






I. SPECIES	<i>Salvia apiana</i> Jepson [updated 2017]
<p>NRCS CODE: SAAP2</p>  <p>1st season seedlings, mid April 2009, western Riverside Co.</p> <p>Photos, A. Montalvo, Riverside Co.</p>	<p>Family: Lamiaceae Order: Lamiales Subclass: Asteridae Class: Magnoliopsida</p> <p>in fruit, persistent calyx</p>    
<p>A. Subspecific taxa</p> <ol style="list-style-type: none"> 1. SAAPA 2. SAAPC 	<ol style="list-style-type: none"> 1. <i>S. apiana</i> Jeps. var. <i>apiana</i> 2. <i>S. apiana</i> Jeps. var. <i>compacta</i> Munz [recognized by USDA PLANTS 2016 and mentioned in a note in Jepson eFlora (Averette 2016)]
<p>B. Synonyms (numbered as above)</p>	<ol style="list-style-type: none"> 1. <i>Audibertia polystachya</i> Benth., <i>Ramona polystachya</i> Briq., <i>Audibertiella polystachya</i> Briq., <i>Salvia californica</i> Jeps., but not the <i>S. californica</i> Brand. described by Brandegee (Epling 1938).
<p>C. Common name (numbered as above)</p>	<ol style="list-style-type: none"> 1. white sage (McMinn 1939, Calflora 2016); also called bee sage (Keator 1994) 2. compact white sage (Calflora 2016, USDA PLANTS 2016)
<p>D. Taxonomic relationships</p>	<p><i>Salvia</i> is a large genus of nearly 1000 species distributed over most continents. White sage belongs to section <i>Audibertia</i> of the subgenus <i>Audibertia</i> which is restricted to the California Floristic Province and adjacent deserts (Walker & Sytsma 2007, Walker et al. 2015). The alignment of white sage with species traditionally classified in <i>Salvia</i> section <i>Audibertia</i> has been supported by combined analysis of DNA molecular data and stamen morphology (Walker & Sytsma 2007, Walker et al. 2015). Recent analyses supported classifying the California <i>Salvia</i> into subgenus <i>Audibertia</i> with two monophyletic sections, <i>Audibertia</i> with 15 species and <i>Echinosphace</i> with four species. Within section <i>Audibertia</i>, the following six taxa are in a single, monophyletic lineage (clade): <i>S. apiana</i>, <i>S. munzii</i> Epling, <i>S. vaseyi</i> Parish, <i>S. eremostachya</i> Jepson, <i>S. clevelandii</i> (A. Gray) Greene, and <i>S. mellifera</i> Greene (Walker et al. 2015).</p>
<p>E. Related taxa in region</p>	<p><i>S. apiana</i> overlaps in distribution with a number of other <i>Salvia</i> species in section <i>Audibertia</i> in southern California, including the subshrubs <i>S. clevelandii</i>, <i>S. eremostachya</i>, <i>S. leucophylla</i>, <i>S. mellifera</i>, <i>S. munzii</i>, <i>S. pachyphylla</i>, and <i>S. vaseyi</i> as well as with the annual herb <i>S. columbariae</i> Benth (Epling 1938, Munz 1974). <i>S. apiana</i> also overlaps with <i>S. carduea</i> Benth, an annual within section <i>Echinosphace</i>.</p> <p>Using a combination of morphological and both nuclear and cytoplasmic DNA data, Walker et al. (2015) reevaluated the relationships among California <i>Salvia</i> and investigated the hypothesis of Epling (1938) that <i>S. vaseyi</i> was the result of hybridization between <i>S. apiana</i> and <i>S. eremostachya</i>. Their analysis was consistent with past hybridization events and chloroplast capture involved in the diversification of subgenus <i>Audibertia</i>. Data suggest <i>S. apiana</i> provided maternal chloroplast DNA to <i>S. vaseyi</i>, and <i>S. eremostachya</i> provided paternal nuclear DNA, consistent with Epling's hypothesis, although other explanations could not be ruled out.</p>
<p>F. Taxonomic issues</p>	<p>The designation of varietal status for <i>S. apiana</i> var. <i>compacta</i> is briefly noted by Averett (2017) in the online Jepson Manual (Jepson eFlora 2017) as used for Baja California plants with condensed panicles. However, the name has also been used for such plants on the edges of California deserts.</p>
<p>G. Other</p>	<p>White sage is an important aromatic subshrub of inland and coastal sage scrub vegetation that has decreased substantially in Riverside Co. in the past 50 years (Roberts et al. 2004).</p>

II. ECOLOGICAL & EVOLUTIONARY CONSIDERATIONS FOR RESTORATION

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

Taxonomic stability - low
 Longevity - few to 50 years
 Parity - polycarpic
 Stress tolerance - high
 Flowering age - 2+ yr (occasionally first year)
 Environmental tolerance - moderately wide
 Reproduction after fire - facultative seeder
 Fragmentation history - recent
 Habitat fragmentation - high
 Distribution - narrow but common, dry sites

Seeds - dormant, refractory, likely long-lived
 Seed dispersal distance - short, local
 Pollen dispersal - intermediate to far
 Breeding system - mixed, mostly outcrossed
 Population structure - unknown, likely intermediate
 Adaptive trait variation - unknown
 Chromosome number - stable
 Genetic marker polymorphism - no data
 Average total heterozygosity - no data
 Hybridization potential - high

SDM projected midcentury suitable habitat - 48–100% stable

SDM projected midcentury habitat gain - gain > loss under 4 of 5 future climate scenarios (assuming unlimited dispersal)

B. Implications for seed transfer (summary)

Fragmentation of coastal sage scrub habitat is some of the most extreme in California. Although Species Distribution Modeling (see V. B. SDM summary) suggests that much of white sage's currently suitable habitat will remain climatically suitable to midcentury; however, its populations have been shrinking and its dispersal ability is unlikely to allow much migration among the lowest elevation habitat fragments of southern California. Dispersal and evolution of this plant may not be able to keep up with potential habitat loss from anthropogenic influences, especially if the most important pollinators (*largeBombus* and *Xylocopa* bees) suffer continued declines. Habitat corridors for pollinators and plants may be especially important to maintain. We suggest it would not be favorable to deploy seeds across Ecological Sections (especially not from west to east) or widely separated Subsections. It would be more suitable to deploy seeds across adjacent Ecological Subsections (see III. B. Distribution in California), while avoiding movement across more than 1000 ft elevation bands, from lower toward higher rainfall Subsections, or from cooler to warmer locations. Data on hybrid inviability and the inability of natural hybrids to spread (see VI. H. Hybridization potential, I. Inbreeding and outbreeding effects) suggests it would be wise to avoid collecting seeds from hybrid zones for use in offsite restoration and revegetation.

