## I. SPECIES

### Artemisia californica Less. [Updated 2017]

<table>
<thead>
<tr>
<th>NRCS CODE: ARCA11</th>
<th>Subtribe: Artemisiinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>(FEIS CODE: ARCAL)</td>
<td>Tribe: Anthemideae</td>
</tr>
</tbody>
</table>

**Family:** Asteraceae

**Order:** Asterales

**Subclass:** Asteridae

**Class:** Magnoliopsida

### A. Subspecific taxa

None. *Artemisia californica* Less. var. *insularis* (Rydb.) Munz is now recognized as *Artemisia nesiotica* P.H. Raven (Jepson eFlora 2017).

### B. Synonyms

*Artemisia abrotanoides* Nuttall; *A. fischeriana* Besser; *A. foliosa* Nuttall; *Crossostephium californicum* (Lessing) Rydberg (FNA 2017).

### C. Common name

California sagebrush. The common name refers to its strong, sage-like aroma and endemism to California and Baja California. Other names include: coastal sage, coast sage, coast sagebrush (Painter 2016).

### D. Taxonomic relationships

The FNA (2017) places this species in subgenus *Artemisia*. The molecular phylogeny of the genus has improved the understanding of relationships among the many species of *Artemisia* and has, at times, placed the species in subgenus *Tridentadae*; morphology of the inflorescences and flowers alone does not place this species with its closest relatives (Watson et al. 2002). The detailed phylogeny is not completely resolved (Hayat et al. 2009).

### E. Related taxa in region

There are 18 species and a total of 31 taxa (including infrataxa) of *Artemisia* in southern California, all of which differ clearly from *A. californica* in habitat affinity, structure, or both (Munz 1974, Jepson eFlora 2017). Within subgenus *Artemisia* (as per FNA 2017), *A. nesiotica* from the Channel Islands is the most similar and was once considered part of *A. californica*; it can be distinguished by its wider leaves with flat leaf margins (not rolled under). *A. ludoviciana* Nutt. overlaps in southern California, but plants are rhizomatous perennials that grow primarily further inland and in the Great Basin.

*Artemisia dracunculus* L. overlaps with *A. californica* in floodplain habitats and alluvial scrub. Plants can easily be distinguished from *A. californica* by their perennial, non-woody habit, often tarragon odor, and glabrous to subglabrous stems and leaves. The shrub *A. tridentata* overlaps in southern California but has short, broad, wedge-shaped leaves with three teeth toward the top end and is generally separated by its interior distribution and occurrence at higher elevation.

### F. Taxonomic issues

None at the species level.

### G. Other

One of the most important and widespread plants of coastal sage scrub vegetation. It is an indicator species frequently used in restoration. Seed transfer guidelines have been developed only for the much more widespread species of sagebrush, *A. tridentata* (Mahalovich & McArthur 2004).
II. ECOLOGICAL & EVOLUTIONARY CONSIDERATIONS FOR RESTORATION

A. Attribute summary list (based on referenced responses in full table)

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxonomic stability</td>
<td>- high</td>
</tr>
<tr>
<td>Longevity</td>
<td>- often reproduces 5-25 yr</td>
</tr>
<tr>
<td>Parity</td>
<td>- polycarpic</td>
</tr>
<tr>
<td>Flowering age</td>
<td>- 2+ yr</td>
</tr>
<tr>
<td>Stress tolerance</td>
<td>- moderate to high</td>
</tr>
<tr>
<td>Environmental tolerance</td>
<td>- moderate</td>
</tr>
<tr>
<td>Reproduction after fire</td>
<td>- facultative seeders</td>
</tr>
<tr>
<td>Fragmentation history</td>
<td>- historical and recent</td>
</tr>
<tr>
<td>Habitat fragmentation</td>
<td>- high</td>
</tr>
<tr>
<td>Distribution</td>
<td>- common in western California</td>
</tr>
<tr>
<td>SDM projected midcentury suitable</td>
<td>- habitat - 96–100% stable</td>
</tr>
<tr>
<td>SDM projected midcentury habitat</td>
<td>- gain &gt; loss under all five future climate scenarios (assuming unlimited dispersal)</td>
</tr>
</tbody>
</table>

B. Implications for seed transfer (summary)

This species grows across a range of temperature, elevation, and precipitation gradients that appear to have influenced differences in adaptation (see VIII. C. Geographic variation), even within Ecological Sections. For other *Artemisia*, seed transfer guidelines state that "when local data suggest moisture gradients and ranges of elevation in excess of 458 m (1500 ft), conservative guidelines could further restrict seed transfer up 153 m (500 ft) in elevation, or down 305 m (1000 ft) in elevation, from the origin collection area" (Mahalovich & McArthur 2004). *A. californica* shares similar reproductive traits and dispersal ability with these other species and shows clinal variation in traits associated with fitness. It is likely highly outcrossed and wind-pollinated, which provides an ability to exchange genes among nearby stands of plants, but dispersal distances are likely too short to surmount the severe level of habitat fragmentation experienced by this species in some locations (see V. B. SDM Summary). Although species distribution modeling projects a high degree of habitat stability under contrasting mid-century climate scenarios, other influences are causing dramatic declines in populations of California sagebrush. Severe habitat fragmentation from land uses and habitat conversion of shrubland to non-native grassland suggest some active movement of seeds may be important to maintain genetic diversity within populations and the potential to adapt to changing conditions. Careful selection of source populations from within Subsections and adjacent Subsections will be important.

