






I. SPECIES	<i>Ceanothus crassifolius</i> Torrey	
<p>NRCS CODE: (CECR)</p>  <p>Note dark hypanthium in center of white flowers. Photos by A. Montalvo.</p> 	<p>Family: Rhamnaceae Order: Rhamnales Subclass: Rosidae Class: Magnoliopsida</p> <p>Lower right: Ripening fruits, two already dehisced. Lower center: Longitudinal channeling in stems of old specimen, typical of obligate seeding <i>Ceanothus</i> (>25 yr since last fire).</p> 	 
A. Subspecific taxa	<ol style="list-style-type: none"> 1. <i>C. crassifolius</i> Torr. var. <i>crassifolius</i> 2. <i>C. crassifolius</i> Torr. var. <i>planus</i> Abrams (there is no NRCS code for this taxon) 	
B. Synonyms	<ol style="list-style-type: none"> 1. <i>C. verrucosus</i> Nuttall var. <i>crassifolius</i> K. Brandegee (Munz & Keck 1968; Burge et al. 2013) 2. <i>C. crassifolius</i> (in part, USDA PLANTS 2019) 	
C. Common name	<ol style="list-style-type: none"> 1. hoaryleaf ceanothus, sometimes called thickleaf ceanothus or thickleaf wild lilac (Painter 2016) 2. same as above; flat-leaf hoary ceanothus and flat-leaf snowball ceanothus are applied to other taxa (Painter 2016) 	
D. Taxonomic relationships	<p><i>Ceanothus</i> is a diverse genus with over 50 taxa that cluster in to two subgenera. <i>C. crassifolius</i> has long been recognized as part of the <i>Cerastes</i> group of <i>Ceanothus</i> based on morphology, life-history, and crossing studies (McMinn 1939a, Nobs 1963). In phylogenetic analyses based on RNA and chloroplast DNA, Hardig et al. (2000) found <i>C. crassifolius</i> clustered into the <i>Cerastes</i> group and in each analysis shared a clade with <i>C. ophiophilus</i>. In molecular and morphological analyses, Burge et al. (2011) also found <i>C. crassifolius</i> clustered into <i>Cerastes</i>. <i>Cerastes</i> included over 20 taxa and numerous subtaxa in both studies. Eight <i>Cerastes</i> taxa occur in southern California (see I. E. Related taxa in region).</p>	
E. Related taxa in region	<p>In southern California, the related <i>Cerastes</i> taxa include: <i>C. cuneatus</i> Nutt. var. <i>cuneatus</i>, two varieties of <i>C. megacarpus</i> Nutt., <i>C. ophiophilus</i> S. Boyd, T. Ross, & L. Arnseth, <i>C. otayensis</i> McMinn, <i>C. perplexans</i> Trel., and <i>C. vestitus</i> Greene (Burge et al. 2011).</p>	
F. Taxonomic issues	<p>Based on a 2011 update of the Taxonomic Integrated System for Rhamnaceae, <i>C. c.</i> var. <i>planus</i> is not recognized by USDA PLANTS (2019), but it is recognized in the online Flora of North America (FNA) and the Jepson eFlora (2019). In most of its range, <i>C. c.</i> var. <i>crassifolius</i> is dominant and easy to identify. The two varieties intergrade in Santa Barbara and Ventura counties (McMinn 1939a, Fross & Wilken 2006) and may represent the extremes of an integrating network which needs more study to see if varietal rank is appropriate (Burge et al. 2013). Introgressive hybridization of var. <i>crassifolius</i> with several other <i>Ceanothus</i> species can occasionally make identification a challenge (Fross & Wilken 2006). The amount that the leaf margins are rolled under and denticulate in var. <i>crassifolius</i> can be variable, even within populations that are outside the range of hybridizing taxa (A. Montalvo pers. obs.).</p>	

II. ECOLOGICAL & EVOLUTIONARY CONSIDERATIONS FOR RESTORATION

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

SDM for:
C. c. var. crassifolius

Taxonomic stability - high (exception-hybrids)
Longevity - moderate-lived (30 to 90+ yr)
Parity - polycarpic
Flowering age - 5+ yr
Stress tolerance - moderate
Environmental tolerance - broad
Reproduction after fire - obligate seeder
Fragmentation history - historically low
Habitat fragmentation - low in mountains, high at low elevations

Seeds - long-lived
Seed dispersal distance - short
Pollen dispersal - intermediate to far
Breeding system - needs study; likely self-compatible with mixed mating system
Population structure - unknown; likely low
Adaptive trait variation - unknown
Chromosome number - stable within entire genus
Genetic marker polymorphism - no data
Average total heterozygosity - no data
Hybridization potential - high where overlaps with other *Cerastes* taxa

For *C. c. var. crassifolius*:

SDM projected midcentury suitable habitat - 93–100 % stable
SDM projected midcentury habitat gain - gain >> loss (assuming unlimited dispersal)

B. Implications for seed transfer (summary)

Gene dispersal of hoaryleaf ceanothus is aided primarily by bees, whereas seed dispersal occurs primarily near the seed-bearing plant. Dense stands of flowering plants can be very attractive to early-emerging bee taxa, including bumblebees which can move pollen hundreds of meters to over a kilometer away. Although plants may suffer and die back after prolonged drought, subsequent fire can rejuvenate populations from long-lived seed banks as long as soil moisture is sufficient, seedlings reach maturity, and fire return intervals are long enough to allow seed numbers to build up in the face of drought and seed losses to seed predators. In areas where populations become fragmented by development or type conversion, restoration may be warranted to reconnect migration corridors. For any planting site, best practices would include using seeds collected from many plants and potentially from several sites within the home ecological region and subregion of the plant, and within 500 feet in elevation. There is insufficient information about local adaptation, population structure, and genetic variation to justify relaxing distances to outside the ecological region of the planting site. When moving seeds within ecological regions, the warming of the climate and increasing climatic water deficit suggests that moving seeds from warmer toward cooler ecological subregions would be more prudent than the reverse.

