

Ceanothus L.

ceanothus

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Growth habit, occurrence, and use. Van Renssler and McMinn (1942) recognized 55 species of *ceanothus*, 25 varieties, and 11 named natural hybrids, all restricted to the North American continent. Most of them are found along the Pacific Coast of the United States, and only 2 are found east of the Mississippi River (Hitchcock and others 1961; Kearney and Peebles 1951; Munz and Keck 1968; Rowntree 1948; Sampson and Jespersen 1963; Schmidt 1993; Van Renssler and McMinn 1942). Forty-three species and 21 varieties are described in the most recent flora of California, which does not recognize hybrid forms (Schmidt 1993). Although hybridization appears to be common in nature, there are few named hybrids (Lentz and Dourley 1981; Schmidt 1993). *Ceanothus* species are mainly evergreen or deciduous shrubs, some of which may attain the height of small trees. In the West, they occur in a diversity of habitats, ranging from interior desert chaparral to moist redwood forest along the Pacific Coast (table 1). *Ceanothus* species are important as wildlife food and shelter, for erosion control, as hedges and shelterbelts, and in soil development and soil nitrogen regimes (Conard and others 1985; Graham and Wood 1991). Deerbrush *ceanothus* is rated as one of the most important summer browse species in California for deer and cattle (Sampson and Jespersen 1963), and redstem *ceanothus* is a key winter browse plant for deer and elk in parts of Idaho, Washington, and Oregon (Hickey and Leege 1970). All species that have been investigated bear root nodules containing a nitrogen-fixing *Frankia* symbiont (for example, Delwiche and others 1965); species from both forest and chaparral systems have been associated with accretion of soil nitrogen over time (Binkley and Husted 1983; Binkley and others 1982; Conard and others 1985; Hellmers and Kelleher 1959; Youngberg and Wollum 1976; Youngberg and others 1979; Zavitkovski and Newton 1968; Zinke 1969).

On forest sites, *ceanothus* species have alternately been considered a problem because they compete with commercial conifers and a benefit because of their nitrogen-fixing ability and their wildlife value (Conard and others 1985). Although there was early experimentation with planting *ceanothus* species for erosion control on chaparral sites (DFFW 1985) and there has been some interest in *ceanothus* establishment for browse or general site improvement in forest sites (Hickey and Leege 1970; Radwan and Crouch 1977), the dominant horticultural uses have continued to be for domestic, commercial, and right-of-way landscapingCparticularly in California and the Pacific Northwest. *Ceanothus* species are valued particularly for their showy flowers (they are sometimes called ACalifornia lilacs@), relatively rapid early growth, drought adaptation, and ability to tolerate landscape watering. Some species have been cultivated for many years (table 2), and the potential for

hybridization has led to the development of numerous cultivars, many of which are available from commercial native plant nurseries (for example, Lentz and Dourley 1981; Perry 1992). Distribution and uses of some of the more common species are described in table 1.

Flowering and fruiting. Flowers are small, bisexual, and regular, and are borne in racemes, panicles, or umbels. The 5 sepals are somewhat petal-like, united at the base with a glandular disk in which the ovary is immersed. The 5 petals are distinct, hooded, and clawed; the 5 stamens are opposite the petals, with elongated filaments. Petals and sepals can be blue, white purple, lavender, or pink. The ovary is 3-celled and 3-lobed, with a short 3-cleft style. Fruits are drupaceous or viscid at first but soon dry up into 3-lobed capsules (figure 1) that separate when ripe into 3 parts. Seeds are smooth, varied in size among species (figures 2 and 3; table 3), and convex on one side.

Flowering and fruiting dates for several species are listed in table 2. Feltleaf ceanothus is reported to begin bearing seeds at 1 year (Van Renssler and McMin 1942), deerbrush ceanothus at 3 years (McDonald and others 1998), hoaryleaf ceanothus at 5 years (Everett 1957), desert ceanothus at 6 to 8 years (Zammit and Zedler 1992), and snowbrush ceanothus at 6 to 10 years (McDonald and others 1998). Thus it appears that most species can be expected to begin producing seed by about 5 to 10 years of age. Fendler ceanothus has been reported to bear good seedcrops annually (Reed 1974). However, hoaryleaf ceanothus, desert ceanothus, chaparral whitethorn, and other species, both annual seed production and the amount of seed stored in the soil may be quite variable (Conard and others 1985; Keeley 1977, 1987b; Zammit and Zedler 1988).

