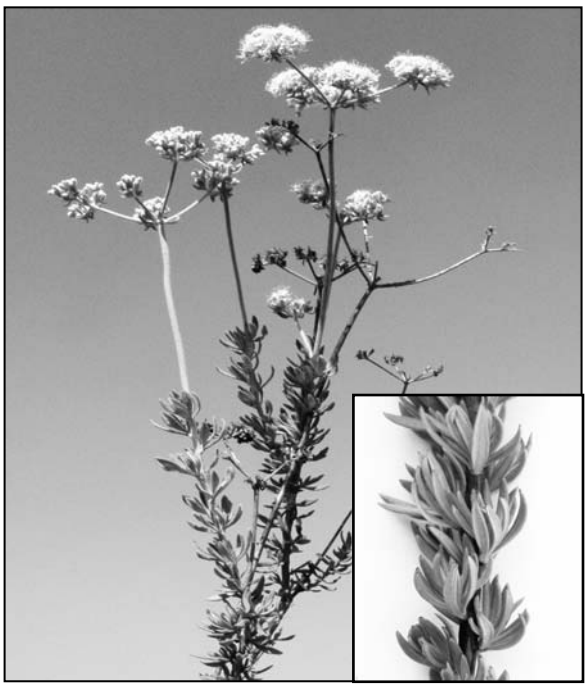
***Eriogonum fasciculatum* Benth.** California buckwheat
POLYGONACEAE

Synonyms: *E. rosmarinifolium* Nutt.
E. fasciculatum var. *maritimum* Parish
E. fasciculatum var. *oleifolium* Gand.
E. aspalathoides Gand.
E. fasciculatum ssp. *aspalathoides* S. Stokes



General Description.—California buckwheat is a widespread and morphologically variable shrub and is one of the most important components of sagebrush scrub, desert scrub, and especially coastal sage scrub (Kirkpatrick and Hutchinson 1977, Westman 1981). Although the four taxonomic varieties partly overlap in geographic distribution each is associated with a different climatic zone and combination of traits, especially color, chromosome number, leaf shape, degree of revolute leaf margins, and pubescence (Munz and Keck 1968, Hickman 1993). All forms have alternate cauline, linear to oblanceolate leaves that are white wooley with appressed hairs beneath, and darker, generally less hairy to glabrous above. Leaves are 1 to 2 cm long and cluster tightly at nodes on short axillary shoots, giving the leaves a fascicled appearance. Flowers are small (about 3 mm long) with six white to pinkish sepals and are born in heads of tightly to loosely packed involucres with few flowers per involucre. The heads (or dense cymes) are born singly or in umbels subtended by long, naked peduncles (often > 5 cm). Branching of the umbels varies from one to four levels. Umbels are rounded to flat-topped depending on the extent of branching. Flowers produce small (about 1.5 to 2 mm long), single seeded achenes that are partially enclosed in a dry, persistent calyx. Below is a summary of diagnostic differences among varieties following Munz and Keck (1968), Reveal (1989), and Hickman (1993).

Range and Taxonomy.—*E. f.* var. *fasciculatum* (see insert) has 2n = 40 chromosomes (Munz and Keck 1968). Shrubs are often low and spreading and 0.6 to 1.2 m tall. Leaves are linear to linear-oblanceolate, green and glabrate above, sparsely pubescent beneath, with leaf margins strongly rolled under (revolute). Involucres and flowers are usually glabrous. Plants occur from nearly sea level to just over 300 m in coastal scrub and sage scrub along coastal bluffs and cliffs, and in canyons and dry slopes of the foothills near the coast from San Luis Obispo Co. south to central Baja California.

E. f. var. *foliolosum* (Nutt.) S. Stokes ex Jones (Munz and Keck 1968), the interior flat-topped buckwheat, is tetraploid with 2n = 80 chromosomes (Stebbins 1942). Shrubs are erect to spreading, 0.5-1.5 m tall and occur on interior slopes and mesas below 1000 m (seldom on coast) in chaparral and sage scrub from Monterey Co., California south to northern Baja California. Leaves are often linear, dark to gray-green and pubescent above, and densely pubescent below. Involucres and perianth are usually pubescent. Synonyms are *E. rosmarinifolium* var. *foliolosum* Nutt., *E. f.* ssp. *foliolosum* S. Stokes, and *E. f.* var. *obtusiflorum* S. Stokes.

E. f. var. *polifolium* (Benth.) Torrey and A. Gray (flowering shoot in photograph) has 2n = 40 chromosomes (Stebbins 1942). These greyish, pubescent, rounded shrubs occur at 600 to 2300 m on dry slopes and washes. They are widespread across inland mountains and deserts of California, from the inner coast ranges of San Luis Obispo and Fresno Cos., south to San Diego Co., eastward into the Mojave Desert to southern Nevada, Utah, and Arizona, and

south into northwestern Senora, Mexico and central Baja California. In inland sage scrub, plants overlap in distribution with var. *foliolosum,* especially in Riverside Co., but occupy drier sites. Leaves are oblanceolate to obovate, densely pubescent beneath, and usually tomentose above with leaf margins sometimes barely revolute. Involucres and sepals are pubescent. Heads tend to be born in simple to once-compound umbels. Reveal (1989) reports hybridization between var. *polifolium* and *E. cinereum* Benth in areas were *E. cinereum* has been introduced within the range of var. *polifolium*. Synonyms are *E. f.* ssp. *p*. S. Stokes and *E. p.* Benth.