III. GENERAL

A. Geographic range

Common at mid-elevations of coastal mountains and valleys of southern California and northern Baja California (Conard & Reed 2008).

B. Distribution in California; ecological section and subsection

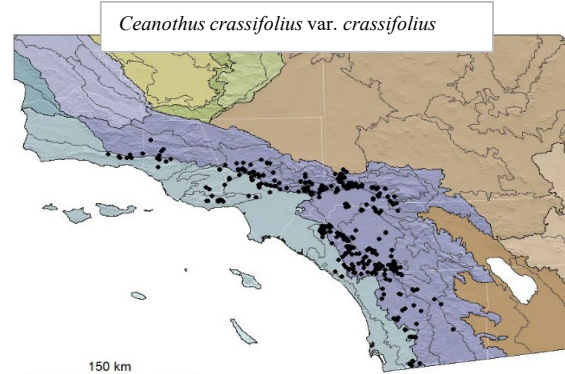
(sensu Goudey & Smith 1994; Cleland et al. 2007)

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

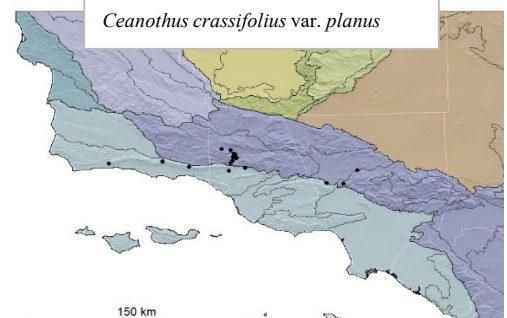
Map includes validated herbarium records (CCH 2016) as well as CalFlora (2016) and field surveys (Riordan et al. 2018).





Legend has Ecological Sections; black lines are subsections.

Ecological Section/subsection:
Southern California Mountains & Valleys
M262B: a,c-h,j,k,l,n,o,p
Southern California Coast 261B: b,e,f,g,i
Mojave Desert 322A: g (bordering M262Bg)



Ecological Section/subsection:
Southern California Mountains & Valleys
M262B: a,c,d
Southern California Coast 261B: b,e



C. Life history, life form	Shrub, polycarpic, evergreen, long-lived, obligate seeder. Lives 90+ years (Keeley 1975, Sawyer et al. 2009).
D. Distinguishing traits	<p>1. Woody shrub, 1–4 m tall; twigs grey to brownish; paired stipules dark, thickened, pointed, and persistent; leaves with petioles, opposite, elliptic to broadly elliptic, 1–3.5 cm long, evenly spaced along stem; blades rigid, single veined from base, with thick usually revolute (rolled under) margins with spinulose teeth, sometimes wavy, pale with dense white tomentose hairs below, and olive-green, glabrous to minutely papillose above; flowers white, with 5 sepals, petals and stamens, a 3-parted ovary and stigma, and dark hypanthial disk, in umbel-like clusters produced towards tips of branches.</p> <p>2. As above except blade margins thick, flat to revolute, usually lacking teeth, with undersides only sparsely to moderately tomentose.</p> <p>Vegetative hoaryleaf ceanothus is separated from co-occurring <i>Ceanothus</i> by their erect stature and thick, conical stipules subtending opposite leaves that are thick, leathery, 1-veined from the base, and somewhat evenly spaced on rigid stems. Leaves of var. <i>crassifolius</i> are also distinctly whitish below and somewhat concave.</p>
E. Root system, rhizomes, stolons, etc.	Branched, shallow spreading root system from short tap root. Hellmers et al. (1955) found an average maximum radial spread of 7.3 ft (2.2 m) and many lateral roots up to 14 ft (4.3 m) long. Long lateral roots were found on plants growing in shallow soil. Roots did not appear able to penetrate fine cracks in unweathered rock.
F. Rooting depth	Shallow. Observed to about 4 ft (1.2 m) deep (Hellmers et al. 1955).
IV. HABITAT	
<p>A. Vegetation alliances, associations</p>  <p>May 17, 2019. Juvenile plant from seed following fire. Plant is about 3 to 4 months old.</p>  <p>March 10, 2019. Seedling at about 1 month old.</p>	<p>Known from many chaparral and some alluvial scrub plant communities (Munz & Keck 1968, Holland 1986, Gordon & White 1994, Sawyer et al. 2009). Plants occur in near monotypic stands or co-codominant with <i>Adenostoma fasciculatum</i>, <i>A. sparsifolium</i>, <i>Malosma laurina</i>, <i>Cercocarpus betuloides</i>, <i>Salvia mellifera</i>, or <i>Xylococcus bicolor</i>. Other commonly associated shrubs include: <i>Arctostaphylos glandulosa</i>, <i>A. glauca</i>, <i>Ceanothus leucodermis</i>, <i>Diplacus</i> species, <i>Eriogonum fasciculatum</i> var. <i>foliolosum</i>, <i>Hesperoyucca whipplei</i>, <i>Keckiella antirrhinoides</i>, <i>Quercus berberidifolia</i> and <i>Rhus ovata</i>. The herbaceous perennial vine, <i>Marah macrocarpa</i>, is also a common associate. After fire, monotypic stands can develop. On more northerly exposures, <i>Heteromeles arbutifolia</i> and <i>Q. berberidifolia</i> sometimes recruit from seeds and transform the community (Sawyer et al. 2009).</p> <p>In chaparral, dominant within the <i>Ceanothus crassifolius</i> alliance (Sawyer et al. 2009) or codominant in the following associations:</p> <p><i>Ceanothus crassifolius</i>–<i>Adenostoma fasciculatum</i>–<i>Xylococcus bicolor</i> scrub; <i>Ceanothus crassifolius</i>–<i>Cercocarpus betuloides</i> scrub; <i>Ceanothus crassifolius</i>–<i>Adenostoma fasciculatum</i>–<i>Malosma laurina</i> scrub; <i>Ceanothus crassifolius</i>–<i>Adenostoma fasciculatum</i>–<i>Rhus ovata</i> scrub; <i>Ceanothus crassifolius</i>–<i>Adenostoma fasciculatum</i>–<i>Salvia mellifera</i> scrub;</p> <p><i>Adenostoma sparsifolium</i> shrubland alliance in:</p> <p><i>Adenostoma sparsifolium</i>–<i>Ceanothus crassifolius</i> scrub; <i>Adenostoma sparsifolium</i>–<i>Adenostoma fasciculatum</i>–<i>Ceanothus crassifolius</i> scrub</p> <p><i>Arctostaphylos glandulosa</i> shrubland alliance in:</p> <p><i>Arctostaphylos glandulosa</i>–<i>Adenostoma fasciculatum</i>–<i>Ceanothus crassifolius</i> scrub</p> <p><i>Arctostaphylos glauca</i> shrubland alliance in:</p> <p><i>Arctostaphylos glauca</i>–<i>Adenostoma fasciculatum</i>–<i>Ceanothus crassifolius</i> scrub</p> <p>Often occurs within the following alluvial scrub alliances/associations (Sawyer et al. 2009):</p> <p><i>Lepidospartum squamatum</i> scrub alliance in:</p> <p><i>Lepidospartum squamatum</i>–<i>Baccharis salicifolia</i> association (Buck-Diaz et al. 2011).</p>
 	