Collection, extraction, and storage. Several useful points on collecting ceanothus seeds have been described (Van Renssler and McMin 1942; Emery 1988). Seeds should be collected only from vigorous plants, as weak, diseased plants do not produce sound seeds. To obtain plants similar to mature specimens, seeds should be collected in single-species stands in the wild or from isolated garden plants. Because many species hybridize freely, asexual propagation is the only certain way of maintaining species or varieties free from hybridization (Lentz and Dourley 1981). As the capsules split, ripe seeds are ejected with considerable force, such that about two-thirds of the seeds fall outside the shrub canopy, to distances up to 9 m (Evans and others 1987). Therefore, a common method of seed collection is to tie cloth bagsCpreferred to paperCsecurely over clusters of green seedpods. It is also possible to cut seedpod clusters before capsules have split, but the degree of maturity of the seeds is critical, as few prematurely collected seeds will germinate. Seeds that contain milky or gelatinous substances are not mature enough to harvest (Emery 1988). Green seeds should be air-dried at 29 to 38 °C.

If necessary, the seeds can be separated from capsule fragments by screening and blowing (Reed 1974), or seeds can be passed through a mill and floated (Plummer and others 1968). Average number of cleaned seeds per weight ranges from 90,000 to over 350,000/kg (41,000 to 178,000/lb), depending on the species (table 3). Adequate information on long-term storage is not available, but the seeds are apparently orthodox in storage behavior. Dry storage at around 4.5 °C should be satisfactory. Quick and Quick (1961) reported good germination in seeds of a dozen ceanothus species that had been stored for 9 to 24 years, with no apparent effect of seed age on viability. Seeds are apparently long-lived in litter; viable seeds of snowbrush ceanothus have been found in the surface soil of forest stands that were between 200 to 300 years old (Gratkowski 1962).

Germination. The long-term viability of seeds of ceanothus species apparently results from a strong seed coat dormancy, which in nature is typically broken by fire but may occasionally be

broken by solar heating or mechanical scarification, such as from forest site preparation activities (Conard and others 1985). Germination of ceanothus seeds generally increases with increasing fire intensity (Conard and others 1985; Moreno and Oechel 1991), although at very high intensities, soil temperatures may be high enough to kill substantial numbers of seeds, resulting in decreased germination (Lanini and Radosevich 1986). In varnishleaf ceanothus, Gratkowski (1962) observed that when seeds were exposed to drying conditions at normal air temperature, the hilum (the attachment scar on the seed, through which the radicle would normally emerge) functioned as a 1-way hygroscopic valve that allowed moisture to pass out, but prevented moisture uptake by the seed. Heat caused a permanent, irreversible opening of the hilar fissure, which rendered the seed permeable to water. However, the seedcoat itself remained impermeable to moisture even after heating. This mechanism likely accounts for the abundant germination of ceanothus species that often occurs after fire on both chaparral and forest sites (Conard and others 1985).

In the laboratory, germination has been induced by soaking in hot water or heating in an oven, with or without a subsequent period of cold stratification (table 4). The typical pattern is that germination increases with the temperature of heat treatments up to a maximum, at which point seed mortality begins to occur. Seed germination and mortality are a function of both temperature and length of exposure, but for most species these optima are poorly defined. For hoaryleaf ceanothus, for example, maximum germination was obtained after heat treatments of 10 minutes to 1 hour at 70 to 80 °C. At higher temperatures, germination dropped off increasingly rapidly with duration of treatment, until at 100 °C there was a linear decrease in germination with times over 5 minutes (Poth and Barro 1986). In the wild, this range of time and temperature optima gives the advantage of allowing dormancy to be broken at a range of soil depths as a function of fire temperature and residence times. Quick and Quick (1961) reported that germination of mountain whitethorn and, to a lesser extent, deerbrush ceanothus began to drop off rapidly after a few seconds to several minutes in boiling water. Although Asteeping® treatments at cooler temperatures (for example, 70 to 95 °C) were also found effective on several species (Quick 1935; Quick and Quick 1961), many investigators have continued to use treatments of boiling water (table 4). Dry heat treatments may be less damaging at higher temperatures than wet heat (table 4), although careful comparisons have not been made. In place of hot water treatments, seeds can also be immersed in sulfuric acid for 1 hour (Reed 1974).