III. GENERAL

A. Geographic range

White sage ranges from Santa Barbara Co., California south to the middle of Baja California and east to the western edge of the Colorado desert (Epling 1938, Munz & Keck 1968).

B. Distribution in California; ecological section and subsection

(sensu Goudey & Smith 1994;
Cleland et al. 2007)

Section Code

■ 261A	■ M261G
■ 261B	■ M262A
■ 262A	■ M262B
■ 263A	■ 322A
■ M261A	■ 322B
■ M261B	■ 322C
■ M261C	■ 341D
■ M261D	■ 341F
■ M261E	■ 342B
■ M261F	□ Salton Sea

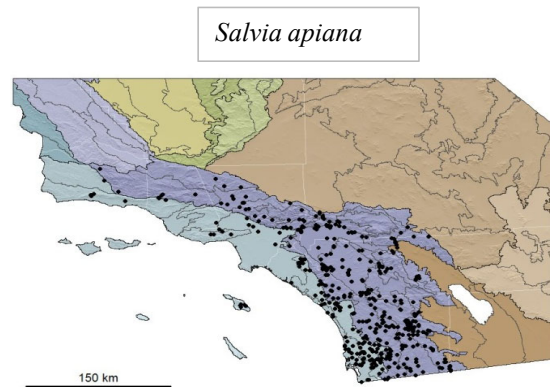
Map includes validated herbarium records (CCH 2016) as well as occurrence data from CalFlora (2016) and field surveys (Riordan et al. 2018).

Peak abundance is in Riverside, Orange, San Bernardino, and San Diego Counties.

Legend has Ecological Sections;
black lines are subsections.

Southern California Coast 261B:
a-b,e-j.

Southern California Mountains & Valleys
M262B: a-d, e (lower elev. edges), f-g,
i-l, (m, lower elev. edges), n-p.




C. Life history, life form

Polycarpic, subshrub, woody at the base (suffrutescent shrub). Reproductive range 2 to 50 years (Sawyer et al. 2009).

