***Encelia farinosa* Gray ex Torr.** brittlebush
ASTERACEAE

Synonyms: none

General Description.—Brittlebush, a dry environment-adapted shrub with weak branches, is also known as incienso because it has fragrant resin, and as desert encelia because it occurs in desert and semidesert habitats. The specific epithet *farinosa* refers to the mealy pubescence of the leaves, which is composed of appressed wooly hairs. These shrubs have dense rounded canopies with alternate whitish to greenish-gray leaves clustered near stem tips. Adults are 0.3 to 1.5 m tall, shallowly rooted (40 cm), with one to several many-branched stems. Leaves are simple, 3 to 8 cm long, ovate to rhombic in outline, with wavy margins, and short petioles. Heads are arranged in loose, naked panicles and have both disk and ray flowers subtended by green, glandular bracts that embrace the flat, obovate, 4.5 mm long achenes. Involucre bracts are imbricate in three to four series. Disk florets are yellow or rich purple and are surrounded by 8 to 12 mm long yellow ray florets (Munz and Keck 1968, Hickman 1993). Munz and Keck (1968) recognize two varieties: *E. f.* var. *radians* Bdg. ex Blake from southeastern California with glabrate leaves and involucre and yellow disk flowers, and *E. f.* var. *phenocodonta* (Blake) Jtn. from the southern Colorado desert with purple disk flowers. Plants have n = 18 chromosomes (Hickman 1993). Brittlebush hybridizes readily with *E. fructescens* (A. Gray) A. Gray, *E. californica* Nutt. and *E. actoni* Elmer (Ehleringer and Clark 1988, Hickman 1993). Intergeneric hybrids with the annual *Gerea canescens* T. & G. have also been reported (Kyhos 1967).

Range.—Brittlebush occurs within sage scrub of the inland valleys of southern California, eastward and southward into arid habitats of the Sonoran and Mojave deserts and into Arizona, northwestern Mexico, southern Nevada, and southwestern Utah at under 1,000 m elevation (Munz and Keck 1968, Hickman 1993, Sandquist and Ehleringer 1997). In California, it has been extending westward and northward due to roadside and other plantings.

Geographic Variation.—Geographic variation and adaptation to local environments have been documented for many brittlebush traits. In particular, adaptation to water availability has been well demonstrated, including genetic differentiation in water use efficiency (Sandquist and Ehleringer 2003). Also, individuals with brown-purple disk florets (var. *phenicodonta*) occur in areas with higher levels of soil moisture and are replaced by the yellow-disked form (var. *farinosa*) in drier sites. This pattern may involve natural selection in response to water availability (Kyhos 1971) but may also be linked to the lower frost tolerance of var. *phenicodonta* (Sandquist and Ehleringer 1996). Similarly, Monson and others (1992) found localized physiological and genotypic differences in water use between plants at the base and the top of a slope that coincided with a moisture stress gradient.

The degree of leaf pubescence varies across regions with different mean annual rainfall, and variation in number of leaf hairs is both a plastic response and genetically determined. Leaves of plants growing in arid regions are more pubescent, thereby having greater control over leaf temperature and water loss, but they have lower photosynthetic capacity due to higher reflectance of light than plants from more mesic regions. Differences are maintained when offspring are planted together in common gardens (Sandquist and Ehleringer 1997, Housman and others 2002). However, an additional plastic response allows plants in more mesic gardens to grow less-pubescent leaves than sibling plants in desert gardens, a response which allows plants to take advantage of higher water availability and increased photosynthetic ability through leaf-hair reduction (Ehleringer and Clark 1988). The inverse relationship for leaf pubescence and photosynthetic activity may involve pleiotropy or linkage to other genetically determined morphological differences between populations or from environments

with different moisture regimes (Housman and others 2002).

There is also clinal variation in production of chemical compounds that provide defense against herbivores. From north to south in Baja California and east to west from the Sonoran desert to coastal regions of California, plants produce progressively less of a sequiterpene and more of a chromene toxin, which may influence local resistance to herbivores (Wisdom 1985, Kunze and others 1995). Seasonal production of these compounds may also influence herbivores (Wisdom and Rodriquez 1983). There are higher concentrations of these chemicals and nitrogen in young tissues. In addition, populations differ in the relative amount of different compounds. The specialist beetle *Trirhabda geminata* Horn experienced lowered larval growth rates when fed higher levels of the secondary compounds.

