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The Role of the Genus *Ceanothus* in Western Forest Ecosystems

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The Role of the Genus *Ceanothus* in Western Forest Ecosystems

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Compilers

Report of a workshop held November 22-24, 1982
Oregon State University, Corvallis, Oregon

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Abstract

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This report was developed from discussions on the role of *Ceanothus* in western forests that took place at a workshop held November 22-24, 1982, at Oregon State University, Corvallis, Oregon. The workshop provided a forum for discussing research relevant to *Ceanothus* management. Major topics were autecology and synecology; interactions between *Ceanothus* species and the soil system; the physiological ecology of *Ceanothus* and associated conifers; and the effects of *Ceanothus* on forest productivity and growth. The workshop was attended by scientists and land managers from government agencies, universities, and forest industry. This report summarizes available information concerning the biology and ecology of *Ceanothus* species in western forest ecosystems; describes and critiques methods, results, and conclusions of past research; discusses current investigations; identifies research needs; and includes an extensive bibliography and a listing of workshop participants involved or interested in *Ceanothus* research and management.

Keywords: *Ceanothus,* competition (plant), ecology (plant), autecology (plant), synecology (plant).

1. Introduction

The impacts of native, symbiotic, nitrogen-fixing plants on conifer productivity, vegetation dynamics, nutrient cycling, and wildlife habitat in forest ecosystems are of considerable ecological and economic interest. The two major genera of nitrogen-fixing woody plants on forest sites in the western United States are *Ceanothus* and *Alnus.*[1] Although *Alnus* is an important component in coastal and mesic low- and high-elevation forests of the Pacific Northwest, the primary nitrogen-fixing shrubs on drier and middle-elevation forest sites are species of *Ceanothus*. Several of these species are frequently dominant components in early successional vegetation following disturbance such as fire.

Two recent publications (Gordon and Wheeler 1983, Gordon and others 1979) provide an excellent overview of current research on the effects of nitrogen-fixing species on forest site productivity; the biology, ecology, and physiology of the host-symbiont relationship; options for integrating nitrogen fixers into forest management; and economic considerations in the management of symbiotic nitrogen fixers. Although these publications summarize much of the available data on *Alnus* and other species, the information they present pertaining to *Ceanothus* is limited.

A fairly large body of research information exists on the biology and ecology of forest species of *Ceanothus*. The literature indicates that *Ceanothus* affects many components of the forest ecosystem, including nitrogen availability, nutrient cycling, conifer establishment and growth, and forage quality for browsing animals.

The workshop on *Ceanothus* was initiated because widely divergent opinions exist among scientists and land managers concerning the relative benefits and negative impacts of *Ceanothus*. The workshop was structured to provide a forum for discussing major research areas relevant to *Ceanothus* management. The three major objectives of the workshop were: (1) to summarize available information concerning the biology and ecology of *Ceanothus* species in western forest ecosystems; (2) to discuss research methods, results, conclusions, and interpretations; and (3) to identify future research needs. Participants included scientists and land managers from government agencies, universities, and forest industry.

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[1] Scientific and common names of species are listed in appendix 1.

Following an overview presentation on the importance of *Ceanothus* species in U.S. forest ecosystems, the workshop was organized into small working groups, each of which focused on one of the four topic areas:

1. The autecology and synecology of *Ceanothus*.

2. Interactions between *Ceanothus* species and the soil system.

3. The physiological ecology of *Ceanothus* and associated conifers.

4. Effects of *Ceanothus* on forest productivity and conifer growth.

Past and current research was discussed in each group; the objective was to summarize available information and identify promising techniques for new or improved studies. Emphasis was placed on including existing studies on *Ceanothus* within a framework of long-term research objectives.

Each participant was provided a preliminary bibliography and a list of recommended reading prior to the workshop. Participants were also encouraged to discuss unpublished research.

This report summarizes and updates workshop presentations and discussions. The introductory remarks by Jerry Franklin and the concluding remarks by John Gordon are based on transcripts from tapes. Summaries of group discussions (sections 3-7) include pertinent published and unpublished results identified by participants, comments on research methods and approaches, and recommendations for future research. These summaries were prepared by the compilers.