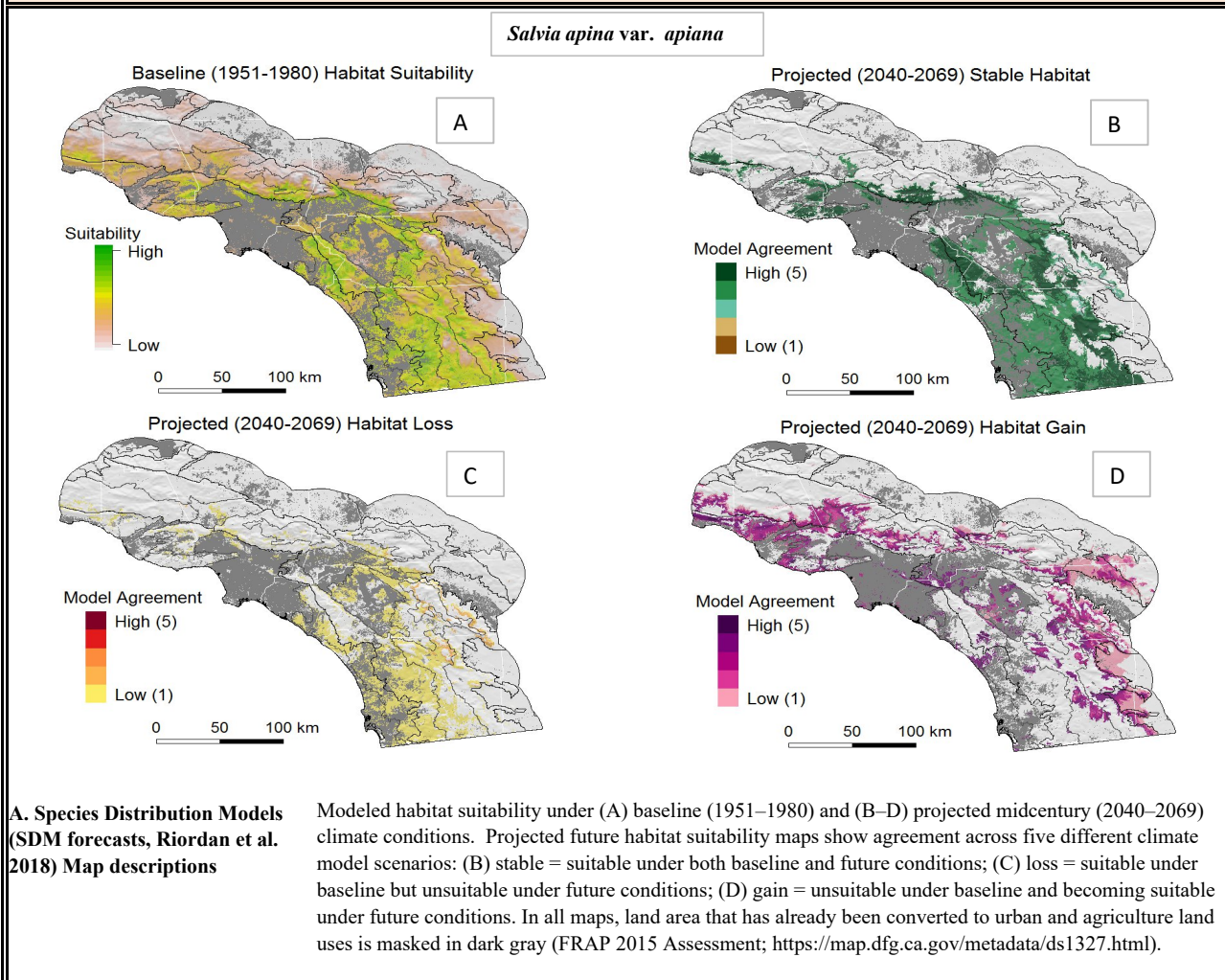
D. Distinguishing traits

White sage is a rounded, 1 to 2.5 m tall subshrub that has highly aromatic, 3 to 9 cm long, whitish to pale gray-green leaves, many of which persist throughout the year. Suffrutescent, nearly herbaceous stems arise from a woody base and produce opposite, lance-oblong, petioled leaves with thick blades. The blades have crenulate margins (small rounded teeth), taper into the petiole, and are covered with short appressed hairs and oil glands that give the leaves a silvery sheen. The attractive white to pale lavender flowers with short greenish calyx are clustered in compact cymose branches of a tall graceful, often pink-tinged inflorescence (thyrsoid panicle) that extends from 0.5 to 1.5 m above the foliage (Munz & Keck 1968). The lower lip of the two-lipped corolla is long and ruffled and obstructs the corolla tube, whereas the upper lip is reduced to a small lobe. The long style ends in a stigma that protrudes forward about 15 mm beyond the floral tube (modified from Montalvo 2004).

S. apiana var. *compacta* is distinguished by its condensed and more spike-like panicle and distribution along the desert edge (Munz 1974).

E. Root system, rhizomes, stolons, etc.	Branched, fibrous root system that extends further laterally than deep (Hellmers et al. 1955). Feeder roots were concentrated in the top foot of soil around the root crown but also extended along major lateral roots.
F. Rooting depth	Roots tend to penetrate less than 1.5 m deep (Hellmers et al. 1955).
IV. HABITAT	
A. Vegetation alliances, associations	Occurs in many plant communities including chaparral, coastal sage scrub, yellow-pine forest, and the upper edges of desert scrub (McMinn 1939, Munz & Keck 1968). Once extensive stands occurred on alluvial fans in alluvial scrub vegetation in San Bernardino Co., especially in the Etiwanda and Cajon Pass, Cable Canyon areas (A. Montalvo, pers. obs.). White sage tends to occur as a dominant or co-dominant plant in shrublands with species such as <i>Artemisia californica</i> Less., <i>Encelia farinosa</i> A. Gray ex. Torr., <i>Eriogonum fasciculatum</i> Benth., <i>Mimulus aurantiacus</i> Curtis, <i>Yucca whipplei</i> Torr., and <i>Malacothamnus fasciculatus</i> (Torr. & A. Gray) Greene (Sawyer et al. 2009). White sage scrub is a sensitive plant community (S3G4).
B. Habitat affinity and breadth of habitat	Plants occupy dry slopes, fans, and low gradient deposits along streams (Munz & Keck 1968, Sawyer et al. 2009). In an extensive study of coastal sage scrub vegetation, plants occupied north and south-facing slopes, and slopes of gentle (0 - 5 °), medium (6 - 15 °) and steep gradients (16 ° and above) nearly equally; plants occupied rocky as well as unconsolidated substrates (Kirpatrick & Hutchinson 1980). 
	White sage is abundant on the Etiwanda alluvial fan at the base of the San Gabriel Mtns. Photo A. Montalvo.
C. Elevation range	Generally from 300 - 1500 m but up to 1600 m (Sawyer et al. 2009, Jepson eFlora 2017).
D. Soil: texture, chemicals, depth	Plants occur on coarse to loamy soils derived from sandstone, conglomerate and sandstone, shale, granitic/dioritic rocks, and volcanic rocks (Westman 1981a). In western Riverside Co., plants also occur on serpentine soil (Montalvo 2004).
E. Precipitation	White sage occupies areas ranging from desert edges with less than 10 in of annual precipitation to coastal areas and foothills with over 25 in of precipitation. Occurs primarily in Mediterranean climate zone with cool to cold moist winters and warm to hot dry summers. Plants typically grow in areas with 10 to 40 inches of precipitation. For ecological sections occupied by white sage, annual normal precipitation ranges from 10 to 40 in (250 to 1,020 mm) in the Southern California Mountains and Valleys (M262B) and from 10 to 25 in (250 to 640 mm) in the Southern California Coast (261B).
F. Drought tolerance	Drought tolerant; plants often thrive in droughty soils and in habitats with high summer temperatures (Montalvo 2004). The crowded, whitish leaves are often held vertically and become folded during drought, likely adaptations for keeping leaves cool. In addition, many leaves are shed late in the dry season. In a desert wash in Baja California during summer drought, leaf conductance, transpiration rates, and turgor potentials were high and plants did not show signs of drought stress (Schmitt et al. 1993). In chaparral, white sage had higher water potentials throughout the day well into the summer drought than did most of the evergreen shrubs measured (Poole & Miller 1975). Water potentials decreased late in the dry season and recovered after November at the end of the seasonal drought. Within a natural hybrid zone, Gill and Hanlon (1998) found that xylem pressure potential was significantly higher in white than in black sage, hybrids were intermediate to the two parental species, and white sage drops fewer leaves during drought. These data support that white sage is more drought adapted than black sage.
G. Flooding or high water tolerance	Generally not flood tolerant. Plants occur in alluvial scrub vegetation on benches and fans that flood rarely (Sawyer et al. 2009).
H. Wetland indicator status for California	None.
I. Shade tolerance	Plants require full sun (Keator 1994).