The risk of maladaptation from translocation is likely to be on a scale of habitat zones, such as between Ecological Sections where east-west, and north-south changes in temperature and precipitation norms can differ sharply over the species' range. Large adaptive differences have been measured among populations from widely separated Subsections and elevations along a north-south gradient (see VIII. C, D, and E). Within ecological Sections, the plant grows on many different soil types, which should be noted and matched when possible.

III. GENERAL

A. Geographic range

Widespread in Central Western and Southwestern California Bioregions (Jepson eFlora 2017), from Contra Costa Co. south into Baja California, including the Channel Islands. Historically, California sagebrush was the dominant shrub on north-facing slopes in coastal sage scrub but has declined to about a third of its past abundance in many areas of southern California, especially inland on north-facing slopes where it is being replaced by exotic annual grasses (Minnich & Dezzani 1998).

B. Distribution in California; ecological section and subsection (sensu Goudy & Smith 1994; Cleland et al. 2007)

- Map includes validated herbarium records (CCH 2016) as well as occurrence data from CalFlora (2016) and field surveys (Riordan et al. 2018).

- Ecological Section/subsection:
  - Northern California Coast 263A: k,l,m
  - Central California Coast 261A: a,b,c,e-h,j,k,l
  - Central California Coast Ranges M262A: a-f,h,j,k
  - Southern California Coast 261B: a-j
  - Southern California Mountains and Valleys M262B: a,b,c,d,e (lower edge),f,g,i,j,k,l,n,o,p (western edge)
  - Mojave Desert 322A: g (bordering M262B)
  - Colorado Desert 322C: a (bordering M262B)

C. Life history, life form

Subshrub, drought deciduous, generally lives for 5 to 25 years (Sawyer et al. 2009).
Generally below 800 m (Munz & Keck 1968, Shultz 2017), but can be higher in some areas of southern California. Breadth of habitat

D. Distinguishing traits

Aromatic, sage-smelling subshrub usually 0.6-1.5 m tall but sometimes only 0.2 m or to 2.5 m (Shultz 2017). Plants tend to be wider than tall with many branches from the base (Munz & Keck 1968, Hickman 1993). Upper branches are somewhat unbranched and the stems are whitish with appressed hairs, long, slender, leafy, and flexible. The somewhat hairy gray-green, alternate leaves are soft, entire to divided into narrow linear segments, giving the entire shrub a wispy appearance. Early and late season leaves differ in morphology, and plants become more brown in hue during the dry summer to fall. Early season leaves tend to be longer and more divided than late season leaves. The many small bisexual flower heads are less than 5 mm wide and nodding at maturity, arranged in many small, branched clusters along the stem (appears like a long narrow panicle), and have 20-40 disk florets per flower head, with about a third of the florets pistillate (Shultz 2017).

E. Root system, rhizomes, stolons, etc.

Branch taproot becomes fibrous. The shallow, branched roots (Harrison et al. 1971) allow for rapid water absorption and growth response to shallow rains (Gray 1982).

F. Rooting depth

Shallow root system (Gordon & White 1994), primarily in top 50 cm of soil (Goldstein & Suding 2014).

IV. HABITAT

A. Vegetation alliances, associations


In southern California, also co-dominant in the shrub layer within woodland alliance associations, including the *Juglans californica–Artemisia californica/Elymus triticaoides* association, *Juniperus californica/Eriogonum fasciculatum–Artemisia californica* association, and the *Quercus engelmannis–Quercus agrifolia/Artemisia californica* association.

B. Habitat affinity and breadth of habitat

California sagebrush is common in sage scrub, alluvial scrub and along the coastal strand on dry slopes and fans and young alluvial wash deposits (McMinn 1939, Munz & Keck 1968, Buck-Diaz et al. 2011). In southern California, plants tend to grow equally on flanks and gentle to steep slopes (Kirkpatrick & Hutchinson 1980). Although shrubs tend to be taller and broader when growing on north-facing slopes than on south facing ones, seed production can be higher on south-facing slopes (DeSimone & Zedler 2001). In a seeding experiment on north versus south-facing slopes, Kimball et al. (2017) found *A. californica* cover varied significantly among years but was nearly neutral to slope aspect.

C. Elevation range

Generally below 800 m (Munz & Keck 1968, Shultz 2017), but can be higher in some areas of southern California. Some records and authors report to about 1200 m (Sawyer et al. 2009).

D. Soil: texture, chemicals, depth

Plants occur on virtually all soil types except serpentine (Westman 1981a), and on a variety of soil textures including loams, clayey loams, sandy loams, and loamy sands (FEIS: Scott 2006). Common on granitic and unconsolidated soils (Kirkpatrick & Hutchinson 1980). See IV. F. Drought tolerance for effect of excess nitrogen.

E. Precipitation

Plants occur in Mediterranean climate regions of California that are typically dry in summer, wet in the cool winter, becoming dry mid to late spring, depending on location. Plants typically grow in areas with 10 to 40 inches of precipitation, but can be higher in northern coastal locations such as coastal Monterey.

For ecological sections occupied by *A. californica*, annual normal precipitation ranges from 10 to 40 in (250 to 1,020 mm) in the Southern California Mountains and Valleys (M262B), from 10 to 25 in (250 to 640 mm) in the Southern California Coast (261B), from 14 to 50 in (350 to 1280 mm) in the Central California Coast (261A), and from 10 to 30 in (250 to 760 mm) in the Central California Coast Ranges (M262A). Annual precipitation normals range from 40 to 100 in (1020 to 2540 mm) in the Northern California Coast (263A), with *A. californica* occurring in the southern and drier portion of this ecological subsection.