Seeds of species found at high elevations also require cold stratification for good germination (Quick 1935; Van Renssler and McMinn 1942). Although some lower-elevation species from chaparral sites can germinate reasonably well without this cold treatment, their germination rates generally increase with stratification (table 4). Cold stratification is accomplished by storing seeds in a moist medium for periods of 30 to 90 days at temperatures of 1 to 5 °C. In general, longer periods of cold stratification are more effective than short ones. For example, Radwan and Crouch (1977) observed increasing germination of redstem ceanothus as cold stratification was increased from 1 to 3 or 4 months; no germination occurred without stratification. Similar patterns were observed by Quick and Quick (1961) for deerbrush ceanothus (increased germination up to 2 months of stratification) and Bullock (1982) for mountain whitethorn (increased germination up to 3 months). In lieu of cold stratification, a chemical treatment with gibberellin and thiourea was used to induce germination of buckbrush ceanothus (Adams and others 1961). Treatment with potassium salts of gibberellin also successfully replaced cold stratification in germination tests on redstem ceanothus

seeds (Radwan and Crouch 1977). Following chemical treatments, seeds may then be germinated or dried again and stored (Adams and others 1961). Although emphasis has been on more natural methods of stimulating germination, seeds of snowbrush *ceanothus* and other species can be germinated quite successfully with acid scarification followed by a gibberellin treatment (Conard 1996).

Specific germination test conditions have not been well defined for most species of *ceanothus*. Sand or a mixture of sand and soil has been used as the moisture-supplying medium in most of the reported germination tests (Emery 1964; Quick 1935; Reed 1974), but filter paper has also been used successfully (Keeley 1987a). Diurnally alternating temperatures of 30 °C in light and 20 °C in darkness have been effective, but constant temperatures of 10 °C (Reed 1974) and 24.5 °C (Emery 1988) also have been suitable for germination. A need for light has not been reported (Keeley 1991), and at least 1 species (deerbrush *ceanothus*) appears to germinate significantly better in the dark (Keeley 1987a). Germination rates resulting from selected pregermination treatments are listed in table 4 for 19 species.

The genus *Ceanothus* includes both species that sprout vegetatively following fire (sprouters) and species that are killed by fire and reproduce only from seed (obligate seeders). Obligate seeders appear to have overall higher germination following heat treatment and to tolerate higher temperatures and longer periods at high temperature without damage to seed viability (Barro and Poth 1987). Germination test results suggest that eastern species may not be dependent on fire to stimulate germination. For western species, however, some level of heat treatment, followed by stratification, will typically enhance germination. Although there has certainly been considerable variability in test results (table 4), a 5- to 10-minute dry heat treatment at 100 °C or a steeping treatment starting with 85 °C water, followed by several months of cold stratification, should effectively stimulate germination in most species.

Nursery practice. Seeding has been done in flats containing a medium of 5 parts loam, 4 parts peat, and 3 parts sand (Van Renssler and McMinn 1942). Leaf-mold may be substituted for the peat, but the peat is preferred because it is comparatively free of fungi. Sand is needed for drainage, a higher proportion being used in the seeding than in the potting medium. Seedlings are sensitive to sowing depth. In a trial by Adams (1962), deerbrush and buckbrush *ceanothus* emerged best when sown at depths of 12 to 25 mm (2 to 1 in), and shading favored emergence of the first 2 species. However, some germination and emergence occurred at sowing depths ranging from 6 to 64 mm (3 to 22 in). Many species are sensitive to damping off, so for safety soil should be sterilized (Van Renssler and McMinn 1942). In California, seeding is usually done in November to January. Germination is epigeal (figure 4). Although all species of *Ceanothus* apparently fix nitrogen symbiotically, there has apparently been little or no research into the efficacy of or need for seed inoculation with *Frankia* to ensure nodulation of seedlings after outplanting. This is not likely to be a problem on soils where *Ceanothus* species are present, as nodulation appears to occur readily (Conard 1996) but may be of concern for horticultural uses of the genus.

Seedling care. When several sets of leaves have formed, the seedlings can be carefully planted into 2- or 3-inch (5- or 7.6-cm) pots. A good potting medium is 5 parts loam, 3 parts peat or leaf mold, and 1 part sand (Van Renssler and McMinn 1942). Care must be taken not to place the seedlings too deep in the soil, with root crowns should be just below the soil surface. Seedlings are susceptible to stem rot, and the loss will be greater if young plants are kept in moist soil that

covers the root crown. The root development should be examined from time to time. When a loose root system has formed on the outside of the ball, the plant is ready for shifting to a larger pot or gallon can. It is best to discard potbound plants rather than to carry them along.