V. CLIMATE CHANGE AND PROJECTED FUTURE SUITABLE HABITAT



B. SDM summary

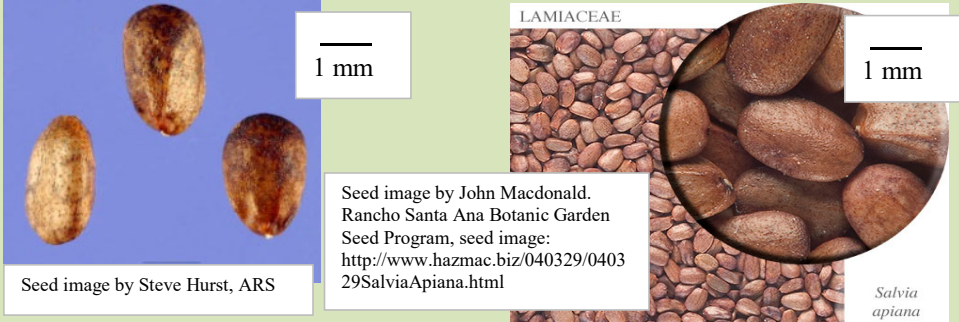
Species distribution model predictions of future suitable habitat for white sage in the 21st century with respect to climate change are variable. Assuming a future of continued high greenhouse gas emissions, Riordan et al. (2018) predicted 48–100% of baseline habitat for white sage in southern California would remain suitable (stable) under mid-century conditions across climate scenarios from five different general circulation models (GCMs) (SDM maps Fig. B). Predicted stable suitable habitat was high ($\geq 93\%$) and gain in suitable habitat (41–54%) exceeded loss under four of five climate scenarios (SDM maps Figs. C-D). Only under the wettest future climate scenario (CNRM) did predicted loss in suitable habitat (52%) exceed gain (15%). Previous SDM studies predicted greater losses in habitat suitability for white sage under projected climate change. Riordan & Rundel (2014) predicted 35–40% loss in suitable habitat by mid-century, rising to 56–63% by the end of the 21st century. Principe et al. (2013) also predicted greater loss in suitable habitat, particularly in the Perris Valley and Hills areas.


Land use, altered fire regimes, invasive species, and their interaction with climate change could negatively affect white sage, even if projected habitat loss 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). White sage is a drought-tolerant facultative seeder, regenerating by both resprouts and seeds after fire (see VI. D. Regeneration after fire or other disturbance). However, repeated burning kills seedling and mature plants, contributing to the conversion of coastal sage scrub to annual grassland (Talluto & Sudding 2008, Zedler et al. 1983). In addition, the high level of habitat conversion and fragmentation across the southern and low elevation portions of the species' range creates a considerable barrier to seed and possibly pollen dispersal. This likely reduces gene dispersal, genetic variation, and the adaptive capacity of the species to respond to changing conditions. Riordan & Rundel (2014) caution that land use may compound projected climate-driven losses in habitat suitability for southern California shrublands. They predict that the combined impacts of projected land use and climate change could result in as much as 66% loss in currently suitable habitat for white sage by the end of the century (Riordan & Rundel 2014).

<p>C. SDM caveat (concerns)</p>	<p>The five GCMs used to predict future habitat suitability assume a ‘business-as-usual’ scenario of high greenhouse gas emissions that tracks our current trajectory (IPCC scenario RCP 8.5). They show how climate may change in southern California and highlight some of the uncertainty in these changes. The true conditions at mid-21st century, however, may not be encompassed in these five models. Predictions of current and future habitat suitability should be interpreted with caution and are best applied in concert with knowledge about the biology, ecology, population dynamics and demographics of the species. They are best interpreted as estimates of exposure to projected climate change, not population-level persistence. Our models characterize habitat suitability with respect to climate and parent geology but do not include other factors, such as biotic interactions or disturbance regimes, that may also influence species distributions. Additionally, they do not include the adaptive capacity of a species, which will affect its sensitivity to changes in climate. See Riordan et al. (2018) for more information on SDM caveats.</p>
<p>VI. GROWTH, REPRODUCTION, AND DISPERSAL</p>	
<p>A. Seedling emergence relevant to general ecology</p>	<p>Seedling emergence and establishment in shrublands is associated with gaps in mature vegetation, and within grasslands in areas where herbs have been removed by gophers (DeSimone & Zedler 1999, 2001).</p>
<p>B. Growth pattern (phenology)</p>	<p>Most seedling and vegetative growth occurs in the cool rainy season between January and April and continues until the soil becomes dry in the late spring to early summer. Seedlings grow relatively fast, have little herbivore damage, and fold their leaves in response to drought (DeSimone & Zedler 2001). Plants tend to mature in the second year but in good years may flower the first year. Inflorescences arise from the upper nodes in spring and produce flowers from April to July, peaking in late May, depending on location (CCH 2016). Leaf growth over the season results in a seasonal dimorphism in leaf size (Westman 1981b). Smaller leaves are produced on short shoots (brachyblasts) that develop from leaf axils along the main elongated stems (dolichoblasts) and are often retained when the older, longer dolichoblast leaves are shed during drought. With the return of seasonal rains, the short shoots elongate into long shoots, and the retained short leaves continue to expand and subtend the next generation of short shoots and leaves.</p>
<p>C. Vegetative propagation</p>	<p>Plants resprout from the base after disturbance such as fire but otherwise do not typically spread vegetatively. In some instances prostrate stems develop roots in unburned sites and may be able to generate new plants (Gordon & White 1994).</p>
<p>D. Regeneration after fire or other disturbance</p> 	<p>White sage is a facultative seeder after fire (Keeley et al. 2006) and fire is a normal disturbance factor of most plant communities within which white sage occurs. Following fire, this shrub frequently sprouts from distinct basal burls (Westman et al. 1981, Keeley 1998), but year-old seedlings are killed by fire, and repeated burning kills mature plants (Zedler et al. 1983). Seedlings can emerge from the seedbank in the first season after fire, but reported densities are low (Zedler et al. 1983, Keeley 1998), and high intensity fires can kill seeds (Keeley & Fotheringham 1998). In a study of many postfire plots, Keeley et al. (2006) found that nearly twice as many white sage seedlings emerged in the third season after fire as in the first and second seasons. They also found many more seedlings in coastal sage scrub plots than in chaparral plots.</p> <div style="border: 1px solid black; padding: 5px; width: fit-content; margin: 10px auto;"> <p>Photo. Resprouting in 2007 after Blue Cut fire. A. Montalvo</p> </div>
<p>E. Pollination</p>  <div style="border: 1px solid black; padding: 5px; width: fit-content; margin: 10px auto;"> <p>Flowers before visited with lip in closed position. A. Montalvo</p> </div>	<p>The flowers of white sage have a specialized pollination mechanism (Ott et al. 2016). The lower lip of the flower blocks access to the nectar reward until the lip is pushed downward, causing the stamens to swing downwards while placing the anthers in a position to contact a large bee. Only large bees are able to trigger the mechanism.</p> <p>Based on the floral morphology and stamen release mechanism, only some of the larger bee visitors are capable of transferring pollen to the highly exerted stigmas. Grant and Grant (1964) report three species of <i>Xylocopa</i> and a species of <i>Bombus</i> as effective pollinators. Hummingbirds, honeybees, bombyliid flies, and small species of native bees (primarily <i>Anthophora</i>, <i>Diadastia</i>, and <i>Osmia</i>) sometimes visit flowers (Grant & Grant 1964) but are thought to be ineffective as pollinators (modified from Montalvo 2004).</p> <p>Recently, Ott et al. (2016) studied pollination of <i>S. apiana</i> in three natural populations in southern California and at Rancho Santa Ana Botanic Garden. They confirmed that only large bees (<i>Bombus</i> and <i>Xylocopa</i>) trigger the release mechanism and observed two species of <i>Xylocopa</i> and two species of <i>Bombus</i> visiting flowers. The largest bee (<i>Xylocopa varipuncta</i>) had the best fit to the flowers and readily transferred pollen to stigmas and also visited fewer flowers within a plant than the other bees. They also moved rapidly between plants, effecting outcrossed pollinations. (It was not mentioned if the visiting <i>Bombus</i> were workers or queens. The size difference can be substantial.)</p>