F. Drought tolerance

Drought tolerant. Plants drop their larger, early season leaves during the summer drought and shift to small leaf production and maintenance. Drought tolerance of seedlings may be affected by nitrogen deposition effects on the microbial communities that form associations with California sagebrush. Valliere & Allen (2016) found seedlings inoculated with soil from a high nitrogen deposition site had a negative response to drought, whereas seedlings inoculated with soil from a low nitrogen deposition site had higher colonization rates by mycorrhizal fungi, higher root:shoot ratios, and a more neutral response to drought.

G. Flooding or high water tolerance

Upland species but also grows in infrequently inundated and well-drained areas of flood plains along streams and on alluvial fans in alluvial scrub vegetation (FEIS: Scott 2006, Burk et al. 2007).
## V. CLIMATE CHANGE AND PROJECTED FUTURE SUITABLE HABITAT

**Artemisa californica**

### A. Species Distribution Models (SDM forecasts, Riordan et al. 2018) Map descriptions

Modeled habitat suitability under (A) baseline (1951–1980) and (B–D) projected midcentury (2040–2069) climate conditions. Projected future habitat suitability maps show agreement across five different climate model scenarios: (B) stable = suitable under both baseline and future conditions; (C) loss = suitable under baseline but unsuitable under future conditions; (D) gain = unsuitable under baseline and becoming suitable under future conditions. In all maps, land area that has already been converted to urban and agriculture land uses is masked in dark gray (FRAP 2015 Assessment; http://frap.fire.ca.gov/data/frapgisdata-sw-fveg_download).

### B. SDM summary

Species distribution modeling suggests *A. californica* could maintain much of its suitable habitat in southern California under projected climate change to mid-century. Assuming a future of continued high greenhouse gas emissions, Riordan et al. (2018) predicted 96–100% of baseline habitat in southern California would remain suitable under mid-century climate conditions across five different general circulation models (GCMs) (SDM maps Fig. B). In addition, the area of habitat suitable for *A. californica* could increase by 37–88%. Predicted gain in suitable habitat far exceeded loss under all five climate scenarios (SDM maps Figs. C-D). Riordan and Rundel (2014) predicted similar high habitat stability: only 4–10% habitat loss by mid-century and 10–15% loss by the end of the 21st century. In contrast, Principe et al. (2013) predict a much greater loss in habitat suitability (78%) by midcentury.

Land use, altered fire regimes, invasive species, and their interactions with climate change could negatively affect *A. californica*, even if projected loss in suitable habitat from climate change alone is relatively low. In southern California human activity is the primary driver of fire (Keeley & Syphard 2016) with fire ignitions and fire frequencies increasing with human population growth (Syphard et al. 2009). *A. californica* is a facultative seeder, but under high fire intensities and frequencies resprouting may fail and seed banks may become depleted, resulting in local extirpations (see VI. D. Regeneration after fire or other disturbance). In addition, the high level of habitat conversion and fragmentation throughout the species’ range creates a barrier to dispersal and gene flow that could negatively affect the adaptive capacity and ability of the species to respond to changing conditions. Much of the currently suitable habitat of *A. californica* in southern California has been developed. Riordan and Rundel (2014) caution that human land use may compound projected climate-driven losses in habitat suitability in southern California shrublands. They predict that the combined impacts of projected land use and climate change could result in as much as 46% loss in currently suitable habitat for *A. californica* by the end of the century (Riordan & Rundel 2014).
### VI. GROWTH, REPRODUCTION, AND DISPERAL

**A. Seedling emergence relevant to general ecology**


**B. Growth pattern (phenology)**

Most plants reach maturity in their second year (Jessica Pratt pers. com.). In California, shoot and new leaf production begins with the winter rains, usually in December, and continues throughout winter and spring. Flower buds are produced in summer, but flowering occurs after the first rains. Flowering of California sagebrush tends to peak in late fall, but in Baja California summer rains may trigger flowering during summer (Minnich 1985). Seeds mature October to January, depending on location and rainfall patterns. The thin leaf cuticle and numerous stomata allow a high photosynthetic rate in response to water availability (Poole & Miller 1975, Gray 1983). Leaves are drought-deciduous and seasonally dimorphic (Westman 1981b, Gray 1982). Leaf drop and production of smaller leaves occurs during the summer drought (Westman 1981b). In areas with coastal fog in late summer, water condensation on leaves may help reduce evapotranspiration and leaf drop (Emery & Lesage 2015, 2017).

**C. Vegetative propagation**

Resprouts from base of plant. Buried stems can sometimes develop roots (FEIS: Scott 2006).

**D. Regeneration after fire or other disturbance**

Faculative seeder, plants regenerate after fire by both sprouting and from seedlings (Keeley 1998, Keeley et al. 2006). Seedling emergence after fire is variable and low (Zedler et al. 1983, Keeley 1998). In a large study in southern California, California sagebrush resprouted after fire about 20 percent of the time within inland areas and 18 percent of the time in coastal areas (Keeley et al. 2006). Over a five year period after fire, about 83% of seedlings emerged in the first two years after fire, falling to 13% in year three. Resprouting appears to be lower in burns through dense vegetation, where plants are older, or if fire intensity is high (Malanson & O'Leary 1982, Keeley 1998, Minnich & Dezzani 1998). Seedlings sometimes appear the second year from seeds of resprouts or seeds blown in from adjacent areas. Under high fire intensities or frequency, California sagebrush will likely be extirpated because of its poor resprouting ability and poor competitive ability of seedlings (Malanson & O'Leary 1982, Malanson & Westman 1991).

