an "undescribed entity in *Lathyrus*"; however, this observation was never published.

The majority of native species of *Lathyrus* that occur along the Pacific Coast of North America can be found in the Klamath Mountains of northwestern California and adjacent Oregon. *Lathyrus* is considered to be Arcto-Tertiary in origin (Raven and Axelrod 1978), and the Klamath Mountains are known to be a center of endemism for relicts of the Arcto-Tertiary Geoflora (Stebbins and Major 1965). Three other species of *Lathyrus* are endemic to the Klamath region: *L. delnorticus*, *L. tracyi*, and the recently described *L. biflorus* (Nelson and Nelson 1983).

ACKNOWLEDGMENTS

I thank Kenton Chambers for checking the Latin diagnosis and for freely sharing his knowledge and experience throughout all stages of this project, Julie Kierstedd for preparing the illustrations, and Thomas Nelson for providing a valuable orientation to northern California and the *Lathyrus* growing there. Funds for this project were provided by the Oregon State University Herbarium and by the National Science Foundation grant DEB-7911543.

LITERATURE CITED

BROICH, S. L. 1983. A systematic study of *Lathyrus vestitus* Nutt. ex T. & G. (Fabaceae) and allied species of the Pacific Coast. Ph.D. dissertation, Oregon State Univ.

HITCHCOCK, C. L. 1952. A revision of the North American species of *Lathyrus.* Univ. Wash. Publ. Biol. 15:1–104.

KUPICHA, F. K. 1977. The delimitation of the tribe Vicieae and the relationships of *Cicer* L. J. Linn. Soc., Bot. 74:131–162.

NELSON, T. W. and J. P. NELSON. 1983. Two new species of Leguminosae from serpentine of Humboldt County, California. Brittonia 35:180–183.

RAVEN, P. H. and D. I. AXELROD. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72:1–134.

STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35:1–35.

WELSH, S. L. 1965. Legumes of Utah. III. *Lathyrus* L. Proc. Utah Acad. Sci. 42: 214–221.

(Received 19 Apr 1985; revision accepted 17 Jan 1986.)

REVIEW

A Field Manual of the Ferns & Fern-Allies of the United States and Canada. By DAVID B. LELLINGER. ix, 389 pp., 45 pp. color photographs (mostly by A. Murray Evans). Smithsonian Institution Press, Washington, DC. 1985. ISBN 0-8747-602-7, $45.00 (hardcover); ISBN 0-87474-603-5, $29.95 (paperbound).

This manual is the most current and complete treatment available for ferns and fern allies of the conterminous United States, Canada, and Alaska. It is written in an easily readable but scientifically accurate style that is suitable for all students of ferns, both professional and laic. Features that make it useful for non-professionals include the extensive illustrated glossary, helpful introduction on various aspects of fern biology and classification, an index to common names, notes on cultivation for each species, and 402 color photographs (nine per page). These features, plus an index to scientific names, keys to families, genera, and species, descriptions for some 406 taxa (species, varieties, hybrids), and the attention paid to nomenclatural details, make it equally useful to those who make a living studying ferns.

The photographs deserve special mention because they distinguish this book from several others that cover similar territory. Generally they are of high quality and helpful in identification. In genera such as *Isoëtes* and *Selaginella,* whose diagnostic characters are largely microscopic and technical, photographs alone will be insufficient, but this is hardly the fault of Evans, who has done an admirable job with difficult subjects. Many very rare or infrequently seen taxa are represented, e.g., *Botrychium mormo* and *Anemia wrightii.* Herbarium specimens provide the basis for photographs of some species, mostly those from western North America.

Deficiencies in this book are few and almost too trivial to mention. There is a slight eastern North American bias to the work (or is it my greater familiarity with western ferns?), which is understandable given the base of operations of the author and photographer. For example, a higher proportion of western taxa are unillustrated (but only ca. 60 of the total 406 taxa are not represented by photographs). Evidently, Evans' photographic trip to the western states was during the dry season, as several illustrations show dormant or dried plants. *Aspidotis carlotta-halliae* (incorrectly treated as a sterile hybrid; p. 313) from California is mentioned only casually, whereas eastern taxa of rarer occurrence (e.g., *Pleopeltis astrolepis, Thelypteris grandis*) are given full treatment (description, habitat, distribution, and photograph). Similarly, several rare eastern hybrids (e.g., *Pteris* ×*delchampsii,* are given full treatment, but the western *Pellaea* ×*glaciogena* receives cursory mention. Distribution statements are generally accurate, but *Woodsia plummerae* is not cited for California, where it is known from the Mojave desert. One will look in vain for *Ophioglossum vulgatum,* a rarity but well documented from California; does it go under a different name now? Because synonymy is not given, it is impossible to tell.

These quibbles and a few others do not detract significantly from an excellent work, which is destined for a long and useful life in our libraries and offices, even considering the high mutation rate of fern nomenclature.—ALAN R. SMITH, Dept. Botany-Herbarium, Univ. California, Berkeley 94720.

NOTES

RANGE EXTENSIONS AND CORRECTIONS FOR *Pinus jeffreyi* AND *P. coulteri* (PINACEAE) IN NORTHERN BAJA CALIFORNIA.—High resolution aerial photography (Mexico Instituto Nacional de Estadistica Geografica e Informatica (INEGI) 1972, Scale 1:40,000; Mexicana Aerofoto, Mexico City 1938, Scale 1:20,000) permits accurate identification and mapping of larger trees occurring in inaccessible terrain of Baja California Norte, Mexico. The holistic view provided by comprehensive aerial coverage permits detailed mapping of species not possible in the field, including discovery of unreported populations and errors in published maps. This note revises the distribution of *Pinus jeffreyi* and *P. coulteri,* which reach their southern limits in northern Baja California (Fig. 1).

Both trees were identified from their morphological structure and color record exclusively, rather than habitat and physiography to avoid circular reasoning attendant with correlation of their distributions with environmental gradients (Minnich et al., U.S.D.I. Contract, Technical Report III, Dept. Earth Sciences, Univ. California, Riverside. 1969; Thorley et al., p. 1353–1426 *in* Bowden and Pruitt, eds., Manual of remote sensing. 1975). *Pinus jeffreyi* was identified by its large height, rounded crown perimeter, flattened crown summits (of mature trees), and blue green hue. *Pinus coulteri* is a shorter tree with larger crown spread; it also prunes poorly with the canopy extending to the ground. To correlate field information with photography, I have trekked through and photographed many forests in several trips to the Sierra San Pedro Mártir (Minnich, Madroño 29:22–31. 1982), along the crest of the Sierra Juárez (La Rumerosa to El Topo, Laguna Juárez, Santa Catarina, and Valle de la Trinidad), and by binocular observation from Mexico Hwys. 3 (Tecate to Ensenada) and 16 (Ensenada to San Felipe). Map accuracy in the Sierra Juárez is simplified by the fact that these pines are the only tall trees in the range. In the Sierra San Pedro Mártir, *P. jeffreyi* is separated from other taxa of mixed conifer forests on the basis of crown perimeter structure.

PINUS JEFFREYI. Four populations (ca. 30 trees total) have been discovered at the north end of the Sierra San Pedro Mártir: two within 1 km southwest and northwest of Cerro San Matias (31°14′N, 115°29′W, elevation 2000 m), one in a basin perched on the mountain divide 2 km to the southwest (1600 m), and another wash 2 km south southeast (place names based on 1:50,000 topographic sheets published by INEGI). The Cerro San Matias populations extend the range about 10 km north of the mapped limit in the San Pedro Mártir (Critchfield and Little, U.S. Forest Serv., Misc. Publ. 991. 1966). To the south, *P. jeffreyi* dominates an extensive mixed conifer forest extending ca. 40 km along the high mountain plateau, except along the eastern wall of the range where forests are dominated by *Abies concolor, Pinus lambertiana,* and *Cupressus montana.* The southern limit of *P. jeffreyi* is in Arroyo Santa Eulalia (30°39′N).

In the Sierra Juárez, *P. jeffreyi* reaches its southern limit in two shallow basins on a plateau (30°40′N, 115°45′W) just south of Moran's (Phytologia 35:205–208.1977) observation of the tree along the bottom of Arroyo Rincón. Basin floors and watercourses in the higher, arid Sierra Juárez volcanic tablelands further south (1600–1800 m) contain only *Quercus peninsularis* and *Pinus quadrifolia.* Well-drained slopes above are covered with chaparral or solid stands of scrubby *Quercus chrysolepis* on northern exposures. The populations on Cerro San Matias and Mesa la Vinata Romero reduce the *P. jeffreyi* disjunction across San Matias Pass to 50 km. *Pinus jeffreyi* forests in the Sierra Juárez are more fragmented than mapped by Critchfield and Little (op. cit.) with most stands occurring along meadows, basin floors, and watercourses (1400–1700 m). Chaparral covers steep slopes to the highest summits (1900 m).

A third population mapped by Critchfield and Little (op. cit.) near the U.S.–Mexican

---

MADROÑO, Vol. 33, No. 2, pp. 144–149, 30 May 1986

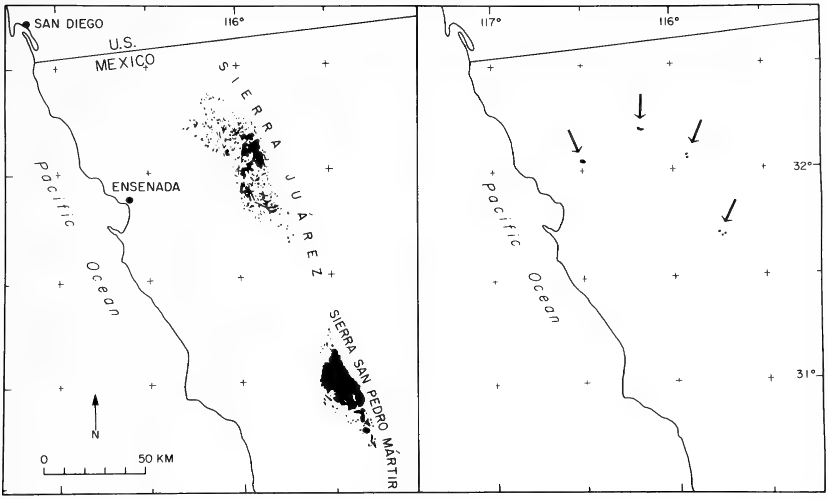


FIG. 1. The distributions of *Pinus jeffreyi* (left) and *P. coulteri* (right) in northern Baja California.

border is in error. The northern limit of *P. jeffreyi* comprises several groves along a wash 3 km north of Valle Los Pinos (15 km ese. of Neji, 32°23′N, 116°10′W). The plateau near the border is apparently too low for the tree (1100–1300 m), which recurs again 60 km north in the Laguna Mountains of San Diego County.

PINUS COULTERI. *Pinus coulteri* is extremely rare in northern Baja California. The most substantial population is also the westernmost: a small forest of ca. 50 ha on Sierra Blanca, just south of Valle Guadelupe, accurately mapped by Critchfield and Little (op. cit.). Scattered groves also occur on Cerro Hanson (La Sierrita), a small peak just northwest of Laguna Juarez (Hanson), including a stand seen by Moran (op. cit.) (32°03′N, 115°56′W). Several populations are found on steep knolls a few km north. In the northern Sierra Juárez plateau, *P. coulteri* is far less extensive than mapped by Critchfield and Little (op. cit.), based on a report by Goldman (Contrib. U.S. Natl. Herb. 16:309–371. 1916). I agree with Moran (op. cit.) that Goldman probably saw the Cerro Hanson groves because the Biological Survey expedition never traveled the wagonroad between Laguna Juárez and Campo (Nelson, Mem. Natl. Acad. Sci. 16. 1921). Aerial photographs record only one cluster of *P. coulteri* groves on rocky slopes immediately southwest of Rancho San Faustino, 7 km north of San Juan De Dios (32°13′N, 116°12′W). Scattered individuals reported on the south and north rims of Arroyo Rincón by Moran (op. cit.) are also clearly visible on photographs, and from Santa Catarina, but no other populations were seen south of there, including the Sierra San Pedro Mártir (Minnich op. cit.).

Most *P. coulteri* grow in thin chaparral on highly resistant granite or steep volcanic mesas so rocky that fire can rarely pass over the stands. Although *P. coulteri* can reproduce immediately after burns owing partly to its semi-serotinous cone habit (Minnich, p. 55–61 *in* Plumb, U.S. Forest Serv. Tech. Rep. PSW-44. 1980; Borchert, Madroño 32:29–48. 1985), these southern populations appear to find refuge in fire resistant habitats. Such stands provide a secure seed source that may become critical when fires are followed by drought severe enough to cause reproductive failure.

Differences in *P. jeffreyi* and *P. coulteri* distribution reported here are not due to actual vegetation changes owing to disturbances. Registration of 1938 and 1972 aerial photographic coverages with a Bausch and Lomb Zoom Transfer Scope reveal nearly identical distributions in spite of widespread burning during the intervening period (fires mostly passed beneath the trees). Forests in the Sierra Juárez were only selectively logged near Laguna Juárez. Sierra San Pedro Mártir forests have never been logged.

The scale of photographs will not permit identification of possible hybrids between *Pinus jeffreyi* and *P. coulteri* (Zobel, Evolution 5:405–413. 1951; Madroño 11:283–284. 1952). However, with the exception for stands above Laguna Juárez, all *P. coulteri* populations are far from *P. jeffreyi* forests. In cursory field observations at Laguna Juárez, I found that the trees occur in ecologically divergent habitats in a characteristic pattern of southern California. *Pinus jeffreyi* occurs on basin floors whereas *P. coulteri* covered chaparral slopes on ridges above. I saw no intermediates.—RICHARD A. MINNICH, Geography Program, Dept. Earth Sciences, Univ. California, Riverside 92521. (Received 4 Apr 1985; revision accepted 13 Nov 1985.)

TAXONOMY OF OREGON SEMAPHORE GRASS, *Lophochlaena oregona* (POACEAE).—The taxonomic status of Oregon semaphore grass remains unsettled. The first collection of the grass in 1886 by W. C. Cusick was misidentified as *Lophochlaena californica* Nees [*Pleuropogon californicus* (Nees) Bentham ex Vasey], which explains why Vasey (U.S.D.A. Bull. 13(2):1–207. 1893) reported that the latter species occurred also in Oregon. After two more collections were made in 1901 and 1927, its distinct specific status was recognized by Chase (J. Wash. Acad. Sci. 28:52–53. 1938), who named it *Pleuropogon oregonus.* Her treatment was accepted by Benson (Amer. J. Bot. 28:358–360. 1941) and by Hitchcock et al. (Vascular Plants of the Pacific Northwest. Part I, Univ. Wash. Press, Seattle. 1969). Löve and Löve (Bol. Soc. Brot. Sér. 2, 53:563–585. 1980) suggested, however, that the taxon is merely a genetic variant of *Lophochlaena refracta* A. Gray [*Pleuropogon refractus* (A. Gray) Bentham ex Vasey]. Their arguments were that (1) a short awn, characteristic of *L. oregona,* was observed on the palea in an individual of the progeny obtained from selfing a plant of *L. refracta* from the Olympic Peninsula, and (2) the taxon could not be rediscovered anywhere in nature after its description.

With the rediscovery of Oregon semaphore grass in Adel, OR (But et al., Madroño 32:189–190. 1985), it is possible to reevaluate its taxonomic status. This grass can be distinguished readily from *L. refracta* by a combination of the following characters: (1) lemmas shorter, 5.5–7 mm long, and prominently scabrous-nerved, (2) palea margins distinctly and consistently bearing an awn 5–12 mm long, (3) spikelets gynomonecious with a special kind of flowering pattern, and (4) caryopses oval and smaller, 2.5–3 mm long. I am of the opinion that Oregon semaphore grass should be treated as specifically distinct from *L. refracta.*

Löve (Taxon 27:375–392. 1978) and Löve and Löve (ibid.) redefined *Pleuropogon* as a monotypic genus consisting solely of an arctic-circumboreal species, *P. sabinii* R. Brown, and referred the western cordilleran species to *Lophochlaena* Nees. Stebbins (*In* Jorgensen et al., Biol. Skr. 9(4):1–172. 1958), Tateoka (Bull. Natl. Sci. Mus. 12: 161–163. 1965), and Tsvelev (Grasses of the Soviet Union, Part II: 545. 1976. Engl. translation 1983) also suggested similar treatment. Concurring with the narrower generic concept of these authors, I propose the following combination:

Lophochlaena oregona (Chase) But comb. nov.—*Pleuropogon oregonus* Chase, J. Wash. Acad. Sci. 28:52. 1938.—TYPE: USA, Oregon, Union Co., Union, 8 Jun 1901, *Leckenby s.n.* (Holotype: US!).

Representative specimens. USA: OREGON: Union Co., Hog Valley, probably near Union, 1886, *Cusick 1316* (ORE, US); Lake Co., 25.8 km w. of Adel, 29 Jun 1937, *Peck 19568* (WILLU); Mud Creek, 25 km w. of Adel on Hwy. 140, 4 Jun 1979, *Kagan 604812* (ORE); 3 Jun 1982, *Crosby 2651* (CUHK, OSC); 11 Jul 1983, *But 83-2* (A, CUHK, IBSC, K, UC, US).

I thank Lincoln Constance, Peter Rubtzoff, George Church, Jimmy Kagan, Virginia L. Crosby, and J. Stephen Shelly for assistance and encouragement in this study, and the curators of A, K, ORE, OSC, UC, US, WILLU for specimen loans. Partial support from the National Science Foundation (BHS75-17083) is acknowledged with gratitude.—PAUL P. H. BUT, Museum of Chinese Medicine, Chinese Medicinal Material Research Center, The Chinese University of Hong Kong, Shatin, N. T., Hong Kong. (Received 5 Jul 1985; revision accepted 12 Jan 1986.)

NOTES ON *Betula* SER. *Humiles* (BETULACEAE) IN IDAHO.—The shrubby members of the genus *Betula* (series *Humiles*) have long been a source of taxonomic uncertainty and debate. Members of this group from the Pacific Northwest have been treated variously as four species, two varieties of a single species, or two species. Butler (Bull. Torr. Bot. Club 36:421–440. 1909) recognized four species from the region: *B. glandulosa* Michx., *B. glandulifera* (*B. pumila* L. var. *glandulifera* Regel—references cited below), *B. hallii* Howell, and *B. crenata* Rydb.; the latter known only from the type locality in western Montana. Hitchcock (*in* Vascular Plants of the Pacific Northwest, Pt. 2, Univ. Wash. Press, Seattle. 1964) included all of the variation in the region under two varieties of *B. glandulosa* (var. *glandulosa* mostly from east of the Cascades, and var. *hallii* from the Cascades and west). He noted, however, that occasional specimens from Idaho, Montana, eastern Washington, and Wyoming represented perhaps a third variety. More recent workers have recognized the presence of both *B. glandulosa* and *B. pumila* var. *glandulifera* in various portions of the northern Rocky Mountains (Brayshaw, Catkin bearing plants of British Columbia. 1976; Scoggan, Flora of Canada. 1978; Moss, Flora of Alberta, 2nd ed. 1983; Dugle, Can. J. Bot. 44:929–1007. 1966, who recognized *B. glandulifera*). The identity of many Idaho specimens, however, has remained uncertain.

Betula pumila var. *glandulifera* is recognized generally by its broad samara wings (>½ as broad as the body), obovate leaves with more than 10 teeth on each side, and stature up to 4 m. *Betula pumila* is tetraploid, $2n = 56$ (Woodworth, Bot. Gaz. 90:108–115. 1930).

In contrast, *B. glandulosa* has narrow samara wings (<½ as broad as the body), broadly ovate to orbicular leaves with less than 10 teeth on each side, and is generally less than 2 m tall. *Betula glandulosa* is diploid, $2n = 28$ (Packer, Can. J. Bot. 42: 473–494. 1964).

In 1982, we discovered 5 populations of birch in extreme northern Idaho that match closely the published descriptions of *B. pumila* var. *glandulifera* (as summarized above). Two representative localities are: Boundary Co., swamp/fen at nw. end of Bonner Lake, 15 km ene. of Bonners Ferry, T62N R3E S18, 760 m, 31 Jul 1982, *Johnson and Brunsfeld 1962* (ID, IDF, V); swamp/fen on e. shore of Perkins Lake, 18 km ene. of Bonners Ferry, T62N R3E S5, 800 m, 29 Oct 1982, *Brunsfeld 2009* (ID, IDF, V). The identification of both of these collections was verified by T. C. Brayshaw (V). This is the first report of this species in Idaho.

For further confirmation of this identification, we germinated seed and made mitotic chromosome counts of root tip cells following procedures outlined by Soltis (Syst. Bot. 5:17–19. 1980). Two counts were obtained from populations in Boundary Co.: 1) $2n = 56$, Perkins Lake, *Brunsfeld 2009*; 2) $2n =$ ca. 56, Skin Cr., 2.5 km n. of Perkins Lake, *Brunsfeld 2015* (ID, IDF). Camera lucida drawings and photomicrographs are on file with the authors. These counts are the first reported for *B. pumila* from western North America. These data and morphological evidence support the identification of these plants as *B. pumila* var. *glandulifera.*

Examination of herbarium specimens (ID, IDF, OSC, ORE, WS, WTU) revealed the presence of two additional major forms of shrubby birch in Idaho. *Betula glandulosa,* as delineated above, and as recognized by Hitchcock (op. cit., var. *glandulosa*), Dugle (op. cit.), and Brayshaw (op. cit.), occurs throughout east-central and southeastern Idaho. Throughout the rest of central and northern Idaho, excluding the small northeastern corner that contains *B. pumila,* a form occurs with characteristics of both *B. pumila* and *B. glandulosa.* Two collections of this material, *Wellner 1388* (ID, IDF, V) and *Johnson 4984* (IDF, V), were confirmed as intermediate by T. C. Brayshaw. About half of the collections we examined of series *Humiles* in Idaho can be placed in this category. This form appears to be what Hitchcock (op. cit.) considered a possible new variety of *B. glandulosa.* In 1960 he annotated an Idaho specimen (*Daubenmire 5299,* WS) of this kind as follows: "Atypical (*B. glandulosa*), perhaps representative of a Rocky Mtn. race." Dugle (op. cit.) studied plants with similar morphology in western Canada and concluded that they were hybrids between *B. glandulosa* and *B. glandulifera* (*B. pumila*). A range in chromosome numbers of $2n =$ 28–56 was reported in the apparent hybrids. Dugle named the hybrid *B.* ×*sargentii* Dugle and reported it as a "very important member of the flora in western Alberta."

This study reveals that *Betula* series *Humiles* in Idaho is represented by *B. pumila* in the far-northern part of the state, by *B. glandulosa* in east-central and southeast Idaho, and by an apparently intermediate form in the area between these two species. It appears likely that the intermediate is *B.* ×*sargentii,* reported from western Canada. By this note we hope to encourage additional biosystematic work on this group.

We thank Douglas Soltis for assistance in obtaining chromosome counts, use of his lab at Washington State Univ., and review of the manuscript; Amy Jean Gilmartin for helpful comments on the manuscript; and the directors of ID, ORE, OSC, WS, and WTU for allowing us to examine their specimens. Funding was provided in part by the C. R. Stillinger Foundation.—STEVEN J. BRUNSFELD and FREDERIC D. JOHNSON, College of Forestry, Wildlife and Range Sciences, Univ. Idaho, Moscow 83843. (Received 5 Apr 1985; revision accepted 13 Jan 1986.)

Salix lanata SUBSP. *calcicola* IN COLORADO.—*Salix lanata* L., an essentially Arctic circumpolar species, occurs in the Colorado alpine as the subspecies *calcicola* (Fern. & Wieg.) Hulten. The following collection represents the first occurrence for Colorado and the contiguous United States, ca. 1600 km sse. of the nearest populations in Banff National Park, Alberta, and 2250 km sw. of the periphery of its main range along the west coast of Hudson Bay: COLORADO, PARK CO., Horseshoe Cirque, Mosquito Range, 5 mi above 4-Mile Campground, sw. of Fairplay, 3650 m, 23 Jul 1984, *W. A. Weber and D. Randolph 17395* (CAN, COLO), determined by George Argus.

This eastern Canadian low-Arctic subspecies is distributed around the shores of Hudson and Ungava bays, and coasts of northern Labrador, southern Baffin Island, and eastern District of Keewatin. Disjunct populations occur in western Newfoundland, the Gaspe Peninsula, and western Alberta. Its distributional pattern parallels that of *S. vestita* Pursh, another calciphile with its main population in eastern Canada and disjunct populations in the western cordillera (Miller and Thompson, J. Arnold Arb. 60:167–218. 1979). The closely related *S. tweedyi* (Bebb) Ball also occurs in the western United States. Both of these taxa have large, precociously flowering, sessile aments that are usually borne at the ends of branches. Their capsules are glabrous and have long styles; the leaves are broadly ovate and are glandular-dotted or finely glandular-serrate on the margins.

Subspecies *calcicola* differs from *S. tweedyi* in having the leaves strongly glaucous beneath. In *S. tweedyi,* the leaves are non-glaucous, but in the field a thin glaucescence may be present that is lost in drying (Dorn, Brunsfeld, pers. comm.). The two differ ecologically; *S. tweedyi* is a subalpine species, occurring on acidic substrates along streams in *Abies bifolia* (*S. lasiocarpa* auctt.) forests, whereas *S. lanata* subsp. *calcicola,* in the Rocky Mountains, is an alpine species growing on basic substrates.

The cirque basin of the Mosquito Range where it occurs in Colorado is part of the most critical floristic site in the state, one noteworthy for extensive exposures of limestone (Leadville Formation) at high altitudes. At Horseshoe Cirque, *S. lanata* subsp. *calcicola* forms low, dense, rounded bushes less than a meter tall on loose limestone detritus above the edge of a tarn, whose shores are dominated by rare alpine species, including *Carex microglochin, Kobresia simpliciuscula, K. sibirica,* and *Saussurea weberi.* A short distance downstream a willow fen supports a small stand of *Baeothryon* (*Scirpus*) *pumilum,* recently rediscovered after having been "lost" since 1862.

We thank Steven J. Brunsfeld, Univ. Idaho, for specimens of *S. tweedyi* and for his helpful comments.—WILLIAM A. WEBER, Campus Box 218, Univ. Colorado Museum, Boulder 80309, and GEORGE ARGUS, National Museum of Natural Sciences, Ottawa K1A 0M8, Canada. (Received 4 Jan 1985; revision accepted 18 Dec 1985.)

NOTEWORTHY COLLECTIONS

ARIZONA

ERIOGONUM RIPLEYI J. T. Howell (POLYGONACEAE).—Yavapai Co., Coconino Natl. For., T16N R3E S26 nw. ¼, just ne., above, and to the left of the flume at the boundary (fence) of Dead Horse Ranch St. Park near Cottonwood, calcareous ridge top, 1044 m, 20 Apr 1985, *Schaack 1458 and Morefield* (DHA); 2.4 km S53°E of Tuzigoot Natl. Mon. and ca. 2.5 km nne. of Cottonwood, on white chalky carbonate of Verde Formation with *Canotia, Cercocarpus, Ceanothus, Cowania* and *Salvia,* 1046 m, 29 Apr 1985, *Morefield 2658, Schaack and P. Boucher* (ASU, DHA, MNA, Morefield, NY, RSA), specimens to be distributed.

Significance. Third known location for the species, ca. 150 km se. of the type locality near Frazier Well in Coconino Co., and ca. 95 km nnw. of the locality at Horseshoe Dam in Yavapai Co. Reveal (Phytologia 34:428. 1976) considers this species rare and threatened by grazing and recreational and horticultural activities.—JAMES D. MOREFIELD and CLARK G. SCHAACK, Deaver Herbarium, Dept. Biological Sciences, Northern Arizona Univ., Flagstaff 86011.

CALIFORNIA

ALLIUM ANCEPS Kell. (ALLIACEAE).—Mono Co., above Hwy. 89 e. of Monitor Pass, 3.5 km w. of the jct. of Hwy. 395 at T9N R22E S10 ne.¼, common in open areas with widely scattered *Artemisia tridentata* and *Purshia tridentata* on a rocky sw.-facing volcanic slope, 1640 m, 2 May 1985 (CPH).

Previous knowledge. Previously reported along e. side of the Sierra Nevada as far

---

MADROÑO, Vol. 33, No. 2, pp. 149–151, 30 May 1986

s. as Carson City, NV and Sierre Valley in Placer Co., CA; extending n. to Harney and Malheur cos., OR and e. to Elko and White Pine cos., NV.

Significance. Southernmost occurrence and a range extension of 60 km. This species and the related *A. lemmonii* Wats. with a similar, though somewhat wider distribution, reach their s. limits here in similar habitats on opposite sides of Monitor Pass. *Allium anceps* occurs on the e. slope and *A. lemmonii* on the w.—DALE W. MCNEAL, Dept. Biological Sciences, Univ. of the Pacific, Stockton, CA 95211.

RHYNCHOSPORA CALIFORNICA Gale (CYPERACEAE).—Butte Co., between Big Chico Creek and the north rim of Big Chico Creek Canyon in Upper Bidwell Park, 8.9 km ne. of Chico, T22N R2E S3&9 at 120 to 170 m. Six populations varying in size from about 25 to over 1000 cespitose tufts are on seeps located on either Tuscan Formation or Lovejoy Basalt rock in foothill woodland community. 14 Jun 1984, *Oswald 1291* (CHSC, CAS) (verified by J. T. Howell, CAS).

Previous knowledge. Known from the type location, Pitkin Marsh, 8 km n. of Sebastopol, Sonoma Co., and from Cunningham and Perry Marsh (the latter now extirpated) in Sonoma Co. and Ledum Swamp in Marin Co. (information from California Natural Diversity Data Base, Dept. Fish and Game, Sacramento).

Significance. This species is currently in List 1B (Plants considered rare and endangered in California and elsewhere) of Smith and York (Special Publication No. 1 (3rd ed.), Calif. Nat. Plant Soc., 1984). These collections extend the range of this plant from the North Coast Ranges of Sonoma Co. 173 km ne. into the foothills of the n. Sierra Nevada.—VERNON H. OSWALD, Dept. Biological Sciences, California State Univ., Chico 95929

ROSA MINUTIFOLIA Engelm. in Parry (ROSACEAE).—San Diego Co., Otay Mesa, head of dry swale in coastal sage scrub, T18S R1W S31 nw.¼ & se.¼, 152 m, 6 Feb 1985, *Reveal 2846* (CAS, RSA, SD, UC); 8 Mar 1985, *Reveal 2847* (ARIZ, ENCB, DES, NY, SD, UCR). Specimens to be distributed.

Previous knowledge. Known only in Baja California from near Ensenada to the vicinity of Misión de San Fernando (Wiggins, Flora of Baja California, p. 798, 1980). Herbaria consulted; SD, RSA.

Significance. First record outside Baja California, a n. range extension of 75 km.—GEOFFREY A. LEVIN, Botany Dept., San Diego Natural History Museum, San Diego, CA 92112. [The same collection was reported recently by Beauchamp (A flora of San Diego Co., California. 1986)—Editor.]

NEVADA

SPHAGNUM FIMBRIATUM Wilson (SPHAGNACEAE).—Elko Co., Jarbidge Mts., n. side of Prospect Peak, in small bog, T45N R59E, 2900 m, 14 Aug 1985, *Rust s.n.* (ALTA, RENO, TEX). (ALTA collection verified by Dale Vitt.)

Significance. First record of this moss genus for Nevada. The occurrence of *Sphagnum* in Nevada is remarkable because of the predominance of dry habitat and limestone substrate. The nearest known localities of this species of *Sphagnum* are in eastern California in the Bodie Hills (lower Cinnabar Cañon), and Osgoods Swamp near Lake Tahoe. Both of these localities lie approximately 600 km to the west of the Nevada locality.—RICH RUST, Dept. Biology, Univ. Nevada, Reno 89557 and MATT LAVIN, Dept. Botany, Univ. Texas, Austin 78713.

OREGON

ASTRAGALUS TEGETARIOIDES Jones (FABACEAE).—Harney Co., head of Smoke-out Canyon, ca. 4.3 km ene. of Little Juniper Mountain, T28S R25E S8 nw.¼, 1500 m, 28 May 1985, *Shelly and G. V. King 984* (OSC, BLM-LK, NY). Mat-forming around cracks in welded tuffaceous rock outcrops, with *Juniperus occidentalis, Artemisia tridentata, A. arbuscula, Chrysothamnus nauseosus.*

Significance. This collection is probably a rediscovery of a 1941 record by M. E. Peck (3 miles e. of Little Juniper Mountain *20853*, WILLU.). Of interest at this site is the plant's lack of association with *Pinus ponderosa,* and the almost complete restriction of the plants to cracks in the pink-colored, welded, tuffaceous rocks. Known also from Deschutes Co. and a limited geographic area ca. 29–40 km n. of Burns, Harney Co., OR, and Lassen Co., CA.

ASTRAGALUS TETRAPTERUS Gray (FABACEAE).—Klamath Co., 11 km n. of Beatty on Godowa Spring Rd., 0.5 km e. of road, w. of Piute Rock, T35S R12E S14 se.¼, 1427 m, 12 Jul 1983, *Shelly 607* (OSC, BLM-LK). In barren volcanic gravels, with *Pinus ponderosa, Juniperus occidentalis, Artemisia tridentata, Purshia tridentata, Penstemon janishiae.*

Significance. A 145 km range extension w. from Guano Valley, Lake Co., OR, and outside the nw. boundary of the Great Basin. Previously known from Lake, Harney, and Malheur Cos., OR, NV, sw. UT, and nw. AZ.

IVESIA SHOCKLEYI S. Wats. (ROSACEAE).—Lake Co., 0.3 km ene. of the summit of Drake Peak, n. Warner Mountains, T38S R22E S3 nw. ¼ & sw. ¼, 2495 m. 22 Jun 1985, *Shelly and G. V. King 1022* (OSC, UC, NY, BLM-LK). On rocky, exposed ridgeline, with *Pinus albicaulis, P. ponderosa* (stunted), *Purshia tridentata, Erigeron compositus, Polemonium pulcherrimum.*

Significance. M. E. Peck's collection (Summit of Drake Mt., *19826,* WILLU) in 1937 was misidentified as *I. gordonii* (Hook.) T. & G. (B. Ertter, pers. comm.). This verifies the continued existence of a population on Drake Peak. The species can be added formally to the OR flora. A n. range extension of ca. 350 km, from the Sierra Nevada in Placer Co., CA, and s. Washoe Co., NV. Previously known from Placer to Inyo Cos., CA, Washoe, Nye, and Lander Cos., NV, and Beaver Co., UT (B. Ertter, pers. comm.).

LOMATIUM PECKIANUM Math. & Const. (APIACEAE).—Klamath Co., 0.8 km e. of Bly Mountain Pass, ca. 15.2 km sw. of Beatty via Hwy. 140, T37S R11E S23 nw.¼, 1640 m, 18 Jun 1984, *Shelly 805* (OSC, UC, BLM-LK); Lake Co., summit of Warner Pass, on e. side of Hwy. 140, T38S R21E S31 nw.¼, 1787 m, 26 Jun 1984, *Shelly and A. V. Munhall 820* (OSC, UC, BLM-LK) (identifications verified by L. Constance). At both sites, growing in thin, gravelly soils, with *Pinus ponderosa, Juniperus occidentalis, Artemisia tridentata, A. arbuscula.*

Significance. First collections in OR since the type collection by M. E. Peck in 1927, near Bly, Klamath Co.; the Lake Co. collection is an ese. range extension of about 67 km from Bly. The Klamath Co. site was initially found on 22 Aug 1983 by Shelly and V. L. Crosby, and post-fruiting material was verified by L. Constance. Also known from Siskiyou Co., CA.

MIMULUS LATIDENS (Gray) Greene (SCROPHULARIACEAE).—Lake Co., dissected uplands e. of Warner Valley, ca. 19 km ne. of Adel, 1.6 km ne. of Fisher Canyon, along drainage flowing into se. side of Wool Lake, T38S R25E S12 se.¼ & ne.¼, 1710 m, 5 Jul 1984, *Shelly 831* (OSC, ORE, BLM-LK) (verified by K. L. Chambers). Ca. 150–200 plants, growing in vernally moist clay soils, with *Chrysothamnus nauseosus, Artemisia cana, Muhlenbergia richardsonis, Camissonia tanacetifolia, Plagiobothrys scouleri.*

Significance. First record for OR, a latitudinal range extension of ca. 320 km nne. from Butte Co., CA, and an upward altitudinal range extension of ca. 950 m from the "2500 ft." (762 m) upper limit given by Munz (A California flora, p. 614, 1959). Previously known from Butte and Lake Cos. to San Diego Co., CA.—J. STEPHEN SHELLY, Bureau of Land Management, P.O. Box 151, Lakeview, CA 97630 (Current address: Montana Natural Heritage Program, State Library, 1515 E. 6th Ave., Helena, MT 59620).

REVIEWS

Inventory of Rare and Endangered Vascular Plants of California. Third Edition. By James Payne Smith, Jr. and Richard York. The California Native Plant Society. 909 12th St., Suite 116, Sacramento, CA 95814. 1984. $10.95 plus $1.50 postage.

Publication of the 3rd edition of the *Inventory of Rare and Endangered Vascular Plants of California* continues the California Native Plant Society's (CNPS) long history of interest in providing *the* handbook source on endangered and rare plant species in the state. This edition expands and refines work first begun in 1967 by G. Ledyard Stebbins as a list of all plants in California with a range of less than 100 miles. That original list, enhanced by Roman Gankin and followed by the tireless efforts of Alice Howard and Robert Powell, culminated in the 1st edition printed in 1974. The 2nd edition, published in 1980, was produced just as the Society joined forces with the computerized California Natural Diversity Data Base (then with The Nature Conservancy, now in the Department of Fish and Game) to track the state's data on rare and endangered plant occurrences. This 3rd edition incorporates the latest Data Base records to cover a total of 1449 species of varying degrees of rarity in the state. Clearly presented and expanded introductory material sets the stage for the four lists of plants that follow. The result is the single most useful compendium on rare and endangered plants of California.

Computerization of the *Inventory* has assured a lower rate of typographical errors for this enormous number of scientific names than in previous editions. The book's format, combined with a clean-looking type font, is quite readable, considering an average page provides facts on 11 different species. Although the general structure follows that of the past editions, several positive changes were incorporated. A major change has occurred in the names and order of the lists of plants. In an effort to align the lists more closely with state law concerning endangered species, the Society adopted the state's definitions of rare and endangered.

List 1 reflects those species that CNPS judges to meet the criteria for state listing. It has been divided into two parts (equivalent to Lists 1 and 2 of the 2nd edition): 1A, those species presumed to be extinct in the state, and 1B, those extant species with active threats to their existence. List 2, "Plants Rare or Endangered in California, But More Common Elsewhere," and the newly created List 3, "Plants About Which We Need More Information," also involve plants that could meet state designation requirements. All told, these three lists focus on over 900 species, at least 15% of the state's flora, that may warrant protection; securing their protection would be a hefty challenge for any conservation group. The final roster, List 4, offers a "watch list" containing approximately 500 plants of regional rarity or localized distribution that may eventually be moved to higher lists of concern should their habitats or numbers decline significantly.

The addition of a data field called "Notes" within each species entry is very helpful. Now under a species entry, one not only finds the common name, family, current legal or suggested status, and readable codes for county and topographic quad of occurrence, but also information about threats to the species, whether or not CNPS has written a status report about it, or importantly, a citation of the original description for species published since Munz's *A California Flora.* Another improvement is the removal of the ever-confusing species acronyms, the "taxon codes." They may be a good shorthand method for working with a small data set, but when dealing with so many species they lose that quick reference appeal. In addition, a typo in a taxon code completely mystifies its meaning. I don't think they will be missed.

To lessen the confusion about which plant is on which legal list, an appendix of state and federally listed species is also included. Finally, the greatly expanded ref-

Madroño, Vol. 33, No. 2, pp. 152–154, 30 May 1986

erence section is also helpful, directing students of our endangered flora to further taxonomic or ecological publications on individual species.

This volume is a must for any rare plant enthusiast, environmental consultant, or agency biologist who deals with endangered, threatened, or rare plants. It is the first step for many professionals faced with conducting a rare plant field survey. The data in the *Inventory* are backed by herbaria and field work records contributed by the Society and other botanists and housed in the Department of Fish and Game's Natural Diversity Data Base. As with any publication of this type, however, it is out of date even before it is off the presses. CNPS recognized this fact, promoting the *Inventory* as a place to start when needing rare plant data, while encouraging use of the Data Base for the latest locational information. CNPS goes one step further, including an excellent discussion by member and botanist James R. Nelson on rare plant inventorying techniques, emphasizing that no survey is complete with only book-learned facts—one must get to the field before deciding on presence or absence of rare plants at a site.

Habitat information is just about the only facet of data missing from these concise species entries. A coding system for habitats is being contemplated by the authors for the next edition. It would be a welcome inclusion. I found only one organizational drawback of the book—its organization by species instead of by geographical location. Users needing to determine which species are found within a particular geographic area must essentially read the entire book, picking out the appropriate quad codes or county names. To reverse the information and print it by quadrangle map with all the species found therein would be marvelous but would just about double the size and cost of the document. It also would be quickly out of date and seeing such lists could lull uninformed consultants or botanists into a false sense of security about the presence or absence of endangered plants. A potential compromise for this problem may be county lists of species, giving those in need a starting point for further investigation.

Students of rare plant distribution will revel in the information crunched into these pages; in today's world of high-priced books, I can't think of a wiser use of funds to start or complete a library on California's endangered and rare plants.—SUSAN COCHRANE, Coordinator, Endangered Plant Program, California Dept. Fish and Game, 1416 9th Street, Sacramento 95814.

The Botany and Natural History of Panama: La Botanica e Historia Natural de Panama. Edited by WILLIAM G. D'ARCY and MIREYA D. CORREA A. Published as volume 10 of Monographs in Systematic Botany from the Missouri Botanical Garden. 455 pp. $48.00 + 4% shipping. ISBN 0-915279-03-7 (paperbound). (Available from Dept. 11, MBG, P.O. Box 299, St. Louis, MO 63166.)

In April 1980, a symposium was convened in Panama to signal the completion of the Missouri Botanical Garden's Flora of Panama project, the publication of which was begun in 1943. That it took nearly 40 years is some indication of the overwhelming diversity in the tropics and the amount of work necessary to try to bring into focus even the basic taxonomy of the tropical biota. The editors deserve high praise for this volume; it reflects what must have been a highly successful symposium.

The volume does not cover, or try to, the spectrum of organisms one might consider significant in tropical regions (bats, for instance, are not covered in any of the 48 articles), but coverage does include zoology, anthropology-ethnology-linguistics, meteorology (one paper), demography and man's influence on the landscape, and conservation, in addition to a broad range of botanical topics. The gaps may reflect merely that the editors are completely at the mercy of whatever symposium participants were available. In a sense, this is a beautifully complementary volume to Janzen's Costa Rican Natural History, a mini-encyclopedia that highlights particular creatures in the forests and details of what they do, also based to some extent on what specialists were available.

The first section of the book includes papers on particular groups of plants and animals (monocots, grasses, orchids, lianas, pteridophytes, mosses, and mangroves; termites, reptiles, birds, and the tamarin), followed by perhaps the strongest part, plants and geography. Those rash enough to consider working directly in the tropical forest canopy will need to be aware of Sugden's technique of constructing aerial walkways. The second part, The Interactions, covers topics in pollination, phenology, dispersal, regeneration, and the ecology and evolution of *Heliconia.*

Contributions in part three, the Human Aspect, were new ground for me and will be for most botanists, perhaps with the exception of the ethnobotany, but I found them all interesting and well worth having just for the general information. Did you know, for instance, that the Kuna Indians have four different vocabularies (and grammars) with which to speak in specific contexts, or that leaves of *Piper auritum* are used as bait in fish weirs in some Panamanian rivers?

Articles in English have brief Spanish summaries interpolated here and there in the text, and Spanish articles are similarly paraphrased in English. Most of the Spanish articles are in the "Modern Man and the Landscape" section.

There are few typographical errors, but one is significant: 12 references have been deleted from the Rockwood literature cited (Seed Size and Plant Habit).—C. DAVIDSON, Idaho Botanical Garden, P.O. Box 2140, Boise 83701.

CBS COUNCIL REQUEST

ARCHIVAL MATERIALS

The Executive Council of the California Botanical Society requests that all members of the Society, readers of Madroño, and other interested persons contribute to the preservation of the history of the Society by assisting with the conservation of archival materials pertinent to the Society's activities. Dr. Elizabeth McClintock, Society Archivist, maintains a collection of archives at the University Herbarium and welcomes all additions to the growing data base of records, correspondence, announcements, etc. The Council is particularly interested in acquiring correspondence and other materials from the earlier years of the Society and we are eager to accept donations of such documents. The collection of archives is available for examination or use at the University Herbarium and is a valuable resource for information on historical botany of California and the West. Your contribution of additional material will be accepted with sincere appreciation and your donation will be housed in a scholarly manner. Donation of archival material or inquiries about the collection should be addressed to Dr. Elizabeth McClintock, University Herbarium, Department of Botany, University of California, Berkeley, CA 94720.

2ND ANNOUNCEMENT

RARE AND ENDANGERED PLANTS—A CALIFORNIA CONFERENCE ON THEIR CONSERVATION AND MANAGEMENT

5–8 November 1986

Location: The conference will be held at the Capital Plaza Holiday Inn, 300 J Street, Sacramento, CA, U.S.A.

The California Native Plant Society (CNPS), in conjunction with government agencies, conservation groups, and private corporations, is organizing a conference on the conservation and management of rare and endangered plants. It is designed to be a forum for information exchange through concurrent sessions, poster sessions, and workshops. Proceedings will be published by CNPS.

Co-sponsors include: California Department of Fish and Game, The Nature Conservancy, California Botanical Society, The Rancho Santa Ana Botanic Garden, Pacific Gas & Electric, Southern California Edison, Bureau of Land Management, and Jones & Stokes Associates.

Keynote speakers include: Dr. Paul Ehrlich (Stanford Univ.), Dr. Daniel Axelrod (Univ. California, Davis), Dr. Ray Dasmann (Univ. California, Santa Cruz), Mr. Ed Hastey (California Director, Bureau of Land Management), Mr. Zane Smith (Regional Forester, U.S. Forest Service), and Dr. Faith Campbell (National Resource Defense Council).

Program topics to include:

—Introduction to California Rare & Endangered Plants
—Factors Endangering Plants Today
—Endangered California Habitats
—Legal Aspects of Plant Protection
—Technical Skills for Surveys & Impact Assessment
—Ecology, Systematics and Population Dynamics of Rare Plants
—Mitigation & Addressing Project Impacts
—Population Monitoring Techniques & How Research Directs Management
—Balancing Conservation & Land Use Planning—Long Range Planning
—Population Size & Long-term Survival—How Much Is Enough?
—Propagation & Reintroduction of Rare Plants
—Preserve Design
—Current Conservation Activities
—Management Plans for Rare Plants
—Habitat Enhancement & Restoration
—Education & Endangered Plants
—Public Involvement with Conservation Issues

Abstracts: due July 1, 1986.

Questions or comments regarding the conference should be directed to: Jim Nelson, Conference Coordinator, California Native Plant Society, 909 12th Street, Suite 116, Sacramento, California, 95814, U.S.A.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

VOLUME 33, NUMBER 3 JULY 1986

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES

NOTEWORTHY COLLECTIONS

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: FRANK ALMEDA, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

First Vice President: PATRICK ELVANDER, 443 Applied Sciences, University of California, Santa Cruz, CA 95064

Second Vice President: KINGSLEY R. STERN, Department of Biology, California State University, Chico, CA 95929

Recording Secretary: V. THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: CHERIE L. R. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928; the *Editor* of MADROÑO; three elected *Council Members:* THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; JOHN MOORING, Department of Biology, University of Santa Clara, Santa Clara, CA 95053; and a *Graduate Student Representative,* NIALL F. MCCARTEN, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

SEGREGATION OF *LOESELIASTRUM* FROM *LANGLOISIA* (POLEMONIACEAE)

STEVEN TIMBROOK
Santa Barbara Botanic Garden, 1212 Mission Canyon Road,
Santa Barbara, CA 93105

ABSTRACT

Morphological and phytochemical studies support the segregation of the zygomorphic-flowered species previously included in *Langloisia* as a separate genus, **Loeseliastrum** (Brand) Timbrook. The two genera differ in aspects of their leaf bristles, corolla, stamens, pollen, trichomes, and capsules, and by the type of flavonoids present. Similarities of leaves, calyces, and growth habit are thought to be due to convergence in strongly selective desert habitats. Two species are recognized in *Loeseliastrum,* **Lo. matthewsii** (=*Langloisia matthewsii*) and **Lo. schottii** (=*Langloisia schottii*), and one species with two subspecies in *Langloisia, La. setosissima* subsp. *setosissima* and **La. s.** subsp. **punctata**. Chromosome counts for all taxa are $2n = 14$. A key and descriptions of the taxa are included.

Langloisia is a small genus of western North American desert annuals erected by Greene in 1896. Milliken (1904) reduced *Langloisia* and four other genera to subgenera of *Gilia,* whereas most subsequent taxonomists such as Jepson (1925, 1943), Mason (1951), Munz (1959, 1974), and Grant (1959) have agreed with Greene in their treatments of the Polemoniaceae of western North America.

Brand (1907) and Cronquist (1959) questioned the integrity of *Langloisia.* Brand divided it into two sections using characters pointed out by Greene in his original description of the genus: sect. *Langloisia* (=sect. *Eulangloisia*) for species with actinomorphic corollas and straight stamens and sect. *Loeseliastrum* for species with zygomorphic corollas and curved stamens. Cronquist called the genus *Langloisia* a "technically weak but habitally well-marked group . . . ." Grant (1959) did not recognize sections in *Langloisia* although he did so in nine genera of Polemoniaceae, which implies he felt infrageneric separation unwarranted.

Studies by Smith et al. (1977) and Timbrook (1978), however, have revealed that the dichotomy between Brand's sections is so strong that they are more appropriately treated as separate genera. This paper summarizes the evidence supporting such a treatment, validates the necessary combinations, and discusses the taxa involved. The new names will be used in the rest of this paper.

MATERIALS AND METHODS

Specimens from my own collections and others represented by over 2000 herbarium sheets from 35 herbaria were examined mor-

---

MADROÑO, Vol. 33, No. 3, pp. 157–174, 1986

TABLE 1. CHARACTERS SEPARATING *Langloisia* AND *Loeseliastrum*.

Characters	*Langloisia*	*Loeseliastrum*
Morphological		
Trichome type	Branched	Uniseriate
Glandular trichomes	Absent	Present
Multiple leaf bristles	Present	Absent
Corolla symmetry	Actinomorphic	Zygomorphic
Stamens	Equally inserted, filaments equal, straight	Subequally inserted, filaments unequal, curved
Pollen color	White to blue	Yellow to gold
Capsule cross section	Triangular	Three-lobed
Capsule valve height/width	3/1	2/1
Seed coat sculpturing	Reticulate	Linear
Chemical		
6-methoxyflavonols		
Eupalitin	Present	Absent
Eupatolitin	Present	Absent
Patuletin	Present	Absent
Common flavonols		
Kaempferol	Absent	Present
Quercetin	Absent	Present

phologically. Scanning electron photomicrographs were made of seed coats and pollen. Flavonoid aglycones were surveyed using the techniques of paper chromatography. Mitotic configurations were prepared from plants transplanted from the field to the glasshouse at SBBG and voucher specimens were deposited at UCSB. Root tips were fixed in ethanol : chloroform : acetic acid (6:3:1, v/v/v) for one hour, hydrolyzed in 1 N HCl at 60°C for eight minutes, and stained in leucobasic fuchsin for one hour. Nomenclature in this paper follows that proposed in the Taxonomic Treatment.

RESULTS

Morphology. Langloisia and *Loeseliastrum* share a growth habit common to many desert plants, that of low-growing annuals with typical mature specimens forming rounded mounds about one-half as high as they are wide. Both genera have actinomorphic calyces with bristle-tipped lobes, a feature that distinguishes them from other genera in the tribe Gilieae. *Navarretia* and *Eriastrum* have zygomorphic calyces, bristle-tipped in *Navarretia,* whereas the calyces of the other genera are actinomorphic and non-spiny.

In contrast to the few shared characters distinguishing *Langloisia* and *Loeseliastrum* from other members of the Gilieae, several characters, both vegetative and floral, distinguish the two from each other

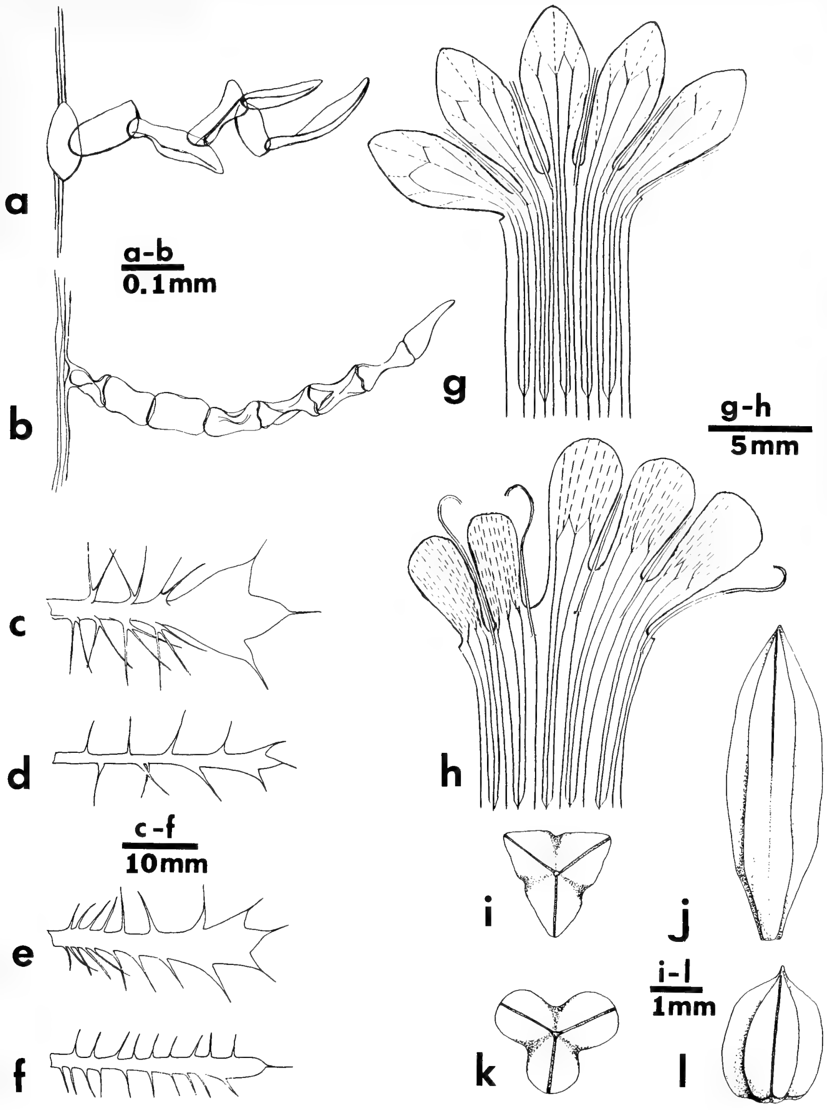


FIG. 1. Morphological comparisons of *Langloisia* (a, c, d, g, i, j) and *Loeseliastrum* (b, e, f, h, k, l). a. Branched trichome of *La.* b. Uniseriate trichome of *Lo.* c. Upper leaf of *La.* always bears some multiple bristles. d. Lower leaf of *La.* may have multiple bristles. e. & f. Upper and lower leaves of *Lo.* lack multiple bristles. g. Opened and flattened corolla of *La.* showing equal lobes and erect filaments. h. Corolla of *Lo.* has unequal lobes and curved, unequal filaments. i. & j. Capsule of *La.* is triangular in cross section and much longer than broad. k. & l. Capsule of *Lo.* is distinctly three-lobed in cross section and slightly longer than broad.

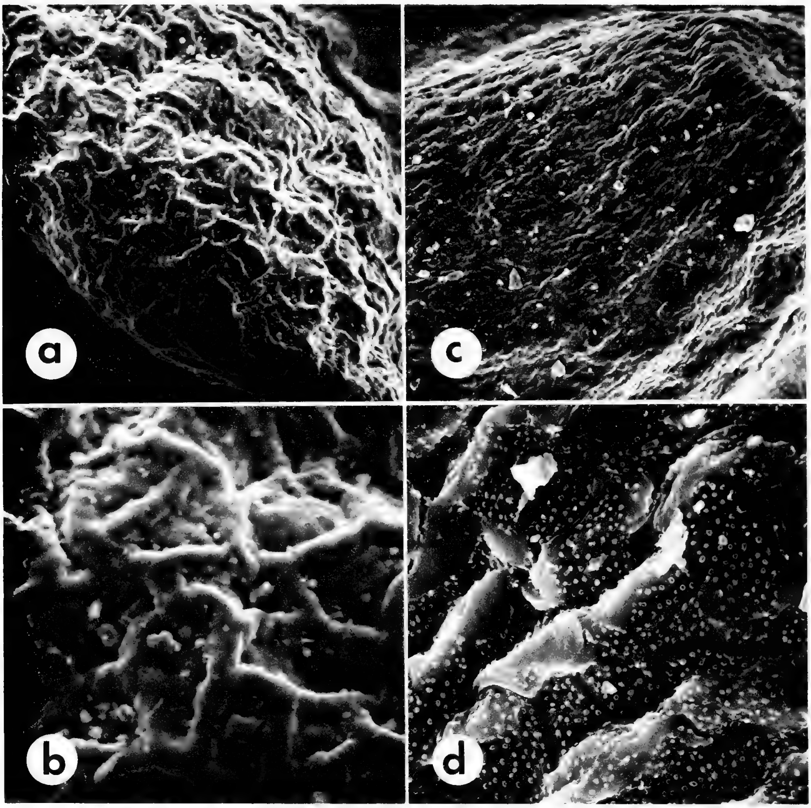


FIG. 2. Seed coat sculpturing of *Langloisia* (a: × 150, b: × 450) shows reticulations without any granular pattern, whereas that of *Loeseliastrum* (c: × 150, d: × 450) consists of short, parallel ridges and has a distinct granular pattern visible at the higher magnification.

(Table 1 and Figs. 1–3). Some of these characters deserve further consideration.

The pubescence of stems, leaves, bracts, and calyces is composed entirely of multicellular, branched trichomes in *Langloisia* (Fig. 1a), a trichome type that has not been reported elsewhere in the Polemoniaceae. *Loeseliastrum* (Fig. 1b) has both multicellular, uniseriate trichomes and, on pedicels and calyces, short glandular trichomes. The leaves and bracts of both genera are similar in shape but *Langloisia* (Fig. 1c, d) always bears at least some multiple bristles on the proximal margins of the upper leaves and bracts, although the lower leaves may bear only single bristles. *Loeseliastrum* (Fig. 1e, f), however, never bears multiple bristles on either lower or upper leaves or on the bracts.

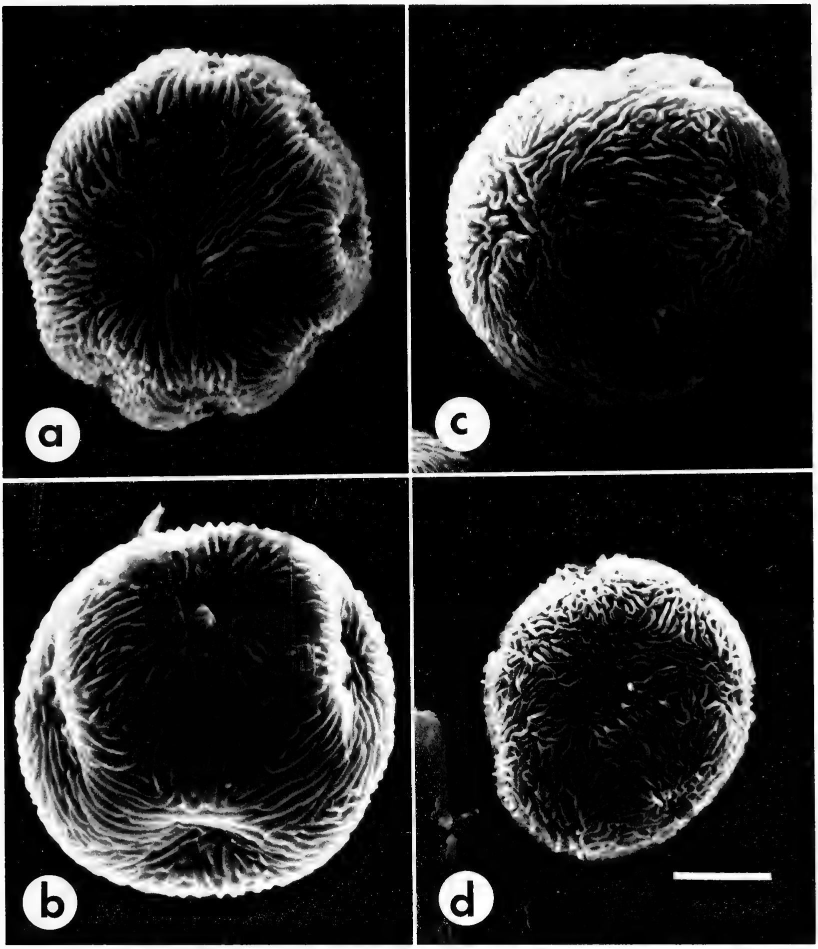


FIG. 3. Pollen grains of *Langloisia* and *Loeseliastrum* are very similar (scale bar = 10 μm). a. *La. setosissima* subsp. *setosissima*. b. *La. s.* subsp. *punctata*. c. *Lo. matthewsii*. d. *Lo. schottii*.

Corollas of *Langloisia* (Fig. 1g) are actinomorphic, with equally inserted stamens having equal, straight filaments, whereas corollas of *Loeseliastrum* (Fig. 1h) are zygomorphic (bilabiate), with subequally inserted stamens having unequal, strongly curved filaments. Capsules of *Langloisia* (Fig. 1i, j) are triangular in cross section with essentially flat outer valve walls, whereas in *Loeseliastrum* (Fig. 1k, l) the outer valve walls are deeply indented between the septa, making the capsule distinctly three-lobed in cross section.

Both genera have seed coats that become mucilaginous when wet-

TABLE 2. CHROMOSOME COUNTS FOR *Langloisia* AND *Loeseliastrum*. Voucher specimens deposited at UCSB.

Langloisia setosissima subsp. *setosissima*; $2n = 14$.
USA: CA, Imperial Co., Crucifixion Thorns Recreation Area, w. of Calif. 98, *Timbrook 553*; San Diego Co., just w. of Imperial Co. line on S-22, *Timbrook 556.*

Langloisia setosissima subsp. *punctata*; $2n = 14$.
USA: CA, San Bernardino Co., 5 mi n. of Fort Irwin Road on road to Lane Mountain, *Timbrook 570.*

Loeseliastrum matthewsii; $2n = 14$.
USA: CA, Los Angeles Co., 3.1 mi w. of 263rd Street East, on Calif. 18, *Timbrook 550*; San Bernardino Co., Lucerne Valley, 0.5 mi e. of Midway Avenue on Calif. 247, *Timbrook 551.*

Loeseliastrum schottii; $2n = 14$.
MEX: BAJA CALIFORNIA NORTE, 5 mi s. of Rancho Chapala on Mexico 1, *Timbrook 559.*

ted, as do many other members of the Polemoniaceae. The seed coat mucilage of *Langloisia* expands more slowly and is more diffuse than that of *Loeseliastrum.* Scanning electron photomicrographs of the seed coats (Fig. 2) show reticulate ridges with no granular pattern in *Langloisia. Loeseliastrum* ridges tend to be parallel, at least for a short distance, and the whole coat has a distinct granular pattern that is seen only at high magnification (×450).