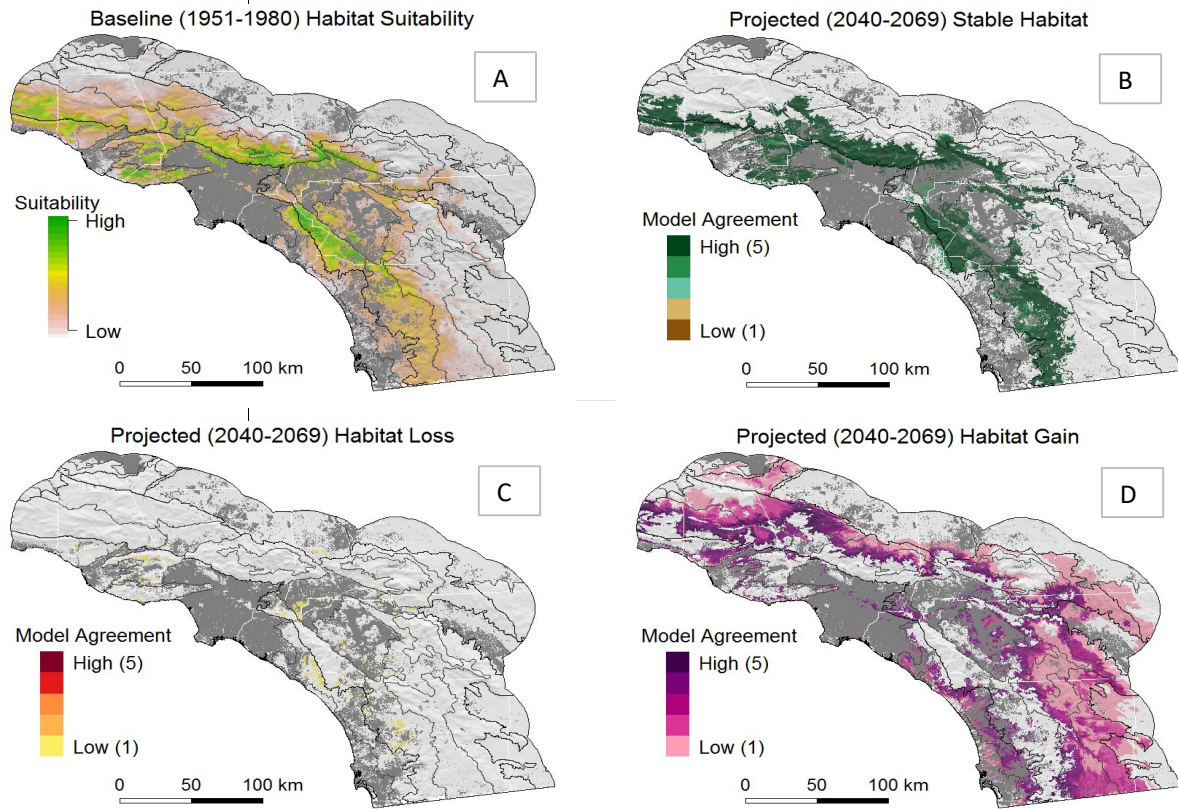
B. Habitat affinity and breadth of habitat	<p>1. <i>C. c.</i> var. <i>crassifolius</i>. Dry slopes and ridges, but also on well-drained alluvium of fans and outwash deposits along streams (Munz & Keck 1968, Buck-Diaz et al. 2011). Most common on coastal range slopes but also at lower elevations of interior mountains. Cover tends to be denser on south-facing than on north-facing slopes (Keeley 1987a, A. Montalvo & E. Riordan unpublished data).</p> <p>2. <i>C. c.</i> var. <i>planus</i>. Described as being restricted to coastal slopes of the Transverse Ranges, and seldom overlapping with var. <i>crassifolius</i> (Fross & Wilkens 2006).</p>
C. Elevation range	60–1,100 m (Fross & Wilken 2006), 40–1,300 m (Sawyer et al. 2009). For the Transverse and Peninsular Ranges, Gordon & White (1994) found elevation range to be 1,600–4,240 ft (488–1,292 m) with average of 3,052 ft (930 m). Davis et al. (2007) found that <i>C. crassifolius</i> was resistant to freezing-induced xylem dysfunction, allowing it to exist in cold-air drainages and at higher elevations than other <i>Ceanothus</i> species in the Santa Monica Mountains (e.g., <i>C. megacarpus</i> , <i>C. spinosus</i>). However, Hanes (1971) did not find <i>C. crassifolius</i> above 4,000 ft in plots surveyed in the San Gabriel and San Bernardino mountains.
D. Soil: texture, chemicals, depth	Occurs on substrates derived from a variety of parent materials (Fross & Wilken 2006). In the Santa Ana Mountains occurs on slopes and ridges with sandy loams to sandy clays derived from granitic and sedimentary rocks (A. Montalvo pers. obs.).
E. Precipitation	Precipitation falls primarily from November through May during the cool season. <i>Ceanothus crassifolius</i> occurs in areas with total annual precipitation ranging from 10 to 40 in (250 to 1020 mm). Annual normal precipitation ranges from 10 to 40 in for the interior Southern California Mountains and Valleys (M262B) and from 10 to 25 in for the Southern California Coast (261B). In these areas, plants tend to occur in areas with 15 to 25 in of precipitation.
F. Drought tolerance	Tolerant. Plants can reduce leaf heating by changing orientation of their leaves relative to the sun (see VIII. B. Plasticity). Hoaryleaf ceanothus are more drought tolerant and able to occupy more droughty soils than resprouting taxa of <i>Ceanothus</i> (Pratt et al. 2007, Pausas & Keeley 2014; see VII. A. Competitiveness). During prolonged drought, plants fail to flower and many plants suffer from the dieback of shoots. Shoot dieback appears to be caused by xylem cavitation followed by hydraulic failure (rather than owing to fungal infection) and may be a mechanism to conserve water (Davis et al. 2002), but some dieback can also be caused by pathogens (see VII. B. Herbivory, seed predation, disease). Prolonged severe drought can cause mortality in shallow-rooted <i>Ceanothus</i> species (Venturas et al. 2016, Jacobsen & Pratt 2018)
G. Flooding or high water tolerance	Plants exist in alluvial scrub in alluvial wash deposits that receive occasional flooding (see IV. A. Vegetation alliances; B. Habitat affinity)
H. Wetland indicator status for California	None.
I. Shade tolerance	Full sun. Seedlings of <i>C. crassifolius</i> grown experimentally in the shade did poorly (Pratt et al. 2012).