E. ... continued	<p><i>Xylocopa</i> were infrequent, and 95% of visits were by the European honey bee (<i>Apis mellifera</i>) which visited many flowers within a plant. Also, honey bees were not a good fit to the flowers and transferred less pollen to stigmas than the larger bees. Overall, seed set of open-pollinated flowers was 56% compared to a maximum of 85% obtained from hand pollinations, suggesting that infrequent visits by the best pollinator (<i>X. varipuncta</i>) limited seed set. Conservation of native bee populations will be especially important for reproduction and gene dispersal among populations. Large bees, including <i>Bombus</i> are in decline in California and elsewhere (Murray et al. 2009).</p>
F. Seed dispersal	<p>The small nutlets fall from the dried calyx but are secondarily dispersed by harvester ants and seed-caching rodents. Seed traps revealed that seeds dispersed up to 3 m away and that there was higher secondary removal rate of seeds in coastal sage scrub (80 percent) than in grassland (0 percent) or the ecotone of the two habitats (about 40 percent) (DeSimone & Zedler 2001). Other modes of dispersal may also occur. When wetted, the surface of the achene is mucilaginous and becomes sticky. Zona (2017) suggests the wet seeds may sometimes stick to animals and disperse.</p>
G. Breeding system, mating system	<p>The flowers of white sage are self-compatible (Ott et al. 2016). Anthers release most pollen prior to maturity of stigmas (protandrous), and the stigma protrudes far beyond the anthers (Montalvo 2004). This configuration ensures that flowers receive pollen from other flowers; however, the inflorescences are large, and there can be many flowers of different stages open at the same time on a plant, making some transfer of pollen to flowers within the same plant possible. Ott et al. (2016) observed bees moving between plants, but also observed bees, especially honey bees (see VI. E. Pollination) transferring pollen among flowers of a single plant. They suggest that most pollinations may be geitonogamous (self-pollen transferred from flowers of same plant). The interplant movements by the most efficient pollinator, <i>Xylocopa varipuncta</i>, protandrous flowers, and presence of interspecific hybrids with <i>S. mellifera</i> suggest that there is also outcrossing and that the mating system is mixed self and outcrossing. It is likely that the degree of selfing will vary among populations and years depending on the relative abundance of honey bees and <i>Xylocopa</i>.</p>
H. Hybridization potential	<p>White sage hybridizes with other <i>Salvias</i> with the same chromosome number, including <i>S. mellifera</i>, <i>S. munzii</i>, <i>S. leucophylla</i>, <i>S. clevelandii</i>, <i>S. eremostachya</i>, <i>S. pachyphylla</i>, and <i>S. vaseyi</i> (Epling 1938, McMinn 1939). Hybrid zones between <i>S. mellifera</i> (black sage) and white sage are especially common (Montalvo 2004). Hybrids exhibit a range of intermediate floral and leaf traits (Epling 1947a, b; Anderson & Anderson 1954) and differ in leaf anatomy (Webb & Carlquist 1964). Most hybrids are thought to be first generation crosses or backcrosses to black sage, and they tend to grow very close to the parental types.</p> <p>Although black sage and white sage overlap in range, they have different habitat affinities. Their ranges overlap in most of coastal southern California, but white sage is not found north of Santa Barbara Co., and it ranges further south into Baja California and eastward into the edge of the desert than does black sage. Both species can occur intermingled, but black sage tends to be found in flatter, more mesic areas, while white sage is usually on drier slopes (Epling 1947a, Anderson & Anderson 1954, Grant & Grant 1964, Gill & Hanlon 1998). As such, most sites contain a single species, but hybrids are often present where the species co-occur (Meyn & Emboden 1987).</p> <p>The potential for reproductive isolation of the species within areas of overlap has been examined most thoroughly by Grant and Grant (1964), augmenting earlier observations (Epling 1947a, Anderson & Anderson 1954). White sage generally flowers later than black sage, and the short overlap in flowering time of one to several weeks limits hybridization. In addition, white sage has large, highly modified flowers that are pollinated almost exclusively by large carpenter and bumblebees (<i>Xylocopa</i> and <i>Bombus</i>), while black sage has smaller, unmodified flowers that are pollinated primarily by honeybees and small native solitary bees.</p>
I. Inbreeding and outbreeding effects	<p>Inbreeding: Hand-self pollinations resulted in 55.8% seed set compared to 85.5% for hand-outcrossed pollinations (Ott et al. 2016). This suggests there is substantial inbreeding depression in seed set. No studies have examined of the success of selfed compared to outcrossed seeds.</p> <p>Outbreeding: There are no comparisons of the effect of matings among populations. Hybrids between black sage and white sage are fully viable but, on average, suffer reduced fertility relative to parental species (Epling 1947a, Meyn & Emboden 1987). There are also fewer seeds per flower in F₁ back crosses to both parental species (Grant & Grant 1964).</p>
VII. BIOLOGICAL INTERACTIONS	
A. Competitiveness	<p>In plots that were hand weeded and seeded in a twice-normal rainfall year, about a quarter of the seedlings survived to the second year (Storms 1999). Seedling survival is expected to be much lower in dry years and weedy areas (Montalvo 2004).</p>