2. The Importance of *Ceanothus* Species in U.S. Forest Ecosystems[1]

This paper discusses autecology, distribution, and taxonomic relationships of the major forest species of *Ceanothus* and considers some of the various roles that *Ceanothus* plays in western forest ecosystems.

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[1] This section prepared by Jerry Franklin, chief plant ecologist, Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station, Corvallis, OR 97331; Charlie Halpern, research assistant, Botany Department, Oregon State University, Corvallis, OR 97331; Brad Smith, research assistant, Botany Department, Oregon State University; and Ted Thomas, research assistant, Forest Science Department, Oregon State University.

Ceanothus is a North American genus of Sierra Madrean origin. Of the 55 species in the genus, 51 of them are found in western North America, four are found in the Eastern United States, and two are isolated in Florida. There are 44 species in the Pacific coast region; 38 of these are restricted to the California floristic province, which includes California, Baja California, southwestern Oregon, and western Nevada. Six species are found in the Rocky Mountains.

Species in the genus *Ceanothus* range from mat-forming shrubs less than 0.3 meter (1 ft) high to small trees as tall as 4 to 9 meters (15-30 ft). Typically, they are shrubs 0.9 to 2.4 meters (3-8 ft) tall. The genus contains both deciduous and evergreen species.

Genus sections.—Two sections of the genus are recognized, *Euceanothus* and *Cerastes;* within each section, the species are highly interfertile. There are many known hybrids, which may account for the variability in the taxonomic treatment of the genus—our treatment follows McMinn (1942). The potential for hybridization and formation of species that can adapt to new environments may be one reason the genus has been successful.

The more ancient section is *Euceanothus*, and it contains about 60 percent of the species (approximately 33). Characteristics of several distinctive species are shown in figure 1. Most have retained the ability to sprout. This is also the section in