**E. Pollination**

Primarily wind pollinated. The reduced flowers are typical of other wind-pollinated species of *Artemisia*. Most of the genus is wind-pollinated (Hayat et al. 2009).

**F. Seed dispersal**

The tiny seeds are thought to be wind dispersed. DeSimone & Zedler (2001) used seed traps to determine dispersal distances away from parent plants. The longest distances recorded were 5 m. Seeds are likely to travel much further during strong winds.

**G. Breeding system, mating system**

Flowers are said to be self-incompatible (Moldenke & Neff 1974), but evidence is lacking. Some species of *Artemisia* have been shown to be self-compatible (Hayat et al. 2009), while others are self-incompatible (Garnock-Jones 1986).

**H. Hybridization potential**

No information on *A. californica*. Hybridization among distantly related populations in mixed plantings is probable if flowering overlaps. There is evidence for hybridization and introgression between subspecies *oA. tridentata* in the Great Basin (Wang et al. 1997).

**I. Inbreeding and outbreeding effects**

Effects of outbreeding among subspecies from adjacent habitats was examined in a closely related species. *A. tridentata* plants were tested in hybrid zone and parental environments of different subspecies *oA. tridentata*. The first generation hybrids were most fit in the ecotone between the two subspecies studied while parents were most fit at contrasting home sites (Graham et al. 1995, Wang et al. 1997). Subspecies and hybrids differed in absorption of elements, and there was local adaptation in uptake of several elements (Wang et al. 1997, 1999). Results suggest the outbreeding depression observed at home sites was due to a breakup of local adaptation.
### VII. BIOLOGICAL INTERACTIONS

**A. Competitiveness**

Competition with invasive species for light and resources appears to limit establishment of *A. californica*. Seedlings can be virtually absent in grasslands adjacent to stands of shrubs (Freudenberger et al. 1987), and seedlings are notably less abundant in annual grasslands than in gaps and small clearings of non-grassland vegetation (DeSimone & Zedler 1999). Seed germination, seedling establishment and survival can be high among shrubs (Goldstein & Suding 2014), but poor in grass dominated areas, in light limited conditions under grass thatch, or amidst even low densities of standing grass (Schultz 1996, Elisson & Allen 1997, Storms 1999), a problem likely exacerbated by much earlier germination and growth of grasses than of sagebrush.

Attempts to use annual legumes as nurse plants in revegetation projects can result in reduced seedling growth and survival (Marquez & Allen 1996), but seedling survival may be unaffected when sown with other native species at low density (Montalvo et al. 2002). Clearing weeds before planting is critical. California sagebrush can return vigorously to areas where all vegetation has first been removed, even when sown with a variety of other species.

Solarization of soil and prescribed burning to kill seeds of non-native grasses at a site in the coastal Santa Monica Mountains significantly improved establishment from seeds and plugs compared to control plots (Moyes et al. 2005). However, *Brassica nigra* was prolific in the burned plots.

**B. Herbivory, seed predation, disease**

High rates of infection by larvae of wood-boring beetle *(Perarthrus vittatus)* have been observed, although it is not known if infection results in death (Tyson 1981). *Artemisia californica* has also been found to host larvae of the scarab beetle *Phobetus comatus* (La Rue 1992). Spittle bugs (*Cercopidae*) are commonly found on *Artemisia* during summer months, but are not known to harm plants significantly (Jutta Burger pers. com.). Plants produce a large number of aromatic compounds known as secondary chemicals, including terpenes (both monoterpenes and sesquiterpenes) that are thought to deter herbivores, but plants host more than 200 species of herbivorous arthropods (Pratt et al. 2014). The terpenes provide the camphor/sage-like aroma of the leaves. Variation in chemical composition may be adaptive and associated with different levels of defense (Pratt et al. 2017, see VIII. E. Phenotypic or genotypic variation in interactions).

**C. Palatability, attractiveness to animals, response to grazing**

Grazing appears to prevent shrub establishment, as seen by differential reinvasion of shrubs into ungrazed and grazed areas (see Freudenberger et al. 1987, Callaway & Davis 1993). Although some grazers may choose to eat young grasses or forbs over fresh shoots of *A. californica* during the growing season, shrubs are vulnerable to grazing by vertebrate herbivores during the summer and fall, when they may be preferentially eaten (Genin & Badan-Dangon 1991, Genin & Pijoan 1993). Plants continually produce basal sprouts during a single shrub’s lifetime, and young shrubs can resprout if clipped at the base (Malanson & Westman 1985).

