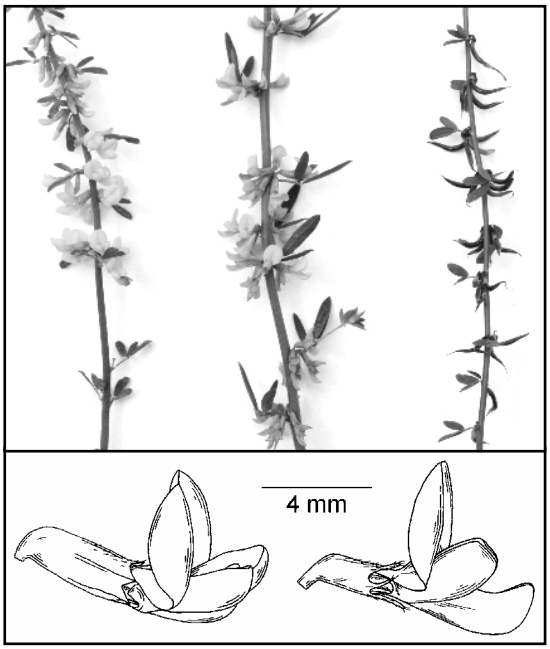
***Lotus scoparius* (Nutt.) Ottley** California broom
FABACEAE

Synonyms: *Hosackia scoparia* Nutt. in T. and G.
Syrmatium galbrum Vogel
Hosackia glaber Greene
Hosackia crassifolia Nutt., not Benth
Lotus glaber Greene, not Mill.



General Description.—California broom is a diverse and widely distributed subshrub (Munz and Keck 1968, Isely 1981, Hickman 1993). The Latin name "scoparius" refers to the broom-like form which is also evident in the common name "California broom." The other common name, "deerweed," refers to its use as browse by deer. Of five previously recognized subspecific taxa (Ottley 1923, Munz and Keck 1968), the three from the Channel Islands were reassigned to *L. dendroideus* (Greene) Greene by Isley (1981). His treatment of the genus recognizes two varieties of *Lotus scoparius* (*L. s*. var. *scoparius* and *L. s*. var. *brevialatus* Ottley) and has been adopted in Hickman (1993). In the former, the keel of the corolla is about as long as the wings and the calyx has broad triangular teeth (figure: top left and bottom left). In the latter, the keel is longer than the shortened wings and the calyx has narrow teeth (figure: top center and bottom right). The erect suffrutescent shrubs grow from 0.4 to 1.5 m tall but prostrate forms often occur along the coastal strand. A spreading, prostrate ecotype occurs on coastal sand dunes at Monterey Bay. The many flexible green branches arise from a woody base, and are mostly glabrous except toward tips. The soft, alternate leaves are pinnately compound with three (occasionally four to five) oblong to oblanceolate leaflets, usually 4 to 10 mm long with short, sparse, appressed hairs, and are subtended by small, gland-like stipules. The sessile, usually two- to seven-flowered, umbellate inflorescences are in the axils of leaves. The yellow pea-like flowers are 7 to 10 (occasionally to 15) mm long, have short pedicels, and sometimes bear a red splotch of varying intensity on the back of the banner. Depending on the plant, flowers fade to dark orange or red following pollination. Plants bear hundreds of inflorescences and are an attractive flag for native bees. The small indehiscent pods (figure: top right) bear one to two (rarely three) seeds that vary from brown to greenish brown with or without dark brown mottling. Seeds of var. *scoparius* are narrow bean-shaped, 1.2 - 2mm long. Seeds of var. *brevialatus* are narrower (ca. 3 x longer than wide). Both varieties have 2n = 14 chromosomes (Munz and Keck 1968, Grant 1995).