Planting stock of most common western ceanothus species is now available from commercial nurseries or botanic gardens, and numerous hybrids and cultivars have been developed for the nursery trade. Cultural notes on some of the commonly available species (table 1) and cultivars (Brickell and Zuk 1997) follow:

- ! feltleaf ceanothus *C. arboreus* which can attain a height of 5 to 8 m and has pale blue flowers, grows best in coastal areas or with partial shade in areas with hot, dry summers.
- ! Fendler ceanothus *C. fendleri* Cup to 2 m tall with pale, bluish-white flowers, has been propagated from seed sown in the spring and from cuttings in autumn. It grows best in light, well-drained soils and can tolerate cold.
- ! camel ceanothus *C. griseus* var. *horizontalis* McMinn Ca spreading, low-growing (to 1 m) variety, is used as ground cover and for slope stabilization. It performs best in mild coastal regions but will do well in partial shade in drier areas with adequate watering. Several named varieties are available.
- ! squaw-carpet *C. prostratus* Ca spreading, prostrate groundcover with small blue flower clusters, usually is propagated by layering. It is best if grown within its native range (for example, ponderosa pine zone of Sierra Nevada) and does not grow well at low elevations.
- ! *C. cuneatus* (Nutt.) Hoover var. *rigidus* cv. Snowball Ca white-flowered cultivar, 1 to 1.5 m tall, recommended for coastal areas from southern California to the Pacific Northwest. Summer water should be restricted. It is a good bank and background plant.
- ! Sierra blue *C. cyaneus* Eastw. × ? Ca medium to large shrub (to 6 m) with showy blue flowers, is a relatively fast grower that will tolerate hot, dry environments with some supplemental summer water.
- ! blue blossom *C. thyrsiflorus* Ca large shrub (2 to 7 m tall) with showy deep blue flowers, is a native of coastal forests. It grows well in its native range (Pacific coastal mountains) and needs shade from afternoon sun on dry inland sites, but requires little summer water once established.

There are many more ceanothus varieties that are excellent candidates for a range of domestic, commercial, or right-of-way landscaping situations. Although they are typically not widely available at retail nurseries, many native plant nurseries within the native range of ceanothus have wide selections. Additional information can be found in Kruckeberg (1982), Lenz and Dourley (1981), Perry (1992), Schmidt (1980), and the Sunset Western (1995) and National (1997) Garden Books, among others.

References

- Adams L. 1962. Planting depths for seeds of three species of ceanothus. Res. Note PSW-194. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 3 p.

- Adams L, Stefanescu E, Dunaway DJ. 1961. Gibberellin and thiourea break seed dormancy in California ceanothus. Res. Note PSW-178. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 4 p.
- Barro SC, Poth M. 1987. A possible advantage for the obligate seeding strategy in *Ceanothus* [unpublished manuscript on file]. Riverside, CA: USDA Forest Service, Pacific Southwest Research Station, Forest Fire Laboratory.
- Binkley D, Cromack K Jr, Fredriksen RL. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. Forest Science 28(4): 720B724.
- Binkley D, Husted L. 1983. Nitrogen accretion, soil fertility, and Douglas-fir nutrition in association with redstem ceanothus. Canadian Journal of Forest Research 13: 122B125.
- Brickell C, Zuk JD. 1997. American Horticultural Society ABZ Encyclopedia of Garden Plants. New York: DK Publishing: 239B241.
- Bullock S. 1982. Reproductive ecology of *Ceanothus cordulatus* [MA thesis]. Fresno: California State University.
- Conard SG. 1996. Unpublished data. Washington, DC: USDA Forest Service, Research and Development.
- Conard SG, Jaramillo AE, Cromack K Jr, Rose S, comps. 1985. The role of the genus *Ceanothus* in western forest ecosystems. Gen. Tech. Rep. PNW-182. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 72 p.
- Delwiche CC, Zinke PJ, Johnson CM. 1965. Nitrogen fixation by *Ceanothus*. Plant Physiology 40(6): 1045B1047.
- DFFW [Department of Forester and Fire Warden]. 1985. Emergency revegetation in Los Angeles County 1919B1984. Los Angeles: County Fire Department. 93 p.
- Emery DE. 1964. Seed propagation of native California plants. Leaflets of the Santa Barbara Botanical Garden 1(10): 90B91.
- Emery DE. 1988. Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanical Garden. 115 p.
- Evans RA, Biswell HH, Palmquist DE. 1987. Seed dispersal in *Ceanothus cuneatus* and *C. leucodermis* in a Sierran oak woodland savanna. Madroño 34(4): 283B293.
- Everett PC. 1957. A summary of the culture of California plants at the Rancho Santa Ana Botanic Garden 1927B1950. Claremont, CA: Rancho Santa Ana Botanic Garden. 223 p.
- Franklin J, Halpern C, Smith B, Thomas T. 1985. The importance of *Ceanothus* species in U.S. forest ecosystems. In: Conard SG, Jaramillo AE, Cromack K Jr, Rose S, comps. The role of the genus *Ceanothus* in western forest ecosystems. Gen. Tech. Rep. PNW-182. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 2B15.
- Furbush PB. 1962. Feed from brush: an evaluation of some important California browse plants. City: California Department of Conservation, Division of Forestry. 24 p.
- Graham R, Wood H. 1991. Morphologic development and clay redistribution in lysimeter soils under chaparral and pine. Soil Science Society of America Journal 55: 1638B1646.
- Gratkowski HJ. 1962. Heat as a factor in germination of seeds of *Ceanothus velutinus* var. *laevigatus* T. & G. [PhD thesis]. Corvallis: Oregon State University.
- Hellmers H, Kelleher JM. 1959. *Ceanothus leucodermis* and soil nitrogen in southern California mountains. Forest Science 5: 275B278.