V. CLIMATE CHANGE AND PROJECTED FUTURE SUITABLE HABITAT

SDM maps

Maps are for models run on *C. c.* var. *crassifolius*. The sample size for var. *planus* was too small.




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; <https://map.dfg.ca.gov/metadata/ds1327.html>). Hi resolution maps are available for download (see Riordan et al. 2018).

B. SDM summary




We project that much (93–100 %) of the current suitable habitat for *C. c.* var. *crassifolius* will remain suitable by midcentury. There was high agreement in future stable habitat suitability under the five general circulation models (GCMs) considered. All (100%) of currently suitable habitat was projected to remain suitable in four of the five GCMs. Gains in habitat suitability were much more variable across GCMs, ranging from 20 to 219% increase relative to current suitable habitat. This makes sense biologically because *C. crassifolius* is highly tolerant to water stress (Pratt et al. 2008) and thus may be able to expand under warmer, drier conditions expected with climate change. Prolonged extreme drought, however, could be detrimental (Davis et al. 2002, Jacobsen & Pratt 2018). Principe et al. (2013) also predicted that most of the currently suitable habitat for *C. crassifolius* var. *crassifolius* will remain climatically suitable by mid-century, but predicted some losses in suitability in lower elevation areas of the Peninsular Ranges.

While our predictions suggest low risk of climate-driven loss in habitat suitability for *C. crassifolius* var. *crassifolius*, branch dieback and plant mortality have been observed during recent prolonged droughts (e.g., Davis et al. 2002 and S. Davis pers. com.). Dieback results in an accumulation of dead fuels and may happen more often if the frequency of extreme heat and prolonged droughts increase as the climate warms. Also, chaparral shrubs with shallow root systems may suffer more mortality in response to extended drought and extreme heat events (Jacobsen & Pratt 2018). This may be less of a problem for *C. crassifolius* in areas with fire return intervals as low as 15 to 25 years, if the seed bank has recovered.

B. SDM summary,continued	<p>The species may also be facing increasing fire risk related to continued population growth, urbanization, and ignition potential (Syphard et al. 2009) in concert with projected climate change and increasing drought stress (Westerling et al. 2011). A long-lived obligate seeder, <i>C. crassifolius</i> depends on fire for recruitment, but repeated fires with short fire return intervals cause population declines in obligate-seeding <i>Ceanothus</i> species (e.g., Zedler et al. 1983) and can contribute to vegetation type conversion (Jacobsen et al. 2004, Keeley & Brennan 2012). The high level of habitat conversion and fragmentation in southern California creates a considerable barrier to dispersal and gene flow that could negatively affect the adaptive capacity and ability of the species to respond to changing conditions. Suitable habitat is already heavily converted in lower elevations of the Transverse and Peninsular Ranges. Continued human land use may compound projected climate-driven losses in habitat suitability for southern California shrublands (Riordan & Rundel 2014).</p>
C. SDM caveat (concerns)	<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, and population dynamics/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>
VI. GROWTH, REPRODUCTION, AND DISPERSAL	
A. Seedling emergence relevant to general ecology	<p>Episodic. Seedlings emerge after fire (Keeley 1987a). A few seeds may germinate between fires but seedlings are quickly eaten by herbivores (Christensen & Muller 1975). The decrease in herbivores after fire may aid survival of seedlings. Drought-induced shrub dieback that opens canopies could lead to soil heating and seed germination as well, leading to seed bank depletion (R. Brandon Pratt, pers. comm.).</p>
B. Growth pattern (phenology)	<p>Seedlings emerge in the first winter following fire (Keeley 1987a). Most growth occurs during the cool, rainy season and most plants begin to flower in 5 years (Sawyer et al. 2009), but this can take longer with drought. Flower buds are produced at the end of the growing season in late spring and bolt in late winter after plants resume growth. Flowering occurs January to April, peaking in March (CCH 2016). Fruit maturation continues into late April, early May. Most fruits release seeds in May. Plants can sometimes live 90+ years (Sawyer et al. 2009), but they are considered to have medium longevity of 20-30 years by some (Burk 1978). These trends may vary depending on temperature and rainfall patterns.</p>
C. Vegetative propagation	<p>None in nature.</p>
D. Regeneration after fire or other disturbance	<p>Shrubs are usually killed by fire. Although many seeds may be killed during fire (Quinn 1994), seed mortality in chaparral shrubs may vary with the depth of seeds in the soil and fire severity (Keeley 1977, Davey 1982). Regeneration is from seeds germinating from long-lived soil seed banks after fire (Hanes 1971, Keeley 1975, Sawyer et al. 2009). In a study of post-fire plots, Keeley et al. (2006) found that nearly all seedlings of <i>C. crassifolius</i> emerged by the first spring after fire (N=13 sites). There was an average of 74 seedlings per pre-fire parent plant in the first postfire year, a ratio that varies widely and may depend on factors such as prefire vegetation composition and time since last fire. Seedling survival decreased each year to about 15% by the sixth postfire year. Recruitment exceeded its prefire proportional representation relative to other species.</p> <div data-bbox="175 1371 435 1577" style="text-align: center;">  </div> <div data-bbox="483 1556 1414 1640" style="border: 1px solid black; padding: 5px; margin-top: 10px;"> <p>left: Seedling with oval cotyledons and first true leaves. <i>C. crassifolius</i> seedlings emerged in February after the Holy Jim fire in the foothills of the Santa Ana Mountains in Riverside Co.</p> </div>
E. Pollination	<p>The small, unspecialized flowers of all <i>Ceanothus</i> species can be pollinated by a variety of insect visitors including small flies, bees, and occasionally butterflies (Moldenke 1976, Fross & Wilken 2006). <i>Ceanothus</i> is an important pollen plant for bumble bees (<i>Bombus</i> species) (Thorp et al. 2002). Moldenke & Neff (1974) documented flower visits to the closely related <i>C. cuneatus</i> or <i>C. perplexans</i> by bees in the genera <i>Lasioglossum</i>, <i>Hylaeus</i>, <i>Megachile</i>, <i>Perdita</i>, <i>Bombus</i> and <i>Andrena</i>.</p>