Range.—California broom occurs primarily after fire or in open areas of coastal sage scrub, chaparral, desert scrub, washes, coastal strand, or along roadsides. The var. *scoparius* is distributed in cismontane California below 1,500 m from Humboldt and Plumas Counties, south into Baja California, primarily in shrublands and associated open areas, and primarily in the coastal regions of California and north of Los Angeles. In addition to the distinct differences in floral form between the two varieties, there is variation in floral form within var. *scoparius* that is associated with coastal verses inland habitats from the Transverse Range of California, northward (author's observation). Variety *brevialatus* occurs from Los Angeles Co., south into Baja California primarily in the hotter and drier interior regions of Riverside, Los Angeles, western San Bernardino, and eastern San Diego Counties. Although the two varieties have somewhat different geographic distributions and are easily distinguished by floral characters (Isely 1981, Steppan 1991), they overlap and hybridize in some areas of Los Angeles, Riverside, and San Diego Counties. Putative hybrids have been observed in contact zones between the two varieties (Isely 1981, Steppan 1991, Montalvo

and Ellstrand 2001). Flowers of synthetic F1 hybrids are somewhat intermediate, but have wings as long as the keel. Many areas of overlap may be due to natural secondary contact, but some are clearly due to seeding projects along highways and utility corridors. The various floral forms are maintained when plants are grown from seed in a common environment (Montalvo and Ellstrand 2000, 2001).

Ecology.—In nature, seeds typically germinate after scarification by fire but some germinate in open, disturbed sites (Munz and Keck 1968, Keeley and Keeley 1984). Between 2 to 3 years after fire in sage scrub vegetation, following a burst of herbaceous species, California broom can become the dominant canopy species, eventually becoming replaced by long-lived shrub species. Its abundance gradually decreases in 5 to 10 years after fire. The branched tap root is relatively shallow (< 1 m), and roots form symbiotic associations with nitrogen fixing bacteria and arbuscular mycorrhizal fungi (author's observation). Plants are facultatively drought-deciduous, a trait commonly associated with shallow-rooted shrubs of coastal sage scrub vegetation in California. Seasonality of leaf production, nutrient accumulation, and leaf drop in response to summer drought has been studied extensively in *L. scoparius* var. *scoparius* (Nilsen and Muller 1980, 1981a,b, 1982, Nilsen and Schlesinger 1981, Nilsen 1982). Other researchers have examined response to photoperiod (Comstock and Ehleringer 1986).

Reproduction.—Seeds of California broom germinate in mid to late winter during the rainy season. Plants establish quickly with normal rainfall and typically reach flowering size the second year. Flowering occurs primarily from March to June but may start as early as January in warm, wet winters, and last much longer in more moist, coastal areas and in years with long-lasting soil moisture. Flowers are self-compatible and insect-pollinated (Moldenke 1976, Hickman 1993, Jones and Cruzan 1999) primarily by native bees in the genera *Bombus, Hoplitus, Anthophora, Habropoda*, *Osmia*, and *Anthidium*, but flowers are also visited by butterflies and non-native honeybees (author's observation, Jones and Cruzan 1999). The indehiscent pods ripen in about 4 to 6 weeks and are primarily passively dispersed short distances. The hard seeds require heat or mechanical scarification to break dormancy. Of several treatments including control, soil heated to 100 ^{o}C for 1 hr, ash /chemical fertilizer, and heat plus fertilizer, Christensen and Muller (1975) found that heat treatment yielded the highest germination. In addition, Keeley (1987) found that heating seeds in their pods to 120 ^{o}C for 5 minutes increased germination over that of unheated controls.

Genetics.—There are significant genetic differences among populations of the two varieties of California broom (Montalvo and Ellstrand 2000, 2001). An analysis of genetic marker data (13 allozyme loci) from three populations of var. *brevialatus* and nine populations of var. *scoparius* showed significant population substructure due primarily to differences among populations of the two varieties. In an analysis of all populations, 18 percent of the variation was due to differences among populations, while analysis of just var. *brevialatus* or var. *scoparius* populations showed only 1 and 8 percent of the variation due to differences among populations. Thus, populations within a variety are substantially more genetically similar to each other than to populations of the other variety. Inbreeding coefficients were low for all populations, a pattern consistent with substantial cross pollination, severe loss of inbred progeny, or both (mean f = 0.09, range = 0.00 – 0.18) (Montalvo, Clegg, and Ellstrand, manuscript in preparation).