**D. Mycorrhizal? Nitrogen fixing nodules?**

Roots form associations with arbuscular mycorrhizal (AM) fungi (Harney et al. 1997), but the beneficial nature of the interaction may be facultative and is potentially affected adversely by human-influenced nitrogen deposition (Sigüenza 2000, Yoshida & Allen 2001, 2004; Valliere & Allen 2016). Vogelsang & Bever (2010) found that *A. californica* growth benefited from inoculation with arbuscular mycorrhizal fungi and that increase in size was highly variable. In a study of root colonization along a nitrogen deposition gradient, colonization of roots of *A. californica* by AM fungi was found to be lowest in areas of high nitrogen deposition (Sigüenza et al. 2006b). In addition, in greenhouse studies, plants that received higher amounts of nitrogen fertilizer had lower growth when inoculated with soil containing AM fungi compared to uninoculated controls (Sigüenza et al. 2006a). Furthermore, inocula collected from high N-deposition sites resulted in the greatest depression in growth (Sigüenza et al. 2006b), especially under drought (Valliere & Allen 2016). Together, these studies suggest N-deposition and its differential impact on species of AM fungi have contributed to declines in the abundance of *A. californica* through changes in the interaction between plants, fungi, and environmental conditions. In a study in Irvine (a low N-deposition area), Kimball et al. (2014) found cover of *A. californica* was highest in plots supplemented with nitrogen under ambient rainfall compared to plots with reduced or added water. A recent study found genetically-based population variation in the response of several traits to added N (Jessica Pratt pers. com.; Meza-Lopez In Review).

**E. Other**

It has been suggested that *Artemisia* and other shrubs of coastal sage scrub produce allelopathic substances that inhibit growth or germination of other plant species (Muller et al. 1964). Studies on chemistry of leaves, litter, and soil below shrubs documented the presence of both soluble compounds and volatile monoterpenes and sesquiterpenes that inhibit germination or growth of some plants (Halligan 1973, 1975, 1976). Small mammalian herbivores and seed eaters often restrict foraging to beneath shrub canopies and to within a short distance of protective cover (Halligan 1973, 1974) and may contribute to the conspicuous bare zones on the edge of shrub stands and under canopies.

### VIII. ECOLOGICAL GENETICS

**A. Ploidy**

Diploid with n = 9 chromosomes (Hickman 1993).

**B. Plasticity**

There is plasticity in flowering time and seed maturation time evident from among-year variation in phenology. Plants in southern California have been observed to be facultatively deciduous in prolonged drought. In a common garden study, Pratt & Mooney (2013) documented plasticity in several traits in response to different precipitation treatments, including Carbon:Nitrogen ratios, average flowering date, and plant size (see VIII. C. Geographic variation).

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C. Geographic variation (morphological and physiological traits)  Near the coast, plants vary in pubescence, color, chemistry, and physiology (O'Brien 1980). Shrubs vary between a green form with sparse hairs on the leaves to a form with dense hairs that give the plants a gray hue. Populations differ in the distinctness of forms and in their relative frequency. Seedlings raised together generally retain the grayness of their parents but can become grayer with age (O'Brien 1980). Differences in pubescence of shoots correspond to differences in water content, rate and timing of shoot elongation, leaf retention, and chemistry. The lower leaf-water content of gray plants negatively affects larval growth and fecundity of the beetle *Triphaga sericotrachyla* (O'Brien 1980).

Recent studies found clinal patterns in secondary chemistry and/or physiological traits and flowering time along a latitudinal, precipitation, and temperature gradient in coastal CA. Pratt et al. (2014) examined variation in terpene chemistry among five populations of California sagebrush collected along a latitudinal gradient consisting of steep precipitation and temperature variability from San Diego County (20 cm annual rainfall) to Mendocino, California (103 cm annual rainfall). Twenty plants derived from cuttings collected from each of the five populations were grown together in an experimental common garden in Orange County under high and low precipitation treatments. They found significant variation in total terpenes and monoterpenes among source populations that was not altered by precipitation treatment, suggesting differences were genetically based. In addition, phenotypic selection analyses showed that increased precipitation selects for decreased monoterpane concentration, suggesting that clinal variation in monoterpane concentration and overall terpene composition (along southwardly increasing temperature and aridity) and decreasing precipitation gradient) is adaptive. Further experiments could test if these traits are adaptive by determining, for example, if monoterpenes are beneficial to plant survival and reproduction in hotter, more arid environments.

In an analysis of other functional traits using plants from the same experiment, Pratt & Mooney (2013) found phenotypic plasticity in several performance traits that correlated with the interannual variability in precipitation of source sites and clinal patterns in growth and flower production response to precipitation treatments. Southern populations were more plastic in total flower production and growth than northern populations.

Sheng (2015) tested for genetically based variation in leaf physiological traits, flowering time, and terpene content by measuring traits on plants grown in a common garden from seeds sourced from 21 natural populations of California sagebrush distributed along a precipitation and temperature gradient along the coast from San Mateo Co. south to San Diego Co. Most traits were also measured on wild plants at five natural sites distributed along the same gradient and data were analyzed in relation to latitude, environmental variables and patterns of variation observed in the common garden. The four climatic variables studied were all significantly associated with latitude, especially low temperature, intra-annual variability of precipitation, and high precipitation (R² all > 0.55). Of the traits measured at the five in situ sites, most varied significantly among sites but only percent leaf water content was congruent with the clinal patterns detected in the common garden (see VII. D. Genetic variation and population structure). The author noted the low number of in situ sites provided low statistical power.

D. Genetic variation and population structure  Prostrate forms have been selected from coastal regions for use as groundcover in landscaping (Perry 2010), suggesting genetic variation among populations in stature.