F. Seed dispersal	<p>When capsules dehisce, the ovary pops off and seeds are explosively ejected. Seeds are secondarily dispersed by animals or erosion events. Most seeds land near parent plants, but some are cast meters away (Sawyer et al. 2009). Seed casting distances were measured in <i>C. cuneatus</i>, a close relative with similar stature, fruit size, fruit position, and seed size (Evans et al. 1987, Pratt et al. 2007). Most seeds were cast in the middle of the day (when temperature highest and relative humidity lowest); 32% of the seeds fell beneath shrubs, 42% at the edges, decreasing outward to 1.9% at 9 m. Very similar results were found for <i>C. leucodermis</i>.</p>
G. Breeding system, mating system	<p>Inconclusive. Likely self-incompatible and outcrossing, but reports have been mixed. Nobs (1963) found some taxa in the <i>Cerastes</i> group to be self-incompatible, while others were "partially" self-fertile. <i>C. crassifolius</i> was not among the taxa reported as self-incompatible. Moldenke (1976) reports <i>Ceanothus</i> as self-incompatible, but Fross & Wilken (2006) concluded from the early studies of McMinn (1944) and Nobs (1963) that most <i>Ceanothus</i> are self-compatible.</p>
H. Hybridization potential	<p>Hybridizes with other species in the <i>Cerastes</i> subgenus causing much taxonomic confusion. Putative hybrids have been found where populations come into contact with <i>C. cuneatus</i>, <i>C. megacarpus</i>, and <i>C. perplexans</i> (Fross & Wilkin 2006). Known to hybridizes with <i>C. ophiochilis</i>, a narrowly distributed species (Boyd & Keeley 2002, Fross & Wilken 2006). Once thought to hybridize with <i>C. vestitus</i> (<i>C. greggii</i> var. <i>vestitus</i>) to form <i>C. x otayensis</i> (McMinn 1939a), but the putative hybrid is now recognized as <i>C. otayensis</i>. Morphometric analysis showed <i>C. crassifolius</i> was not a likely parental taxon (Boyd & Keeley 2002).</p> <p>In a greenhouse and garden setting, Nobs (1963) conducted crosses among taxa of the <i>Cerastes</i> group and also attempted crosses between <i>Cerastes</i> and <i>Euceanothus</i> group taxa (subgenus <i>Ceanothus</i>). All interspecific hybrids within <i>Cerastes</i> were fertile and produced highly fertile pollen, normal seed set, and viable F1 progeny, including a <i>C. crassifolius</i> cross with <i>C. gloriosus</i>, a prostrate, blue flowered taxon from coastal bluffs of Point Reyes. However, hybridization between taxa from different subgenera nearly always failed indicating genetic barriers to hybridization.</p>
I. Inbreeding and outbreeding effects	<p>No studies have examined the potential for inbreeding depression or effects of crossing distant populations.</p>