Stuchlik (1967a,b), using transmitted light microscopy, found that *Langloisia setosissima* subsp. *setosissima, L. s.* subsp. *punctata,* and *Loeseliastrum matthewsii* all have the same pollen type, which he called Gilia I. It also was found in *Collomia* sect. *Collomiastrum* in the Polemonieae and, in the Gilieae, in *Eriastrum, Ipomopsis* sect. *Phloganthea,* and all five sections of *Gilia.* All supraspecific taxa in the Gilieae with Gilia I pollen, except *Langloisia, Loeseliastrum,* and *Gilia* sect. *Gilia,* also had species with other pollen types. Scanning electron photomicrographs show the similarity of *Langloisia* and *Loeseliastrum* pollen (Fig. 3).

Phytochemistry. Smith et al. (1977) surveyed flavonoid distribution in the Polemoniaceae and found three main groups of compounds: Group A consists of the common flavonols kaempferol, quercetin, and myricetin; Group B of the rare 6-methoxyflavonols patuletin, eupalitin, and eupatolitin; and Group C of C-glycosylflavones based on apigenin and luteolin. In most of the family, the genera as defined by Grant (1959) contain only one of these flavonoid groups; but in the Gilieae the situation is not as clear. In *Gilia,* the most heterogeneous genus in the tribe (Grant 1959), all three groups were found, even though only seven of the approximately 56 species were surveyed by Smith et al. *Linanthus* and *Navarretia* have both

Group A and Group B compounds, even in the same species in some cases. *Ipomopsis* and *Eriastrum,* the genera considered closest to *Langloisia* sensu lato, have only Group B compounds, as does *Langloisia* sensu stricto. *Loeseliastrum,* in contrast, has only Group A compounds.

My data (Timbrook 1978), obtained from 26 additional populations of *Langloisia* and 48 of *Loeseliastrum,* confirmed the conclusion of Smith et al. that *Langloisia* contains only Group B compounds, whereas *Loeseliastrum* contains only Group A compounds. Although *Langloisia* and *Loeseliastrum* are readily distinguished by their flavonoid aglycones, within each genus the flavonoid aglycones are uniform.

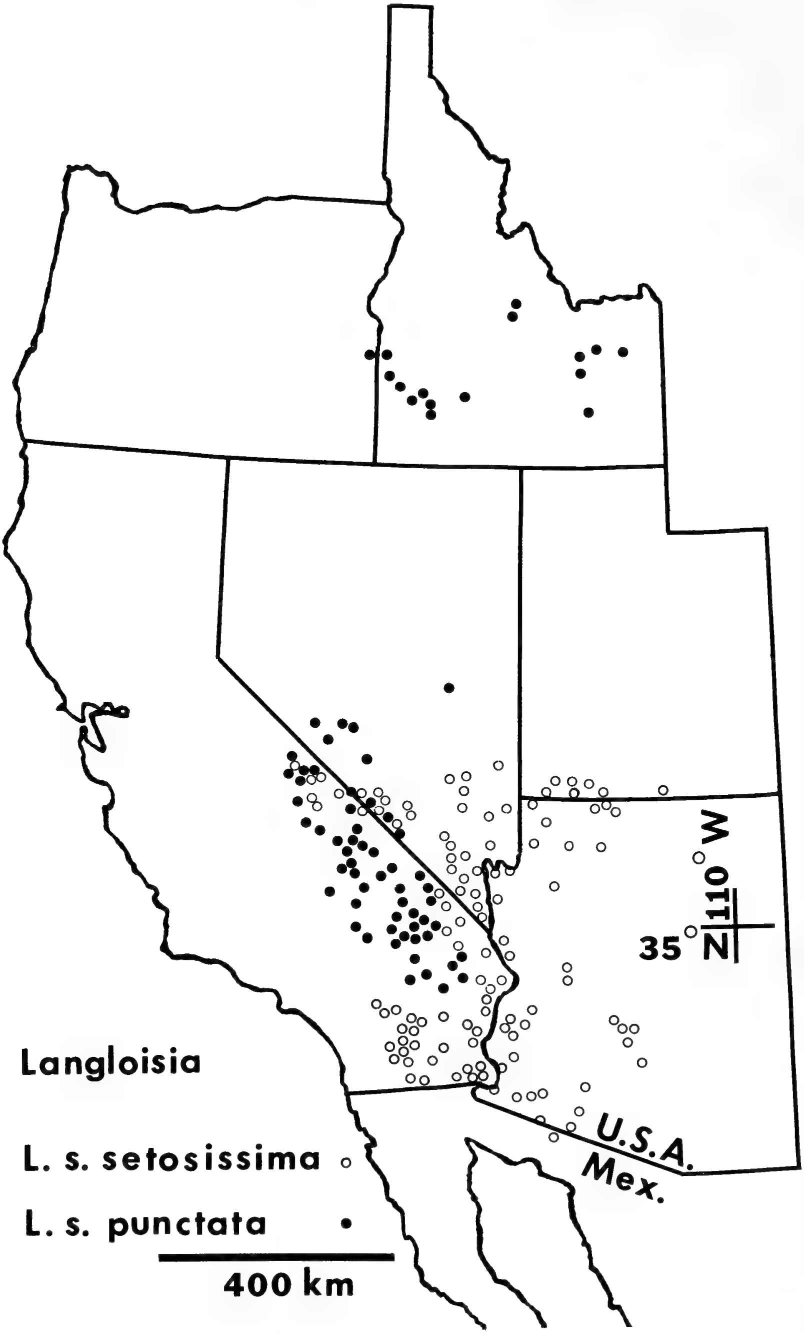
Smith et al. (1977) devised a flavonoid numerical advancement index based upon 1) loss of substances considered primitive in the angiosperms and 2) addition of others considered advanced, and assigned values to each species studied. Values in the family range from a primitive value of zero in one species of *Linanthus* to 12 in three species of *Eriastrum.* On this scale, *Langloisia* has a value of 11 for both of its taxa, *Loeseliastrum matthewsii* has a value of two, and *Lo. schottii* a value of one. *Loeseliastrum matthewsii* has no glycoflavones, compounds considered primitive, giving it a higher advancement value than *Lo. schottii.*

Chromosome counts. All taxa of *Langloisia* and *Loeseliastrum* have $2n = 14$, as do *Ipomopsis* and *Eriastrum* in the Gilieae and *Phlox* in the Polemonieae (Table 2).

Phytogeography. Langloisia and *Loeseliastrum* are desert endemics that are sympatric over the greater part of their respective ranges (Figs. 4, 5), although *Langloisia* occurs farther north as a disjunct series of populations in the valleys of the Snake and Salmon rivers in Idaho and Oregon. Future collecting in Mexico may extend the known southern limits of both genera.

Langloisia and *Loeseliastrum* are restricted to coarse-textured well-drained soils, with the densest and most extensive stands of *Langloisia* on well-developed desert pavement and those of *Loeseliastrum* on sandy soils. When the two genera occur together, *Langloisia* tends to occupy the rockier sites and *Loeseliastrum,* the sandier sites. Populations of both genera are found from below sea level to over 2100 m, but usually occur below 1800 m. Seeds generally germinate after fall or winter rains, overwinter as small rosettes of leaves, and bloom in late spring or early summer as temperatures rise and soil moisture drops. They bloom later than most annual desert Polemoniaceae, but earlier than *Eriastrum* and *Ipomopsis.*

Affinities with other genera. Greene (1887) wrote concerning the Polemoniaceae, "The one general conclusion reached by me, after


Langloisia
L. s. setosissima ○
L. s. punctata ●
400 km
35 N
110 W
U.S.A.
Mex.

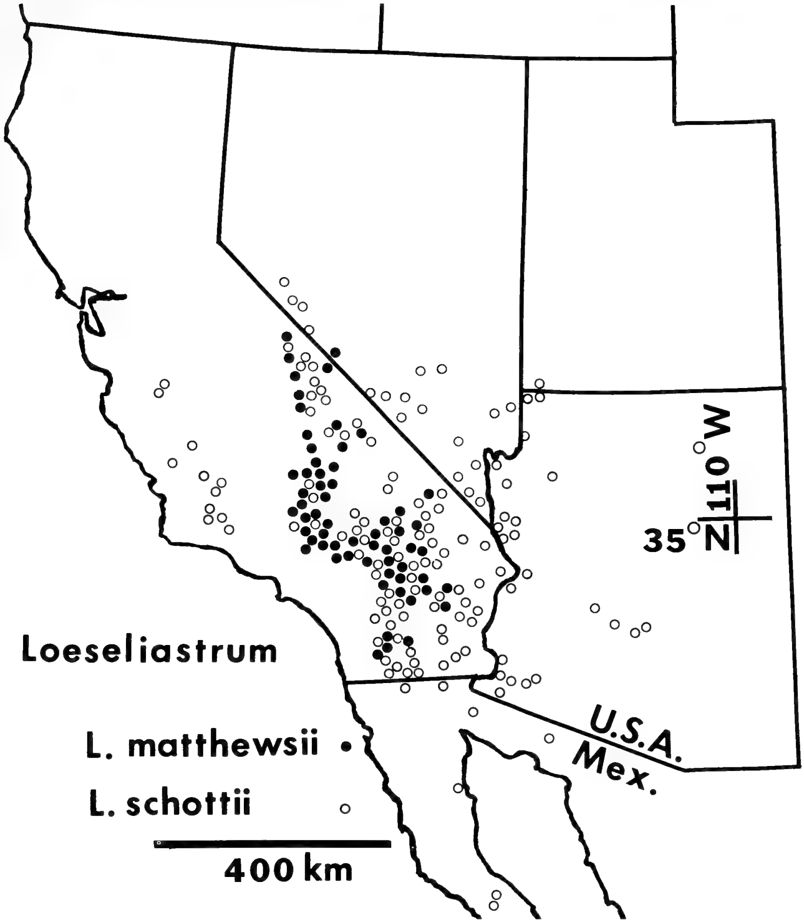


FIG. 5. *Loeseliastrum matthewsii* (●) is primarily a species of the Mojave Desert with outlying populations in eastern San Diego Co., California, at the western edge of the Sonoran Desert, separated from the Mojave Desert by the low elevation Coachella Valley and Salton Sink in Riverside and Imperial cos., California. *Lo. schottii* (○) is well represented in the Mojave and Sonoran deserts, and extends slightly into the Great Basin. A few disjunct populations occur on the southwestern margins of California's central valley.

⟵

FIG. 4. *Langloisia setosissima* subsp. *setosissima* (○) and *La. s.* subsp. *punctata* (●) are mostly allopatric, with a narrow zone of overlap along the California-Nevada border where several populations show intergrading corolla morphology. There are disjunct populations of *La. s.* subsp. *punctata* in the Snake and Salmon river valleys of Idaho and eastern Oregon.

eighteen years of field experience with these plants is, that characters of form of corolla and length, insertion, direction, etc. of stamens may be set aside as wholly incompetent to furnish means of defining genera; and that, by the calyx alone, especially as it appears not in flower, but in its after developments, in and of itself and in its relation to the fruit, we may limit and define good acceptable genera, made up of plants agreeing in habit, and in some other minor points." He modified this view five years later (Greene 1892), writing, ". . . only upon habit, strengthened in four or five instances by some characters of the calyx, can any genera of Polemoniaceae find confirmation." In his original publication of *Langloisia,* however, Greene (1896) reiterated his idea that, ". . . the calyx in the Polemoniaceae is the floral organ which affords the best characters for the definition of genera."

The morphological characteristics distinguishing *Langloisia* and *Loeseliastrum* are so evident it is doubtful that they would have been treated as a single genus were it not for weight attached to calyx morphology in the past. Although both genera are low bristly annuals, their habit is one that appears in *Eriastrum, Ipomopsis,* and *Navarretia* of the Polemoniaceae, and in desert members of several other plant families, suggesting that the habit is a result of convergent evolution. During field studies, and in the examination of over 2000 herbarium sheets of *Langloisia* and *Loeseliastrum,* no specimens were found that might represent intergeneric hybrids, even though the two taxa are occasionally found flowering in mixed stands. Every specimen, even early non-flowering material, could be easily assigned to one genus or the other.

Langloisia appears to share affinities with *Eriastrum* and *Ipomopsis.* All three genera have 6-methoxyflavonols, seven pairs of chromosomes, and at least some species with Gilia I pollen. Perhaps *Langloisia* is somewhat closer to *Eriastrum* than to *Ipomopsis* because the latter genus has larger chromosomes (Grant 1959). There is little evidence, however, to recommend joining *Langloisia* and *Eriastrum* in a single genus. *Eriastrum* is distinguished from other genera by a combination of zygomorphic calyces, cobwebby pubescence of uniseriate long-celled thin trichomes, and largely non-spiny leaves and bracts, quite unlike *Langloisia.*

Determining the affinities of *Loeseliastrum* is more difficult. It shares chromosome number and habit with *Eriastrum, Ipomopsis,* and *Langloisia,* and calyx morphology with *Langloisia. Loeseliastrum,* however, has the common flavonols and the presence of these compounds rather than the 6-methoxyflavonols seems indicative of a different ancestry. Perhaps its closest affinities lie with *Gilia,* although it would be difficult to support its inclusion in that genus, which has large chromosomes (Grant 1959) with numbers based on $x = 9$. Smith et al. (1977) suggest that thorough analysis of the flavonoid diversity in *Gilia* could provide for further dismemberment of the genus, another argument in favor of treating *Loeseliastrum* as a separate genus so that its taxonomic visibility will invite comparative studies.

TAXONOMIC TREATMENT

Key to Taxa of *Langloisia* and *Loeseliastrum*

A. Corollas actinomorphic; capsules triangular in cross section; trichomes branched; upper leaves and bracts with some multiple bristles; pollen white to blue .... *Langloisia*
  B. Corolla lobes ⅓ to ½ the length of the tube, unmarked to streaked with purple, but seldom dotted; filaments less than 3 mm long .... 1a. *La. setosissima* subsp. *setosissima*
  B. Corolla lobes ½ to nearly the length of the tube, dotted with purple; filaments more than 3 mm long, somewhat less in Idaho and Oregon populations .... 1b. *La. setosissima* subsp. *punctata*
A. Corollas zygomorphic; capsules 3-lobed in cross section; trichomes unbranched; bristles of leaves and bracts all simple; pollen yellow .... *Loeseliastrum*
  C. Corolla 11 to 21 mm long, the upper lip ¾ to 1½ times the length of the tube; longest filaments equal to upper lip of corolla; calyx (excluding bristles) ½ to ¾ the length of the corolla tube .... 1. *Lo. matthewsii*
  C. Corolla 8 to 15 mm long, upper lip ½ to ¾ times (rarely equal) the length of the tube; longest filaments shorter than upper lip of corolla; calyx ¾ to nearly the length of the corolla tube .... 2. *Lo. schottii*

LANGLOISIA Greene, Pittonia 3:30. 1896.—*Gilia* subg. *Langloisia* Milliken, Univ. Calif. Publ. Bot. 2:25. 1904.—*Langloisia* sect. *Eulangloisia* Brand in Engler, Pflanzenr. IV. 250:169. 1907.—LECTOTYPE: *Langloisia setosissima* (Torr. & A. Gray) Greene (*Navarretia setosissima* Torr. & A. Gray). See Timbrook (1985) for a discussion of lectotypification of *Langloisia*.

Low, often rigidly branched, taprooted annuals; lower stems often naked, upper very leafy. Leaves alternate, linear to oblanceolate, cuneate, pinnately toothed, the lobe tips protracted into bristles, these simple on distal lobes, the proximal lobes of upper leaves reduced to a cluster of 2–3 bristles; pubescence non-glandular, trichomes branched. Flowers sessile to short pedicellate, in terminal, bracteate heads, the bracts leaf-like, dentate cuneate, with lobes bristle-tipped; calyx actinomorphic, the lobes equal or subequal, bristle-tipped, the narrow hyaline membrane in sinuses rupturing early with the enlargement of capsule; corolla actinomorphic, funnelform, white to blue or lavender, often purple-dotted; stamens inserted at or just below the sinuses, equal, straight, exserted, the anthers oval; pollen white to blue; style exserted. Capsule oblong-lanceolate, triangular in cross section, 3-celled, disarticulating on dehiscence, the outer wall of capsule valve flat. Seeds small, ovoid, tan to brown, mucilaginous when wetted.

One species with two subspecies, native to deserts of western North America.

1. Langloisia setosissima (Torr. & A. Gray) Greene, Pittonia 3: 30. 1896.—For synonymy and typification see the subspecific headings.

Plants low, (0.15–)0.3–2.5 dm wide; stem short, upright, the branches horizontal or ascending; herbage sparsely to densely pubescent, the trichomes branched. Leaves 1–3 cm long, narrow at base and expanded into 3(–5) lobes at apex, these with single bristles, the proximal lobes of upper leaves reduced to long bristles, these connate at base forming clusters of 2–3 bristles, especially on upper leaves and bracts. Calyx lobes 5–10 mm long, with terminal bristles 2–6 mm long; corolla actinomorphic, funnelform; stamens regularly inserted, the filaments straight; pollen white to blue. Capsule oblong-lanceolate, 4.5–7.5 mm long, triangular in cross section, 3-celled, the outer valve walls nearly flat. Seeds 1 mm long, 2–10 per cell.

The two taxa of *Langloisia* are treated here as subspecies, a departure from their usual treatment. Coville (1892) described plants of *Gilia setosissima* (=*La. setosissima*) from Inyo County, California, as *G. setosissima* var. *punctata.* These plants have larger flowers and fruits than plants from other areas and have purple-dotted corollas. He also noted intergradation between var. *setosissima* and var. *punctata.* Goodding (1904) elevated var. *punctata* to specific rank, but the specimens [Rioville, NV, *Goodding 716* (RM)] he apparently used to support the change in status clearly belong to *L. setosissima* subsp. *setosissima.* Unfortunately, he did not cite his collection number, but this is the only collection of his from Rioville that I have seen, and it bears his handwritten identification "*Langloisia punctata*". Jepson (1925, 1943), Mason (1951), and Munz (1959, 1974) followed Goodding in recognizing the *punctata* taxon at the specific rank. This may reflect that most of the zone of overlap of the two subspecies lies in Nevada, or just at the periphery of the area covered in their treatments in northern Inyo County, California. In other parts of California, the two taxa are allopatric and easily distinguished, and these authors may not have been aware of the intergradation of the two forms. In the zone of sympatry, I have collected specimens with intermediate floral morphology in terms of corolla patterning, corolla lobe to tube ratio, and filament length. I also have seen specimens of *Langloisia setosissima* subsp. *setosissima* adjacent to the zone of sympatry that bear dots on the corolla, suggesting introgression of genes from *La. setosissima* subsp. *punctata.* In view of the largely allopatric nature of the two taxa and their intergradation in the zone of sympatry, they do not merit specific status.

1a. LANGLOISIA SETOSISSIMA subsp. SETOSISSIMA—*Navarretia setosissima* Torr. & A. Gray in Ives, Report upon the Colorado River of the West 22. 1860.—*Gilia setosissima* (Torr. & A. Gray) A. Gray, Proc. Amer. Acad. Arts 8:271. 1870.—*Loeselia setosissima* (Torr. & A. Gray) A. Gray ex Peter in Engler & Prantl, Nat. Pflanzenfam. IV(3a):54. 1891.—LECTOTYPE: "Most westerly part of N. Mex. near Virgen R.", actually referring to the Virgin River of Utah (Cronquist 1984), *Fremont 414* (Lectotype: NY!; isolectotype: GH!). See Cronquist (1984) and Timbrook (1985) for a discussion of lectotypification.

Langloisia setosissima (Torr. & A. Gray) Greene var. *campyloclados* Brand in Engler, Pflanzenr. IV.250:171. 1907.—SYNTYPES: "Near St. George, Southern Utah", *Parry 190*; "Ft. Mohave, Arizona", *Lemmon & Wife s.n.*; "The Needles, California, *Jones 3786*". Brand cites Herb. Boissier for *Parry 190* and for *Lemmon & Wife s.n.* and these are at G. Because I have seen only photocopies of them, I shall not designate a lectotype. Isosyntypes: *Parry 190* (F!, G, GH!, MO!, ND!, NY!, US!); *Lemmon & Wife s.n.* (G, UC!, US!); *Jones 3786* (ARIZ!, CAS!, DS!, F!, MICH!, NY!, POM!, UC!, US!).

Corolla lavender to blue, unmarked or with purple guidelines, rarely (introgressive forms?) dotted or flecked as in *Langloisia setosissima* subsp. *punctata,* the tube 10–14 mm long, sometimes surpassing the calyx bristles, the lobes 3–5(–7) mm long, ⅓–½ the length of the tube; stamen filaments less than 3 mm long; $2n = 14$.

Langloisia setosissima var. *campyloclados* seems to be based on a large, well-branched specimen that falls within the variation seen in *La. s.* subsp. *setosissima.* Brand's (1907) description contains an apparent typographical error. "Elatior, usque ad 15 mm alta . . ." should probably read "15 cm." Many collections I have examined contain plants approaching this stature along with much smaller mature specimens. The large plants are not worthy of taxonomic distinction.

1b. **Langloisia setosissima** subsp. **punctata** (Coville) Timbrook comb. et stat. nov.—*Gilia setosissima* (Torr. & A. Gray) A. Gray var. *punctata* Coville, Proc. Biol. Soc. Wash. 7:72. 1892.—

Navarretia setosissima Torr. & A. Gray var. *punctata* (Coville) Coville, Contr. U.S. Natl. Herb. 4:154. 1893.—*Langloisia punctata* (Coville) Goodding, Bot. Gaz. 37:58. 1904.—*Langloisia punctata* (Coville) Heller, Muhlenbergia 1:57. 1904.—*Gilia punctata* (Coville) Munz, Man. S. Calif. Bot. 402. 1935.—TYPE: USA, CA, Inyo Co., "Surprise Cañon, Panamint Mts., Alt. 800 meters", *Coville & Funston 716* (Holotype: US!; isotypes: GH!, MO!, UC!, US!).

Langloisia lanata Brand in Engler, Pflanzenr. IV.250:169. 1907.—TYPE: USA, NV, Mineral Co., "Candelaria", *Jones 3965* (Holotype: B, lost during war (Leuenberger, pers. comm.); lectotype here designated: US!; isotypes: CAS!, DS!, MO!, NY!, POM!, UC!, US!).

Corolla white to light blue, heavily marked with purple dots, often with 2 yellow spots in the middle of each lobe, rarely lightly marked to unmarked, the tube 8.5–13 mm long (6.5–11 mm in Idaho and Oregon populations), the lobes 5–9.5 mm long (4.5–8 mm in Idaho and Oregon populations), the lobes ½ to nearly the length of the tube; stamen filaments 3.5–7.6 mm long (2.5–5 mm in Idaho and Oregon populations); $2n = 14$.

Langloisia lanata was based upon a single collection with distinctly pedicellate flowers and dense woolly pubescence. Pedicel length in *La. setosissima* subsp. *punctata* varies from 0–2.1 mm, and pubescence from nearly glabrous to dense and woolly. Both characters can vary within a population and some individual plants have both pedicellate and sessile flowers.

Loeseliastrum (Brand) Timbrook stat. nov.—*Gilia* sect. *Chaetogilia* A. Gray, Syn. Fl. N. Amer., ed. 2, 2(1, Suppl.):409. 1886.—*Loeselia* subg. *Chaetogilia* A. Gray ex Peter in Engler & Prantl, Nat. Pflanzenfam. IV(3a):54. 1891.—*Langloisia* sect. *Loeseliastrum* Brand in Engler, Pflanzenr. IV.250:169. 1907.—LECTOTYPE: *Loeseliastrum matthewsii* (A. Gray) Timbrook based upon *Loeselia matthewsii* A. Gray according to Grant (1959) who selected it as the type of *Gilia* sect. *Chaetogilia* and *Langloisia* sect. *Loeseliastrum* Brand even though Grant did not use sections in his treatment of *Langloisia* sensu lato.

Low, rigidly branched, taprooted annuals; lower stems naked, upper leafy. Leaves alternate, linear to oblanceolate, pinnately toothed, the lobes protracted into a single bristle; pubescence of multicellular uniseriate trichomes, and with short, glandular trichomes on pedicels and calyces. Flowers sessile to short-pedicellate, in terminal bracteate heads or the lower solitary in leaf axils, the bracts leaf-like, dentate, with bristle-tipped lobes, the bristles always simple; calyx actinomorphic, the lobes equal or subequal, bristle-tipped, with narrow hyaline membrane in sinuses rupturing early with enlargement of capsule; corolla strongly bilabiate to nearly regular, funnelform, white to pink or rose, the upper lip of 3 lobes, heavily to faintly marked with maroon arches above throat, the lower lip less heavily marked to unmarked; stamens subequally inserted at or just below the sinuses, unequal, curved, weakly to strongly exserted, the anthers oval. Capsule ovoid, strongly 3-lobed in cross section, 3-celled, the whole capsule disarticulating on dehiscence, the outer wall of capsule valve indented between the septa. Seeds small, ovoid, tan to brown, mucilaginous when wetted.

Two species, native to deserts of western North America.

1. **Loeseliastrum matthewsii** (A. Gray) Timbrook comb. nov.—*Loeselia matthewsii* A. Gray, in Watson, Bot. Calif. 2:466. 1880.—*Gilia matthewsii* (A. Gray) A. Gray, Syn. Fl. N. Amer., ed. 2, 2(1, Suppl.):409. 1886.—*Navarretia matthewsii* (A. Gray) Coville, Contr. U.S. Natl. Herb. 4:135. 1893.—*Langloisia matthewsii* (A. Gray) Greene, Pittonia 3:30. 1896.—TYPE: USA, CA, Inyo Co., "Camp Independence", *Matthews s.n.* (Holotype: GH!).

Plants mounded, 0.3–2.1 dm wide, the branches spreading divaricately, horizontal or ascending, naked on proximal portion, leafy on distal; herbage subglabrous to villous, with pubescence of multicellular uniseriate trichomes, the pedicels and calyces with short glandular trichomes. Leaves broadly linear to oblanceolate, 1–3.5 cm long, pinnately lobed or toothed, the lobes and teeth with single bristles at tip. Calyx 4–7(–8) mm long, the lobes villous-margined, bristle-tipped; corolla strongly bilabiate, white to more commonly pink to deep rose-purple, the upper lip ¾–1½ times the length of the tube, 5–11 mm long, mostly with 3 lobes, heavily marked with maroon arches and white blotch at base of each lobe, the lower lip 4–7 mm long, mostly with 2 lobes, less heavily marked, the tips of the lobes of both lips truncate, 3-toothed or retuse with a mucro in the notch, infrequently rounded, often with inward-directed palate-like projections in sinuses on either side of middle lobe of upper lip; stamens subequally inserted, the filaments unequal, strongly exserted, strongly curved, the longest as long as the upper corolla lip; pollen yellow to gold; style strongly exserted. Capsule ovoid, 3–5 mm long, strongly 3-lobed in cross section, 3-celled, the whole capsule disarticulating on dehiscence, the outer wall of capsule valve indented between the septa. Seeds 1 mm long, 2–6 per cell, ovoid, tan to brown, mucilaginous when wetted; $2n = 14$.

Loeseliastrum matthewsii is primarily a species of the Mojave Desert, although a few of its most northerly populations in Inyo and Mono cos., California, and Nye County, Nevada, fall just within the southwestern boundary of the Great Basin floristic division of Cronquist et al. (1972). A more significant occurrence outside the limits of the Mojave Desert is in eastern San Diego Co., California, where populations from the western edge of the Sonoran Desert are separated from the nearest Mojave Desert populations by the low elevation Coachella Valley and Salton Sink in Riverside and Imperial cos., California. The only known collection from Mexico is *Palmer 127* (ND, NY) from "Los Angeles Bay, Gulf of California, 1887." Some sheets of *Palmer 127* (NY, US), however, bearing the same species, are labeled, "7–15 Jun 1888, N fork of Kern River, Kern Co., California." The Los Angeles Bay sheets may actually be duplicates of the Kern County collection. Because of this uncertainty, the Mexican collection has not been included in Fig. 5.

2. **Loeseliastrum schottii** (Torr.) Timbrook comb. nov.—*Navarretia schottii* Torr., Bot. Bound., *In* Emory, Rep. U.S. Mex. Bound. 2:145. 1859.—*Gilia setosissima* (Torr. & A. Gray) A. Gray var. *exigua* A. Gray, Proc. Amer. Acad. Arts 8:271. 1870.—*Gilia schottii* (Torr.) Watson, Botany, *In* King, United States geological exploration of the fortieth parallel 267. 1871.—*Loeselia schottii* (Torr.) A. Gray, *In* Watson, Bot. Calif. 2:466. 1880.—*Langloisia schottii* (Torr.) Greene, Pittonia 3:30. 1896.—TYPE: "Colorado Desert, Sonora", *Schott s.n.* (Lectotype here designated: NY!; isolectotypes: F!, GH!).

Langloisia flaviflora Davidson, Bull. S. Calif. Acad. Sci. 21:39. 1922.—TYPE: USA, CA, Kern Co., "roadside, Willow Springs, Mojave Desert", *Davidson 3506* (Holotype: LAM!, isotypes: DS!, GH!, POM!, UC!, US!).

Plants low, 0.2–2 dm wide, sometimes unbranched, or erect, short stemmed, with divaricately spreading branches, these horizontal or ascending, naked on proximal portion, leafy on distal portion; herbage subglabrous to villous, with pubescence of multicellular uniseriate trichomes, the pedicels and calyces with short glandular trichomes. Leaves broadly linear to oblanceolate, cuneate, 1–3 cm long, pinnately lobed, the lobes with single bristles at tip. Calyx 4–6(–7) mm long, the lobes villous-margined, bristle-tipped; corolla weakly to moderately bilabiate, white to pink, rarely deep rose-purple, the upper lip ½–¾ (rarely as long as) the length of the tube, 3–7 mm long, mostly with 3 lobes, marked with maroon streaks at base of each lobe, the lower lip mostly with 2 lobes, the lobe tips acute to apiculate, rarely rounded; stamens subequally inserted, the filaments weakly curved in less zygomorphic forms to moderately or strongly curved in more zygomorphic forms, unequal, the longest shorter than the upper lip of the corolla, weakly to moderately exserted; pollen yellow; style weakly to moderately exserted. Capsule ovoid, 2.5–5 mm long, strongly 3-lobed in cross section, 3-celled, the whole capsule disarticulating on dehiscence, the outer wall of capsule valve indented between the septa. Seeds 1 mm long, 2–6 per cell, ovoid, tan to brown, mucilaginous when wetted; $2n = 14$.

Loeseliastrum schottii is well represented in both the Sonoran and Mojave deserts, and extends slightly into the Great Basin. A few disjunct populations occur on the southwestern margins of California's central valley. There is a sheet of *Lo. schottii,* [*M. E. Jones s.n.* (MICH)] from El Paso, Texas, the only known collection from Texas. Because *Lo. schottii* is not known from New Mexico and the eastern halves of Arizona and Utah, the validity of the Texas collection is somewhat doubtful. It has not been included in Fig. 5.

Langloisia flaviflora was recognized on the basis of a single collection of yellow-flowered plants with short styles. Populations of *Loeseliastrum schottii* often contain a few yellow-flowered individuals, and there is much variation in flower color with age of the flower, even in a single plant; thus, the occurrence of occasional populations with predominantly yellow-flowered plants does not seem worthy of taxonomic recognition.

ACKNOWLEDGMENTS

Appreciation is extended to the curators and staff of the following herbaria for loans of specimens: ARIZ, ASU, CAS, CS, COLO, DS, F, GH, ID, IDS, JEPS, LA, LAM, MICH, MO, ND, NY, OSC, POM, RENO, RM, RSA, SD, TEX, UC, UCLA, UNM, US, USC, UT, UTC, WS, and WTU. Specimens were also studied at SBBG and UCSB. I am grateful to Drs. R. W. Patterson, R. N. Philbrick, and D. M. Smith for comments on an earlier version of the manuscript; to Drs. A. Cronquist, J. McNeill, D. Nicolson, and E. G. Voss for comments concerning typification; to J. F. Timbrook for line drawings; and to the Department of Biological Sciences, University of California at Santa Barbara, and Sigma Xi for grants-in-aid of research. Reviews by Drs. M.E. Barkworth and A. Day were very helpful in revising the manuscript.

LITERATURE CITED

BRAND, A. 1907. Polemoniaceae. *In* A. Engler, Das Pflanzenreich IV. 250:1–203.

COVILLE, F. V. 1892. Descriptions of new plants from southern California, Nevada, Utah, and Arizona. Proc. Biol. Soc. Wash. 7:65–80.

———. 1893. Botany of the Death Valley expedition. Contr. U.S. Natl. Herb. 4:1–363.

CRONQUIST, A. 1959. Polemoniaceae. *In* C. L. Hitchcock, A. Cronquist, H. Ownbey, and J. W. Thompson, Vascular plants of the Pacific Northwest 4:95–145. Univ. Washington Press, Seattle.

———. 1984. Polemoniaceae. *In* A. Cronquist, A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren, Intermountain flora: vascular plants of the Intermountain West, U.S.A. Vol. 4. New York Botanical Garden, New York.

———, A. H. HOLMGREN, N. H. HOLMGREN, and J. L. REVEAL. 1972. Intermountain flora: vascular plants of the Intermountain West, U.S.A. Vol. 1. Hafner Publ. Co., Inc., New York.

GOODDING, L. N. 1904. Southwestern plants. Bot. Gaz. (Chicago) 37:53–59.

GRANT, V. 1959. Natural history of the *Phlox* family: systematic botany. M. Nijhoff, The Hague.

GREENE, E. L. 1887. Some American Polemoniaceae I. Pittonia 1:120–139.

———. 1892. Some American Polemoniaceae II. Pittonia 2:251–260.

———. 1896. A new genus of Polemoniaceae. Pittonia 3:29–30.

JEPSON, W. L. 1925. Manual of the flowering plants of California. A.S.U.C. Bookstore, Berkeley, CA.

———. 1943. Polemoniaceae. *In* A flora of California 3:131–222. A.S.U.C. Bookstore, Berkeley, CA.

MASON, H. L. 1951. Polemoniaceae. *In* L. Abrams, Illustrated flora of the Pacific states 3:396–474. Stanford Univ. Press, Stanford, CA.

MILLIKEN, J. 1904. A review of Californian Polemoniaceae. Univ. Calif. Publ. Bot. 2:1–71.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

———. 1974. A flora of southern California. Univ. California Press, Berkeley.

SMITH, D. M., C. W. GLENNIE, J. B. HARBORNE, and C. A. WILLIAMS. 1977. Flavonoid diversification in the Polemoniaceae. Biochem. Syst. Ecol. 5:107–115.

STUCHLIK, L. 1967a. Pollen morphology in the Polemoniaceae. Grana Palynol. 7: 146–240.

———. 1967b. Pollen morphology and taxonomy of the family Polemoniaceae. Rev. Palaeobot. Palynol. 4:325–333.

TIMBROOK, S. 1978. Biosystematic studies of *Langloisia* and *Loeseliastrum*. Ph.D. dissertation, Univ. California, Santa Barbara.

———. 1985. Problems of lectotypification in *Langloisia* (Polemoniaceae). Taxon 34:522–524.

(Resubmitted 27 Sep 1985; revision accepted 3 Apr 1986.)

HASTINGSIA ATROPURPUREA (LILIACEAE: ASPHODELEAE), A NEW SPECIES FROM SOUTHWESTERN OREGON

RUDOLF W. BECKING
College of Natural Resources, Humboldt State University,
Arcata, CA 95521

ABSTRACT

Hastingsia atropurpurea Becking was discovered recently along the slopes of the Woodcock and Tennessee Mountains in southwestern Oregon. It is distinguished from *Hastingsia bracteosa* by a distinct, dark purple perianth, larger bulb size, larger and more robust scape, longer and wider, more glaucous leaves, shorter and more branched racemes, larger number of veins in the leaves, shorter floral and inflorescence bracts, and greater density of flowers in the raceme. It is sympatric with *H. bracteosa* only at three isolated localities, where there is no evidence of hybridization.

An unusual collection of *Hastingsia* (Liliaceae: Asphodeleae) was made in June 1982, in conjunction with a survey of the status of *H. bracteosa,* an endangered species. Between 1983 and 1985, further explorations revealed considerable range extensions of this unknown plant. In 1984, 22 specimens were collected and deposited in major herbaria, and herbarium materials of *Hastingsia* species from many institutions were studied. These studies resulted in the distinction of a new species, which is supported by statistical analysis.

Hastingsia atropurpurea Becking, sp. nov.

Herba typice plerumque alterioris; scapus unus per annuum, 71–99 cm altus; racemibus terminalibus, 20–70 floribus, erectibus, solitaribus, non rarifer ramificantibus. Bulbus oblongatus vel infrequenter ovatus, grandioris; 28–54 mm longus, 18–30 mm latus. Folia graminifolia, glauco-virida, 25–55 cm longi, 6–12 mm lati. Sepala vel corolla atropurpurea cum vena centralis pallida virida, 9–12 mm longi, 2 mm lati, lanceolata, acuminata. Capsula oblonga. Fig. 1.

Perennial herbs typically more robust than *Hastingsia bracteosa.* Scape single, arising from the top of the bulb, 71–99 cm tall. Bulb oblong or infrequently more oblong-ovate; 28–54 mm long and 18–30 mm wide; bulb scales light brownish, fleshy, densely packed forming the bulb; bulb with a blackish exterior tunica consisting of hardened dried vein remnants. Terminal raceme 20–70 flowered, erect, solitary; often the scape is branched below the terminal raceme with 1 to 3 shorter lateral ascending racemes. Leaves distinctly grass-like, deeply to distinctly keeled or V-shaped, bluish-green, glabrous,

MADROÑO, Vol. 33, No. 3, pp. 175–181, 1986

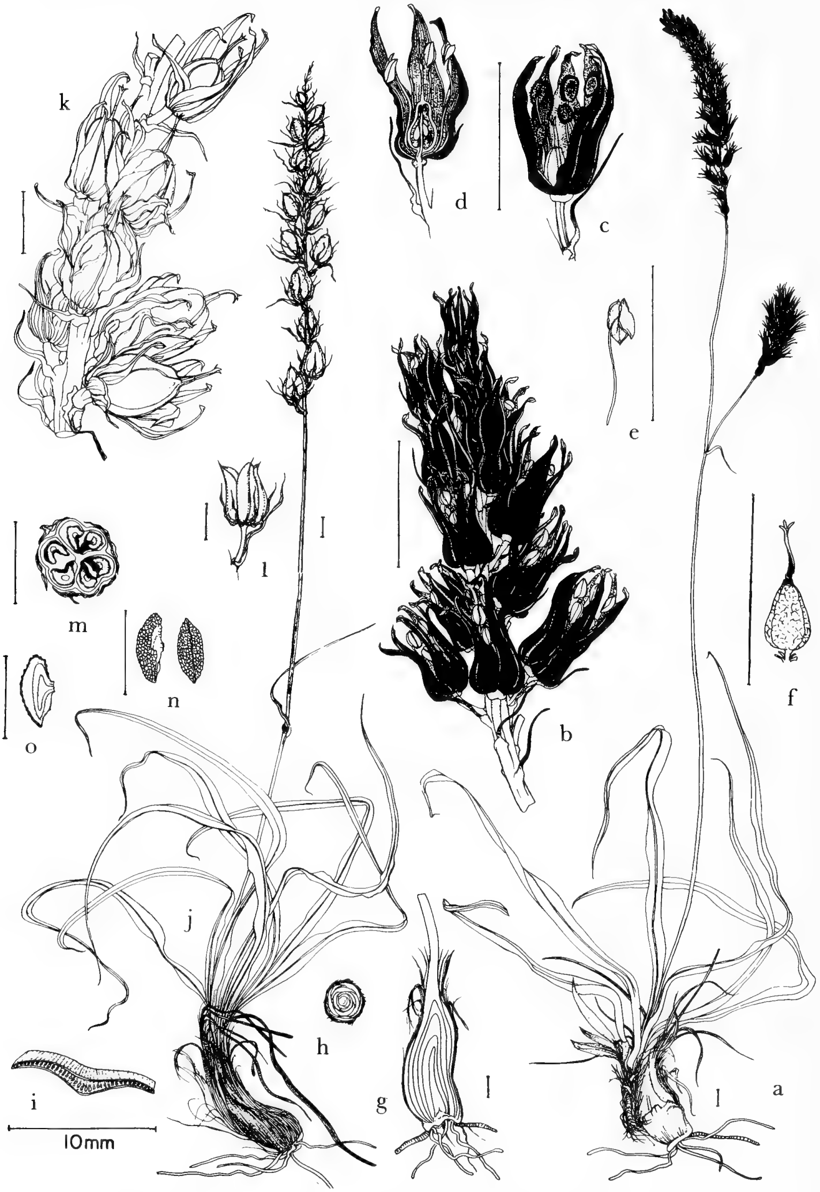


FIG. 1. *Hastingsia atropurpurea.* a. Flowering plant. b. Top of flowering raceme. c. Flower. d. Lengthwise cross section of flower. e. Stamen. f. Pistil. g. Lengthwise cross section of bulb. h. Cross section of bulb. i. Cross section of leaf blade. j. Fruiting plant. k. Part of fruiting raceme. l. Capsule. m. Cross section of capsule. n. Seeds. o. Lengthwise section of seed. All bar scales are 10 mm long.

25–55 cm long and 6–12 mm wide. Mature plants often have abundant dead, blackish, and shriveled foliage persisting at the base of the scape at soil level. Sepals and petals lanceolate, 9–12 mm long, 2 mm wide, erect and forming a closed perianth, trinerved, purple-black with a pale green central vein; discoloring often in herbarium specimens to dark purple; each perianth segment narrowing into a flattened and triangular tip, whitish in color with minute dense stiff hairs along the tip margins. Capsule oblong to oblong-ovate, broadly 3-lobed and slightly constricted ⅓ below its top, 2 seeds per locus. Seed fusiform, elongate with two laterally flattened sides, shiny, black with irregular reticulation on the rounded surface.

TYPE: OR, Josephine Co.: O'Brien, Woodcock Mt., *Darlingtonia* bog, T39S R8W S31 se.¼, 123°41′48″W, 42°7′29″N, 1520 ft. elev., 4 Jul 1984. *R. W. Becking 840700.* (Holotype: CAS; isotypes: CAS, DS, GH, HSC, ORE, OSC, PUA, RSA, SOC, UBC, US.) The most typical fruiting specimen is *Becking 840700(14)* (CAS).

PARATYPES: OR, Josephine Co.: Woodcock Mt., 24 Jun 1982, *Becking 820658* (HSC); Woodcock Mt., 17 Jun 1982, *Becking 820633* (HSC); Canyon Creek, 5 Jul 1984, *Becking 840723* (HSC); Mikes Gulch, 3 Jul 1984, *Becking 840706* (HSC); Upper Josephine Creek, 30 May 1985, *Becking 850551* (CAS, HSC, UBC); Parker Creek, 28 May 1985, *Becking 850540* (CAS, HSC, OSC, UBC); Canyon Creek, 29 May 1985, *Becking 850546* (CAS, HSC, OSC, UBC); Josephine Creek, Cutlers Cabin, 5 Jul 1984, *Becking 840727* (CAS); Upper Josephine Creek, 6 Jul 1984, *Becking 840730* (HSC); Canyon Creek, 8 Jul 1984, *Becking 840740* (CAS, RSA); Woodcock Mt., 4 Jul 1984, *Becking 840712, 840713* (HSC, RSA); Woodcock Mt., Mendenhall Creek, 5 Jun 1985, *Becking 850608* (CAS); Eight Dollar Mt., USFS Road No. 3843 bridge, 17 Jun 1982, *Becking 820600* (CAS).

Distinction between species. The distinctions between *Hastingsia atropurpurea* and *H. bracteosa* are readily observed in the field, even on mature sterile plants. These differences are summarized in Table 1. No evidence for hybridization between *H. atropurpurea* and *H. bracteosa* has been observed.

Hastingsia atropurpurea (dark purple) can be separated from *H. bracteosa* (yellowish white) by the distinctive perianth color and its more glaucous leaves. Flower color is very distinctive in the Liliaceae. In the Tribe Asphodeae to which *Hastingsia* belongs, flower color has been used as the simplest and most reliable difference between *Schoenolirion croceum* (yellow) and *Schoenolirion wrightii* (white) (Sherman 1969). In *Chlorogalum,* a closely related genus, flower color is used to distinguish *Chlorogalum purpureum* (purple) and *C. parvifolium* (white). *Hastingsia bracteosa* and *H. atropur-*

TABLE 1. DISTINCTIONS BETWEEN *Hastingsia atropurpurea* AND *H. bracteosa.* All characters listed had significant differences at the 0.01 probability level by t-test analysis. 1. Leaf length, leaf width and leaf vein number were measured on 2–3 undamaged leaves at about the middle of the leaf length to establish the range of these characters. 2. Floral bracts support individual flowers. 3. Inflorescence bracts support raceme branches. 4. Density of flowers is the number of flowers per 10 cm raceme length. Most often, counts per 5 cm lengths were executed and converted per 10 cm lengths. The most dense and least sparse (open) raceme portions were selected for counting the range of flower density.

	Hastingsia atropurpurea		*Hastingsia bracteosa*	
	Mean ± s.e.	(sample size)	Mean ± s.e.	(sample size)
Bulb length	41.1 ± 12.5 mm	(44)	34.6 ± 8.4 mm	(38)
Bulb width	24.4 ± 6.1 mm	(44)	21.0 ± 5.7 mm	(38)
Scape length	801.9 ± 186.9 mm	(55)	655.3 ± 217.2 mm	(45)
Scape base	3.3 ± 0.8 mm	(57)	2.8 ± 0.8 mm	(46)
Dead leaves	usually present		often absent	
Leaf length[1]				
Max	439.9 ± 111.0 mm	(62)	381.8 ± 141.3 mm	(45)
Min	372.6 ± 118.0 mm	(62)	314.1 ± 129.4 mm	(43)
Leaf width[1]				
Max	9.8 ± 1.8 mm	(62)	6.7 ± 1.4 mm	(45)
Min	8.4 ± 1.7 mm	(62)	5.8 ± 1.3 mm	(43)
Leaf vein number[1]				
Max	27.4 ± 4.0	(62)	23.0 ± 3.6	(43)
Min	24.2 ± 3.9	(62)	20.3 ± 3.5	(43)
Floral bract[2]				
Length max	7.2 ± 2.3 mm	(57)	8.7 ± 2.9 mm	(48)
Inflor. bract[3]				
Length min	16.1 ± 8.4 mm	(44)	21.5 ± 7.5 mm	(33)
Ovary color	dark purple	(46)	dark gray-green	(45)
Capsule style	2.5 ± 0.5 mm	(26)	2.1 ± 0.3 mm	(12)
Capsule color	purplish-green		gray to yellow-green	
Raceme branches	1.7 ± 1.3	(44)	1.0 ± 1.0	(36)
Density flowers[4]				
Max	36.1 ± 6.9	(42)	30.0 ± 6.7	(36)
Min	30.3 ± 6.9	(42)	24.7 ± 7.4	(36)

purea can be separated from *H. alba* by their closed, more campanulate perianth with filaments distinctly shorter than the perianth.

Statistical analysis. Discriminant Analysis (Wilkinson Lambda; Nie et al. 1975) was used to test classification of 62 herbarium specimens of *Hastingsia atropurpurea* and 50 specimens of *H. bracteosa.* Some 47 different quantitative and 8 qualitative characters were measured or assessed; all specimens with one or more missing characters were excluded from the Discriminant Analysis. The re-

TABLE 2. DISCRIMINANT ANALYSIS RESULTS USING SPECIMENS OF *Hastingsia atropurpurea* AND *H. bracteosa.* Key: *H. a* and *H. b* = *Hastingsia atropurpurea* and *H. bracteosa,* respectively; % = percent of correct classification; r = canonical correlation coefficient; # = number of significant characters used. Total number of specimens is 112.

Character group tested in discriminant analysis	Number of specimens		%	r	#
	H. a	*H. b*			
Bulb, scape, foliage, flower, and raceme	21	20	100	0.999643	14
Scape, foliage, flower, and raceme	28	23	100	0.985042	14
Bulb, scape, foliage, capsule, and seed	11	6	100	0.993476	9
Scape, foliage, capsule, and seed	14	7	100	0.998970	13

sults are summarized in Table 2. The segregations of the two species were highly effective (Canonical r = 0.985042 to 0.999643) and 100% correct classification occurred, with 9–14 characters selected as highly significant.

The t-test analysis was applied to the 112 available specimens and the 55 quantitative or qualitative characters selected for comparison at the individual character level. The significant characters were identified (Table 1). In addition, some 20 characters were examined and were found to have no significant differences: max/min petal length and width, long and short filaments, ovary length and width, ovary stalk, ovary style, max/min capsule length and width, raceme openness and density, and max/min seed length and width.

Distribution and ecology. The ranges of *Hastingsia atropurpurea* and *H. bracteosa* do not overlap (Fig. 2), with only a few exceptions. Both species are limited almost exclusively to ultramafic rock formations (Borine 1983, Ramp 1979), and both usually grow on open, sunny, and continuously wet sites. *Hastingsia bracteosa* is common only on Eight Dollar Mt. near Selma, Oregon. It occurs elsewhere, however, at the mouth of Josephine Creek and the lower parts of Mikes Gulch, Days Gulch, and Fiddler Gulch. It has been observed only in *Darlingtonia californica* bogs. *Hastingsia atropurpurea* is common on Woodcock Mt. near O'Brien, Oregon, on Tennessee Mt., and the middle and upper parts of the Josephine Creek watershed. Along the east bank of Josephine Creek opposite the mouth of Fiddler Gulch, however, both species occur together in limited numbers in a small *Darlingtonia* bog. This bog is utilized as a source of spring water and is grazed intensively. Here, both species occur along the small creek that is shaded heavily by *Chamaecyparis lawsoniana* (A. Murr.) Parl.

Herbarium specimens of *H. atropurpurea* have been collected in the past in two isolated locations. In 1932, Applegate collected a single specimen on Eight Dollar Mt. [*Applegate 7266* (DS)]. Two

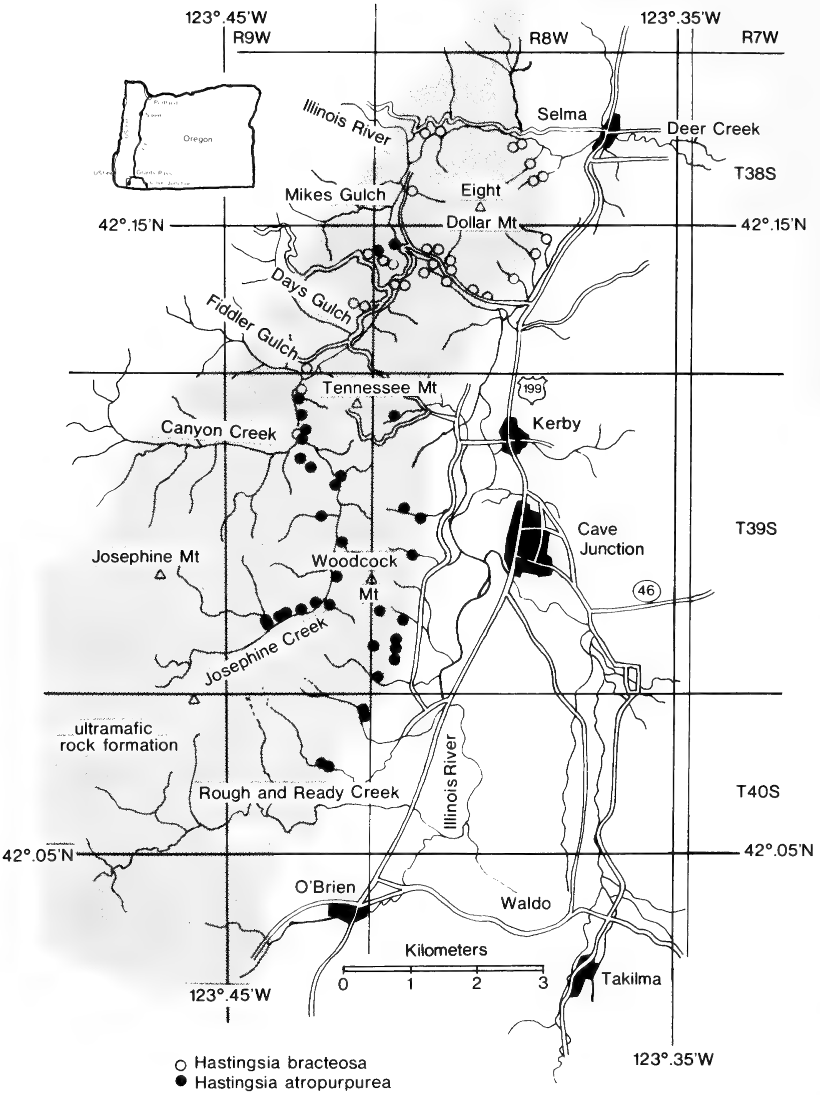


FIG. 2. Distribution map for *Hastingsia atropurpurea* and *Hastingsia bracteosa* near Cave Junction, southwestern OR.

other specimens were collected at a marsh along Josephine Creek [25 Jun 1930, *L. Leach s.n.* (OSC); 25 Jun 1930, *J. R. Leach 2968* (ORE)]. All three specimens were labeled *H. bracteosa.*

My first collection of *H. atropurpurea* was another specimen from an isolated locality. This specimen was found in the rocky flood plain of the Illinois River [17 Jun 1982, *Becking 820600* (CAS)]. In 1984, a few additional specimens of *H. atropurpurea* were collected in the Mikes Gulch area, immediately uphill from this latter collection site [3 Jul 1984, *Becking 840706* (HSC)].

Recommendation. Hastingsia bracteosa is listed as an endangered species (U.S. Fish and Wildlife Service, 1980). The same endangered species status should be given to *H. atropurpurea* because of its equally restricted distribution and sensitive habitat, which is threatened by mining and grazing.

ACKNOWLEDGMENTS

I am grateful for the excellent cooperation of the directors of many herbaria (CAS, DS, GH, HSC, JEPS, ORE, OSC, PUA, ROPA, RSA, SOC, UBC) for their hospitality during visits and the loan of herbarium specimens. I thank Dr. F. Raymond Fosberg (US), the reviewers, and the editor for constructive comments. I also thank Six Rivers National Forest, Eureka, CA; Siskiyou National Forest, Grants Pass and Cave Junction, OR; and the Bureau of Land Management, Medford, OR for logistical support and unpublished information. Valuable field assistance by James M. Lenihan and Esteban Muldavin and computer assistance by Steven A. Harris is acknowledged. A complete listing of measurements and specimen data is available upon request.

LITERATURE CITED

BECKING, R. W., J. A. LENIHAN, and E. MULDAVIN. 1982. Final report *Schoenolirion bracteosum.* Ecological investigations. Contract #43-9A4-0-1645. Six Rivers Nat. Forest, Eureka, CA.

BORINE, R. 1983. Soil survey of Josephine County, Oregon. U.S.D.A., Soil Conservation Service, Grants Pass, OR.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. L. BENT. 1975. SPSS: statistical package for the social sciences. McGraw-Hill, Inc., New York.

RAMP, L. and N. V. PETERSON. 1979. Geology and mineral resources of Josephine County, Oregon. Dept. Geology & Mineral Resources, State of Oregon. Bull. 100.

SHERMAN, H. L. 1969. A systematic study of the genus *Schoenolirion* (Liliaceae). Ph.D. dissertation, Vanderbilt Univ., Nashville, TN.

U.S. FISH AND WILDLIFE SERVICE. 1980. Endangered and threatened wildlife and plants: review of plant taxa for listing as endangered or threatened species. Federal Register vol. 45 No:242:82480–82569.

(Received 4 Mar 1985; revision accepted 16 Apr 1986.)

A NEW SPECIES OF *COURSETIA* (FABACEAE: ROBINIEAE) FROM THE CHIHUAHUAN DESERT, MEXICO

MATT LAVIN
Department of Botany, University of Texas,
Austin 78713

ABSTRACT

Coursetia insomniifolia is herein described from Coahuila, Mexico. It is the only member of the genus to inhabit the Chihuahuan Desert, and its relationship with other species of *Coursetia* is obscure. *Coursetia axillaris* and *C. glandulosa,* both inhabitants of northern Mexico and adjacent U.S.A., are probably its closest relatives.

During the course of a systematic revision of *Coursetia,* I detected an undescribed species in the form of a specimen collected by Thomas Van Devender in 1984 from Mexico. Initially I was not certain of the identity of the specimen, so I tentatively referred it to an undescribed species of *Genistidium* I. M. Johnston, an endemic genus of the Chihuahuan Desert. It was only after subsequent field investigations that I was able to conclude that the plant was a member of the genus *Coursetia.*

Coursetia insomniifolia Lavin, sp. nov.

Coursetiae axillari accedens sed foliolis lineari-ellipticis raro 2 saepe 4, ovariis glabris, rachidibus racemorum 0.2–4 cm longis, ramis nonfloriferis intricate ramosis apicibus debiliter spinosis (Fig. 1).

Shrubs 0.2–1.5 m high. Stems intricately branched, greenish, borne from a thick, knotty root system; branches glabrous, young growth with a whitish, finely appressed indumentum, the distal ends blunt to spine-tipped. Leaves paripinnate, 0.4–1.5 cm long, petiole and rachis canaliculate, exstipellate; leaflets (2)4 per leaf, linear-elliptic, 4–15 mm long, 1–3(4) mm wide, finely sericeous, rounded-apiculate distally, usually readily caducous from the persistent rachis; stipules subspinescent, 1–2 mm long; stipels obsolete. Inflorescence of axillary racemes, rachis of raceme 0.2–4 cm long, bearing at most 1 flower at anthesis per day; floral bracts linear, subulate, persistent to caducous, 1 mm long. Flower with a pedicel 1.5–2.5 mm long; calyx sericeous, the tube 2.5–3.5 mm deep, the lobes 2–3 mm long, triangular acuminate; petals all clawed, yellow; banner orbicular, emarginate, 7–9 mm long, gradually contracted into a short claw, aging slightly reddish, calluses and inflexed auricles slightly devel-

---

MADROÑO, Vol. 33, No. 3, pp. 182–185, 1986

oped; keel 7–9 mm long; wings 7–9 mm long; staminal tube 9+1 diadelphous; ovary nearly glabrous with 6–9 ovules; style 6–8 mm long, hairy the distal one-half to full length. Legume glabrous, 1–9 seeded, 1–3 cm long, 3.5–4.5 mm wide. Seeds 2.4–3.5 mm diameter, mottled, accumulating canavanine (here reported). Chromosome number $n = 8$ (here reported from *Lavin et al. 5732*).

TYPE: Mexico, Coahuila, Puerto de Ventanillas, 42 km n. of San Pedro along Hwy 30, 26°02′34″N, 102°44′23″W, 1450 m, 18 Oct 1985, *Lavin, Nesom and Scott 5732* (Holotype: MEXU; isotypes: ARIZ, MO, NY, TEX, US).

PARATYPE: Mexico, Coahuila, Puerto de Ventanillas, 25 mi ne. of San Pedro on Mexico Hwy 30, 25 Oct 1984, *T. Van Devender et al. 84-577* (TEX).

Distribution. Coursetia insomniifolia is known only from the type locality and vicinity in Coahuila, Mexico (Fig. 1). The population at this locality is large and has a great diversity in age-class. The plants are restricted to sloping limestone bed-rock where they are dominant with *Agave lechuguilla* Torr., *Heteropogon contortus* (L.) Beauv., *Janusia gracilis* A. Gray, *Carlowrightia serpyllifolia* A. Gray, and *Opuntia* spp.

Discussion. The single known population was in flower and fruit in late October of 1984 and 1985. Flowering apparently begins with fall rains during September and continues through October.

The seedling morphology is typical of the genus: germination is epigeal; the cotyledons are foliar; the eophyll is unifoliolate; the metaphylls are similar to mature leaves; and the leaf rachis of all leaves is canaliculate and exstipellate. Axillary branching occurs very early during development with the base of the branch being very thick (grown from seed of *Lavin et al. 5732*).

I originally thought *Coursetia insomniifolia* pertained to *Genistidium* because both 1) are multi-branched shrubs with photosynthetic bark, 2) possess small leaves with leaflets that have inconspicuous venation and do not undergo nyctinastic movements, 3) have yellow flowers of approximately similar dimensions, and 4) occupy a similar geographic region (Fig. 1). *Coursetia insomniifolia* differs most notably from *Genistidium,* however, by 1) its 4-foliolate, paripinnate leaves (i.e., lacking a terminal leaflet), 2) the inflorescence that is an indeterminant, simple, axillary raceme, and 3) the legume with an endocarp that at maturity forms a compartment for each seed. The latter two features are unique to *Coursetia* (Lavin in press). *Genistidium* possesses 1–3 foliolate leaves, an inflorescence that is reduced to a single (rarely two) axillary flower, and a legume with an endocarp that does not compartmentalize the seeds. Although the chromosome number of *Genistidium* ($2n = 16$, Goldblatt 1981) is the same as that for *Coursetia,* the similarities of *C. insom-*

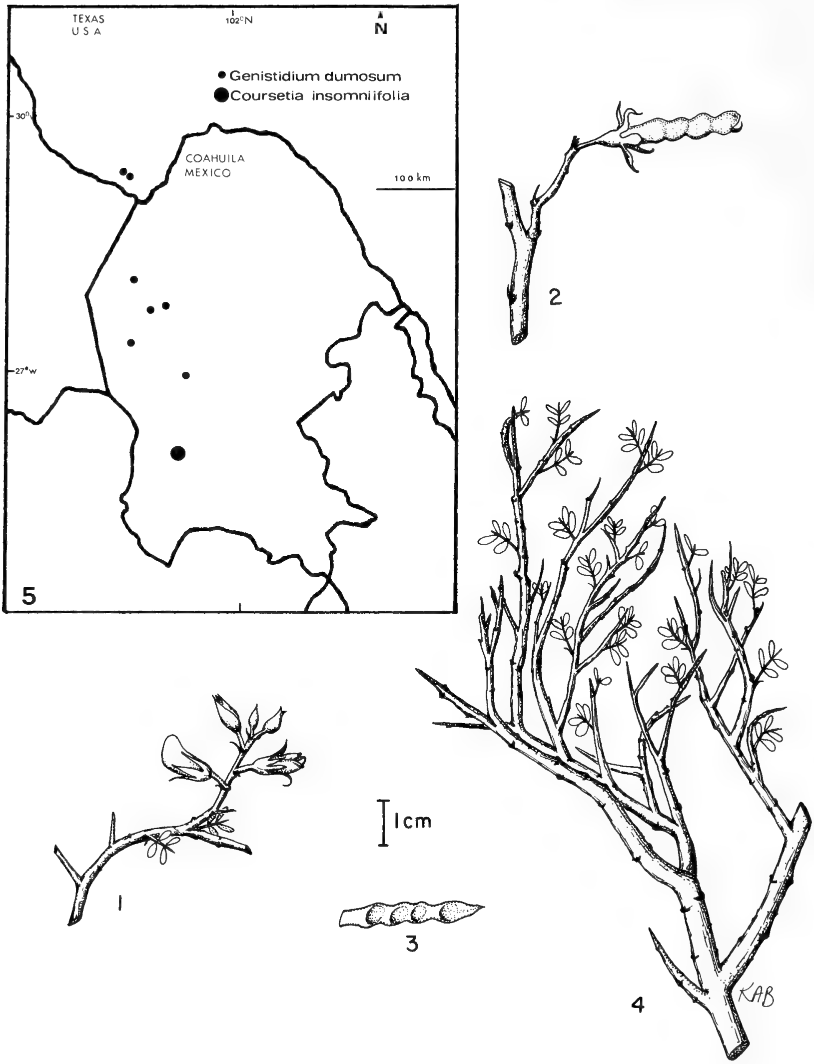


Fig. 1. *Coursetia insomniifolia.* 1. Inflorescence. 2. Infructescence. 3. Inside of pod valve showing seed compartments. 4. Habit. 5. Distribution.

niifolia and *Genistidium* are perhaps the result of convergence. The possibility of a close relationship between *Genistidium* and *C. insomniifolia* remains unknown, but the reduction of the inflorescence, pod, and leaves of *Genistidium* precludes such inferences from these characters.