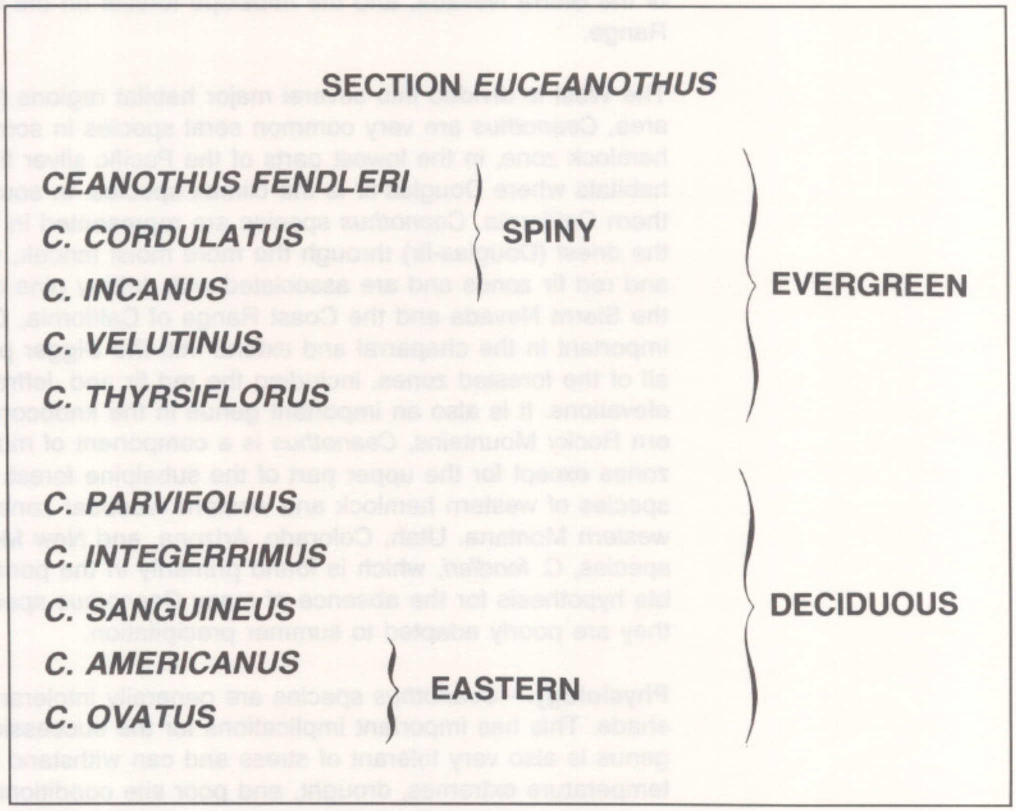

Figure 1.—Ecological characteristics and common forest species of section *Euceanothus* in the genus *Ceanothus*.

which most of the important forest species are found. Both evergreen and deciduous species and both spiny and nonspiny species are included. The four species in the Eastern United States are found in this section.

The other section, *Cerastes,* has about 26 species, and some people believe it contains the most long-lived ones. The species in this section do not sprout, and only a few of them are important forest species *(C. cuneatus, C. prostratus,* and *C. pumilus). C. greggii* is, however, an important desert and chaparral species (USDA Forest Service 1937). The purported longevity of these species supports a hypothesis that seed reproduction rather than sprouting tends to be characteristic of long-lived species.

Distribution.—Many *Ceanothus* species occur in chaparral and desert habitats at elevations below forest sites or at the forest-nonforest interface. Approximately a third of *Ceanothus* species (20 to 25) are forest oriented. These species, with a few exceptions, are important components of the communities in most western forest zones except in the coldest zones and in moist habitats, such as the Sitka spruce zone and the wetter parts of the western hemlock zone. Generally, *Ceanothus* species are not found in subalpine forests except at the lowest elevations of the zone. *Ceanothus* distribution is skewed toward the driest forest zones—ponderosa pine and the Douglas-fir series—and toward early successional stages of midslope zones in the Rocky Mountains, the Sierra Nevada, and the Cascade Range. This includes the mixed conifer zone of the Rocky Mountains, the mixed conifer forests of the Sierra Nevada, and the midslope forests on the east slope of the Cascade Range.

The West is divided into several major habitat regions (fig. 2). In the northwestern area, *Ceanothus* are very common seral species in some parts of the western hemlock zone, in the lowest parts of the Pacific silver fir zone, and especially in habitats where Douglas-fir is the climax species. In southwestern Oregon and northern California, *Ceanothus* species are represented in all the forest zones, from the driest (Douglas-fir) through the more moist tanoak, western hemlock, white fir, and red fir zones and are associated with Jeffrey pine on serpentine habitats. In the Sierra Nevada and the Coast Range of California, *Ceanothus* species are very important in the chaparral and extend into the Digger pine and oak woodlands and all of the forested zones, including the red fir and Jeffrey pine forests at higher elevations. It is also an important genus in the knobcone pine forests. In the northern Rocky Mountains, *Ceanothus* is a component of most of the important forest zones except for the upper part of the subalpine forest. *Ceanothus* are seral species of western hemlock and western redcedar zones in northern Idaho and western Montana. Utah, Colorado, Arizona, and New Mexico have only one species, *C. fendleri,* which is found primarily in the ponderosa pine zone. A possible hypothesis for the absence of many *Ceanothus* species in the southwest is that they are poorly adapted to summer precipitation.

Physiology.—*Ceanothus* species are generally intolerant to very intolerant of shade. This has important implications for the successional role that they play. The genus is also very tolerant of stress and can withstand both cold and hot temperature extremes, drought, and poor site conditions.