VII. BIOLOGICAL INTERACTIONS

A. Competitiveness	<p>Seedlings of <i>C. crassifolius</i> are more drought tolerant and resistant to xylem cavitation than seedlings of co-located sprouting species of <i>Ceanothus</i> (Davis et al. 1999), enabling them to re-establish populations after fire kills adult plants. They can survive periods of drought that cause branch die-back on sprouting congeners and co-occurring chaparral species (Davis et al. 2007, Pratt et al. 2014).</p>
B. Herbivory, seed predation, disease <div style="text-align: center; margin-top: 20px;">  </div> <div style="text-align: center; margin-top: 5px;"> <div style="border: 1px solid black; padding: 2px; width: fit-content; margin: 0 auto;">Beetle larva from seed.</div> </div>	<p>After dispersal, predation of <i>Ceanothus</i> seeds by mammals and birds can be high (Sawyer et al. 2009, Warzecha & Parker 2014). Davey (1982) observed post-dispersal seed predation of hoaryleaf ceanothus by rodents, birds, and harvester ants; the majority of seeds added to the seed bank in one season were gone by the end of one year. Seeds were removed at a uniform rate when they were abundant. Build-up of seed banks after fire can take many seasons, especially when seed inputs are variable.</p> <p>Predation of seeds also occurs before dispersal (see photo of larva retrieved from seed). Many seeds have exit holes from seed predators and seeds are often empty and float during processing. A fraction of floating seeds may also contain a single beetle larva which consumes the entire embryo (Montalvo pers. obs.). Chalcid wasps also utilize the seeds. Bugbee (1971) reported high rates of seed predation in the related <i>C. greggii</i> by the chalcid wasp <i>Eurytoma ceanothi</i>. Other chalcids may be parasitoids on larvae that occur in the seeds (Bugbee 1967).</p> <p>Allen & Roberts (2013) describe slow root herbivory by the ceanothus rain beetle (<i>Pleocoma puncticollis</i> Rivers) where the beetle is completely dependent on species of <i>Ceanothus</i> for its survival.</p> <p><i>C. crassifolius</i> was shown to be susceptible to infection by <i>Botryosphaeria dothidea</i> (Brooks & Ferrin 1994) which causes lesions. Endophytic fungi in the genera <i>Botryosphaeria</i> and <i>Sclerophoma</i> have been isolated from proximal stems of the plant and the fungi are thought to be common in stands of this plant (Davis et al. 2002). Inoculation of healthy stems with isolates of the fungi did not produce pathogenic effects, but the relationship could become detrimental under extreme drought.</p> <div style="display: flex; justify-content: space-around; margin-top: 20px;"> <div style="text-align: center;">  </div> <div style="text-align: center;"> <div style="border: 1px solid black; padding: 5px; width: fit-content;">Chalcid wasp that emerged from seeds of <i>C. crassifolius</i> from the Santa Ana Mountains.</div> </div> <div style="text-align: center;">  </div> </div>

C. Palatability, attractiveness to animals, response to grazing	Leaves are tough and leathery. Substantial herbivory of seedlings can occur after fire, such that community species composition may be affected (Quinn 1994). Seedlings of another obligate seeder, <i>C. megacarpus</i> , that were browsed by deer early in the growing season exhibited increased branching in response (Frazer & Davis 1988); <i>C. crassifolius</i> is likely to respond similarly. Quinn (1994) observed that regrowing <i>C. crassifolius</i> in the open were shorter than plants protected from herbivores for up to a decade post-fire and had a hedged appearance until they grew tall enough to exceed the reach of mule deer.
D. Mycorrhizal? Nitrogen fixing nodules?	Actinorhizal. Develops symbiotic association with an endophytic, filamentous N-fixing bacteria in the genus <i>Frankia</i> (Murry 1971). <i>Frankia</i> forms nodules on the roots. It is likely that <i>C. crassifolius</i> also forms associations with arbuscular mycorrhizal and/or ectomycorrhizal fungi. All eight actinorhizal <i>Ceanothus</i> species examined by Rose (1980) formed arbuscular mycorrhizae simultaneously (Rose 1980). Most actinorhizal plants also form mycorrhizae (Rose 1980, Chaia et al. 2011).
E. Insect pollinators	The insect pollinators of <i>C. crassifolius</i> flowers (see VI. E. Pollination) are likely the same or similar to those that visit other taxa in the <i>Cerastes</i> group of <i>Ceanothus</i> . Some of the bee genera known to visit <i>Ceanothus</i> (see VI. C. Pollination) are known to have species that forage over large distances, which may facilitate intermediate to long-distance pollen flow. Several species of <i>Bombus</i> were found to fly distances of 1,000 to 10,000 m, and several species of <i>Andrena</i> , <i>Lassioglossum</i> , and <i>Megachile</i> were found to forage over hundreds of meters (Zurbuchen et al. 2010). However, the way different species of bees travel across fragmented habitat or respond to the spatial scale of urbanization varies (Schochet et al. 2016). Small flies and beetles were also found to visit flowers but they tend to move pollen short distances and are less likely than the bees to move pollen among plants.

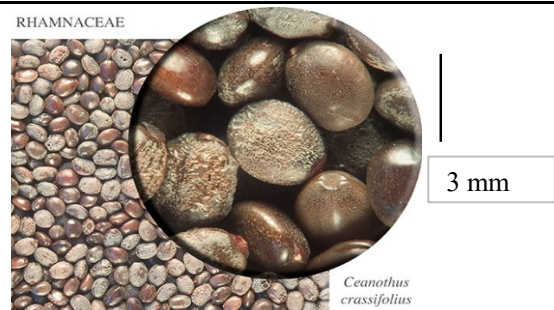
VIII. ECOLOGICAL GENETICS

A. Ploidy	2n = 24 (Nobs 1963). This is common to the many <i>Ceanothus</i> taxa counted as of 1963.
B. Plasticity	No information found on growth plasticity in general. Shrubs change the orientation of leaves relative to the sun as water potentials become more negative during summer; this reduces absorption of solar radiation and leaf heating (Comstock & Mahall 1985). Leaves become more horizontal in winter and early spring when temperatures are cooler.
C. Geographic variation (morphological and physiological traits)	No studies found.
D. Genetic variation and population structure	No studies found.
E. Phenotypic or genotypic variation in interactions with other organisms	Murry (1997) detected different strains of <i>Frankia</i> in hoaryleaf ceanothus compared to other <i>Ceanothus</i> species sampled, but the degree of host specificity is unknown. Biogeographic patterns have been found in host specificity among <i>Frankia</i> strains and several other species of <i>Ceanothus</i> sampled across contrasting bioregions California (Oakley et al. 2004, Chaia et al. 2010).
F. Local adaptation	No studies found.
G. Translocation risks	There is no direct information on translocation. However, plant taxa with populations distributed over a variety of habitats frequently differ in their ability to survive and reproduce in the different environments. Hoaryleaf ceanothus populations occur over an intermediate range of precipitation and temperature normals.

IX. SEEDS

Seed image by John Macdonald (RSA Seeds 2016).

In photo, seeds with wrinkled seed coats were immature when collected. Mature seeds have shiny, dark brown to black seed coat.