E. f. var. *flavoviride* Munz & Johnson has n = 20 chromosomes (Reveal 1989) and is 2 to 3 dm tall. The rounded shrubs occur on dry rocky slopes and washes from 200 to 1300 m in creosote bush scrub of the southern Mojave Desert, San Bernardino Co., south through eastern Riverside Co. to far eastern San Diego Co., and south to central Baja California. Leaves are light green to yellowish-green, linear, strongly revolute, and glabrous above. Peduncles are glabrous; involucres and sepals are subglabrous. Synonym is *E. f.* ssp. *flavoviride* S. Stokes.

Ecology.—California buckwheat occurs on dry slopes and often granitic substrate (Westman 1981). The woody, branched roots penetrate to under 1.5 m (Kummerow and others 1977). Plants lose some leaves in the dry season and can shed many leaves in severe drought. Plants are vulnerable to hot fires so resprout success is low and most regeneration is from seeds (Keeley 1998). Frequent fires deplete the seed bank, making populations vulnerable to local extinction. In Riverside Co., this shrub has decreased dramatically since the 1940's, with the largest decreases on alluvial soils (Minnich and Dezzani 1998). Decreases are attributed to a combination of competition with exotic annual grasses, too frequent a fire interval, that is exacerbated by weeds which carry fire, and by atmospheric deposition of nitrogen, which encourages growth of competing weeds. California buckwheat does well on rocky road cuts and in shallow soils that are inhospitable to annual grasses.

Reproduction.—Plants flower from early spring through summer. The four taxa have slightly shifted flowering times, with var. *flavoviridae* having the earliest season (Munz and Keck 1968) and var. *polifolium* flowering before the other two. In all taxa, stamens and stigmas are exerted and open to generalist pollinators, including honey bees and many species of small native bees, flies, wasps, and beetles. Achenes mature from June to September and disperse when dried inflorescences shatter in autumn. The dry calyx provides buoyancy to detached achenes and assists dispersal by wind and water. Harvester ants also disperse achenes (DeSimone and Zedler 1999). Seedlings emerge in the rainy season in mid to late winter within light gaps and open areas. Survival is unusually high as shown by studies in a variety of sites and years, often ranging from 80 to 90 percent (Wright and Howe 1987, Miriti and others 1998, Montalvo and others 2002). Most shoot elongation and leaf growth occurs before flowering from late winter to mid spring (Cole 1967). Plants can reach maturity in 1 to 2 years.

Seed Germination.—Light improves germination (Cole 1967, Keeley 1987). Atwater (1980) suggests that light increases permeability of seed coats, water adsorption, and possibly leaching of inhibitors, allowing seeds to germinate. Light-induced seed coat permeability would allow some buried seeds to remain viable and dormant in the seed bank, a bet-hedging strategy. Cole (1967) found coastal populations germinated at 15 to 25 ^{o}C while inland populations germinated over a larger range of 5 to 35 ^{o}C. Keeley (1987) examined the effects of light, dark, heat, and leachate through charred wood (charrate) on germination. Seeds germinated equally well on soil vs. filter paper, and light controls had a two-fold increase in germination compared to dark controls (83 vs. 45 percent germination). Charrate did not affect germination. In light, seeds exposed to 120 ^{o}C for 5 min suffered a large decrease in germination under all conditions relative to seeds heated to 70 or 100 ^{o}C, suggesting fire may kill many seeds in the upper centimeter of the seedbank. Heat sensitivity and a light requirement for germination encourage colonization of disturbed or open sites.

Horticulture.—Plants can be propagated from seeds or rooted from cuttings. Seeds and container plants should be planted in the fall to early winter to take advantage of the moist cool season for growth. In one study, seeds planted by seed imprinting and hydroseeding, shallow methods that allow light to reach planted seeds, had at least twice the emergence success as drilling that covered seeds with 0.5 to 1 cm of soil (Montalvo and others 2002). Seeds germinate within 2 weeks if soil is moist and over about 15 ^{o}C. Plants require full sun and good drainage. No irrigation is required if planted before seasonal rains.

The grey-green var. *polifolium* provides a nice contrast to the other green varieties in the garden, but all do well in dry landscaping. The flowers last far into the summer and become an attractive rusty-brown in fruit. Some prostrate cultivars of California exist, including "Theodore Payne," "Prostrata," "Dana Point," and "Wildwood" (Perry 1992).

Greenhouse studies indicate that California buckwheat forms facultative associations with arbuscular mycorrhizal fungi (Egerton-Warburton, Montalvo, and Allen, unpublished report). The plant's facultative dependence on mycorrhizal fungi may be instrumental to successful colonization of barren sites. Montalvo and others (2002) found that plants grew quickly to maturity on a graded site with low organic matter and nutrients, but establishment, growth, and flowering all decreased significantly with decreasing soil nitrogen (NO_3-N mean = 7.89 mg/g, range = 0.8-69 mg/g in the study plot).