Coursetia insomniifolia is readily distinguished from all other species of the genus by its very small, 4-foliolate leaves. Such leaves are rivaled only by the distantly related *Notodon,* a Cuban genus that also possesses small, 4-foliolate, paripinnate leaves. *Coursetia insomniifolia* is named for its leaves that do not undergo nyctinastic movements (i.e., "sleep movements"). All other species of the genus that possess paripinnate leaves have a peculiar type of evening leaf movement in which the leaflets fold back strictly along the rachis exposing only the abaxial surface.

Coursetia insomniifolia also possesses subspinescent stipules and flowers that are yellow at anthesis, two features that are otherwise unknown in Mexican *Coursetia.* This species probably has its closest relatives in *Coursetia axillaris* Coult. & Rose and *C. glandulosa* A. Gray; both species are inhabitants of northern Mexico and adjacent U.S.A. This supposition, however, is based only on the paripinnate leaf condition and the similarity of their geographical ranges.

Key to Mexican *Coursetia* with Paripinnate Leaves

1. Leaflets (6)8–22 per leaf, orbicular-elliptic; mature leaves 2.5–6 cm long; flowers predominantly whitish at anthesis; racemes commonly several per leaf axil and clustered on short shoots; anthesis occurring before the leaves.
    2. Inflorescence, ovary, and pod glandular-sericeous; axillary short shoots bearing 2–4 racemes; shrubs and trees with long slender stems, 1–8 m long; Pacific cordilleras from Arizona s. to Oaxaca .... *C. glandulosa* A. Gray
    2. Inflorescence, ovary, and pod white sericeous; axillary short shoots bearing 1–2 racemes; short, commonly gnarled shrubs of the Tamaulipan thorn-scrub of ne. Mexico and adjacent Texas .... *C. axillaris* Coult. & Rose
1. Leaflets (2)4 per leaf, linear-elliptic; mature leaves 0.4–1.5 cm long; flowers yellow at anthesis; racemes single in leaf axils; anthesis occurring with mature leaves; Chihuahuan Desert .... *C. insomniifolia* Lavin

ACKNOWLEDGMENTS

Financial assistance was supported by the National Science Foundation (BSR-8421262). I am especially grateful to Thomas Van Devender for sharing his important collection. I also thank B. L. Turner and A. Whittemore for useful comments, Katie Bear for the illustration, Marshall Johnston for the Latin diagnoses, and the following herbaria for loan of pertinent material: ARIZ, GH, LL, MEXU, MO, NY, TEX.

LITERATURE CITED

GOLDBLATT, P. 1981. Cytology and the phylogeny of the Leguminosae. *In* R. M. Polhill and P. H. Raven, eds., Advances in legume systematics, part 1, p. 427–463. Royal Botanic Gardens, Kew.

LAVIN, M. (in press). A cladistic analysis of the tribe Robinieae (Papilionoideae, Leguminosae). *In* C. H. Stirton, ed., Advances in legume systematics, part 3. Royal Botanic Gardens, Kew.

(Received 3 Dec 1985; revision accepted 18 Apr 1986.)

CHROMOSOME COUNTS IN *ERIOPHYLLUM* (COMPOSITAE: HELENIEAE)

JOHN S. MOORING
Biology Department, University of Santa Clara,
Santa Clara, CA 95053

ABSTRACT

Chromosome numbers, mostly from microsporocytes, were obtained from greenhouse- or garden-grown seedlings or transplants. Chromosome numbers of $2n = 7\text{II}$ were found in *Eriophyllum nubigenum* and in *E. nubigenum* var. *congdonii,* and of $2n = 8\text{II}$ in varieties and intermediates of the *E. lanatum* complex: *croceum, grandiflorum, hallii, integrifolium,* and *obovatum.* In one population of *E. lanatum* var. *integrifolium* and in a population intermediate between vars. *achillaeoides* and *arachnoideum,* $2n =$ ca. 16II. Root tip counts in another population of var. *integrifolium* and in two populations of var. *leucophyllum* showed that $2n = 16$. The counts for *E. nubigenum* and *E. lanatum* var. *hallii* are first reports, the others supplement previous reports.

These chromosome counts are part of a long-term study of *Eriophyllum,* especially *E. lanatum.* Three of the individuals examined were transplanted from natural populations, the others were greenhouse- or garden-grown from fruits collected in nature. Microsporocytes or, in five cases, root tips were squashed in acetocarmine, the former after fixation in 1:3 acetic alcohol, the latter after 6–8 minutes in 1:1 concentrated HCl–95% ethanol (Mooring 1975). The counts for *E. lanatum* (Pursh) Forbes var. *hallii* Constance and *E. nubigenum* Greene are first reports.

The *Eriophyllum lanatum* complex has diploid, tetraploid, hexaploid, and octoploid populations (Mooring 1975). The diploid ($2n = 8\text{II}$ or $2n = 16$) counts from vars. *croceum* (Greene) Jepson, *grandiflorum* (Gray) Jepson, *integrifolium* (Hook.) Smiley, *leucophyllum* (DC.) W. R. Carter, *obovatum* (Greene) Hall, and certain populations intermediate between vars. *achillaeoides* (DC.) Jepson, *arachnoideum* (Fisch. & Avé-Lall.) Jepson, and *grandiflorum,* and the $2n =$ ca. 16II counts for var. *integrifolium* and an *achillaeoides-arachnoideum* intermediate (Table 1) supplement those reported earlier (Mooring 1966, 1973, 1975). These counts come from heretofore unsampled populations and are congruent with the geographic and taxonomic distribution of ploidy levels in this complex (Mooring 1975). The single count of $2n = 8\text{II}$ for *E. lanatum* var. *hallii* (Table 1) is a first report for this rare taxon. It should be corroborated by additional counts from the only known population, discovered by Clifton Smith in 1975, and, if possible, by counts from the other

MADROÑO, Vol. 33, No. 3, pp. 186–188, 1986

TABLE 1. CHROMOSOME COUNTS IN *Eriophyllum*. All populations except that of *E. lanatum* var. *hallii* were collected by the author, and collection numbers are my own unless otherwise noted. Voucher specimens have been deposited in the University of Santa Clara Herbarium. Numbers in parentheses indicate number of individuals counted, if more than one; locations are approximate. An asterisk shows cases where the plant died before it could furnish a herbarium specimen.

Eriophyllum lanatum (Pursh) Forbes
- var. *croceum* (Greene) Jepson. $2n = 8\mathrm{II}$. CA: Fresno Co., Badger, *3452*; Tulare Co., Pinehurst, *3485*.
- var. *grandiflorum* (Gray) Jepson. $2n = 8\mathrm{II}$. CA: Mariposa Co., Pilot Peak, *3544*; Sierra Co., Downieville, *3510*; Tuolumne Co., Long Barn*; Clark Fork Campground*.
- var. *hallii* Constance. $2n = 8\mathrm{II}$. CA: Santa Barbara Co., Cuyama Valley, *Clifton Smith s.n.*, 6 June 1974 (UC).
- var. *integrifolium* (Hook.) Smiley. $2n = 16$ (root tip counts). CA: Alpine Co., Highland Lakes* (2). $2n = 8\mathrm{II}$. CA: Lassen Co., Antelope Mountain*. OR: Union Co., Elgin, *2487*. $2n =$ ca. $16\mathrm{II}$. ID: Blaine Co., Carey, *2476*.
- var. *leucophyllum* (DC.) W. R. Carter. $2n = 16$ (root tip counts). WA: Clallam Co., Hurricane Ridge*; Skagit Co., Rosario Beach*.
- var. *obovatum* (Greene) Hall. $2n = 8\mathrm{II}$. CA: San Bernardino Co., Snowbear*; Running Springs, *2528*.

INTERMEDIATES

- var. *achillaeoides* (DC.) Jepson.–var. *arachnoideum* (Fisch. & Avé-Lall.) Jepson. $2n =$ ca. $16\mathrm{II}$. CA: Sonoma Co., Mark West Creek, *3401*.
- var. *achillaeoides* (DC.) Jepson.–var. *grandiflorum* (Gray) Jepson. $2n = 8\mathrm{II}$ (2). CA: Tuolumne Co., Groveland, *3541*.
- var. *arachnoideum* (Fisch. & Avé-Lall.) Jepson.–var. *grandiflorum* (Gray) Jepson. $2n = 8\mathrm{II}$. CA: Humboldt Co., Carlotta, *3500*.

Eriophyllum nubigenum Greene. $2n = 7\mathrm{II}$ (6). CA: Mariposa Co., Pilot Peak, *3529*.
- var. *congdonii* (Bdg.) Constance. $2n = 7\mathrm{II}$ (4). CA: Mariposa Co., Trumbull Peak, *3525*.

---

known sites, where collections have not been made since 1905 (Constance 1937).

The counts of $2n = 7\mathrm{II}$ for *Eriophyllum nubigenum* Greene var. *congdonii* (Bdg.) Constance agree with reports by Carlquist (1956) and Johnson (1978) for Merced River populations near El Portal, but come from a population 1000 meters above the river ones, and only 11 km from the Pilot Peak population of *E. nubigenum*, where counts of $2n = 7\mathrm{II}$ were obtained (Table 1). This is a first report for that rare taxon. My crosses between these two taxa yielded large numbers of achenes with embryos, and the relationship between these two taxa will be the subject of a future report.

ACKNOWLEDGMENTS

I thank Dr. Lincoln Constance for sending me viable fruits of *Eriophyllum lanatum* var. *hallii*, and Drs. Carl Sharsmith and Jan van Wagtendonk for assistance in obtaining fruits of *E. nubigenum* and *E. nubigenum* var. *congdonii*. John Strother's eye for verbiage shortened the manuscript; I thank him also.

LITERATURE CITED

CARLQUIST, S. 1956. On the generic limits of *Eriophyllum* (Compositae) and related genera. Madroño 13:226–239.

CONSTANCE, L. 1937. A systematic study of the genus *Eriophyllum* Lag. Univ. Calif. Publ. Bot. 18:69–136.

JOHNSON, D. 1978. Systematics of Eriophyllinae (Compositae). Ph.D. dissertation, Univ. California, Berkeley.

MOORING, J. 1966. Chromosome numbers in the *Eriophyllum lanatum* (Compositae, Helenieae) complex. Madroño 18:236–239.

———. 1973. Chromosome counts in *Eriophyllum* and other Helenieae (Compositae). Madroño 22:95–97.

———. 1975. A cytogeographic study of *Eriophyllum lanatum* (Compositae, Helenieae). Amer. J. Bot. 62:1027–1037.

(Received 9 Dec 1985; revision accepted 28 Feb 1986.)

ANNOUNCEMENT

A NEW SECTION FOR MADROÑO

Beginning with Volume 33, each issue of MADROÑO will contain an editorial page on which comments by the editor, invited contributions, unsolicited letters, and other remarks will be featured. This editorial page will serve as a vehicle for communication among our members and could include, for example, opinions of authorities on current trends in botany, rebuttals or comments on papers published in MADROÑO, letters from the President of our society, and other noteworthy communications. The editors invite all members to participate in this forum; however, all editorials will be published at the discretion of the editors.

SECONDARY SUCCESSION AND THE FATE OF NATIVE SPECIES IN A CALIFORNIA COASTAL PRAIRIE COMMUNITY

THEODORE C. FOIN
Division of Environmental Studies, University of California,
Davis 95616

MARY M. HEKTNER
U.S. National Park, Service, Redwood National Park,
Orick, CA 95555

ABSTRACT

Secondary succession in former sheep pastures in the northern California coastal prairie favors cover dominance by perennials, especially grasses. Studies of secondary succession at Sea Ranch, Sonoma County, show that the relative cover is dominated increasingly by *Anthoxanthum odoratum,* an introduced perennial grass. Native species are not successful at increasing their cover during succession and are unlikely to regain cover dominance in the coastal prairie.

Historically, large parts of the California coastal prairie were used for grazing by domestic animals. One of the main effects of grazing in this grassland is a change in species composition, accomplished by selection against grazing-intolerant species. Grazing has been implicated as a major factor in the change of vegetation in the Central Valley (Burcham 1957), and is likely to have been important in the coastal zone as well, although such changes have never been documented.

Secondary succession may be defined as the predictable sequence of species replacements occurring after a disturbance such as grazing defoliation. It differs from primary succession only in that the latter is assumed to start from a substrate that has not been occupied previously by any vegetation. Secondary succession is the key ecological process governing change in species composition once grazing pressure is reduced or eliminated, and thus successional studies may reveal whether or not the natural recovery process can ameliorate the effects of grazing (see McIntosh 1980).

The classic expectation of the effects of secondary succession are based on early work by Clements (1916), who argued that succession would favor native species, which are well adapted to each other and their physical environment. Invaders and weedy species, however, would be crowded out eventually and recovery to the original climax vegetation would be complete. More recently, Heady and others (1977) have predicted that "introduced plants will continue

MADROÑO, Vol. 33, No. 3, pp. 189–206, 1986

to be abundant on many hectares of coastal prairie, but succession will apparently move rapidly toward dominance of perennial grasses if land management practices are suitable." This is a modified Clementsian view, which recognizes that invading species may not be so easily displaced. Heady refers specifically to the replacement of introduced annuals by native perennial grasses in the coastal prairie. Although introduced Mediterranean annuals are commonly treated as the dominant vegetation of interior valleys, they have been as abundant in the coastal prairie flora, at least in range systems.

Studies in secondary succession would appear to be useful in California prairies for several basic and applied reasons. There are a number of succession models proposed (e.g., Connell and Slatyer 1977, Shugart 1984) that could be tested using California vegetation. On the other hand, range and reserve managers could use such information in management and restoration activities. Despite the obvious need, secondary succession in the coastal prairie is not well known at present. Those few studies that exist suggest that native species may dominate the vegetation as succession proceeds. Huffaker and Kennett (1959) showed that perennial grasses, especially one native species (*Danthonia californica*) replaced an introduced perennial (*Hypericum perforatum*) known as Klamath weed, following successful biological control by the Klamath weed beetle (*Chrysolina hyperici*) in the coastal prairie of Humboldt County.

Elliott and Wehausen (1974) analyzed cover in three plots with different grazing pressure in Point Reyes National Seashore. Their data predict that the coastal shrub *Baccharis pilularis* and the native perennial bunchgrass *Deschampsia holciformis* would increase during succession. Lathrop and Gogan (1985) surveyed the Tule Elk Range at Tomales Point, immediately to the north of the area studied by Elliott and Wehausen. They argued that shrubs would dominate secondary succession in wind-protected areas, but that perennial grasses would also increase (particularly the native perennial *Stipa pulchra* Hitchcock). The invasion of prairie by northern coastal scrub is indicated by their data, and is more strongly suggested by the work of McBride and Heady (1968) and McBride (1974). It is not clear, however, that the coastal prairie is a seral stage whose climax is ultimately shrub or forest dominated.

Despite the evidence suggesting the successional superiority of native species over introduced species, it is far from conclusive. A number of counter examples, demonstrating the tenacity of invading species, also exists; perhaps the best example is that of *Bromus tectorum* in the Great Basin (Harris 1967, Mack 1981). The literature pertaining to the emergence of natives during succession in California prairies also does not support the theory. White (1967) claimed that *Stipa pulchra* should be one of the climax dominants in the oak woodland at Hastings Reservation in Carmel Valley, and Burcham

(1957) hypothesized that the same species dominated the primeval Central Valley prairies. On the other hand, Wester (1981) has used historical records to argue that perennial grasses did not dominate the inland prairies now dominated by introduced annuals, except in wet places. Bartolome and Gemmill (1981) showed experimentally that *Stipa pulchra* was competitively inferior to *Bromus mollis* at high densities. Their evidence makes it clear that there may be great differences between species, and that being "native" does not necessarily confer a competitive advantage over introduced species.

Even the theoretical expectation is fragile because it was based on a number of assumptions that have been proven erroneous, the largest of which was the assumption of evolutionary advantage in a highly coevolved plant community (for a good discussion of the contribution of Clements to modern plant ecology see McMahon 1980). These arguments may be used to challenge the importance of the community in succession and to emphasize the importance of the population dynamics of "key" species in governing the outcome of succession (Foin and Jain 1977, Westoby 1979, McIntosh 1981).

To evaluate the dominance of native versus introduced plants in secondary succession of coastal prairie, we conducted chronosequential studies at Sea Ranch, Sonoma Co., California (38°40′N, 123°24′W) in 1974. An earlier paper (Hektner and Foin 1977) examined differences in the vegetation in different areas of the Sea Ranch coastal prairie using the data obtained in the summer of 1974. The present paper reports the results of succession based on the 1974 census and additional samples taken in 1975–1978. Detailed information on site conditions, species present, and land use history may be found in the 1977 paper.

STUDY AREAS

Sea Ranch is a recreational subdivision 180 km north of San Francisco. It occupies 16 km of the coastal terrace from Stewarts Point northward to the Mendocino Co. line. Homesites have been developed such that large areas of meadow and forest have been preserved as permanent open space. Sea Ranch includes two uplifted marine terraces with sandy loams (Baywood and Rohnerville series: U.S. Dept. Agr. 1972) overlying sandstone and basalt. All study areas reported in this paper are located in the commons areas of the first terrace (that terrace adjacent to the coast) and were protected from grazing, fire, mowing, and other overt management for the duration of the study. Disturbance of the vegetation was not excluded completely because soil disturbance by gophers and moles, grazing by insects, rabbits, deer, and mice, and limited trampling by hikers were all present. Three study areas were sampled, the names of which

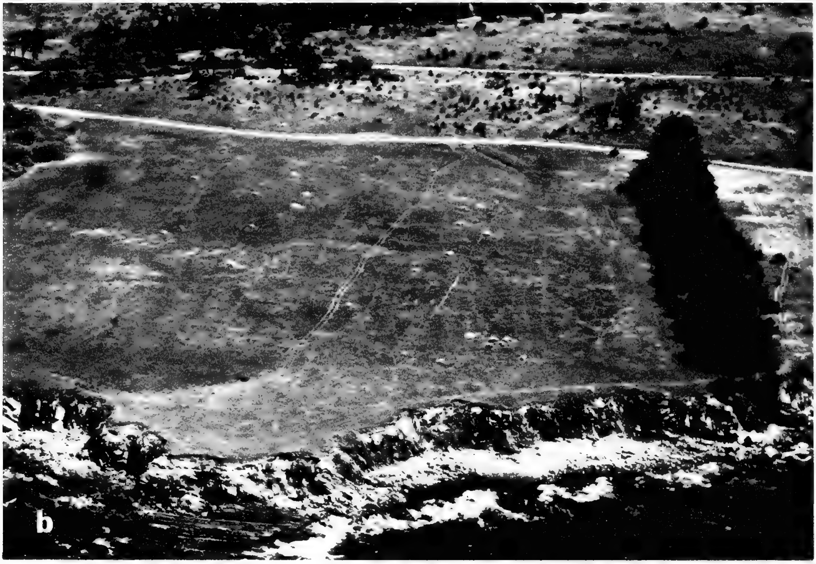


Fig. 1a. Photograph of Lone Tree Meadow taken in June 1984. The photograph was taken from the top of the slope looking to the northwest. The white stakes mark the location of soil moisture monitoring stations. The light-colored vegetation in the foreground is an annual-*Rytidosperma* patch. The vegetation behind it is the wet-type (*Deschampsia-Holcus-Anthoxanthum*). The vegetation to the left side is mostly *Anthoxanthum odoratum.*

Fig. 1b. Aerial photograph of Buck Meadow looking east-northeast, 8 Jul 1975. There is a prominent hedgerow (composed of Monterey cypress) to the right. The light dots are scattered *Lupinus arboreus* Sims. One set of vehicle tracks and several trails made during the 1974 vegetation survey are evident in the photograph.

are traditional ones used by the previous owner of the ranch (the late E. J. Ohlson).

Lone Tree Meadow. This study area is a 160 × 80 m rectangular grid located on a northwest-facing slope, approximately 300 m from the ocean to its western boundary (Fig. 1a). The site is unprotected from the prevailing northwesterly winds. It was the one area of the former sheep ranch that was used most intensively, particularly for year-round herds of ewes and their lambs. Estimates of stocking rates are not available.

Buck Meadow. This study area is a 200 × 300 m rectangle with the seaward edge 100 m from the coast bluff (Fig. 1b). This site is flat, with no pronounced slope. It was named for its grazing history: it was used as the ram (buck) pasture. Ohlson noted that ram densities were always low, particularly in later years when stock densities were falling rapidly.

Stable Meadow. This site is the only study area available on Sea Ranch that is still grazed. The area is fenced-off and used as a pasture and paddock for horses. Use rates are low but continuous, on the order of 2 animals per ha. Vegetative biomass is low, making the site visually distinctive, and there appears to be at least as much damage from hooves breaking the soil surface as from defoliation. The area sampled (50 × 50 m) is approximately 120 m from the coastal bluff, in the center of the pasture, with a gentle west-facing slope towards the ocean. Other than its present use, Stable Meadow is very similar in slope and aspect to Buck Meadow.

The Sea Ranch lands were used for grazing purposes from the late 19th century to 1968. Small parts were used experimentally for agriculture, but those experiments were unsuccessful. In 1965, when the ranch was sold for development, sheep were removed progressively from south to north, until the last sheep were sold in 1968. Lone Tree and Buck meadows remained under grazing until 1968.

METHODS

Sampling procedure. The sampling methodology followed in this study used line transects established for the initial survey in 1974. Complete details of the methodology are found in Hektner and Foin (1977). In brief, line transects were established randomly, one transect each 10 m, and sample locations were taken randomly, one for each 10 m of transect length. Cover estimations were made using the Domin index, as modified by Major from Evans and Dahl (1955), using 0.25 m^2 circular quadrats.

Stable Meadow was sampled using 30 quadrats in 1978 to establish a frame of reference for the other two sites. Lone Tree Meadow was sampled three times (1974, 1976, 1978) at 143 quadrat locations.

Buck Meadow was sampled twice (1975, 1978) at 242 quadrat locations.

Two possible problems exist in the methodology used. First, placement of the quadrat sampling ring was not centered on the permanent marking stake (which was on the transect line), but was offset to avoid sampling pathways. This procedure did not permit precise relocation of the quadrat in subsequent censuses. Second, all sites were sampled late in the summer (August and September). This is an artifact of the first census (1974) because all later censuses were made at the same time to maximize year-to-year comparability. Sampling earlier in the summer, when the grass species were clearly identifiable, but annuals were more evident in the field, would have been preferable. Although annuals, especially forbs, were undoubtedly underrepresented in our results, it is the comparative aspect and trend in time that we required. These two aspects of the data are least sensitive to absolute bias in cover estimates.

Treatment of cover data. The Domin value of each species in each quadrat was converted first from its index value, each of which covers a range of percent cover, to the midpoint of the range for that value. This follows the procedure used by Hektner and Foin (1977). The converted Domin values were then calculated to yield four indices: *absolute cover,* the sum of converted Domin values for each species over all quadrats; *relative cover,* the percent representation of a given species over all quadrats as a fraction of the cover attributable to all species; *mean cover,* the mean absolute cover per quadrat; and *adjusted mean cover,* the mean absolute cover calculated only for those quadrats in which the species occurred.

Error bars were taken as ± 2 s.e. (standard errors) on mean cover. Nonoverlapping error bars were used as tests of significant differences between means with $\alpha = 0.05$. This procedure is more conservative, i.e., it has smaller Type I error, than standard parametric confidence limits unless $\text{df} \leq 5$ (see Steele and Torrie 1960). None of the comparisons was based on so few degrees of freedom.

Assignments of life form were made using Reed et al. (1963). Five classes were used: annual forbs, perennial forbs, annual grasses, perennial grasses, and "other life forms". The last category is composed primarily of three species: *Pteridium aquilinum* var. *pubescens, Rubus ursinus,* and *Linum bienne.* All nomenclature follows Munz (1973), except for *Deschampsia holciformis* (Crampton 1974) and *Rytidospermum pilosum* (=*Danthonia pilosa*).

RESULTS

Successional Changes in Life Form Composition

Species data from the three censuses of Lone Tree Meadow are aggregated into life form groups and plotted in Fig. 2. This plot

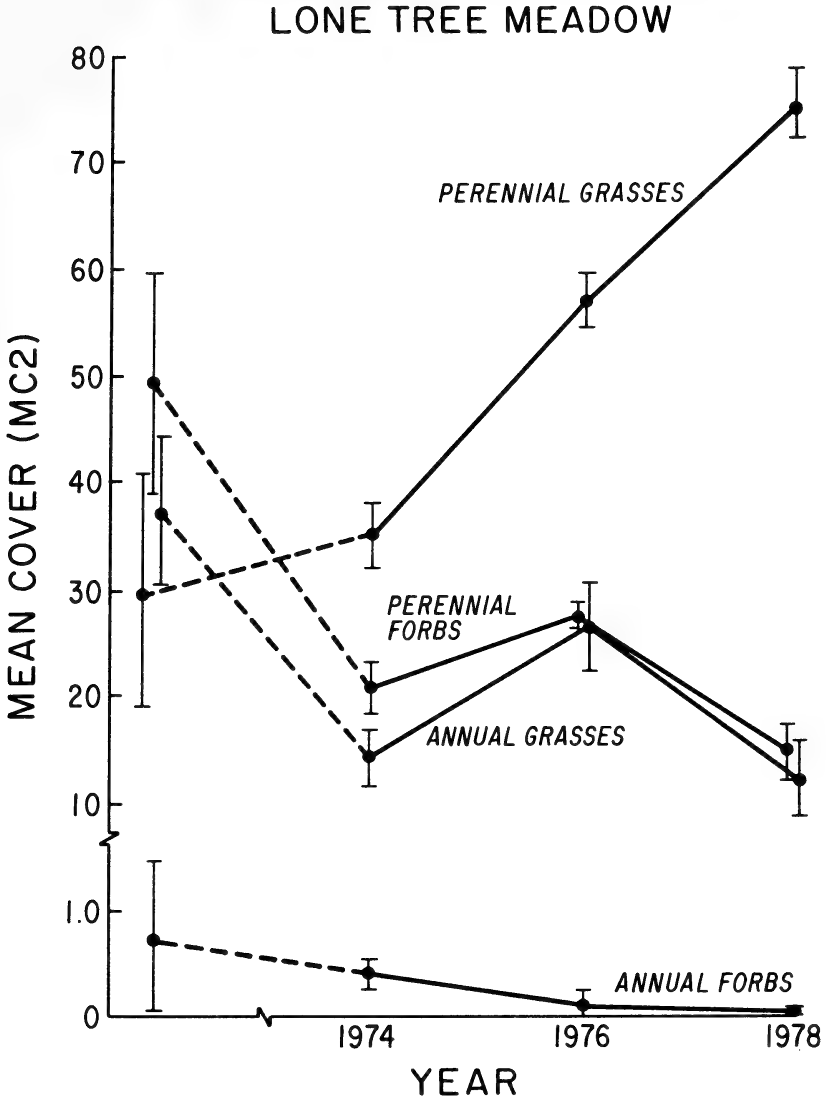


FIG. 2. Mean cover trends (MC2) for life forms in Stable Meadow (leftward points) and Lone Tree Meadow, 1974–1978. Error bars are ±2 standard errors.

shows mean cover for each of the major life forms except "other life forms". The three censuses in Lone Tree Meadow are plotted with the data from Stable Meadow displayed at the extreme left. The Stable Meadow data are included to provide an indication of the structure of the presuccessional coastal prairie vegetation. Because these data are only an indication of life form mean cover values for Lone Tree Meadow, these points are connected to the 1974 data with dashed lines. In any case, the extrapolations must be viewed cautiously, because environmental differences between sites and differences between sheep and horse grazing could be very important (Harper 1977). Note that annual forbs comprise so little of the total cover that the ordinate in Fig. 2 must be broken in order to include them. Two s.e. confidence intervals do not overlap in the following comparisons: 1) the mean cover of annual forbs decreased from 1974–1978; 2) annual grasses increased from 1974 to 1976 and decreased from 1976–1978; 3) perennial forbs increased from 1974 to 1976, and decreased from 1976–1978 and from 1974–1978; and 4) perennial grasses increased in cover at each sampling period. Lone Tree Meadow had less cover for annual grasses and perennial forbs than Stable Meadow for all three sampling periods, and had greater cover in perennial grasses for 1976 and 1978.

Figure 3 shows the cover data for Buck Meadow arranged in the same fashion as the data in Fig. 2. Using the same comparisons, annual grasses showed a decrease in cover, whereas perennial grasses showed an increase over the period 1975 to 1978. Neither forb group showed a significant change over this period. Comparison to Stable Meadow data shows (1) no significant differences for annual forbs; (2) significantly higher cover for annual grasses in Buck Meadow in 1978; (3) significantly lower cover in perennial forbs for both years; and (4) a significant difference for perennial grasses by 1978.

Comparison of Figs. 2 and 3 illustrates that trends in life forms in each site were similar. Annual forbs were not common in either site and did not have significantly higher cover in Stable Meadow. This situation, however, is likely to be an artifact of the timing of sampling, because adjacent sheep meadows can support a variety of annual forbs, especially when heavily grazed. Both annual grasses and perennial forbs decreased during succession, which is particularly evident in the Lone Tree Meadow data. Perennial grasses increased significantly to similar cover values in both sites. Lone Tree and Buck Meadows showed decreasing cover in perennial forbs and, with time, more perennial grasses than Stable Meadow.

This trend can be seen more easily in a plot of relative cover (Fig. 4). These data are separate estimates for Lone Tree and Buck Meadows, except for 1978, which is the arithmetic average for both sites. The figure shows a decrease in relative cover for all categories and for bare ground, except for perennial grasses and "other life forms". Bare ground never exceeded 5% relative cover at Sea Ranch, and decreased to less than 1% of the relative cover in the 1978 censuses.

Successional Changes in Species Composition

Principal seral dominants during succession. The majority of the species encountered in the quadrats were infrequent and low in

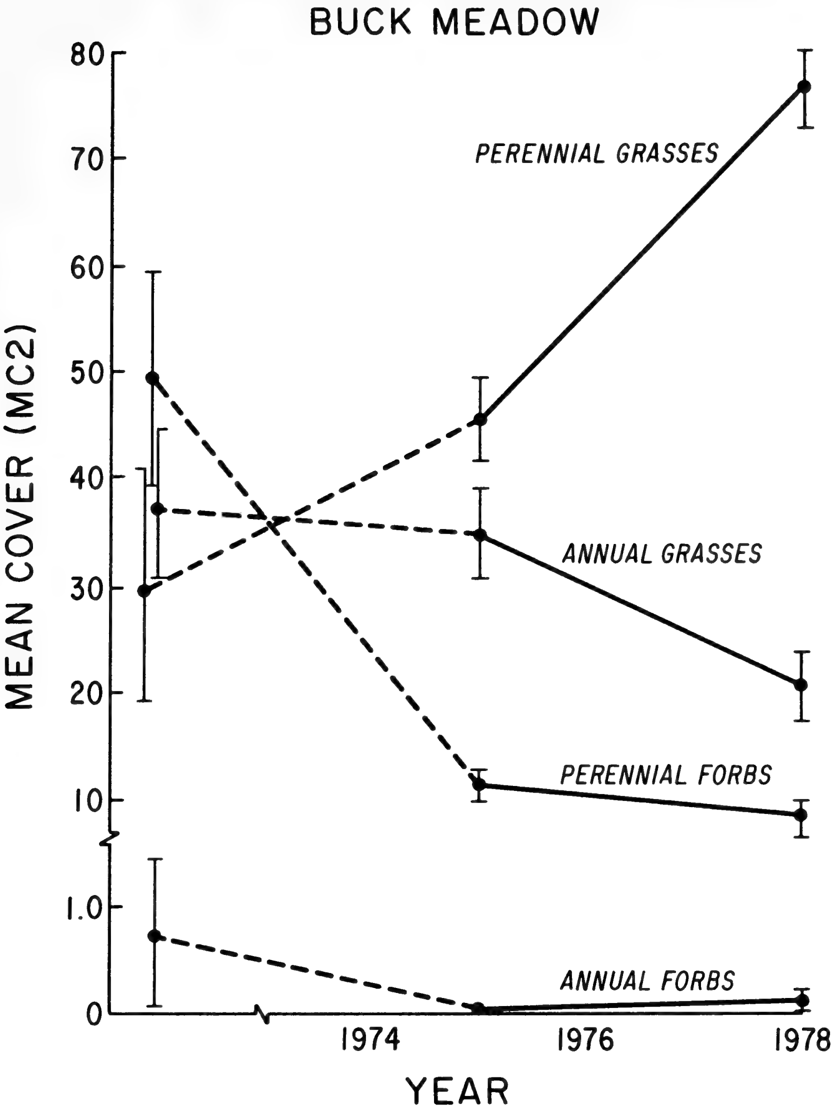


FIG. 3. Mean cover trends for Stable Meadow compared to Buck Meadow, 1975–1978. Arrangement of this figure corresponds to that of Fig. 2.

cover. We used two criteria to single out those species that had high cover values at one census or another: 1) any species that occurred in five or more quadrats at any one of the three sites in one or more census periods, and 2) that also had 1% relative cover in the site for which criterion (1) was met. Application of these criteria excludes all annual forbs and reduces the list to 19 species (Table 1).

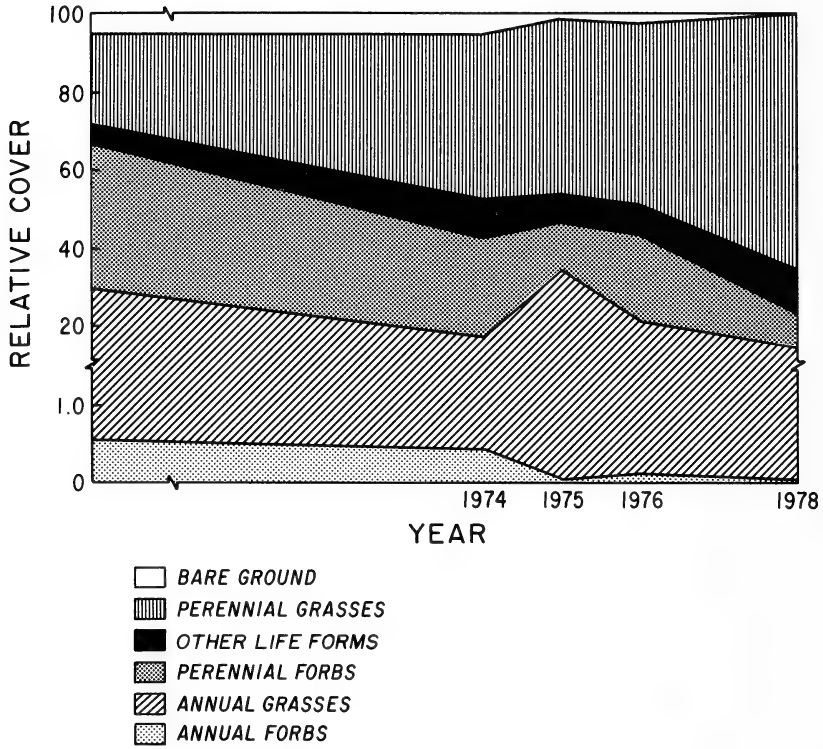


FIG. 4. Relative cover assigned to all life forms and to bare ground for Lone Tree and Buck Meadows; 1978 is the average for both sites. Relative cover for Stable Meadow is given at the left end of the abscissa, as done in Figs. 2 and 3.

The species in Table 1 are arranged by life form. Absolute cover (AC) and frequency in sample quadrats are tabulated for all 19 species meeting the criteria outlined above for each survey of the three sites sampled. There is sufficient consistency among the results shown in Table 1 to suggest successional patterns in the species as well as the life forms. The species that had high frequency also had high absolute cover. The dominants of early and later stages in succession are readily identified from this table, assuming Stable Meadow represents the starting point. *Cynosurus echinatus* is an example of an annual that showed high cover and frequency in Stable Meadow and in early surveys of the other two sites. Other examples of characteristic species of earlier successional stages, which followed the termination of grazing, include *Plantago lanceolata, Linum bienne, Lolium perenne,* and *Rytidosperma pilosum.*

Changes in species composition may be identified by considering significant changes in mean cover (Table 2). All but one of the early

TABLE 1. IMPORTANT SPECIES IN THE SUCCESSIONAL SEQUENCE IN THE COASTAL PRAIRIE AT SEA RANCH. N = native species; I = introduced species. Frequency is in quadrats and absolute cover is the sum of mean Domin values for each species.

	Lone Tree Meadow						Buck Meadow				Stable Meadow	
	Frequency			Absolute cover			Frequency		Absolute cover		Frequency	Absolute cover
Species	1974	1976	1978	1974	1976	1978	1975	1978	1975	1978	1978	1978
Annual grasses												
Aira caryophyllea (I)	90	51	31	345	179	368	104	21	422	128	5	47
Bromus mollis (I)	66	54	18	58	1399	118	171	101	6722	2458	25	254
Cynosurus echinatus (I)	94	83	44	1538	1144	124	62	9	127	49	20	494
Hordeum leporinum (I)	0	0	0	0	0	0	0	0	0	0	5	188
Vulpia bromoides (I)	43	25	31	26	382	1182	169	69	1128	2064	20	114
Perennial forbs												
Corethrogyne californica (N)	1	0	0	2	0	0	18	4	564	204	0	0
Hypochoeris radicata (I)	42	42	7	102	398	78	53	12	62	46	4	18
Iris douglasiana (N)	26	31	33	375	450	709	0	1	0	42	2	50
Plantago lanceolata (I)	106	100	76	2284	2415	1048	195	92	1530	566	27	1402
Rumex acetosella (I)	16	12	3	16	29	6	102	69	454	472	0	0
Perennial grasses												
Anthoxanthum odoratum (I)	102	111	131	2062	4514	7540	170	192	6298	10,038	0	0
Rytidosperma pilosum (I)	91	60	46	1210	936	638	184	159	3272	5598	9	118
Deschampsia holciformis (N)	34	34	29	1547	1888	1761	4	9	251	396	0	0
Holcus lanatus (I)	31	23	37	174	352	758	87	85	939	1986	0	0
Lolium perenne (I)	22	28	7	12	202	6	0	0	0	0	19	779
Other life forms												
Juncus bufonius (N)	4	0	0	16	0	0	0	0	0	0	9	69
Linum bienne (I)	67	51	34	62	68	56	67	40	34	92	19	130
Pteridium aquilinum (I)	13	15	13	158	266	210	50	82	1200	2482	0	0
Rubus ursinus (N)	62	62	83	774	905	1412	39	53	335	652	0	0
Total actual cover				11,976	17,884	16,798			23,962	28,490		3965
Total quadrat	143	143	143				242	242			30	

Table 2. Mean Cover Estimates and Standard Errors for the Nineteen Species Listed in Table 1. * = occurred in one sample only; no variance estimate possible.

	Lone Tree Meadow			Buck Meadow		Stable Meadow
Species	1974	1976	1978	1975	1978	1978
Annual grasses						
Aira caryophyllea	3.8 ± 1.5	13.0 ± 5.2	11.9 ± 5.1	4.1 ± 2.05	6.1 ± 6.1	9.4
Bromus mollis	0.9 ± 0.2	25.9 ± 7.5	6.6 ± 6.1	39.3 ± 5.4	24.3 ± 5.3	10.2
Cynosurus echinatus	16.4 ± 4.8	13.8 ± 1.9	2.8 ± 1.9	2.0 ± 2.1	5.4 ± 8.6	24.7
Hordeum leporinum	0	0	0	0	0	37.7
Vulpia bromoides	0.6 ± 0.1	15.3 ± 8.2	38.1 ± 10.0	6.7 ± 2.2	27.9 ± 6.5	5.7
Perennial forbs						
Corythrogyne californica	2.0—*	0	0	31.3 ± 9.9	50.9 ± 8.6	0
Hypochoeris radicata	2.4 ± 1.0	9.5 ± 2.7	11.1 ± 11.1	1.2 ± 0.4	3.8 ± 2.4	4.4
Iris douglasiana	14.4 ± 6.4	14.5 ± 7.4	21.5 ± 5.8	0	42.0—*	24.8
Plantago lanceolata	21.5 ± 3.4	24.1 ± 3.5	13.8 ± 3.7	7.8 ± 4.5	6.1 ± 3.5	51.9
Rumex acetosella	1.0 ± 0.9	2.4 ± 1.4	2.0 ± 0.0	4.5 ± 2.9	6.8 ± 1.1	0
Perennial grasses						
Anthoxanthum odoratum	20.2 ± 4.1	40.7 ± 6.2	57.6 ± 5.6	37.0 ± 5.1	52.0 ± 4.5	0
Rytidosperma pilosum	13.2 ± 4.2	15.6 ± 5.4	13.9 ± 5.0	17.8 ± 4.7	35.2 ± 4.9	13.1
Deschampsia holciformis	45.5 ± 8.6	55.5 ± 10.1	60.7 ± 10.8	62.8 ± 14.5	44.1 ± 14.3	0
Holcus lanatus	5.6 ± 3.1	15.3 ± 0.8	20.5 ± 7.9	10.8 ± 3.4	23.4 ± 5.1	0
Lolium perenne	0.6 ± 0.5	7.2 ± 3.7	0.9 ± 0.5	0	0	41.0
Other life forms						
Juncus bufonius	0	0	0	0	0	7.7
Linum bienne	0.9 ± 0.5	1.3 ± 1.0	1.7 ± 0.6	0.5 ± 0.0	2.3 ± 0.8	6.8
Pteridium aquilinum	12.2 ± 5.3	17.7 ± 5.7	16.2 ± 4.6	24.0 ± 4.5	30.3 ± 3.7	0
Rubus ursinus	12.5 ± 2.4	14.6 ± 3.2	17.0 ± 2.7	0	12.3 ± 1.1	0

dominants (the exception being *Rytidosperma pilosum*) decreased significantly ($p < 0.05$) in Buck and Lone Tree Meadows by 1978.

The dominant species in the latest surveys were mostly perennial grasses. *Anthoxanthum odoratum* and *Holcus lanatus* were two introduced species absent from Stable Meadow that showed significant increases in mean cover in the other sites. *Anthoxanthum odoratum* had higher cover values, greater dispersion over the successional sites, and higher rates of increase than most other species. In Lone Tree Meadow, *Anthoxanthum odoratum* reached 69% of the relative cover (Fig. 5a) of the perennial grasses in 1978, occupied 91% of the sample quadrats, and had increased 266% in actual cover. In Buck Meadow, the corresponding figures were 54% (Fig. 5b), 80%, and 59%. *Holcus lanatus* increased significantly in both meadows and showed higher percent rates of increase than did *A. odoratum.* Its frequency values were lower, reflecting high patchiness and locally high cover. *Rytidosperma pilosum* was the only perennial grass to show differences between sites. In Lone Tree Meadow, *R. pilosum* disappeared from half the quadrats in which it occurred and lost 47% of its cover. In Buck Meadow, *R. pilosum* increased significantly (71%), despite a reduction in frequency, because its mean cover increased in those plots occupied at the beginning of the study in 1975. *Deschampsia holciformis,* a large native bunchgrass characteristic of wetter sites, did not show significant change in time and may represent a relict species that survives grazing rather than a later successional dominant. Other species that showed significant increases in cover include *Vulpia bromoides* (=*Festuca dertonensis*) and *Rubus ursinus. Rubus ursinus* is characteristic of heavy stands of perennial grass, especially in wetter areas. *Vulpia bromoides* was unique in that its frequency decreased, whereas cover increased in the remaining quadrats. This pattern of locally patchy occurrence in perennial stands persists to the present time.

Representation of native species in secondary succession. Table 3 shows that native species are present at all stages of succession, but at low cover values. There is no significant temporal increase in the representation of native species, with the exception of *Rubus ursinus.* We see little evidence suggesting that a major increase in native species, at least in the herbaceous vegetation, is to be expected in the future. *Deschampsia holciformis,* however, is one native species that could be a successional dominant, but it has a static population at Sea Ranch with no evidence suggesting dominance at climax, contrary to what Elliott and Wehausen (1974) suggest for Point Reyes.

Two other well-known natives are relatively rare and likely to remain so. *Stipa pulchra* is uncommon at Sea Ranch. It tends to be concentrated along roadsides and in relict annual-dominated patches. Our observations on this species at Sea Ranch support the conclu-

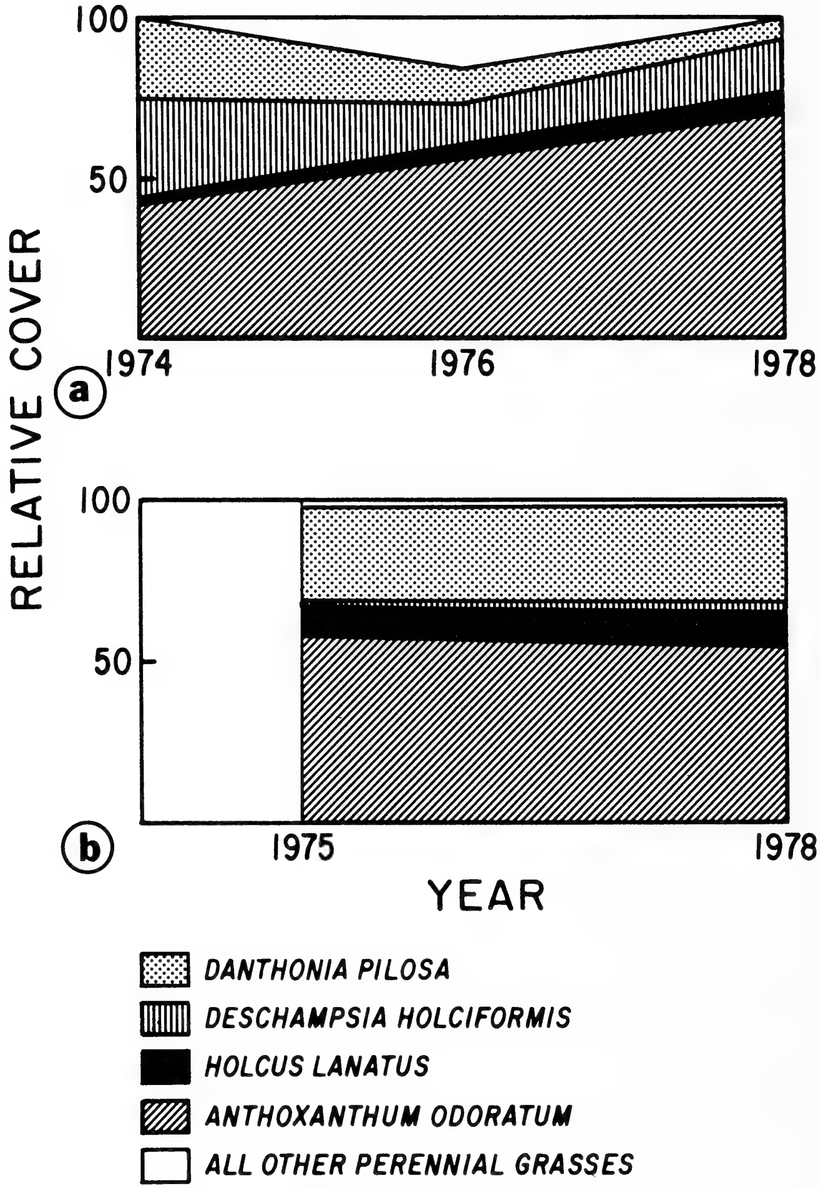


FIG. 5. Relative cover for perennial grasses in Lone Tree Meadow (Fig. 5a) and Buck Meadow (Fig. 5b).

TABLE 3. REPRESENTATION OF NATIVE SPECIES IN SECONDARY SUCCESSION IN THE SEA RANCH COASTAL PRAIRIE. Statistics are absolute cover (AC) assigned to the 19 native and introduced species of Table 1.

Site and year	AC native species	AC all species	Proportion of natives
Stable Meadow			
1978	119	3663	0.032
Lone Tree Meadow			
1974	2714	10,761	0.252
1976	3243	15,527	0.209
1978	3882	16,014	0.242
Buck Meadow			
1975	1150	12,338	0.093
1978	1294	27,273	0.047

sions drawn by Bartolome and Gemmill (1981). *Danthonia californica* is a low-growing, native, perennial that is restricted to the low vegetation found on exposed bluffs (see Hektner and Foin 1977). It has never been found inland in the taller vegetation.

DISCUSSION

Secondary succession in the California coastal prairie. Our data show that secondary succession in the Sea Ranch coastal prairie is characterized by rapid replacement of annuals by perennials and subsequently the concentration of dominance within a small number of mostly introduced species of perennial grasses. The replacement of annuals by perennials is most easily explained as a decline in yearly establishment by annuals because perennials utilize most of the soil surface. Peart and Foin (1985) have shown that establishment is strongly retarded by biomass at Sea Ranch. As succession has progressed, biomass has accumulated (much of it standing dead material and litter). The cause of the replacement of annuals and perennial forbs by perennial grasses is more speculative at this time, but may be a function of competition for light and soil moisture. Peart (1982) measured light levels beneath the grass canopy using a light meter measuring only the photosynthetically active spectrum. He found that light values beneath the grass canopy were typically much less than at the floor of nearby redwood forests. Because most of the forbs at Sea Ranch are low-growing, it is easy to imagine that they would be readily overtopped and shaded out.

The replacement of some perennial grasses by others at Sea Ranch is exemplified most strikingly by the increase in *Anthoxanthum odoratum*. This species has continued to increase; at present, it has even larger cover values than those presented in this paper (the informal estimate for 1985 in Lone Tree Meadow is greater than 70%). Explanation of the success of this species is still incomplete, although there are suggestions in some of our current work that soil moisture is an important, perhaps the most important, explanation. Peart and Foin (1985) showed in experimental invasion studies that *Anthoxanthum odoratum* was the best at colonizing the stands of annual-perennial forb-*Rytidosperma* that were present with the sheep. Differences in colonizing ability are adequate to explain the changes in secondary succession reported in this paper, but newer data (Foin, unpublished) strengthen the argument by showing the role of soil moisture in the dynamics of the dominant perennial species.

Succession and the native vegetation. Our research at Sea Ranch demonstrates that native species cannot be expected to recover in the coastal prairie in the face of competition from a small number of well-adapted introduced species. Even with intensive management, species like *Anthoxanthum odoratum* and *Holcus lanatus* probably cannot be eliminated from the prairie community. This is because the coastal climate is mild enough in the summer to permit the survival of perennials, and because these two introduced species are opportunistic and adapted to a wide variety of environmental conditions. The research reported here suggests that, under mesic conditions on the northern coast, these two introduced species are the prairie dominants and likely to remain so. Barry and Schlinger (1977) have shown that introduced perennial grasses dominate at Inglenook fen, and recently Saenz and Sawyer (1986) have drawn a similar conclusion about introduced species in Humboldt County. The Sea Ranch data also are in harmony with the replacement of natives by introduced annuals in the interior valleys. Thus, Heady and others (1977) were correct in their prediction that introduced species would continue to persist in the coastal prairie, but they did not foresee that persistence also would mean even greater dominance.

ACKNOWLEDGMENTS

Support for this work was provided by the National Science Foundation (DEB 76-82503), the Rockefeller Foundation, and the Opportunity Program for Ecological Research, University of California. We are grateful to the members and staff of The Sea Ranch Association, particularly George Wickstead, the late Larry Marshall, Robert Kirkwood, and Ruth Riordan, for their generous assistance over the years. We also thank Harold Heady and Carla Scheidlinger for their extensive comments on the manuscript.

LITERATURE CITED

BARRY, W. J. and E. I. SCHLINGER. 1977. Inglenook Fen. Dept. Parks and Recreation, State of California.

Bartolome, J. W. and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madroño 28:172–184.

Burcham, L. T. 1957. California rangeland. Calif. Div. Forestry, Sacramento.

Clements, F. E. 1916. Plant succession. Publ. Carnegie Inst. Wash., no. 242.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Naturalist 111:1119–1144.

Crampton, B. 1974. Grasses of California. Univ. California Press, Berkeley.

Elliott, H. W. and J. D. Wehausen. 1974. Vegetational succession on coastal rangeland of Point Reyes Peninsula. Madroño 22:231–238.

Evans, F. C. and E. Dahl. 1955. The vegetational structure of an abandoned field in southeastern Michigan and its relation to environmental factors. Ecology 36: 635–706.

Foin, T. C. and S. K. Jain. 1977. Population biology and ecosystem analysis: lessons for the development of community ecology. BioScience 27:532–538.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol. Monogr. 37:89–111.

Heady, H. F. 1975. Rangeland management. McGraw-Hill, New York.

———, T. C. Foin, M. M. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1977. Coastal prairie and northern coastal scrub. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 733–759. Wiley-Interscience, New York.

Hektner, M. M. and T. C. Foin. 1977. Vegetation analysis of a northern California coastal prairie: Sea Ranch, Sonoma County, California. Madroño 24:83–103.

Huffaker, C. B. and C. E. Kennett. 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. J. Range Managem. 12: 69–82.

Lathrop, K. T. and P. J. P. Gogan. 1985. Plant communities of the Tule Elk Range, Point Reyes National Seashore. Tech. Report 18, Cooperative National Park Resources Studies Unit, Univ. California, Davis.

McBride, J. 1974. Plant succession in the Berkeley Hills, California. Madroño 22: 317–329.

——— and H. F. Heady. 1968. Invasion of grassland by *Baccharis pilularis* DC. J. Range Managem. 21:106–108.

McIntosh, R. P. 1980. The relationship between succession and the recovery process in ecosystems. *In* J. Cairns, Jr., ed., The recovery process in damaged ecosystems. Ann Arbor Science Press, Ann Arbor, MI.

———. 1981. Succession and ecological theory. *In* D. C. West, H. H. Shugart, and D. B. Botkin, eds., Forest succession. Springer-Verlag, New York.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agroecosystems 7:145–165.

McMahon, J. A. 1980. Ecosystems over time: succession and other types of change. *In* R. H. Waring, ed., Forests: perspectives from ecosystem analysis. Oregon State Univ. Press, Corvallis.

Munz, P. A. 1973. A California flora and supplement. Univ. California Press, Berkeley.

Peart, D. R. 1982. Experimental analysis of succession in a grassland at Sea Ranch, California. Ph.D. dissertation, Univ. California, Davis.

——— and T. C. Foin. 1985. Analysis and prediction of population and community change: a grassland case study. *In* J. White, ed., The population structure of vegetation. W. Junk, The Hague.

Reed, M. J., W. R. Powell, and B. S. Bal. 1963. Electronic data processing codes for California wildland plants. U.S. Forest Service Research Note PSW-N20.

Saenz, L. and J. O. Sawyer, Jr. 1986. Grasslands as compared to adjacent *Quercus* *garryana* woodland understories exposed to different grazing regimes. Madroño 33:40–46.

SHUGART, H. H. 1974. A theory of forest succession. Springer-Verlag, New York.

STEELE, R. G. D. and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

UNITED STATES DEPT. OF AGRICULTURE. 1972. Soil survey of Sonoma County, California. United States Government Printing Office, Washington, DC.

WESTER, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. Madroño 28:231–241.

WESTOBY, M. 1979. Elements of a theory of vegetation dynamics in arid rangelands. Israel J. Bot. 28:169–194.

WHITE, K. L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation. Ecology 48:949–955.

(Received 6 Sep 1985; revision accepted 20 Apr 1986.)

ANNOUNCEMENT

SYMPOSIUM TO HONOR G. LEDYARD STEBBINS

An International Symposium will be held in Davis, California, on 12–14 September 1986, to honor Professor G. Ledyard Stebbins in the year of his 80th birthday. Invited talks by leading plant biologists will include topics in population and ecological genetics, organelle and nuclear molecular genetics, morphogenesis and plant development, and evolution and systematics. For further information please contact: Dr. L. D. Gottlieb, Department of Genetics, or Dr. S. K. Jain, Department of Agronomy and Range Science, University of California, Davis, CA 95616.

DIFFERENCE IN SEEDLING GROWTH MORPHOLOGY AS A FACTOR IN THE DISTRIBUTION OF THREE OAKS IN CENTRAL CALIFORNIA

KOZUE MATSUDA[1] and JOE R. MCBRIDE
Department of Forestry and Resource Management,
University of California, Berkeley 94720

ABSTRACT

Seedling growth morphology and initial elongation of roots of *Quercus douglasii, Q. lobata,* and *Q. agrifolia* were compared in artificial and field environments. *Quercus douglasii* had established longer main roots by spring than the other two species. This was attributed to its early germination and high rate of root elongation. *Quercus douglasii* has the smallest leaf area/root weight ratio among the three species, which enables it to occupy xeric sites. Restriction of *Q. agrifolia* to mesic sites is related to its relatively slow germination, low rate of root elongation, and larger leaf area/root weight ratio.

Vegetation in California, which has developed under summer drought, has been related to depth of water table and the rate of drying of surface soils after winter rains (Cannon 1914a,b, Cooper 1922, 1926, Helmers et al. 1955, Griffin 1967, Krause and Kummerow 1977, Ng and Miller 1980, Arkeley 1981, Kummerow and Mangan 1981). Oaks dominate many of the California plant communities that cover the area from coastal regions up to the middle elevation of the mountainous regions. Griffin (1971, 1973, 1976) discussed the distribution and regeneration of California oaks in relation to moisture availability of habitats. The amount of available water in soils and the growth characteristics of individual species, such as a germination time, root growth rate of seedlings, material distribution within a seedling, etc., apparently have important effects on success or failure of seedling establishment. Information on such autecological aspects is necessary for better understanding the difference in distribution of species.

Quercus agrifolia Née, *Q. douglasii* H. & A., and *Q. lobata* Née dominate the local foothill woodland, although they are generally segregated along gradients of moisture availability (Griffin 1973). *Quercus agrifolia,* which is the only evergreen species of the three, occupies mesic sites, such as canyon bottoms or north-facing slopes, and *Q. douglasii* occupies xeric sites, such as south-facing slopes adjacent to chaparral vegetation. *Quercus lobata* occurs on alluvial

---

[1] Present address: Dept. Biology, Tokyo Metropolitan Univ., Setagaya-ku, Tokyo 158, Japan.

MADROÑO, Vol. 33, No. 3, pp. 207–216, 1986

terraces and natural levees along rivers and also on ridge tops (Griffin 1977).

The aim of this study is to clarify the relationship between seedling growth characteristics and the habitats of the three oaks. We examined seedling growth morphology, the effects of temperature on initial root growth, and the rate of root elongation of these oaks, together with germination and root growth under the field conditions.

MATERIALS AND METHODS

Mature acorns were collected from 10 trees of each species in the Central Coast ranges of California during October and November, 1981 and 1982. Acorns of *Q. agrifolia* were collected in the Berkeley Hills, 190 to 300 m above sea level, and in Carmel Valley (100 to 300 m). Those of *Q. douglasii* were collected in Mt. Diablo State Park, near Walnut Creek (800 to 1000 m) and at the Hastings Reservation (550 to 600 m); those of *Q. lobata* were collected near Pine Grove (760 m) and at the Hastings Reservation (550 to 600 m). Acorns were sealed in plastic bags and stored at temperatures between 2.5° and 5°C until used in the experiments, except for an outdoor experiment when they were planted immediately following collection. The storage period was two to three months.

Seedling growth morphology. For each species, 70 acorns (seven from each of the 10 seed source trees) previously germinated on moist vermiculite were planted in tar paper tubes (6 × 90 cm) filled with U. C. mix (25% top soil, 25% organic matter, and 50% sand) in late December to early January. The tar paper tubes were placed in a lath house and protected from precipitation by a transparent (polyethylene) roof. The tubes were watered when the soil surface appeared to be dry. The epicotyl length of each seedling was measured every four days. Forty of the seedlings of each species were harvested one by one when their epicotyls grew over 2 cm tall. Leaves had not appeared yet at this stage. The 30 remaining seedlings of each species were transferred to a warm greenhouse to accelerate shoot growth. These seedlings were harvested one by one when the last leaf from the initial bud on each seedling had fully expanded. Main root length, shoot length, and leaf area of each seedling were measured. Seedlings were then divided into leaves, stems, and roots and dried at 80°C.

Effects of temperature on root growth. Seedlings were grown in two temperature-controlled greenhouses: 1) high temperature, 20°C day (12 hr) and 15°C night (12 hr); 2) low temperature, 10°C day (18 hr) and 5°C night (6 hr). Forty germinated acorns of each species, four from each of the ten seed source trees, were planted into tar paper tubes and grown until epicotyls were 2 cm tall. The seedlings were then harvested and the main root length and root weight were measured.

Root elongation rate. The relationship between acorn size and the rate of root elongation was tested by using only *Q. agrifolia* and *Q. lobata.* From each of the 10 seed source trees, a relatively large, a relatively small, and a medium-sized acorn were selected, totaling 30 acorns for each species. The fresh weight of each acorn was recorded prior to germinating on moist vermiculite. Once germinated, each acorn was transferred to one of five root observation boxes (30 × 30 × 120 cm) filled with U. C. mix. The front side of each box was made of glass set at an oblique angle so the roots of each seedling could be observed as they grew in contact with the glass. The glass was covered to screen the developing roots from light. The length of each main root was measured every three days, from January to June, until each main root touched the bottom of the box. Dry weight of cotyledons inside acorns at the beginning of the experiment was estimated from a correlation between acorn fresh weight and dry weight of cotyledons. The correlation was established by measurement on 50 extra acorns of each species, five from each of the 10 seed source trees. The amount of storage material in cotyledons utilized during seedling development was obtained by subtracting the weight of the shrivelled cotyledons at the end of the experiment from the estimated weight of cotyledons at the beginning.

Germination and root growth under outdoor conditions. The experiment was conducted in the shade of an oak woodland canopy at the University of California Botanical Garden in Berkeley. Twenty to 30 acorns of each of the 10 seed source trees of *Q. douglasii, Q. lobata* and *Q. agrifolia* were sown on the soil surface soon after collection and covered with oak litter. Acorns were observed once a week and germination was recorded separately for each of the seed source trees. Germinated acorns were transplanted in tar paper tubes (6 × 90 cm) buried vertically in the ground. Seedlings were harvested on 3 March 1982, and the length of main roots was measured.