A. General	In good years, plants produce large numbers of seeds (Davey 1982). Seeds are broadly oblong and oval in cross section, 2 to 3 mm long and 1.5 to 2 mm wide. When seeds are ejected from the fruit, they are black and shiny, but when collected before capsules dehisce can be dark brown.
B. Seed longevity	Long-lived. Accumulate in soil seed bank. Quick & Quick (1961) tested seeds of numerous other species of <i>Ceanothus</i> that varied from 9.5 to over 20 years old and found high germination rates after treatment. The seeds had been dried and stored in air-tied tins at 37 °F. The closely related obligate seeder <i>C. cuneatus</i> whose seeds had been stored for 17 years and 5 months reached 98% germination after heat treatment (boiled 10 sec) and 98 days of stratification at 36 °F.
C. Seed dormancy	Dormant. Seed coat is impermeable and embryo is sometimes additionally dormant. Seeds are refractory – heat shock from fire breaks dormancy by scarifying the seed coat (Quick 1935, Keeley 1991), but a cold period following heat shock may be needed to break embryo dormancy (see IX. B. Seed longevity; H. Seed germination). Quick & Quick (1961) found that for 12 other <i>Ceanothus</i> species stored under dry, cold conditions for many years, boiling seeds for 10 to 20 seconds followed by cold stratification provided high germination rates.
D. Seed maturation	Seeds mature in the late winter to early spring and tend to disperse in early May (A. Montalvo pers. obs.) Seeds are shiny and black when mature. Crack open unpoped capsules to determine ripeness.
E. Seed collecting and harvesting	Collect from healthy stands that are separated from species with which hoaryleaf ceanothus hybridizes readily. Fruit production is highly variable among years (Keeley 1987a). Because the capsules dehisce explosively, collect when capsules are brown, but before they pop and release seeds. Alternatively, branches with fruits can be bagged with netting to capture seeds when capsules dehisce, but this is a very intensive process. Collecting in the morning hours will ensure the highest number ripe capsules before they pop. Pluck clusters of capsules into open containers (such as paper or breathable fabric bags). Collect from many plants, spacing the collections across the population with at least 10 m between collections to ensure genetic diversity in the collection.
F. Seed processing	Processing is difficult unless capsules are collected just before they pop or collected by bagging (see IX. E. Seed collecting and harvesting, above). Dry incoming seed lots in well ventilated space. If unpoped capsule collection is well timed, capsules can be placed in cloth or paper bags in a warm place to pop on their own (R. Brandon Pratt pers. com.). They can then be cleaned as described below. For collections that don't pop, we recommend sending large collections to a seed extractory with specialized equipment. For small collections, processing is similar to that described for <i>C. macrocarpus</i> (Wall & Macdonald 2009). The fruits are very hard when dry and require pounding or cracking open with a rolling pin to macerate fruits before screening to separate most seeds from fruit walls. Alternatively, Quick (1935) rubbed the dried fruits between boards to break them open. Continue to macerate by rubbing broken fruits over a medium screen to release seeds. Once broken up and screened, repeated blowing at blower speed of 4.0 or higher is needed to separate seed from fruit casings, small twigs and empty seeds. Seeds with larvae do not all blow off, but they float whereas filled seeds sink. Float off hollow seeds and seeds with larvae (A. Montalvo pers. obs.).
G. Seed storage	Store dried seed in dry conditions away from direct heat. Cool, dry storage at 4.5 to 8 °C is likely satisfactory (Conard & Reed 2008 suggest 4.5 °C).
H. Seed germination	Seed germination is not light sensitive (Keeley 1991, Conard & Reed 2008), but scarification of the seed coat by fire (heat shock) breaks physical dormancy (Keeley & Fotheringham 2000). Various heat treatments can succeed, but heat treatment followed by cold stratification provides the best results for many species of <i>Ceanothus</i> (Conard & Reed 2008). Quick (1935) found 48% germination of hoaryleaf ceanothus seeds suspended in 70 °C water and allowed to cool to room temperature, but this increased to 76% when followed by cool, moist stratification at 2.5 °C for 3 months. Various other heat treatments worked to a lesser degree, including boiling in water for 1 or 5 min or suspending in 80 °C water, then cooling. In other studies, heat shock of dry seeds at 105 °C for 5 min resulted in means of 87% or 90% germination, increasing to 99% and 92% when followed by treatment in GA ₃ , gibberellic acid (Keeley & Fotheringham 1998, 2000). This may be superior to the Emery (1988) recommendation for hot water soak followed by stratification for 2–3 mo or boiling seeds 1 min then soaking in 400 ppm GA ₃ for 13 hours. After treatment, it can take three weeks to three months for full germination at 10–20 °C (Conard & Reed 2008), with shorter times expected after cold stratification or treatment with GA ₃ .