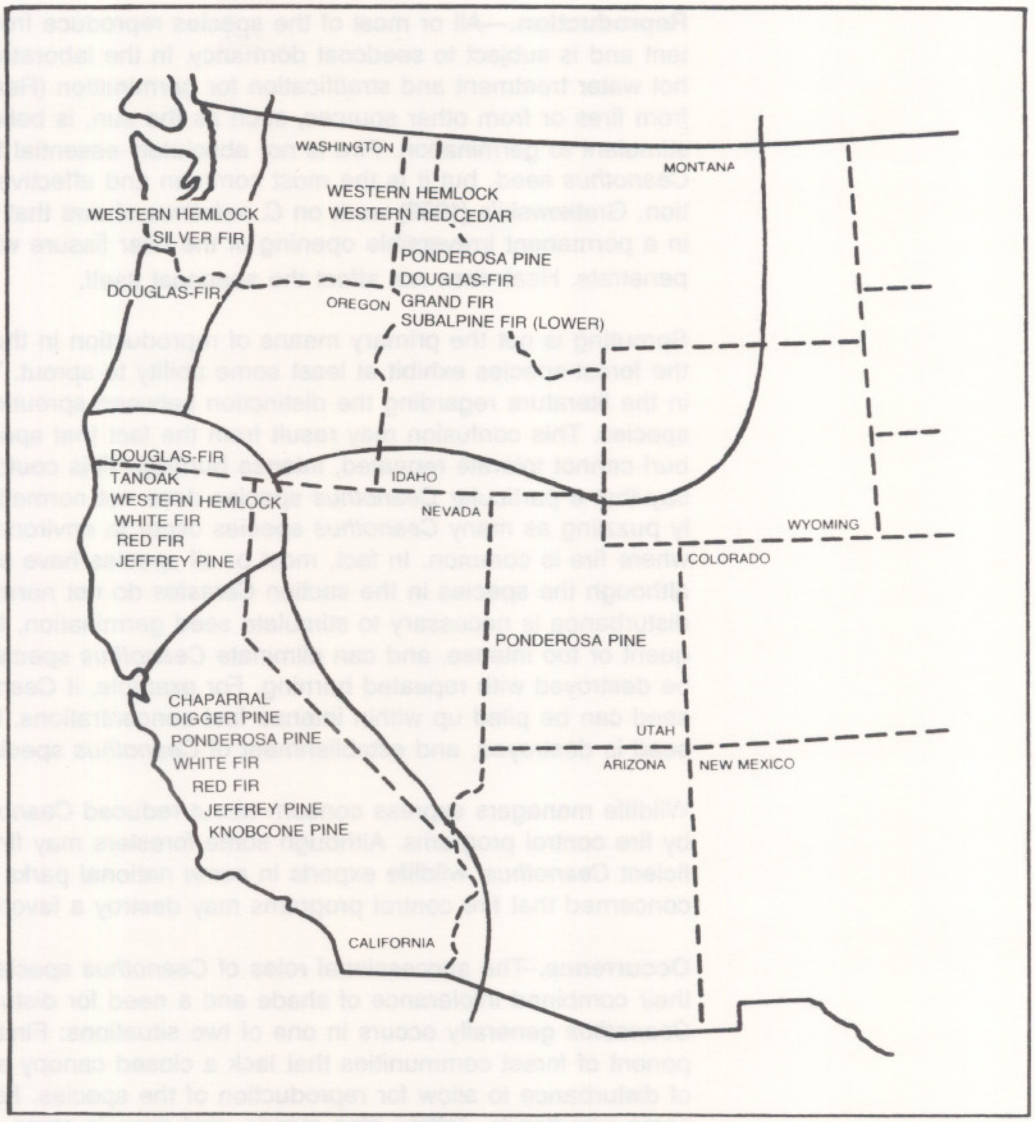

Figure 2.—Zones or community series in which one or more *Ceanothus* species play important roles.

Ceanothus species have the potential to fix nitrogen. Although the occurrence of nodules on *Ceanothus* has been known for a long time, demonstration of the ability of the plants to actually fix nitrogen is a relatively recent discovery (Bond 1957). The ability of *Ceanothus* to fix nitrogen has been demonstrated in the laboratory for all species that have been examined in detail. Delwiche and others (1965), for example, worked with 12 species using excised nodules and found that in all cases when these species are nodulated they are capable of fixing nitrogen. Field demonstrations of net nitrogen accretion are much more limited and are somewhat controversial. Probably all the species have the potential to fix nitrogen on at least some sites at least part of the time.