Ecology.—In sage scrub, brittlebush occurs on flats and slopes, primarily on weathered sandstone, granite, diorite, and alluvial deposits; in the desert it occurs on rocky slopes, flats, and in washes (Munz and Keck 1968, Hickman 1993). Studies on the adaptive significance of variation in leaf form and pubescence both within and among populations is reviewed by Housman and others (2002) and by Sandquist and Ehleringer (1997, 1998). Plants react to seasonal increase in water stress at the end of the rainy season by replacing the larger, less hairy leaves produced earlier in the growing season with more pubescent leaves that are smaller and thicker. This reduces water loss and regulates leaf temperature, but it also decreases photosynthetic capacity. Prolonged drought leads to dormancy and leaf drop.

Brittlebush shows variation among individuals and populations in water-use efficiency (the ratio of photosynthesis to transpiration, or delta value). Individuals with a high delta have a higher growth response if water stress is decreased but perform poorly in response to drought stress, while those with a low delta show lower growth response under low water stress and a greater capacity to survive drought conditions (Ehleringer 1993). In general, however, brittlebush is drought adapted and responds quickly to water addition through rapid CO_2 uptake, leaf production, and stem growth (Nobel and others 1998).

Reproduction.—Brittlebush flowers from March through May (Munz and Keck 1968) and individuals must be cross-pollinated in order to produce seed (Ehleringer and Clark 1988). Flowers are visited by various insects including butterflies, moths, flies, bees, wasps, and beetles (Kyhos 1971, Moldenke 1976). In one study, a beetle (Malachiidae) was found to be 10 times more common than all other insect species combined (Kyhos 1971). These potential pollinators do not discriminate between plants with different disk-flower color (Kyhos 1971). Achenes are collected from May to July (Mirov and Kraebel 1939) with about 770,000 bulk seeds/kg (personal communication with S&S seeds, Carpenteria, CA). Seed viability varies among years, with as few as 35 percent of seeds viable (personal communication with M. Wall, Rancho Santa Ana Botanical Garden, Claremont, CA). Seed production is influenced by water stress heightened by competition. In a desert study in which nearby neighbors were removed, shrubs experienced lower water stress, had higher survival, grew to nearly twice the mass, and produced 53 percent more flower heads per twig and 220 percent more achenes per head than shrubs with brittlebush neighbors within 2 m (Ehleringer 1984).

Establishment and Growth.—Brittlebush becomes established rapidly following disturbance. Seedlings emerge and become established in open areas in the winter rainy season. Plants become dormant and drop many leaves during the dry season and then sprout new leaves with the onset of winter rains. Plants can reach maturity within 2 years and often live for 10 to 15 years. In sage scrub vegetation, resprouting success of shrubs from the base is inversely related to fire intensity (Westman and others 1981, Martin 1984). In one study, 2 to 30 percent of brittlebush resprouted on slopes previously dominated by the shrub, and resprouts and seedlings surpassed prefire densities within 2 years (Martin 1984). For coastal sage scrub in general, both resprouting and seedling emergence from a soil seed bank are negatively correlated with fire intensity (Keeley 1998).

Seed germination.—Some authors report seed germination without pretreatment (Mirov and Kraebel 1939, Emery 1988), but pretreatment can increase otherwise low germination rates. Padgett and others (1999) found that seed stored for 6 months at room temperature had 2 to 4 percent germination while seed stored at 5 to 10 ^{o}C in a refrigerator had 10 to 12 percent germination. In addition, treatment with gibberelic acid or $Ca(NO_3)_2$ increased germination of both warm- and cold-stored seeds approximately two-fold, and leaching with water for several days increased germination by about 50 percent.