Benefits.—California buckwheat provides habitat and food for numerous animals. Osborne (1998) found high abundance and diversity of arthropod species on California buckwheat. Some are species-specific feeders such as the larvae of the moth, *Hemileuca electra* (Wright) (Rubinoff 1998). Numerous species of butterfly larvae feed on California buckwheat and specialize on different plant parts and taxa (Howe 1975), sometimes according to timing of growth. For example, the larvae of the butterfly, *Apodemia mormo* (Felder & Felder), has three biotypes in the Mojave Desert. The spring morph feeds on California buckwheat while the others feed on species with different flowering times. *E. parvifolium* Sm. in Rees. is the host of the rare El Segundo blue butterfly (*Euphilotes bernardino allyni* Shields). When California buckwheat was planted instead of later flowering *E. parvifolium,* competing insect species used California buckwheat, built up populations, and then competed with the rare butterfly for *E. parvifolium* flowers (Longcore and others 2000).

Vertebrates also use California buckwheat. The rare orange-throated whiptail is associated with open vegetation with this shrub (Brattstrom 2000). Rare California gnatcatchers (*Polioptila californica californica*) forage and nest in the shrub. California buckwheat and *Artemisia californica* Less. are dominant shrubs used by gnatcatchers (Mock and Bolger 1992). The rare mountain sheep (*Ovis canadensis nelsoni*) browses on California buckwheat in the San Gabriel Mountains of southern California (Perry and others 1987), and deer eat the inflorescences (Schopmeyer 1974).

Genetics, Geographic Variation, Hybridization, and Fitness.—Stebbins (1942) hypothesized that tetraploid populations of var. *foliolosum* arose from hybridization between diploid var. *fasiculatum* and var. *polifolium* (= *E. f.* subsp. *foliolosum*, *E. f.* subsp. *typicum*, and *E. f.* subsp. *polifolium*, respectively, in the paper). He examined the distribution of taxa in relation to climatic factors and concluded that the morphology and ecological tolerances of var. *foliolosum* combined the morphology and tolerances of the two diploid taxa. The variety *polifolium* was in areas with some snow, frost, and only 10 to 13 cm of rainfall, *fasciculatum* was in the areas with no frost, often frequent fog, and 22 to 37 cm of rainfall, and *foliolosum* often occurred in habitats intermediate to the two diploids. Cole (1967) tested assumptions about the distribution of morphology and ecological tolerances of vars. *fasciculatum* and *foliolosum*. Cole compared their physiologies over an ecological gradient from the cool coast across the mountains to the hot inland valleys and found that coastal var. *fasciculatum* were the least hairy, and populations of var. *foliolosum* became more hairy inland. There was a clear morphological cline from the coast to the interior among and within ecotypes that correlated with habitat. Photosynthesis vs respiration ratios and photosynthetic rates and respiration rates all varied in a clinal manner that correlated with morphological characters. The variety *fasciculatum* forms a distinctly adaptive coastal ecotype, while var. *foliolosum* forms an inland ecotype.

Analysis of eight allozyme loci for eight populations of var. *foliolosum* and four *fasciculatum* revealed ample genetic variation (Montalvo, Ellstrand, and Clegg, unpublished data). All loci were polymorphic and there was an average of 5.7 alleles/locus. Expected heterozygosity was also high at 0.42. Nei's genetic distances among populations ranged from 0 to 0.074, with the largest distance between varieties. Overall, the proportion of total variation explained by differences among populations (G_{ST}) was 0.025. By itself, the tetraploid var. *foliolosum* had no significant structure (G_{ST} = 0.005), while G_{ST} = 0.028 for var. *fasciculatum*. These values suggest high levels of gene flow and outbreeding.

Seed Collection and Processing.—Seeds are collected after heads have turned rusty brown. The chaff can be separated from seeds by pushing seeds through a screen and then separating seeds from chaff with an air separator or fan (author's observation). Commercial seed companies usually skip the screening and just break up the chaff, air separate the seeds from crude chaff, and sell seeds with the persistent calyx intact. A recommended target for minimum quality of purchased seeds is 15 percent purity and 65 percent germination. Here, a bulk seed pound with about 990,000 seeds/kg, would have about 96,800 pure live seeds (personal communication, S & S Seeds, Carpenteria, CA).

Growth and Management.—Seeds have been widely planted for restoration, roadside erosion control, slope stabilization, landscaping, and apiary (Schopmeyer 1974, Perry 1992). Despite the clear geographic pattern and ecological affinities of the four taxonomic varieties, most researchers and consultants fail to

designate taxonomic variety on publications, plant lists, or plant palettes. They also commonly fail to specify appropriate ecological zone for seeds used in wildland plantings. This has resulted in extensive plantings outside natural ranges and habitats (Reveal 1989). Projects should use seeds of appropriate taxa to maximize project success.

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