RESULTS

Seedling growth morphology. During the first period of seedling development, until the epicotyl was 2 cm tall, significantly more root growth was exhibited by *Q. douglasii* than by *Q. agrifolia* or *Q. lobata* (Table 1). Main root length of *Q. douglasii* averaged 36% greater than that of both *Q. agrifolia* and *Q. lobata.* In fully developed seedlings, the length of main roots of *Q. douglasii* and *Q. lobata* were not significantly different from each other, but both were significantly longer than that of *Q. agrifolia.* Corresponding to the

TABLE 1. SEEDLING MORPHOLOGY OF *Quercus agrifolia, Q. lobata,* AND *Q. douglasii.* For each characteristic, values attached by a same superscript are not significantly different from each other ($p < 0.05$, Student's t-test). *$D^2 \times L$ = (diameter)^2 × length of acorns and is correlated with cotyledon dry weight ($r > 0.8$). **Number of days between germination and sampling.

Characterstics	Species *Q. agrifolia*	 *Q. douglasii*	 *Q. lobata*
Seedlings with 2 cm epicotyls			
Length of main roots (cm)	34.6^a	49.0	37.3^a
Root weight (g)	0.139	0.404^a	0.301^a
$D^2 \times L$ of acorns* (cm^3)	5.51	8.11	10.51
Number of days**	42^a	55	40^a
Seedlings with fully expanded leaves			
Main root length (cm)	69.8	86.1^a	86.2^a
Main root diameter at base (cm)	0.306^a	0.320^a	0.399
Root weight (g)	0.306	0.667	1.070
Leaf number	5.6^a	6.1^a	6.2^a
Leaf area (cm^2)	45.1	24.9	66.8
Leaf weight (g)	0.279^a	0.159	0.326^a
Stem length (cm)	7.0^a	5.1	8.2^a
Stem weight (g)	0.116	0.084	0.191
Leaf area/root weight (cm^2/g)	145.0	41.3	67.2
Total seedling weight (g)	0.701	0.910	1.580
$D^2 \times L$ of acorns* (cm^3)	4.29	7.53	13.02
Number of days**	64^a	78	66^a

increase in the acorn size, total seedling weight and root weight increased in the order of *Q. agrifolia, Q. douglasii,* and *Q. lobata. Quercus douglasii,* however, showed the smallest values in leaf area, leaf weight, stem length, and stem weight. Leaf area/root weight ratio was smallest in *Q. douglasii* and largest in *Q. agrifolia.*

Effects of temperature on root growth. Low temperature increased significantly the length and weight of roots of the three species built in the first period of seedling development (Table 2). At both temperatures, *Q. douglasii* exhibited greatest and *Q. agrifolia* least root length. Roots of *Q. lobata,* however, were heavier than those of *Q. douglasii* in the low temperature greenhouse ($p < 0.05$).

Root elongation rate. The correlation coefficient (r) between estimated dry weight of the cotyledons and the root elongation rate was 0.64 ($p < 0.005$) for *Q. agrifolia* and 0.11, not significant, for *Q. lobata* (Fig. 1). The amount of storage material utilized during seedling development in *Q. agrifolia* also showed a good correlation ($r = 0.65$, $p < 0.005$) with root elongation rate, but this was not true in *Q. lobata* ($r = 0.12$, not significant). Elongation rates also were estimated from the data of seedling morphology mentioned

TABLE 2. ROOT LENGTH AND WEIGHT OF OAK SEEDLINGS WITH 2 CM EPICOTYLES GROWN IN HIGH (20°–15°C) AND LOW (10°–5°C) TEMPERATURE GREENHOUSES. Intraspecific differences between values of the temperature treatments are significant for all species ($p < 0.05$, Student's t-test). Interspecific differences between values of any two species under the same temperature treatment are significant ($p < 0.05$) except for marked (a) pairs. *Number of days between germination and sampling.

Quercus species	No. of days*		Root length (cm)		Root weight (g)	
	High	Low	High	Low	High	Low
Q. agrifolia	17[a]	61	25.4	31.4	0.069	0.129
Q. douglasii	21	71[a]	39.8	53.9	0.182[a]	0.396
Q. lobata	18[a]	79[a]	32.7	42.1	0.215[a]	0.651

above. Main root length of the seedlings harvested with 2 cm epicotyls was divided by the number of days between germination and harvesting. The rate of growth for *Q. agrifolia* was 0.78 cm/day; for *Q. douglasii,* 0.86 cm/day; and for *Q. lobata,* 0.93 cm/day (significantly different from one another, $p < 0.05$).

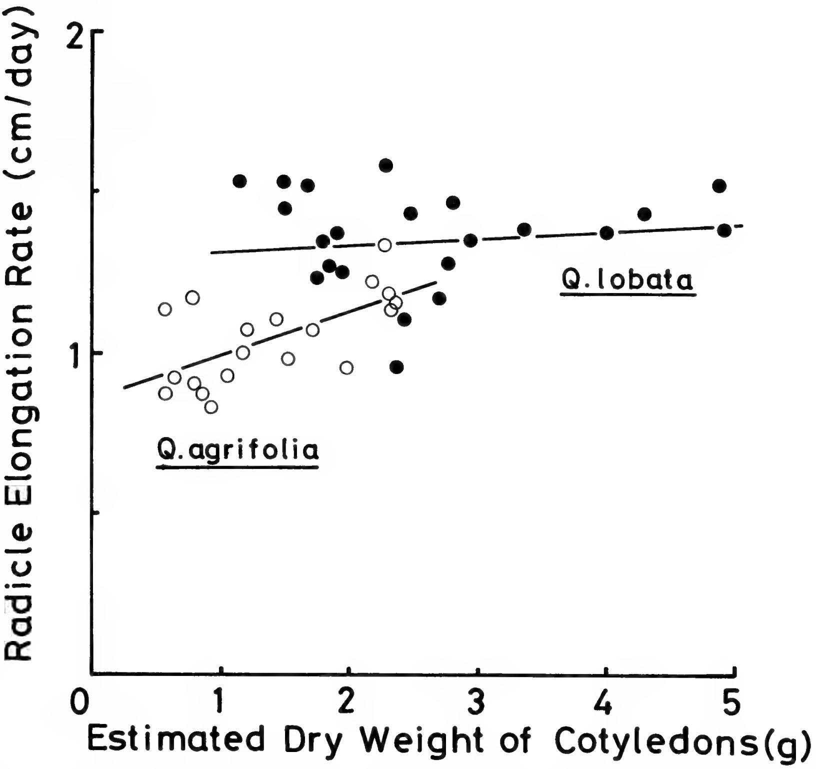


FIG. 1. Correlation between elongation rates of main roots and estimated dry weight of cotyledons of *Q. agrifolia* (○) and *Q. lobata* (●).

TABLE 3. MEAN MAXIMUM AND MINIMUM AIR TEMPERATURES AND THE AMOUNT OF PRECIPITATION RECORDED IN THE UNIVERSITY OF CALIFORNIA BOTANICAL GARDEN IN BERKELEY.

1981–1982	Oct	Nov	Dec	Jan	Feb	Mar
Mean maximum (°C)	21.2	18.3	15.6	12.8	17.7	15.6
Mean minimum (°C)	7.3	8.1	6.0	2.0	5.2	5.1
Precipitation (cm)	9.3	20.3	12.1	28.3	13.8	26.1

Germination and root growth under outdoor conditions. Weather records during the observation period are shown in Table 3. Soil temperatures recorded weekly for the experimental site were 5.1°C lower (average maximum), and 4.2°C higher (average minimum) than the air temperatures.

Quercus douglasii germinated from late October to early November, promptly after planting, although germination of *Q. agrifolia* did not occur until mid-November to mid-December. Acorns of *Q. lobata* showed a large tree to tree variation for germination time (Fig. 2); these results were consistent with those of Griffin (1971). By March, *Q. douglasii* and *Q. lobata* had produced significantly longer main roots than had *Q. agrifolia* (Fig. 3).

DISCUSSION

Seedling growth morphology demonstrated in the present study is consistent with the results of field observation by Griffin (1971). He investigated seedling establishment of the three species at Hastings Reservation near Carmel, California. On grass-covered south-facing slopes, all seedlings of all species died in the first growing season after a dry winter. When grasses were removed, most of the *Q. douglasii* seedlings survived, although *Q. lobata* and *Q. agrifolia* seedlings were less successful. After a wet winter, most of *Q. douglasii,* a smaller number of *Q. lobata,* and no *Q. agrifolia* seedlings survived the summer drought. He demonstrated that less precipitation in addition to competition with annual grasses greatly reduced the successful seedling establishment. The present study showed that *Q. douglasii* had significantly longer main roots than either *Q. agrifolia* or *Q. lobata* when shoots started growing, with 2 cm epicotyls (Table 1). Grown under different temperature conditions, the results were similar (Table 2).

Deep rooting in the early stage of development seems to be of primary importance for *Q. douglasii* to survive in xeric habitats. The seedling roots grow below the rooting zone of annual grasses before soil moisture is depleted by evapotranspiration. In the field condition, earlier germination of *Q. douglasii* than *Q. agrifolia* (Fig. 2) assured the production of longer roots by spring of the former

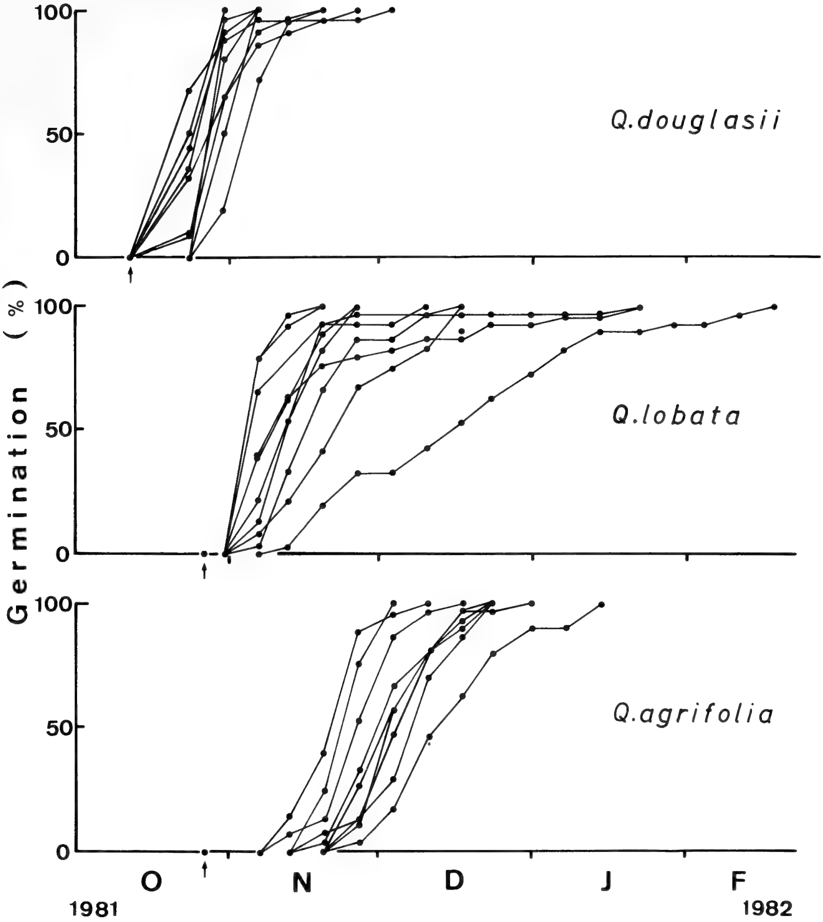


FIG. 2. Germination of oaks under outdoor conditions. Each line shows a time course of germination recorded on thirty acorns collected from each of ten seed source trees. Arrows indicate the time of acorn planting.

(Fig. 3). The long roots of *Q. douglasii* might be attributed in part to their greater growth at low temperature during winter. In fact, low temperature itself suppressed root growth in length and weight, but the start of shoot growth was greatly delayed under low temperature. As a result, longer and heavier roots had been produced, when compared at the same developmental stage of epicotyls (Table 2). *Quercus agrifolia* also developed longer and heavier roots in the low temperature greenhouse than it did in the high temperature one (Table 2). The delay in germination, however, may reduce the benefits from cold soils under field conditions.

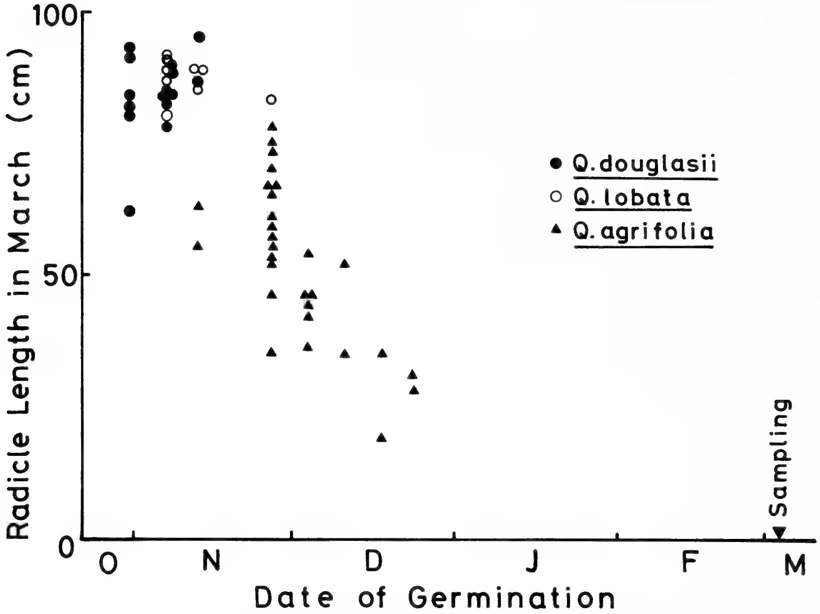


FIG. 3. Length of main roots in March of outdoor-grown oak seedlings. Seedlings germinated at the indicated date were grown outdoors until the sampling on 3 March 1982. The root length of *Q. douglasii* and *Q. lobata* was underestimated, because most of the roots had grown through the bottom of tubes, 90 cm tall, when sampled.

Root elongation rate was found to be different among the three species. The increase of the root elongation rate corresponded to the increase of the mean acorn size. Small elongation rate of *Q. agrifolia* might be responsible for its short root length in spring (Fig. 3), together with its late germination (Fig. 2). Intraspecifically, the root elongation rate of small-seeded *Q. agrifolia* correlated positively with its estimated dry weight of cotyledons; however, that of large-seeded *Q. lobata* did not (Fig. 1). Whalley et al. (1966) also showed that the rate of seedling height growth correlated with the seed size in species with small seeds, but not in a species with large seeds. There seems to be a saturation point in root elongation rate, which would be accelerated by the increase of the seed weight.

Balance between water absorption by roots and transpiration from leaves determines water economy of plants. Small leaf area/root weight ratio, therefore, can be regarded as a morphological adaptation developed by xerophytes and large leaf area/root weight ratio for that by mesophytes. Long radicles and a small leaf area/root weight ratio of fully developed *Q. douglasii* seedlings help explain its distribution in the most xeric environment. In contrast, short roots and the largest leaf area/root weight ratio of *Q. agrifolia* seedlings might restrict its distribution in the mesic sites. Cooper (1926) found that *Q. lobata* grew on alluvial terraces with deeper water tables than those supporting *Q. agrifolia.* Longer roots and smaller leaf area/root weight ratio of *Q. lobata* than *Q. agrifolia* at the seedling stage might be important for survival in such an environment. *Quercus lobata,* however, had a larger leaf area/root weight ratio than did *Q. douglasii.* This characteristic might prevent *Q. lobata* from establishment in the xeric habitat occupied by *Q. douglasii.*

Griffin (1971) observed a high percentage of *Q. douglasii* with desiccated stems at the end of the first growing season. Many of these plants resprouted the following spring. *Quercus douglasii* allocated only 27% of its dry weight to leaves and stems, which was smaller than either *Q. lobata,* 33%, or *Q. agrifolia,* 56% (Table 1). By maintaining a larger percentage of material below ground, *Q. douglasii* minimizes the desiccation of the material and can utilize it for resprouting the following spring. This may be a further adaptation of *Q. douglasii* to its xeric environment. In contrast, *Q. agrifolia* apparently does not occur in similar desiccating environments because of the large percentage of material allocated to its evergreen leaves.

ACKNOWLEDGMENTS

We thank Pamela Muick, Christine Reid, and Dr. James R. Griffin for their assistance in the preparation and review of this manuscript. We are also indebted to Jim Griffin for his help in locating seed-producing trees and collecting acorns.

LITERATURE CITED

ARKELEY, R. J. 1981. Soil moisture use by mixed conifer forests in a summer dry climate, Sierra Nevada and San Bernardino Mountains of California. J. Soil Sci. Soc. Am. 45:423–427.

CANNON, W. A. 1914a. Specialization in vegetation and in environment in California. Plant World 17:223–237.

———. 1914b. Tree distribution in central California. The Popular Science Monthly 85:417–427.

COOPER, W. S. 1922. The broad-sclerophyll vegetation of California—an ecological study of the chaparral and its related communities. Carnegie Inst. Wash. Publ. 319:1–124.

———. 1926. Vegetational development upon alluvial fans in the vicinity of Palo Alto, California. Ecology 7:1–30.

GRIFFIN, J. R. 1967. Soil moisture and vegetation patterns in northern California forests. Res. Paper PSW-46. U.S.D.A. Pacific Southwest Forest and Range Exp. Sta., Forest Service.

———. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology, 52:862–868.

———. 1973. Xylem sap tension in three woodland oaks of central California. Ecology 54:152–159.

———. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. Amer. Midl. Nat. 95:422–435.

———. 1977. Oak woodland. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 383–415. John Wiley and Sons, New York.

HELMERS, M., J. S. MORTON, G. JUHREN, and J. O'KEENE. 1955. Root systems of some chaparral plants in southern California. Ecology 36:667–678.

KRAUSE, D. and J. KUMMEROW. 1977. Xerophytic structure and soil moisture in the chaparral. Oecol. Plant. 12:133–148.

KUMMEROW, J. and R. MANGAN. 1981. Root systems in *Q. dumosa* Nutt. dominated chaparral in southern California. Acta Oecologia 2:177–188.

NG, E. and P. C. MILLER. 1980. Soil moisture relations in the southern California chaparral. Ecology 61:98–107.

WHALLEY, R. D. B., C. M. MCKELL, and L. R. GREEN. 1966. Seedling vigor and early nonphotosynthetic stage of seedling growth in grasses. Crop Science 5:147–150.

(Received 11 Mar 1985; revision accepted 17 Mar 1986.)

ANNOUNCEMENT

SYMPOSIUM ON MULTIPLE-USE MANAGEMENT OF CALIFORNIA'S HARDWOOD RESOURCES

12–14 November 1986
California Polytechnic State University,
San Luis Obispo

Papers will be presented on scientific, technological, economic, sociological, and legal phenomena relevant to the management of California's hardwood resources.

Keynote speakers: Zane Smith, Regional Forester, USFS; Harold Walt, Chairman, Board of Forestry; Jerry Partain, Director, CDF.

For information contact Julie Oxford, Conference Coordinator, NRM Dept., Cal Poly, San Luis Obispo, CA 93407. For general information call (805) 546-1402.

Symposium sponsored by California Polytechnic State University, USDA—Forest Service (PSW & Region 5), California Dept. of Forestry, USDI—Bureau of Land Management, UC Cooperative Extension, and the Society of American Foresters.

OPAL PHYTOLITHS AS EVIDENCE FOR DISPLACEMENT OF NATIVE CALIFORNIAN GRASSLAND

JAMES W. BARTOLOME and STEVEN E. KLUKKERT
Department of Forestry and Resource Management,
University of California, Berkeley 94720

W. JAMES BARRY
Department of Parks and Recreation,
The Resources Agency, State of California,
P.O. Box 2390, Sacramento 95811

ABSTRACT

Opal phytoliths are produced by plants and persist in soils as microfossils with taxonomically distinct morphology. We found phytoliths produced by the original native perennial species in soil under an annual grassland, thus providing the first direct evidence that the Californian grassland was formerly dominated by panicoid opal-producing grass. The most common panicoid-type opals were probably produced by *Stipa pulchra.* Frequencies of opal phytoliths from native grasses were greater at 10 cm depth than at the soil surface beneath the annual grassland. Comparison of opal phytolith frequencies from 10 cm deep at the annual site and an adjacent relict perennial grassland site suggested that the density of panicoid opal-producing native grasses on the annual site was once similar to the relict grassland.

Reconstruction of pristine plant communities in California is constrained by limited techniques for establishment and maintenance of natural vegetation, and by a lack of recorded knowledge about the composition of those historical communities. The evidence for previous vegetation includes results from pollen studies, macrofossils, observation of succession, and the composition of present vegetation on selected relict sites. One technique, which has not been applied to any California plant community, uses opal phytoliths to identify historical species assemblages.

Plant opals are microscopic, translucent particles that occur in plants and persist for long periods in soil as opal phytoliths. They are formed within plant cells and cell walls through the passive uptake of monosilicic acid by way of the transpiration stream from soil solution (Jones and Handreck 1967). They are composed of amorphous silica, which also contains some additional carbon, water, and cations (Wilding et al. 1975). Opals are most common in leafy portions of plants but are also present in stems, roots, and other parts. Biogenic opal particles range in size from less than one micron to over 500 microns; however, the majority of diagnostic forms range from two to 50 microns.

MADROÑO, Vol. 33, No. 3, pp. 217–222, 1986

Research on opal phytoliths initially emphasized investigations of biogeochemical processes, genesis of paleosols and of catenas, and loess deposition, in which phytoliths were studied as components of soil (Wilding et al. 1975, Twiss et al. 1969, Moore 1978). Plant ecologists and paleoecologists have now begun to use phytoliths to document vegetation change, post-glacial succession, type distributions, and shifting ecotones such as grassland-forest boundaries (Wilding et al. 1975, Moore 1978, Rovner 1983, Palmer 1976).

Plant anatomists refer to opals as "silica bodies" or "silica idioblasts." They are useful in taxonomic descriptions and have been useful in classification of monocots (Metcalfe 1960). Members of the Poales (grasses and sedges) have a significant propensity to form opals. In the Poaceae (Gramineae), silica body morphology is considered diagnostic at the subfamily and tribal levels. There are at least three recognized types of silica bodies in grasses: festucoid, panicoid, and chloridoid (Twiss et al. 1975), which suggests a correlation between opal cell morphology and C3 and C4 type photosynthesis (Rovner 1983, Palmer 1976).

These taxonomic affinities are useful to differentiate Californian grasses. The common grasses that now dominate the Californian grassland are festucoid species introduced from the Mediterranean (Heady 1977). Native perennials assumed to have dominated the pristine grassland, *Stipa* spp. and *Danthonia californica* Boland., contain significant amounts of panicoid opals (Barkworth 1981, DeWet 1956, Bartolome and Gemmill 1981); others, including the genera *Deschampsia* and *Distichlis,* are exclusively festucoid. The typical "dumbbell" or "hourglass" shape of panicoid opals is readily distinguished from the elliptical disc or "hat"-shaped festucoid types and from silicified, dumbbell-shaped, stomatal guard cells (Figs. 1a, 1b). Several distinctive types of silicified trichomes (unicellular or bicellular hairs) also are associated with particular tribes or genera (Metcalfe 1960, Barkworth 1981, DeWet 1956).

This paper describes the use of opal phytoliths from two soil depths to document replacement of native vegetation by exotics on Jepson Prairie Reserve in Solano County, California (Lat. 38°N, Long. 122°W), 75 km northeast of San Francisco. The Prairie contains a small remnant of the California Valley Grassland or California Prairie, which may have covered much of the Central Valley (Heady 1977). The vegetation on all but a few hectares of the 1000 ha reserve, described in detail by Barry (1972), is now dominated by annual grasses from the Mediterranean region.

STUDY SITES

The study contrasted two locations. One location is dominated by native grasses and forbs, including *Stipa pulchra* Hitchc. and

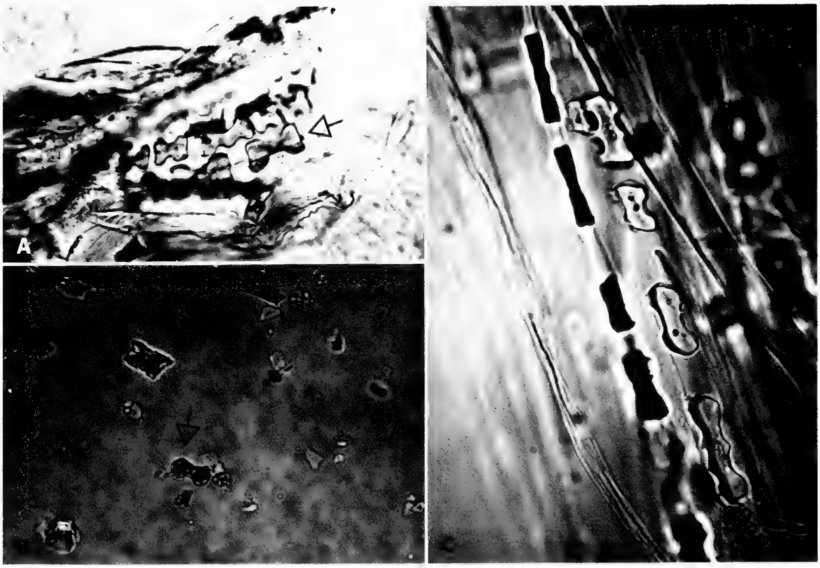


FIG. 1. Photomicrographs of opal phytoliths. a. Dumbbell-shaped panicoid opals (length = 25 microns), isolated from leaf tissue of *Danthonia californica,* are visible in the center of the photomicrograph. b. Opal phytoliths isolated from annual grassland soil, 10 cm depth (480 × magnification). The arrow points to a phytolith produced by a perennial, *Stipa pulchra.* c. Linear arrangements of panicoid opals (length = 20 microns) in leaf tissue of *Stipa pulchra.* Dark rectangular shapes are opals viewed on edge.

Deschampsia danthonioides (Trin.) Munro ex Benth. This pasture has been grazed lightly by sheep for at least the last 100 years. Stands of *S. pulchra* averaged 4.2 plants/m^2 when sampled in the spring of 1985 on 30 permanently marked 25 cm × 25 cm plots (B. Leitner, pers. comm.). Frequency of *S. pulchra* measured 23.3 percent on these same plots, with the remainder of the vegetation exotic and native annuals. This density is typical of relict non-coastal sites (Bartolome and Gemmill 1981).

The second pasture also is part of the Reserve and is less than one km away, but it has been in different ownership and grazed by cattle. Annual grasses of Mediterranean origin, including the genera *Bromus, Avena, Vulpia,* and *Hordeum,* dominate the second location. It contains no native tussock-forming bunchgrasses and only a few scattered plants of rhizomatous *Distichlis spicata* (L.) Greene. The nearest native bunchgrasses are 200 meters from the second sample location. The soils are similar, sandy loam or loam derived from sedimentary alluvium, and classified as Palexeralfs or Natrixeralfs. "Hogwallow" or mima-mound topography with vernal pools typifies undisturbed portions of both the sites.

TABLE 1. RATIO OF DUMBBELL OPAL PHYTOLITHS PRODUCED BY NATIVE PERENNIAL GRASSES TO TOTAL OPAL PHYTOLITHS FOR SOIL SAMPLES FROM THE JEPSON PRAIRIE AND FREQUENCY OF FIELDS WITH DUMBBELL OPAL. Sample size numbered 400 from each depth and location. Numbers in parentheses are 95 percent confidence intervals for each value from binomial distribution.

	Annual grassland		Perennial grassland	
Depth	Ratio	Dumbbell opal freq.	Ratio	Dumbbell opal freq.
Surface	0.056 (0.03–0.08)	0.45 (0.39–0.51)	0.154 (0.10–0.19)	0.89 (0.85–0.92)
10 cm	0.144 (0.10–0.18)	0.75 (0.70–0.80)	0.169 (0.13–0.22)	0.80 (0.75–0.84)

METHODS

In August 1984, we collected soil from the surface (0–1 cm) and from 10 cm depth at ten randomly located sites in each of the two locations. Collected samples were air-dried, and the gravel and organic debris removed. The five to 10 g of fine material remaining was sieved through 240 micron mesh plankton netting (Cwynar et al. 1969). Organic matter was removed using 30 percent hydrogen peroxide. Mechanical shaking in a sodium hexametaphosphate (0.5–1 molar)–sodium pyrophosphate (10%) solution dispersed aggregates. Dispersed soil was then wet-sieved through 107 micron mesh plankton netting. Microscopic inspection of coarser material verified that essentially all the opal had passed the sieve.

Particle sizing was performed by sedimentation and decantation using standard procedures (Jackson 1979) adjusted for specific gravity of opal (2.2 g/cc). Soil smears were prepared from a dilute, ammoniated soil/water suspension (Smithson 1961) and placed onto a standard microscope slide and mounted in cedarwood oil. Separate microscope counts were made on the medium silt (5–20 microns) fraction, at 400× magnification using a 0.2 × 0.4 mm grid system. A maximum of 50 fields/slide were used to record frequency of distinctive dumbbell phytoliths, tallied as ratio of dumbbell to total phytoliths.

RESULTS AND DISCUSSION

Dumbbell opal phytoliths, which could have been produced only by native grasses, were, as expected, more frequent in the surface soil of perennial grassland than of the annual grassland (Table 1). Dumbbell opals were nearly as frequent in the annual site subsurface soil as in the perennial site subsurface. Most of these opals are probably from *Stipa pulchra.* The low density of panicoid phytoliths in the surface of the annual grassland site apparently resulted from the replacement of native perennials by introduced annuals and the influx of non-panicoid opal.

Although the replacement of the native grassland by introduced species has been widely hypothesized (Heady 1977), using circumstantial sources of evidence such as the presence of relict stands of natives in presumed undisturbed sites, this study has produced the first documentation of replacement based on more direct evidence. The annual site apparently had a cover of native perennial bunchgrass vegetation. Since settlement by people of European origin, the bunchgrasses were replaced by introduced annuals on the present annual grassland site. Number and composition of panicoid-type phytoliths (Fig. 1c), including some "fan"-or "keystone"-shaped forms (Wilding et al. 1975, Metcalfe 1960) at 10 cm depth, suggests that the present perennial grassland site is similar to the original grassland in density of panicoid opal-producing native bunchgrasses.

Phytoliths show much potential as a tool to study historical changes in vegetation. At the Jepson Prairie, we were able to characterize vegetation change from a grassland dominated by perennial species, which produce panicoid-type phytoliths, to an annual grassland without panicoid opals. We were able to take advantage of a situation ideally suited to the use of opal phytolith characteristics. In other vegetation types, the changes will be more difficult to detect. However, even where the types of opal phytolith produced do not change at detectable levels, the relative abundance of opal in soil can be a useful diagnostic aid. Changes most likely to show large differences in the quantity of opal in the soil occur on grass/shrub or grass/tree boundaries because of the great difference in opal production between grasses and woody species. The invasion of meadows by trees, for example, should be readily detectable with opal phytolith studies. Because of the complementarity of pollen and opal phytoliths (the two tend to differentiate into taxonomic categories differently) and the different dispersal potential of phytoliths, the dual use of phytoliths and pollen for studies of vegetation history should increase.

ACKNOWLEDGMENTS

We thank representatives of the University of California Natural Reserves System and the Nature Conservancy for permission to work on the Jepson Prairie. Emeritus Professor Hans Jenny suggested this study and contributed his inspiration and advice. Professors Roger Byrne, Don Erman, and Paul Zinke lent use of their laboratories and equipment. Funds were provided by the California Department of Parks and Recreation.

LITERATURE CITED

BARKWORTH, M. E. 1981. Foliar epidermes and taxonomy of North American Stipeae (Gramineae). Syst. Bot. 6:136–152.

BARRY, W. J. 1972. The central valley prairie. Calif. Dept. Parks and Recr., Sacramento.

BARTOLOME, J. W. and B. G. GEMMILL. 1981. Ecological status of *Stipa pulchra* (Poaceae) in California. Madroño 28:172–184.

CWYNAR, L. C., E. BURDEN, and J. H. MCANDREWS. 1979. An inexpensive sieving method for concentrating pollen and spores from fine-grained sediments. Can. J. Earth Sci. 16:1115–1120.

DEWET, J. M. J. 1956. Leaf anatomy and phylogeny in the tribe Danthonieae. Am. J. Bot. 43:175–182.

HEADY, H. F. 1977. Valley grassland. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 491–514. Wiley-Interscience, New York.

JACKSON, M. L. 1979. Soil chemical analysis. 2nd ed. M. L. Jackson, Madison, WI.

JONES, L. H. P. and K. A. HANDRECK. 1967. Silica in soils, plants, and animals. Adv. Agron. 19:107–149.

METCALFE, C. R. 1960. Anatomy of the monocotyledons. Vol. I. Gramineae. Clarendon Press, Oxford.

MOORE, P. D. 1978. Botanical fingerprints. Nature 274:18.

PALMER, P. G. 1976. Grass cuticles: a new paleoecological tool for East African lake sediments. Can. J. Bot. 54:1725–1734.

ROVNER, I. 1983. Plant opal phytolith analysis: major advances in archaeobotanical research. Adv. Arch. Meth. and Theory 6:225–266.

SMITHSON, F. 1961. The microscopy of the silt fraction. Soil Sci. 12:145–157.

TWISS, P. C., E. SUESS, and R. M. SMITH. 1969. Morphological classification of grass phytoliths. Proc. Soil Sci. Soc. Amer. 33:109–115.

WILDING, L. P., N. E. SMECK, and L. R. DRESS. 1975. Silica in soils: quartz, cristabolite, tridymite, and opal. *In* J. B. Dixon and S. B. Weed, eds., Minerals in soil environments, p. 471–552. Soil Science Soc. Amer. Spec. Publ. Series.

(Received 1 Aug 1985; revision accepted 28 Apr 1986.)

NOTES

OBSERVATIONS AND AN EXPERIMENT ON SYNCHRONOUS FLOWERING.—Interspecific comparisons of flowering phenology show there is no single pattern for a given climate or vegetative phenology. Although the diversity of patterns ultimately must be accounted for in terms of external selective factors, proximal cues must be defined to comprehend and predict temporal variability and assess its effects. The variations can be investigated by natural and contrived experiments; several factors have been implicated, as reviewed briefly by Opler et al. (J. Biogeog. 3:231–236, 1976).

In the tropical deciduous forest at Chamela, Jalisco, México (109°30′N, 105°03′W; av. annual precip. 74.8 cm), a natural experiment in cueing of flowering to rainfall occurred in 1983. Following 18 rainless weeks, and over two weeks before the normal start of the rainy season, hurricane Adolfo passed by offshore bringing 14.9 cm of rainfall on 26 May (17.7 cm in four days). Some species that showed abrupt, generalized flowering in response to this rainfall were the following: *Zanthoxylum fagara* (L.) Sarg. (Rutaceae) began flowering on day two after the rain; *Bernardia spongiosa* McVaugh (Euphorbiaceae) on day three; *Hybanthus mexicanus* Ging. (Violaceae) on day four; *Samyda mexicana* Rose (Flacourtiaceae) and *Tabebuia chrysantha* (Jacq.) Nichols. (Bignoniaceae) on day six; *Erythroxylum havanense* Jacq. (Erythroxylaceae) on day eight; and *E. mexicanum* HBK. on day 11. Between days 10 and 14, several other species showed synchronous, short episodes of flowering. These plants included *Prockia crucis* P. Browne and *Casearia corymbosa* HBK. (Flacourtiaceae), *Hiraea reclinata* Jacq. (sensu lato), *Malpighia* sp. nov. (Malpighiaceae), and three species of *Randia* (Rubiaceae). In these cases, flowering ended within two to eight days, and did not occur again in 1983. In contrast, all typically flower at the start of the rainy season in late June or July.

To confirm the rainfall cue while separating root and bud wetting, to investigate the response to different magnitudes of soil wetting, and to test the effect of extraordinary events on normal flowering, I performed an experiment with *Erythroxylum havanense* (*Bullock 1345, 1346,* MEXU). This species is an understory shrub up to 200 cm tall; stem basal areas of the sample plants ranged from 0.64 to 19.42 cm^2. All experimental and control plants were located in one plot of 0.1 ha. On 23 May 1984, I watered the soil within 25 cm radius of each plant, as defined by a 10 cm high circular border. There were three water treatments [1.5 cm of water ($n = 12$ plants), 4.5 cm ($n = 12$), and 13.5 cm ($n = 4$)], in addition to the unwatered controls ($n = 12$). This year was rainless from 31 January through 10 June. Average soil moisture at 4–8 cm depth adjacent to five control plants was at 9.6 percent of field capacity. In monitoring the plants from 28 May to 3 June, I recorded the presence of buds and the number of flowers, as well as tendencies to leaf expansion.

Control plants and the 1.5 cm group produced no buds. All except two plants in the 4.5 cm and 13.5 cm groups produced both flower buds and leaf buds. On days seven and seven to eight after watering, two plants of the 4.5 cm group flowered; no leaves expanded. On days seven to eight or seven to nine, all plants of the 13.5 cm group flowered; leaves expanded to a variable extent but soon desiccated. Three of these plants flowered maximally on day seven, two on day eight, and one on day nine.

Without developing mature leaves or fruits, 81 percent of the experimental plants that responded to watering flowered again at the start of the rainy season (third week of June), as did all the controls. The possibility of repeated flowering in the other species mentioned above remains to be demonstrated. The delays from strong cue to flowering noted in 1983 may reflect the time for differentiation and/or growth of buds. The developmental cycles (Borchert, Biotropica 15:81–89, 1983) are unknown, but only *Bernardia spongiosa* and *Zanthoxylum fagara* have macroscopic resting buds. Multiple rains and flowerings during the dry season, as occur in Costa Rica and Panama (Opler et al., op. cit.; Augspurger, Ecology of a tropical rain forest:

MADROÑO, Vol. 33, No. 3, pp. 223–226, 1986

seasonal rhythms and long-term changes, p. 133–150, 1982), are not known at Chamela.

For *E. havanense,* a single rain of the middle magnitude may be sufficient for flowering, because rain does not leave small spots surrounded by dry soil. The waterings, however, were more effective than equivalent rain because interception by the forest canopy was avoided. Despite their survival in a comparatively dry climate, with seasonally extreme soil dryness, *E. havanense* and other species at Chamela probably require more rainfall to cue flowering than do similar species in central Panama (Augspurger, op. cit.). Most rains at Chamela are <1 cm (Bullock, Arch. Met. Geoph. Biocl. Ser. B, in press), so threshold moisture is probably approached sporadically in most years, but spatial unevenness in rainfall, canopy, and soil conditions must promote local asynchrony within species.

The manuscript benefited from comments by J. Henrickson and other reviewers.—STEPHEN H. BULLOCK, Estación de Biología Chamela (UNAM), Apartado Postal 21, San Patricio, Jalisco 48980, México. (Received 10 Jul 1985; revision accepted 23 Mar 1986.)

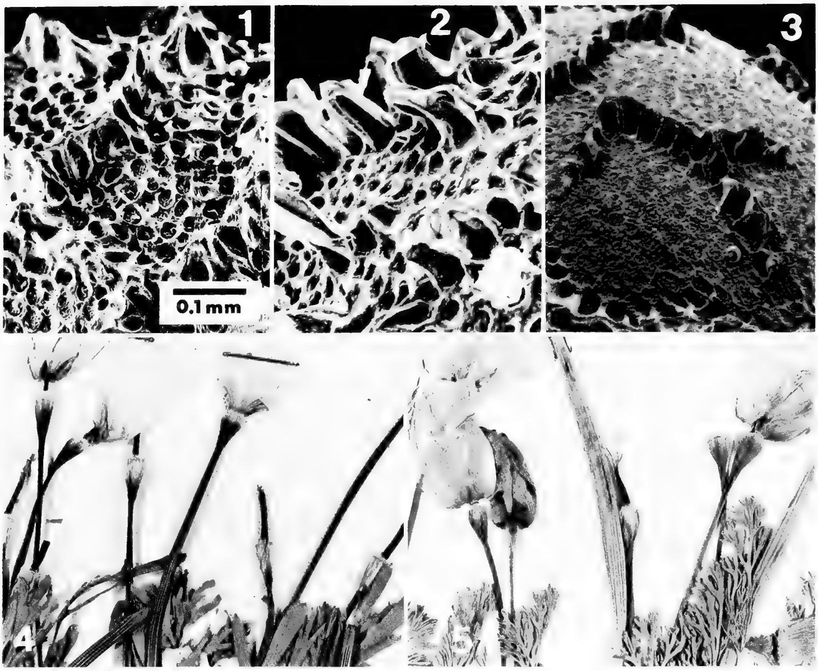
Eschscholzia lemmonii SUBSP. *kernensis* (PAPAVERACEAE), A NEW COMBINATION FOR THE TEJON POPPY.—While studying seed coat microsculpturing of *Eschscholzia* (Clark and Jernstedt, Syst. Bot. 3:386–402, 1978), I noticed that a collection labeled *E. caespitosa* Benth. subsp. *kernensis* Munz [6 May 1935, *Wolf 6738* (UC)] had seed coats unlike those of other samples of that species. This collection was made later in the same year and at the locality of the type specimen of this subspecies.

Although the seeds were unlike those of *E. caespitosa,* they were very similar to the seeds of *E. lemmonii* Greene (Figs. 1–3). Both have serrate ridge crests and foveate facet cells. Subspecies *kernensis* cells have micropapillae, which are somewhat unusual in *E. lemmonii,* and the ridges are more elevated, giving the seeds a somewhat "burlike" appearance, but they resemble the seeds of *E. lemmonii* more than those of any other species. In contrast, the ridges of seed coats of *E. caespitosa* are lower and the crests are generally uniform. Micropapillae are absent and the facet cells are generally polygonal or obscure, but never foveate.

Although the holotype of subsp. *kernensis* lacks the pubescent and nodding buds that are used to distinguish *E. lemmonii* in identification keys, it agrees in many other respects. Both plants have large turbinate receptacles (Figs. 4, 5), large, deep orange flowers, and stout stems and pedicels, contrasted with the small, obconical receptacles, smaller yellow flowers, smaller fruits, and slender stems and pedicels of *E. caespitosa.*

Twisselmann (Fl. Kern County, CA, 1967) also noticed these similarities, commenting that subsp. *kernensis* was "difficult to distinguish from glabrous forms of *E. lemmonii.*" These glabrous forms, unusual in the field, are common in greenhouse-grown plants, which may also have erect buds. Twisselmann's account of the range of the subspecies places it between the main range of *E. lemmonii* in the inner south Coast Ranges and its eastern extent in the northern Tehachapi Mountains, in the same grassland habitats. Both the range and the habitat differ sharply from those of *E. caespitosa,* which occupies open sites in oak woodland and chaparral at higher elevations.

Thus, subsp. *kernensis* differs from *E. lemmonii* consistently only by its burlike seeds. Munz apparently made the decision to include it in *E. caespitosa* because of its erect, glabrous buds, but it shares with *E. lemmonii* a number of features unique in the genus. Therefore, I propose the following combination.



FIGS. 1–3. Scanning electron micrographs of seed coats of *Eschscholzia*. 1. *Eschscholzia lemmonii* subsp. *lemmonii* (*Clark 556*). 2. *Eschscholzia lemmonii* subsp. *kernensis* (*Wolf 6738*). 3. *Eschscholzia caespitosa* (*Clark 570*). Scale refers to each figure. FIG. 4. Holotype of *Eschscholzia lemmonii* subsp. *kernensis* (*Wolf 6358*). Note the turbinate receptacles, similar to those in the next figure. FIG. 5. *Eschscholzia lemmonii* subsp. *lemmonii* (*Clark 556*).

Eschscholzia lemmonii Greene subsp. **kernensis** (Munz) C. Clark comb. nov.— *Eschscholzia caespitosa* Benth. subsp. *kernensis* Munz, Aliso 4:90. 1958.—TYPE: California, Kern Co., Tejon Hills 2 mi nw. of Tejon Ranch Headquarters, 15 Apr 1935, *Wolf 6358* (Holotype, RSA 12994!).

—CURTIS CLARK, Biological Sciences, California State Polytechnic University, Pomona 91768. (Received 16 Oct 1985; revision accepted 7 Feb 1986.)

A NOTE ON THE STATUS OF *Sidalcea nelsoniana* (MALVACEAE).—*Sidalcea nelsoniana* Piper is reported to be endemic to the Willamette Valley of Oregon. Hitchcock et al. (Vasc. Plants Pac. Northw. 3:428, 1961) give its distribution within the Willamette Valley as being from Salem to Portland, west to eastern Tillamook Co. It is reported as endangered by Ayensu and DeFilipps (Endang. Threat. Pl. U.S., Smithsonian Inst. and World Wildl. Fund, Wash., DC, 1978); and as rare and critically endangered, presently known from only two small roadside populations, by Siddall, Chambers, and Wagner (Rare, Threat., Endang. Vasc. Pl. Oregon, Oregon Nat. Area Preserves Advisory Comm., 1979). The Oregon Natural Heritage Data Base (pers. comm., 1984) lists 24 sites where *S. nelsoniana* is reported to occur. Of these sites, specimens were collected at 15, incorrectly identified from three, and unconfirmed at six.

The discovery of a population of *S. nelsoniana* in the area of a proposed water supply reservoir led to a distributional and ecological study of the species during the 1985 growing season. As a result of this cooperative study, involving the City of McMinnville Water and Light Department and the Salem Area Office of the Bureau of Land Management, the number of known populations has been increased and the geographic range of this species has been extended. In this study, 24 populations of *S. nelsoniana* were located. Six had been reported previously; 18 are new populations. The populations ranged in size from a few plants to several thousand plants. The species is presently found in the Coast Range of Tillamook and Yamhill cos. and in the Willamette Valley from Yamhill Co. south to central Benton and Linn cos.

Hitchcock (U. Wash. Pub. Biol. 18:1–79, 1957) reported that *S. nelsoniana* grew in more or less gravelly, well-drained soils. Our study demonstrated that it is not restricted to this type of soil, but is found more commonly in poorly drained, silty-clay loam soils that are subject to seasonal high water tables. It is, however, not found in soils that are wet throughout the year.

Sidalcea nelsoniana also is reported to be restricted to undisturbed remnants of Willamette Valley prairie grasslands and intolerant of disturbance (Beebe et al., Botanical field inventories, monitoring, planning. Ann. Report., U.S. Bur. Land Manage., Salem, OR, 1984; Meinke, Threat., Endang. Vasc. Pl. Oregon, U.S. Fish and Wildl. Serv., Portland, OR, 1982). The species is frequently found, however, in weedy meadows and roadside ditches dominated by introduced species. Such habitats are probably not prairie remnants, nor are the sites where Coast Range populations occur. Roadsides are areas often disturbed by mowing or construction, activities to which *S. nelsoniana* is at least fairly tolerant. A roadside population of *S. nelsoniana* on Meadow Lake Road in Yamhill Co. is subject to mowing, yet the population has increased in size in recent years. The largest Willamette Valley population occurs at the Oregon State University poultry farm and is mowed periodically. A Coast Range population grew, flowered, and set seed despite being run over by a bulldozer early in the growing season. *Sidalcea nelsoniana* also is able to colonize any suitable site and compete well with other vegetation. For example, the Meadow Lake Dam broke in 1964 and the Nestucca River cut a meandering course through the silted bed of the former reservoir. Several colonies of *S. nelsoniana* now occur on either side of the river in very weedy meadows. *Sidalcea nelsoniana* also can colonize roadsides following construction. The species may occur in prairie remnants and has been found associated with open stands of mature *Fraxinus latifolia* Benth., but is not restricted to that habitat. It is generally a component of seral communities and as such would disappear as succession proceeds.

Sidalcea nelsoniana is not as rare as earlier thought. It has been collected infrequently but this may be related to misleading information about its habitat. It usually occurs in weedy or seral communities, habitats not in danger of extinction. Finally, from the results of this study, the species range in Oregon is now known to include the Willamette Valley from Yamhill Co. south to central Benton and Linn cos. and can be extended into the Coast Range of western Yamhill and eastern Tillamook cos.—RICHARD R. HALSE, 4535 NW Beta Place, #3, Corvallis, OR 97330; JUDITH B. GLAD, 1400 N Holman, Portland, OR 97217. (Received 5 Nov 1985; revision accepted 17 Mar 1986.)

NOTEWORTHY COLLECTIONS

CALIFORNIA (LICHENS)

SPHINCTRINA LEUCOPODA Nyl. (CALICIACEAE).—Santa Barbara Co., Santa Cruz Island, along Islay Canyon Road halfway to Ridge Road, 33°59′30″N, 119°44′30″W, on *Pertusaria* sp. on *Quercus douglasii,* ca. 200 m, 14 Mar 1983, *C. Bratt 3032* (UPS). (Determined by L. Tibell, UPS.)

Significance. First record for CA. Although not listed by Hale and Culberson (Bryologist 73:499–543, 1970), Tibell considers it common further north (e.g., Minnesota: pers. comm.).

CYPHELIUM PINICOLA Tibell (CYPHELIACEAE).—Ventura Co., Pine Mountain Ridge, Pine Mountain Campground, T6N R23W S4, on decorticated branch found under *Pinus jeffreyi,* ca. 1825 m, 9 Nov 1985, *C. Bratt 4911* (Bratt). (Determined by L. Tibell, UPS.)

Significance. Second collection in CA, first since 1903. Although a Hasse collection of 1903 from Murietta in Riverside Co. is cited by Tibell (Symb. Bot. Upsal. XXI: 54, 1975), it is not included in Tucker and Jordan (Wasmann J. Bio. 36:1–105, 1978). It also should be noted that the spore size (9–10.5 × 6.5–7 μ) of the Bratt collection is smaller than that (13–17 × 7–9 μ) cited by Tibell in his monograph.

HYPOTRACHYNA REVOLUTA (Flk.) Hale (PARMELIACEAE).—Santa Barbara Co., Santa Cruz Island, Western (Christy) pines, 34°00′30″N, 119°49′00″W, on *Pinus remorata,* ca. 400 m, 6 Aug 1983, *C. Bratt 3489A* (US, Bratt). (Determined by M. E. Hale, US.)

Significance. First record of this genus in CA. Although common on the pines of Santa Cruz Island, it has not been found in similar habitats on the mainland.

CALOPLACA ROSEI Hasse (TELOSCHISTACEAE).—Santa Barbara Co., Santa Barbara Island, along trail to Webster Point, 32°28′30″N, 119°02′00″W, ca. 60 m, 8 Oct 1983, *C. Bratt 3684, 3685* (Bratt). (Determined by W. A. Weber COLO.)

Significance. Second or possibly first collection in CA. This species was described by H. E. Hasse (Bryologist 14:10, 1911). It was collected by Dr. J. N. Rose of the Smithsonian Institution at "San Roque, California". Because Hasse did not include this species in his 1913 publication (Lichen Flora of Southern California, U.S. National Herbarium 17:1–132, 1913), it is possible that "San Roque" referred to by him was in Baja California, which would make this a first collection in California.

Caloplaca rosei is a very distinctive species because of its pale yellow to white lacy hypothallus. In 1968, it was collected by G. F. Otto near Vancouver, British Columbia. It is probably more widespread than reported.—CHARIS C. BRATT, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Rd., Santa Barbara, CA 93105.

MONTANA

ARCTOSTAPHYLOS PATULA Greene subsp. PLATYPHYLLA (Gray) Wells (ERICACEAE).—Previously unrecorded in state and widely disjunct here—Lake Co. (nw. Montana), ridgetop 2.1 km n. of Lake Mary Ronan (townsite) and 14 km nw. of Dayton, T25N R22W S3 ne., at 1280 m, approximately 40 shrubs, 6–10 dm high in rocky, quartzite-derived soil with scattered *Pinus ponderosa, Pseudotsuga menziesii,* and *Juniperus communis,* 25 May 1984, *Lesica 2950* (MONTU, KANU, UC); same location, 10 Aug 1984, *Lesica 3420* (MONTU, KANU, UC); same location, 25 Jun 1976, *Lackschewitz, Stickney and Rumely 6514* (MONTU). Occurs sympatrically with the prostrate *A. uva-ursi* (L.) Spreng., a circumboreal species that is widely abundant here and elsewhere in the Rocky Mountains. The Montana colony of *A. patula* has apparently hybridized to some extent with *A. uva-ursi* as there are individuals of intermediate stature and leaf morphology, a situation strikingly similar to the pattern

---

MADROÑO, Vol. 33, No. 3, pp. 227–231, 1986

observed on the Uncompahgre Plateau of Colorado by Rollins (Rhodora 39:462–463, 1937). *Arctostaphylos patula* subsp. *platyphylla* from Colorado was described as *A. pinetorum* Rollins and the hybrid with *A. uva-ursi* as *A. coloradense* Rollins.

Significance. Previously known from as far n. as w. CO, central and w. (Deep Creek Range) UT, the Snake Range of eastern NV and the Cascade Mountains n. to Klickatat Co., sw. WA, the firm identification of *A. patula* subsp. *platyphylla* from Montana establishes an extraordinary northward range extension of 900 km from NV or 600 km from WA. Plants from the MT population have the golden glandulosity and broadly ovate leaves of typical *A. patula* and the absence of burl with vegetative proliferation by peripheral layering that characterize subsp. *platyphylla.* Although this widely disjunct colony of *A. patula* subsp. *platyphylla* could be the product of a long-range dispersal event, there is the possibility that this taxon had a wider distribution during the warmer phases of the Holocene and a search for other colonies at intermediate points (as in Idaho, where it is unrecorded) may be fruitful. The manzanita population from Lake Mary Ronan has been known since at least 1969 (specimens in MRC); this colony of *A. patula* subsp. *platyphylla* is apparently the basis for a report of *A. pungens* HBK. from Montana by Hitchcock and Cronquist (Fl. Pacific Northwest, 1976).—PETER LESICA, Dept. Botany, Univ. Montana, Missoula 59812 and PHILIP V. WELLS, Botany Dept., Univ. Kansas, Lawrence 66045.

NEVADA

ASTRAGALUS CERAMICUS Sheldon var. CERAMICUS (FABACEAE).—Lincoln Co., Dry Lake Valley, ca. 28 km w. of Pioche, common on semi-barren habitats with *Chrysothamnus* etc., T1N R64E, 1426 m, 23 May 1985, *R. Nichols 456* (NY).

Significance. First record for NV and a wsw. range extension of about 80 km from Beaver Co., UT. Previously known from e. MT and adjacent ND to w. OK, NM, AZ and UT.

GILIA CONGESTA var. CREBRIFOLIA (Nutt.) A. Gray (POLEMONIACEAE).—White Pine Co., Snake Range, 2.9 km e. of Murphy Wash road on road to Big Springs Wash, s. end of the range, growing in the cracks of limestone rock outcrops, T10N R68E, 1966 m, 23 May 1985, *Tiehm 9478* (CAS, NY, RSA, UTC).

Significance. First record for NV and a 50 km range extension from the Wah Wah Mountains of Beaver and Millard cos., UT. Previously known from sw. MT and n. WY to NM and UT.

RANUNCULUS NATANS var. INTERTEXTUS (E. L. Greene) L. Benson (RANUNCULACEAE).—Elko Co., O'Neil Basin, Cottonwood Creek at the Cottonwood Ranch, common along the creek, T45N R61E S31, 1829 m, 2 Aug 1985, *Tiehm 10076* (CAS, NY, RSA, UTC).

Significance. First record for Nevada and a s. range extension of over 250 km from central ID. Previously known from s. Canada s. to CO and ID.—ARNOLD TIEHM, The New York Botanic Garden, Bronx, NY 10458.

OREGON

ALLIUM ACUMINATUM Hook. (LILIACEAE).—Benton Co., ca. 6.5 km nw. of Philomath along U.S. Hwy. 20 at The Nature Conservancy's Wren Prairie Preserve, under a canopy of *Pseudotsuga menziesii* and *Quercus garryana,* within 5 m of a forest-meadow ecotone dominated by *Festuca rubra, Toxicodendron diversilobum,* and *Pteridium aquilinum,* 265 m, 14 Jul 1985, *Meinke 3225* (OSC); ca. 3.5 km se. of downtown Corvallis in Willamette Park, in gravel floodplain ca. 150 m w. of the Williamette River with numerous native and introduced herbaceous species—probably a waif, 78 m, 2 Jun 1985, *Meinke 3155*—(OSC); "Dimple Hill, near Corvallis", ca. 250 m, 10 Jul 1933, *Barss s.n.* (OSC); Linn Co., "Saddle Butte, on open slopes on north side", 185 m, 26 Jun 1947, *Evenden s.n.* (OSC).

Significance. First records for w. OR, a range extension of ca. 140 km from the main distribution of the species e. of the Cascade Mtns.; also known w. of the Cascades ca. 500 km to the n. on Vancouver Is., BC and adjacent parts of nw. WA, in the general region influenced by the Olympic Mtns. rainshadow. In w. OR, populations often are affiliated with relict stands of native prairie.

ALLIUM TOLMIEI Baker var. PERSIMILE Ownbey (LILIACEAE).—Wallowa Co., Wallowa-Whitman Natl. Forest (Hell's Canyon Natl. Rec. Area), rocky slopes in the vicinity of Buckhorn Springs Observation Site overlooking the Imnaha River drainage, locally common with *Phlox viscida* and *Eriogonum* spp., 1640 m, 15 May 1982, *Meinke 2983* (OSC).

Significance. First record for OR, a range extension of ca. 55 km nnw. from the s. end of the Seven Devils Range in Adams Co., ID. Population scattered over about 4 ha.

ALLIUM TOLMIEI Baker var. PLATYPHYLLUM (Tidestrom) Ownbey (LILIACEAE).—Baker Co., Wallowa-Whitman Natl. Forest, 4.5 km n. of China Spring and 0.5 km e. of Forest Service Rd. S-77, in extremely rocky soil along ridge with *Artemisia rigida, Poa cusickii,* and *Eriogonum thymoides,* 1350 m, 15 Jun 1978, *Meinke 1981* (OSC); ca. 2.0 km n. of State Hwy. 86, along ridge ca. 0.5 km e. of Forest Service Rd. S-77, 1310 m, 11 Jun 1978, *Meinke 1941* (Forest Serv. Herb.—Baker, OR).

Significance. A county record and s. range extension of ca. 80 km from n. Union and Wallowa cos., representing an extensive series of populations occurring along the s. flank of the Wallowa Mtns. This and the preceding report demonstrate that the currently recognized varieties of *A. tolmiei* are not strictly allopatric, as suggested by Ownbey (*in* Vasc. Plants Pac. Northw. 1:758, 1969). The presence of significant numbers of individuals "keyable" to var. *persimile* within predominantly var. *platyphyllum* populations, and vice versa, indicates at least a local breakdown of morphological separation as well.

ARABIS CRUCISETOSA Const. & Rollins (CRUCIFERAE).—Wallowa Co., Wallowa-Whitman Natl. Forest (Hell's Canyon Natl. Rec. Area), n. end of Summit Ridge between Fingerboard Gulch and Deep Cr., ca. 5.0 km n. of Lord Flat in a n.-facing *Pseudotsuga menziesii* thicket with *Physocarpus* and *Cerastium,* T3N R49E S25, 1385 m, 14 Jun 1979, *Leary and Leary 3275* (OSC).

Significance. First record for OR, a range extension of 30–50 km from se. WA and w. ID. This corrects a perpetuated misunderstanding that the single OR station for this species occurs at or very near Hat Point, actually 24 km to the s. (see Siddall et al., Rare, Threat., Endang. Vasc. Plants in Oregon—an interim report. Oregon Div. of State Lands, Salem, 1979; Vorobik, A key to the species and varieties of *Arabis* that occur in Oregon, 1985 [unpubl. ms. on file at OSC]).

BUPLEURUM AMERICANUM Coult. & Rose (UMBELLIFERAE).—Wallowa Co., Wallowa-Whitman Natl. Forest in the Wallowa Mtns., along Wing Ridge at the head of Little Sheep Cr. in reddish basaltic scoria, T4S R45E S24, 2710 m, 5 Aug 1982, *Johnson s.n.* (Forest Serv. Herb.—Baker, OR; OSC).

Significance. A county record and range extension of 90 km ne. from the Elkhorn Range, the only other locality for this species in the Pacific states (Meinke, Bull. Torr. Bot. Club 105:232, 1978); otherwise known from AK s. through the Rocky Mtns. into MT, e. ID, and WY.

CASTILLEJA CHLOROTICA Piper (SCROPHULARIACEAE).—Deschutes Co., ca. 9.5 km s. of Millican, on knoll e. of Pine Mtn. Observatory with *Artemisia tridentata, Chrysothamnus viscidiflorus,* and *Festuca idahoensis,* T20S R15E S33, 1905 m, 22 Jul 1980, *Kennison 153* (OSC, NY).

Significance. Only the third locality known for this species, a range extension of

70 km e. from the Tumalo Cr. area and 160 km n. from Gearhart Mtn. This collection confirms the existence of undetected, intervening populations predicted by Holmgren (Mem. N.Y. Bot. Gard. 21:28, 1971).

LOMATIUM GREENMANII Math. (UMBELLIFERAE).—Wallowa Co., Wallowa-Whitman Natl. Forest in the Wallowa Mtns., just s. of Ruby Pk. summit on reddish mudstone, in alpine community with *Ivesia,* T2S R44E S31, 2730 m, 26 Aug 1984, *Kierstead s.n.* (OSC).

Significance. Only the second known population of this rare species; otherwise only found 18 km to the se. on the summit of Mt. Howard (Meinke and Constance, Madroño 29:13–18, 1982), where it is under constant threat of extirpation from intensive recreational activities.

LYTHRUM HYSSOPIFOLIA L. (LYTHRACEAE).—Linn Co., 1.0 km e. of Willamette River off of State Hwy. 34, along sandy shore of large pond formed in abandoned gravel excavation with *Gratiola ebracteata* and *Downingia yina,* 80 m, 15 Jun 1985, *Rimbach s.n., Meinke 3156* (OSC).

Significance. County record and only the third collection of this cosmopolitan species recorded from the Willamette Valley of w. OR; otherwise chiefly coastal in the Pac. Northw.

ONOBRYCHIS VICIAEFOLIA Scop. (LEGUMINOSAE).—Union Co., e. edge of La Grande along Geckler Ln. in waste field, with *Bromus tectorum* and *Tragopogon dubius,* 845 m, 6 Jun 1978, *Meinke 1890* (OSC); Baker Co., along shoulder of I-84 ca. 3.0 km s. of North Powder, T6S R39E S26, 1015 m, 4 Jun 1978, *Leary and Leary 2536* (OSC); Grant Co., 4.5 km due s. of Seneca, w. of Silvies Valley, T17S R31E S15, 1425 m, 10 Jul 1980, *Wright 1369* (OSC).

Significance. First records of the spontaneous spread and establishment of this European weed in OR. Since the initial documentation reported here, the species has expanded its ne. OR range and now occurs at many locations along the I-84 corridor between the towns of Baker and La Grande. *Onobrychis* was first introduced in OR in 1940 at the Oregon St. Univ. Squaw Butte Exp. Sta., Harney Co., 220 km sw. of Baker (series of collections at OSC by G. Powell).

PETASITES FRIGIDUS (L.) Fries var. PALMATA (Ait.) Cronq. (COMPOSITAE).—Umatilla Co., Umatilla Natl. Forest, along Umatilla River (N. Fork), ca. 4.5 km sse. of Bingham Springs, T3N R37E S22, 740 m, 24 Apr 1982, *Meinke 2912*; Umatilla Natl. Forest, "Off the trail in N. Fork Umatilla River Campground", ca. 735 m, 11 Apr 1985, *Rule 5* (OSC).

Significance. Only the second w. U.S. locality for this species e. of the Cascade Mtns.; a range extension of ca. 270 km from the main distribution of the species in and w. of the Cascades, and ca. 75 km nw. from the only previously reported disjunct population in the w. U.S. (Meinke, Northw. Sci. 54:237–243, 1980).