In a common garden study Pratt et al. (2014) and Pratt & Mooney (2013) found evidence for genetic differences in terpene concentrations, water-use-efficiency, growth rates, flowering time, and Carbon:Nitrogen ratios. The variation in most traits correlated with environmental differences in a clinal pattern (see VIII. C. Geographic variation). In the subsequent common garden study by Sheng (2015, see VIII. C. Geographic variation), both plant biomass and inflorescence production differed among sources, indicating genetic differences, with a pattern of decreasing biomass and inflorescence production with increasing latitude. In addition, the onset of flowering was associated with latitude (but not to single climate variables), whereas specific leaf area, leaf water content, and nitrogen content increased with source site mean temperature, and sesquiterpene concentration decreased with increasing mean annual precipitation.

E. Phenotypic or genotypic variation in interactions with other organisms  In *A. tridentata*, a reciprocal transplant study of seedlings and soil suggested that the microorganisms with which the plants interact may be adapted to native soil, and that the plants in turn, may be adapted to native microorganisms (Miglia et al. 2004).

Pratt et al. (2017) found significant differences in arthropod (insects, spiders) communities and densities among populations of *A. californica* grown together in a common garden. The garden populations were sourced from along a south to north gradient, and the density of arthropods hosted by the plant populations increased from south to north. The arthropod communities on the two southern California source populations also differed from those on the three northern California populations. The pattern of northward increases in arthropod density was associated with changes in a number of plant traits including decreases in water use efficiency, plasticity in phenology, the ratio of carbon to nitrogen, and the concentration of monoterpenes. Arthropod community composition was also associated with terpene composition.
F. Local adaptation

There appear to be suites of adaptive differences in populations along a latitudinal, temperature, and aridity gradient from Mendocino County to Baja California (see VII. C. Geographic variation, E. Phenotypic or genotypic variation in interactions). Pratt et al. (2014) and Pratt & Mooney (2013) found clinal patterns of variation in terpenes and various growth traits and hypothesized that aridity and herbivory influence adaptive differences in terpene composition. They also suggest variability in environmental conditions influence the evolution of adaptive plastic responses. Results of studies by Pratt et al. (2017) are consistent with clinal variation in adaptive traits related to arthropod use (see VII. E. Phenotypic or genotypic variation in interactions). The patterns detected in the common garden study by Sheng (2015) (see VII. C. Geographic variation and D. Genetic variation) are also consistent with local adaptation in co-varying traits associated with physiology and water economy.

Evolutionary divergence in adaptive traits has also occurred within other species of *Artemisia*. Rogers & Montalvo (2004) outlined ample evidence of differences in adaptation among populations of the related, but more widespread, shrub *A. tridentata*. For example, in a study of 69 source populations involving three subspecies, there were habitat-correlated patterns in seed germination response within and among taxa (Meyer & Monsen 1992); the number of days it took for 50% of seeds to germinate at 1°C was negatively correlated with the mean January temperature of source sites, suggesting adaptation to home-site temperature regimes.

G. Translocation risks

Common garden studies and the clinal patterns associated with latitude and environmental variables suggest differences in adaptation among populations of California sagebrush and potential risks to moving populations to very different sites (Pratt & Mooney 2013, Pratt et al. 2014, Sheng 2015, Pratt et al. 2017). However, we did not find a study on the fitness effects of moving plants different distances along an environmental cline.

IX. SEEDS

Seed image by John Mcdonald Rancho Santa Ana Botanic Garden Seed Program (RSA Seeds 2016).

A. General

The small achenes (dry, one-seeded fruits) are tiny (about 60 micrograms) and build up in the soil seed bank (DeSimone & Zedler 2001). They are about 1.2 mm long, obovate, yellowish brown with a thin, white, membranous fruit coat (Wall & Macdonald 2009). Low purity (5–15%) and 60% minimum germination are common standards (Jody Miller, S&S Seeds, pers. comm., Stover Seed Company 2010).

B. Seed longevity

Other species of *Artemisia* do not form long-lived seed banks, but seeds are potentially viable for 5 years if stored dry at under 10°C (Meyer 2008). See seed storage below.

C. Seed dormancy

Seeds have physiological dormancy. In tests on the combined effects of light and fire components on germination, 73% of seeds exposed to light germinated on soil, but seeds in the dark did not germinate (Keeley 1987). These results are consistent with field data that show germination may be limited by reduced light (Eliason & Allen 1997, Montalvo et al. 2002).

D. Seed maturation

The single-seeded fruits (achenes) ripen in December to January (sometimes as early as October), with variation among years and habitats (Eliason & Allen 1997, DeSimone & Zedler 1999).

E. Seed collecting and harvesting

Mature inflorescences with ripe seeds are brown to golden brown, and seeds fall easily from the small heads. Seeds and seed heads generally fall easily from the inflorescence when ripe and dry (A. Montalvo pers. obs.). Meyer (2008) describes seed collecting methods for other species of *Artemisia*, and these methods work for A. californica (A. Montalvo pers. obs.). Seeds tend to be retained in heads when plants are wet. Heads should be dry and seeds brownish when collected. To collect seeds, gently shake, strip, or beat branches with a racket over an open tub, tarp, or hopper to collect ripe seeds.

F. Seed processing

It is not necessary to remove all the chaff from the seed heads when processing seeds for seeding projects. For bulk collections and cleaning up to 15% purity, material of *Artemisia* can be run through a debearder and screened to separate seeds and large chaff (Stevens et al. 1996).

