

***Salvia mellifera* Greene**
LAMIACEAE

black sage

Synonyms: *Audibertia stachyoides* Benth.
Ramona stachyoides Briq.
Audibertiella stachyoides Briq.



General Description.—Black sage has a dark appearance, especially during drought. *Salvia* is derived from the Latin word for safe and refers to the medicinal properties of sages. The specific epithet “*mellifera*” means “honey producing” and refers to its use by nectar foraging bees. Shrubs are open, 1 to 2 m tall with twisted, furrowed woody stems at the base, and herbaceous greenish branch tips that are square in cross section. Twigs and leaves are glandular, highly aromatic, and opposite. The oblong-elliptical blades are 2 to 6 cm long, dark green and rugulose above (convex between obvious veins) with crenulate (finely scalloped) margins, and taper to a few to 12 mm long petiole (Munz and Keck 1968). Many small, 6- to 12-mm long, two-lipped flowers occur in compact clusters subtended by green bracts and are spaced 2 to 6 cm apart along the often branched inflorescence. Corollas vary from pure white to pale blue or lavender. The style and stamens extend just beyond the corolla tube. Flowers bear four oblong nutlets (single-seeded fruits) within a persistent calyx. Nutlets vary from mottled gray to dark brown and are about 1 mm wide and 2 mm long.

Range.—Black sage occurs on dry slopes and alluvial fans within interior and coastal sage scrub and lower montane chaparral from sea level to 1,200 m, ranging from Contra Costa County, CA (near San Francisco) south to northern Baja California (Munz and Keck 1968, Hickman 1993). On leeward slopes of the Coast Ranges it extends into desert scrub (Keeley 1986). It is one of the dominant shrubs of sage scrub (Westman 1983), and can form dense, nearly monospecific stands on steep slopes.

Ecology.—Black sage occurs on a variety of soils derived from sandstone, shale, granite, and especially serpentinite, and gabbro basalt (Westman 1981). Plants produce numerous volatile compounds, including camphor, cineole, terpenes, and sesquiterpenes (Neisess and others 1987, Gonzalez and others 1992, Arey and others 1995), which may be important in herbivore or pathogen defense.

Black sage is semideciduous, depending on site and severity of drought, and shallow rooted. Plants are drought tolerant by leaf curling rather than drought avoiding through leaf drop (Gill and Hanlon 1998). Leaf drop is drought induced possibly due to embolisms that occur in xylem tissues (Kolb and Davis 1994). At Stanford, CA, leaves began to senesce and drop in October in both irrigated and unirrigated treatments, leaf stomata did not control transpiration when xylem water potentials were low, and rates of photosynthesis did not decline until after leaf drop (Gigon 1979). In Santa Barbara County, CA, most leaves senesced between May and July, 32 percent persisted into the following growing season, leaf curling and uncurling was related to water stress, and leaf drop was more related to photoperiod than to low xylem potentials (Gill and Mahal 1986).

Reproduction.—The timing of growth and flowering is closely adapted to the Mediterranean climate of southern California, with cool wet winters and hot dry summers (Grant and Grant 1964, Gill and Mahall 1986). Common garden studies with 12 populations revealed that date of first flowering varies with source population and ranged from early February to early May (Montalvo, unpublished data). Also, shifts in

flowering time occur in years with contrasting rainfall patterns (Meyn and Emboden 1987).

The self-compatible flowers are hermaphroditic with stamens dispersing pollen before stigmas are receptive. Flowers are pollinated by small to medium-sized solitary bees in families Andrenidae, Anthophoridae, Halictidae, Megachilidae, and Xylocopinae as well as introduced honey bees (Grant and Grant 1964). Rarer visitors include large-bodied *Bombus* and *Xylocopa* bees, syrphid and bombyliid flies, and Anna's hummingbirds. Each flower produces up to four seeds that are gravity dispersed in June and July from the dry, persistent calyces, and can be secondarily dispersed by ants. Seeds accumulate in a dormant seed bank (Keeley 1986).

Establishment and Growth.—Black sage occurs in plant communities adapted to fire and drought. Seedlings emerge in clearings between adult shrubs, but most emerge in the first 2 years following fire, primarily from February to April (Keeley 1986, Westman and O'Leary 1986). Plants take two or more growing seasons to reach maturity. After fire, plants sometimes resprout from the base (Went and others 1952, Keeley 1986, 1998). However, where fire intensity is high, shrubs tend to be killed, and recruitment is primarily by seed. Across a range of conditions, resprouting success averaged 15.8 percent, and shrubs that resprouted had significantly smaller basal diameters, suggesting resprouting decreases with age (Keeley 1998). The seasonal pattern of growth and dormancy varies both geographically and between years. Generally, seasonal growth begins after the start of fall rains, most new leaves are produced by mid March, and flowering occurs from late winter to late spring.