POTENTILLA RECTA L. (ROSACEAE).—Union Co., hills w. of La Grande, very abundant on e.-facing slope with *Trifolium plumosum* and *Agropyron spicatum,* T3S R38E S7, 925 m, 5 Jul 1978, *Leary 2697* (OSC).

Significance. First record of the spontaneous establishment of this Eurasian weed in OR; also known from e. WA and nw. MT, and apparently common in the e. U.S.—ROBERT J. MEINKE, Herbarium, Dept. Botany & Pl. Path., Oregon St. Univ., Corvallis 97331; PATRICK J. LEARY, Science Dept., Clark Co. Comm. Coll., 3200 E. Cheyenne, North Las Vegas, NV 89030; and JULIE KIERSTEAD, Berry Botanic Garden, 11505 SW Summerville, Portland, OR 97219.

UTAH

SANGUISORBA MINOR Scop. subsp. MURICATA Briquet (ROSACEAE).—Washington Co., Zion National Park, weedy margin of parking lot at Kolob Canyon overlook, 37°25′40″N, 113°11′50″W, elev. ca. 1900 m, 15 Sep 1984, *Clark 634* (CSPU).

Significance. Evidently the first report for UT. The species is an occasional European garden escape in CA (E. McClintock, pers. comm.), infrequent elsewhere in the west. Kearney and Peebles (Arizona Flora, 1951) report it from Maricopa Co., AZ, and Hitchcock and Cronquist (Fl. Pacific Northwest, 1973) report it as a garden escape in the w. Cascade Mtns. It is not included in McDougall (Seed Pl. N. Arizona, 1973). The species may be more frequently collected by students in introductory taxonomy courses and not identified; the achenes are tightly invested by the hypanthium, giving the appearance of an inferior ovary, which, coupled with its lack of petals, is confusing to a novice not familiar with the genus.—CURTIS CLARK and NANCY CHAREST, Biol. Sci. Dept., California St. Polytechnic Univ., Pomona 91768.

REVIEWS

A Preliminary Verified List of Plant Collectors in Mexico. Compiled by IRVING W. KNOBLOCH. iv + 179 pp. Bibliography. Phytologia Memoirs VI. Moldenke and Moldenke, 303 Parkside Road, Plainfield, NJ. 1983. Offset. $16.00 domestic, $17.00 foreign surface mail, and $19.00 foreign air mail.

Over the decades botanists have found great value in lists of miniscule biographic sketches of the motley group of collectors who gathered the plant specimens on which systematic botany is based. The immense growth in numbers of such contributors has required the publication of national and regional lists to which botanists could turn for information on even obscure collectors and their work. The areas visited, dates and kinds of collections, extent and places of deposit of gatherings are all of interest to the systematist who cites herbarium specimens collected by persons unfamiliar to him. It is too much to hope that any list of collectors will be so exhaustive that all collectors will be included or that all collecting activities of any one will be detailed. The value of each compilation, however, must be judged by the quantity and quality of the information offered. This list consists of names arranged alphabetically and usually accompanied by one or more citations of publications in which, presumably, information or verification may be found.

One expects in a treatment of the botanical collectors of an area two very definite qualities. First, it should be clear that all persons included have performed meaningful botanical collecting in significant quantity and evidence of this should be furnished as the basis of the compiler's judgment. Second, information on geographic and phylogenetic characteristics of collections and the abundance and distribution in herbaria of specimens, to the extent that these are known, should be offered relative to each collector. In this list citations to literature, which contains such information, are offered in lieu of facts. The reader has every right to expect the facts to be offered at least in economical outline form. The average reader, moreover, simply does not possess the library required to use this list.

This treatment is an outgrowth of Knobloch 1979, *The plant collectors of northern Mexico.* The scope and mass of the earlier list are vastly extended in the present effort, but the word "preliminary" in the title is still more accurate than the word "verified". The compiler's effort to avoid omission of significant collectors has ap-

---

MADROÑO, Vol. 33, No. 3, pp. 231–233, 1986

parently resulted in the inclusion of trivial and incidental collectors for whom no evidence of serious botanical effort is known. In this age of easy transportation, considerable numbers of plant collections result from rather well-attended social events, and everyone's name appears on the herbarium label. Somewhat less clearly trivial is the second name on a joint collection cited in a taxonomic paper. It seems very doubtful, however, that such a collector is truly significant unless many more examples of his or her participation come to light. It might have been desirable to limit the list to those known to be significant botanical collectors. The true verification of all included collectors, however, will have to be undertaken one day, perhaps by the author of the next list of collectors of Mexican plants. This author of a future time will find the Knobloch list a massive source of literature citations bearing upon a great many nominees for inclusion. He would have difficulty finding a better starting point for his work. For this reason, all institutional botanical libraries should shelve a copy of this booklet.—C. H. MULLER, Dept. Biological Sciences, Univ. California, Santa Barbara 93106.

The Solanaceae of New Guinea. By D. E. SYMON. Journal of the Adelaide Botanic Gardens. Volume 8. Adelaide Botanic Gardens, North Terrace, Adelaide, South Australia. 1985. (No price given.) ISSN 0313-4083.

David Symon has given us the first comprehensive treatment of the family Solanaceae for New Guinea and the offshore islands, including the Solomon Islands. Keys are provided and full descriptions and specimen citations are given for all of the species. The only native genus is *Solanum,* for which 59 species are recognized, seven of which are introduced and 19 of which are described as new. Excellent illustrations, either drawings or photographs, are included for all of the species of *Solanum.* The ten other genera that are present represent naturalized or cultivated plants, all but one of which come from tropical America. The presence of some species in New Guinea raises interesting phytogeographic problems. For example, one of the new species described, *Solanum atheniae,* is tentatively placed in the section *Lasiocarpa,* whose species are predominantly American.—CHARLES HEISER, Dept. Biology, Indiana Univ., Bloomington 47405.

Manual de Herbario, Administración y manejo de colecciones, técnicas de recolección y preparación de ejemplares botánicos. By ANTONIO LOT y FERNANDO CHANG. Consejo Nacional de la Flora de México. 1986. 142 pp. $6.00. [Or it may be purchased directly from the Departmento de Botánica del Instituto de Biología, UNAM, Apdo. Postal 70-233, 04510 México, D.F.]

Various manuals for preparation of herbarium specimens and the care and management of herbaria have been published, but heretofore nothing of the wide scope of this *Manual de Herbario.* The first third of the Manual presents a general discussion of the structure and organization of an herbarium. First, obtaining the specimens, then processing them for inclusion in permanent housing, details of management, use of computers in a herbarium, etc. Included in this first part is a bibliographical guide by Armando Butanda C. (pp. 31–44). This provides valuable references for all aspects of managing a herbarium as well as important works and periodicals treating taxonomy.

Two-thirds of the volume is devoted to detailed instruction for techniques of collecting and preparing herbarium specimens in various groups: algae, fungi, lichens, bryophytes, pteridophytes, vascular aquatics, Gramineae, succulents, epiphytes, palms, and trees. Most of these sections are well illustrated and they all include special bibliographic references. For example, Hermilo Quero of the Jardín Botánico, in his discussion of palms, not only discusses the difficulties of making palm collections, but also provides four pages of figures illustrating the essential parts of a palm that should be included in or noted for a palm specimen.

The Manual will be a valuable reference work, not only for those scientists embarking on the establishment of a herbarium, but also for an established herbarium. The portion of the volume dealing with field techniques for special groups will be invaluable for collectors. The extensive bibliographic sections provide a ready source of indispensable reference material.

Preparation of this manual was promoted by the National Council of the Flora of Mexico to advance the orderly increase of Mexican collections.—ANNETTA CARTER, Herbarium, Department of Botany, University of California, Berkeley 94720.

LETTERS

Dear Editor:

I read the note (Madrono V. 33, No. 1, pp. 76–78, 27 March 1986) about presence and absence of spines in petioles in *Washingtonia filifera* by James W. Cornett and would like to suggest an alternate hypothesis. Instead of the notion that the palm ceases petiole spine production in taller individuals because of the absence of (very) tall herbivores, I would like to suggest the possibility that some simple physiological mechanism (for example, increased water stress with increased height and exposure) might be responsible. We should remember, after all, the simple sun and shade variations in the foliage of many plants.

Stephen D. Veirs, Jr.
Redwood National Park
1125 16th Street
Arcata, CA 95521

Dear Editor:

Here is my written response to Stephen D. Veirs, Jr., who wrote concerning my explanation for the absence of petiole spines in tall individuals of *Washingtonia filifera.*

If one accepts the notion that petiole spines evolved as a result of the protection afforded the apical meristem, then, in the absence of any documentation to the contrary, one must also assume that the selective pressure favoring the development of petiole spines decreases with height. That is what the data in Table 1 indicates at this time. Further, is it merely a coincidence that the percentage of each petiole covered with spines begins to markedly decrease at the uppermost reach of the largest known Pliocene-Pleistocene herbivore? Any other explanation must answer this question and deal with the demise of the spines instead of some other trait of the species. I'll stick with my hypothesis for the time being.

James W. Cornett
Natural Science Department
Palm Springs Desert Museum
101 Museum Drive
Palm Springs, CA 92263

MADROÑO, Vol. 33, No. 3, p. 233, 1986

COMMENTARY

PRONUNCIATION OF SCIENTIFIC NAMES

I attended the Tercentenary of the Edinburgh Botanical Garden a few years ago and found myself in the unenviable position of having to read Peter Raven's paper on the Mediterranean Flora, Peter having been quarantined at the Zurich airport after exposure to some epizootic. If any of you have ever had to do this you realize that it is a thankless job; you won't do it well, and your listeners will resent the fact that they are not getting the word from the "horse's mouth".

After a few seconds of cogitation, I thought I had something that would put the audience in the palm of my hand. When I got to the rostrum, I announced that Peter was not here to give his presentation, a fact that I regretted as much as they did, but that to compensate them I would offer them a bonus: I would pronounce the scientific names in "European". I did, and they were overjoyed because they could understand me without having the words written out. After the reading, Dr. Clapham came up to me and said: "You know, I really think that we English-speakers should make some effort to meet the Europeans half-way." A remarkable statement considering the source, and ever since that day I have been teaching and preaching this to my students and colleagues.

For some reason, it seems to me that Americans and Englishmen try very hard to understand Europeans; we mentally translate their broken English into our equivalent, for we know they are trying a lot harder than we ever could to master a horrible foreign language. On the other hand, when the Amerenglish speak to Europeans about plants and animals and use scientific names one can almost see the hands instantly clap themselves against their ears; they do not even try to understand us; our pronunciation is, as one German colleague put it, "quite something other". This is true of our students as well. Try to give any group of students a list of plant names, orally, and see the spellings they come up with!

William T. Stearn, in his chapter on *The Latin Alphabet and Pronunciation,* in "*Botanical Latin*", approaches this middle ground, especially in his recommendations on the sounds of letters. But he still likes the Classical Latin pronunciation of the words. Nevertheless, he says: "How they are pronounced really matters little provided they sound pleasant and are *understood by all concerned.*" Here is the crux of the matter. I choose to play down the rules on stress and antepenultimates in favor of understanding. My rules are simple:

1. Try to approach the style of pronunciation of the person you are talking to. This is the cardinal rule.

2. Remember these things about European pronunciation of the letters: *i* is never pronounced "*eye*", always as in "*see*" or as in "*sit*". Terminal double *ii* can be slightly separated but not necessarily. *A* is never "*ay*" but always "*ah*". *Y* is not as in "cipher", but as in "cynical". *E* is never *ee* but *eh.* Consonants are not so simple, their sound often depending on the listener's nationality. Try "*Halerpestes* on for size. The Russians make it *Khal-yer-pyes-tyes.* But *ti* can be *tsi* but never "*sh*".

3. Most important to my thesis of "understandability", and this goes against classical pronunciation: try not to distort the sound of the various word stems by accenting unimportant connecting vowels, particularly "*o*". *Phyl*lo-*phor*a, rather than phyll*oph*-ora. Try not to change the sound of the person or place of honor: *nut*tall-i, not nut-*tallee*-eye (Hulten hated that pronunciation with a white passion; he would grit his teeth and rub it in my nose with a vengeance); *We*ber-i, not We*beer*ee-eye; *E*ric-a, not Er-*eye*-ca.

That's all there is to it. Of course there are purists who insist that if there are rules

MADROÑO, Vol. 33, No. 3, pp. 234–235, 1986

of Classical Latin we should stick to them. At the expense of communication? I think not. As Stearn also points out, "The relation of botanical Latin to classical Latin is that of a former dependency which by vigorous economic growth over many years has established traditions and divergencies arising out of its special conditions and history that must be accepted, if need be, by proclaiming its status as a language in its own right."

Nobody can honestly say that Amerenglish pronunciation of the vowels and consonants is Latin, so why should we worry about the accentuation either? We are in a smaller world now, and spoken science is more common among the peoples of our world than it was when Classical Latin was important. As Clapham suggested, "Let's meet them half way!"

William A. Weber
Campus Box 218
Univ. Colorado Museum
Boulder, CO 80309

FINAL ANNOUNCEMENT

RARE AND ENDANGERED PLANTS—A CALIFORNIA CONFERENCE ON THEIR CONSERVATION AND MANAGEMENT

5–8 November 1986

Location: The conference will be held at the Capital Plaza Holiday Inn, 300 J Street, Sacramento, CA, U.S.A.

The California Native Plant Society (CNPS), in conjunction with government agencies, conservation groups, and private corporations, is organizing a conference on the conservation and management of rare and endangered plants. It is designed to be a forum for information exchange through concurrent sessions, poster sessions, and workshops. Proceedings will be published by CNPS.

Co-sponsors include: California Department of Fish and Game, The Nature Conservancy, California Botanical Society, The Rancho Santa Ana Botanic Garden, Pacific Gas & Electric, Southern California Edison, Bureau of Land Management, Jones & Stokes Associates and U.S. Fish and Wildlife Service.

Keynote speakers include: Dr. Paul Ehrlich (Stanford Univ.), Dr. Daniel Axelrod (Univ. California, Davis), Dr. Ray Dasmann (Univ. California, Santa Cruz), Mr. Ed Hastey (California Director, Bureau of Land Management), Mr. Zane Smith (Regional Forester, U.S. Forest Service), and Dr. Faith Campbell (National Resource Defense Council).

Questions or comments regarding the conference should be directed to: Jim Nelson, Conference Coordinator, California Native Plant Society, 909 12th Street, Suite 116, Sacramento, California 95814, U.S.A.

ANNOUNCEMENT

EDGAR T. WHERRY COLLECTION

Some members of the Delaware Valley Chapter of the American Rock Garden Society have volunteered to locate and catalog letters and other written material, slides and photographs, and memorabilia relating to the life and work of our respected friend, the late Dr. Edgar T. Wherry.

Arrangements have been made to house and service the Wherry Collection in the library of the Academy of Natural Sciences of Philadelphia for the benefit of future students and researchers.

If you have such material in your files—or if you know someone or some institution that might have—I would appreciate hearing from you with the goal in mind of receiving such material or copies thereof. Suggestions for expanding this search will be greatly appreciated, too.—MILTON LADEN, 334 Wellesley Road, Philadelphia, PA 19119.

ANNOUNCEMENT

THE JEPSON MANUAL OF VASCULAR PLANTS OF CALIFORNIA

120 authors are now committed to writing portions of THE JEPSON MANUAL. About 15% of draft text is now in hand, covering all or part of more than 30 families; illustrations are being prepared as rapidly as authors provide detailed guidelines and will eventually cover ca. 3000 taxa. THE JEPSON MANUAL will be oriented to a diversity of users and will highlight plants that are rare or endangered, have potential for native gardens, are toxic to humans or livestock, or are invasive weeds. The INTRODUCTION and FAMILY KEYS will be distributed early, allowing time for substantial pre-publication review. Funding in addition to Jepson's endowment is being sought aggressively; a "Friends" organization is being established this summer, with Margedant Hayakawa and G. Ledyard Stebbins as Co-chairs.

Additional authors are still sought. Contact James C. Hickman (Botany Dept., U. of California, Berkeley, CA 94720; 415-643-7008) if you wish more information, are interested in joining this project, or know of those we might invite to participate.

Groups available: 13 Apocynaceae; 4 Aristolochiaceae; 100 misc. Asteraceae; 7 Betulaceae; 125 misc. Boraginaceae; 7 Callitrichaceae; 18 Capparidaceae; 8 misc. Convolvulaceae; 3 Frankeniaceae; 4 Haloragaceae; 3 Krameriaceae; 44 misc. Lamiaceae; 7 Polygalaceae; 24 misc. Portulacaceae; 20 misc. Rhamnaceae; 8 Salicaceae (*Populus*); 20 Verbenaceae; 40 Violaceae; 4 Vitaceae; 90 misc. Liliaceae; 200 misc. Poaceae.

Volume 33, Number 3, pages 157–236, published 5 September 1986

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $3.00 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

CALIFORNIA BOTANICAL SOCIETY

VOLUME 33, NUMBER 4 OCTOBER 1986

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

NOTES

NOTEWORTHY COLLECTIONS

(*Contents continued on back cover*)

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: $25 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

Editor—WAYNE R. FERREN, JR.
Associate Editor—BARRY D. TANOWITZ
Department of Biological Sciences
University of California
Santa Barbara, CA 93106

Board of Editors
Class of:

1986—AMY JEAN GILMARTIN, Washington State University, Pullman
ROBERT A. SCHLISING, California State University, Chico
1987—J. RZEDOWSKI, Instituto de Ecologia, A.C., Mexico
DOROTHY DOUGLAS, Boise State University, Boise, ID
1988—SUSAN G. CONARD, USDA Forest Service, Riverside, CA
WILLIAM B. CRITCHFIELD, USDA Forest Service, Berkeley, CA
1989—FRANK VASEK, University of California, Riverside
BARBARA ERTTER, University of California, Berkeley
1990—STEVEN TIMBROOK, Santa Barbara Botanic Garden
THOMAS R. VAN DEVENDER, Arizona–Sonora Desert Museum, Tucson

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1985–86

President: FRANK ALMEDA, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

First Vice President: PATRICK ELVANDER, 443 Applied Sciences, University of California, Santa Cruz, CA 95064

Second Vice President: KINGSLEY R. STERN, Department of Biology, California State University, Chico, CA 95929

Recording Secretary: V. THOMAS PARKER, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132

Corresponding Secretary: JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Treasurer: THOMAS F. DANIEL, Department of Botany, California Academy of Sciences, San Francisco, CA 94118

Financial Officer: CHERIE L. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President,* CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928; the *Editor* of MADROÑO; three elected *Council Members:* THOMAS FULLER, 171 Westcott Way, Sacramento, CA 95864; ANNETTA CARTER, Department of Botany, University of California, Berkeley, CA 94720; JOHN MOORING, Department of Biology, University of Santa Clara, Santa Clara, CA 95053; and a *Graduate Student Representative,* NIALL F. MCCARTEN, Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

DISTRIBUTION AND MORPHOLOGY OF *HAPLOPAPPUS* HYBRIDS (ASTERACEAE: ASTEREAE) IN THE MOJAVE DESERT

Martin L. Cody and Henry J. Thompson
Department of Biology, University of California,
Los Angeles 90024

Abstract

At several sites in the Mojave Desert, shrubs occur that are intermediate in morphology between *Haplopappus cooperi* and *H. linearifolius.* Where these species occur together and both are common, intermediates generally comprise about one per 300 of the combined populations. Morphological features readily recognized in the field are plant stature, number and size of flower heads per flowering stem, peduncle lengths, and leaf size and shape. In all respects, the distributions of characters in the intermediates lie between those of *H. cooperi* and *H. linearifolius.* As each species varies morphologically among sites, the morphology of the intermediates also varies and retains its intermediacy. We conclude that the intermediates are sterile hybrids of *H. cooperi* and *H. linearifolius* and that these two species belong in the same section of the genus as suggested recently.

During the last 10 years of field work (e.g., Cody 1978) on the distribution and ecology of *Haplopappus, Chrysothamnus,* and related genera of Asteraceae in the Mojave Desert, we have encountered numerous examples of plants that are morphologically intermediate between species that traditionally have been placed in different sections of the genus *Haplopappus.* Hall (1928) placed *H. cooperi* (A. Gray) Hall in sect. *Ericameria* and *H. linearifolius* DC. in sect. *Stenotopsis,* and did not recognize a close relationship between them. Urbatsch and Wussow (1979), however, identified hybrids between both species from herbarium specimens, deduced their close relationship, and assigned them to *Ericameria* sect. *Stenotopsis.*

In this paper, we support a hypothesis of close relationship between *H. cooperi* and *H. linearifolius* and present morphological and distributional data on hybrids, which are numerous and distributed widely in natural populations. We describe the hybrids and document their occurrence along transects only in habitats where the two putative parents co-occur. Our data show that the morphology of the hybrids is intermediate between that of the putative parents, and follows variations in parental morphology among different sites in the Mojave Desert.

Methods

Observations were made on morphologically intermediate shrubs in the New York Mountains, Mid Hills, and Granite Mountains in

Madroño, Vol. 33, No. 4, pp. 237–243, 1986

the central Mojave Desert, and on the north slope of the San Gabriel Mountains in the western Mojave Desert. Intermediates were found at many sites between 1200 and 1350 m on the central desert ranges, but were found at lower elevations (to 900 m) in the western desert where winter rainfall totals are higher. Collections were made at the base of Prospect Canyon at 35°18′N 115°18′W on the north side of the New York Mountains at 1218 m; from near Mexican Water Spring at 35°07′N 115°29′W in the Mid Hills at 1290 m; near Granite Cove Spring at 34°48′N 115°37′W on the northeast side of the Granite Mountains at 1215 m; and from a site on the Valyermo Road near its crossing of the California Aqueduct at 34°30′N 117°53′W on the north slope of the San Gabriel Mountains at 977 m.

Distributional data were collected in the Mid Hills from three N-S belt transects that were 2 m wide, 250 m apart, and spanning the elevational range 1220–1290 m. Counts of plants were made from 10 × 2 m quadrats (n = 148) along 1480 m on the belt transects. We characterized each quadrat by its slope angle and the percentage of rock cover (rocks > 10 cm in average diameter) on the surface of the ground beneath the measuring tape.

Morphological measurements were made on plants from the New York Mountains, Mid Hills, Granite Mountains, and San Gabriel Mountains. *Haplopappus cooperi, H. linearifolius,* and intermediate shrubs have leafy stems culminating in either branched or simple peduncles that bear either solitary or several to many (up to ca. 30) flowering heads. Leaves are fascicled and possess a single primary leaf and a pair of smaller, secondary leaves at each fascicle, as well as additional, smaller leaves per fascicle in *H. cooperi.* The following characteristics were measured for putative parents and hybrid individuals: number of flowering heads per leafy stem; peduncle lengths (using vernier calipers); receptacle diameter, in March 1984, of the previous year's blooms (using a digital caliper); leaf length and width of primary and secondary leaves; and stature (using a meter stick) for intermediate shrubs and other *Haplopappus* species in their immediate vicinity.

Flowering material was collected in late May 1984 from parents and intermediates (20–30 flowering heads from 3–8 individuals), and was numbered but not labeled by MLC in late May 1984. Pollen stainability was estimated by mounting pollen in lacto-phenol cotton blue; the percentage of full, stained grains was assessed by HJT for each sample. Achenes were checked for the presence of plump embryos.

RESULTS

At all sites where intermediate shrubs were encountered, henceforth called hybrids, mature individuals of *H. cooperi* and *H. linearifolius* were found in the immediate vicinity. These sites are gen-

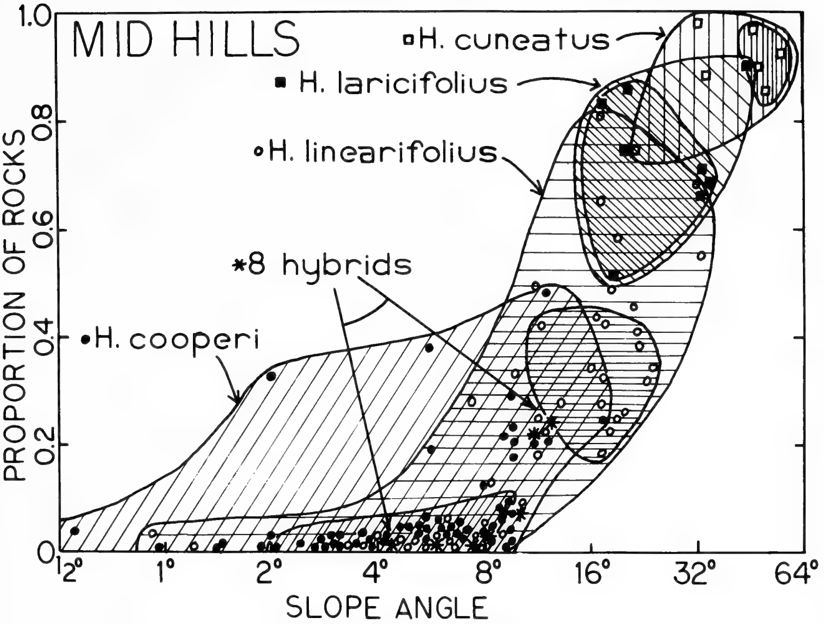


FIG. 1. Distribution of four shrub species of *Haplopappus* over an environmental gradient from sandy flats to rocky cliffs in the Mid Hills, central Mojave Desert. The envelope of the range of each species is shown; the doubly hatched regions indicate where each species reaches 50% or more of its maximum density on belt transects sampled in 10 × 2 m quadrats. The positions on the gradient of eight hybrid individuals (asterisks) are indicated.

erally intermediate between the flatter, sandier areas on which *H. cooperi* is common, and the steeper, stonier slopes on which *H. linearifolius* is common.

Distribution. Some 68 woody plant species were found in the sample areas in the Mid Hills: 1012 individuals of *H. cooperi* (23% of the total woody plants) and 140 individuals of *H. linearifolius* (3.2%) were encountered. The counts also included 22 individuals of *H. laricifolius* A. Gray (0.5%) and 11 individuals of *H. cuneatus* A. Gray (0.25%). Five hybrids were found within the belt transects, and three additional hybrids were located immediately adjacent to them. Distributional data are plotted in Fig. 1, on which is located each 10 × 2 m sample in the plane of slope angle (abscissa) and percentage rock cover (ordinate). The distributional ranges of the *Haplopappus* species are outlined and the shaded areas indicate the locations of samples in which each of the four species reached 50% or more of its maximum density (Fig. 1). These maximum counts are 24 individuals per quadrat in *H. cooperi,* 11 in *H. linearifolius,* four in *H. laricifolius,* and two in *H. cuneatus.* The positions of eight

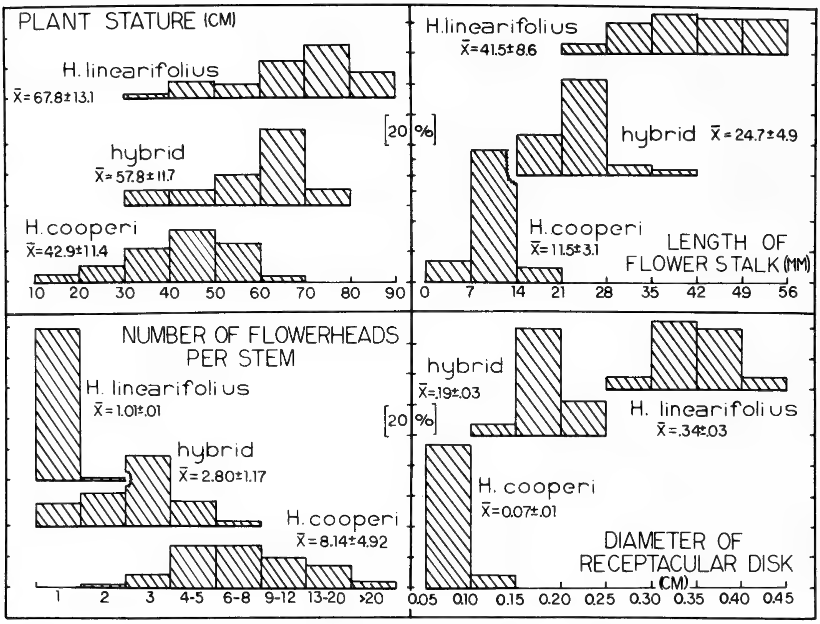


FIG. 2. Frequency distributions from the Mid Hills of four morphological variables in the putative parents *Haplopappus linearifolius* and *H. cooperi* and also in intermediate individuals that are putative hybrids. For plant stature, sample size n = 35, 10 (8 on belt transects, 2 off the transects), and 69 for *H. linearifolius,* hybrids, and *H. cooperi,* respectively; for numbers of flower heads per stem, length of flowering stalk, and diameter of receptacle, n = 30, from 6–12 individuals, in all cases. The means of the parent distributions and of each of the parent-hybrid distributions are significantly different in all cases.

hybrid individuals are indicated, suggesting that hybrids occur in habitats co-occupied by *H. cooperi* and *H. linearifolius* and are scattered between habitats in which these two species reach their highest densities.

Morphology. Field characters that distinguish the intermediate shrubs from their putative parents are shown in Fig. 2. In stature, *H. cooperi* is significantly smaller and *H. linearifolius* is significantly taller (t-test on the means, with equal variances but unequal sample sizes, $p < 0.05$ in all pairwise cases) than the putative hybrids.

Flowering heads normally occur singly on unbranched peduncles in *H. linearifolius* (two of 180 stems from ca. 20 individuals had two flowering heads). Peduncles are produced from branched stalks in *H. cooperi* and averaged eight heads per stem (30 individuals); stalks branched less in the hybrids and averaged 2.8 heads per stem (30 individuals). All pairwise t-tests on means (with unequal variances) show that the three distributions differ significantly from each other ($p < 0.001$; Fig. 1, lower left).

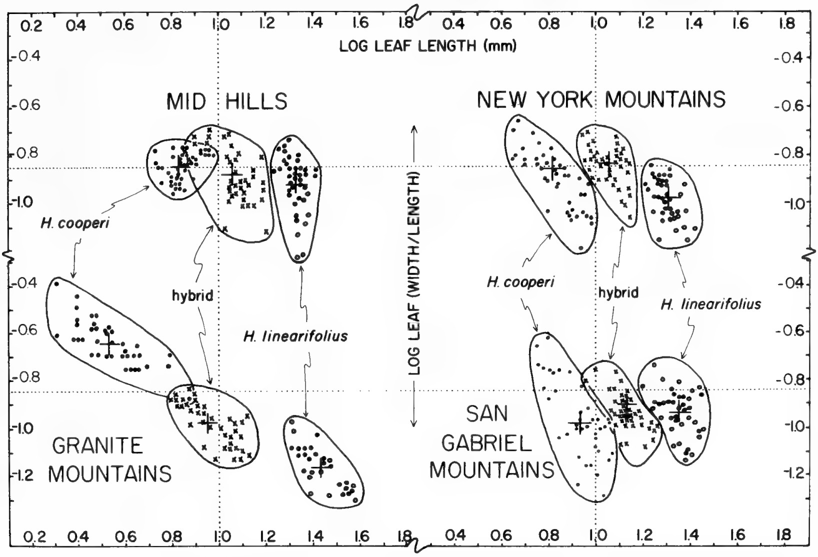


FIG. 3. The morphology of primary leaves is displayed in the plane of log (leaf length) vs. log (leaf width/length) for parent species *Haplopappus linearifolius* and *H. cooperi* and hybrids at each of four sites: the Mid Hills, Granite Mountains, New York Mountains, and San Gabriel Mountains. The relative leaf morphologies can be seen with respect to the dotted lines. Although parent leaf morphology differs between sites, and is especially different at the Granite Mountains, hybrids fall into intermediate positions at all sites. Means are indicated by cross-hatches.

Peduncles average 41.5 mm in *H. linearifolius,* but are much shorter ($\bar{x} = 11.5$ mm) in *H. cooperi* (Fig. 2, upper right). The hybrids are intermediate with a mean peduncle length of 24.7 mm. Receptacles are much larger in *H. linearifolius* (Fig. 2, lower right), reflecting their larger heads. In *H. cooperi,* receptacle diameters are only one-fifth as large as *H. linearifolius,* whereas the hybrids average one-half the mean of *H. linearifolius.* Each pairwise comparison (t-tests) for each of these two characters shows that the hybrids differ significantly from each of the putative parents and are also different from each other ($p < 0.001$ in all cases).

Two characteristics of hybrid plants were compared to adjacent individuals of *H. linearifolius* and *H. cooperi* in the Granite Mountains: number of inflorescences per stem and peduncle length. In *H. cooperi* at the Granite Mountains, the mean number of inflorescences per stem is 12.2, significantly more (t-test; $p < 0.001$) than the average 8.1 in the Mid Hills. Although no double inflorescences were found in *H. linearifolius* in the Granite Mountains, their mean inflorescences per stem (1.00) is not significantly different from the mean of 1.01 calculated for the Mid Hills. At the Granite Mountains, however, hybrids average 4.0 inflorescences per stem, 44% higher than in the Mid Hills, and corresponding to a 49% increase in this character in *H. cooperi.* Peduncles are significantly longer (36%) in *H. cooperi* in the Granite Mountains relative to the Mid Hills populations ($p < 0.001$), and also are longer (6%), but not significantly so, in *H. linearifolius.* In the hybrids, peduncles average 38% longer in the Granite Mountains. Thus, hybrid morphology shifts in intermediate character with changes in the parent plants.

Plants on the north slope of the San Gabriel Mountains were compared in numbers of inflorescences per stem; *H. cooperi, H. linearifolius,* and hybrids averaged 8.4, 1.37, and 3.76 inflorescences per stem, respectively. The hybrids were intermediate and shifted in this feature similar to changes in the parents relative to other sites.

Lastly, the results of leaf morphology measurements are shown in Fig. 3, in which log (leaf length) is plotted against log (leaf width/leaf length) for primary leaves. In the Mid Hills, *H. linearifolius* leaves averaged three times longer (21.5 mm vs. 7.1 mm), with width/length ratios reaching 84% of those in *H. cooperi* (0.119 vs. 0.141). Hybrid individuals have leaves that are exactly intermediate in both respects. In the Granite Mountains, *H. linearifolius* and *H. cooperi* are more dissimilar in leaf morphology than they are in the Mid Hills, with the former's leaves significantly longer and narrower (means 27.1 mm and 1.84 mm, respectively; $p < 0.01$ by t-tests), and the latter's significantly shorter (mean 3.4 mm; $p < 0.001$ by t-test). In the Granite Mountains, the leaves of the hybrids are shorter (9.0 mm vs. 11.7 mm) and relatively narrower (0.11 vs. 0.13 width/length; both means significantly different from the Mid Hills measurements at $p < 0.001$). Leaf morphology of the hybrids is intermediate to the two parents. Leaf morphology data from the remaining two sites, New York Mountains and San Gabriel Mountains, are included in the figure, in which the intermediate morphology of the hybrids once more follows the shifting morphological differences between the parents at the two sites.

Pollen and embryos. Pollen samples from three individuals of *H. linearifolius* ($n = 725$ counts) and *H. cooperi* ($n = 218$ counts) showed 99% full and stained pollen. Counts from flowers on three different hybrid individuals showed 65% ($n = 361$), 68% ($n = 268$), and 61% ($n = 332$) good pollen. No embryos could be found in ovaries from the hybrid samples, in contrast to the large and normal embryos in *H. linearifolius* achenes. *Haplopappus cooperi* ovaries were too immature to assess the condition of embryos.

DISCUSSION AND CONCLUSIONS

The morphology of the hybrids follows the variations in the morphology of the two parents among sites and indicates that the hybrids are produced locally at each site. Although chromosomes were not examined, this parallel morphological variation among sites suggests the hybrids are not fertile tetraploids formed by alloploidy. There is no evidence, furthermore, of introgression or back-crossing to the parents and no hybrid swarm. These observations together with the pollen data demonstrate that the hybrids are sterile.

Both *H. linearifolius* and *H. cooperi* flower in the spring with more than 90% overlap in their blooming season; *H. linearifolius* typically flowers earlier than *H. cooperi.* Another potential parent is *H. laricifolius,* but this species differs in flowering season (it flowers in late fall to early winter), in morphology (peduncles are axillary on leafy stems rather than terminal and ± branched), and in habitat (it occurs on steeper and rockier slopes).

Our data indicate that intermediate individuals between *H. linearifolius* and *H. cooperi* occur commonly where these two species are sympatric at various sites in the Mojave Desert, and that sterile hybrids are produced by these two species. The close relation between the taxa *H. linearifolius* and *H. cooperi* is confirmed, and their combination either in the same section of *Haplopappus* or in a section of *Ericameria* as proposed by Urbatsch and Wussow (1979) is supported.

ACKNOWLEDGMENTS

Our work on desert plant communities has been supported by the Research Committee of the University of California at Los Angeles and by a grant to the first author from Resources for the Future; we express our thanks to both sources. We also thank the editors, B. Prigge, J. Strother, and H. Wells for critical improvements to the manuscript.

LITERATURE CITED

CODY, M. L. 1978. Distribution ecology of *Haplopappus* and *Chrysothamnus* in the Mojave Desert. I. Niche position and niche shifts on north-facing granitic slopes. Amer. J. Bot. 65:1107–1116.

HALL, H. M. 1928. The genus *Haplopappus*: a phylogenetic study in the Compositae. Carnegie Inst. Washington Publ. 389:1–391.

URBATSCH, L. E. and J. R. WUSSOW. 1979. The taxonomic affinities of *Haplopappus linearifolius* (Asteraceae—Astereae). Brittonia 31:265–275.

(Received 14 Mar 1985; revision accepted 20 May 1986.)

NATURAL HYBRIDIZATION BETWEEN *LAYIA GLANDULOSA* AND *L. PANICULATA* (ASTERACEAE: MADIINAE)

Barry D. Tanowitz and John W. Adams
Department of Biological Sciences, University of California,
Santa Barbara 93106

Abstract

A large putative hybrid swarm between *Layia glandulosa* and *L. paniculata* was found at La Purisima Mission State Historic Park in northern Santa Barbara Co., California. *Layia glandulosa* is a self-incompatible, morphologically and ecologically polytypic, annual, diploid species ($n = 8$) that occurs in open, relatively dry habitats. By contrast, *L. paniculata* is a self-compatible, morphologically and ecologically uniform, annual, tetraploid species ($n = 16$) that occurs in shaded, relatively moist habitats. Putative hybrids occur in two contrasting areas. In one habitat, hybrids were found in an interface between coastal sage scrub community on sandy soils on a southwest-facing slope and oak woodland–valley grassland community with sandy and clay loam soils on a north-facing slope. In the other habitat, hybrids were found in open, sandy areas between large, scattered shrubs of a coastal sage scrub–dune scrub community at the top of a mesa. Morphological analyses showed the hybrids to be intermediate in most vegetative and floral characters. The hybrid haploid chromosome number ($n = 12$) is intermediate. A meiotic analysis indicates that the modal synaptic configuration is $8_{II} + 8_{I}$ and suggests that these two species share a common genome. The low degree of fertility (<6%) in the hybrids presumably is the result of genic and/or chromosomal differences between the parents.

Natural hybridization has been shown to occur in several genera of tarweeds (Heliantheae: Madiinae) (Clausen 1951, Venkatesh 1958, Tanowitz 1977, Carr and Kyhos 1981). Many of these hybrids are found between species of different ploidy levels (Clausen et al. 1945, Venkatesh 1958, Tanowitz 1977, Carr and Kyhos 1981), different ecological preferences (Clausen 1951, Tanowitz 1977), and between species that are strikingly different morphologically (Kobayashi 1973, Tanowitz 1977, Carr and Kyhos 1981). Although natural hybrids occur in the Madiinae, strong external and internal reproductive isolating mechanisms operate among most members of this group (Tanowitz 1980, 1985). *Layia,* in particular, displays distinct geographical distributions among species (Clausen et al. 1945, Clausen 1951). Typically, cytological differences or strong ecological preferences are evident whenever two or more species of *Layia* occur sympatrically. Therefore, it was interesting to find a large hybrid population that occurred between two species of *Layia* that differed markedly both cytologically and morphologically.

Putative hybrids between the annual species *Layia glandulosa* (Hook.) H. & A. and *L. paniculata* Keck were found during a floristic

Madroño, Vol. 33, No. 4, pp. 244–252, 1986

and vegetation study of La Purisima Mission State Historic Park in northern Santa Barbara Co., California (Ferren et al. 1984). *Layia glandulosa* (sensu lato) is self-incompatible, and highly morphologically and ecologically variable; it has large, showy heads and a chromosome number of $n = 8$; and it grows in open, relatively dry habitats (Keck 1959). At La Purisima Mission, *L. glandulosa* is found in association with coastal sage scrub and valley grassland communities in light, sandy loam soils. By contrast, *L. paniculata* is self-compatible with relatively little morphological and ecological amplitude; it has small, inconspicuous heads, and a chromosome number of $n = 16$; and it grows in shaded, relatively moist habitats (Keck 1959). At La Purisima Mission, *L. paniculata* is found in association with two distinct habitats (vegetation classification according to Cheatham and Haller 1975). The first is an oak woodland community dominated by *Quercus agrifolia* Nee in which *L. paniculata* occurs as a component of the understory on sandy and clay loam soils of north-facing slopes. The second is an unusual community that is a mixture of dune scrub dominated by *Lupinus arboreus* Sims and *L. chamissonis* Eschs. in association with typical coastal sage scrub dominated by *Baccharis pilularis* DC. subsp. *consanguinea* (DC.) C. B. Wolf in which *L. paniculata* occurs at the bases of shrubs on sandy soils on the top of a mesa. In the first habitat, hybrids occur where the coastal sage scrub community borders the oak woodland–valley grassland community where slopes were slumped and eroded. In the second habitat, hybrids occur in open areas among dominant shrubs. The latter area shows minimal natural disturbance, but significant man-made disturbance, and was the site where most of this investigation was done. Through the use of morphological, ecological, and cytological analyses, it is our purpose to document hybridization that occurs between *L. glandulosa* and *L. paniculata* and to discuss the relationships between them.

MATERIALS AND METHODS

Vegetative and floral material was prepared for observation with a dissecting scope and SEM by rehydration according to the method of Hardin (1981). For observation with the SEM, the material was critical-point dried, mounted, and sputter coated using standard procedures. Samples were examined with an Hitachi-S 415A SEM at an accelerating voltage of 25 kV.

Cytological material was examined and pollen fertility was estimated according to the methods found in Tanowitz (1985). Voucher specimens are deposited at UCSB.

RESULTS

Morphological features are shown in Table 1. Several distinctive features of *L. glandulosa* and *L. paniculata* distinguish the hybrids

TABLE 1. SALIENT MORPHOLOGICAL FEATURES EMPHASIZING THE DIFFERENCES AMONG *Layia glandulosa, L. paniculata,* AND THEIR HYBRIDS. Mean ± standard deviation (and range) of measurements of parents and hybrids are from 50 individuals with one measurement for each character per individual. All length and width measurements in mm.

Trait	*L. glandulosa*	Hybrids	*L. paniculata*
Stem color	Anthocyanous; not dotted	Anthocyanous; dots scattered	Anthocyanous below; dotted throughout
Stem pubescence	Puberulent	Hispidulous-hispid	Hispid
Lower leaf shape	Deeply pinnatifid	Pinnatifid-dentate	Dentate
Cauline leaf margin	Entire	Subentire-denticulate	Denticulate
Involucre length	7.7 ± 1.2 (5.5–14.0)	6.1 ± 0.6 (5.0–7.5)	4.9 ± 0.5 (3.5–6.0)
Involucre width	11.2 ± 1.5 (7.0–14.5)	8.6 ± 1.7 (4.0–12.0)	8.0 ± 1.2 (5.5–11.0)
Receptacular bract shape	Lanceolate	Lance-linear	Linear
Number ray flowers/head	9.0 ± 2.0 (5–13)	9.4 ± 2.0 (5–13)	8.5 ± 1.4 (6–13)
Ray corolla length	16.2 ± 3.2 (9.0–21.5)	7.0 ± 1.1 (4.5–9.0)	3.9 ± 0.6 (2.5–6.0)
Ray corolla width	8.1 ± 2.0 (3.5–15.0)	3.3 ± 0.6 (1.5–4.5)	1.8 ± 0.3 (1.5–3.0)
Ray corolla color	White	Cream	Yellow
Ray achene length	3.4 ± 0.6 (2.5–6.0)	3.2 ± 0.5 (1.5–4.5)	2.8 ± 0.5 (1.0–4.0)
Number disc flowers/head	64.5 ± 12.6 (33–98)	45.7 ± 10.9 (17–70)	40.0 ± 8.6 (21–58)
Anther color	Yellow	Red—Brown	Black
Number disc flowers/number ray flowers	7.4 ± 1.8 (4.4–12.8)	4.9 ± 0.9 (2.6–7.3)	4.7 ± 0.8 (3.4–7.7)
Disc corolla length	4.8 ± 0.7 (2.5–6.0)	3.8 ± 0.5 (3.0–5.0)	3.1 ± 0.4 (2.5–4.0)
Disc achene length	3.6 ± 0.7 (1.5–5.0)	3.3 ± 0.7 (1.5–4.5)	3.2 ± 0.4 (2.5–4.5)
Pappus color	White	Light Brown—White	Rufous
Ray corolla length/disc corolla length	3.4 ± 0.7 (1.7–5.0)	1.8 ± 0.2 (1.2–2.7)	1.3 ± 0.2 (0.8–1.6)

from these species in the field. For example, *L. glandulosa* has large, showy heads with broad, trilobate, white rays, whereas *L. paniculata* has smaller heads with inconspicuous, strap-shaped, yellow rays. Putative hybrids typically displayed intermediate-sized heads with conspicuous cream-colored rays. Hybrids showed some variation in ray corolla color, but no hybrids were observed to possess either all white or all yellow corollas. Qualitative characters (e.g., stem color,

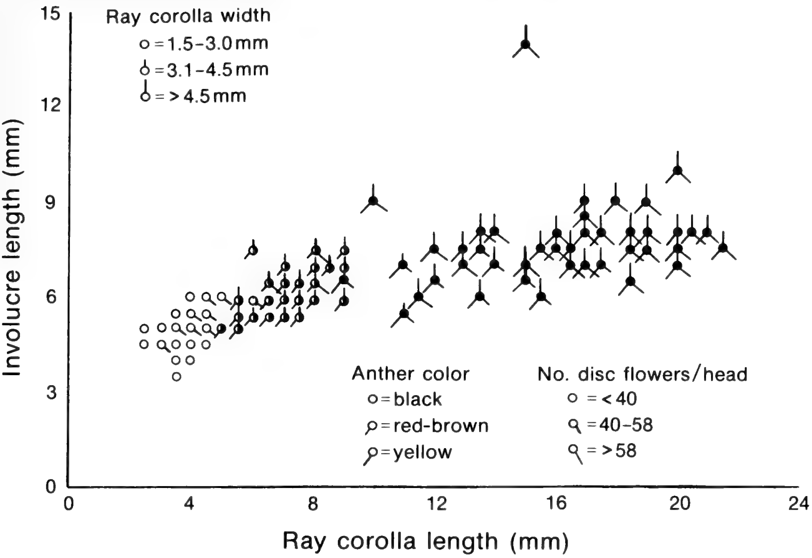


FIG. 1. Scatter diagram that depicts 50 individuals each of *Layia glandulosa, L. paniculata,* and their hybrids from the study site. Closed circles represent white ray corollas of *L. glandulosa*, open circles represent yellow ray corollas of *L. paniculata,* and half circles represent cream-colored ray corollas of hybrids. Several individuals with a similar morphology overlap and are not indicated.

branching) showed similar patterns of variation that suggest simple dominance is lacking in these features. In most other instances, hybrids were intermediate in vegetative and floral characters. Both parental species have a campanulate involucre, but *L. glandulosa* has larger heads with greater numbers of ray and disc flowers per head.

An SEM analysis of the vesture of the stem, lower and cauline leaves, and involucre revealed distinct differences in types and density of trichomes between the parental species. Hybrids typically showed intermediacy in density and possessed combinations of both parental trichome types on all structures examined. For example, *L. paniculata* possesses sessile, biseriate, glandular trichomes on the involucre, which are lacking in *L. glandulosa* (cf. Carlquist 1958, Figs. 3, 8). These trichomes were found on the involucre in all hybrid individuals, but had a more scattered distribution. The setose pappus elements are barbellate in both species, but the shorter outer elements of *L. paniculata* were found to be tightly spiralled and hygroscopic in action. Spiralled pappus elements were lacking in *L. glandulosa,* but occurred in some hybrids.

Morphological data for individuals are depicted in a scatter diagram (Fig. 1). The shape of the recombination spindle suggests that the putative hybrids are F_1's. The majority of hybrids exhibited character states intermediate to one or the other parental species. No evidence of introgression or backcrossing was present. The scatter diagram revealed further that individuals of *L. paniculata* are clustered tightly, which suggests that this population is relatively uniform morphologically. This is in contrast to individuals of *L. glandulosa* that display scattered points, which presumably reflect the greater morphological amplitude in this population. Although a few individuals of *L. paniculata* had numerous disc flowers (n = >58), most individuals of *L. glandulosa* had disc flowers well in excess of those of *L. paniculata.* Moreover, those *L. glandulosa* individuals with fewer disc flowers also were those that possessed smaller involucres and shorter ray corollas. Only three hybrid individuals showed numbers of disc flowers greater than 58, and none had ray corollas longer than 9 mm.

An analysis of meiotic features was performed using pollen mother cells (PMC's) obtained from buds of the parents and putative hybrids. *Layia glandulosa* (12 individuals, 84 PMC's) showed a chromosome number of $n = 8$, whereas *L. paniculata* (15 individuals, 67 PMC's) showed a chromosome number of $n = 16$. Meiosis in both species appeared normal in all instances and showed no apparent structural heterozygosity in the population. Putative hybrids (10 individuals, 127 PMC's) had a chromosome number of $2n = 24$. The modal synaptic configuration at diakinesis or metaphase I was $8_{II} + 8_{I}$. Six PMC's showed $1_{III} + 6_{II} + 9_{I}$, with the association of three as a chain. One PMC showed $1_{IVch} + 6_{II} + 8_{I}$, whereas four PMC's had fewer bivalents and more univalents (maximum of 12). Anaphase I and II cells showed no evidence of any major structural chromosomal rearrangements (e.g., bridges or fragments); however, unpaired chromosomes often were observed lagging on the equator. In three PMC's, two to three bivalents appeared to undergo asynchronous disjunction. Telophase II cells showed micronuclei.

Fifty individuals each of *L. glandulosa* and *L. paniculata,* used in morphological analyses, were examined for pollen fertility (500 grains/individual). Pollen stainability in both species averaged above 98% and ranged 87–100% in *L. glandulosa,* and 81–100% in *L. paniculata.* Similarly, 50 hybrid individuals were examined for pollen fertility. Pollen stainability averaged nearly 1% and ranged 0–6% (500 grains/individual).

Over 2000 fruits were visually examined in each species and over 6000 among all hybrids. Fruit set was 73% in *L. glandulosa,* 77% in *L. paniculata,* and 0% in the hybrids.

DISCUSSION

Natural hybridization between *L. glandulosa* and *L. paniculata* is apparent from the morphological data. The large morphological differences evident between the parental species were found to be intermediate in the hybrid population in most features. Cytological data showed a triploid condition in hybrids and so provide additional evidence for hybridity. Furthermore, we consider all hybrid individuals studied in the population to be F_1's, based on extremely high pollen sterility, meiotic anomalies, and lack of fruit set.

In spite of striking, obvious, morphological differences, *L. glandulosa* and *L. paniculata* share less obvious features (e.g., involucral shape, pappus morphology, and vesture). These characters, although found in other members of the genus, are confined principally to what comprises a morphologically and cytologically closely related phyletic group (Clausen 1951, Tanowitz unpublished). These phenotypic similarities presumably reflect genic and chromosomal similarities. Cytogenetic analyses suggest that the two species share a common genome. Additional meiotic analyses of artificial hybrids, in progress, should reveal the extent of homology that occurs between *L. glandulosa* and *L. paniculata.*

Layia glandulosa and *L. paniculata* are ecologically distinct throughout most of their respective ranges. Even in areas of close sympatry these species typically retain strong microhabitat preferences. Several distinct populations of *L. glandulosa* and *L. paniculata* occur at La Purisima Mission (Ferren et al. 1984). In only one area of high disturbance do the ecological barriers break down sufficiently to provide an intermediate habitat to support both parents and their hybrids. The other habitat in which hybrids occur is unusual. This habitat represents a unique association and provides a situation that also results in the breakdown of ecological barriers. Because the morphological and cytological differences between the parents do not preclude crossability, it appears then that the reproductive isolating mechanisms are fundamentally external. Following the breakdown of external barriers, internal mechanisms, such as hybrid sterility, presumably reinforce their distinctness in contiguous populations.

Although natural hybridization in Madiinae has been well-documented (Clausen et al. 1945, Clausen 1951, Carr and Kyhos 1981, Tanowitz 1977, 1980), studies of artificial hybridization in the subtribe suggest that the potential for hybridization is even greater than observed in nature (Clausen 1951, Carr 1975, 1977, 1978, Tanowitz 1980). Ecological and distributional factors operate as strong reproductive isolating mechanisms in the Madiinae. Clausen (1951) noted that many genera, including *Layia,* display strong ecological preferences and distributional disjunctions. Clausen (1951) further noted that where *Layia* species occur sympatrically they typically comprise two fundamentally different cytological groups (species complexes) that display strong barriers against interbreeding. *Layia glandulosa* and *L. paniculata* are in the same phyletic group, but are considered to be in a different morphological complex from their common cytological group (Clausen 1951). *Layia glandulosa* has the greatest eco-distributional amplitude of any taxon in the subtribe (Clausen et al. 1945). The distribution of *L. glandulosa* completely encompasses that of *L. paniculata,* yet they are distinct ecologically. Thus, the lack of natural hybridization in these two species is not unexpected.

Hoover (1970) reported a natural hybrid between *L. glandulosa* and *L. hieracioides* (DC.) H. & A. (*Hoover 8369* OBI!) in San Luis Obispo Co. The parentage of this hybrid is problematical. The diploid *L. hieracioides* is one of the presumed progenitors of the tetraploid *L. paniculata.* Preliminary investigations of these two species indicate that their distributions overlap, ecological preferences are similar, and morphological characters used in their discrimination segregate randomly among populations (Tanowitz, unpublished). Hoover (1970) reported no cytological information and so it is difficult to decide whether *Hoover 8369* is a cross of *L. glandulosa* with *L. hieracioides* or with *L. paniculata.*

The only other report of natural hybridization in *Layia* was reported by Clausen et al. (1945). They discovered a putative hybrid individual between *L. pentachaeta* A. Gray ($n = 8$) and *L. platyglossa* (Fisch. Meyer) A. Gray ($n = 7$) in southeastern Monterey Co., California. This individual showed an intermediate morphology, a chromosome number of $2n = 15$, and was highly sterile. It also shared morphological and cytological similarities with an artificially produced hybrid of the same combination (Clausen et al. 1945). They showed that through spontaneous chromosome doubling, the artificial hybrid gave rise to a tetraploid individual, and designated it as '*L. pentaglossa*'. They suggested that the presence of unreduced gametes found in the artificial hybrid increased the possibility that the tetraploid could occur in nature. This possibility appears remote, however, because '*pentaglossa*' was derived from obligate outcrossing species and, thus, would have to pass through a bottleneck. A similar origin for the self-fertile, tetraploid *L. paniculata* is more likely because it was apparently derived, in part, from a self-fertile species, *L. hieracioides.*

It has been suggested that a relatively common mechanism for speciation in the Madiinae is through hybridization and subsequent chromosomal repatterning that may or may not result in aneuploidy (Venkatesh 1958, Carr 1975, 1977, Tanowitz 1977, 1985). Speciation occurring without change in chromosome number has been documented in a number of examples in this group, although several genera show aneuploid series (Carr 1975, 1977, Tanowitz 1980, Carr and Kyhos 1981). In contrast, speciation as the result of hybridization and subsequent polyploidy in the Madiinae is apparently uncommon. Along with genetic and ecologic isolation factors, this mode of speciation is a result presumably of the bottleneck effect through which species must pass (Stebbins 1950). Clausen et al. (1945), however, demonstrated that the hexaploid *Madia citrigracilis* Keck ($n = 24$) resulted from a cross of *M. gracilis* (Sm.) Keck ($n = 16$) with *M. citriodora* Greene ($n = 8$). It appears that most, if not all, polyploid species in this group are self-fertile and have been derived from at least one parent that is self-fertile. Therefore, the possibility exists that hybridization and subsequent polyploidy could serve as a mechanism for speciation among self-fertile species in the Madiinae.

ACKNOWLEDGMENTS

Research was partially supported by a University of California President's Undergraduate Fellowship to JWA. We thank Susan Leone for aid in handling the specimens; Dennis Odion, Robert Gill, and the Department of Biological Sciences for use of the SEM; and Drs. R. Patterson, J. Strother, J. Mooring, and D. Pinkava for reviews of the manuscript. We especially thank Melissa Cummings for aid in field work, Wayne R. Ferren, Jr. for bringing the problem to our attention and for valuable discussions, and Eric T. Andresen for aid with the morphological analysis.

LITERATURE CITED

CARLQUIST, S. 1958. Structure and ontogeny of glandular trichomes of Madiinae (Compositae). Amer. J. Bot. 45:675–682.

CARR, G. 1975. Chromosome evolution and aneuploid reduction in *Calycadenia pauciflora* (Asteraceae). Evolution 29:681–699.

———. 1977. A cytological conspectus of the genus *Calycadenia* (Asteraceae): an example of contrasting modes of evolution. Amer. J. Bot. 64:694–703.

———. 1978. Chromosome numbers of Hawaiian flowering plants and the significance of cytology in selected taxa. Amer. J. Bot. 70:744–755.

——— and D. W. KYHOS. 1981. Adaptive radiation in the Hawaiian silversword alliance (Compositae—Madiinae). I. Cytogenetics of spontaneous hybrids. Evolution 35:543–556.

CHEATHAM, N. H. and J. R. HALLER. 1975. An annotated list of California habitat types. University of California Natural Land and Water Reserves System.

CLAUSEN, J. 1951. Stages in the evolution of plant species. Hafner Publ. Co., New York.

———, D. D. KECK, and W. M. HIESEY. 1941. Experimental taxonomy. Carn. Inst. Wash. Year Book No. 40:160–170.

———, ———, and ———. 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from the Madiinae. Carn. Inst. Wash. Publ. 564.

FERREN, W. R., JR., H. C. FORBES, D. A. ROBERTS, and D. M. SMITH. 1984. The botanical resources of La Purisima Mission State Historic Park. The Herbarium, Dept. Biological Sciences, Univ. California, Santa Barbara, Publ. No. 3.

HARDIN, J. W. 1981. Atlas of foliar surface features in woody plants. II. *Broussonetia, Morus, Maclura* of North America. Bull. Torrey Bot. Club 108:338–346.

HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. Univ. Calif. Press, Berkeley.

KECK, D. D. 1959. *Layia. In* P. A. Munz, A California flora. Univ. Calif. Press, Berkeley.

KOBAYASHI, H. K. 1973. Putative generic hybrids of Haleakala's silversword and Kupaoa (*Argyroxiphium sandwicense* × *Dubautia menziesii*) Compositae. Pac. Sci. 27:207–208.

STEBBINS, G. L. JR. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.

TANOWITZ, B. D. 1977. An intersectional hybrid in *Hemizonia* (Compositae: Madiinae). Madroño 24:55–61.

———. 1980. Evolutionary patterns in the genus *Hemizonia* DC. sect. *Madiomeris* Nutt. (Asteraceae: Madiinae). Ph.D. dissertation, Univ. California, Santa Barbara.

———. 1985. Systematic studies in *Hemizonia* (Asteraceae: Madiinae): hybridization of *H. fasciculata* with *H. clementina* and *H. minthornii.* Syst. Bot. 10:110–118.

VENKATESH, C. S. 1958. A cyto-genetic and evolutionary study of *Hemizonia,* section *Centromadia.* Amer. J. Bot. 45:77–83.

(Received 21 Jan 1986; revision accepted 21 Apr 1986.)

NATURAL HYBRIDIZATION BETWEEN *MALACOTHRIX INCANA* AND *M. SAXATILIS* VAR. *IMPLICATA* (ASTERACEAE: LACTUCEAE) ON SAN MIGUEL ISLAND, CALIFORNIA

W. S. Davis
Department of Biology, University of Louisville,
Louisville, KY 40292

Ralph Philbrick
Santa Barbara Botanic Garden,
Santa Barbara, CA 93105

Abstract

Evidence from 1) plants grown in cultivation, 2) herbarium specimens, and 3) natural populations suggests that hybridization between the perennials *Malacothrix incana* and *M. saxatilis* var. *implicata* occurs on San Miguel Island, California. *Malacothrix incana* has yellow corollas, a chromosome number of $2n = 14$, and is self-compatible. *M. s.* var. *implicata* has white corollas, a chromosome number of $2n = 18$, and is self-incompatible. Three hybrids were grown in cultivation from achenes collected from *M. s.* var. *implicata* on San Miguel Island, and all had $2n = 16_I$. Hybrids in cultivation and in the field had pale yellow corollas. All hybrids had less than 4% stainable pollen and were intermediate between the parents in leaf and involucre morphology. Cross-pollinations between the parents in cultivation produced no hybrids, and hybrids apparently are relatively rare in natural populations. All of the evidence suggests that the parents are separated by generally effective isolating mechanisms and that hybridization in nature has not proceeded beyond the F_1 level. Hybrids were found on San Miguel Island in all areas where the parents were seen together, and no single zone of hybridization was found. The presence of hybrids of different ages suggests that there have been several hybridization events. The parents have different habitat preferences, but changes in edaphic factors on San Miguel Island during historic time probably have allowed *M. incana* to invade areas occupied by *M. s.* var. *implicata* so that cross-pollination can occur often enough to produce hybrids.

Three of the ca. 24 species now included in *Malacothrix* (Asteraceae) are perennials. One, *M. xantii* A. Gray, behaves predominately as an annual and is not considered here. The other two perennials are *M. incana* (Nutt.) Torr. & A. Gray, and the *M. saxatilis* (Nutt.) A. Gray complex. These two taxa are sufficiently morphologically distinct from the annuals and each other that they were considered separate genera by Nuttall (1841). The *M. saxatilis* complex originally included six species, but later taxonomic treatments (Williams 1957, Abrams and Ferris 1960) have reduced them to varietal rank. The corollas of *M. incana* are yellow and the chromosome number is $2n = 14$. Evidence from recent studies (Davis 1980) suggests that *M. incana* is closely related to diploid, annual

Madroño, Vol. 33, No. 4, pp. 253–263, 1986

taxa that are endemic to the California islands. Members of the *M. saxatilis* complex have white corollas and a chromosome number of $2n = 18$. The complex is internally coherent but has no clear morphological or cytological relationship to any of the known annual species and is under current investigation by the senior author.

We observed that *M. saxatilis* var. *implicata* (Eastw.) Hall, endemic to the California islands, and *M. incana* were sympatric on San Miguel Island, California and evidence from a preliminary study (Philbrick 1980) suggested that hybridization was occurring. In the present paper, we report evidence that documents hybridization between these two taxa, and we discuss the evolutionary and systematic implications of this hybridization.