B. Herbivory, seed predation, disease	Urn-shaped insect galls form on leaves (Clarke et al. 2007).
C. Palatability, attractiveness to animals, response to grazing	The essential oils and terpenoid compounds found throughout the plants may deter many herbivores (Dentali & Hoffman 1992).
D. Mycorrhizal? Nitrogen fixing nodules?	The roots of white sage form associations with arbuscular mycorrhizal fungi that may also assist plants in low nutrient and droughty habitats (Volgelsang et al. 2004).
E. Insect pollinators	The bee genera that best pollinate white sage (<i>Bombus</i> , <i>Xylocopa</i> , see VI. C. Pollination) have been shown to fly distances of 1,000 to 10,000 m (Zurbuchen et al. 2010). Declines in native bee populations are of great concern (Murray et al. 2009). Habitat fragmentation from agriculture and urbanization have resulted in declines in pollinator populations and decreases in pollination services (e.g., Kremen et al 2002). The most common species of <i>Bombus</i> in southern California are particularly sensitive to urban development (Schochet et al. 2016) with each species responding differently to habitat variables at a range of spatial scales (variables such as amount of sage plant cover – either <i>S. apiana</i> or <i>S. mellifera</i> – impervious surfaces, distances to major roads, and distance to coast for habitat reserves, fragments, and urban areas). Habitat corridors are used by bees and are needed to help maintain bee and plant populations (Townsend & Levey 2005).
VIII. ECOLOGICAL GENETICS	
A. Ploidy	Plants are considered diploid (2 n = 30); counts show a haploid count of n = 15 chromosomes (Epling et al. 1962).
B. Plasticity	No published data.
C. Geographic variation (morphological and physiological traits)	There is a north to south and east to west geographic gradient in floral morphology (Meyn & Emboden 1987). For example, the lip of the corolla and stamen filaments are longer toward the coast. Other than this and the more compact inflorescences on the desert edge for var. <i>compacta</i> , no other reports of geographic variation were found in the literature. Studies are needed to determine if the gradients in flower lip and stamen filament lengths are under genetic control or caused primarily by plastic response to the environment.
D. Genetic variation and population structure	No published data. The potential for mixed mating in this species together with restricted seed dispersal, but potentially long pollen dispersal distances suggest that variation among nearby populations that flower at the same time is relatively low. When populations are connected by gene dispersal, variation in genetically-controlled morphological traits would be unlikely to correlate with gradients in the environment, except under strong selection.
E. Phenotypic or genotypic variation in interactions with other organisms	No published data found.
F. Local adaptation	No published data. This species occupies sites that vary sufficiently in elevation and rainfall patterns to have likely developed differences in adaptive traits such as timing of flowering, leaf flush, tolerance to freezing, and water use efficiency. It is not known if the switch to a more compact form inflorescence in what has been called <i>S. apiana</i> var. <i>compacta</i> or the changes that occur in flower morphology from the coast to inland sites are adaptive traits. It has been suggested that the compact form may be a result of past hybridization with another taxon (e.g., Walker et al. 2015). However, it is not unusual for plants on the more arid end of an environmental gradient to develop adaptations that aid in water use efficiency or reduction of water loss. In addition, populations in desert scrub are likely to be more cold tolerant than those from coastal locations (Montalvo 2004).
G. Translocation risks	Risks from hybridization among populations from different ecological sections are unstudied, but hybridization is very likely. Hybrids between white sage and black sage tend to be better adapted to sites intermediate between the parental species (Anderson & Anderson 1954, Meyn & Emboden 1987, Gill & Hanlon 1998). Data on the inability of hybrids to spread suggests they may not be as fit as their parental lines.