Roots are colonized by arbuscular mycorrhizal (AM) fungi. After 4 months of growth in a greenhouse, root and shoot mass was higher in seedlings inoculated with AM fungi than in controls, but in younger plants the opposite occurred (E. Allen, L. Egerton-Warburton, A. Montalvo, unpublished report).

Seed germination.—Seeds of black sage often have low germination rates unless exposed to light or components of fire such as charred wood, smoke, or KNO_3 (Keeley 1986, Thanos and Rundel 1995, Keeley and Fotheringham 1998). Exposure to dry cool smoke for 5 min (Keeley and Fotheringham 1998) yields higher germination than charred wood. A 12 to 15 hour soak in a 1:25 dilution of Regen 2000 Smokemaster, a liquid smoke product, also breaks dormancy (author's observation). Heat of fire may reduce germination of seeds from sage scrub populations (Keeley and Fotheringham 1998). Oddly, seeds from desert

populations, where fires are less frequent, were stimulated to germinate by heat and charred wood, but not by light (Keeley 1986).

Genetics, Geographic Variation, and Fitness.—Black sage is genetically variable over its geographic range. In a survey of 12 populations (Montalvo, Clegg, and Ellstrand unpublished, 14 allozyme loci), expected heterozygosity was high ($H_e = 0.23$) and alleles averaged 2.81 per locus. Within sites, a low inbreeding coefficient ($f = 0.072$) suggests the protandrous flowers and pollinators combine to promote outcrossing. There is significant but low structure both among and within populations, and results are consistent with a relatively high level of historical gene flow (Theta-p ($\sim F_{ST}$, sites relative to total population) = 0.041; Theta-s (plots relative to sites) = 0.057; and $F(F_{IT}) = 0.125$).

Populations cluster by genetic similarity, and geographic floristic associations and this is somewhat mirrored by distribution patterns of morphological variation and timing of flowering. Flowers from populations in the Santa Monica Mountains and Simi Hills can be strikingly bluish. In the drier, more interior hills and valleys of Riverside Co., flowers tend to be white to pale blue or lavender, and plants flower earlier. These differences are retained in common gardens. Differences in timing of flowering could affect seed production of translocated populations if pollinator activity, seed predation, or important physical environmental factors differ from home sites. Plants from contrasting populations also smell different, likely due to differences in composition of volatile chemicals. Such differences among populations may be adaptive and contribute to their success under particular environments. Montalvo and Ellstrand (unpublished) evaluated seedling survival, growth and reproduction of 12 populations in a common garden. A combination of climatic data and soil traits was used to calculate environmental similarity among garden and source sites. After three growing seasons, populations from sources most similar to the garden site were the most successful (measured as survival x flower production). This effect was small ($r^2 = 0.18$) but is consistent with the presence of weak adaptive differences among source populations.

Hybridization.—Black sage hybridizes with the shrubs *S. apiana* Jeps. ($n = 15$), *S. leucophylla* Greene ($2n = 30$), and *S. clevelandii* (Gray) Greene ($2n = 30$), and rarely with annuals *S. columbariae* Benth ($n = 13$) and *S. carduacea* Benth ($n = 16$) (Epling 1938, 1947a, Epling and others 1962, Munz and Keck 1968). Most hybridization is with *S. apiana*. These hybrids are fully viable but suffer reduced pollen fertility (Epling 1947a, Meyn and Emboden 1987) and numbers of

seeds/flower in F1 back crosses to parental species (Grant and Grant 1964). Hybrids differ from both parental species by a range of intermediate floral, leaf, and anatomical traits (Epling 1947a, b, Anderson and Anderson 1954, Webb and Carlquist 1964). Most are thought to be F1s or backcrosses to *S. mellifera* and tend to grow near parental types. Hybrid zones can be stable in position but may shift in morphology (Meyn and Emboden 1985). This suggests differences in the relative success of hybrids and backcrossed progeny over time. The influence of gene exchange on floral form of black sage does not appear to extend beyond hybrid zones (Epling 1947a, b).