- Hickey, WO, Leege TA. 1970. Ecology and management of redstem ceanothus: a review. Wildlife Bull. 4. Boise: Idaho Department of Fish and Game. 18 p.
- Hitchcock CL, Cronquist A, Owenbey M, Thompson JW. 1961. Vascular plants of the Pacific Northwest: 3. Saxifragaceae to Ericaceae. Seattle: University of Washington Press. 614 p.
- Hubbard RL. 1958. Hot water and thiourea break dormancy of wedgeleaf ceanothus seed. Res. Note PSW-143. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 4 p.
- Kearney TH, Peebles R. 1951. Arizona flora. Berkeley: University of California. 1032 p.
- Keeley JE. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 58: 820B829.
- Keeley JE. 1987a. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68(2): 434B443.
- Keeley JE. 1987b. Fruit production patterns in the chaparral shrub *Ceanothus crassifolius*. Madroño 34(4): 273B282.
- Keeley JE. 1991. Seed germination and life history syndromes in the California chaparral. Botanical Review 57(2): 81B116.
- Kruckeberg AR. 1982. Gardening with native plants of the Pacific Northwest. Seattle: University of Washington Press.
- Lanini WT, Radosevich SR. 1986. Response of three conifer species to site preparation and shrub control. Forest Science 32: 61B77.
- Lenz LW, Dourley J. 1981. California native trees and shrubs for garden and environmental use in southern California and adjacent areas. Claremont, CA: Rancho Santa Ana Botanic Garden. 232 p.
- McDonald PM, Laurie WD, Hill R. 1998. Early growth characteristics of planted deerbrush and greenleaf manzanita seedlings. Res. Note PSW-RN-422. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 6 p.
- McMinn HE. 1964. An illustrated manual of California shrubs. Berkeley: University of California Press: 278B320.
- Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: Civilian Conservation Corps. 42 p.
- Moreno JM, Oechel WC. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. Ecology 72(6): 1993B2004.
- Munz PA, Keck DD. 1968. A California flora with supplement. Berkeley: University of California Press: 977B984.
- Perry B. 1992. Landscape plants for western regions, an illustrated guide to plants for water conservation. Claremont, CA: Land Design Publishing. 318 p.
- Poth M, Barro SC. 1986. On the thermodynamics of heat survival by seeds [unpublished manuscript on file]. Riverside, CA: USDA Forest Service, Pacific Southwest Research Station, Forest Fire Laboratory.
- Plummer AF, Christensen DR, Monsen SB. 1968. Restoring big-game range in Utah. Pub. 68-3. Salt Lake City: Department of Natural Resources, Division of Fish and Game. 182 p.
- Quick CR. 1935. Notes on the germination of ceanothus seeds. Madroño 3: 135B140.
- Quick CR, Quick AS. 1961. Germination of ceanothus seeds. Madroño 16: 23B30.