Growth and Management.—Maximum growth of roots occurs in the winter and early spring (Drennan and Nobel 1996), so plants will establish best if sown in late fall. Planting brittlebush seeds can yield vegetative cover and visual appeal relatively quickly. However, seed mixtures should be balanced carefully because overuse can retard establishment of other species (Went 1942, Gray and Bonner 1948). Ample

evidence for local adaptation in this species underscores the need to collect seed material for wildland restoration from within the same ecological zone and vegetation type as the targeted planting site so as to maximize success of planting projects. Because of potential competition and hybridization, it is also important that correct native species are specified and used. Mistaken plantings of *E. californica* instead of brittlebush, or vice versa, abound (authors' observation), and hybrids between species have been found in such locations (personal communication with A. Sanders, University of California, Riverside). Improper seed choices can compromise the success of restoration efforts and the genetic integrity of wild populations.

Benefits.—Brittlebush was used by native tribes for medicinal and other purposes. The resinous gum, heated or made into a salve, was applied to the chest to relieve pain and loosen bronchial mucous. A decoction of boiled blossoms, leaves, and stems was held in the mouth to relieve gum and tooth ache (Bean and Saubel 1972, Moore 1989). In addition, tea made from the gum has a numbing effect and was used to relieve arthritic pain (Moore 1989). The resin was also burnt as incense or melted and used as a varnish (Moore 1989, Hickman 1993).

Brittlebush feeds numerous pollinators and herbivores. It is an important nectar and pollen source of the bee, *Calliopsis pugionis* Cockerell, which is the host of the rare cleptoparasitic bee, *Holcopasites ruthae* Cooper in Riverside County, CA (Visscher and Danforth 1993). Mountain sheep eat brittlebush, but it is only found in fecal pellets in spring, summer, and fall in trace amounts (Perry and others 1987). The dominant herbivores on brittlebush leaves are the larvae and adults of the beetle, *Trirhabda geminata* (Wisdom 1985). The fly *Neotephritis finalis* Loew lays its eggs between the florets, and the larvae feed on the achenes (Goeden and others 1987).

Horticulture.—Brittlebush does best with full sun and good drainage (Hickman 1993, Keator 1994). The rounded form with striking yellow flowers is attractive near the back of borders or rock gardens, and it is especially suitable on dry slopes (Perry 1992, Keator 1994). Plants can be established quickly from seed or containers (Perry 1992). Provision of occasional summer water allows plants to remain attractive throughout the year (Keator 1994).

References

Bean, J.L. and K.S. Saubel. 1972. Temalpakh: Cahuilla Indian Knowledge and Usage of Plants. Malki Museum Press, Morongo Indian Reservation, CA. 225 p.

Drennan, P.M. and P.S. Nobel. 1996. Temperature influences on root growth for *Encelia farinosa* (Asteraceae), *Pleuraphis rigida* (Poaceae), and *Agave deserti* (Agavaceae) under current and doubled CO_2 concentrations. American Journal of Botany 83: 133-139.

Ehleringer, J.R. 1984. Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinosa*. Oecologia 63: 153-158.

Ehleringer, J.R. 1993. Variation in leaf carbon isotope discrimination in *Encelia farinosa*: implications for growth, competition, and drought survival. Oecologia 95: 340-346.

Ehleringer, J.R. and C. Clark. 1988. Evolution and adaptation in *Encelia* (Asteraceae). In: L. Gottlieb, L. Jain and S. Jain, eds. Plant Evolutionary Biology. Chapman and Hall, London. p. 221-248.

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

Goeden, R.D., T.D. Cadatal, and G.A. Cavender. 1987. Life history of *Neotephritis finalis* (Loew) on native Asteraceae in southern California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 89: 552-558.

Gray, R. and J. Bonner. 1948. An inhibitor of plant growth from the leaves of *Encelia farinosa*. American Journal of Botany 35: 52-57.

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

Housman, D.C., M.V. Price, and R.A. Redak. 2002. Architecture of coastal and desert *Encelia farinosa* (Asteraceae): consequences of plastic and heritable variation in leaf characters. American Journal of Botany 89: 1,303-1,310.

Keator, G. 1994. Complete garden guide to the native shrubs of California. Chronicle Books, San Francisco, CA. 314 p.

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 Publishers, Leiden, Netherlands. p. 69-90.