For high purity processing, dry material down and separate dehisced loose floral material from the bottom of the collection bin/bag through a #25 sieve to remove bulk of the chaff (Wall & Macdonald 2009). Wall & Macdonald (2009) then recommend gently rubbing the material over a #45 sieve or a rubber mat to separate the achenes from the flowers and then reprocessing material through the #25 sieve to separate seeds from most chaff. A blower can then be used followed by sieving the captured material through the #25 sieve to catch remaining small twigs and chaff. Blower speed will depend on the particular blower and seed lot.
### G. Seed storage
Store seeds dry under cool conditions. Meyer (2008) warns that seeds of other *Artemisia* hold viability for only 2 to 3 years under warehouse conditions. She also notes that if seed quality is initially low, that viability may decrease faster than high quality seed lots. In addition, if seeds are dried down to an optimal moisture content of 6 to 8%, storage at under 10°C is likely to extend longevity.

### H. Seed germination
Baskin & Baskin (1998) and NPNPP (2016) recommend 23°C in light and seeds germinate about 21 days after sowing (Young in NPNPP 2016). Seeds will germinate when fresh, but stored seeds may need cold stratification to enhance germination (De Hart 1994). When one-year-old seed stored at room temperature was tested at 19/26°C (night/day) on moist filter paper with 12h light, germination was less than 10% both with and without gibberellic acid treatment (J. Burger pers. com.). Certain components of fire also influence germination. In light, treatment with leachate from charred wood (charate) alone or with heat increases germination by 5 to 14 percent, but germination is about a third lower when seeds are subjected to high temperatures (70–120°C). In contrast, in darkness both heat and charate alone stimulate germination, although heat and charate together generally decrease germination. Thus buried seeds may require some exposure to fire in order to germinate, but such exposure yields inferior germination compared to light alone (Keeley 1987).

### I. Seeds/lb
- 1,034,280 seed/bulk lb (S&S Seeds 2016 database).
- 6,000,000 seed/lb (Stover Seeds 2010 database).

### J. Planting
**Horticulture:** For sowing containers, mix the tiny seeds with washed fine sand or potting soil to dilute seeds and sow on surface of potting soil (NPNPP 2016, A. Montalvo pers. obs.).

**Outplanting:** For direct seeding, California sagebrush should be planted using shallow seeding methods such as hydroseeding or dry broadcasting and tamping or dry broadcasting followed by seed imprinting. Shallow methods are superior to planting with a range drill because the seeds need light for germination (Montalvo et al. 2002). As in Montalvo et al. (2002), the tiny seeds can be mixed with bran or other carrier to help distribute seeds at intended seeding rates. In seeding trials on slopes comparing hydroseeding, drilling, hand-sowing, and hand-sowing covered with jute netting (jute method), Tamura et al. (2017) found the highest seedling emergence after hydroseeding on moderate slopes and after the jute method on steep slopes.

Meyer (2008) provides detailed information for seeding of *A. tridentata* that may be useful for *A. californica*. For example, she recommends that seeds be planted at or near the surface of a firm seed bed. Too much compaction can be a problem, and seed can get buried too deeply if drilled or broadcast on too loose a seed bed. Bowler et al. (1994) had success salvaging seedlings from a nearby site and transplanting them into a restoration site in Orange Co. The transplants were watered about once a month the first year.

### K. Seed increase activities or potential
Yes. *Artemisia californica* is being grown for seed increase in Orange County, CA by the Irvine Ranch Conservancy (J. Burger & M. Garrambone pers. com.), where 2 1/2 inch liners were planted in November at three foot spacing (1 plant/28 sq. ft) in drip-irrigated raised beds. Plants provided with limited supplemental water produced 100% cover and had flower buds by September (in 10 months). Mean yield over four years was 27 PLS pounds, but seed production was highly variable over years and at different locations. After four seasons of production, year 2 (the wettest during a drought) had the highest production. Years 3 and 4 had yields similar to year 1. At a new growing site, odd rainfall patterns the first year resulted in 25% of the crop flowering out of the normal season and non-viable seed. IRC plans no more than four years of production for a single crop. Orders for production require at least two years advanced notice because first-year seed crops are ready after the seeding season.

Seed increase has also been done successfully with three subspecies of *A. tridentata* in Utah (Stevens et al. 1996). Generally, plants were placed 5–7 feet apart within rows that were also spaced 5–7 feet. Depending on subspecies, about 20–50% of the seed crop was produced during the second growing season relative to the highest production year. Seed production increased to 80 to 100% by the third year. Production was 1000 to 2000 lbs/acre at 15% purity and production stands lasted at least 15 years.
### X. USES