- Radwan MA, Crouch GL. 1977. Seed germination and seedling establishment of redstem ceanothus. *Journal of Wildlife Management* 41(4): 760B766.
- Reed MJ. 1974. *Ceanothus* L., ceanothus. In: Schopmeyer CS, tech. coord. Seeds of woody plants of the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 284B290.
- Rowntree L. 1948. Flowering shrubs of California. Standford, CA: Stanford University Press: 23B86.
- Sampson AW, Jespersen BS. 1963. California range brushlands and browse plants. Manual 33. Berkeley: University of California Agricultural Experiment Station, Extension Service: 102B112.
- Schmidt CL. 1993. *Ceanothus*. In: Hickman JC, ed. The Jepson manual: higher plants of California. Berkeley: University of California Press: 932B938.
- Schmidt MG. 1980. Growing California native plants. Berkeley: University of California Press. 366 p.
- Sunset National Garden Book. 1997. *Ceanothus*. Menlo Park, CA: Sunset Publishing Corp.: 235.
- Sunset Western Garden Book. 1995. *Ceanothus*. Menlo Park, CA: Sunset Publishing Corp.: 212B214.
- Swingle CF, comp. 1939. Seed propagation of trees, shrubs and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 198 p.
- Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: U.S. Department of Agriculture. 362 p.
- Van Renssler M, McMinn HE. 1942. *Ceanothus*. Berkeley, CA: Gillick Press. 308 p.
- Youngberg CT, Wollum AG II. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. *Soil Science Society of America Journal* 40(1): 109B112.
- Youngberg CT, Wollum AG II, Scott W. 1979. *Ceanothus* in Douglas-fir clearcuts: nitrogen accretion and impact on regeneration. In: Symbiotic nitrogen fixation in the management of temperate forests conference: proceedings of the symposium; 1979 April 2B5; Corvallis, OR. Corvallis: Oregon State University. 224B233.
- Zammit CA, Zedler PH. 1988. The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. *Vegetatio* 75: 175B187.
- Zammit CA, Zedler PH. 1992. Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *Journal of Ecology* 81: 499B511.
- Zavitkovski J, Newton M. 1968. Ecological importance of snowbrush (*Ceanothus velutinus*) in the Oregon Cascades. *Ecology* 49(6): 1134-1145.
- Zinke PJ. 1969. Nitrogen storage of several California forest soil-vegetation systems. In: Biology and ecology of nitrogen: proceedings of a conference; 1967 November 28BDecember 1. Washington, DC: National Academy of Sciences: 40B53.

Table 1C *Ceanothus*, ceanothus: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
<i>C. americanus</i> L. North Dakota, S to Florida & Texas	New-Jersey-tea , Jersey-tea, redroot	Dry woods, Ontario to Manitoba, Maine to
<i>C. arboreus</i> Greene <i>C. arboreus</i> var. <i>glabra</i> Jepson	feltleaf ceanothus , island myrtle, Catalina ceanothus	Larger islands of Santa Barbara Channel, California; up to 300 m; dry slopes, chaparral
<i>C. cordulatus</i> Kellogg whitethorn ceanothus	mountain whitethorn , snowbush, E to Nevada; 900B2,900 m, rocky ridges,	Baja California & mtns of S California, N to SW Oregon, ponderosa pine to red fir forest
<i>C. crassifolius</i> Torr.	hoaryleaf ceanothus	Cismontane southern California & Baja California; to 1,100 m; dry slopes and ridges, chaparral
<i>C. cuneatus</i> (Hook.) Nutt. wedgeleaf ceanothus, <i>C. rigidus</i> Nutt.	buckbrush ceanothus , California N into Oregon, S to Baja California; hornbrush, buckbrush	Inner coast range & Sierra Nevada foothills, 100B1,800 m elevation; chaparral & ponderosa pine forests
<i>C. cuneatus</i> var. <i>rigidus</i> (Nutt.) Hoover <i>C. rigidus</i> Nutt.	Monterey ceanothus	San Luis Obispo Co., N through Mendocino Co., California; up to 200 m; coastal bluffs, closed-cone pine forests
<i>C. diversifolius</i> Kellogg	trailing ceanothus , pinemat, Calistoga ceanothus	Westside Sierra Nevada, spotty in northern coast range, California; 900B1,800 m; under oaks, pines
<i>C. fendleri</i> Gray	Fendler ceanothus , buckbrush	South Dakota to New Mexico, Arizona, & Mexico; 1,500 to 3,000 m; ponderosa pine to dry Douglas-fir forests
<i>C. greggii</i> Gray	desert ceanothus	W Texas to S California, Utah, & N Mexico; 300B2,300 m, chaparral & desert chaparral
<i>C. impressus</i> Trel.	Santa Barbara ceanothus	Coastal areas in Santa Barbara & San Luis Obispo Cos., California; to 200 m; dry, sandy flats and slopes
<i>C. integerrimus</i> Hook & Arn. <i>C. andersonii</i> Parry	deerbrush ceanothus , sweet-birch, blue bush, deer brush	N California, Oregon, Washington to S California, Arizona, & New Mexico; 300B2,100 m; ponderosa pine to western hemlock, white fir forests; chaparral in SW
<i>C. leucodermis</i> Greene	chaparral whitethorn	S California to N Baja California; to 1,800 m; chaparral, dry slopes
<i>C. megacarpus</i> Nutt.	bigpod ceanothus	California
<i>C. oliganthus</i> Nutt.	hairy ceanothus	Coastal ranges, San Luis Obispo & Santa