MATERIALS AND METHODS

Plants representing natural populations of *Malacothrix incana* and *M. s.* var. *implicata* were grown in UC soil mix B at the University of Louisville in a Sherer-Gillet walk-in chamber (2.0 × 2.5 × 2.5 m). Photoperiod and temperature were reset every 15 days to match photoperiod and mean day and night temperatures for Los Angeles, California, over a 12 month cycle; these conditions were chosen for general studies of species of *Malacothrix* in cultivation and have been used for the past 12 years.

Beginning in 1974, plants were propagated from achenes taken from herbarium specimens at SBBG. Forty-nine plants of *M. incana* have been grown in the growth chamber: three from achenes of specimens collected at the mouth of the Santa Maria River, Santa Barbara Co.; one from an achene of a specimen from Santa Rosa Island; four from achenes of a single specimen collected at Montaña de Oro State Park, San Luis Obispo Co.; and 41 plants grown from achenes collected during trips to San Nicolas and San Miguel islands in 1984. Thirty-nine plants of *M. s.* var. *implicata* have been grown in the growth chamber: 15 from achenes collected on Anacapa Island in 1982; three from achenes collected on San Nicolas Island in 1984; 12 from achenes collected on San Miguel Island in 1984; and nine from achenes collected on Santa Cruz Island in 1985. Voucher specimens for all plants grown in cultivation are deposited at DHL.

Plants in cultivation were used in all cross-pollinations. Percentages of filled achenes were recorded for all crosses.

We examined 46 herbarium specimens of *M. incana, M. s.* var. *implicata,* and hybrids from Cuyler Harbor, San Miguel Island, and 98 specimens from other areas of the island. Forty-seven specimens of *M. incana* and *M. s.* var. *implicata* from other California islands, and 46 specimens of *M. incana* from mainland California also were studied. A list of specimens is available from the senior author.

We studied parents and hybrids in the field on flats near the Ranch airstrip, slopes above Cuyler Harbor, north-facing slopes of San Miguel Hill, and slopes near the ocean at Tyler Bight during a visit to San Miguel Island, 24–27 May 1984.

Meiotic behavior in cultivated plants was studied using standard acetocarmine squash techniques, and 20 PMC's were analyzed for each plant studied. Pollen stainability was determined for plants from natural populations, plants in cultivation, and all herbarium specimens using 1% cotton blue-lactophenol; 100 pollen grains were analyzed for each specimen. For studies of mitosis, five-day-old seedlings from achenes from mainland and island locations were placed in 0.002 M 8-hydroxyquinoline for three hours, then fixed and root tips stained using the Feulgen technique.

Achenes for scanning electron microscopy (SEM) were mounted on stubs, coated with 9 nm gold, and viewed with either a Cambridge or an SPI Model 40 SEM.

RESULTS

Morphology of parents. Morphological characters, as observed in the growth chamber, on herbarium specimens, and in natural populations, clearly distinguish *Malacothrix incana* from *M. s.* var. *implicata* (Table 1). The cauline leaves of *M. incana* have entire margins or possess broad, short lobes with blunt apices. Less often, the lobes are long and narrow (Fig. 1A). The leaves and stems are glabrous on some plants and densely tomentose on others. The outer phyllaries are ovate or broadly linear (Fig. 1A) and the surface of the receptacle is umbonate and without chaff. The corollas are yellow. The achenes have an inner pappus composed of a ring of bristles connate at their bases, but lack an outer pappus (Fig. 2A). The spines on the achene wall are less than 50 μm long.

The cauline leaves of *M. s.* var. *implicata* are irregularly bipinnatifid with numerous, linear divisions; apices are generally attenuate-acute (Fig. 1C). The young leaves and stems are hairy, but glabrate at maturity. The outer phyllaries are lanceolate with acuminate apices (Fig. 1C). Chaff up to 40 μm in length occurs on the surface of the receptacle. The corollas are white, with an abaxial lavender stripe on each ligule. The achenes have an inner pappus composed of bristles connate at their bases, and an outer pappus composed of white scarious teeth that extend above the apex of the achene wall (Fig. 2C). The achene surface is covered with spines, 110–170 μm long.

Cytology of parents. Meiotic behavior appeared to be normal in 11 cultivated plants of *M. incana* and all had $2n = 7_{\text{II}}$ (Fig. 3A); root tip mitosis was examined in eight plants and all had $2n = 14$. Meiotic behavior appeared normal in 10 cultivated plants of *M. s.* var. *implicata* and all had $2n = 9_{\text{II}}$ (Fig. 3C); root tip mitosis was

TABLE 1. A COMPARISON OF FEATURES IN *Malacothrix incana, Malacothrix saxatilis* VAR. *implicata,* AND INTERSPECIFIC HYBRIDS. Mean ± s.d. is given for stainable pollen: N = number of plants analyzed.

	M. incana	Hybrids	*M. saxatilis* var. *implicata*
Vestiture	stem and leaves densely hairy or essentially glabrous	stem and leaves densely hairy or essentially glabrous	young stems and leaf axils with scattered hair
Receptacle	umbonate, smooth, without chaff	umbonate, but with scattered chaff	foveolate, with chaff to 40 μm long
Corolla color	dark yellow, with no adaxial stripes on ligules	pale yellow, often with abaxial reddish stripes on ligules	white with abaxial lavender stripes on ligules
Achene wall	spines on rims of lacunae 30–50 μm long	spines on rims of lacunae 70–80 μm long	spines on rims of lacunae 110–170 μm long
Outer pappus	none	irregular scarious teeth	dense ring of irregular scarious teeth
Chromosomes at diakinesis	$2n = 7_{II}$	$2n = 16_{I}$	$2n = 9_{II}$
Percent stainable pollen	94.8 ± 4.3 (N = 59)	1.1 ± 2.6 (N = 45)	96.2 ± 3.3 (N = 32)

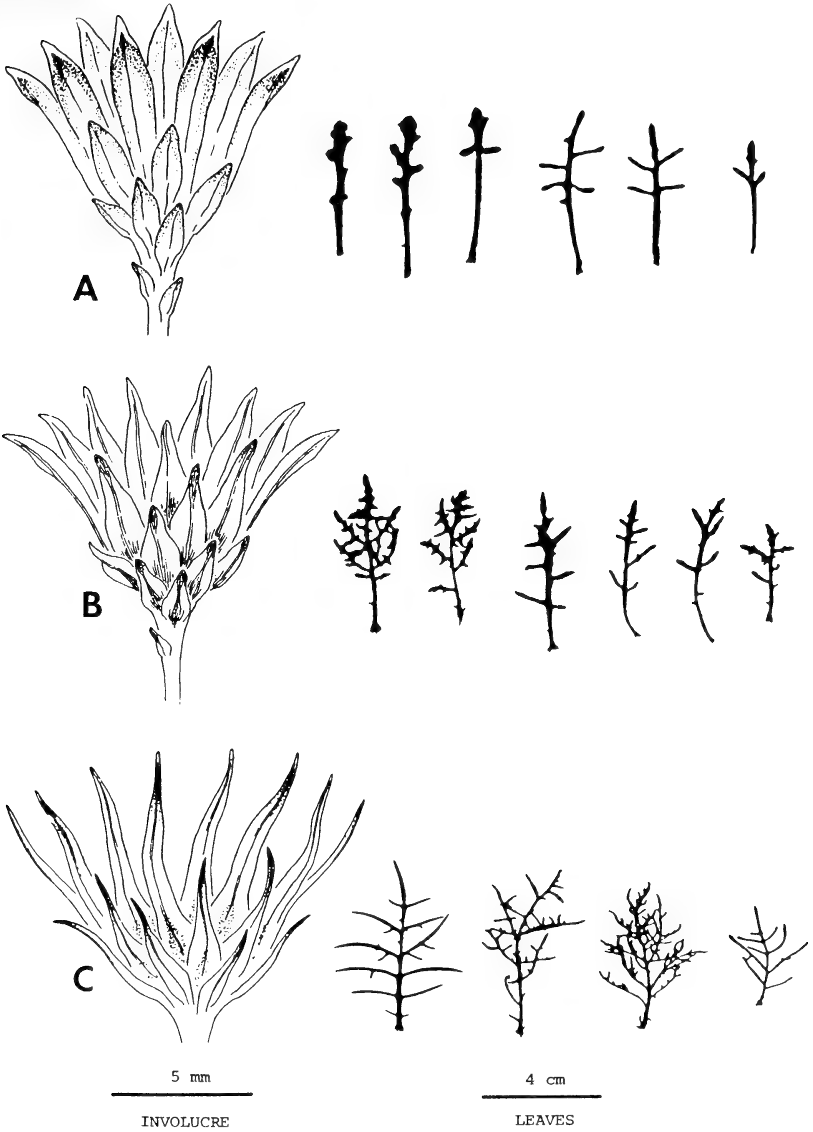


FIG. 1. Representative involucres and cauline leaves from plants grown in cultivation. A. *Malacothrix incana*. B. Hybrids between *M. incana* and *M. saxatilis* var. *implicata*. C. *M. saxatilis* var. *implicata*.

studied in eight plants and all had $2n = 18$. Pollen stainability of *M. incana* and *M. s.* var. *implicata* was 80% or more in all growth chamber plants, herbarium specimens, and natural populations. All plants of *M. s.* var. *implicata* in growth chamber conditions were

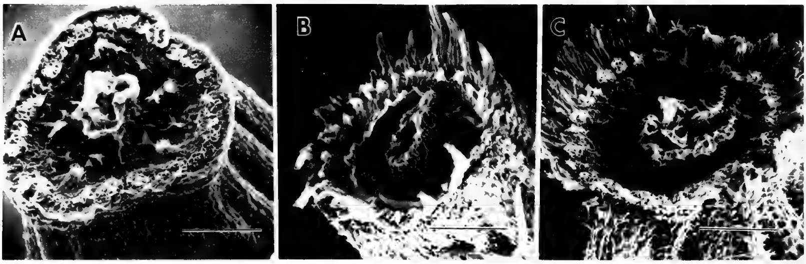


FIG. 2. Scanning electron micrographs of the apical portions of achenes of parents and hybrid. A. *Malacothrix incana.* B. Hybrid between *M. incana* and *M. saxatilis* var. *implicata.* C. *M. saxatilis* var. *implicata.* (Bars = 100 μm.)

found to be self-incompatible. In contrast, all plants of *M. incana* were found to be self-compatible.

Growth chamber experiments. We were unable to obtain mature hybrid plants from achenes produced by cross-pollinations in cultivation. Fifty-four filled achenes were produced from 12 crosses involving *M. s.* var. *implicata* as the female parent and *M. incana* as the male parent. From these, only five plants were produced, and all were of non-hybrid origin. These individuals were possibly products of the mentor effect, in which the presence of foreign compatible pollen allows the self-incompatibility mechanism to be bypassed (Nettancourt 1977). Achenes taken from *M. incana* following cross-pollinations with *M. s. implicata* produced only non-hybrid plants.

Three hybrid plants were grown in the growth chamber from wild achenes. One plant was grown from an achene taken from a specimen of *M. s.* var. *implicata* collected at Cuyler Harbor in 1973. The other two hybrids were grown from achenes collected in 1984 from plants identified in the field as *M. s.* var. *implicata*: one at Tyler Bight and one at Cuyler Harbor. All three hybrids had less than 4% stainable pollen, and 16 univalents were observed in meiosis in all specimens (Fig. 3B).

Hybrids from all sources were intermediate between the parents in leaf and involucre morphology (Fig. 1B). The stems and leaves of the hybrids varied from glabrate to densely tomentose. Receptacles were umbonate with scattered chaff. Achenes had an inner pappus and an outer pappus composed of white, scarious teeth (Fig. 2B). The outer pappus of hybrids was consistently less well-developed than the outer pappus of *M. s.* var. *implicata.* The achene walls of hybrids had spines that were 70–80 μm long.

In the growth chamber and in the field, corollas of hybrids were pale yellow and often had a reddish streak along the abaxial surface of each ligule. One of the cultivated hybrid plants grew at a faster rate and flowered sooner during its first year of growth than indi-

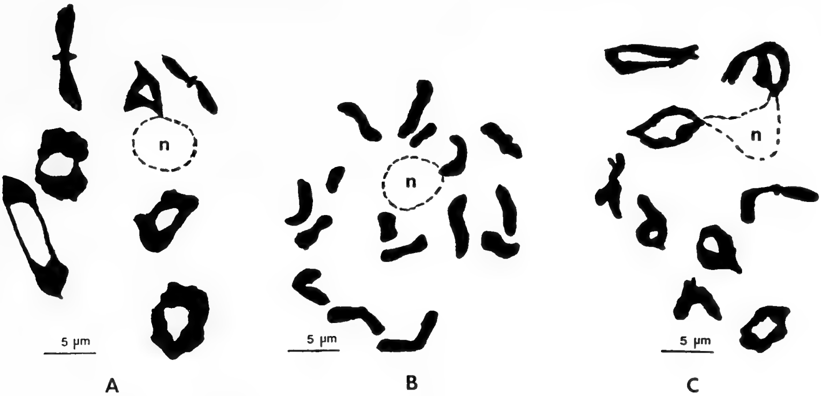


FIG. 3. Meiotic configurations at diakinesis in PMC's of parents and hybrid. A. *Malacothrix incana,* 7_{II}. B. Hybrid between *M. incana* and *M. saxatilis* var. *implicata,* 16_{I}. C. *M. s.* var. *implicata,* 9_{II}.

viduals of either parent growing with it. The other two hybrid plants died after flowering in their first year of growth. Cross-pollinations between cultivated hybrids with either *M. s.* var. *implicata* or *M. incana* produced abortive ovaries.

Field observations. On San Miguel Island in 1984, *M. incana* was found on the flats and slopes across the surface of the island and on the slopes, bluffs, and unstabilized sand dunes near the ocean. Along the west slope of San Miguel Hill, *M. incana* was abundant and grew scattered on stabilized sand. In contrast, *M. s.* var. *implicata* was not observed on the upper flats and slopes of the island, but was common on the slopes and bluffs adjacent to the ocean.

We found 38 putative hybrids on San Miguel Island, 20 on the slopes above Cuyler Harbor, 14 above Tyler Bight, two above Cardwell Point, one in Willow Canyon, and one in upper Cañada del Mar. These hybrids were found in a variety of habitats on the island, but occurred only where the parents also were present. Parents and hybrids occasionally were intermixed, with one of the taxa growing among the stems of the others. Parents and hybrids were vigorous and well-developed on the north-facing slopes above Cuyler Harbor, but were noticeably less robust on the southwest-facing slopes above Tyler Bight. All the hybrids had light yellow corollas and leaves intermediate in morphology between those of the parents; stainable pollen ranged from 0–4%. In 113 mature heads (1–7 from each plant) collected in the field, 10 normal-appearing achenes were found among a total of 9615. None of these achenes germinated when planted; five had poorly developed embryos, but the others contained embryos that appeared to be normal.

Although *M. incana* was found on unstabilized sand dunes and on stabilized sand, hybrids were found only on stabilized sand. The composition of the vegetation was conspicuously different, however, in different areas where hybrids were found. The following descriptions of three areas on the north-facing slopes above Cuyler Harbor illustrate some of these vegetation differences: 1) *M. incana* abundant, few plants of *M. s.* var. *implicata* present, patches of bare soil interspersed among the herbaceous cover; 2) *M. incana* uncommon, *M. s.* var. *implicata* common as part of a shrubby assemblage that included *Lupinus albifrons* Benth., *Baccharis pilularis* DC., and *Haplopappus venetus* (HBK) Blake; 3) parents relatively uncommon, no bare soil patches visible, no shrubby vegetation present. Hybrids were generally well-developed with thick basal stems 2–4 cm in diameter, and evidence of previous years' growth could be seen. Estimates of the ages of hybrid plants on San Miguel Island were made using evidence from a study of the rate of increase in stem diameter of a hybrid plant growing in cultivation for six years. From this comparison, most wild hybrid plants appeared to be four years of age or older, but one flowering hybrid was found with a stem diameter and branching pattern that suggests it was no more than two years old.

Pollinators. Thirty-one pollinating and herbivorous insects were collected from *Malacothrix* parents and hybrids (Miller and Davis 1985). Three species of insects were collected from both parents and the hybrids, and the parents shared an additional four species of visitors that were not observed on the hybrids. Both parents and hybrids were in flower with up to 250 open flower heads on individual plants. On parents and hybrids, the heads opened about 0700 h and among the first visitors to the two parents was the native bee *Agapostemon texanus* Cresson, which appears to be the major pollinator of *Malacothrix* species on San Miguel Island. The relatively large, metallic green females were numerous in the morning hours, and a majority of the pollen taken from 11 females of this species from San Miguel Island was from *Malacothrix.* On four occasions we saw individuals of *A. texanus* move from flowers of one parent to flowers of the other parent.

DISCUSSION

Evidence from the present study suggests that hybridization between *Malacothrix incana* and *M. saxatilis* var. *implicata* occurs on San Miguel Island when the two are found in sympatry. Hybrids are less abundant than the parents. For example, only 20 hybrids were found along the slopes above Cuyler Harbor where thousands of plants of each parent occur. The presence of a young hybrid plant on the island and the wide range of apparent ages of the other hybrids suggest that hybridization is a continuing phenomenon.

We have found no evidence that natural hybridization has proceeded beyond the F_1 level and the production of F_2 segregates is improbable. All of the hybrids were sterile, less than 0.1% of the achenes from heads of hybrids were filled, and no chromosome associations were observed in hybrids grown in the growth chamber. Parents and hybrids were identified easily in nature, as herbarium specimens, or in the growth chamber; no combinations of character states were found that suggested segregation beyond the F_1 level.

The achenes of the parents are dispersed easily because of their small size (length ca. 1 mm), light weight (ca. 0.05 mg), and the presence of a ring of inner pappus bristles that may remain attached to the fruit and can function as a parachute. Achenes from mature heads of cultivated parents often were seen floating in the air from one end of the growth chamber to the other. During each growing season, seedlings of *M. incana* regularly appeared in pots containing mature plants of other species of *Malacothrix.* Because of the almost constant wind and its relatively high velocity on San Miguel Island, it is likely that achenes of both species have had a chance to be distributed throughout the island. The general pattern of distribution of *M. incana* and *M. s.* var. *implicata* on San Miguel Island, however, suggests that each species has different habitat preferences. This view is supported by observations from San Nicolas Island where both *M. incana* and *M. s.* var. *implicata* are found and by the distribution of *M. incana* on mainland California. At mainland sites, *M. incana* is restricted to coastal strand communities where stable sand dunes are found. Williams and Potter (1972) found that *M. incana* was restricted to the stable dune area at Morro Bay State Park (San Luis Obispo Co.) where it formed conspicuous scattered colonies. On San Nicolas Island, we recently found *M. incana* to be distributed widely on portions of the island where the substrate is stabilized sand and also near the ocean on stabilized or unstabilized sand dunes. We found *M. s.* var. *implicata* growing only on more compacted sandy-clay soils, either on bluffs away from the main beach areas or along the ocean on the leeward side of the island. We found no habitats on San Nicolas Island where *M. incana* and *M. s.* var. *implicata* were sympatric.

Johnson (1980) suggested that recurrent episodes of vegetation stripping and soil erosion have occurred during late Pleistocene to recent historic time on San Miguel Island. Historic stripping episodes have followed droughts, overgrazing, and farming activities. Landscape modification has included dune encroachments and wind erosion. An aerial photograph taken on 1 April 1960 (Johnson 1980) showed strips of sands that ran from one side of the island to the other. The distribution of *M. incana* across the slopes of Green Mountain and San Miguel Hill is generally correlated with these stabilized sandy areas. Such changes in edaphic factors apparently have played the primary role in allowing *M. incana* and *M. s.* var. *implicata* to grow sympatrically.

Natural hybridization between *Malacothrix incana* and *M. saxatilis* var. *implicata* suggests a relationship between the *M. saxatilis* complex and the main body of *Malacothrix.* With respect to most morphological features, however, the *M. saxatilis* complex is less similar to *M. incana* and related annual species than it is to some of the mainland annual species. For example, an outer pappus similar in construction to the one in the *M. saxatilis* complex is found in *M. glabrata* A. Gray, and the receptacles of most annual mainland species are foveolate and bear chaff. White corollas similar to those in the *M. saxatilis* complex are found in *M. floccifera* (DC.) Blake, but the latter has no outer pappus. Natural hybridization between *M. incana* and *M. s.* var. *implicata* and the fact that a number of morphological features of the *M. saxatilis* complex occur in other species in the genus support the idea that *Malacothrix* is natural as currently defined. There is no extant mainland species with a suite of morphological features that match it with members of the *M. saxatilis* complex, however, and the precise placement of the complex in *Malacothrix* remains to be determined.

ACKNOWLEDGMENTS

We thank the curators of the following herbaria for loans of specimens: CAS, COLO, DAV, DS, GH, JEPS, LA, LAM, MO, ND, OBI, POM, RM, RSA, SBBG, SEM, TEX, UC, UCSB, UNM, US, UT. Original field collections were made by the junior author with Michael Benedict or Donald Ricker. During the 1984 visit to San Miguel Island, Steve Junak assisted with vegetation analysis and field tasks. Collection and later identification of insects was arranged by Scott Miller. The assistance of the U.S. Park Service and particularly Ranger Tom Cox is acknowledged gratefully. Involucre drawings were rendered by Rosemary Bauman. The helpful comments of Dr. Henry J. Thompson on the first draft of the manuscript are appreciated. The editor and reviewers provided valuable comments and suggestions.

LITERATURE CITED

ABRAMS, L. and R. S. FERRIS. 1960. An illustrated flora of the Pacific states, Vol. 4. Stanford University Press, Stanford, CA.

DAVIS, W. S. 1980. Distribution of *Malacothrix* (Asteraceae) on the California islands and the origin of endemic insular species. *In* D. M. Power, ed., The California islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

JOHNSON, D. L. 1980. Episodic vegetation stripping, soil erosion, and landscape modification in prehistoric and recent historic time, San Miguel Island, California. *In* D. M. Power, ed., The California islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

MILLER, S. E. and W. S. DAVIS. 1985. Insects associated with the flowers of two species of *Malacothrix* (Asteraceae) on San Miguel Island, California. Psyche 92: 547–555.

NETTANCOURT, D. DE. 1977. Incompatibility in angiosperms. Springer-Verlag, New York.

NUTTALL, T. 1841. Descriptions of new species and genera of plants in the natural order of the Compositae, collected in a tour across the continent to the Pacific. Trans. Amer. Philos. Soc. II, 7:440.

Philbrick, R. 1980. Distribution and evolution of endemic plants of the California islands. *In* D. M. Power, ed., The California islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Williams, E. W. 1957. The genus *Malacothrix* (Compositae). Amer. Midl. Naturalist 58:494–517.

Williams, W. T. and J. R. Potter. 1972. The coastal strand community at Morro Bay State Park, California. Bull. Torrey Bot. Club 99:163–171.

(Received 6 Sep 1985; revision accepted 16 Jul 1986.)

ANNOUNCEMENT

UCSB HERBARIUM PUBLICATION SERIES

The UCSB Herbarium Publication Series is issued at irregular intervals from the Herbarium, Dept. of Biological Sciences, University of California, Santa Barbara, CA 93106. Manuscripts accepted for publication in the Series include primarily those with a floristic emphasis and those for which voucher specimens are deposited at UCSB. The most recent issue, *A flora of Dry Lakes Ridge,* is a product of research conducted by a herbarium staff member, David Magney, and was compiled originally for his senior thesis. Copies of this and other publications are available from the UCSB Herbarium; checks should be made payable to the UCSB Foundation.

Howald, A. M. 1981. A flora of Valentine Eastern Sierra Reserve, Part I: Valentine Camp. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Publication No. 1, p. 1–55. (A limited number of free copies are available.)

Orr, B. K. 1981. A flora of Valentine Eastern Sierra Reserve, Part II: Sierra Nevada Aquatic Research Laboratory. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Publication No. 1, p. 57–97. (A limited number of free copies are available.)

Fletcher, M. 1983. A flora of Hollister Ranch, Santa Barbara County, California. The Herbarium Department of Biological Sciences, University of California, Santa Barbara, Publication No. 2. 77 p. (Out of print.)

Ferren, W. R., Jr., H. C. Forbes, D. A. Roberts, and D. M. Smith. 1984. The botanical resources of La Purisima Mission State Historical Park, Santa Barbara County, California. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Publication No. 3. 159 p. ($6.00)

Ferren, W. R., Jr. 1985. Carpinteria Salt Marsh: environment, history and botanical resources of a southern California estuary. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Publication No. 4. 300 p. ($15.00)

Magney, D. L. 1986. A flora of Dry Lakes Ridge, Ventura County, California. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Publication No. 5. 110 p. ($8.00)

CHROMOSOME COUNTS IN *MIMULUS* SECT. *ERYTHRANTHE* (SCROPHULARIACEAE). III

Robert K. Vickery, Jr., Byoung-Ky Kang, Thuong K. Mac
Department of Biology, University of Utah,
Salt Lake City 84112

Steven R. Pack
School of Medicine, University of Utah,
Salt Lake City 84132

Dennis A. Phillips
College of Pharmacy, University of Utah,
Salt Lake City 84132

ABSTRACT

Chromosome counts of $n = 8$ were obtained for greenhouse grown plants of seven populations and color morphs of *Mimulus cardinalis* Douglas, four populations of *M. lewisii* Pursh, and two populations of *M. verbenaceus* Greene. These counts include distinctive populations from the extreme southern peripheries of the ranges of *M. cardinalis* (1 population—3 color morphs) and *M. verbenaceus* (2 populations). Populations of these three species, widespread *M. lewisii* Pursh ($n = 8$), and the rare, narrow endemic, *M. rupestris* Greene ($n = 8$), were hybridized experimentally in 10 intraspecific and interspecific combinations. Eight of the resulting F_1 hybrids showed $n = 8$ and regular chromosome pairing, whereas the other two F_1 hybrids also had two or more regular diploid plants ($n = 8$), but in addition, each had one triploid plant with $n = 12 \pm 1$ or 2.

Evolutionary divergence that involves, for example, chromosome number or homology has been postulated to be both important and likely in isolated peripheral populations or narrow endemic species (Mayr 1976). The purpose of our investigation was to test this hypothesis in *Mimulus* sect. *Erythranthe* by 1) determination of the chromosome numbers in populations of *M. cardinalis* Douglas, *M. lewisii* Pursh, and *M. verbenaceus* Greene, particularly of those from the periphery of their species' ranges, and 2) the study of chromosome pairing in F_1 hybrids, particularly in hybrids between more centrally distributed and more peripheral populations or narrow endemic species (Fig. 1). This investigation is part of the authors' long range experimental study of the evolution of species in sect. *Erythranthe* (Vickery 1978, 1984, Wullstein and Vickery in press).

MATERIALS AND METHODS

Six or more plants of each population were grown in the University of Utah greenhouse (Table 1). The plants were obtained either as

Madroño, Vol. 33, No. 4, pp. 264–270, 1986

TABLE 1. CHROMOSOME COUNTS IN *Mimulus* SECT. *Erythranthe.* Populations are arranged by species, locality, collector, culture number. Each culture number is followed by the initial of its species to facilitate recognition.

M. cardinalis Douglas. $n = 8$

U.S.A., CA, Yosemite National Park: Chinquapin, 1858 m, 23 Aug 1984, *S. Sutherland s.n., 13,359C*; Upper Yosemite Falls, ca. 1540 m, 23 Aug 1984, *S. Sutherland s.n., 13,360C*; South Gate, 1544 m, 23 Aug 1984, *S. Sutherland s.n., 13,361C*; Wawona campground, ca. 1230 m, 24 Aug 1984, *S. Sutherland s.n., 13,363C.*

Mexico, Baja California del Norte, Cedros Island, Aguaje Vargas, 600 m, 25 Oct 1981, *S. Sutherland s.n.*, red-flowered morph = *13,248C*; orange-flowered morph = *13,249C*; yellow-flowered morph = *13,106C* and *13,250C.*

M. lewisii Pursh. $n = 8$

U.S.A., WA, Umatilla National Forest, ca. 1250 m, Aug 1980, *R. Jorgensen s.n., 13,098L*; CA, Yosemite National Park, Raisin Lake, 2123 m, 25 Aug 1984, *S. Sutherland s.n., 13,357L*; east of Porcupine Flat, 2461 m, 25 Aug 1984, *S. Sutherland s.n., 13,358L*; UT, Little Cottonwood Canyon, Snowbird, Big Emma, ca. 2525 m, 18 Sept 1984, *R. K. Vickery, Jr. 2928, 13,466L.*

M. verbenaceus Greene. $n = 8$

Mexico, Sonora, Baconora, 770 m, 24 Apr 1982, *D. A. Polhemus s.n., 13,255V*; Yecora, 1550 m, 25 Apr 1982, *D. A. Polhemus s.n., 13,256V.*

---

transplants from the wild, seeds collected in the wild, or seeds harvested from these sources. Each population was assigned a culture number when it was collected by one of us or when it was obtained from other collectors following the practice of Hiesey et al. (1971).

Experimental hybridizations were made among 10 populations of sect. *Erythranthe* (Table 2) with the goal of assessing chromosome homology, as gauged by chromosome pairing, in the interpopulation and interspecific F_1 hybrids obtained. The populations hybridized included three newly counted ones (Table 1) and seven from an earlier study (Vickery 1978) representative of *M. cardinalis, M. lewisii,* and *M. rupestris* Greene. The crosses were carried out in an insect-free greenhouse. At first, flowers were emasculated, but in later crosses, this practice was discontinued in order to allow some self-pollination. Capsules that contained at least a few seeds resulting from self-pollination developed, whereas capsules with apparently only hybrid seeds often aborted. Also, after the seeds were sown and the seedlings emerged and grew, the "selfed," maternal type seedlings provided an excellent control against which to verify the validity of the F_1 hybrids. Each hybrid combination was assigned a culture number. In experimental studies such as this, culture numbers provide an efficient way of keeping track not only of parental populations (see above), but also of the numerous F_1, F_2 and backcross hybrids studied.

For the chromosome pairing study, six or more plants of each F_1 hybrid combination were propagated in the greenhouse.

TABLE 2. INTERPOPULATION AND INTERSPECIFIC F_1 HYBRIDS OF *Mimulus* ARRANGED BY F_1 HYBRID CULTURE NUMBER, FEMALE PARENT, MALE PARENT, AND UT VOUCHER NUMBER. All parents have $n = 8$ chromosomes. Geographical locations are indicated briefly. For full details of parental populations not listed in Table 1, see Vickery et al. 1958, 1963, 1982; McArthur et al. 1971.

Female parent	Male parent	F_1 culture number
A. *Diploids, n* = 8 (all have regular chromosome pairing in Metaphase I of meiosis followed by occasional, slightly irregular segregations).		
M. cardinalis, 7120C Los Trancos, CA	*M. cardinalis, 7113C* Mt. San Antonio, CA	*13,178*
M. cardinalis, 13248C-red Cedros Is., B.C., Mex.	*M. lewisii, 6103L* Ice Lake, CA	*13,293*
M. cardinalis, 13106C-yellow Cedros Is., B.C., Mex.	*M. lewisii, 6103L* Ice Lake, CA	*13,258*
M. verbenaceus, 5924V Grand Canyon, AZ	*M. lewisii, 6103L* Ice Lake, CA	*13,180*
M. lewisii, 5875L Alta, UT	*M. lewisii, 6103L* Ice Lake, CA	*13,374*
M. lewisii, 6103L Ice Lake, CA	*M. lewisii, 5875L* Alta, UT	*13,375*
M. lewisii, 5875L Alta, UT	*M. cardinalis, 13248C*-red Cedros Is., B.C., Mex.	*13,289*
M. lewisii, 13257L Raisin Lake, Yosemite Nat. Park, CA	*M. cardinalis, 13363C* Wawona, Yosemite Nat. Park, CA	*13,468*
M. lewisii, 5875L Alta, UT	*M. rupestris, 9102R* Tepoztlan, Morelos, Mex.	*13,288*
M. rupestris, 9102R Tepoztlan, Morelos, Mex.	*M. cardinalis, 7113C* Mt. San Antonio, CA	*13,179*
B. *Triploids, n* = 12 ± 1 or 2 (each plant exhibited ± 8 bivalent chromosome associations plus 1–6 univalent chromosomes).		
M. rupestris, 9102R Tepoztlan, Morelos, Mex.	*M. cardinalis, 7113C* Mt. San Antonio, CA	*13,179*
M. lewisii, 5875L Alta, UT	*M. cardinalis, 13248C*-red Cedros Is., B.C., Mex.	*13,289*

Flower buds were removed and the anthers squashed in a drop of aceto-carmine stain. The slides were immediately observed under a phase contrast microscope, an improvement over our earlier method (Vickery et al. 1963). Cover slips were ringed with dental sticky wax, which avoided dehydration and permitted observation for two to three weeks. Usually the chromosomes had taken up sufficient stain to be clearly visible after one or two days. Sketches and camera lucida drawings were made of representative cells. Chromosome number determinations and pairing behavior were based on observations of 20 or more PMC's typically from two to six plants. Vouchers of the plants counted are deposited in the Herbarium of University of Utah (UT).

RESULTS AND DISCUSSION

All the native populations counted have $n = 8$ (Table 1). This result confirms previous reports (Brozek 1932, Sugiura 1940, Vickery et al. 1958, 1963, 1982, Hiesey et al. 1971, McArthur et al. 1971) of a uniform $n = 8$ chromosome number in sect. *Erythranthe.* The native, parental populations counted include three from the extreme southern peripheries of the ranges of two species: the populations of *M. verbenaceus* Greene from Baconora and Yecora, Sonora, Mexico and the population of *M. cardinalis* from Cedros Island, Baja California del Norte, Mexico (Table 1). In all cases, the populations had normal meiosis.

The plants of the peripheral populations of *M. verbenaceus* have much narrower leaves compared with plants farther north, particularly those from populations in Arizona that include a topotype from the Verde Valley (Vickery 1978). The narrow leaves of plants from the Baconora and Yecora populations appear intermediate between the lanceolate leaves of typical *M. verbenaceus* and the extremely narrow leaves of *M. nelsonii* Grant (see illustration in Vickery et al. 1963) from Durango and Sinaloa farther south in the Sierra Madre. Plants of *M. cardinalis* populations from Cedros Island are unusual in that individuals have orange, bright yellow, or normal cardinal-red flowers. The three wild color morphs proved to be interfertile as Brožek (1932) had found previously for similar, horticulturally-derived color forms (obtained from Vilmorin et Cie, Paris).

Most of the intra- and interspecific F_1 hybrids (Table 2) exhibited regular chromosome pairing (8 bivalents) in Metaphase I, with occasional irregularities in chromosome segregation in the later stages of meiosis (Fig. 2). Occasional cells with $n = 6$, 7, 9 or 10 chromosomes instead of $n = 8$ were observed. For example, the chromosome counts for one F_1 hybrid (culture no. *13,258*, *M. lewisii* × *M. cardinalis*) were $n = 6$, 1 cell; $n = 7$, 6 cells; $n = 8$, 30 cells; $n = 9$, 2 cells; and $n = 10$, 1 cell.

One plant of each of two of the interspecific F_1 hybrids [culture no. *13,179* = *M. rupestris* (*9102R*) × *M. cardinalis* (*7113C*); and culture no. *13,289* = *M. lewisii* (*5875L*) × *M. cardinalis* (*13,248C*)] were found to be triploids with $n = 12 \pm 2$ chromosomes. The other plants of both F_1 hybrid combinations had $n = 8$ chromosomes and exhibited essentially regular pairing as above. The only other *Erythranthe* polyploid known to us is a single tetraploid F_1 hybrid [*M. nelsonii* (El Salto, Durango, Mexico) × *M. lewisii* (Timberline, Mono Co., CA)] reported by Hiesey et al. (1971). These authors suggest

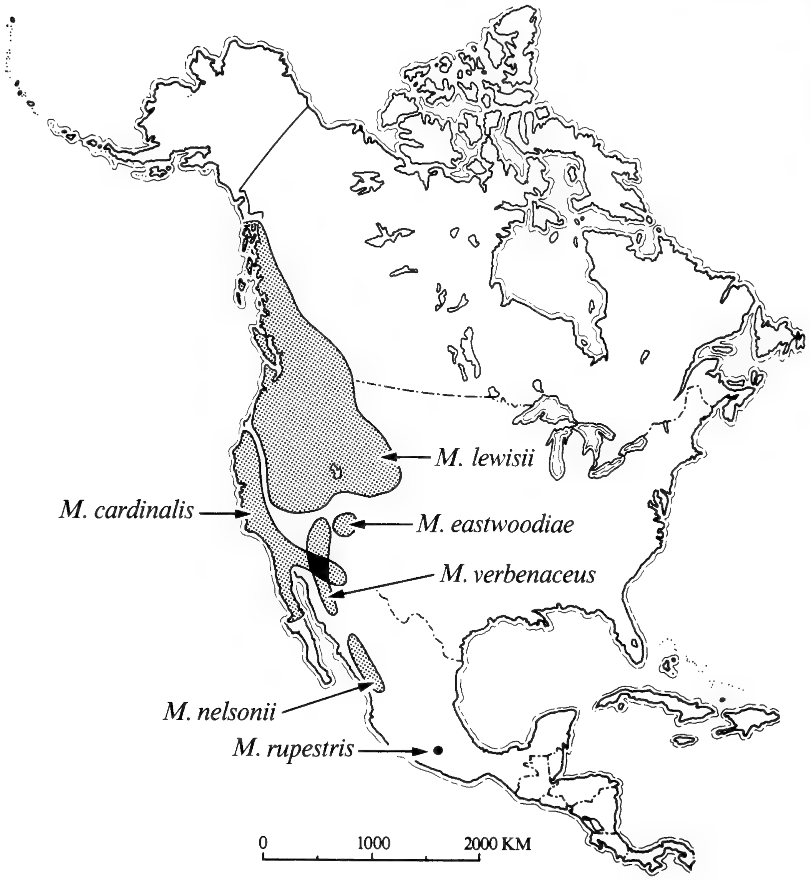


FIG. 1. Distribution map of the species of *Mimulus* sect. *Erythranthe.*

that the formation of this amphiploid tetraploid stresses the genetic distinctness of the *M. cardinalis–lewisii* complex from the *M. eastwoodiae* Rydberg–*verbenaceus–nelsonii* complex to which we have shown *M. rupestris* to belong also (Vickery 1978). Our finding of the triploid F_1 hybrids both within and between these complexes sheds no further light on the relationships of the complexes.

CONCLUSIONS

The peripheral populations of *M. cardinalis* and *M. verbenaceus* have $n = 8$ in accord with other wild populations of sect. *Erythranthe.* No reduction in chromosome pairing or polyploidy was detected in peripheral populations of sect. *Erythranthe* as were observed in sect. *Simiolus,* particularly in *M. guttatus* Fisch. ex DC. (Vickery 1978).

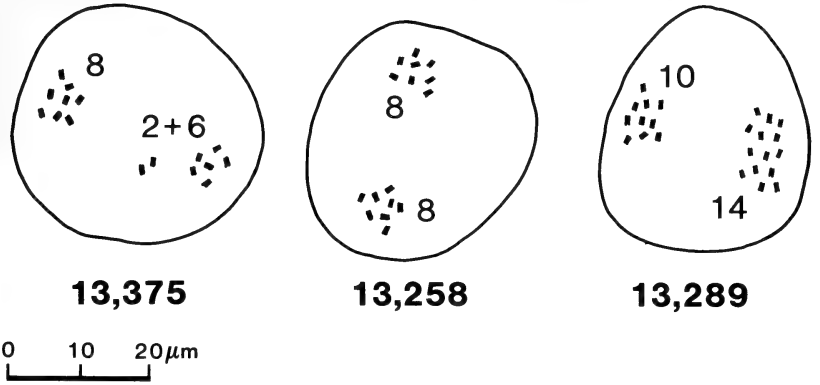


FIG. 2. Camera lucida drawings of representative chromosome configurations at Metaphase II of meiosis. Cultures *13,375* and *13,258* illustrate, respectively, irregular and regular segregations in diploid, $2n = 16$, F_1 hybrids. Culture *13,289* illustrates a typical, irregular segregation in a triploid, $3n = 24$, F_1 hybrid.

The intra- and interspecific F_1 hybrids between populations from the central regions of their species' ranges and peripheral populations showed a similar level of near normal chromosome pairing as did F_1 hybrids both of whose parents came from the central regions of their species' ranges. The F_1 hybrids involving the narrow endemic, *M. rupestris,* also showed normal chromosome pairing. There was no indication that the chromosomes of either the peripheral or narrow endemic populations have evolved to the point where a reduction in homology causes a significant reduction in chromosome pairing.

Our finding of the two rare triploid F_1 hybrid plants suggests to us that polyploidy probably occurs at a very low frequency in any sect. *Erythranthe* population or hybrid as observed in the *M. glabratus* HBK complex (Tai and Vickery 1970). Thus, although the peripheral and narrow endemic populations have diverged morphologically, they do not appear to have diverged in chromosome number or homology in sect. *Erythranthe.*

ACKNOWLEDGMENTS

We thank Drs. Stephen Sutherland, Dan A. Polhemus, and Richard Jorgensen for their helpful collections. We thank N.I.H. (grant no. 507-RR07092) and N.S.F. (grant no. DEB79-11554) for financial support.

LITERATURE CITED

BROŽEK, A. 1932. Mendelian analysis of the "red-orange-yellow" groups of flower colours in *Mimulus cardinalis.* Hort. Preslia 11:1–10.

HIESEY, W. M., M. A. NOBS, and O. BJÖRKMAN. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics, and physiological ecology of the *Erythranthe* section of *Mimulus.* Carnegie Inst. of Wash. Publ. no. 628, Washington, DC.

MAYR, E. 1976. Evolution and the diversity of life. Harvard University Press, Cambridge.

MCARTHUR, E. D., R. K. VICKERY, JR., and A. E. ANDERSON. 1971. Scrophulariaceae. *In* IOPB chromosome number reports XXXI, presented by A. Löve. Taxon 20:157–160.

SUGIURA, T. 1940. Studies in the chromosome numbers in higher plants. V. Cytologia 10:363–370.

TAI, W. and R. K. VICKERY, JR. 1970. Cytogenetic relationships of key diploid members of the *Mimulus glabratus* complex (Scrophulariaceae). Evolution 24: 670–679.

VICKERY, R. K., JR. 1978. Case studies in the evolution of species complexes in *Mimulus*. *In* M. K. Hecht, W. C. Steere, and B. Wallace, eds., Evolutionary biology 11:405–507. Plenum Press, New York.

———. 1984. Biosystematics 1983. *In* W. F. Grant, ed., Plant biosystematics, p. 1–24. Academic Press, Montreal.

———, B. B. MUKHERJEE, and D. WIENS. 1958. Chromosome counts in section *Erythranthe* of the genus *Mimulus* (Scrophulariaceae). Madroño 14:150–153.

———, ———, and ———. 1963. Chromosome counts in section *Erythranthe* of the genus *Mimulus* (Scrophulariaceae). II. Madroño 17:53–56.

———, S. A. WERNER, and E. D. MCARTHUR. 1982. Scrophulariaceae. *In* IOPB chromosome number reports LXXV, presented by A. Löve. Taxon 31:342–368.

WULLSTEIN, B. M. and R. K. VICKERY, JR. In press. Comparison of six approaches to the classification of section *Erythranthe* of the genus *Mimulus*. Systematic Botany.

(Received 23 Oct 1985; revision accepted 6 June 1986.)

MIMULUS SHEVOCKII (SCROPHULARIACEAE), A NEW SPECIES FROM DESERT HABITATS IN THE SOUTHERN SIERRA NEVADA OF CALIFORNIA

Lawrence R. Heckard and Rimo Bacigalupi
Jepson Herbarium, Department of Botany,
University of California, Berkeley 94720

Abstract

Mimulus shevockii, a new species in sect. *Paradanthus* from desert habitats in the southern Sierra Nevada of Kern County, California, is described and illustrated. Its corolla is unique: four upper lobes are small, entire, and maroon-purple; the lowest lobe is much larger, bifid, and bright yellow. Vegetative and pollen morphology of *M. shevockii* resembles members of the *M. rubellus* and *M. palmeri* groups of sect. *Paradanthus.*

Several collections of *Mimulus* dating back to 1932 were made in the desert region of the southern Sierra Nevada near Kernville. The specimens, which did not clearly show the corolla, remained unidentified or were tentatively assigned to *M. barbatus* Greene, a species of meadow borders or damp granitic sands primarily in Jeffrey pine forests of higher elevations on the Kern Plateau. James R. Shevock, intrigued by the striking difference in the two habitats, searched for and found the puzzling desert plants. He has supplied excellent field study notes, photographs, and specimens documenting the plants as a distinctive new species with a highly limited distribution. We are pleased to name the species in honor of this energetic and effective botanist who has contributed greatly to our knowledge of the plants of the southern Sierra Nevada.

Mimulus shevockii Heckard and Bacigalupi, sp. nov.

Herba annua minute glandulosa usque ad 12 cm alta. Folia sessilia amplectentia connataque lanceolato-ovata vel anguste ovata aliquantum succulenta concavaque. Flores axillares pedicellis 10–15 (–20) mm longis. Calyx vasiformis angulatus costis leviter incrassatis apud florem 4–6 mm apud fructum 6–7 mm longis dentibus 0.7–1.0 mm longis truncatis vel rotundatis saepe mucronulatis. Corollae tubus faucesque 8–12 mm longi, labiis usque ad 10–15 mm ampliatis; labium superiorum duobus brevibus rotundatis marronino-purpureis lobulis; labium inferiorum duobus lateralibus marronino-purpureis lobulis et unico lobo magno flavido leviter lato quam longo et 5–10 mm longo instructis. Stigmata ciliato-papillata et stamina ex ore corollae parum exsert (Figs. 1, 2).

Madroño, Vol. 33, No. 4, pp. 271–277, 1986

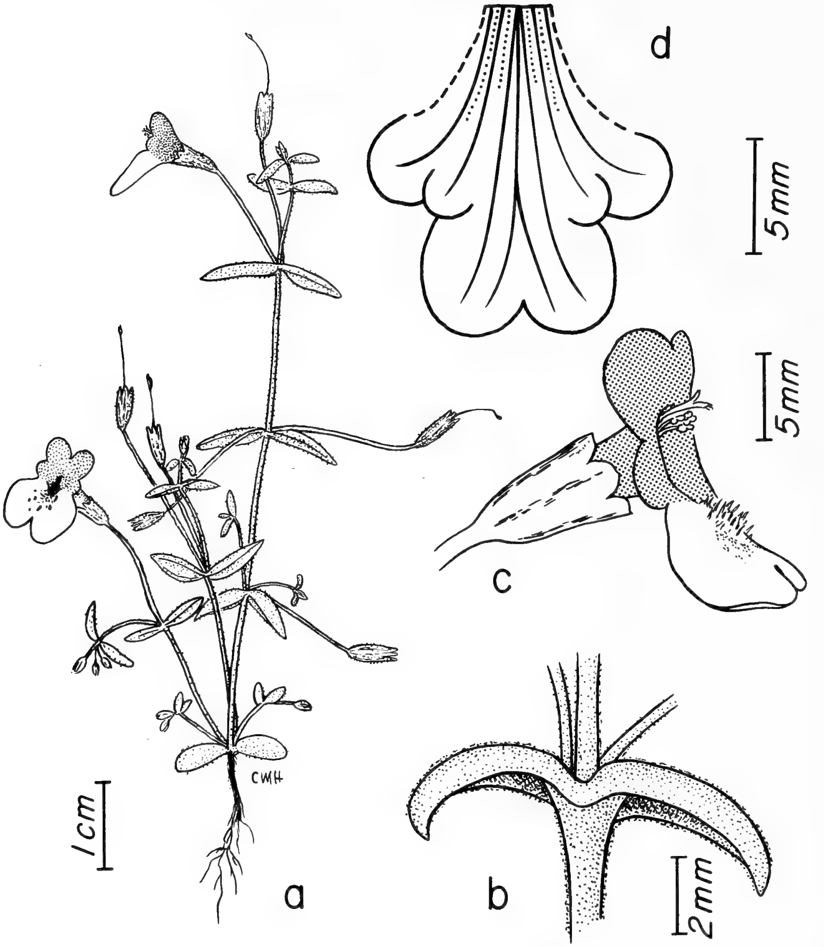


FIG. 1. *Mimulus shevockii.* a. Habit. b. Nodal region with lowermost pair of connate leaves. c. Flower. d. Corolla opened dorsally, showing major veins. From *Bacigalupi 9446.*

Minutely glandular-puberulent annual; stems erect to 12 cm, simple or branched at lowermost nodes. Cotyledons persistent, rotund to ovate, 5–10 mm long, the bases clasping. Leaves 1–10 pairs, sessile, the lowermost ovate to lanceolate, usually connate at base, 5–10 mm long, somewhat fleshy, purplish below and slightly concave with entire thickened margins, obscurely palmately veined with five (three in upper leaves) sunken veins; upper leaves reduced and narrowed, clasping but not connate at base, often reflexed with deflexed tip. Flowers axillary from first leaf node upward; pedicels 10–15(–20) mm long, exceeding internodes in length, ascending or becoming

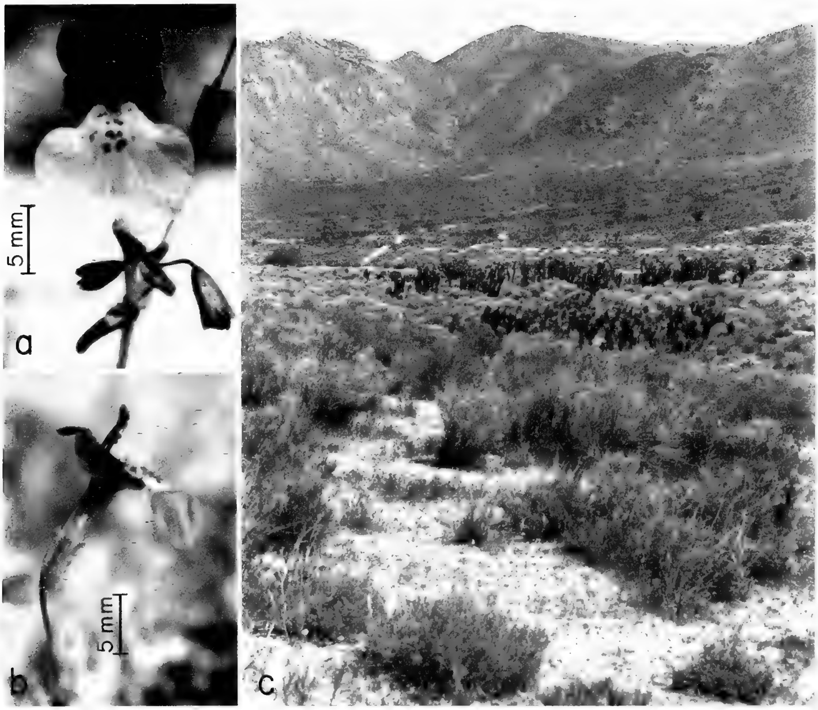


FIG. 2. *Mimulus shevockii.* a. Flower, face view. b. Flower, side view. c. Habitat, region of Joshua tree woodland in Kelso Creek Valley; type locality.

divergent or declinate with upturned apices, mostly glabrous; calyx vase-shaped, angled, 4–7 mm long, elongating in fruit only slightly or not at all but becoming distended by maturing capsule, the ribs slightly thickened and often greenish-yellow with several elongated reddish spots or solid red, weakly glandular-puberulent; calyx teeth 0.7–1.0 mm long, rounded to acute, often mucronulate. Corolla bilabiate, tube-throat 8–12 mm long, the lips widely and unequally spreading 10–15 mm, upper lip with two short (3–5 mm) rounded (sometimes weakly mucronulate) maroon-purple lobes, the lower lip with two short (1–3 mm) lateral maroon-purple lobes (below the lobes of upper lip and appearing to be a part of it) and one large yellow bifid lobe 5–10 mm long, 8–15 mm broad; throat and base of lowermost lobe of lower lip with two palatal folds, maroon-purple spotted and bearded with trichomes up to 1 mm long; tube-throat maroon-purple distally, pallid below. Stamens glabrous, exserted 1–2(–4) mm, upper pair 4–6 mm long, lower pair 7–8 mm long, attached slightly lower in tube, anthers connivent in pairs, filaments dark red. Stigma exserted, slightly exceeding anthers, dark red, lobes equal, irregularly ciliate-papillose, the style weakly puberulent below stigma, sometimes breaking proximally and leaving apiculation on mature capsule; capsule ellipsoid, 5–6 mm long, barely included in calyx-tube at maturity, dehiscent at apex and along both sutures, the placenta splitting to ⅓ or less its length. Seeds many (more than 100), ellipsoid to ovoid, tan, faintly reticulate, ca. 0.5 mm long. Chromosome number $n = 16$.

TYPE: USA, CA, Kern Co.: w. side of Kelso Creek along dirt road to Cortez Canyon, n. of Kelso Creek, 1067 m, T27S R35E S34 w.½, 16 Apr 1983, *Shevock 10319* (Holotype: JEPS; isotypes: CAS, GH, MO, NY, RM, RSA, SBBG, US).

PARATYPES: USA, CA, Kern Co.: near Kernville, 12 Apr 1932, *Bangsberg s.n.* (JEPS); Cyrus Canyon, *Twisselmann 14087* (CAS, JEPS), *14097* and *17640* (CAS); Cyrus Canyon, e. of Sierra Way Rd., T26S R33E S6I, *Shevock 10267* (CAS, JEPS, SBBG), *Shevock 10327* (CAS, JEPS, RSA), *Norris 370* (CAS, JEPS); Kelso Creek, *Luthey 341-B* (CAS); Kelso Creek, w. side, along road to Cortez Canyon, T27S R35E S34, *Shevock 9321* (CAS, JEPS, RSA), *10266* (CAS, FSC, MO, NY, RSA), *10368* (CAS, JEPS, RSA); Kelso Creek, w. side, 1 mile nw. of Bird Spring Pass road junction, T27S R35E S28, *Shevock 10322* (CAS, JEPS, MO, RSA), *Norris 375* (JEPS), *Bacigalupi 9346* (JEPS), *Heckard 6225* (JEPS); Kelso Creek, w. side, just s. of Bob Rabbit Canyon, T27S R35E S20, *Shevock 10383* (CAS, JEPS, NY, RSA); Cortez Canyon, T28S R35E S05, *Shevock 10320* (CAS, JEPS, NY, RSA).

Distribution and ecology. Mimulus shevockii occurs predominantly in loamy, coarse sands on alluvial fans and deposits of granitic origin (Fig. 2c). The Cyrus Canyon population, however, grows on finer soils developed from metasedimentary rocks. All populations are within Joshua tree or California juniper woodlands, or their transition at 975–1250 m, with a mean annual precipitation of about 20 cm. Flowering occurs April–May.

Even though hundreds of hectares appear to contain suitable habitat, only six populations of *Mimulus shevockii* have been discovered, all within a relatively limited geographical area of the southern Sierra Nevada within the Kern River drainage in the Lake Isabella region. Five of the six populations are located at the northeast base of the Piute Mountains north of Kelso Peak within 3 km of Kelso Creek. A sixth population, collected by Ernest Twisselmann in 1968 and by Shevock in 1983 is disjunct about 22 km northwestward in Cyrus Canyon near Kernville.

Associated species (at all localities): *Anisocoma acaulis, Camissonia graciliflora, Canbya candida, Ephedra nevadensis, Eriogonum fasciculatum subsp. polifolium, Eriophyllum pringlei, Haplopappus linearifolius, Hymenoclea salsola, Linanthus aureus, L. parryae, Lu-*

pinus concinnus var. *orcuttii, Mimulus androsaceus, M. fremontii, Opuntia echinocarpa, Pectocarya penicillata, P. setosa,* and *Salvia dorrii.*

Relationships. According to the comprehensive treatment of the genus *Mimulus* by Grant (1924), *M. shevockii* belongs to sect. *Paradanthus,* a large group that she proposed to accommodate a diverse assemblage of species. Some of these species she admitted were quite unrelated and even possibly derived from different sections. The relationship of *M. shevockii* within the section is problematic. Its corolla is unique in lobe configuration and color pattern. The two lateral lobes of the lower lip are reduced and raised to a horizontal position (Fig. 1c) and are colored the same as the upper lip (rather than having the lips of separate colors as in other species with bicolored corollas). Thus, only the much enlarged central lobe of the lower lip is yellow. Only one example of a similar color pattern is known and that was recently observed and photographed in *M. pulchellus* A. L. Grant (sect. *Oenoe*) at Yosemite National Park (S. Botti pers. comm.). The photographs show considerable variation in corolla ranging from the usual pattern (upper lip purplish and lower lip yellow) through intermediate conditions to corollas in which the lower lip has lateral lobes purplish and the central lobe yellow as in *M. shevockii.* This would seem to indicate that the color pattern in the corolla of *Mimulus* is more capable of evolutionary modification than previous evidence indicated.

Vegetative morphological features of *Mimulus shevockii* are close to those of species in the *M. rubellus* and *M. palmeri* groups as circumscribed and discussed by Grant (1924, p. 110–111). Several species (e.g., *M. androsaceus* Curran ex Greene, *M. barbatus* Greene, *M. gracilipes* Robinson, and *M. purpureus* A. L. Grant) in these groups are similar to *M. shevockii* in their small leaves with clasping-connate leaf bases, long and spreading to ascending pedicels, and calyx with short rounded, often mucronulate lobes. None of these species, however, has any hint of the unusual corolla features of *M. shevockii. Mimulus androsaceus,* which grows with *M. shevockii,* is remarkably similar in vegetative features, including a leaf that is purplish and marginally thickened abaxially.

Evidence from chromosome number for the relationship of *Mimulus shevockii* is minimal but does not negate a connection with those species of sect. *Paradanthus* that most resemble it vegetatively. The chromosome number for *M. shevockii,* kindly supplied by Dr. T-I. Chuang, is $n = 16$ (based on *Shevock 10322*). This number, along with $n = 8$, is the most common number in sect. *Paradanthus,* occurring in 13 of the 16 known counts (Vickery 1978, Heckard and Shevock 1985, Chuang and Heckard unpubl.). Three counts are available for species of the *M. rubellus* and *M. palmeri* groups that vegetatively resemble *M. shevockii* and these are also $n = 8$ and 16.

Pollen features also are equivocal. Argue (1980, letter 1985) considers pollen of *M. shevockii* to be Type IIb, indistinguishable from that of *M. barbatus* and similar to that of *M. rubellus* Gray and *M. discolor* Grant. These three species are in the *M. rubellus* group and are similar vegetatively to *M. shevockii. Mimulus dudleyi* Grant and *M. repens* R. Br., however, which are morphologically unrelated, also have very similar pollen of Type IIb. Less similar Type IIb pollen is known in six other species of sect. *Paradanthus.* Pollen of many taxa remains to be studied with SEM. Therefore, the systematic significance of pollen morphology remains unclear within sect. *Paradanthus,* but pollen data do not contradict deductions of relatedness from vegetative morphology.

Mimulus barbatus, which occurs in meadow borders at higher elevations in the nearby Kern Plateau, has been confused with *M. shevockii,* but the corollas of the two species are highly dissimilar, especially in shape. *Mimulus barbatus* also has a bicolored corolla, but the corolla lobes are each cleft and the upper lip of two lobes is reddish-purple (rather than maroon-purple) and the lower lip has three downward projecting yellow lobes. If *M. barbatus* is the closest relative to *M. shevockii,* then the corolla of the latter has evolved considerably. Another difference, although one in which *M. shevockii* has an intermediate condition in the section, is that the placenta of the dehiscing capsule splits to about ⅓ its length whereas that of *M. barbatus* separates to near the middle.

The distinctive color pattern and lobe configuration of the corolla of *Mimulus shevockii* raises a question as to which lobes make up the two corolla lips. Our interpretation of what constitutes the upper and lower lips of the corolla is based on evidence from the venation of the corolla. In other *Mimulus* species examined, each of the five corolla lobes has a major vein from the base, thus two veins run to the two lobes of the upper lip and three to the three lobes of the lower lip. The four stamens each have a vein and these four veins alternate with those of the five corolla lobes except in the upper lip where the two lobe veins are adjacent due to the evolutionary loss of the fifth stamen in this position. In *M. shevockii* (Fig. 1d), two veins run between the veins of the upper stamens and clearly define the upper lip with its two lobes. The large emarginate lower lobe has one vein (dividing into three, then four, branches) and the two lateral lobes each have a major vein indicating that these three lobes with their three veins make up the lower lip.

ACKNOWLEDGMENTS

We thank James Shevock for gathering and sharing his knowledge of *Mimulus shevockii.* We also thank Charles L. Argue for information on pollen morphology, Tsan-Iang and Fei-Mei Chuang for the chromosome count, Larry L. Norris for photographs, and the following colleagues for helpful comments on the manuscript: James A. Bartel, Lincoln Constance, James C. Hickman, and Alan R. Smith.

LITERATURE CITED

ARGUE, C. L. 1980. Pollen morphology in the genus *Mimulus* (Scrophulariacae) and its taxonomic significance. Amer. J. Bot. 67:68–87.

GRANT, A. L. 1924 (publ. Jan 1925). A monograph of the genus *Mimulus.* Ann. Missouri Bot. Gard. 11.

HECKARD, L. R. and J. R. SHEVOCK. 1985. *Mimulus norrisii* (Scrophulariaceae), a new species from the southern Sierra Nevada. Madroño 32:179–185.

VICKERY, R. K. 1978. Case studies in evolution of species complexes in *Mimulus.* Evol. Biology 11:405–507.

(Received 15 Apr 1986; revision accepted 6 Jun 1986.)

COMPARISON OF FIRE OCCURRENCE IN DESERT AND NONDESERT VEGETATION IN TONTO NATIONAL FOREST, ARIZONA

GARRY F. ROGERS
Department of Geography, 1255 Bunche Hall,
University of California, Los Angeles 90024

ABSTRACT

A 29-yr (1955–1983) record of fires in Tonto National Forest, Arizona was used to compare fire occurrence in desert and nondesert vegetation. Nondesert fires were more numerous, but desert fires were larger, with the result that the mean area burned per square kilometer per year was similar. This similarity in the size of the area burned probably is not representative of prehistoric conditions, but instead may be a result of more effective fire suppression in nondesert vegetation. I speculate that finer fuels and higher rates of spread may allow desert fires to become larger than nondesert fires before being controlled.

Recognition of the ecological linkage among fire frequency, adaptive traits of plants, and the structure of plant communities has improved predictive capabilities, and has contributed to more effective fire management (Bratten 1984). Rogers and Steele (1980) concluded that the frequency of desert fires is impossible to discern in most areas because few desert plants produce annual growth rings that would permit dating of past fires. Because of the discontinuous spacing of desert plants, it has been assumed that fires were infrequent and thus were unimportant ecologically in most of the Sonoran Desert (Humphrey 1974).

Vint and Rogers (in press) used a record of individual fire reports for the period 1955–1983 to estimate fire intervals of 275 and 295 yr for the 391,000 ha desert portion of Tonto National Forest (TNF). The 275-yr value represents the time required for an area equal in size to that of the TNF desert to burn. The 295-yr value represents the time required for all of the TNF desert to burn at least once. The 295-yr value also represents the typical number of years between fires at individual sites in the desert. I use the terms frequency and interval in this manner. The lengths of the intervals estimated by Vint and Rogers (in press) agree with the assumption that desert fires are infrequent, and they agree with the observed low tolerance to burning of most desert plants (Rogers 1985). Vint and Rogers (in press) did not compare the estimated TNF desert intervals with data for the same time period at other sites. In this paper, I assess the accuracy of the intervals by comparing the desert-fire data and results of Vint and Rogers (in press) with data on nondesert-fire occurrence in the remainder of TNF.