There is also genetically based geographic variation in floral form in this species. In San Diego Co., Steppan (1991) detected distinct discontinuities in floral morphology between varieties and moderate correlations among environmental variables and floral traits of wild populations. Montalvo and Weaver (unpublished data) measured floral traits on 12 populations of plants raised in a common environment and made pairwise comparisons of genetic, floral, geographic, and environmental distances of source populations. Floral morphological distance correlated with environmental distance, genetic distance correlated with floral distance, but genetic distance did not correlate with geographic distance until var. *brevialatus* was removed from the analysis. Results were consistent with floral form having a genetic basis and with environmental factors playing a role in the evolution of floral divergence.

The substantial genetic differentiation of populations has implications for translocation of California broom for restoration. Common garden experiments testing plants originating from seed collected from 12 source populations (both varieties represented) demonstrated a significant home site advantage (Montalvo and Ellstrand 2000). Furthermore, Montalvo and Ellstrand (2001) directly tested the potential for "outbreeding depression," a loss of fitness upon crossing genetically differentiated populations, by crossing individuals from six populations of the two varieties in every combination and testing the progeny in two common gardens at wild sites. Seeds per flower and seedling emergence decreased significantly with an increase in genetic distance of the crossed parental populations. Among variety crosses were only 70 percent as fit as within

variety crosses by the time seedlings emerged, and further fitness differences accumulated after seedlings were outplanted into field plots. In these common gardens, success of progeny decreased with increasing differences between parental environments and the transplant location. Results indicate that careful attention should be given to the similarity of taxonomic position and environment of source populations relative to planting location, especially when choosing source populations for restoration, mitigation, and roadside landscaping.

Interspecific Hybridization.—Putative hybrids have been reported between California broom and *L. junceus* (Benth.) Greene and *L. benthamii* Green in central and northern California, as well as between other members of the species complex (Isely 1981), but there have not been any genetic studies confirming introgression. Liston and others (1990), however, did genetic studies on San Clemente Is. and documented hybridization between the rare *L. dendroideus* (Greene) Greene var. *traskiae* (Nodden) Isely, formally *L. scoparius* ssp. *traskiae* (Noddin) Raven, and the more widespread *L. argophyllus* (A. Gray) E. Greene var. *ornithopus* (E. Greene) Ottley. They concluded that genetic assimilation of the rare species by the widespread species is possible.

Growth and Management.—The small pods of California broom can be collected from May to July depending on location. Pods or cleaned seeds can be covered with boiling water and left to soak to break dormancy (Atwater 1980, Young and Young 1986, Emery 1988, Montalvo and Ellstrand 2000, 2001), or exposed to dry heat (Keeley 1987). Whole pods can be dry or wet broadcast in the fall for revegetation and restoration. Seedlings plugs can also be used for small projects. In greenhouse plantings, seeds germinate best when planted less than 2 mm deep (author's observation). Despite the strong geographic and morphological differences, the two varieties have been used indiscriminately in many seeding projects. Due to the adaptive differences and the observed outbreeding depression following hybridization, land managers should use the variety native to the planting location.

Benefits.—California broom is an important, fast growing, early successional species used extensively in erosion control, post-fire mitigation, and habitat restoration in California, especially in the rapidly disappearing coastal sage scrub. The flowers and seeds are an important food resource for a variety of insects and seed foraging rodents and birds (Duncan 1968). The plants provide valuable forage for deer, especially in drought years when growth of herbaceous vegetation is sparse (Dale 2000).

References

Atwater, B.R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. Seed Science and Technology 8: 523-573.

Christensen, N.L. and C.H. Muller. 1975. Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. The American Midland Naturalist 93: 71-78.

Comstock, J. and J.R. Ehleringer. 1986. Photoperiod and photosynthetic capacity in *Lotus scoparius*. Plant, Cell and Environment 9: 609-612.