IX. SEEDS	 <p>Seed image by Steve Hurst, ARS</p> <p>Seed image by John Macdonald. Rancho Santa Ana Botanic Garden Seed Program, seed image: http://www.hazmac.biz/040329/040329SalviaApiana.html</p> <p>LAMIACEAE</p> <p>Salvia apiana</p>
A. General	The four nutlets are about 2 to 3 mm long, somewhat rectangular, narrow in cross-section, keeled on one side, convex on the other side, and often grey-brown to light brown (Montalvo 2004). Seed lots often obtain 70% purity and 50% germination (Mirov & Krabel 1939; Jody Miller, S&S Seeds, pers. com.). A generic germination test for shrubby sages is incubation at 15/25 °C or 20/30 °C in the light, with first count at 7 days and last count at 21 days, followed by tetrazolium (TZ) staining of ungerminated seeds to determine if they are dormant (Meyer 2008).
B. Seed longevity	A dry seed lot (mostly stored in a Mason jar) tested at Rancho Santa Ana Botanic Garden after 24 years under variable storage conditions (transferred between room temperature, refrigeration, and freezing) had 43% germination (Michael Wall, pers. com.). Seeds are potentially long-lived in soil seed banks (Sawyer et al. 2009) and likely in dry storage (Meyer 2008).
C. Seed dormancy	Dormant seeds of <i>Salvias</i> may build up in the soil and form a persistent seed bank (Keeley & Keeley 1984, Meyer 2008).
D. Seed maturation	Seeds mature mid to late summer within the persistent calyx (Montalvo 2004). Within a site, seed filling tends to be higher on north compared to south-facing slopes (DeSimone & Zedler 2001). Seeds tend to be filled only in good rainfall years (Clarke et al. 2007).
E. Seed collecting and harvesting	Seeds are collected from the dry, fruiting inflorescences, usually in July and August, depending on site (Montalvo 2004).
F. Seed processing	Process seeds to remove chaff and insects. Wall and Macdonald (2009) report first rubbing the dry, ripened flower clusters with the persistent calyx over a medium screen, then lightly rubbing and sorting material through #14 and #25 sieves. A blower can then be used to remove the empty nutlets and chaff; blower speed set to low to separate chaff, and higher speed to remove sterile seed.
G. Seed storage	Cold dry storage. Seeds stored in sealed warehouse storage or at 4 °C had little loss in viability during 5 to 7 years, but seeds in unsealed storage with fluctuating relative humidity had losses in viability; seeds also increased in germination (from 19 to 43%) after a year in warehouse storage, suggesting a dry after-ripening requirement (report by Kay & Young in Meyer 2008).
H. Seed germination	<p>Seed lots usually have a fraction of seeds that germinate without pretreatment, with maximum germination around 42% (Meyer 2008), although up to 70% germination had been reported (Mirov & Kraebel 1931). Others have found seeds germinate at higher percentages after "fire" treatments, indicating there may be variation among seed lots and populations in germination response. Keeley (1987) showed that exposure to 70 °C for 1 hour followed by incubation in light substantially increased germination over controls, that heat shock for 5 minutes at 100 °C had no effect, and that exposure for 5 min at 120 °C killed seeds. Leachate made from water and charred wood did not increase germination (Keeley 1987), but cool smoke treatment increased germination (Keeley & Fotheringham 1998). Liquid smoke products can also be used to significantly increase germination (Montalvo 2004).</p> <p>In a recent experiment comparing seed germination treatments in the related <i>S. mellifera</i>, treatment with liquid smoke (Wright's Hickory Seasoning, B&G Foods, Inc.) resulted in significantly higher germination rates than the controls. Successful liquid smoke treatments included soaking seeds in pure liquid smoke or in dilutions of 1 part liquid smoke with 10 to 2000 parts water for 10 min. In black sage, heating seeds for 5 min at 70°C resulted in about twice the germination relative to the best liquid smoke treatment. All treatments were followed by cold stratification for one month at 4 °C.</p>
I. Seeds/lb	341,000 seeds/lb (Mirov & Krabel 1939); 324,000 seeds/lb (Meyer 2008); Average of 93,900 live seeds/bulk lb. (S&S Seeds 2016).
J. Planting	Plant seeds approximately 2 mm (1/8 inch) deep in plug flats with well drained seedling mix. Untreated seeds often begin to germinate in about 4 days (Everett 2012), but treating seeds with smoke prior to planting may increase germination (see IX. H. Seed germination). For seeding for restoration, see X. B. Habitat restoration.