Several authors have speculated on the factors promoting hybridization while also maintaining black and white sage as distinct species. While ranges overlap in most of southern California, *S. apiana* is not found north of Santa Barbara County and it ranges farther south into Baja California and eastward. In areas of contact, *S. mellifera* tends to occur in flatter and wetter microsites, while *S. apiana* occurs on drier slopes (Epling 1947a, Anderson and Anderson 1954, Grant and Grant 1964, Meyn and Emboden 1987, Gill and Hanlon 1998). Hybrids also occur in recently disturbed areas, suggesting that hybrids are adapted to intermediate habitats (Anderson and Anderson 1954, Meyn and Emboden 1987). Within a hybrid zone, Gill and Hanlon (1998) found that xylem pressure potential was significantly higher in white than in black sage and that putative hybrids were intermediate to the two parental species. These data support that *S. apiana* is more drought adapted than *S. mellifera*, and that the hybrids are intermediate. In addition, reproductive isolation is favored by flowering differences. *S. apiana* flowers later than black sage, limiting opportunities to hybridize (Grant and Grant 1964). In addition, white sage has larger, highly modified flowers that are pollinated almost exclusively by large bees in *Xylocopa* and *Bombus*. Black sage has smaller, two-lipped flowers that are rarely visited by these large-bodied bees.

Growth and Management.—Seeds are collected from June-August and should be cleaned to remove seed predators. Air separation can be used to remove lighter unfilled seeds that are sometimes abundant. There are about 1,375,000 seeds/bulk kg (personal communication with Victor Schaff, S&S Seeds, Carpinteria, CA). Treatment of seeds with dry or liquid smoke increases germination substantially. Seeds should be air-dried before handling. Plants can be sown in flats for subsequent transplanting or directly sown into the ground in the fall. Plants can be started from cuttings, but this should be avoided for restoration because it reduces genetic variation. Prostrate cultivars (e.g., Clebsch 1997) should not be used in restoration.

Black sage grows in well-drained soil and can tolerate some summer water in a garden.

Benefits.—Black sage is important for restoration, erosion control, and native landscape gardening in California. Plants provide cover and seeds for wildlife, and in western Riverside Co. the listed California gnatcatcher frequently nests in vegetation containing black sage (Weaver 1998). The seeds were eaten and the leaves used for flavoring by native California tribes (Bean and Saubel 1972). In addition, the leaves have a long history of medicinal use by native tribes (Bocek 1984). Their diterpene compounds have antimicrobial activity against gram (+) bacteria (Moujir and others 1996).

Decreasing Populations.—Black sage populations are declining. Increased ignition sources and invasion of shrublands by annual grasses have increased fire frequency, jeopardizing recovery of seed banks (Westman and O'Leary 1986, Haidinger and Keeley 1993, Minnich and Dezzani 1998). Black sage is also inhibited by exotic annual grasses, black mustard (Went and others 1952, Storms 1999), and air pollution (Westman 1985, Preston 1988).

References

- Anderson, E. and B. R. Anderson. 1954. Introgression of *Salvia apiana* and *Salvia mellifera*. *Annals of the Missouri Botanical Garden* 41: 329-338.
- Arey, J., D.E. Crowley, M. Crowley, M. Resketo, and J. Lester. 1995. Hydrocarbon emissions from natural vegetation in California's south coast air basin. *Atmospheric Environment* 29: 2,977-2,988.
- Bean, J. and K. Saubel. 1972. *Temalpakh: Cahuilla Indian knowledge and usage of plants*. Malki Museum Press, Morongo Indian Reservation, CA. 225 p.
- Bocek, B. 1984. Ethnobotany of Costanoan Indians, California, based on collections by John P. Harrington. *Economic Botany* 38: 240-255.
- Clebsch, B. 1997. *A Book of Salvias: Sages for Every Garden*. Timber Press, Portland, OR. 221 p.
- Epling, C. 1938. The California salvias. *Annals of the Missouri Botanical Garden* 25: 95-188.