<i>C. hirsutus</i> Nutt. <i>C. divaricatus</i> Nutt.	Jim brush	Barbara Cos. & San Gabriel Mtns to Humboldt Co., California; to 1,300 m; chaparral
<i>C. prostratus</i> Benth. squaw mat	squaw-carpet, mahala mat, California; higher mtns of Oregon & Washington, W	Sierra Nevada & N coast range S to Calaveras Co., Nevada; 900B2,200 m; common in ponderosa & Jeffrey pine forests
<i>C. sanguineus</i> Pursh <i>C. oreganus</i> Nutt.	redstem ceanothus, Oregon-tea tree	N California, Oregon, Idaho, Washington, & W Montana to S British Columbia; around 1,200 m; ponderosa pine, Douglas-fir/mixed conifer, western hemlock zones
<i>C. sorediatus</i> Hook. & Arn. <i>C. intricatus</i> Parry <i>C. oliganthus</i> var. <i>sorediatus</i> (Hook. & Arn.) Hoover	jimbrush ceanothus, jimbrush	Coast ranges in Los Angeles & Riverside Cos., Parry to Humboldt Co., California; 150B1,000 m; chaparral
<i>C. thyrsiflorus</i> Eschsch. <i>C. thyrsiflorus</i> var. <i>repens</i> McMinn	blue blossom, wild lilac	Coastal mountains Santa Barbara Co., California, to Douglas Co., Oregon; sea level to 600 m; coast redwood, mixed-evergreen, Douglas-fir forest, & chaparral
<i>C. velutinus</i> Dougl. ex Hook.	snowbrush ceanothus, mountain balm, sticky-laurel, tobacco brush	Coast ranges, British Columbia to Marin Co., California, Siskiyou Mtns, Sierra Nevada/Cascade axis E to SW Alberta, Montana, South Dakota, & Colorado; to 3,000 m; many forest types, ponderosa pine to subalpine
<i>C. velutinus</i> var. <i>hookeri</i> (M.C. Johnston) <i>C. velutinus</i> var. <i>laevigatus</i> Torr. & Gray	varnish-leaf ceanothus, snowbrush, Hooker ceanothus	Same as above, but more common near coast

Sources: Franklin and others (1985), Hitchcock and others (1961), Lenz and Dourley (1981), McMinn (1964), Munz and Keck (1968), Reed (1974), Sampson and Jespersen (1963), Schmidt (1993).

Table 2C *Ceanothus*: phenology of flowering and fruiting, height, and year of first cultivation

Species	Flowering dates	Fruit-ripening dates	Height at maturity (m)	Year first cultivated
<i>C. americanus</i>	MayBJuly	AugBearly Oct	0.5B1	1713
<i>C. arboreus</i>	FebBAug	MayBearly Oct	3B9	1911
<i>C. cordulatus</i> :			0.6B2.5	C
California	MayBJune	JulyBSept	C	C
Oregon	JuneBJuly	AugBSept	C	C
<i>C. crassifolius</i>	JanBJune	MayBJune	1.2B3	1927
<i>C. cuneatus</i>	MarBJune	AprBJuly	1B4.5	1848
<i>C. cuneatus</i> var. <i>rigidus</i>	DecBApr	MayBJune	1B2.1	1847
<i>C. diversifolius</i>	spring	JuneBJuly	0.3 or less	1941
<i>C. fendleri</i> (Arizona)	AprBOct	AugBDec	0.2B1	1893
<i>C. greggii</i> (Arizona*)	MarBApr	July	0.6B1.8	C
<i>C. impressus</i>	FebBApr	June	C	C
<i>C. integerrimus</i>	AprBAug	JuneBAug	1B5.5	1850
<i>C. leucodermis</i>	C	JulyBAug	C	
<i>C. oliganthus</i>	FebBApr	MayBJune	1.2B7.5	C
<i>C. prostratus</i>	AprBJune	July	.05B.15	C
<i>C. sanguineus</i>	AprBJune	JuneBJuly	1.5B3	1812
<i>C. sorediatus</i>	MarBApr	MayBJuly	1B5.5	C
<i>C. thyrsiflorus</i>	JanBJune	AprBJuly	1.2B8	1837
<i>C. velutinus</i>			0.6B2.4	1853
Calif.	JuneBAug	JulyBAug	C	C
N IdahoH	May 20BJuly 25	July 15BAug 1	C	C
W Montanal	June 25BJuly 15	Aug 10BSept 10	C	C
SW Oregon	MayBJuly	JulyBSept	C	C
Utah		Aug 1BAug 30	C	C

Sources: Evans and others (1987), Furbush (1962), Hitchcock (1961), Hubbard (1958), Kearney (1951), McMin (1964), Mirov and Kraebel (1939), Plummer and others (1968), Reed (1974), Rowntree (1948), Sampson and Jespersen (1963), Swingle (1939), Van Dersal (1938), Van Rensselaer (1942).