<p>K. Seed increase activities or potential</p>	 <p>Juvenile plant in seed increase field. Photo: J. Burger 2010.</p> <p>The Irvine Ranch Conservancy planted a one-acre field with 2-inch liners in fall 2009 to establish a seed increase field. Plants received some supplemental irrigation and the first individuals flowered by the end of the first spring. Over four years of harvest, three of which were in drought years, peak production was in year two, the wettest year. Average yield was 10 pure live seed pounds (PLS)/acre. At a second farm site planted in 2015, the first yield was 24 PLS lb/acre. The generally low yields were likely due to the low number of flowers per plant, pollination issues, and drought. Seed harvest was relatively easy (data provided by J. Burger & M. Garrambone, pers. com.).</p>
<p>X. USES</p>	
<p>A. Revegetation and erosion control</p>	<p>White sage is used in many restoration and roadside revegetation projects. Newton & Claassen (2003) list white sage as suitable for dry slopes in southwestern California (planted as seed or containers). Its fast growth helps to achieve vegetative cover quickly.</p>
<p>B. Habitat restoration</p>	<p>White sage is used frequently in the restoration of coastal sage scrub in southern California, in part because it has decreased dramatically in percent cover in western Riverside Co. since the early 1930s (Minnich & Dezzani 1998). Successful restoration will depend on controlling the factors associated with its decrease, especially invasive plants and short fire-return intervals so that shrubs can establish, reach maturity, and build-up a seed bank (Montalvo 2004).</p> <p>Plants can be established by direct seeding in the fall before the onset of early rains, or in early January without irrigation (e.g., DeSimone 2011). Later sowing allows for control of early germinating weed species before sowing. If seed germination tests show low germination but high seed viability, seeds can be treated with dry or liquid smoke before sowing. If liquid smoke is used, seeds must be air-dried prior to dry broadcasting, keeping in mind that dormant seeds can result in a beneficial seed bank and establishment over several years (Montalvo 2004). Kimball et al. (2014) found significantly higher germination in hand-broadcast plots compared to drilled plots. Shallow planting methods, such as hand-broadcasting, hydroseeding and imprinting, are likely to produce higher germination than drilling because seed germination is improved with exposure to light (Keeley 1987, Montalvo 2004). Hydroseeding can be very successful on steep slopes and road cuts. Dry broadcasting seeds over a seed bed shallowly scarified with a springtooth harrow followed by dragging the harrow upside down has also been successful in Riverside Co. (A. Montalvo pers. obs.). In hand-sown plots, DeSimone (2011) found significantly higher seedling densities of white sage when the sowing was followed by tamping. Tamping was done with a lawn roller. Based on seedling survival data (Storms 1999, DeSimone & Zedler 2001), even under well-weeded and rainy conditions, fewer than 25% of seedlings should be expected to survive through their first year.</p> <p>Plants can also be established from container plants or plugs using supplemental irrigation in the first year. However, planting from seed decreases the likelihood of spreading disease from the nursery to wild sites (DeSimone 2011).</p>
<p>C. Horticulture or agriculture</p>	<p>Horticulture: The generally rounded form with attractive whitish leaves and long graceful, pink-tinged inflorescence stalks make this an attractive shrub for background areas of dry landscape gardens (Keator 1994, Clebsch 1997, Perry 2010). Plants require full to nearly full sun, well-drained soil, do not tolerate constantly damp conditions, and are sensitive to temperatures below 7°C (Keator 1994, Clebsch 1997). Nursery stock is readily produced from seeds or softwood cuttings. Seeds are recommended for production of nursery stock for habitat restoration so that more genetic diversity is represented in the outplanted plants. Detailed protocols for propagation from cuttings are provided by the Catalina Island Conservancy and USDA Plants (see links below for NPNPP 2016 or USDA Plants database: https://plants.usda.gov/plantguide/pdf/cs_saap2.pdf).</p> <p>Agriculture: Plant in fall or very early winter. Fields can be started from seeds or from plants started in containers (see IX. K. Seed increase potential).</p>
<p>D. Wildlife value</p>	<p>White sage leaves are an important browse of mountain sheep in the winter and spring (Perry et al. 1987). Deer, antelope, elk, and rabbits also browse plants (Stevens & O'Brien 2016). The woodrats <i>Neotoma lepida</i> and <i>N. bryanti</i> eat the leaves (Torregrossa & Dearing 2009). Birds such as quail and grouse and small mammals eat the seeds (Stevens & O'Brien 2016).</p>
<p>E. Plant material releases by NRCS and cooperators</p>	<p>None.</p>

F. Ethnobotanical	<p>Leaves contain essential oils and a variety of diterpenes and triterpenes, including carnosic acid, oleolic acid, and ursolic acid, some of which have been linked to the medicinal use of white sage by native tribes (Dentali & Hoffman 1992). A tincture of the leaves has been used internally as a diaphoretic and diuretic and externally to wash skin. The tincture may have antimicrobial and other medicinal properties. Antibacterial and antifungal activity of several compounds have been verified in vitro (Dentali & Hoffmann 1992). Allison et al. (2016) isolated flavonoid chemicals from leaves and stems and found a the compound jaceosidin known to have anti-inflammatory, anti-allergenic, and antibacterial properties. They also found two other flavonoids and examined mechanisms of antibacterial action. Furthermore, root extracts were found to inhibit the growth of the <i>Staphylococcus aureus</i>, <i>Streptococcus pyogenes</i>, <i>Enterococcus faecalis</i> and <i>Candida albicans</i> (Córdova-Guerrero et al. 2016).</p> <p>In addition to medicinal use, the dried leaves have been used as a smudge and crushed as a soapless shampoo (Bean & Saubel 1972, Moore 1989). Other uses are described in NAE (2016) and Stevens & O'Brien (2016).</p> <p>Seeds have been used as food and leaves for flavoring by native peoples. The seeds were an important component of pinole, a staple food (NAE 2016, Stevens & O'Brien 2016).</p>
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XII. CITATION	<p>Montalvo, A. M., E. C. Riordan, and J. L. Beyers. 2017. Plant Profile for <i>Salvia apiana</i>, Updated 2017. Native Plant Recommendations for Southern California Ecoregions. Riverside-Corona Resource Conservation District and U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Riverside, CA. Available online: https://www.rcrec.org/plant-profiles</p>
X. III. LINKS TO REVIEWED DATABASES & PLANT PROFILES	
Fire Effects Information System (FEIS)	No matches: https://www.feis-crs.org/feis/
Calflora	https://www.calflora.org/cgi-bin/species_query.cgi?where-calrecnum=7298
Jepson Interchange	https://ucjeps.berkeley.edu/cgi-bin/get_cpn.pl?43038
Jepson eFlora (JepsonOnline, 2nd ed.)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=43038
USDA PLANTS	https://plants.usda.gov/core/profile?symbol=SAAP2
Native Plant Network Propagation Protocol Database (NPNPP)	https://npr.rngr.net/propagation
Native Seed Network (NSN)	https://nativeseednetwork.org/
GRIN (provides links to many resources)	https://npgsweb.ars-grin.gov/gringlobal/taxonomydetail.aspx?id=32906
Wildand Shrubs	https://www.fs.usda.gov/treesearch/pubs/27005
Flora of North America (FNA) (online version)	no matches: http://www.efloras.org/flora_page.aspx?flora_id=1
Native American Ethnobotany (NAE)	http://naeb.brit.org/uses/search/?string=Salvia+apiana
Woody Plant Seed Manual	https://www.fs.usda.gov/nsi/nsi_wpsm.html
XIV. IMAGES	<p>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. Image in cell IX. K. courtesy of Jutta Burger, Irvine Ranch Conservancy (copyright 2017). All other images by Arlee Montalvo (copyright 2017) unless otherwise indicated with rights reserved. 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.</p>

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