MADROÑO, Vol. 33, No. 4, pp. 278–283, 1986

STUDY AREA

The desert portion of TNF contains shrub- and cactus-dominated vegetation representative of the Arizona Upland subdivision of the Sonoran Desert (Brown 1982). It is believed generally that fire occurrence in the Arizona Upland requires the presence of annual plants to provide enough continuous fuel for fire to spread (Lotan et al. 1981, McLaughlin and Bowers 1982). McLaughlin and Bowers (1982) hypothesized that annuals would be most abundant after two consecutive wetter-than-normal winters, because increased seed reserves produced during the first winter would be available for germination during the second. Rogers and Vint (in press) found that fires were more abundant after two wet winters as anticipated by McLaughlin and Bowers (1982).

The nondesert vegetation of TNF includes interior chaparral, conifer woodland, conifer forest, semidesert grassland, and evergreen woodland. Interior chaparral and conifer woodland occupy an area approximately equal to the area of the desert; coniferous forest covers an area approximately one fourth the size of the desert area, and semidesert grassland and evergreen woodland occupy smaller areas. Descriptions of these communities are given in the review by Brown (1982). Fire history for the kinds of nondesert vegetation present in TNF is better known than it is for the desert vegetation (Wright and Bailey 1982). Prehistoric intervals between fires are reported to range from a few years in *Pinus ponderosa* forests (Dieterich 1980) and desert grassland (Humphrey 1958) to 10–30 yr in pinyon-juniper (Wright and Bailey 1982), and less than 100 yr in interior chaparral (Brown 1982).

Fire-history studies in many regions and vegetation types have shown that fire intervals have been abnormally long during the past century (Gruell 1983). Fire frequencies are thought to have declined because of fuel reduction by domestic grazers, inadvertent creation of fire breaks by road construction, and fire prevention and suppression (Humphrey 1958, Gruell 1983). Fires were probably smaller throughout TNF during the 1955–1983 period. Technological advances in fire detection and control, and improved prefire organization probably reduced fire sizes during this period. The use of aircraft to fight fires began in the 1950's (Linkewich 1972); aerial infrared radiation detection systems were introduced in the early 1960's (Hirsch 1962); lightning detection systems in use by the late 1960's have steadily improved (Hawe and Fuquay 1969, Latham 1983); and in 1972, the U.S. Forest Service expanded its fire preparedness and prevention programs (U.S. Forest Service 1977).

MATERIALS AND METHODS

The 29-yr TNF fire record provides detailed information in regard to fire occurrence for an area of 1,205,000 ha. The record consists

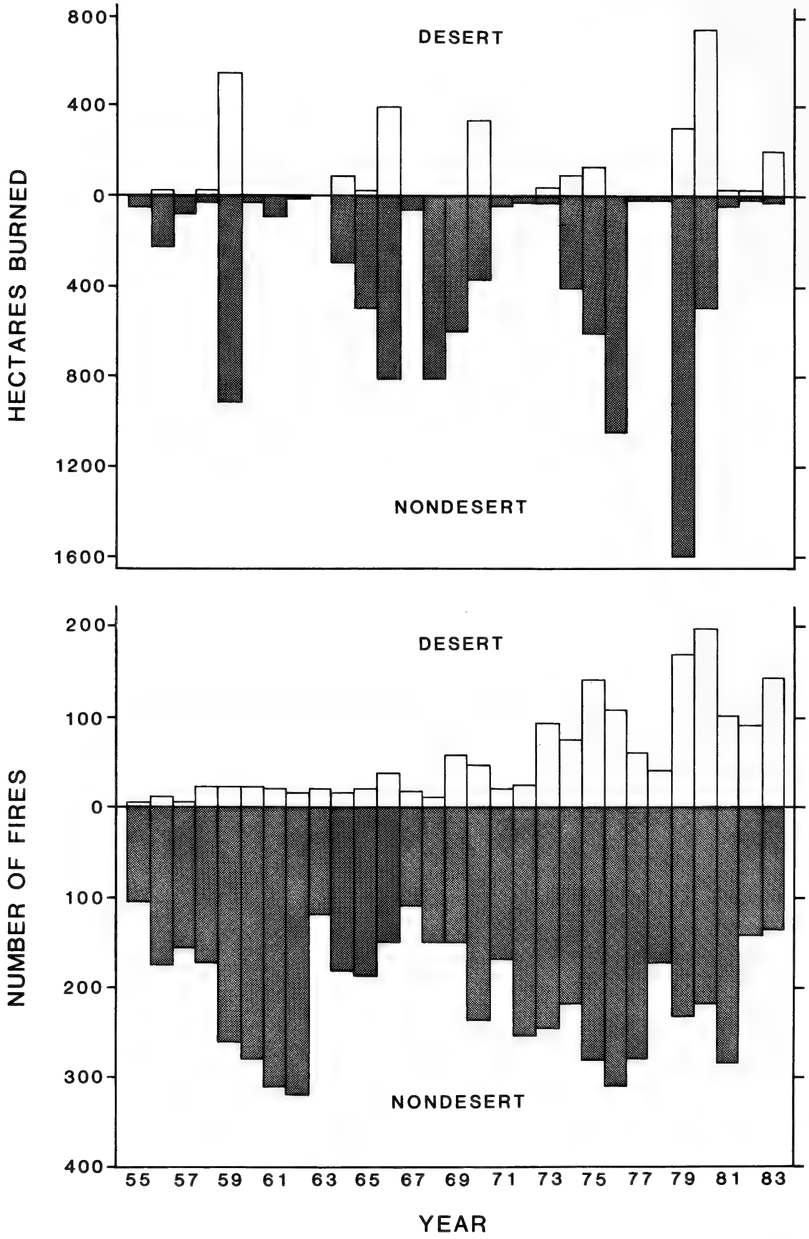


FIG. 1. Annual number of fires and hectares burned in the desert and nondesert portions of Tonto National Forest during the period 1955–1983.

TABLE 1. COMPARISON OF MEAN ANNUAL NUMBERS OF FIRES AND HECTARES BURNED PER KM^2 BETWEEN DESERT (total area = 3800 km^2) AND NONDESERT (total area = 8140 km^2) PORTIONS OF TONTO NATIONAL FOREST. Values are means ± s.e. (range in parentheses). * $p < 0.05$, ^{ns} $p > 0.05$.

n	Annual desert fires per km^2	Annual nondesert fires per km^2	*t*	Sign rank
Annual numbers of fires/km^2				
29	0.015 ± 0.003 (0.001–0.053)	0.025 ± 0.002 (0.013–0.040)	3.92*	—
Annual hectares burned/km^2				
29	0.352 ± 0.101 (0.000–1.939)	0.362 ± 0.092 (0.002–1.973)	—	28.5^{ns}

of individual fire report forms, computer summaries, and maps. This record includes location (Township, Range, and Section), date, size, and cause, and for fires ≥40 ha, maps (1:125,000) showing areas burned for all fires. The location information was used to classify desert and nondesert fires by plotting fire transferred from maps by Brown (1973) and Turner (1974). The vegetation maps are drawn at medium scales (1:500,000 and 1:250,000), and it is possible that small errors in boundary location resulted in misclassification of some fires. The record does not include size for fires that burned less than 0.11 ha. The size of these fires is recorded as 0.05 ha.

Vint and Rogers (in press) used regression analysis to test for annual trends (i.e., increases or decreases) in the number of fires and ha burned by nondesert fires. I repeated this analysis for nondesert fires (significance was tested using F for r^2, and t for slope), and I used correlation analysis to compare desert and nondesert fire occurrence. The assumption that desert fires are rare was tested by calculating and comparing ratios (t-test) of annual number of fires and ha burned per square kilometer (km^2) in the desert and nondesert vegetation of TNF.

RESULTS AND DISCUSSION

Trends in nondesert fire occurrence were too small to measure using regression. For the desert vegetation Vint and Rogers (in press) reported positive trend (increase) in number of fires, but no trend in ha burned. The correlation of desert and nondesert fire occurrence was small: the Spearman rank-order correlation coefficient was 0.26 ($p > 0.05$) for annual number of fires and 0.47 ($p < 0.01$) for annual ha burned.

During the 29-yr period the total number of fires per km^2 in the desert (0.42/km^2) was 58% of the nondesert (0.73/km^2) fires. The mean number of fires per km^2 per year was smaller in the desert (Fig. 1, Table 1). Due to the increasing frequency of desert fires (Vint and Rogers in press), however, the difference declined over the period, and in five of the last nine years desert fires were more numerous than nondesert fires. The total number of ha burned per km^2 was about the same in TNF desert and nondesert vegetation (Table 1). Unlike number of fires, there was no trend in the difference in ha burned between desert and nondesert vegetation.

The similarity in area burned by desert and nondesert fires was not expected. A likely explanation is that fire suppression was less effective in limiting desert fires than nondesert fires because of the greater flammability of desert fuels. Regardless of fire suppression goals, actual achievements depend on several factors that include site accessibility and rate of fire spread. Accessibility is probably similar, but fire spread can be much faster typically in desert in comparison with nondesert vegetation because of fuel differences. Rate of spread depends on fuel compactness, fuel moisture content, and burning conditions (Rothermel 1983). Annual plants, principal fuels of desert fires, are well aerated. In June, when most desert fires occur, high temperature and low humidity lead to exceptionally low fuel moisture levels and highly favorable burning conditions. Lower temperatures, higher humidity, and more living plant material contribute to slower fire spread outside the desert, thus increasing opportunities for forces to limit fire size.

ACKNOWLEDGMENTS

Jerry Ewart, Tim Bos, and Tom Tillman, Tonto National Forest fire managers, supplied the fire records, and Mary Vint organized them and helped with their analysis. Jonathan Sauer and two anonymous reviewers read the manuscript and suggested improvements.

LITERATURE CITED

BRATTEN, F. W. 1984. Fire occurrence probabilities in the northern Rocky Mountain-Intermountain zone: an estimation technique. U.S.D.A. For. Serv., Pacific Southwest Range Exp. Sta., Res. Note PSW–366.

BROWN, D. E. 1973. The natural vegetative communities of Arizona. Ariz. Res. Inform. Syst., Phoenix, Arizona, map.

———, ed. 1982. Biotic communities of the American Southwest—United States and Mexico. Desert Plants 4:3–341.

DIETERICH, J. H. 1980. Chimney Spring forest fire history. U.S.D.A. For. Serv., Intermountain For. Range Exp. Sta., Res. Pap. RM–220.

GRUELL, G. E. 1983. Fire and vegetative trends in the Northern Rockies: interpretations from 1871–1982 photographs. U.S.D.A. For. Serv., Intermountain For. Range Exp. Sta., Gen. Techn. Rept. INT–158.

HAWE, R. G. and D. M. FUQUAY. 1969. Remote sensing of lightning in forest fire behavior. Proc. of the International Symp. on Rem. Sens. of Environ. 6:1193–1203.

HIRSCH, S. N. 1962. Infrared as a fire control tool. Proc. of Ann. Meeting, W. For. Fire Res. Comm., W. Forestry and Conserv. Assoc., Seattle.

HUMPHREY, R. R. 1958. The desert grassland. Bot. Rev. 24:193–253.

———. 1974. Fire in desert and desert grasslands of North America. *In* T. T.

Kozlowski and C. E. Ahlgren, eds., Fire and ecosystems, p. 365–400. Academic Press, NY.

LATHAM, D. 1983. LLAFFS—a lightning-locating and fire-forecasting system. U.S.D.A. For. Serv., Intermountain For. Range Exp. Sta., Res. Pap. INT–315.

LINKEWICH, A. 1972. Air attack on forest fires, history and techniques. D. W. Fiesen and Sons, Calgary, Alberta.

LOTAN, J. E., M. E. ALEXANDER, S. E. ARNO, R. E. FRENCH, O. G. LANGDON, R. M. LOOMIS, R. A. NORWIN, R. C. ROTHERMEL, W. C. SCHMIDT, and J. VON WAGTENDONK. 1981. Effects of fire on flora: a state-of-the knowledge review. U.S.D.A. For. Serv., Gen. Techn. Rept., W0–16.

MCLAUGHLIN, S. P. and J. E. BOWERS. 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 63:246–248.

ROGERS, G. F. 1985. Mortality of burned *Cereus giganteus*. Ecology 66:630–632.

——— and J. STEELE. 1980. Sonoran Desert fire ecology. U.S.D.A. For. Serv., Rocky Mtn. For. Range Exp. Sta., Gen. Techn. Rept. RM-81.

——— and M. K. VINT. In press. Winter precipitation and fire in the Sonoran Desert. J. of Arid Environs.

ROTHERMEL, R. C. 1983. How to predict the spread and intensity of forest and range fires. U.S.D.A. For. Serv., Intermountain For. Range Exp. Sta., Gen. Techn. Rept. INT–143.

TURNER, R. M. 1974. Map showing the vegetation in the Phoenix area, Arizona. U.S.D.I. Geol. Survey, Denver, CO.

U.S. FOREST SERVICE. 1977. Evaluation of fire management activities on the National Forests, Policy Analysis Staff Report, U.S.D.A. For. Serv., Washington, DC.

VINT, M. K. and G. F. ROGERS. In press. Trends in fire occurrence in the Arizona Upland subdivision of the Sonoran Desert, 1955–1983. Southw. Naturalist.

WRIGHT, H. A. and A. W. BAILEY. 1982. Fire ecology, United States and Canada. John Wiley & Sons, New York.

(Received 20 Nov 1985; revision accepted 9 Jun 1986.)

NICHE PARTITIONING IN *DOWNINGIA BELLA* AND *D. CUSPIDATA* (CAMPANULACEAE) IN THE VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA

Bradford D. Martin and Earl W. Lathrop
Department of Biology, Loma Linda University,
Riverside, CA 92515

Abstract

Downingia bella and *D. cuspidata* were sympatric in 10 of 13 study pools. Of the three pools where they were allopatric, two pools were relatively shallow, dried up early, and contained only *D. cuspidata.* In pools where the species were sympatric, flowering of *D. bella* was correlated positively with pool depth, whereas flowering of *D. cuspidata* was correlated negatively. Peak flowering periods of *D. bella* usually occurred 2–4 weeks later than *D. cuspidata. Downingia bella* was significantly larger than *D. cuspidata* for seven morphological characters measured. Pollinators of *D. bella* were primarily *Bombus californicus* and *B. sonorus. Downingia cuspidata* was visited by numerous insect species, but neither species of *Bombus* was observed. Niche partitioning of the two *Downingia* species, which are sympatric in most of the vernal pools on the Santa Rosa Plateau, was demonstrated through differences in distribution, flowering phenology, morphology, and pollinators.

Downingia is a genus of semi-aquatic annual plants (Campanulaceae: subfam. Lobelioideae). Fourteen species of *Downingia* are distributed in western North America and in South America in ephemeral aquatic habitats (Weiler 1962). Thirteen species occur in North America with six of these indigenous to California. In South America there are two species, one of which occurs in both California and Chile. Most species of *Downingia* are restricted to vernal pools (Weiler 1962). When these seasonal habitats begin to dry up in the spring, growth of *Downingia* is rapid and masses of blue or purple flowers are produced from thousands of plants.

The presence of two or three sympatric *Downingia* species in many vernal pools (Weiler 1962, Lin 1970, Foster 1972, Rickabaugh 1974, Macdonald 1976, Holland and Jain 1977, 1984, Gunn 1982, Schlising and Sanders 1982) indicates that there are considerable niche similarities between species. Holland and Jain (1981) found that niche partitioning in vernal pools occurs largely at the level of genera, with species replacing each other along a regional pattern. There are several regions with overlapping ranges of two or more species of *Downingia,* but "true" sympatry was found in less than 10% of the vernal pools in California (Holland and Jain 1977). *Downingia bella* Hoov. and *D. cuspidata* (Greene) Greene (Figs. 1, 2) are found sympatrically in many vernal pools at different locations in California (Holland

Madroño, Vol. 33, No. 4, pp. 284–299, 1986

FIGS. 1, 2. *Downingia* corollas. 1. *Downingia bella,* ×2. 2. *Downingia cuspidata,* ×2.

and Jain 1977, Lathrop and Thorne 1983). Both species have protandrous, resupinate flowers, bilocular ovaries, haploid chromosome numbers of 11, and are indigenous to California (Weiler 1962). *Downingia bella* differs from *D. cuspidata* in having three dark pur-

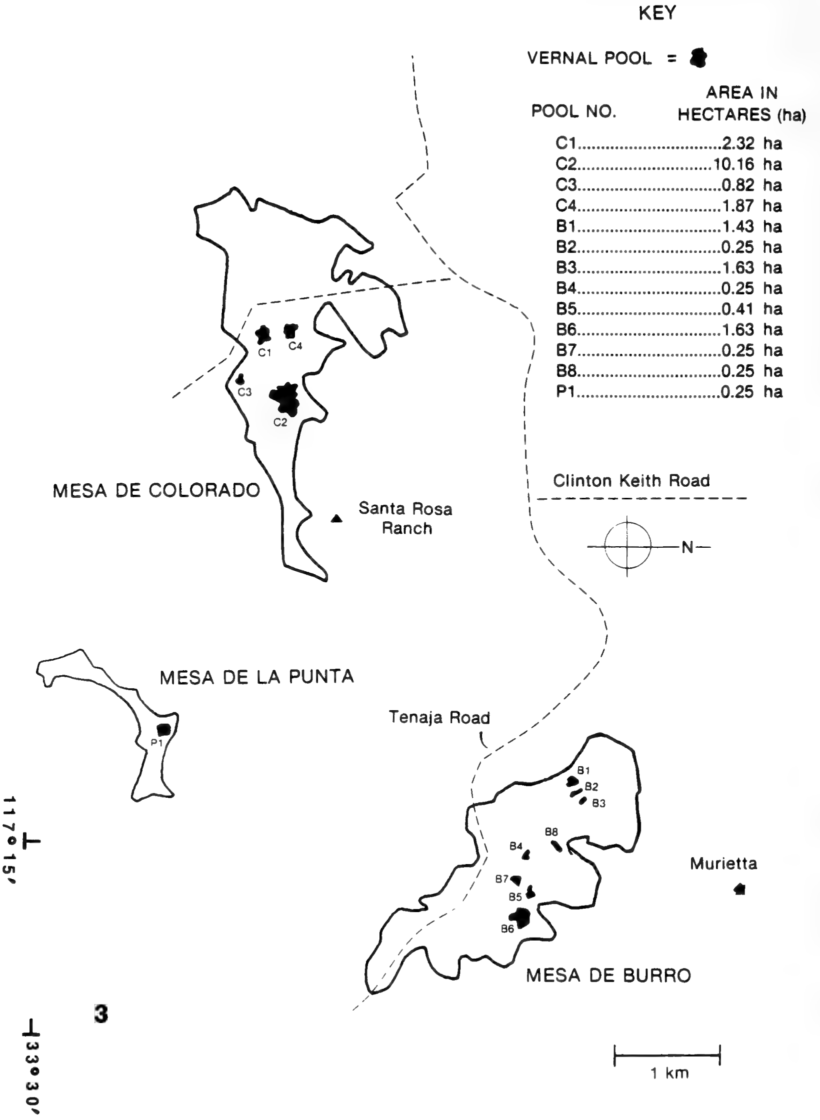


FIG. 3. Distribution of vernal pools on three mesas of the Santa Rosa Plateau Preserve. Map used by permission of *Aliso.*

ple spots at the corolla throat, indehiscent fruits, and longitudinally striate seeds.

The objective of this study was to test distribution, phenology, morphology, and pollination of *Downingia bella* and *D. cuspidata* to determine if these species occupy different niches when they are sympatric.

STUDY AREA

Field work for this research was conducted in the spring and summer of 1982 in the vernal pools of the Santa Rosa Plateau Preserve (Lathrop and Thorne 1985a) located on the Santa Rosa Plateau (Lathrop and Thorne 1985b), Riverside County, California. Thirteen vernal pools are located on three lava-capped mesas; eight on Mesa de Burro, four on Mesa de Colorado, and one on Mesa de la Punta (Fig. 3). Pool sizes, including the zone of influence around each pool, range from 0.25–10.16 ha (Fig. 3). *Downingia bella* and *D. cuspidata* occur sympatrically in 10 of the 13 pools (Lathrop and Thorne 1983).

METHODS

Distribution. Intrapool distribution, flowering frequency (%), relative abundance (%), and plant density (n/m^2) of *D. bella* and *D. cuspidata* were determined from quadrat measurements at various times throughout the 1982 season in pools B1, B5, B6, C1, C2, C3, and C4 (Fig. 3). Belt transects (0.3 × 1.8 m), marked off into 24 quadrats (225 cm^2), were placed perpendicular to a radius of each of the seven pools at regular intervals along 7–15 transect lines running from the edge to the center of the pool. All quadrats, at a particular distance from the edge of the pool, were summed together to get flowering frequency (%) and mean plant density (n/m^2) at that distance. At each placement of the belt transect, all 24 quadrats were measured for flowering frequency, and three randomly selected quadrats were measured to determine plant density (n/m^2). The plane-table method (Compton 1962) was used to survey pools B1 and C2 for pool depth profiles. Depth profiles for all the remaining pools measured were taken from Stagg and Lathrop (1984). Weekly surveys of the 13 vernal pools were conducted between April and September 1982 to determine presence, relative abundance, and distribution in the different vernal pools through time. Linear correlation was used to analyze the relationship of the flowering frequency of *D. bella* and *D. cuspidata* with pool depth. Because flowering was nearly simultaneous throughout the pool in pools B1, B6, C1, C3, and C4, linear correlation was analyzed one date only. Flowering occurred in temporal bands following the receding water in pools B5 and C2. Pool depth was compared with highest frequency of flowering for both species on three different dates in these pools.

Flowering phenology. Data from weekly surveys and quadrat measurements were used to analyze the flowering phenology of *D. bella*

TABLE 1. RELATIVE ABUNDANCE (%) AND THE SEASON'S HIGH MEAN ($\bar{x}$ ± s.d.) DENSITY (n/m^2) OF *Downingia bella* AND *D. cuspidata* IN 13 VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA. Relative abundance was determined from quadrat data (B1, B5, B6, C1, C2, C3, C4) and from count data (B2, B3, B4, B7, B8, P1). K = number of 225 cm^2 quadrats.

	Relative abundance				High mean density			
	D. bella		*D. cuspidata*		*D. bella*		*D. cuspidata*	
Pool	n	%	n	%	K	n/m^2	K	n/m^2
B1	3824	55	3159	45	24	237 ± 191	24	152 ± 218
B2	1075	72	410	28				
B3			1201	100				
B4	4	12	29	88				
B5	638	11	5359	89	30	18 ± 46	30	406 ± 384
B6	89,154	93	6291	7	21	351 ± 216	21	233 ± 182
B7			1812	100				
B8	69	20	269	80				
C1	2592	74	931	26	36	41 ± 37	36	92 ± 189
C2	182,710	81	43,068	19	30	356 ± 260	30	350 ± 352
C3	527	15	7407	85	36	30 ± 88	36	221 ± 197
C4	7	<1	1635	>99	30	1 ± 8	30	65 ± 61
P1	1	100						

and *D. cuspidata.* Peak flowering for each pool was designated as a two week period when flowering plants were at their highest frequency or abundance. The inundation/desiccation condition of the vernal pools was noted throughout the season during weekly surveys. Desiccation dates were recorded when pool beds became dry and hard. Linear correlation was used to compare the peak flowering periods for *D. bella* and *D. cuspidata* with pool desiccation dates.

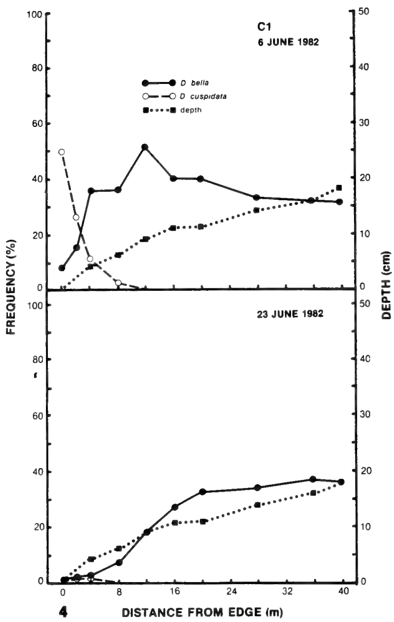
Morphology. Seven morphological characters were measured. From pools B6 and C2 where the two species were sympatric, mature sample specimens of *Downingia bella* (n = 40) and *D. cuspidata* (n = 36) were collected at random, pressed, dried, and taken to the lab for measurements. Parameters measured for each specimen and flower were: 1) linear measurements of plant height, and leaf, ovary, sepal, and tube length; 2) number of flowers per plant; and 3) number of open flowers per plant. One-way ANOVA was used for statistical comparison of these morphological parameters.

Pollination. During weekly surveys, 10 minute observations were made at each pool that contained both species. Insects visiting each species were observed and specimens collected. Chi-square contingency analysis was used to compare the visitation frequency of two of the pollinators (*Bombus californicus* and *B. sonorus*) on both *Downingia* species.

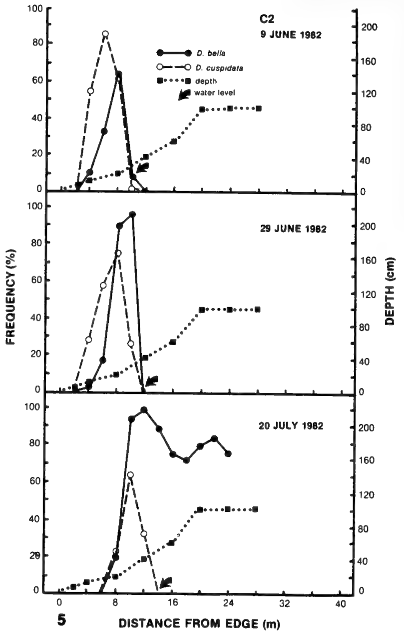
RESULTS

Interpool distribution. Downingia bella and *D. cuspidata* were found sympatrically in 10 of the 13 vernal pools of the Santa Rosa Plateau Preserve (Table 1). In the remaining three pools, *D. cuspidata* was found exclusively in two pools, whereas *D. bella* was found exclusively in only one. Although pool C4 had both species present, it mostly contained *D. cuspidata. Downingia cuspidata* was dominant in five of the 10 sympatric pools. *Downingia bella,* however, was four times more abundant than *D. cuspidata* when all pools were totaled (Table 1). This high relative abundance was due to the dominance of *D. bella* in four of the five largest vernal pools on the plateau.

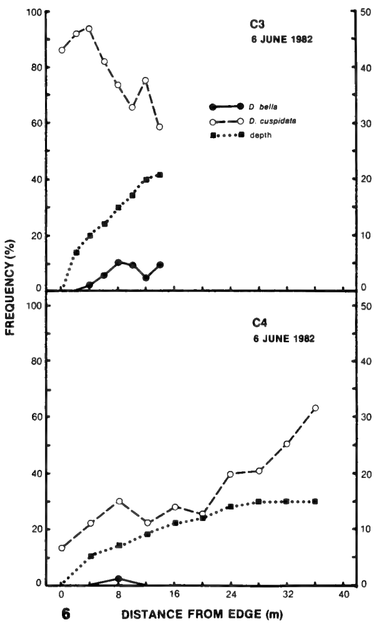
Intrapool distribution. Intrapool flowering frequency patterns varied considerably for both species (Figs. 4–7). In some pools, flowering was nearly simultaneous throughout the entire pool (Figs. 4, 6, 7). Other pools exhibited temporal flowering bands that followed the receding water (Fig. 5). Despite this variability, there was a spatial segregation of the two species in all the pools. While one species increased in flowering frequency, the other decreased. In all pools except pool C4, *D. bella* reached its highest flowering frequency towards the center of the pool, whereas *D. cuspidata* reached its



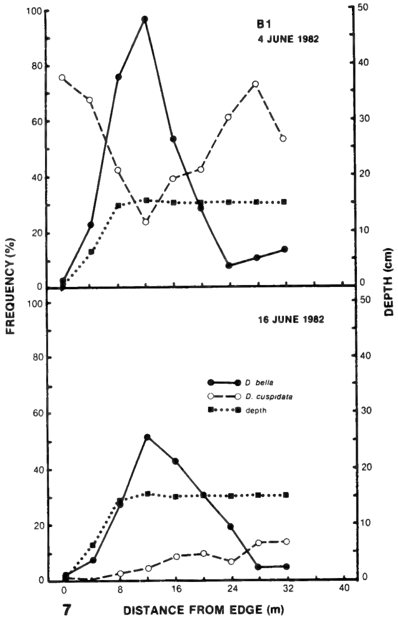
4



5



6



7

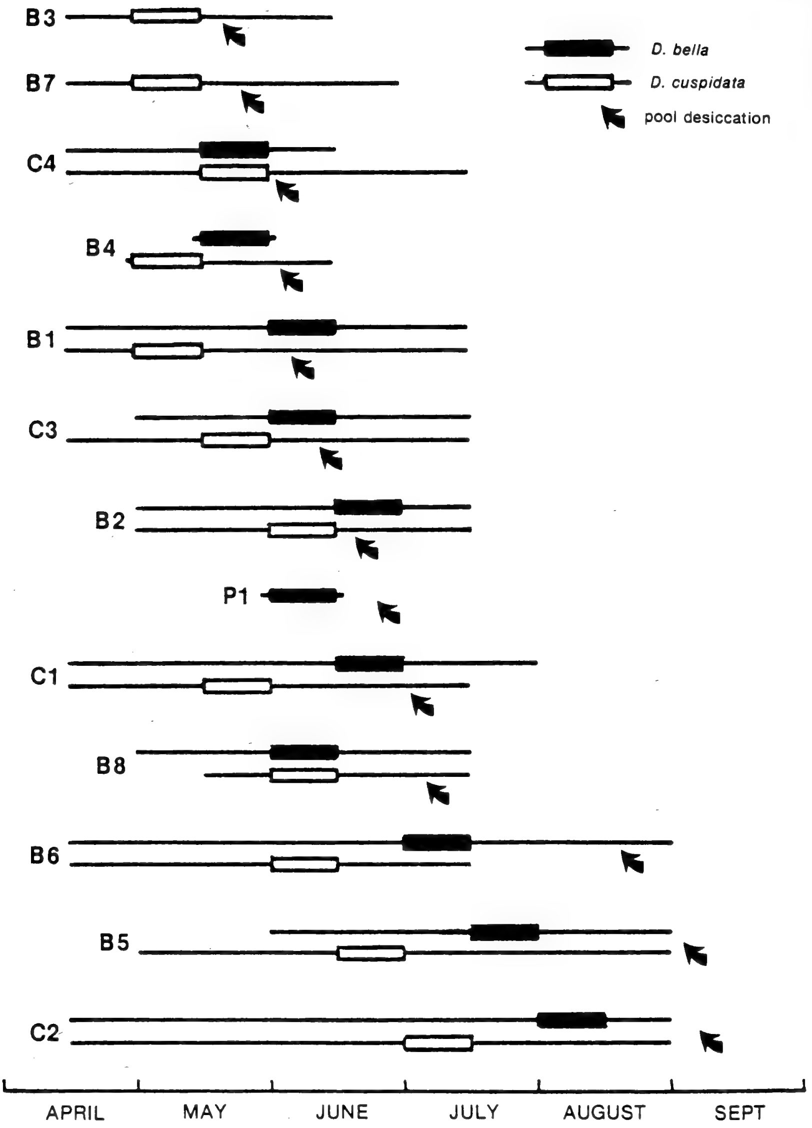
FIGS. 4–7. Flowering frequency of *Downingia bella* and *D. cuspidata* with pool depth at different distances from the edge of the pool. 4. Pool C1. 5. Pool C2. 6. Pools C3 and C4. 7. Pool B1.

highest frequency on the periphery. Pure stands of *D. bella* were observed in the center of pools B6, C1, and C2 after the last frequency measurements were taken. The most peculiar distribution pattern of all the pools was exhibited in pool B1, where *D. cuspidata* was distributed in a bimodal pattern with *D. bella* in a complementary unimodal pattern (Fig. 7). In general, however, flowering frequency of *D. bella* was correlated positively ($r = +0.79$) with pool depth, whereas frequency of *D. cuspidata* was correlated negatively ($r = -0.86$). Flowering frequency of *D. cuspidata* in pool C4 was correlated positively with pool depth, but individuals of *D. cuspidata* composed 99.6% of *Downingia* in this pool (Table 1). Plant density was correlated positively with flowering frequency for both *D. bella* ($r = +0.91$) and *D. cuspidata* ($r = +0.92$). Highest mean densities for *D. bella* and *D. cuspidata* were 356 and 406 plants/m^2, respectively.

Flowering phenology. Peak flowering periods for *D. bella* and *D. cuspidata* were positively correlated with pool desiccation dates ($r = +0.94$ and $+0.89$, respectively). Peak flowering of both species was delayed in vernal pools that had desiccation dates later in the season (Fig. 8). Peak flowering periods of the study species were segregated temporally at each pool (Fig. 8). The peak flowering period of *D. bella* usually occurred 2–4 weeks after the peak period for *D. cuspidata.* The first vernal pools to dry up in the 1982 season were pools B3, B7, and C4 (Fig. 8). *Downingia bella* was absent in pools B3 and B7 and nearly absent in pool C4. These pools appeared to be the shallowest pools. The last pools to desiccate were the deepest (pool B5) and the largest (pool C2). Dense stands of *D. bella* were observed flowering above water approximately 0.5 m deep during July in pools B6 and C2 (Fig. 5). *Downingia cuspidata* was not observed flowering while it was still in the open water zone.

Morphology. Downingia bella had significantly higher mean values ($p < 0.01$ or $p < 0.001$) for all seven morphological characters measured in comparison with *D. cuspidata* (Table 2). Plant height, and leaf, ovary, and corolla lengths, were more than 1.5 times larger in *D. bella.* Both species had numerous flowers per plant, with means of 9.1 and 6.5 for *D. bella* and *D. cuspidata,* respectively. The proportion of total flowers that were mature and open was 35% for *D. bella* and 43% for *D. cuspidata.*

Pollination. Downingia bella was visited only by hymenopterans. Principal visitors were *Bombus californicus* and *B. sonorus* (Table 3). *Downingia cuspidata* was visited by insects of several families (Table 3). The most common were *Syrphus* sp., a species of Calliphoridae, *Plebejus acmon acmon,* and *Vanessa virginiensis.* Visitors usually landed on the lower lobes of the corolla and appeared to



8 TIME (months)

FIG. 8. Flowering phenologies for *Downingia bella* and *D. cuspidata* in 13 vernal pools of the Santa Rosa Plateau Preserve. Rectangles represent the peak flowering periods. Arrows show pool desiccation dates.

probe for nectar inside the corolla tube. Neither species of *Bombus* was observed visiting *D. cuspidata* even though *D. cuspidata* was abundantly present.

DISCUSSION

The differences demonstrated in distribution, flowering phenology, morphology, and pollinators of *D. bella* and *D. cuspidata* indicate that the two species occupy different niches. The main parameter of niche partitioning demonstrated was that of spatial segregation. Certain characteristic vernal pool species segregate into distinct zones or gradually change along the pool gradient (Lin 1970, Kopecko and Lathrop 1975, Schlising and Sanders 1982, Holland and Jain 1984, Zedler 1984). Species segregation usually is attributed to the gradual physical differences found between the extremes of the center of a pool and the adjacent higher grounds (Lathrop 1976, Linhart 1976, Holland and Jain 1984, Zedler 1984). The center of the pool has greater water availability and soil moisture stability when compared to the periphery. Species adapted to wetter environments are restricted to the deeper, more central areas of the pool. Conversely, species that can withstand greater variation in moisture conditions are often found in zones closer to the periphery of the pool.

Observations from our study indicate that *D. bella* requires a wetter, more stable niche than *D. cuspidata,* which perhaps accounts for the niche partitioning of the species. Two results demonstrate that the distribution of *D. bella* is limited by moisture: 1) flowering frequency of *D. bella* was correlated positively with pool depth; 2) *D. bella* was absent in the pools that desiccated earlier in the season. Also, Martin (1984) reported that percent germination of *D. bella* seeds was significantly higher in moister conditions. Lathrop (1976) found that the only soil characteristic of vernal pools that correlated with plant zonation was soil moisture. Moisture also seems to be the limiting factor in the distribution of *D. bella* between and within the vernal pools of the Santa Rosa Plateau Preserve.

Downingia cuspidata, like *D. bella,* is normally restricted to vernal pools. *Downingia cuspidata,* however, occupies a drier, more unpredictable niche. *Downingia cuspidata* was confined to the vernal pool because of moisture requirements, but was correlated negatively with pool depth. In pools where both species were sympatric, *D. cuspidata* was absent in the central areas of these pools.

Conceivably, physical factors other than moisture could exclude *D. cuspidata* from the centers of these pools. Lathrop (1976) reported that soil pH is more alkaline in the center of pool C2. The soil where *D. cuspidata* typically occurs in pool C2, along the periphery and outer zone of the pool, had a pH of 5.7, whereas the center area of the pool, where *D. bella* is more frequent, had a pH of 6.7. *Downingia*

Table 2. Morphological Characters (Mean ± s.d.) of *Downingia bella* and *D. cuspidata* from Two Vernal Pools of the Santa Rosa Plateau Preserve, California. Plants were sampled in areas of each pool where the two species were sympatric. All morphological characters were significantly different ($p < 0.01$ or $p < 0.001$) between the two species. n = number of individuals sampled.

			Morphological characters						
Species	Pool	n	Plant height (cm)	Leaf length (mm)	Ovary length (cm)	Sepal length (mm)	Corolla tube length (mm)	Number of flowers/plant	Number of open flowers/ plant
D. bella	B6	40	30.0 ± 6.6	10.5 ± 15.2	5.7 ± 1.0	5.6 ± 0.7	5.0 ± 0.3	11.6 ± 7.7	3.8 ± 2.0
	C2	40	23.3 ± 5.0	12.0 ± 16.6	5.0 ± 0.9	5.9 ± 0.9	5.1 ± 0.3	6.5 ± 5.3	2.6 ± 1.7
		$\bar{x}$ =	26.6 ± 5.8	11.3 ± 15.9	5.4 ± 1.0	5.8 ± 0.8	5.1 ± 0.3	9.1 ± 6.5	3.2 ± 1.9
D. cuspidata	B6	31	19.9 ± 5.2	6.7 ± 3.9	3.5 ± 0.7	4.4 ± 0.7	3.4 ± 0.5	6.5 ± 2.5	2.7 ± 1.3
	C2	31	14.2 ± 2.2	7.1 ± 1.2	2.8 ± 0.5	3.7 ± 0.5	3.1 ± 0.2	6.4 ± 3.3	2.8 ± 1.4
		$\bar{x}$ =	17.1 ± 3.7	6.9 ± 2.6	3.2 ± 0.6	4.1 ± 0.6	3.3 ± 0.4	6.5 ± 2.9	2.8 ± 1.4

TABLE 3. INSECTS OBSERVED VISITING FLOWERS OF *Downingia bella* AND *D. cuspidata* IN VERNAL POOLS OF THE SANTA ROSA PLATEAU PRESERVE, CALIFORNIA. Listed by family, and by genus and species when known. * = fewer than 25 individuals. ** = more than 25 individuals.

Plant species	Insect visitors	Abundance
D. bella	Hymenoptera	
	Anthophoridae	*
	Apidae	
	Apis mellifera	*
	Bombus californicus	**
	B. sonorus	**
	Halictidae	
	Halictus sp.	*
D. cuspidata	Coleoptera	
	Chrysomelidae	
	Diabrotica undecimpunctata	*
	Coccinellidae	
	Coccinella california	*
	Hippodamia convergens	*
	Diptera	
	Calliphoridae	**
	Syrphidae	
	Syrphus sp.	**
	Tabanidae	
	Chrysops sp.	*
	Tachinidae	*
	Hymenoptera	
	Apidae	
	Apis mellifera	*
	Halictidae	
	Halictus sp.	*
	Vespidae	
	Polistes fuscatus aurifer	*
	Lepidoptera	
	Hesperiidae	*
	Lycaenidae	
	Plebejus acmon acmon	**
	Nymphalidae	
	Vanessa virginiensis	**
	Pieridae	**

bella is known to be an alkali-tolerant species (Luckenbach 1973, Holland and Jain 1977, 1984). Water pH can also vary in vernal pools of different size. Lin (1970) reported that water pH in Solano County vernal pools ranged from 6.6–6.85 and that water in the smaller pools was more acidic. Thus, exclusion of *D. cuspidata* from the central areas of the deeper, larger pools may be due to differences in pH.

The role of competitive exclusion also must not be overlooked because it is known to play a role in plant zonation of vernal pools

(Linhart 1976, Ornduff 1976). Plant frequency of *D. cuspidata* was correlated negatively with pool depth in these pools containing both species, but a positive correlation was noted in pool C4 where *D. bella* was virtually absent. *Downingia cuspidata* may not compete well with *D. bella* or species associated with *D. bella* in the centers of the deeper pools. The pure stands of *D. bella* in the centers of pools B6, C1, and C2 were associated with dense stands of perennial *Eleocharis* spp. *Eleocharis* spp. were very sparse in pools B1 and B5 where *D. cuspidata* occurred at high frequencies in the central, deeper sections. Holland and Jain (1977) and Zedler (1984) also reported an increase in cover of *D. cuspidata* towards the center in pools at Rancho Seco and Kearny Mesa, respectively. Unlike findings in the present study, *D. bella* increased in cover along with *D. cuspidata* in the Rancho Seco pools. No *Eleocharis* spp. occurred at Rancho Seco, but they were infrequent at Kearny Mesa. Holland and Jain (1984) calculated depth preferences for 35 vernal pool species, including *D. bella* and *D. cuspidata. Downingia cuspidata* had a greater depth preference (11.1 cm) than *D. bella* (7.7 cm), which is contradictory to the results of this study. Most of the pools reported by Holland and Jain (1984), however, were much shallower ($\bar{x} = 17$ cm) than those in the present study ($\bar{x} = 53$ cm). Perhaps *D. cuspidata* is relatively scarce in the central portions of the deeper pools on the Santa Rosa Plateau because it apparently does not compete well with the perennial *Eleocharis* spp. due to its relatively small size. *Downingia bella* may be able to compete with *Eleocharis* in this central region, however, due to its larger size.

The temporal segregation of peak flowering periods observed for *D. bella* and *D. cuspidata* in the vernal pools of the Santa Rosa Plateau Preserve indicates niche partitioning between the species. Temporal segregation, however, appears to be an artifact of pool desiccation rather than due to genetically determined factors. Peak flowering periods were correlated positively with desiccation dates. Pools that retained water longer had peak flowering periods later in the season. The earlier desiccation around the periphery of the pool appeared to cause *D. cuspidata* to flower first. Competition for pollinators is decreased when flowering periods of the species are separated (Heinrich and Raven 1972).

Insect species observed visiting *D. bella* and *D. cuspidata* also demonstrate niche partitioning. The most important pollinators of *Downingia* are species of Hymenoptera, Diptera, and Coleoptera (Weiler 1962, Thorp 1976). The results of our study support this statement. Weiler (1962) reported some of the same species of insects observed in the present study as potential pollinators of *Downingia.* It was difficult to determine which species was the primary pollinator for *D. cuspidata.* Syrphid flies are thought to be pollinators for *D. concolor* (Weiler 1962, Linhart 1972) and could be primary pollinators of *D. cuspidata* because many were observed visiting this species. The primary pollinators of *D. bella* appeared to be *Bombus californicus* and *B. sonorus.* Martin (1984) reported that the mean corolla throat diameter of *D. bella* (x̄ = 0.29 cm) was significantly larger than *D. cuspidata* (x̄ = 0.17 cm), which would accommodate the larger *Bombus* pollinators. Both *Bombus* species apparently frequent *D. bella* equally and may be in competition for the same food source. Resource partitioning in *Bombus* on the same species is common (Morse 1977, Inouye 1978). *Bombus californicus* and *B. sonorus* showed flower constancy. Bumblebees are sensitive to UV, blue-violet, and yellow light (Macior 1978) and *Downingia* corollas reflect all three wavelengths, which makes them especially attractive to bumblebees. Possibly *B. californicus* and *B. sonorus* are capable of distinguishing between the two species by the corolla throat pattern (Martin 1984). Although bees orient to UV cues on flowers (Jones and Buchmann 1974) and bumblebees often exhibit flower constancy (Free 1970, Heinrich 1976), Weiler (1962) observed that *Bambus* spp. visited both *D. bicornuta* and *D. cuspidata* indiscriminantly.

Niche partitioning of *D. bella* and *D. cuspidata* was demonstrated by differences in the following: 1) *D. bella* occupied the deeper, central areas of the pools, whereas *D. cuspidata* was found around the periphery; 2) *D. bella* had peak flowering periods 2–4 weeks later than *D. cuspidata*; 3) *D. bella* was significantly larger than *D. cuspidata* for seven morphological characters; and 4) *D. bella* was pollinated primarily by *Bombus californicus* and *B. sonorus,* whereas *D. cuspidata* was pollinated by much smaller and more diverse insect species.

ACKNOWLEDGMENTS

We thank all those who made this study possible, particularly G. Bradley, R. Ryckman, R. Tkachuck, and A. Zuccarelli for their advice and guidance. A special thanks to R. Thorne for his assistance in the field and his helpful suggestions during the preparation of the manuscript. We are grateful to the editors of *Aliso* for use of the vernal pool map. Insect visitors to the study species were identified by E. Schwab. G. Bradley and D. Hergert assisted with the statistical analysis. We thank KACOR Development Company and the Nature Conservancy for permission to work on their land. This work was funded in part by grants from Loma Linda University.

LITERATURE CITED

COMPTON, R. R. 1962. Manual of field geology. John Wiley and Sons Inc., New York.

FOSTER, R. I. 1972. Explosive chromosome evolution in *Downingia yina.* Ph.D. dissertation, Univ. California, Berkeley.

FREE, J. B. 1970. The flower constancy of bumblebees. J. Anim. Ecol. 39:395–402.

GUNN, P. 1982. Vernal pools and rare plants of Haystack Mountain. Fremontia 9: 3–10.

HEINRICH, B. 1976. The foraging specializations of individual bumblebees. Ecol. Monogr. 46:105–128.

——— and P. H. Raven. 1972. Energetics and pollination ecology. Science 176: 597–602.

Holland, R. F. and S. K. Jain. 1977. Vernal pools. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 515–533. Wiley-Interscience, New York.

——— and ———. 1981. Insular biogeography of vernal pools in the central valley of California. Amer. Naturalist 117:24–37.

——— and ———. 1984. Spatial and temporal variation in plant species diversity of vernal pools. *In* S. Jain and P. Moyle, eds., Vernal pools and intermittent streams, p. 198–209. Inst. of Ecol. Publ. No. 28, Univ. California, Davis.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. Ecology 59:672–678.

Jones, C. E. and S. L. Buchmann. 1974. Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. Anim. Behav. 22:481–485.

Kopecko, K. J. and E. W. Lathrop. 1975. Vegetation zonation in a vernal marsh on the Santa Rosa Plateau of Riverside County, California. Aliso 8:281–288.

Lathrop, E. W. 1976. Vernal pools of the Santa Rosa Plateau, Riverside County, California. *In* S. Jain, ed., Vernal pools: their ecology and conservation, p. 22–27. Inst. of Ecol. Publ. No. 9, Univ. California, Davis.

——— and R. F. Thorne. 1983. A flora of the vernal pools on the Santa Rosa Plateau, Riverside County, California. Aliso 10:449–469.

——— and ———. 1985a. A new preserve on the Santa Rosa Plateau. Fremontia 13:15–19.

——— and ———. 1985b. A flora of the Santa Rosa Plateau, southern California. S. California Bot., Spec. Publ. No. 1.

Lin, J. W. 1970. Floristics and plant succession in vernal pools. M.A. thesis, San Francisco State College.

Linhart, Y. B. 1972. Differentiation within natural populations of California annual plants. Ph.D. dissertation, Univ. California, Berkeley.

———. 1976. Evolutionary studies of plant populations in vernal pools. *In* S. Jain, ed., Vernal pools: their ecology and conservation, p. 40–46. Inst. of Ecol. Publ. No. 9, Univ. California, Davis.

Luckenbach, R. 1973. Pogogyne, polliwogs, and puddles: the ecology of California's vernal pools. Fremontia 1:9–13.

Macdonald, R. 1976. Vegetation of the Phoenix Park vernal pools on the American River Bluffs, Sacramento County, California. *In* S. Jain, ed., Vernal pools: their ecology and conservation, p. 69–76. Inst. of Ecol. Publ. No. 9, Univ. California, Davis.

Macior, L. W. 1978. Pollination ecology of vernal angiosperms. Oikos 30:452–460.

Martin, B. D. 1984. Distribution and niche partitioning of *Downingia bella* and *Downingia cuspidata* (Campanulaceae) in the vernal pools of the Santa Rosa Plateau Preserve, California. Ph.D. dissertation, Loma Linda University, Loma Linda, CA.

Morse, D. H. 1977. Resource partitioning in bumblebees: the role of behavioral factors. Science 197:678–680.

Ornduff, R. 1976. Sympatry, allopatry, and interspecific competition in *Lasthenia*. *In* S. Jain, ed., Vernal pools: their ecology and conservation, p. 46–50. Inst. of Ecol. Publ. No. 9, Univ. California, Davis.

Rickabaugh, H. 1974. Boggs Lake: the story of a vernal pool. Fremontia 2:3–5.

Schlising, R. A. and E. L. Sanders. 1982. Quantitative analysis of vegetation at the Richvale vernal pools, California. Amer. J. Bot. 69:734–742.

Stagg, C. M. and E. W. Lathrop. 1984. Distribution of *Orcuttia californica* (Poaceae) in vernal pools of the Santa Rosa Plateau, Riverside County, California.

In S. Jain and P. Moyle, eds., Vernal pools and intermittent streams, p. 250–254. Inst. of Ecol. Publ. No. 28, Univ. California, Davis.

THORP, R. W. 1976. Insect pollination of vernal pool flowers. *In* S. Jain, ed., Vernal pools: their ecology and conservation, p. 36–40. Inst. of Ecol. Publ. No. 9, Univ. California, Davis.

WEILER, J. H. 1962. A biosystematic study of the genus *Downingia.* Ph.D. dissertation, Univ. California, Berkeley.

ZEDLER, P. H. 1984. Micro-distribution of vernal pool plants of Kearny Mesa, San Diego County. *In* S. Jain and P. Moyle, eds., Vernal pools and intermittent streams, p. 185–197. Inst. of Ecol. Publ. No. 28, Univ. California, Davis.

(Received 11 Mar 1985; revision accepted 13 Jun 1986.)

LETTERS

Dear Editor:

In a recent article by R. Becking (Madroño 33:175–181, 1986), *Hastingsia bracteosa* (=*Schoenolirion bracteosum*) is cited as a species listed as endangered by the U.S. Fish and Wildlife Service. In fact, *H. bracteosa* is merely a *candidate* for such status according to the reference given by Dr. Becking (USFWS, Federal Register 45:82479–82569, 1980). While this may seem a minor point, there are tremendous legal differences between formally listed taxa and those under consideration for listing. It is therefore imperative that we clearly and accurately define the status of rare species discussed in our papers. Powell and Howard (Madroño 25:59, 1978) emphasize the importance of addressing the subjects of rarity and potential endangerment of plant species in published research. In echoing their plea, I would respectfully add that we choose our wording carefully in order to avoid further complication of an intricate land management issue.

Robert J. Meinke
Herbarium
Department of Botany and Plant Pathology
Oregon State University
Corvallis, OR 97331

Dear Editor:

In reading the recent article describing *Hastingsia atropurpurea* (Madroño 33:175–181, 1986), the author, Rudolf Becking, erroneously reported that *H. bracteosa* was "an endangered species", citing a notice published by the U.S. Fish and Wildlife Service in the *Federal Register* (45:82479–82569, 1980). However, this notice only indicated that *Schoenolirion bracteosa* was a category 1 "candidate" species (taxa for which the Service currently has on file substantial information on biological vulnerability relating to autecology and distribution and threat(s) to support the appropriateness of proposing to list the taxa as endangered or threatened species), not an "endangered" species under the Endangered Species Act of 1973. The generic epithet was changed to *Hastingsia* in the *Federal Register* (48:53651) in 1983. The most-recent notice in the *Federal Register* (50:39554, 1985) reaffirmed the 1983 notice. Copies of all three notices may be obtained from my office upon request.

James A. Bartel
Staff Botanist
U.S. Fish and Wildlife Service
Sacramento Endangered Species Office
2800 Cottage Way, Rm. E-1823
Sacramento, CA 95825-1846

NOTES

NECTAR-SUGAR COMPOSITION IN AN INDIVIDUAL OF *Ruellia peninsularis* (ACANTHACEAE).—The pioneering nectar analyses of Wykes (New Phytol. 51:210–215, 1952) and Percival (New Phytol. 60:235–281, 1961) showed that floral nectars apparently exhibit a high degree of constancy in regard to nectar-sugar composition. Percival analyzed nectars of 899 species and established that less than 7% (61 species) varied significantly from sample to sample. More recently, Walker et al. (Crop Sci. 14:235–238, 1974) and Loper et al. (HortSci. 11:416–417, 1976) have described changes in nectar-sugar ratios in *Medicago sativa* L. and *Citrus* species (*C. macrophylla, C. depressa,* and the hybrid Fairchild tangerine), respectively. Frey-Wyssling et al. (Experienta 10:490–492, 1954) stated that enzymes, including invertase, are secreted by nectaries and can cause changes in the sucrose : hexose ratios in nectar. It is not known presently, however, if invertase in the nectar is universally, or even commonly, responsible for such changes when they do occur. During a study of intra-plant variability of nectar composition of individual flowers on single plants, I discovered that an individual of *Ruellia peninsularis* (Rose) I. M. Johnstn. (purchased at Boyce Thompson Southwestern Arboretum, Superior, Arizona), grown in a greenhouse at UTEP, showed remarkable interfloral sugar-ratio variability. Sucrose composition ranged from 27% to 79% in an initial sample from 20 flowers. The present study was done to determine if flower temperature at the time of secretion, flower age, or enzymatic activity was responsible for the differences.

Ruellia peninsularis is found near the southern tip of Baja California and in west-central Sonora, Mexico (Wiggins, Flora of Baja California, 1980). Flower size and shape are typical of the genus, and the color is purplish-blue (Exotica Horticultural Color Guide). Flowers typically open about 0300 h and the corollas are often open but sometimes not fully expanded by 0800 h. The anthers have dehisced by the time the corolla opens. Flowers usually remain fresh for about 24 h under greenhouse conditions and the corolla is shed about 1200 h the second day. Pollinators are not reported in the literature, but floral size, morphology, and color suggest large bees as the primary pollinators for this species. In an urban setting in Phoenix, Arizona, however, a plant was visited by small bees (T. F. Daniel pers. comm.).

Methods. Sugar composition of the nectar samples was determined by High-Performance Liquid Chromatography (HPLC) as outlined by Freeman et al. (Bot. Gaz. 145:132–135, 1984). All nectar samples were dried on filter paper disks for storage until analyzed. To assess the effect of flower age on nectar-sugar composition, open flowers were removed at dusk of the day preceding nectar sampling. Flowers that had opened during the night were marked the next morning and nectar-sugar compositions were followed throughout the flower duration. Eighteen flowers were sampled nondestructively at specific time intervals from November to January 1984–85. Ten flowers were sampled at 0830–0900 h, 1230–1300 h, and 1530–1600 h of the first day and at 0830–0900 h the second day. To determine whether the removal of the nectar pool at mid-day affected the sugar composition of the late afternoon sample, eight flowers were sampled at the same time intervals except that the mid-day sampling was omitted. The plant was placed in a growth chamber overnight at either 10°C, 19°C, or 30°C before the nectar samples were collected to determine if temperature at the time of nectar secretion influenced sugar composition. Sampling occurred at previously specified times during the first day of flower life.

Two experiments were conducted to determine the presence of invertase in the nectar. In the first experiment, nectar samples were collected in early morning and a portion of the sample analyzed. The remaining nectar was placed in sealed micropipets at room temperature for 19 h and then reanalyzed. In the second experiment, a 10 μl sample of nectar was added to 90 μl of a 20% sucrose solution as measured by a pocket refractometer. The mixture was held at 30°C. Samples were then drawn for

TABLE 1. CARBOHYDRATE COMPOSITIONS FROM NECTARS OF FLOWERS OF A SPECIMEN OF *Ruellia peninsularis.* Data are mean ± standard deviation; ranges are in parentheses. D1 = day one; D2 = day two of sampling. F = fructose, G = glucose, and S = sucrose.

D1 0830–0900 h	D1 1230–1300 h	D1 1530–1600 h	D2 0830–0900 h
Mean % F			
14.2 ± 2.4 (10.5–20.5)	18.5 ± 2.6 (14.6–22.3)	21.1 ± 4.6 (17.7–26.7)	32.1 ± 4.2 (26.0–42.2)
Mean % G			
8.5 ± 2.1 (4.0–12.8)	13.4 ± 2.9 (8.1–16.5)	16.7 ± 3.2 (12.0–23.5)	22.2 ± 3.4 (18.0–27.5)
Mean % S			
77.3 ± 4.1 (70.5–84.9)	68.1 ± 5.4 (62.0–77.3)	61.2 ± 5.8 (50.2–70.3)	45.7 ± 6.7 (26.7–53.7)

analysis at time 0, 0.5, 1, 4, and 24 h. Sugar concentrations of nectars also were measured with a pocket refractometer during day one. Statistical comparisons of sugar compositions were by 1-way analysis of variance (ANOVA) on arcsine transformed proportions.

To determine the fate of sucrose in the nectar pool, experiments were conducted using sucrose uniformly labeled with carbon-14 (ICN, Irvine, CA, USA). The specific activity was 12.3 mCi/mM and the total activity was 50 μCi. The solid was dissolved in 1.0 ml of water. Five μl of the labeled sucrose solution was added to each of six flowers and the nectar pool collected after 15 min. This determined the amount of labeled sucrose that could be recovered at time 0. Three 5 μl aliquots were measured and counted to determine the number of dps that were being added to the nectar pool at time 0. Six other flowers were injected with the labeled sucrose solution and allowed to remain undisturbed for 8 h (1630 h). The nectar was removed from the flower and the corolla tube washed with 5 μl of water. The total volume was measured with a Hamilton microsyringe (25 μl). This sample was mixed thoroughly and divided into two equal samples. One portion was counted to determine the amount of activity that remained in the nectar after 8 h. The other portion was separated into the constituent sugars by HPLC and the fractions were collected for counting. Sample radioactivities were quantified by scintillation spectrophotometry using Aquasol-2 (New England Nuclear Corp., Boston, MA, USA). Emissions were determined by a variable window discriminator to exclude activity from substances other than carbon-14.

Results. The relationship between flower age and nectar composition is shown in Table 1. In no case did the 10-flower group differ from the eight-flower group at equivalent sampling intervals and, thus, the two groups were combined. The percentage of sucrose declined from a mean of 77.3% in the early morning of the first day to 45.7% in the early morning of day two. Thus, the nectar composition changed from sucrose-dominant to sucrose-rich (see Baker and Baker, *In* Handbook of Exper. Poll. Biol., p. 117–141, 1983). The range of sucrose composition closely approximated the range found in the preliminary 20-flower sample. Fructose was always present in significantly higher quantities than glucose.

Nectar was not produced at 10°C. No significant difference in sugar composition was found in first-day flowers between constant 19°C and 30°C temperatures at 1600 h [F(1,12) = 0.649]. In addition, a percent sucrose comparison of first-day flowers at 1600 h from the greenhouse with the constant temperature trials at the same time interval showed no significant difference [F(2,30) = 0.173]. Therefore, flower temperature at the time of secretion did not significantly affect nectar-sugar composition in this case.

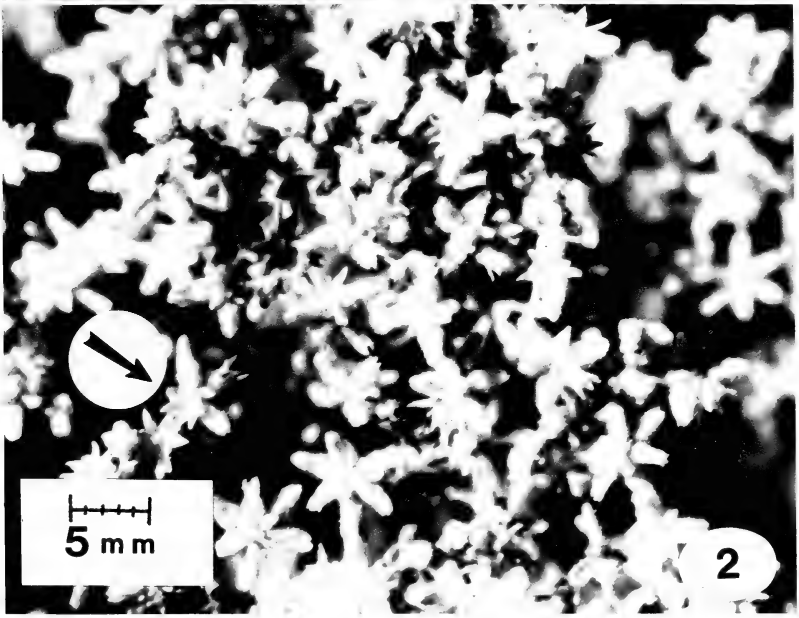
In the invertase activity experiments, holding a high-sucrose nectar from young flowers for 19 h had no significant effect on its sugar composition [F(1,14) = 3.90]. Furthermore, placing nectar samples in volumes of pure sucrose solution had no detectable effect on the mixture. Thus, there is no evidence for the presence of invertase in the nectar. Apparently, nectar must change as the flower ages. The failure of the nectar in the eight flowers to show a significant difference from the 10-flower sample (sampled at mid-day) suggests that it is constantly secreted and reabsorbed by the nectaries, rather than nectar of one composition secreted as others are removed from the flower.

The radioactive sucrose experiments showed that an average of 20.6% of the sucrose was reabsorbed by the flower during the 8 h period. This corresponds to the 20.8% decline in sucrose observed during the same period in Table 1. Furthermore, 85.2% of the radioactivity after 8 h was still in the sucrose form, with 7.8% and 7.0% present as labeled fructose and glucose, respectively. It seems that these changes are of sufficient magnitude to explain the decrease in nectar sucrose during the first day. Reabsorption of radioactive sucrose has been confirmed previously by Pederson, LeFevre, and Wiebe (Science 127:758–759, 1958) who also demonstrated that carbon-14 was translocated to other parts of the plant, particularly actively growing areas. Labeled sucrose was undetectable in the nectars of other flowers because of the low levels of radioactivity used.

Discussion. The sort of nectar changes documented herein are similar in magnitude to those recorded in Loper et al. (op. cit.) and reconfirm Baker and Baker's (op. cit.) emphasis on sampling of freshly produced nectar. Also, this study shows that single nectar samples can be misleading as to the composition of a species. Variability could arise by intrinsic physiological processes or could be related to visitation by pollinators. Possibilities in the second category include regurgitation of invertase from the digestive system of the pollinator during feeding and/or micro-organismal contamination of the nectar by the pollinator (P. G. Kevan pers. comm.). In the case of *R. peninsularis,* intrinsic physiological factors clearly are implicated. If the nectar changes described herein have a selective basis, their significance in terms of pollination success is presently obscure. Perhaps, it is a mechanism by which plants can attract a wider range of pollinators. Different groups of visiting insects would find at least some flowers with acceptable nectars. These different groups of visitors, therefore, might continue to visit flowers seeking suitable nectars and transfer pollen. The increased number of potential pollinators could help assure successful seed set in that species. Caution must be used in interpreting these data, however, because only one plant under greenhouse conditions was studied.—C. EDWARD FREEMAN, Dept. of Biological Sciences, University of Texas at El Paso, El Paso 79968-0519. (Received 28 Jan 1985; revision accepted 20 Jun 1986.)