Reproduction.—All or most of the species reproduce from seed, which is persistent and is subject to seedcoat dormancy. In the laboratory, most species require a hot water treatment and stratification for germination (Reed 1974). In nature, heat from fires or from other sources, such as the sun, is believed to be the major stimulant to germination. Fire is not absolutely essential for germination of *Ceanothus* seed, but it is the most common and effective way to stimulate germination. Gratkowski's (1962) work on *C. velutinus* shows that heating the seed results in a permanent irreversible opening of the hilar fissure which allows moisture to penetrate. Heat does not affect the seedcoat itself.

Sprouting is not the primary means of reproduction in the genus, although most of the forest species exhibit at least some ability to sprout. There is some confusion in the literature regarding the distinction between sprouting and nonsprouting species. This confusion may result from the fact that species without a root crown burl cannot tolerate repeated, intense burning. This could be why many ecologists say that a particular *Ceanothus* species does not normally sprout. This is especially puzzling as many *Ceanothus* species occur in environments such as chaparral where fire is common. In fact, most or all species have some sprouting ability, although the species in the section *Cerastes* do not normally do so. Even though disturbance is necessary to stimulate seed germination, fire can be either too frequent or too intense, and can eliminate *Ceanothus* species. Seed and plants can be destroyed with repeated burning. For example, if *Ceanothus* is windrowed, the seed can be piled up within intense fuel concentrations. In such situations, much seed is destroyed, and establishment of *Ceanothus* species is often very low.

Wildlife managers express concern about reduced *Ceanothus* occurrence caused by fire control programs. Although some foresters may find it hard to imagine insufficient *Ceanothus,* wildlife experts in some national parks in the Sierra Nevada are concerned that fire control programs may destroy a favorite browse for wildlife.

Occurrence.--The successional roles of *Ceanothus* species are a consequence of their combined intolerance of shade and a need for disturbance for regeneration. *Ceanothus* generally occurs in one of two situations: First, it can be a regular component of forest communities that lack a closed canopy and that have some level of disturbance to allow for reproduction of the species. For example, in chaparral, some woodlands, Jeffrey pine stands, and even in some ponderosa pine and Douglas-fir stands, the canopy never gets sufficiently dense to shade out the species. *Ceanothus* could be a basic component of the stable forest on such sites. Second, *Ceanothus* may exist as an early successional species on sites that develop a closed forest canopy; for example, snowbrush *(C. velutinus)* in the mixed conifer forests of the northern Rocky Mountains or in the western hemlock zone of the Cascade Range. These are situations in which *Ceanothus* reproduces following a disturbance such as logging, burning, or wildfire. It grows until it is overtopped by the trees, and it persists as seed until the next major disturbance.

In many young forests, the canopy can be dense enough to shade out *Ceanothus,* but in mature stands there are many canopy openings. Many of the Sierra mixed conifer forests, for example, have a very open canopy and in a mature forest, *Ceanothus* can be a permanent member of those forested communities. Some of the Douglas-fir climax sites in southwestern Oregon and some of the drier sites in the Rocky Mountains are similar. Whether the genus is pioneer or climax, many *Ceanothus* species also have the ability to retard succession by forming brushfields.