Dale, N. 2000. Flowering Plants: The Santa Monica Mountains, Coastal and Chaparral Regions of Southern California. California Native Plant Society, Sacramento, CA. 240 p.

Duncan, D.A. 1968. Food of California quail on burned and unburned central California foothill rangeland. California Fish and Game 54: 123-127.

Emery, D.E. 1988. Seed propagation of native California Plants. Santa Barbara Botanical Garden, Santa Barbara, CA. 23 p.

Grant, W.F. 1995. A chromosome atlas and interspecific-intergenic index for *Lotus* and *Tetragonolobus* (Fabaceae). Canadian Journal of Botany 73: 1,787-1,809.

Hickman, J.C., ed. 1993. The Jepson Manual: Higher Plants of California. University of California Press, Ltd., Berkeley, CA. 1,400 p.

Isely, D. 1981. Leguminosae of the United States III subfamily Papilionoidae: tribes Sophoreae, Podalyrieae, Loteae. In: Memoirs of the New York Botanical Garden. Volume 25. The New York Botanical Garden, Bronx, NY. p. 127-191.

Jones, C.E. and M.B. Cruzan. 1999. Floral morphological changes and reproductive success in deer weed (*Lotus scoparius;* Fabaceae). American Journal of Botany 86: 273-277.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68:434-443.

Keeley, J.E. and S.C. Keeley. 1984. Postfire recovery of California coastal sage scrub. The American Midland Naturalist 111: 105-117.

Liston, A., L.H. Rieseberg, and O. Mistretta. 1990. Ribosomal DNA evidence for hybridization between island endemic species of *Lotus*. Biochemical Systematics and Ecology 18: 239-244.

Moldenke, A.R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305-361.

Montalvo, A.M. and N.C. Ellstrand. 2000. Transplantation of the subshrub *Lotus scoparius*: testing the home site advantage hypothesis. Conservation Biology 14: 1034-1045.

Montalvo, A.M. and N.C. Ellstrand. 2001. Non-local transplantation and outbreeding depression in the subshrub *Lotus scoparius* (Fabaceae). American Journal of Botany 88: 258-259.

Munz, P.A. and D.D. Keck. 1968. A California Flora with Supplement. University of California Press, Berkeley, CA. 1,681 + 224 p.

Nilsen, E.T. 1982. Productivity and nutrient cycling in the early postburn chaparral species *Lotus scoparius*. In: C. E. Conrad and W. C. Oechel, eds. General Technical Report PSW-58. Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, Berkeley, CA. p. 291-296.

Nilsen, E.T. and W.H. Muller. 1980. An evaluation of summer deciduosness in *Lotus scoparius* (Nutt.) T.& G. The American Midland Naturalist 103: 88-95.

Nilsen, E.T. and W.H. Muller. 1981a. The influence of low plant water potential on the growth and nitrogen metabolism of the native California fire response shrub *Lotus scoparius*. American Journal of Botany 68: 402-407.

Nilsen, E.T. and W.H. Muller. 1981b. Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. Ecological Monographs 51: 323-341.

Nilsen, E.T. and W.H. Muller. 1982. The influence of photoperiod on drought induction of dormancy in *Lotus scoparius*. Oecologia 53: 79-83.

Nilsen, E.T. and W.H. Schlesinger. 1981. Phenology, productivity, and nutrient accumulation in the post-fire chaparral shrub *Lotus scoparius*. Oecologia 50: 217-224.

Ottley, A.M. 1923. A revision of the Californian Species of *Lotus*. University of California Publication in Botany, Berkeley, CA. 10: 189-305.

Steppan, S.J. 1991. Geographic distribution of flower morphological traits in subspecies of *Lotus scoparius*. Journal of Biogeography 18: 321-331.

Young, J.A. and C.G. Young. 1986. Collecting, Processing, and Germinating Seeds of Wildland Plants. Timber Press, Portland, OR. 236 p.

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