Kunze, A., C. Muller, and P. Proksch. 1995. Chemical variation and defense of *Encelia farinosa*. Biochemical Systematics and Ecology 23: 355-363.

Kyhos, D.W. 1967. Natural hybridization between *Encelia* and *Geraea* (Compositae) and some related experimental investigations. Madroño 19: 33-43.

Kyhos, D.W. 1971. Evidence of different adaptations of flower color variants of *Encelia farinosa* (Compositae). Madroño 21: 49-61.

Martin, B.D. 1984. Influence of slope aspect on postfire reproduction of *Encelia farinosa* (Asteraceae). Madroño 31: 187-189.

Mirov, N.T. and C.J. Kraebel. 1939. Collecting and handling seeds of wild plants. Forestry Publication 5. Civilian Conservation Corps, United States Government Printing Office, Washington, D.C.

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

Monson, R.K., S.D. Smith, J.L. Gehring, W.D. Bowman, and S.R. Szarek. 1992. Physiological differentiation within an *Encelia farinosa* population along a short topographic gradient in the Sonoran Desert. Functional Ecology 6: 751-759.

Moore, M. 1989. Medicinal Plants of the Desert and Canyon West. Museum of New Mexico Press, Santa Fe, NM. 184 p.

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

Nobel, P.S., H. Zhang, R. Sharifi, M. Castañeda, and B. Greenhouse. 1998. Leaf expansion, net CO_2 uptake, rubisco activity, and efficiency of long-term biomass gain for the common desert subshrub *Encelia farinosa*. Photosynthesis Research 56: 67-73.

Padgett, P.E., L. Vázquez, and E.B. Allen. 1999. Seed viability and germination behavior of the desert shrub *Encelia farinosa* Torrey & A. Grey (Compositae). Madroño 46: 126-133.

Perry, B. 1992. Landscape Plants for Western Regions: an Illustrated Guide to Plants for Water Conservation. Land Design Publishing, Claremont, CA. 318 p.

Perry, W.M., J.W. Dole, and S.A. Holl. 1987. Analysis of the diets of mountain sheep from the San Gabriel Mountains, California. California Fish and Game 73: 156-162.

Sandquist, D.R. and J.R. Ehleringer. 1996. Potential adaptability and constraints of response to the changing climates for *Encelia farinosa* var. *phenicondonta* from southern Baja California, Mexico. Madroño 43: 465-478.

Sandquist, D.R. and J.R. Ehleringer. 1997. Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa* associated with contrasting desert environments. New Phytologist 135: 635-644.

Sandquist, D.R. and J.R. Ehleringer. 1998. Intraspecific variation of drought adaptation in brittlebush: Leaf pubescense and timing of leaf loss vary with rainfall. Oecologia 113: 162-169.

Sandquist, D.R. and J.R. Ehleringer. 2003. Carbon isotope discrimination differences within and between contrasting populations of *Encelia farinosa* raised under common-environmental conditions. Oecologia 134: 463-470.

Visscher, P.K. and B.N. Danforth. 1993. Biology of *Calliopsis pugionis* (Hymenoptera: Andrenidae): nesting, foraging, and investment sex ratio. Annals of the Entomological Society of America 86: 822-832.

Went, F.W. 1942. The dependence of certain annual plants on shrubs in southern California deserts. Bulletin of the Torrey Botanical Club 69: 100-114.

Westman, W.E., J.F. O'Leary, and G.P. Malanson. 1981. The effects of fire intensity, aspect and substrate on post-fire growth of California coastal sage scrub. In: N.S. Margaris and H.A. Mooney, eds. Components of Productivity of Mediterranean-Climate Regions: Basic and Applied Aspects. W. Junk Publishers, Boston, MA. p. 151-179.

Wisdom, C.S. 1985. Use of chemical variation and predation as plant defenses by *Encelia farinosa* against a specialist herbivore. Journal of Chemical Ecology 11: 1,553-1,565.

Wisdom, C.S. and E. Rodriguez. 1983. Seasonal age-specific measurements of the sesquiterpene lactones and chromenes of *Encelia farinosa*. Biochemical Systematics and Ecology 11: 345-352.

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