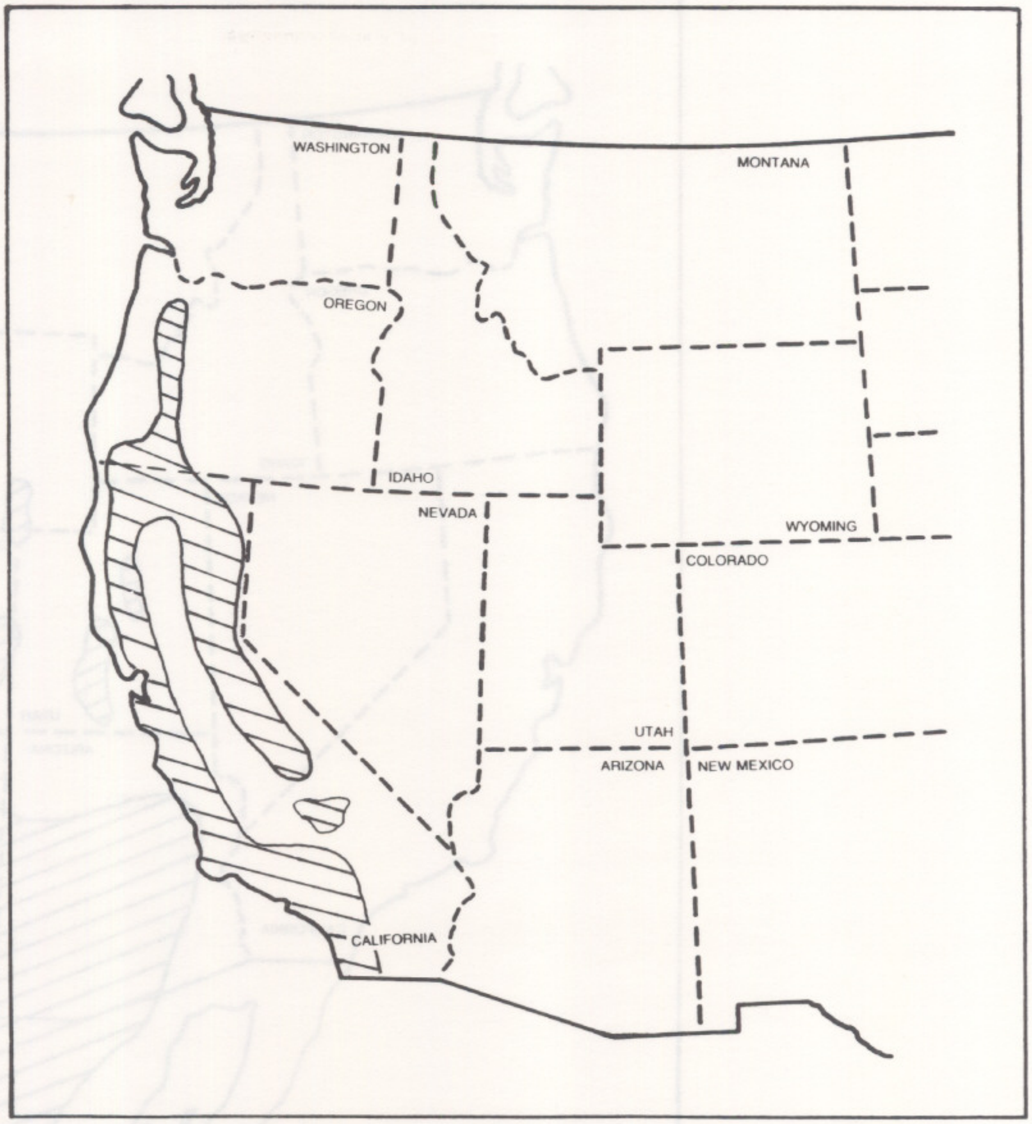

Figure 3.—Distribution of *Ceanothus cuneatus.* Range information from McMinn (1942), Hitchcock and Cronquist (1961), and Sampson and Jesperson (1963).

Ecology and distribution of selected western *Ceanothus* species.—*Ceanothus cuneatus,* (wedgeleaf ceanothus or buckbrush, fig. 3) is primarily a chaparral species, but it also occurs in ponderosa pine and other dry forests. Typical of shallow soils and dry sites, it is a very drought-resistant species. It is a vigorous, aggressive species that can form impenetrable thickets. Because of its palatability, it is an important winter food for deer in many areas.