OBSERVATIONS ON THE POLLINATION OF *Dedeckera eurekensis* (POLYGONACEAE).—The California flora has a relatively large number of phyletically isolated monotypic genera with highly restricted geographic distributions. *Dedeckera eurekensis* is a recently discovered genus of this nature (Reveal and Howell, Brittonia 28:245–251, 1976). This shrub is known only from a number of disjunct localities in the Inyo, Last Chance, Panamint, and White Mountains at the northwestern fringes of the Mojave Desert (Morefield, Madroño 32:122–123, 1985). Populations range in size from only two plants to those with scores of individuals.

The reproductive biology of species with narrowly restricted distributions is of interest because of the high risk of extinction. *Dedeckera* is of further interest because



FIGS. 1, 2. *Dedeckera eurekensis.* 1. Habitat: Coldwater Canyon, White Mts., Mono Co., California. 2. Inflorescence: arrow denotes individual cluster of four flowers (open flower at end of arrow, two unopened buds above and below open flower, closed flower following anthesis at far right).

it flowers during midsummer when the majority of desert shrubs are dormant and annuals generally have completed their life cycles. The following preliminary observations are offered with the hope that they will stimulate more detailed studies of the reproductive biology of *D. eurekensis* and other narrow endemics.

We studied (5–6 July 1985) the floral biology of the population located ca. 1 km up Coldwater Canyon in the White Mountains, northeast of Bishop, California. The population is the largest known and the only one to border a riparian community. It is composed of scattered plants on a steep north-facing talus slope (Fig. 1). The species was not observed on the adjoining south-facing slope.

The plants grew to 1 m, are rounded in form and usually broader than tall. They produce thousands of small flowers (ca. 1–2 mm across) that literally cover the entire surface of the plant (Fig. 2). The small flowers might suggest autogamy, but this is rare (possibly unknown) among long-lived woody perennials [Wiens, Oecologia (Berlin) 64:47–53, 1984]. Examination of the floral morphology indicated that the flowers are protandrous, and therefore not autogamous.

During the male phase, the styles are strongly reflexed against the ovary. Following pollen dispersal, the styles become erect and receptive. The temporal sequences and compatibility relationships are unknown. During the female phase, the minute stigmatic tips become sticky. The flowers are odoriferous and the scent is reminiscent of honey. The sepals are pubescent both adaxially and abaxially. During anthesis, swollen areas (nectaries?) at the base of the sepals where the filaments arise appear to secrete a moist film, but no nectar-pooling was observed. Perhaps this secretory film also is the source of the odor. Following the female phase the sepals closely invest the pistil. Possibly this is a mechanism to protect seed development during the heat of midsummer (temperatures will usually exceed 38°C). The pubescence inside the flowers might serve a similar function by preventing desiccation of the basal secretory film of the flower during anthesis.

Twenty-eight insects were captured during a morning and afternoon of observation. Sixteen were Diptera, mostly several species of Sarcophagidae. The remainder were three species of wasps, a species of damsel fly (Zygoptera), a species of ambush bug (Phymatidae), and a lace wing (Chrysopidae). Syrphid flies were observed, but none was captured. The sarcophagid flies generally carried *Dedeckera* pollen about the proboscis and sternum, but in small quantities. *Dedeckera* pollen also was observed on one wasp in moderate quantities on the sternum. Because Polygonaceae have a single ovule per flower, large pollen loads are perhaps less important. Pollen was examined from insects by methods found in Beattie (Pan-Pacific Entomology 47:82, 1971).

The insect species captured on *D. eurekensis* do not represent all the species that visit the flowers, because many more insects were observed on the flowers than could be caught. Little insect activity was noted between ca. 0500 h and full sunlight at ca. 0700 h. The earliest visitors were the sarcophagids, whose activity increased markedly about this time, followed by the various other visitors. Insect activity was prevalent throughout the day, but dropped off appreciably around 1600 h when it became windy. After 1800 h there was little insect activity until dark at ca. 2150 h. A larger number of insects appeared to visit plants near (within ca. 10 m) the stream than visited plants farther up the steep scree slope.

These observations suggest that sarcophagid and perhaps other short-tongued scavenger flies are probably the most numerous insect visitors that could effect pollination, followed by species of wasps, and possibly syrphid flies. These insects are attracted presumably by the odor and probe for moisture at the base of the flowers. The floral tube approximates the length of the proboscises (ca. 2–3 mm) of most visitors. The other insects mentioned are predators of other insects, and ineffective pollinators.

The only other plant flowering in the vicinity was *Petalonyx nitidus* Wats., which has a long, narrow tube. It was visited and presumably pollinated by a long-tongued fly (Bombyliidae?), which was not collected. This species was not observed visiting *Dedeckera.*

These strictly preliminary observations suggest that *D. eurekensis* is most likely pollinated by short-tongued sarcophagid flies and perhaps secondarily by wasps and syrphid flies. Few species pollinated by generalist flies have been studied thoroughly, and more information on this type of pollination system would be useful. It also would be interesting to investigate reproductive success in more depauperate *Dedeckera* populations such as that at ca. 1100 m in the Last Chance Mountains east of the Eureka Dunes, which consists of only two plants.—DELBERT WIENS, Dept. of Biology, University of Utah, Salt Lake City 84112; MARY DEDECKER, Box 506, Independence, CA 93526; and CAROL DEDECKER WIENS, 1763 Ann Dell Lane, Salt Lake City, UT 84121. (Received 21 Nov 1985; revision accepted 17 Jul 1986.)

SOME RESPONSES OF *Sidalcea calycosa* (MALVACEAE) TO FIRE.—Fire in California's introduced annual grassland is commonplace, but its effects usually are limited in extent and duration (Heady, *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, Wiley Interscience, 1977). Fires from the grassland frequently burn into the adjacent, predominately native vegetation of vernal pools where the role of fire has not been examined. To begin evaluation of the effects of fire on vernal pool plants, density and fruit production were studied in burned and unburned portions of a population of *Sidalcea calycosa* Jones. The autecology of this annual California endemic, which is common to some vernal pool margins and similar areas, has not been investigated previously.

Study site. The study site is at an elevation of 75 m and 1 km east of Chico, Butte Co., California. The topography is mostly flat with several channel-like depressions about 5 m wide and 0.25 m deep that are separated by broad mounds less than 1 m in height. These depressions are without natural outlets and maintain standing water for a maximum of about ten days following rainfall. Soil type is Tuscan stony clay loam (Watson et al., Soil Survey Chico Area, U.S.D.A., 1929). *Sidalcea calycosa* is the most abundant plant in the depressions; associates include *Limnanthes floccosa* Howell subsp. *californica* Arroyo and *Eryngium vaseyi* Coult. & Rose var. *vallicola* Munz. *Erodium* spp. and *Bromus mollis* L. are common in the annual grassland between the low areas. The climate is Mediterranean with an average rainfall of 660 mm; precipitation in the 1984–85 wet season was 512 mm and for 1985–86 was about 835 mm. Average daily temperatures for January and July 1984 were 8°C and 28°C (Chico Univ. Farm, Climatological data, Chico, CA. 1984–86). Domestic live-

TABLE 1. MEAN NUMBER OF FRUITS PER PLANT OF *Sidalcea calycosa* IN BURNED AND UNBURNED AREAS AT THE END OF THE FIRST AND SECOND POST-FIRE SEASONS. Three plants in the southeastern corner of each quadrat were evaluated; 120 plants were used for each treatment in the first season; excluding quadrats infested by *Colletotricum malvarum* during the second season, $n = 84$ and $n = 39$ plants for burned and unburned areas, respectively; values are ± one standard error; ns = $p > 0.05$; s = $p < 0.001$.

Season	Burned areas	Unburned areas	p
First	5.4 ± 0.33	3.4 ± 0.19	s
Second	1.71 ± 0.17	1.21 ± 0.23	ns

TABLE 2. MEAN DENSITY OF *Sidalcea calycosa* IN 1.5 × 2.0 DM QUADRATS IN BURNED AND UNBURNED AREAS DURING FIRST AND SECOND POST-FIRE SEASONS. Total number of individuals in quadrats for each treatment for each season are in parentheses; 40 quadrats were used for each treatment both seasons; values are mean ± one standard error; ns = $p > 0.05$; s = $p < 0.01$.

Season	Burned areas	Unburned areas	p
First	23.6 ± 2.25 (944)	30.9 ± 3.05 (1234)	ns
Second	23.8 ± 1.9 (952)	12.0 ± 1.7 (479)	s

stock have not grazed here for at least five years. In early July 1984, a wildfire burned a portion of the site during hot, dry, and windy conditions.

Methods. Transects were placed systematically across depressions. For every transect in the burn, a corresponding transect was placed in the same depression, but at an unburned location with similar width, depth, and continuity of plant cover. Five 1.5 × 2.0 dm quadrats were located within depresssions at 1 m intervals along each transect. Eight transects yielded 40 quadrats for each treatment. Prior to peak flowering in the first post-fire season (1 April 1985), the number of individuals per quadrat and the proportion of these in flower were measured. At the end of the growing season (5 May 1985), the number of fruits on the three plants in the southeastern corner of each quadrat were counted. During the second post-fire season (19 March 1986), the number of individuals per quadrat were measured again. During late March and early April 1986 an outbreak of the parasitic fungus *Colletotricum malvarum* (A. Br. et Casp.) Southw. caused extensive plant mortality before seed set in 12 of the burn quadrats and 27 of the unburned quadrats. On 29 March 1986, the proportion of early flowering plants in quadrats unaffected by the pathogen was determined and on 26 April 1986 the final number of fruits on the three plants in the southeastern corner of the unaffected quadrats were counted. Chi squares were used to determine if proportions were significantly different, and a one-way ANOVA was used to determine if means were significantly different.

Results. Thirty two percent of the plants in the burned area were flowering by 1 April 1985 compared to 6% of the plants in the unburned area. Larger plants also were observed in post-burn areas at this time. The difference in the proportions of early flowering individuals between treatments in the first season was significant ($p < 0.001$). On 29 March 1986, 19% of the plants in burned locations and 15% of the plants in unburned locations were in flower. The difference in proportions of early flowering individuals in the second post-fire season was not significant. Although significantly more fruits per plant were produced at burned locations during the first season, no difference in fruit production between treatments existed during the second season (Table 1). The specific factors that caused more vigorous early flowering and increased fruit production in the first post-fire season are unknown for *Sidalcea calycosa.* In some grassland herbs, a similar increase in flowering activity follows litter removal, which allows the unshaded young plants to grow earlier and more efficiently (Daubenmire, Ecology of fire in grasslands, Advan. Ecol. Res., 1968).

Table 2 compares the density of *S. calycosa* in burned and unburned areas for the first and second post-fire seasons and shows a significantly greater number of individuals per quadrat in the burned area only during the second season. Interpretation of the density data is difficult, but higher densities in the burned area during the second season following fire may be due to the larger seed crop produced here the first season.

Discussion. Fire may be important to *Sidalcea calycosa* by reducing sources of inoculum for pathogens that can hamper fruit production. Unburned quadrats had increased *Colletotricum malvarum* infestation and the degree of infestation decreased with increasing distance away from the unburned area. The direct role of fire in the reproduction of this vernal pool species, however, is limited because increased flower and fruit production were not apparent after the first post-fire season.

I thank Robert A. Schlising for advice and support, Steven Webster for field work, and Edward E. Butler for pathogen identification.—JOHN E. HUNTER, Dept. Biological Sciences, Chico State Univ., Chico, CA 95929. (Received 27 Nov 1985; revision accepted 25 Jun 1986.)

VESTA FLORENCE HESSE, 1901–1982.—Vesta Hesse was a keen observer of variability in plants and one of the most astute students of the flora of Santa Cruz Co., California. Her botanical collections resulted in a greater completeness of the *Flora of the Santa Cruz Mountains of California* (Thomas, J. H., Stanford University Press, 1961). In 1982 in honor of her botanical contributions, she was elected Second Vice-President of the California Botanical Society. Her name is commemorated in *Calyptridium parryi* Gray var. *hesseae* Thomas, an endemic of the Santa Cruz Mountains.

Vesta Hesse, next to youngest of eight children, was born and grew up on the outskirts of Boulder Creek, Santa Cruz Co., where her father had settled in 1885. She attended the University of California where she majored in Physics, graduating in 1924. After two years of teaching high school at Angels Camp, Calaveras Co., she decided that teaching was not her forte. The "Depression" of the period made it difficult to find a position elsewhere, so, following the death of her father in 1930,

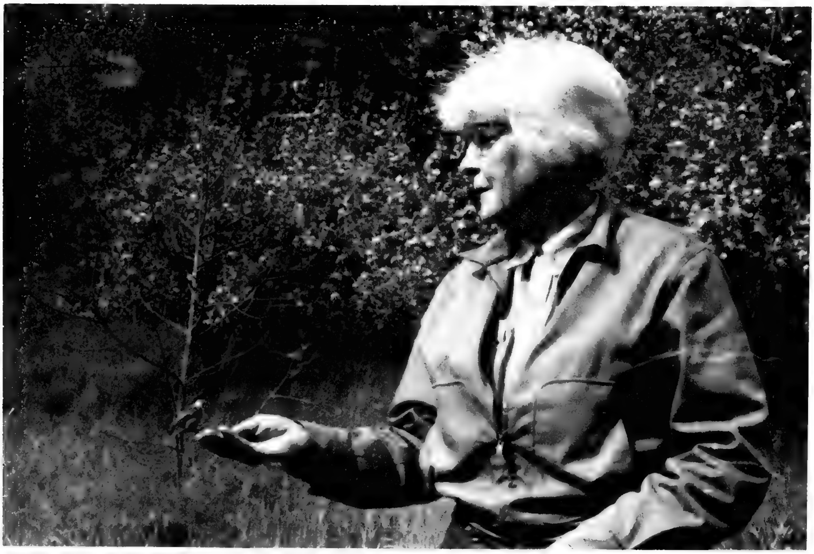


FIG. 1. Vesta Hesse feeding a chickadee.

she returned to Boulder Creek to be with her mother and care for an apple orchard that contained many apple varieties planted by her father. She became interested in the flora of the Santa Cruz Mountains during the mid-1930's and also began corresponding with botanists at a number of institutions. Most of this correspondence concerned the identifications of her specimens, but occasionally the letters revealed interesting facets of her correspondents as well as of her own character.

She corresponded with Dr. Willis Linn Jepson, then Professor of Botany at Berkeley, from 1939 to 1945. He appreciated her keen observations and encouraged her to send him specimens.

Vesta continued to send Santa Cruz County specimens to Jepson—always accompanied by careful notes as to variation and habitat. One such plant was a *Mimulus* from the Ben Lomond sand hill area that she first sent in 1942 and again in 1944. Because she had received no comment on it, she sent a specimen to John Thomas Howell at the California Academy of Sciences, San Francisco. Mr. Howell replied: "The mimulus . . . seems to be an undescribed species. It is related to *M. palmeri,* a Sierran + S. Calif. plant with much longer flowers. If it is alright, I shall name it, using your specimen as the type."

At once, Vesta wrote Dr. Jepson, ". . . I would like you to have the first opportunity to name it if you wish to do so . . .", to which Jepson replied, "It is my custom to inform those who collect regularly for the Flora of California of the proper practices regarding disposal of specimens. I deeply regret this was not done in your case. The situation brought up by your letter . . . is painfully embarrassing. None of the correspondents who support the Flora of California ever send material elsewhere. Not in the least would I labor for years to get results and have these results anticipated by the sending of specimens elsewhere." Vesta then wrote Mr. Howell asking him not to publish the *Mimulus.* He graciously acquiesced. She then wrote Jepson to assure him that no others would see the material until after the publication of the Scrophulariaceae in the *Flora.* (Currently, this Ben Lomond specimen is treated as *M. androsaceous.*)

After Jepson's death in 1946, Vesta continued to correspond with other botanists. She maintained active botanical interactions with Rimo Bacigalupi and Annetta Carter at Berkeley, John Thomas Howell at the California Academy of Sciences, and Roxana Ferris and John H. Thomas at Stanford until about 1968, when she stopped collecting plants. In all, Vesta made about 3350 numbered collections. The first set she bequeathed to the junior author and duplicates of many of these are housed at CAS, DS, and UC. Most of her collections were of vascular plants, although in later years she also collected lichens and bryophytes. She published five papers or notes, three of which were printed in Madroño.

After a long bout with cancer, Vesta died in Berkeley on December 9, 1982 at the home of her nephew, Siegfried Hesse. The Boulder Creek Historical Society has entered her name on their plaque as one of Boulder Creek's outstanding citizens.—ANNETTA M. CARTER, Dept. of Botany, Univ. of California, Berkeley 94720 and JOHN H. THOMAS, Dept. of Biological Sciences, Stanford Univ., Stanford, CA 94305. (Resubmitted 13 Nov 1985; revision accepted 17 Jul 1986.)

NOTEWORTHY COLLECTIONS

CALIFORNIA

ERIGERON SUPPLEX A. Gray (ASTERACEAE).—Sonoma Co., two localities on The Sea Ranch and e. of Coast Hwy., T10N R14W S35: 5.1 km s. of Mendocino Co. line

---

MADROÑO, Vol. 33, No. 4, pp. 308–315, 1986

on firebreak and in adjacent grassy area, 40–48 m, 34 small colonies, 8 Jun 1984, *Wells 338* (CAS); 3.1 km s. of the first locality, on private drive-bank w. of forest, near top of ridge, 79 m, 4 small plants, 13 Jun 1985, *Wells 516* (CAS).

Previous knowledge. Known in Humboldt Co., only one collection (1868–9, *Kellogg and Harford 382*, CAS); in Mendocino Co. from Mendocino, Little River, Point Arena, Gualala, and Havens Neck (the latter has the largest colony, ca. 60 plants); and in Sonoma Co., collected previously only near Stewart's Point (1937, *Vestal s.n.*, DS). Since *Wells 516,* George Snyder has found 20–30 plants 1.3 km s. of Gualala on The Sea Ranch bluff. Another specimen (1900, *Davy 6772,* UC) was collected somewhere at Point Reyes in Marin Co.

Significance. First reported collection from Sonoma Co. since 1937. Its presence in that county apparently was unknown to Cronquist (Brittonia 5:12, 1947) or to Munz (Fl. California and Suppl., 1968). Because *E. supplex* has been found in n. Sonoma Co. and not since 1900 in Marin Co., it is possible that those authors have questioned the location (Marin Co.) given for the Davy specimen. Smith and York (Invent. rare and endang. vasc. plants of California, 3rd ed., 1984) list *E. supplex* as confined to several populations, not endangered, and endemic to California. They also note, "We have one 1984 occurrence, but all the others are very historic . . .", which refers to Humboldt, Marin, and Sonoma Cos. and to *Wells 338* for the 1984 listing.—MARY P. WELLS, 684 Benicia Drive, Apt. 15, Santa Rosa, CA 95405.

STIPA DIEGOENSIS Swallen (POACEAE).—Santa Barbara Co., SAN MIGUEL ISLAND: sea cliff, ne. end, 20 Apr 1932, *Hoffmann s.n.* (SBBG); sea cliffs n. of Cardwell Point near Triangulation Point "Nob", 90 ft., 22 May 1963, *Piehl 63-396* (SBBG); w. wall of lower part of largest canyon s. of Green Mtn., 125 ft., 24 May 1963, *Piehl 63-472* (SBBG). SANTA CRUZ ISLAND: [no locality] 28 Mar 1925, *Hoffmann s.n.* (SBBG); 2 mi e. of Main Ranch, 24 Mar 1932, *Wolf 2861* (RSA); Smuggler's Cove, 21 Mar 1932, *Fosberg 7610* (PENN); Central Valley, 1 km w. of Nature Conservancy cabins, n. bank of stream, 34°00′15″N 119°44′50″W, 24 Mar 1986, *Ferren—UCSB Bot. Soc. 2559* (UCSB); Islay Canyon Rd., ca. 2 km w. of Reserve Station, 20 Mar 1984, *Ferren—UCSB Bot. Soc. 779* (UCSB); Hill 789, ca. 1 km sw. of Prisoners' Harbor, s.-facing slope, 300 ft., 25 Mar 1983, *Ferren and Frank—UCSB Bot. Soc. 2222* (UCSB); 0.5 km wnw. of Los Pinos del Sur, s.-facing slope, 820 ft., 23 Mar 1982, *F.* and *D. Roberts* and *Pierce—UCSB Bot. Soc. 644* (UCSB, SBBG); first canyon e. of rd. to Coches Prietos ca. 0.4 mi s. of Ridge Rd., ne.-facing slope, 24 Mar 1983, *Ferren and Forbes—UCSB Bot. Soc. 748* (UCSB). SANTA ROSA ISLAND: rocky slope, 26 Mar 1927, *Hoffmann s.n.* (SBBG); above Water Canyon, 18 Apr 1932, *Hoffmann 683* (POM); Cherry Canyon at the foot of Black Mtn., hillside with grass under *Quercus* and *Adenostoma,* 300 ft., 5–10 Apr 1960, *Blakley 3155* (SBBG); Torrey Pine grove about ¼ mi se. of Triangulation Point "Drift", 200 ft., 18 Feb 1965, *Philbrick B65-243 and Haller* (SBBG, UCSB). Ventura Co., MIDDLE ANACAPA ISLAND: cliff break above East Fish Camp, s. side, 31 Mar 1962, *Blakley 4925* (SBBG); onshore slopes above Sea Arch Peninsula, 150 ft., 1 May 1986, *Junak MA-193* (SBBG). WEST ANACAPA ISLAND: onshore slope just w. of Frenchy's Cove, n.-facing slope, 40 ft., 23 Apr 1982, *Junak WA-193* (SBBG); near ridge on n. slope below Camel Peak, 650 ft., 10 May 1963, *Piehl 63-242* (SBBG). SAN NICOLAS ISLAND: e. fork of Celery Canyon, w.-facing slope, 200 ft., 23 May 1985, *Junak SN-158* (SBBG); lower Mineral Canyon, n.-facing slope, 150 ft., 28 May 1986, *Junak SN-191* (SBBG).

Previous knowledge. Known previously from San Diego Co. at Proctor Valley, Jamul Mt., McGinty Mt., near Lee Valley, and Otay Mt. (Beauchamp, Fl. of San Diego Co., 1986) and in Baja California Norte s. to Agua de Tánilo near Santa María (Gould and Moran, The grasses of Baja California, Mexico, 1981), including Isla de Todos Santos (Thorne, Notes on the fl. of the Todos Santos Islands, Crossosoma 6(2):1–2, 1980).

Significance. New records for the California Islands, particularly the Channel Islands, and for Santa Barbara and Ventura cos. Range extensions between ca. 275–360 km nw. (largely over water) of the mainland localities in San Diego Co. Plants from San Diego Co. flower May–June and occur at 300–700 m (Beauchamp, op. cit.), whereas island plants flower Feb–May and occur at ca. 30–285 m. Various early collections of *Stipa diegoensis* have been identified as *S. lepida* var. *andersonii,* from which the former is distinguished by longer paleae.

Many taxa characteristic of n. latitudes in mainland California are known to reach the s. limits of their range on the Northern Channel Islands (C. Smith, A fl. of Santa Barbara Reg., California, 1976; Wallace, Vasc. pl. of Channel Islands of s. California and Guadalupe Is., Baja California, Mexico, 1985). Few taxa, however, share the distribution pattern of *Stipa diegoensis.* Other plant taxa that reach the n. limit of their range on the mainland in San Diego Co. or in nw. Baja California and also are known from the Northern Channel Islands include *Camissonia robusta, Plagiobothrys collinus* var. *gracilis,* and *Salvia brandegei.*

We thank curators of the cited institutions for loans or access to specimens and members of the UCSB Botanical Society for discovering the "unknown"*Stipa* on Santa Cruz Island and for assistance.—WAYNE R. FERREN, JR., Dept. Biological Sciences, Univ. California, Santa Barbara 93106; STEVEN A. JUNAK, Santa Barbara Botanic Garden, 1212 Mission Canyon Rd., Santa Barbara, CA 93105; and MARY E. BARKWORTH, Dept., Biology, Utah State Univ., Logan 84322.

MONTANA

AGASTACHE CUSICKII (Greenm.) Heller (LAMIACEAE).—Beaverhead Co., Tendoy Mts., steep s.-facing slope above Big Sheep Creek 19 km sw. of Lima, T15S R10W S10, common in limestone talus with *Artemisia tridentata* and *Oryzopsis hymenoides,* 2070 m, 13 Jul 1985, *Lesica 3519* (MONTU, MONT, NY) (verified by A. Cronquist, NY).

Significance. First report for MT, a range extension of ca. 80 km e. of central ID.

CAREX COMOSA Boott (CYPERACEAE).—Flathead Co., n. end of Flathead Lake 2 km w. of Bigfork, T27N R20W S35 nw.¼, small population in a marsh at the edge of a small pond with *Phalaris arundinacea* and *Carex diandra,* 885 m, 27 Jul 1985, *O'Brien 6* (PH) (verified by A. Schuyler, PH); same location, 30 Jul 1985, *Lesica 3592* (MONTU, MONT, NY).

Significance. First report for MT, a range extension of ca. 180 km e. of northern ID.

DRABA MACOUNII Schulz. (BRASSICACEAE).—Glacier Co., Glacier National Park, n. side of Mt. Jackson above Gunsight Lake 9 km s. of Logan Pass, common on limestone cliffs with *Silene acaulis* and *Hedysarum sulphurescens,* 2255 m, 24 Jul 1984, *Lesica and DeBolt 3193* (MONTU, GH); head of Lunch Creek 2 km ne. of Logan Pass, common in moist, mossy soil along a small meltwater stream with *Salix arctica* and *Saxifraga debilis,* 2345 m, 22 Aug 1985, *Lesica and DeBolt 3283* (MONTU, GH) (both specimens determined by R. Rollins, GH).

Significance. First report for MT and the U.S. A range extension of 400 km s. from Alberta.

DROSERA LINEARIS Goldie (DROSERACEAE).—Lewis and Clark Co., Indian Meadows 19 km nne. of Lincoln, T16N R8W S34 se.¼, locally common in a floating mat near the center of a fen with *Carex limosa* and *C. livida,* 1800 m, 19 Jun 1985, *Pierce 1304* (MONTU, NY); same location, 7 Aug 1985, *Pierce 1378* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. First report for MT and the western continental U.S., a range extension of 615 km s. of Alberta.

HETERANTHERA DUBIA (Jacq.) MacMill. (PONTEDERIACEAE).—Sanders Co., lower Flathead River 6.5 km w. of Dixon, T18N R22W S9 se.¼, in 30 cm of water in a backwater area on the s. side of the river with *Potamogeton natans, P. richardsonii* and *P. pectinatus,* 770 m, 8 Aug 1985, *Gregory and Kiser s.n.* (MONTU, MONT, PH) (determined by A. Schuyler, PH); Flathead Co., w. arm of Egan Slough 5 km sw. of Creston, common in 60 cm of water at the s. end of the slough with *Potamogeton gramineus* and *Elodea canadensis,* 885 m, 16 Aug 1985, *Lesica and DeBolt 3642* (MONTU, PH)

Significance. First report for MT, a range extension of ca. 650 km e. of w. WA.

KOBRESIA SIMPLICIUSCULA (Wahl.) Mack. (CYPERACEAE).—Glacier Co., Glacier National Park, Lunch Creek 2 km ne. of Logan Pass, common in moist peaty soil on a moderate s.-facing slope with *Pinguicula vulgaris* and *Carex capillaris,* 2190 m, 22 Aug 1984, *Lesica and DeBolt 3277* (MONTU, NY) (verified by A. Cronquist, NY); benches on the s. side of Mt. Reynolds 3 km s. of Logan Pass, common in wet bog areas with *Carex scirpoidea* and *Salix arctica,* 2315 m, 18 Aug 1985, *Lesica 3655* (MONTU, RM).

Significance. First report for MT, a range extension of ca. 70 km s. of s. Alta.

PHACELIA INCANA Brand (HYDROPHYLLACEAE).—Beaverhead Co., Tendoy Mts., above Johnson Gulch 16 km se. of Grant, T11S R11W S17, common on an e.-facing limestone scree slope with *Mimulus suksdorfii,* 2160 m, 6 Jul 1984, *Lesica 3105* (MONTU, NY) (verified by A. Cronquist, NY).

Significance. First report for MT, a range extension of ca. 80 km e. of central ID.

PRIMULA ALCALINA Cholewa & Henderson (PRIMULACEAE).—Beaverhead Co., Monida, 17 Jun 1936, *F. H. Rose 471* (MONTU) (determined by D. Henderson, ID).

Significance. First report for MT, a recently described species (Cholewa and Henderson, Britt. 36:59–62, 1984) known previously only from Clark and Lemhi cos., ID.

SAGINA NIVALIS (Lindbl.) Fries (CARYOPHYLLACEAE).—Glacier Co., Glacier National Park, n.-facing cliffs on Mt. Kipp 14 km se. of Waterton Lake, common in moist gravelly soil with *Carex bipartita* and *Sagina saginoides,* limestone parent material, 2380 m, 3 Aug 1985, *Lesica & DeBolt 3604* (MONTU, NH) (verified by G. Crow, NH).

Significance. First confirmed report for MT and the continental U.S., a range extension of 400 km s. of Alberta. A previous report of this species for CO (Rydberg, Fl. Colorado, 1906) was based apparently on a misidentified specimen (W. A. Weber, CO, pers. comm.). Specimens from CO, WY, and UT are intermediate between *S. nivalis* and *S. saginoides* (Crow, Rhodora 80:57, 1978).

SCIRPUS CYPERINUS (L.) Kunth (CYPERACEAE).—Sanders Co., Noxon Resevoir, 1 km n. of Trout Creek along Hwy. 200, large colonies near the shore in shallow water with *Carex athrostachya, C. retrosa* and *Galium trifidum,* 700 m, 12 Aug 1983, *Lackschewitz 10649* (MONTU).

Significance. First report for MT, a range extension of ca. 600 km e. of Columbia Co., OR.

SHOSHONEA PULVINATA Evert & Constance (APIACEAE).—Carbon Co., Pryor Mts., e. rim of Lost Water Canyon ca. 22 km w. of Warren, T8S R27E S26 se.¼, scarce in a windblast area, limestone parent material, 1910 m, 15 Aug 1984, *Pierce 1250* (MONTU) (verified by E. F. Evert); Beartooth Mts., ridgetop n. of the North Fork Grove Creek 10 km se. of Red Lodge, T8S R20E S26, very common in gravelly, limestone-derived soil with *Cymopterus hendersonii* and *Eritrichium howardii,* 2135 m, 17 Jun 1985, *Lesica 3417* (MONTU, MONT, RM, UC) (verified by L. Constance, UC).

Significance. First report for MT. A recently described species (Evert and Constance, Syst. Bot. 74:471–475, 1982) previously known only from Park Co., WY.

TOWNSENDIA FLORIFER (Hook.) Gray (ASTERACEAE).—Beaverhead Co., along the Sage Creek Rd. 16 km e. of Kidd, T12W R8W S2 sw.¼, uncommon in dry, open alkaline soil with *Chrysothamnus nauseosus* and *Heterotheca villosa,* 1965 m, 10 Jun 1985, *Lesica 3377* (MONTU, NY) (verified by A. Cronquist, NY); buttes just s. of White Hills 17 km ne. of Kidd, T8S R8W S25, uncommon in sandy, calcareous soil on steep, s.-facing, eroding slopes with *Penstemon aridus* and *Lesquerella alpina,* 1980 m, 10 Jun 1985, *Lesica 3380* (MSC) (verified by J. Beaman, MSC).

Significance. First report for MT, a range extension of ca. 60 km n. of eastern ID. *Lesica 3380* consists of nearly discoid and apparently apomictic plants (J. Beaman pers. comm.).

TOWNSENDIA SPATHULATA Nutt. (ASTERACEAE).—Beaverhead Co., just s. of Sheep Corral Gulch 11 km ne. of Clark Canyon Reservoir, T8S R12W S35, ca. 50 plants in thin soil on a limestone outcrop with *Oxytropis lagopus* and *Cymopterus bipinnatus,* 1950 m, 9 Jun 1985, *Lesica 2978* (MONTU, NY) (verified by A. Cronquist, NY); Broadwater Co., Limestone Hills 5 km w. of Townsend, uncommon in thin soil of a limestone bench on an e.-facing slope with *Artemisia nova* and *Lesquerella alpina,* 1375 m, 21 May 1985, *Lesica 3325* (MONTU, BD) (verified by J. Beaman, BD).

Significance. Range extensions of 375 km e. and 300 km ne. of a recently reported station (Dorn, Vascular plants of Montana, 1984) in extreme s.-c. MT.—PETER LESICA, KLAUS LACKSCHEWITZ, and JOHN PIERCE, Botany Dept., Univ. Montana, Missoula 59812; SHARI GREGORY, Natural Resources Division, Confederated Salish and Kootenai Tribes, Pablo, MT 59855; and MARIA O'BRIEN, Univ. Montana Biological Station, Bigfork, 59911.

OREGON

LIMONIUM CALIFORNICUM (Boiss.) Heller (PLUMBAGINACEAE).—Lincoln Co., Waldport, across the road from the Waldport High School, in a salt marsh with *Distichlis spicata* and *Jaumea carnosa,* T13S R11W S19, 29 Jul 1983, *Dennis 4727* (OSC); Waldport, marsh, 30 Jul 1939, *Overlander s.n.* (OSC).

Significance. First report for OR for this CA salt marsh species.

PANICUM DICHOTOMIFLORUM Michx. (POACEAE).—Benton Co., Corvallis, at junction of 53rd St. and Reservoir Rd., growing in gravel along roadway, T12S R5W S38, 81 m, 2 Oct 1982, *Dennis 4694* (OSC); Jackson Co., near Talent, Sep 1940, *Reimer s.n.* (OSC, WTU); Malheur Co., Ontario, 13 Sep 1963, *Bailey s.n.* (OSC).

Significance. First report for OR for this native of the c. and e. US, which has become established as a weed in a few localities in CA and ID.

PEPLIS PORTULA L. (LYTHRACEAE).—Linn Co., Truax Slough, off Riverside Drive, T11S R4W S28, 70 m, 3 Oct 1984, *Dennis s.n.* (OSC); Marion Co., Aumsville, s. side Mill Creek behind Santiam Valley Bank, T8S R2W S2, 96 m, 26 Jul 1980, *Ertter 3844* (OSC); Multnomah Co., confluence of the Sandy and Columbia rivers, T1N R3E S24, 5 Oct 1982, *Kemp 82108* (OSC); Polk Co., sw. of Monmouth, 10630 Elkins Road, T9S R5W S13, 75 m, 4 Jun 1984, *Halse 2838* (OSC).

Significance. First report for OR. This European species is known from Placer and Yuba cos., CA and Wahkiakum and Pacific cos., WA.

RANUNCULUS PARVIFLORUS L. (RANUNCULACEAE).—Polk Co., Independence, weedy vernal area at the edge of a *Poa pratensis* field across from 2045 Greenwood Road, T8S R4W S4, 52 m, 18, 21 May 1981, *Halse 2638, 2645* (OSC).

Significance. First report for OR. This European species is known from Humboldt and Monterey cos., CA and the c. and e. US.

VERATRUM INSOLITUM Jeps. (LILIACEAE).—Polk Co., in the Coast Range ca. 12 air km ne. of Valsetz Lake, T7S R8W S24, 819 m, 19 Jul 1985, *Halse 3169* (OSC).

Significance. First record for Polk Co., a n. range extension of ca. 85 km from the Coast Range populations in Lane Co. This species, known primarily from sw. OR and n. CA, is reported from Benton Co. but no vouchers were found in ORE, OSC, WILLU.—RICHARD R. HALSE, 4535 NW Beta Pl. No. 3, Corvallis, OR 97330 and LA REA DENNIS JOHNSTON, Dept. Botany Plant Pathol., Oregon State Univ., Corvallis 97331.

WYOMING

ARCTOSTAPHYLOS RUBRA (Rehd. & Wilson) Fern. (ERICACEAE).—Park Co., Absaroka Range, at the base of the Cathedral Cliffs, ca. 3.2 km e. of Crandall Ranger Station scattered in open, calcareous bog on hummocks and in wet spruce forest, T56N R106W S11 and 14, 2012 m, 12 Aug 1984, *Evert 7494* (MOR, RM), *Dorn 4119* (NY, RM), *Hartman 18548* (RM), *Lichvar 7041* (RM).

Significance. First record for WY and the contiguous US. This disjunct population is ca. 900 km from the nearest known populations in sw. Alberta and adjacent BC.

BROMUS VULGARIS (Hook.) Shear (POACEAE).—Yellowstone National Park, immediately e. of the outlet of Lewis Lake, mixed coniferous forest, 2373 m, 4 Aug 1985, *Evert 9112* (MOR, RM, YELLO), *Dorn 4306* (RM); Teton Co., Teton Range, along N. Fk. Teton Creek, mixed coniferous forest, T44N R117W S20 sw.¼, 2195–2377 m, 9 Aug 1985, *Evert 9209, 9220* (MOR, RM); along S. Fk. Teton Creek, T44N R117W S29, 2195 m, 10 Aug 1985, *Evert 9301* (MOR, RM).

Significance. First collections in WY since this species was first collected in the state (13 Jul 1901, *Merrill and Wilcox 244,* RM) at Teton Pass.

CAREX LIMOSA L. (CYPERACEAE).—Park Co., Absaroka Range, at the base of the Cathedral Cliffs, ca. 3.2 km e. of Crandall Ranger Station, abundant in open calcareous bog on marl-peat substrates with *Carex buxbaumii, Carex simulata, Eriophorum viridicarinatum,* and *Triglochin maritimum,* T56N R106W S11, 2012 m, 12 Aug 1984, *Evert 7505* (MOR, RM), *Dorn 4128* (NY, RM), *Hartman 18559* (RM), *Lichvar 7026* (RM).

Significance. Second report of this species in WY. Previously known (18 Aug 1951, *Beetle 11653,* RM) in WY from Bighorn Co., 275 km se. of the location reported here.

CAREX LIVIDA (Wahlenb.) Willd. (CYPERACEAE).—Location, habitat, and elev. the same as the *C. limosa* collection (above), 21 Jun 1985, *Evert 7867* (MOR, RM).

Significance. First record for WY, a range extension of ca. 385 km from Teton Co., MT and the first report of this species in the Rocky Mtns. s. of n. MT and n. ID.

CAREX MICROGLOCHIN Wahlenb. (CYPERACEAE).—Location, habitat, and elev. the same as the *C. limosa* collection (above), 12 Aug 1984, *Evert 7506* (RM), *Dorn 4145* (RM), *Lichvar 7028* (RM).

Significance. First record from WY, a range extension of ca. 545 km from nw. MT and ne. UT.

CAREX SCIRPIFORMIS Mack. (CYPERACEAE).—Location, habitat, and elev. the same as the *C. limosa* collection (above), 12 Aug 1984, *Dorn 4142* (RM); 21 Jun 1985, *Evert 7868* (MOR, RM).

Significance. First record for WY.

FESTUCA SUBULATA Trin. (POACEAE).—Sheridan Co., ca. 3.2 km w. of Story, fish hatchery grounds along Spring Creek, *Pinus ponderosa* forest, T53N R84W S13 nw.¼, 1646 m, 24 Jul 1982, *Evert 4431* (MOR, RM).

Significance. Second report for WY. Previously known in WY from a single collection (13 Jul 1901, *Merrill and Wilcox 243,* RM) from Teton Pass ca. 346 km sw. of the collection reported here.

KOBRESIA SIMPLICIUSCULA (Wahlenb.) Mack. (CYPERACEAE).—Location, habitat, and elev. the same as the *Carex limosa* collection (above), 12 Aug 1984, *Evert 7503* (MOR, RM), Dorn 4141 (NY, RM), *Lichvar 7021* (RM).

Significance. First record for WY, a range extension of 193 km from the nearest known population in Teton Co., ID.

LOLIUM MULTIFLORUM Lam. (POACEAE).—Park Co., Absaroka Range, ca. 64 km w. of Cody, just n. of Hwy 14 along Gunbarrel Creek, disturbed soil around lodge buildings and corrals, T52N R107W S19 sw.¼, 1951 m, 15 Sep 1982, *Evert 5017* (MOR, RM); Weston Co., near Newcastle, pond shore, T45N R61W S28, 1347 m, 11 Jul 1982, *Hallsten, Skinner and Beetle* (RM).

Significance. First records of this naturalized grass for WY.

OPHIOGLOSSUM VULGATUM L. var. PSEUDOPODUM (Blake) Farw. (OPHIOGLOSSACEAE).—Yellowstone National Park, Shoshone Geyser Basin along Shoshone Creek under small *Pinus contorta* with *Juncus tweedyi, Tofieldia glutinosa,* and *Vaccinium caespitosum,* 2377 m, 5 Aug 1985, *Evert 9156* (MOR, RM, YELLO), *Dorn 4316* (MO, NY, RM), *Lichvar 7095* (RM).

Significance. First record for WY, a range extension of ca. 400 km from Missoula Co., MT.

PRIMULA EGALIKSENSIS Wormskj. (PRIMULACEAE).—Location, habitat, and elev. the same as the *C. limosa* collection (above), 12 Aug 1984, *Evert 7501* (MOR, RM), *Hartman 18561* (RM).

Significance. First record for WY. Previously this species was known in the contiguous US from only Park Co., CO. The population reported here represents a range extension from CO and se. BC of 675 km and 820 km, respectively.

SALIX MYRTILLIFOLIA Anderss. var. MYRTILLIFOLIA (SALICACEAE).—Park Co., Absaroka Range, at the base of the Cathedral Cliffs, ca. 3.2 km e. of Crandall Ranger Station, wet spruce forest at edge of calcareous bog, T56N R106W S14, 2012 m, 12 Aug 1984, *Evert 7489* (MOR, RM), *Dorn 4118* (RM), *Lichvar 7039* (RM).

Significance. First record for WY and the contiguous US, a range extension of ca. 550 km from sw. SK.

SAXIFRAGA NIDIFICA Greene var. NIDIFICA (SAXIFRAGACEAE).—YELLOWSTONE NATIONAL PARK: Absaroka Range, ca. 4.8 km e. of Sylvan Pass, wet, rocky s.-facing slope n. of Hwy 14, 2377 m, 12 Jul 1982, *Evert 4199* (MOR, RM, UC, YELLO); ca. 3.2 km e. of Sylvan Pass, ridge n. of Hwy 14, vernal seepage areas, 2560 m, 14 Jul 1982, *Evert 4214* (MOR, RM, YELLO); PARK CO.: Absaroka Range, ca. 0.2 km e. of Pahaska, seepage area and intermittent drainage, T52N R109W S3 se.¼, 2042 m, 16 Jul 1982, *Evert 4274* (RM); along Eagle Creek ca. 8 km sw. of Hwy 14, seepage areas above cr., T51N R109W S3 se.¼, 2195 m, 18 Jul 1982, *Evert 4314* (MOR, RM); ridge w. of Fishhawk Creek ca. 2.4 km s. of Hwy 14, seepage areas, T52N R108W S34 sw.¼, 2 Jul 1984, *Evert 6814* (MOR, RM); ridge w. of Kitty Creek, ca. 4.8 km sw. of Hwy 14, rocky, seepage areas, T52N R108W S33 sw.¼, 2438 m, 5 Jul 1984, *Evert 6853* (MOR, RM); TETON CO.: n. of Teton Forest Camp near N. Fk. Teton Creek, T44N R117W S20, 2195 m, 2 Jun 1956, *Anderson 271* (UTC). (*Evert 4199* and *Anderson 271* determined by P. G. Elvander.)

Significance. First records for WY, a range extension of 160 to 130 km from Gallatin Co., MT.

SCIRPUS PUMILUS Vahl (*Cyperaceae*).—Location, habitat, and elevation the same as the *C. limosa* collection (above), 12 Aug 1984, *Evert 7498* (MOR, RM), *Dorn 4133* (RM), *Lichvar 7035* (RM).

Significance. First record for WY. This inconspicuous and infrequently collected species was previously known from only CA, CO, and MT in the contiguous US.

SILPHIUM INTEGRIFOLIUM Michx. var. LAEVE T. & G. (ASTERACEAE).—Laramie Co., Crow Cr. flood plain just w. of Cheyenne, T14N R67W S27 n.½, 1890 m, 30 Aug 1984, *Dorn 4171* (NY, RM).

Significance. First record for WY, a range extension of ca. 240 km from NE and Yuma Co., CO.

TRAUTVETTERIA CAROLINIENSIS (Walt.) Vail (RANUNCULACEAE).—Yellowstone National Park, immediately ne. of the outlet of Lewis Lake, wet–moist, mixed coniferous forest and seepage, 2373 m, 14 Aug 1984, *Evert 7508* (RM, YELLO).

Significance. Second record for WY. This specimen represents the first WY collection of this species in 100 years. It was collected previously from the same general area (Yellowstone National Park, Lewis Lake, Aug 1884, *Tweedy 302*). The nearest known populations to that reported here are in Custer Co., ID and Missoula Co., MT.—ERWIN F. EVERT, 1476 Tyrell Avenue, Park Ridge, IL 60068; ROBERT D. DORN, Box 1471, Cheyenne, WY 82001; RONALD L. HARTMAN, Dept. Botany, Univ. Wyoming, Laramie 82071; and ROBERT W. LICHVAR, 1216 West 31 St., Cheyenne, WY 82001.

REVIEWS

Flowering Plants, the Santa Monica Mountains, Coastal and Chaparral Regions of Southern California. By NANCY DALE. 239 pp. Capra Press, Santa Barbara, CA. 1986. ISBN 0-88496-239-0, $15.95 (paperbound).

Students interested in the botany of the Santa Monica Mountains have long been in need of a well-illustrated guide book for the local flora. Now, two books have recently appeared to fill this void. The first is *Wildflowers of the Santa Monica Mountains* by Milt McCauley, and the most recent and the subject of this review is *Flowering Plants, the Santa Monica Mountains* by Nancy Dale.

Dale's book is aimed at beginning students. It also will serve more experienced students who like to refer to illustrations for help with the keys found in technical floras. The introduction briefly summarizes the interesting and complex geology, describes the climate and plant communities, and reviews the rare and endangered plants of the range. There are 249 species described and each is accompanied by either a color photograph or a simple line drawing. In addition, another 133 species are mentioned or distinguished. In total, one may be able to identify 382 species or 43% of the total flora of the Santa Monica Mountains—quite a sizable number for a popular work. Several appendices (wildflower trips, botanic gardens specializing in native plants, nature clubs, docent organizations, and public agencies) and a map of the range are included to help those who are new to the range become acquainted with the native flora.

MADROÑO, Vol. 33, No. 4, pp. 315–317, 1986

The format of the family and species discussion is uniform and simple. Dale has not overwhelmed her readers with technical terms. Some essential botanical terms that she uses are defined and illustrated in the preface, and the rest are defined in the glossary. Interesting information on uses of the plants by Indians and early settlers is presented, and the Latin names are translated or discussed giving those who are unfamiliar with scientific names some understanding and an appreciation for the names.

The species are arranged alphabetically (families are alphabetical within their subclass; species, within their family). This facilitates comparisons with some recent floras that also are alphabetical and avoids some of the problems that beginning students have with phylogenetic arrangements, but retains some of the advantages of a phylogenetic system by keeping all the taxa of a family together. Unlike books arranged by flower color, the alphabetical system may be too cumbersome for beginners. Until they learn most of the families, they will rely heavily on the index arranged by flower color for identification.

The technical aspects are well done and have resulted in a very attractive book. Typographical errors or mispellings are almost nonexistent. Photographs are very good, and their colors are as true-to-life as possible. With as many color photographs as there are in this book, it is amazing that only a couple of the photographs came out too dark. The line drawings done by Marianne Wallace are clean and neat, and she has done an admirable job in capturing the likeness of the plants with simple pen strokes and stippling.

There are few flaws or shortcomings. One error is the description of the scientific name in the preface where the specific epithet is incorrectly stated to be the species name. Trees are treated separately at the end after the section on wildflower trips, and there they appear to be a late addition, but one that certainly will be appreciated. The second index, which is alphabetical by family, is superfluous because the arrangement is the same as the text. The exclusion of most of the wind pollinated taxa (grasses, sedges, and rushes) is a shortcoming, but one not uncommon for guide books. It is unfortunate that these plants, which are often common and distinctive, are ignored even though a photograph or illustration can make identification of many of these species easy.

Nancy Dale has done a fine piece of work. *Flowering Plants, the Santa Monica Mountains* will undoubtedly become a very popular field guide to the range and other coastal sage scrub and low elevation chaparral communities of southern California.—Barry A. Prigge, Dept. Biology, Univ. California, Los Angeles 90024.

A Flora of San Diego County, California. By R. Mitchel Beauchamp. xii + 241 pp. Sweetwater River Press, P.O. Box 985, National City, CA 92050. 1986. ISBN 0-931950-01-5, $28.95 (hardcover); ISBN 0-931950-00-7, $22.95 (paperbound).

Mitchel Beauchamp grew up in San Diego County, interested in natural history since high school. He started this flora for a master's thesis but had to cut back to a more time-realistic goal. Working since as an environmental consultant in the County, he has kept up with local botany, finished writing the flora, and formed his own company to publish it. His wife input the text to a word processor, and the rest was almost automatic. It is a well printed book that a new publisher can be proud of.

One chapter, mainly from Thomas A. Oberbauer, tells of plant communities in the County; and Oberbauer's map, spread over eight pages, shows where they are. A short chapter on floral diversity and endemism discusses "floral districts" and lists significant plants.

The bulk of the book, an even 200 pages, succinctly catalogues the vascular flora of 1980 species (1516 native) and 230 lesser taxa (225 native)—a remarkable total for one county. Keys are adapted from Munz's *A flora of southern California.* Under each major subdivision, the families, genera, and species are alphabetic, for easy finding; and an index gives quick reference. Running heads show family and generic names, but not alternately on left and right. Entries are short and concise, commonly just two to four lines. Following the name (starred if the plant is not native) are any pertinent synonyms and usually a common name. Then come statements of abundance, habitat or plant community, region in the County, and elevation, followed by a dozen or so representative localities or, for less common plants, as many as known. Last are flowering months and chromosome numbers. Type localities are given if in the County, for rejected as well as for accepted taxa. There are few other notes.

Mitchel Beauchamp knows his plants in the field, keeps up on names, has combed several herbaria for records, and is thorough and consistent in his catalogue. The last County flora was Ethel Bailey Higgins' *Annotated distributional list of ferns and flowering plants of San Diego County, California,* 1949, long out of print and longer out of date. Everyone interested in San Diego County plants will welcome this up-to-date and basically much better successor.—Reid Moran, Emeritus Curator of Botany, San Diego Museum of Natural History, Box 1390, Balboa Park, San Diego, CA 92112.

REVIEWERS OF MANUSCRIPTS

The editors thank all reviewers listed below for their assistance with papers published in volume 33. We are grateful for their generous contributions of time and effort toward maintaining the quality of papers published in Madroño.

Daniel I. Axelrod
Herbert G. Baker
Mary E. Barkworth
Spencer C. H. Barrett
James A. Bartel
James W. Bartolome
Jerry M. Baskin
J. M. Brach
T. Christopher Brayshaw
Bert G. Brehm
Dean Capralis
Anita F. Cholewa
Susan A. Cochrane
William B. Critchfield
Robert W. Cruden
Christopher Davidson
Darleen A. DeMason
Melinda F. Denton
Wayne J. Elisons
Barbara Ertter
Thomas C. Fuller
Amy Jean Gilmartin
James R. Griffin
J. Robert Haller
Ronald L. Hartman
Harold F. Heady
Lawrence R. Heckard
James Henrickson
Ann M. Howald
Marshall Johnston
David J. Keil
Jon E. Keeley
Walter Knight
Ronald M. Lanner
William J. Libby
R. John Little
Jack Major
Jack Maze
Elizabeth McClintock
Steven P. McLaughlin
Robert J. Meinke
John S. Mooring
Cornelius H. Muller
Katherine Muller
Rodney G. Myatt
Daniel H. Nicolson
Erik T. Nilsen
Dennis O. Odion
Robert Ornduff
Thomas V. Parker
David Parsons
Arthur M. Phillips, III
Donald J. Pinkava
Barry A. Prigge
Charles F. Quibell
Fred M. Roberts, Jr.
Peter Rowlands
Phillip Rundel
J. Rzedowski
John O. Sawyer, Jr.
Carla R. Scheidlinger
Mark A. Schlessman
Robert A. Schlising
Richard J. Shaw
James R. Shevock
Dale M. Smith
Clifton F. Smith
James P. Smith
Peter F. Stickney
John L. Strother
Barry D. Tanowitz
Ronald J. Taylor
Harry D. Thiers
John H. Thomas
Robert F. Thorne
John M. Tucker
Thomas R. Van Devender
Frank C. Vasek
Grady L. Webster
H. Wells
Dieter H. Wilken

COMMENTARY

Message From the Past CBS President

Several months ago I was asked by our new Editor to contribute the first of what is projected to be a continuing series of presidential "end-of-term notes" wherein the out-going president shares his or her views on the current status of the Society. Most members have regular contact with the Society only through Madroño and perhaps at the annual February meetings, and it was felt that many might appreciate a periodic status report.

Perhaps I can begin by saying that I have been on the Executive Council in one or another capacity almost continuously since 1973. As with most professional organizations, there have been many things that have remained unchanged: we still meet on third Thursdays in Berkeley with an invited speaker to stimulate discussion of one or another botanical subject; Herbert and Irene Baker are almost invariably in attendance, along with numerous other consistent supporters of the Society; and officers are still elected at the January meeting by a "white ballot".

Other things have undergone a bit of evolutionary change, however. As you are well aware, single member dues have increased from $8.00 to $18.00 over this period; the Executive Council has been expanded to include a graduate student representative; and the format of Madroño has developed several mutations, some more permanent than others.

One of these changes was the adoption in 1979 of a Society logo, the silhouette of a well-shaped *Arbutus menziesii* Pursh, selected from a number of designs submitted by the membership. However, I was amused recently when a former Council member, albeit a specialist in cryptogams, referred to "that oak tree on the back cover". Perhaps we need a new contest.

On a more serious note, if you have yet to sense it, your new Editor, Wayne Ferren, Jr., is developing a style that is transforming our journal from being simply an organ of communication for new botanical knowledge, into a more vital and effective vehicle of communication among the members. Be alert for new columns and formats and don't hesitate to communicate your reactions and/or suggestions, either directly to the Editor or to any member of the Executive Council.

As the preceding paragraph should indicate, I am generally pleased with current and future status of the California Botanical Society, even though there was a period in the mid-seventies when the financial picture looked rather bleak. In fact, at one point we were briefly dipping into the Endowment Funds to pay for printing several numbers of the journal. Two things that quite effectively corrected this were a series of increases in the membership fees and the very astute and vigorous investment policy established by Dr. John Thomas during his tenure as CBS Treasurer.

During the first half of this decade, interest rates were generally high, a condition that unfortunately no longer continues. As a result of this and the fact that there has been no dues increase for five years, it probably will be necessary for your Council to institute one for the next calendar year if we are to maintain our newly regained healthy financial condition. This also will allow our continued support of such worthwhile endeavors as the CBS Graduate Students Meetings; the conference on rare and endangered plants held in Sacramento this fall; and the very exciting Jepson Herbarium project to revise the *Manual of the Flora of California,* about which you will be hearing more in the near future.

My final observations have to do with changes I perceive occurring in the membership as represented by those who attend the monthly meetings and the annual banquet. I had earlier been privately concerned that the average age of CBS members had been climbing over the last several years, but recently I have noticed that more and more young new members are in evidence, perhaps at least partially a reflection of our fostering of the Graduate Student Meetings throughout the State.

Madroño, Vol. 33, No. 4, pp. 318–319, 1986

And last but not least, I am pleased to note that there has been a very significant increase in active Society involvement by individuals representing the several public agencies that have been gaining long-due responsibilities for locating and maintaining populations of rare or threatened taxa on public lands. To me this is a good and healthful trend, both for the Society and for the native flora.—CHARLES F. QUIBELL, Department of Biology, Sonoma State University, Rohnert Park, CA 94928.

EDITOR'S REPORT FOR VOLUME 33

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in MADROÑO and to comment on other aspects of the journal. Between 1 July 1985 and 30 June 1986, 90 manuscripts were received (41 articles, 10 notes, and 39 individual noteworthy collections). The current status of all unpublished manuscripts, including those received after 30 June 1986, is 23 in review (14, 1, 8), 18 in revision (16, 2, 0), six awaiting decision by the editors (6, 0, 0) and 12 accepted for publication (11, 0, 1). There are two unpublished book reviews and five in preparation. Volume 33 included 114 published manuscripts (27, 12, 75), 9 book reviews, and 7 editorials, commentaries, or letters to the editor. The period between submittal and publication has averaged about 1⅓ years.

This is the first entire volume completed during my editorship. I am grateful for the opportunity to contribute to this exceptional regional journal. The success of the past year, however, would not have been possible without the help of the past Associate Editor, J. Robert Haller, who contributed to the first three issues, and the current Associate Editor, Barry D. Tanowitz, who contributed to the last two issues. Their dedication to the journal and their editorial and scientific assistance is appreciated greatly.

I also thank the members of the Board of Editors for their assistance with the review of manuscripts. A few, such as Bill Critchfield and Frank Vasek, reviewed more than their share of the burden and I extend special thanks to them. Of particular note is Steven Timbrook, who replaced Barry Tanowitz when Barry assumed the position of Associate Editor. Steven compiled the Contents and Index to Volume 33, an achievement all readers of MADROÑO will appreciate. Thanks Steve! Additionally, a total of 81 reviewers assisted with at least one manuscript review each for papers published in Volume 33; many commented on several different papers. This unsung burden is a critical aspect of any journal and their role here is appreciated deeply. The organization, readability, and style of all papers reflect ideas provided by our reviewers and the general high quality of papers in MADROÑO can be attributed in part to their sincere efforts. I look forward to future assistance by them and others.

Most important is the contribution by our authors. The strength of MADROÑO depends on the quality and quantity of manuscripts. A scan of this year's papers reveals the great breadth of investigations by members of the California Botanical Society, which in Volume 33 have included contributions in systematics, nomenclature, floristics, phytogeography, ecology, paleobotany, cytology, phenology, plant/animal interactions, hybridization, and morphology. These papers also covered many regions of western North America, including Mexico, and concerned various plant groups such as bryophytes, lichens, gymnosperms, and angiosperms. Additionally, editorials, commentaries, announcements, and letters to the editor have sparked debate, created other interactions among members of the Society, and demonstrated even further the important vehicle of communication that MADROÑO continues to be. The editors welcome all contributions and suggestions from authors and other members to help us maintain or improve the status of MADROÑO as an important botanical journal.—W.R.F. 14 Oct. 1986.

INDEX TO VOLUME 33

Classified entries: major subjects, key words, and results; botanical names and plant families (new names are in **boldface**); geographical areas; reviews; letters; commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state, or country. Authors and titles are listed alphabetically in the Table of Contents.

ANNOUNCEMENT

THE 1986 JESSE M. GREENMAN AWARD

The 1986 Jesse M. Greenman Award has been won by David H. Lorence for his publication "A Monograph of the Monimiaceae (Laurales) in the Malagasy Region (Southwest Indian Ocean)", which appeared in the *Annals of the Missouri Botanical Garden,* volume 72, number 1. The publication is derived from a Ph.D. dissertation from Washington University under the direction of Alwyn H. Gentry. This comprehensive account of fifty-five species, all endemic to the region, is based on herbarium and extensive fieldwork. It includes information on pollination syndromes in relation to floral morphology, cytological investigations, population biology,vernacular names, and economic uses.

The Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the *previous* year. Papers published during *1986* are now being considered for the 19th annual award, which will be presented in the summer of 1987. Reprints of such papers should be sent to: Greenman Award Committee, Department of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1987 award, reprints must be received by 1 July 1987.

CALIFORNIA BOTANICAL SOCIETY

SCHEDULE OF SPEAKERS

1986–1987

8:00 PM University of California, Berkeley LSB 2507**

DATE	SPEAKER & TOPIC
SEP 18	Ray Collett, Arboretum Director, UC Santa Cruz "Getting a garden off the ground (and how to make it different!)"
OCT 16	Tom Daniel, Botany Dept., Cal. Acad. of Sci. "Vegetation and Flora of Arizona"
NOV 20	Bob Patterson, Dept. of Biology, SF State Univ. "An evening with 'Flaxflowered Flaxflowers': evolutionary patterns in *Linanthus*"
JAN 15	Elizabeth Bell, Biology Board, UC Santa Cruz "Milkweeds and their Monarchs"
FEB 21*	Arturo Gomez-Pompa, Director, MEXUS Program, UC Riverside "Maya Vegetation Designs: studies from *Ethnoflora Yucatanense*"
MAR 19**	Jim Affolter, Botanical Garden, UC Berkeley "UC Berkeley Botanical Garden: an inside look at expanding collections and sources of new plants"
APR 16	Bruce Pavlik, Dept. of Biology, Mills College "Islands in a dry sea: sand dunes of the Great Basin and Mojave Deserts"
MAY 21**	Steve Junak, Santa Barbara Botanic Garden "Flora and vegetation of Santa Cruz Island"

* **Annual Banquet**—location to be announced.

** Except Mar 19 & May 21, at UC Berkeley Botanical Garden.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XXXIII
1986

Published quarterly by the
California Botanical Society, Inc.
Life Sciences Building, University of California, Berkeley 94720

Printed by Allen Press, Inc., Lawrence, KS 66044

We take great pleasure in dedicating Volume 33 of Madroño to Marion Stilwell Cave, an outstanding contributor to our knowledge of the embryology and cytology of Liliaceae and Agavaceae. As a long-time researcher in the Department of Botany and Botanical Garden, University of California, Berkeley, she has been a cytological collaborator in the taxonomy of the Hydrophyllaceae and Volvocales. She founded and, from 1956 to 1964, was editor of Index to Plant Chromosome Numbers, currently being published by Missouri Botanical Garden. Her paper, demonstrating that there is a free nuclear stage in embryo development in California species of *Paeonia,* was a botanical coup.

Through the years Marion has been, and still is, a generous and enthusiastic advisor, warm friend, and valued tutor to a succession of graduate students. She also has introduced them to photography and darkroom techniques, where, as in all things, she is a perfectionist. It is Marion who saw the need for a photographic record of staff and students in the Department and is responsible for our "rogues' gallery".

TABLE OF CONTENTS

Dates of publication of MADROÑO, volume 33

No. 1, pp. 1–84: 27 Mar 1986
No. 2, pp. 85–156: 30 May 1986
No. 3, pp. 157–236: 5 Sep 1986
No. 4, pp. 237–328: 23 Dec 1986

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals ($18 per year; students $10 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships ($20) include one ten-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available ($25). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to ⅔ original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted ten pages in MADROÑO each year or 20 pages over a two-year period. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of $60.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ $35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ $4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.

(*Continued from front cover*)

CALIFORNIA BOTANICAL SOCIETY