| A. Revegetation and erosion control | California sagebrush is an important, fast growing shrub used extensively in roadside revegetation, erosion control, post-fire mitigation, and habitat restoration in coastal California and its inland valleys, especially in coastal sage scrub (Montalvo & Koehler 2004). Newton and Claassen (2003) recommend use of this plant for disturbed lands within the Central Western California and Southwestern California Regions. In about 2006, CalTrans decided the shrub was too flammable to use in revegetation of right of ways in Riverside County (Montalvo pers. obs.). The shrub has a high flammability index due to its chemistry (particular volatile chemicals), dry deciduous leaves in summer, and fine branching structure (FEIS: Hauser 2006). Studies are needed to see if roadside fires spread as efficiently through a closed canopy of mixed shrub species, including *A. californica*, than shrubs mixed with invasive annual grasses. |
| B. Habitat restoration | Used extensively in restoration of inland and coastal sage scrub vegetation. Recommended for use in the Central Western California and Southwestern California regions (Newton & Claassen 2003). Plants can be established from shallowly planted seeds or from container stock. For wildland sites, use of seeds reduces risk of disease transfer from nurseries (see X. C. Horticulture). Burger et al. (2003) found that although *A. californica* in restoration plots supported a higher arthropod abundance and richness than natural stands, their diversity was lower when corrected for number of arthropods sampled. Diversity and abundance may have differed because of the relatively young age of restored plants as compared to naturally-established ones. There are attempts to restore areas that have been type converted to non-native grassland, and this requires control of the grasses. Cox & Allen (2008) found that three years of exotic grass control (grass-specific herbicide, thatch removal, mowing combinations) significantly reduced grass cover over the short term. Continual control of grasses was necessary to prevent their reinvasion into plots seeded with *A. californica* and other native shrubs and herbs. In addition, non-native forbs, especially *Erodium cicutarium*, were problematic. In degraded, natural stands of coastal sage scrub invaded with non-native grasses and forbs, persistent weed control promotes success of California sagebrush seedlings where there is an intact seedbank or seed dispersal from nearby plants (A. Montalvo pers. obs.). |
| C. Horticulture or agriculture | Agriculture: Spring rains or artificial late fall and spring irrigation may enhance survival of seedlings (Williams & Hobbs 1989, Eliason & Allen 1997, Padgett et al. 2000). However, in experiments by Padgett et al. (2000) where supplemental irrigation occurred in the first year, the increase in seedlings in irrigated plots was erased by the end of two years. Furthermore, in another study late-season watering in wet years did not enhance survival (DeSimone & Zedler 2001). Horticulture: Root rot caused by *Phytophthora tenaculata* has been detected in nursery stock in California (Rooney-Latham et al. 2015). Plants should to be grown in a well-drained mix in disinfected pots and off the ground using best management practices to prevent spread of pathogens. California sagebrush can be compact if kept pruned and subjected to occasional pinching. These aromatic plants remain attractive in the dry season with occasional water (Schmidt 1980, Keator 1994) and prefer well-drained soils and low organic matter content (Wasowski & Wasowski 1995). Naturally occurring prostrate or low-mounding varieties are in cultivation (Browse 1987, Wasowski & Wasowski 1995, Perry 2010) and look good in dry borders or as a foreground to contrasting taller shrubs (Keator 1994). *Artemisia 'Canyon Grey'* was selected from San Miguel Island and has a prostrate growth habit; *A. c.* 'Montara' from coastal San Mateo Co. has a low spreading form (Perry 2010). Planting away from structures is recommended owing to the fine fuels possessed by this species (Paolini et al. 2014). |
| D. Wildlife value | As a dominant member of coastal sage scrub, *A. californica* provides habitat for many plant and animal species. It is preferred food for dusky-footed and desert woodrats and it is an important component of habitat for the federally threatened California gnatcatcher (*Polioptila californica*) and the endemic Bell’s sage sparrow, a state-listed species of special concern (Hauser 2006). Gnatcatcher habitat may consist primarily of *Eriogonum fasciculatum*–*A. californica* and *Encelia californica*–*A. californica* shrub associations (Weaver 1998). Foraging may preferentially occur in *Artemisia* and *Eriogonum* shrubs (Beyers & Wirtz 1997), in part because they house a high number of arthropods (see Osborne 1998). An arthropod sampling study in sage scrub of southwestern Riverside County found that *A. californica* supports fewer species of arthropods than the co-dominant shrub *E. fasciculatum* (218 vs. 265, respectively) but higher abundances (266 vs. 147 individuals per plot, respectively); the relative abundance of the two shrub species does not alter the arthropod use patterns of the shrubs. Both are important to the maintenance of high arthropod species richness and abundance in coastal sage scrub (Osborne 1998) and thus to the overall health of the community. |
| E. Plant material releases by NRCS and cooperators | None. |
| F. Ethnobotanical | Leaves of California sagebrush have been used by Native Americans for smoking, in sweat-houses, and various other purposes (Bean & Saubel 1972). The Cahuilla used the plant to ensure proper maturation of girls into women. It is said to stimulate the uterine mucosa, ensuring rapid childbirth and, if regularly consumed as a decoction prior to the onset of each menstruation, to prevent menstrual cramps and alleviate menopausal trauma. Fresh or dried leaves were chewed to alleviate colds (Bean & Saubel 1972). Costanoan Indians applied leaves to wounds or aching teeth for pain reduction, used a decoction to bathe patients with colds, coughs and rheumatism, or consumed leaves and used them as a poultice for treatment of asthma (Bocek 1984).
California sagebrush contains a variety of monoterpenoids, flavonoids, and sesquiterpenes, some of which have medicinal value; of the monoterpenoid compounds, camphor and eucalyptol react with pain receptors to reduce pain (Fontaine et al. 2013). |
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| XIV. IMAGES | Seed images by John Macdonald used with permission from Rancho Santa Ana Botanic Garden Seed Program (RSABG Seed Program), with rights reserved by RSABG. Images may not be used for commercial purposes. Images in cell IX. K. curtesy of Jutta Burger, Irvine Ranch Conservancy. All other images by Arlee Montalvo (copyright 2017) unless otherwise indicated with rights reserved by the Riverside-Corona Resource Conservation District (RCRCD). Photos may be used freely for non-commercial and not-for-profit use if credit is provided. All other uses require permission of the authors and the Riverside-Corona Resource Conservation District. |
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