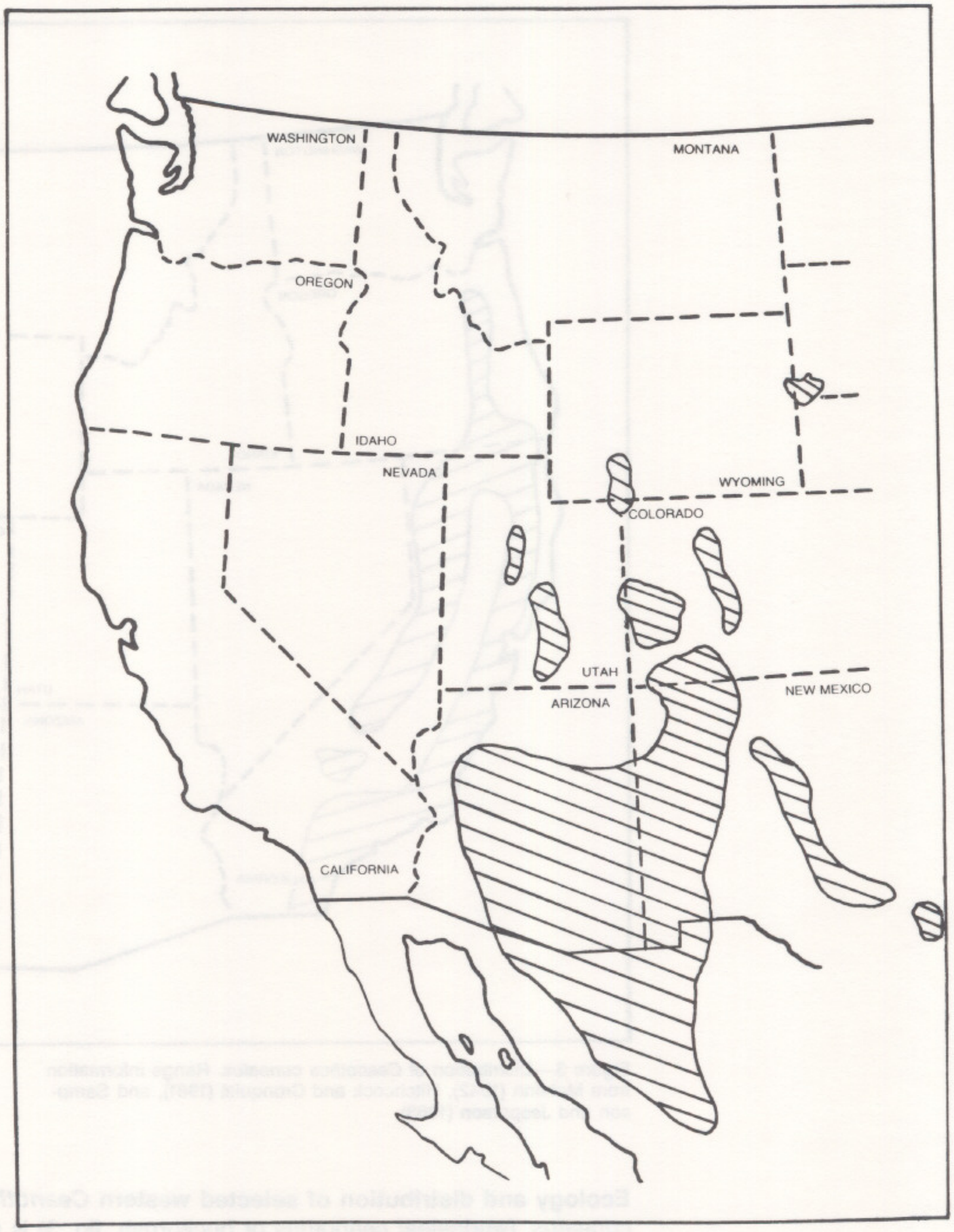

Figure 4.—Distribution of *Ceanothus fendleri*. Information from McMinn (1942).

Ceanothus fendleri (Fendler ceanothus, fig. 4) occurs in the ponderosa pine zone in the Rocky Mountains. It also occurs in some of the drier Douglas-fir habitats of the Southwest (Alexander and others 1984) but is generally absent from white fir forests. A nonsprouter, it germinates following fire and is a component of the stable mature forest. *C. fendleri* is an important browse plant for deer and is often mentioned in connection with deer management.