Elevations: * 900B1,500 m. H 700 m. I 1,650 m.

Table 3C *Ceanothus*, ceanothus: thousands of cleaned seeds per weight

Species	/kg	Range	/kg	Average	Samples
		/lb		/lb	
<i>C. americanus</i>	212B291	96B132	247	112	5
<i>C. arboreus</i>	106B110	48-50	108	49	2
<i>C. cordulatus</i>	311B396	141B179	366	166	4
<i>C. crassifolius</i>	73B143	33B65	117	53	3
<i>C. cuneatus</i>	80B123	36B56	108	49	3
<i>C. cuneatus</i> var. <i>rigidus</i>	C		159	72	1
<i>C. diversifolius</i>	C		185	84	1
<i>C. greggii</i>	C		51	23	C
<i>C. impressus</i>	C		245	111	1
<i>C. integerrimus</i>	128B179	58B81	154	70	2
<i>C. oliganthus</i>	137B161	62B73	148	67	2
<i>C. prostratus</i>	82B98	37B45	90	41	3
<i>C. sanguineus</i>	282B291	128B132	287	130	2
<i>C. sorediatus</i>	267B269	121B122	C	C	2
<i>C. thyrsiflorus</i>	106B400	48B181	C	C	C
<i>C. velutinus</i>	135B335	61B152	207	94	5

Sources: Emery (1964), Hubbard (1958), Mirov and Kraebel (1939), Plummer and others (1968), Quick (1935), Quick and Quick (1961), Reed (1974), Swingle (1939).

Table 4C *Ceanothus*, *ceanothus*: pregermination treatments and germination test results

Species	Pregermination treatments			Germination test duration (days)	Germination rate	
	Hot water soak		Cold stratification (days)		Ave. (%)	Samples
	Temp. (°C)	Time* (min)				
<i>C. americanus</i>	C	0	90	50	65	4
	77B100	ttc	60	30	32	1
<i>C. arboreus</i>	71B91	ttc	0	40B112	90	3+
<i>C. cordulatus</i>	90	ttc	94	35	74	4
	85	ttc	94	35	90	4
	80	ttc	94	35	74	4
<i>C. crassifolius</i>	71	ttc	90	21B90	76	1+
	71	ttc	0	90	48	1+
<i>C. cuneatus</i>	71	ttc	90	21B90	92	1+
	120H	5	30	21	28	3
	100	5	30	21	38	3
	70	60	30	21	3	3
	C	0	30	21	10	3
<i>C. cuneatus</i> var. <i>rigidus</i>	71	ttc	0	60B112	85	2+
<i>C. diversifolius</i>	77B100	ttc	60	60	61	1+
<i>C. fendleri</i>	C	0	0	C	16	C
<i>C. greggii</i>	100	1	30B60	17	51	C
<i>C. impressus</i>	77B100	ttc	60	30	73	1+
<i>C. integerrimus</i>	85	ttc	56	C	100	1
	71	ttc	90	20	85	1+
<i>C. leucodermis</i>	120H	5	30	21	68	3
	100	5	30	21	50	3
	70	60	30	21	47	3
	C	0	30	21	7	3
<i>C. megacarpus</i>	120H	5	30	21	88	3
	100	5	30	21	53	3
	70	60	30	21	54	3
	C	0	30	21	6	3
<i>C. oliganthus</i>	71	ttc	0	70	62	1+
<i>C. prostratus</i>	100	0.5	115	C	92	C
	77B100	ttc	90	30	71	1+
<i>C. sanguineus</i>	100	1	120	32	97	3
	100	5	120	32	92	3
	100	15	120	32	41	3
	100	1B5	0	32	0	3
<i>C. sorediatus</i>	100	5	90	30	100	1+
	100	5	0	30	38	1
<i>C. thyrsiflorus</i>	71	ttc	90	60	83	1+
	71	ttc	0	60	73	1
<i>C. velutinus</i>	90	ttc	63B84	B	82	1
	71	ttc	90	30	70	2+

Sources: Emery (1964), Keeley (1987a), Mirov and Kraebel (1939), Quick (1935), Quick and Quick (1961), Radwan and Crouch (1977), Reed (1974), Van Dersal (1938).

* ttc = Atime to cool@ (to room temperature) varied from several hours to overnight.

H Results reported here are for dry heat treatments, with germination in the dark; see Keeley (1987) for data on light germination.