- Epling, C. 1947a. The genetic aspects of natural populations: actual and potential gene flow in natural populations. *The American Naturalist* 81: 104-113.
- Epling, C. 1947b. Natural hybridization of *Salvia apiana* and *S. mellifera*. *Evolution* 1: 69-78.
- Epling, C., H. Lewis, and P.H. Raven. 1962. Chromosomes of *Salvia*: section *Audibertia*. *Aliso* 5: 217-221.
- Gigon, A. 1979. CO₂-gas exchange, water relations and convergence of Mediterranean shrub-types from California and Chile. *Oecologia Plantarum* 14: 129-150.
- Gill, D.S. and B.J. Hanlon. 1998. Water potentials of *Salvia apiana*, *S. mellifera* (Lamiaceae), and their hybrids in the coastal sage scrub of southern California. *Madroño* 45: 141-145.
- Gill, D.S. and B.E. Mahall. 1986. Quantitative phenology and water relations of an evergreen and deciduous chaparral shrub. *Ecological Monographs* 56: 127-143.
- González, A.G., L.S. Andrés, Z.E. Aguiar, and J.G. Luis. 1992. Diterpenes from *Salvia mellifera* and their biogenetic significance. *Phytochemistry* 31(4): 1,297-1,305.
- Grant, K.A. and V. Grant. 1964. Mechanical isolation of *Salvia apiana* and *Salvia mellifera* (Labiatae). *Evolution* 18: 196-212.
- Haidinger, T.L. and J.E. Keeley. 1993. Role of high fire frequency in destruction of mixed chaparral. *Madroño* 40: 141-147.
- Hickman, J.C., editor. 1993. *The Jepson Manual: Higher Plants of California*. University of California Press, Ltd., Los Angeles, CA. 1,400 p.
- Keeley, J.E. 1986. Seed germination patterns of *Salvia mellifera* in fire-prone environments. *Oecologia* 71: 1-5.
- Keeley, J.E. 1998. Postfire ecosystem recovery and management: The October 1993 large fire episode in California. In: J. M. Moreno, ed. *Large Forest Fires*. Backbuys, Leiden, The Netherlands. p. 69-90.
- Keeley, J.E. and C.J. Fotheringham. 1998. Smoke-induced seed germination in California chaparral. *Ecology* 79: 2,320-2,336.
- Kolb, K.J. and S.D. Davis. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* 75: 648-659.
- Meyn, O. and W.A. Emboden. 1987. Parameters and consequences of introgression in *Salvia apiana* X *S. mellifera* (Lamiaceae). *Systematic Botany* 12: 390-399.
- Minnich, R.A. and R.J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris plane, California. *Western Birds* 29: 366-391.
- Moujir, L., A.M. Gutiérrez-Navarro, L. San Andres, and J.G. Luis. 1996. Bioactive diterpenoids isolated from *Salvia mellifera*. *Phytotherapy Research* 10: 172-174.
- Munz, P.A. and D.D. Keck. 1968. *A California Flora with Supplement*. University of California Press, Berkeley, CA. 1,681 + 224 p.
- Neisess, K.R., R.W. Scora, and J. Kumamoto. 1987. Volatile leaf oils of California *Salvias*. *Journal of Natural Products* 50: 515-517.
- Preston, K.P. 1988. Effects of sulphur dioxide pollution on a Californian coastal sage scrub community. *Environmental Pollution* 51: 179-195.
- Storms, N. 1999. Restoration of a native shrubland in an area of frequent disturbance and high nitrogen deposition. Master of Science in Botany Thesis. University of California, Riverside. 60 p.

Thanos, C.A. and P.W. Rundel. 1995. Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* 83: 207-216.

Weaver, K.L. 1998. Coastal sage scrub variations of San Diego County and their influence on the distribution of the California gnatcatcher. *Western Birds* 29: 392-405.

Webb, A.-A. and S. Carlquist. 1964. Leaf anatomy as an indicator of *Salvia apiana-mellifera* introgression. *Aliso* 5: 437-449.

Went, F.W., G. Juhren, and M.C. Juhren. 1952. Fire and biotic factors affecting germination. *Ecology* 33: 351-364.

Westman, W.E. 1981. Factors influencing the distribution of species of California coastal sage scrub. *Ecology* 62: 439-455.

Westman, W.E. 1983. Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. *Vegetatio* 52: 3-19.

Westman, W.E. 1985. Air pollution injury to coastal sage scrub in the Santa Monica Mountains, southern California. *Water, Air, and Soil Pollution* 26: 19-41.

Westman, W.E. and J.F. O'Leary. 1986. Measures of resilience: the response of coastal sage scrub to fire. *Vegetatio* 65: 179-189.

Arlee M. Montalvo. Plant Population Biologist, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124 and Paul A. McMillan. Coordinator, Biology Department, Capilano College, 2055 Purcell Way, North Vancouver, British Columbia, Canada V7J 3H5