I. Seeds/lb	Seed mass averaged 5.18 mg (N=100) from plants sampled in the Santa Monica Mountains (Pratt et al. 2007), suggesting there are roughly 87,500 seeds in a pound. However, live seed content of seed lots can be variable owing to seed predation (see VII. B. Herbivory, seed predation, disease) and processing methods. Based on three samples, Conard & Reed (2008) report a range of 33,000–65,000 seeds/lb and an average of 53,000 seeds/lb. Values were for clean seed and appear to be for live, or filled seeds per bulk pound. For commercial seed lots, S&S Seeds (2019) reports an average of 37,500 live seeds/ bulk pound.
J. Planting	In the nursery, plant seeds 0.25 to 1.5 inches (6 to 38 mm) deep in a well-drained mix with plenty of sand or perlite because seedlings of <i>Ceanothus</i> are sensitive to damping off (Smith 1986, Conard & Reed 2008). In the closely related <i>C. cuneatus</i> , Adams (1962) planted seeds in flats at 0, 1, 1.5, 2 and 2.5 inches (0, 25, 38, 51 and 64 mm) deep in sun and shade. The highest emergence occurred for the 1 and 1.5 inch planting depths. For seeds of <i>C. integerimus</i> and <i>C. lemmonii</i> planted at depths of 0, 0.25, 0.5, 1 and 1.75 in (0, 6, 12, 25 and 45 mm), the highest emergence occurred for the 0.5 and 1.0 inch (12 and 25 mm) planting depths in sun and 0.25 and 0.5 inches (6 and 12 mm) in shade. None of the surface-planted seeds produced seedlings in sun, and only a few emerged in shade. It may be good to plant treated seeds of hoaryleaf ceanothus 1–1.5 inches (25–38 mm) deep in the field.
K. Seed increase activities or potential	Growing many large plants would ensure productive seed crops, but current use is limited and seed farms would not be financially practical. Collection from large wild populations in good years and storage of cleaned, long-lived seeds for future use is encouraged.
X. USES	
A. Revegetation and erosion control	Post-fire seeding efforts in the 1940s used native shrubs, including <i>Ceanothus</i> species, but found that establishment was no faster than natural regeneration (Department of Forester and Fire Warden 1985). Post-fire seeding with annual grasses may reduce density of chaparral seedlings, including <i>Ceanothus crassifolius</i> (Nadkarni & Odion 1986). <i>C. crassifolius</i> is often recommended for stabilizing banks (e.g., Calscape 2019).
B. Habitat restoration	No studies found. After fire, plants emerge readily from the seed bank, but increased fire frequency can eliminate obligate-seeding species like this one from stands if they burn before reproductive maturity or before seeds have a chance to accumulate in the seed bank (Zedler et al. 1983, Jacobsen et al. 2004). We expect that <i>C. crassifolius</i> will become an increasingly important plant choice in restoring low elevation chaparral that has become partially type-converted from chaparral to non-native grassland due to species loss and non-native annual grass invasion.
C. Horticulture or agriculture	No known horticultural varieties. Used in native habitat demonstration gardens or as a background plant or in screens (A. Montalvo pers. obs.). Excellent for dry gardens with summer heat and full sun (Keator 1994). Seed increase activities not known. Container plants are susceptible to root rot and need to be grown in a well-drained medium using best management practices to avoid fungal infections. Propagation from cuttings: For <i>Cerastes</i> group <i>Ceanothus</i> , the hardened stems tend to need stronger rooting hormones (e.g., 0.5% or more IBA/NAA) and longer rooting times than other <i>Ceanothus</i> (subgenus <i>Ceanothus</i>) species (Smith 1986). Cutting stock should be well watered and free of drought stress. Cuttings are susceptible to fungal infections; often fungicides are often applied before cutting, and cuttings are often treated with fungicide prior to application of rooting hormones. Misting is also reduced. Propagation from seeds: After planting seeds (see IX. J. Planting) that have been heat treated and cold stratified treated to break dormancy (see VIII. C. Seed dormancy and H. Seed germination), seedlings begin to emerge in in 8 to 10 days with most germination completed by 30 days (Everett 2012). Once seedlings have developed two to four true leaves, shift into 2 to 3 inch wide pots with well-drained mix. If production is for field sites, conetainers or D-40 pots (two in. diam., 9 in deep) to allow deeper roots and easier planting to field sites depending on timing for outplanting. Seedlings may be inoculated with <i>Frankia</i> (see VII. D. above) when shifting from flats to pots, however studies are needed to determine inoculation need and success. Conard & Reed (2008) suggest inoculation would not be needed for plants to be added to sites where <i>Ceanothus</i> taxa are present.
D. Wildlife value	Provides nesting sites, cover, and food for a variety of wildlife. Although many species of <i>Ceanothus</i> are import browse plants, hoaryleaf ceanothus is not discussed in Sampson & Jespersen (1963). However, Quinn (1994) found substantial removal of <i>C. crassifolius</i> from post-fire chaparral plots outside of an enclosure compared to within one; mammalian herbivores, including rabbits and deer, were assumed to cause the loss. Flowers produce both nectar and pollen and provide food for a variety of bees (see VI. E. Pollination). The plants and seeds are important to a variety of birds, lepidopterans and other insects (see VII. B. Herbivory). Calscape (2019) lists 86 butterfly and moth taxa that utilize the plant. Nitrogen fixation by associated root symbionts (see VII. D. Mycorrhizae) may have indirect effects on wildlife by supplementing the nitrogen budget of the communities in which they are present (R. B. Pratt pers. com.).

E. Plant material releases by NRCS and cooperators	None.
F. Ethnobotanical	An infusion of the bark or the bark itself was used on open wounds to stop bleeding (Garcia & Adams 2009). The flowers and young fruits were also used to make a lather for washing hands or bathing, wood was used for digging sticks, and the roots were used to make a red dye for basketry. Garcia & Adams discuss the active compounds including alkaloids and flavonoids found in <i>Ceanothus</i> .
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XII. CITATION	Montalvo, A. M., E. C. Riordan, and J. L. Beyers. 2020. Plant Profile for <i>Ceanothus crassifolius</i> . 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. Online: https://www.rcrcd.org/plant-profiles
XIII. LINKS TO REVIEWED DATABASES & PLANT PROFILES	
Fire Effects and Information System (FEIS)	https://www.feis-crs.org (no review available as of February 2020)
Calflora	https://www.calflora.org/cgi-bin/species_query.cgi?where-taxon=Ceanothus+crassifolius
Calscape	https://calscape.org/Ceanothus-crassifolius-()
Jepson eFlora (JepsonOnline, 2nd ed.)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=18433
Jepson eFlora (JepsonOnline, 2nd ed.)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=71709
Jepson eFlora (JepsonOnline, 2nd ed.)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=56082
USDA PLANTS	https://plants.usda.gov/core/profile?symbol=CECR
Native Plant Network Propagation Protocol Database (NPNPP)	https://npn.rngr.net/propagation
Native Seed Network (NSN)	https://nativeseednetwork.org/
GRIN (provides links to many resources)	https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch.aspx
Flora of North America (FNA) (online version)	http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250101430
Ethnobotanical	http://naeb.brit.org/
Woody Plant Seed Manual	https://www.fs.usda.gov/nsl/nsl_wpsm.html
Rancho Santa Ana Botanic Garden Seed Program, seed photos	http://www.hazmac.biz/040712/040712CeanothusCrassifolius.html
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