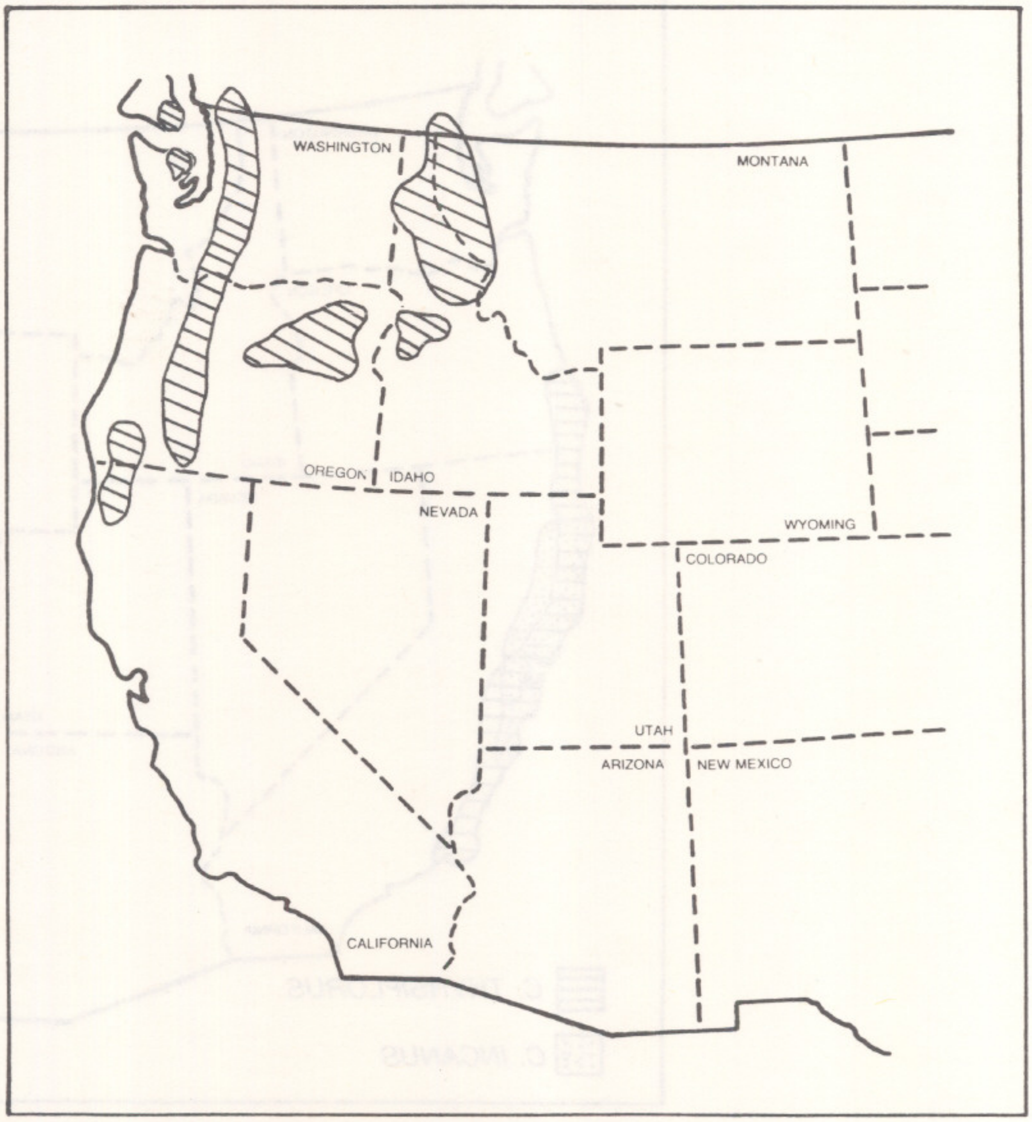

Figure 5.—Distribution of *Ceanothus sanguineus.* Information from McMinn (1942), Hitchcock and Cronquist (1961), and personal observations of the authors.

Ceanothus sanguineus (redstem ceanothus, fig. 5) is found primarily in the ponderosa pine zone and in parts of the mixed conifer and western hemlock zones in both the Cascade Range and in the northern Rocky Mountains. In the Cascades, it is common on sites in the Douglas-fir habitat series, particularly after logging and burning. *C. sanguineus* is considered excellent browse for wildlife.

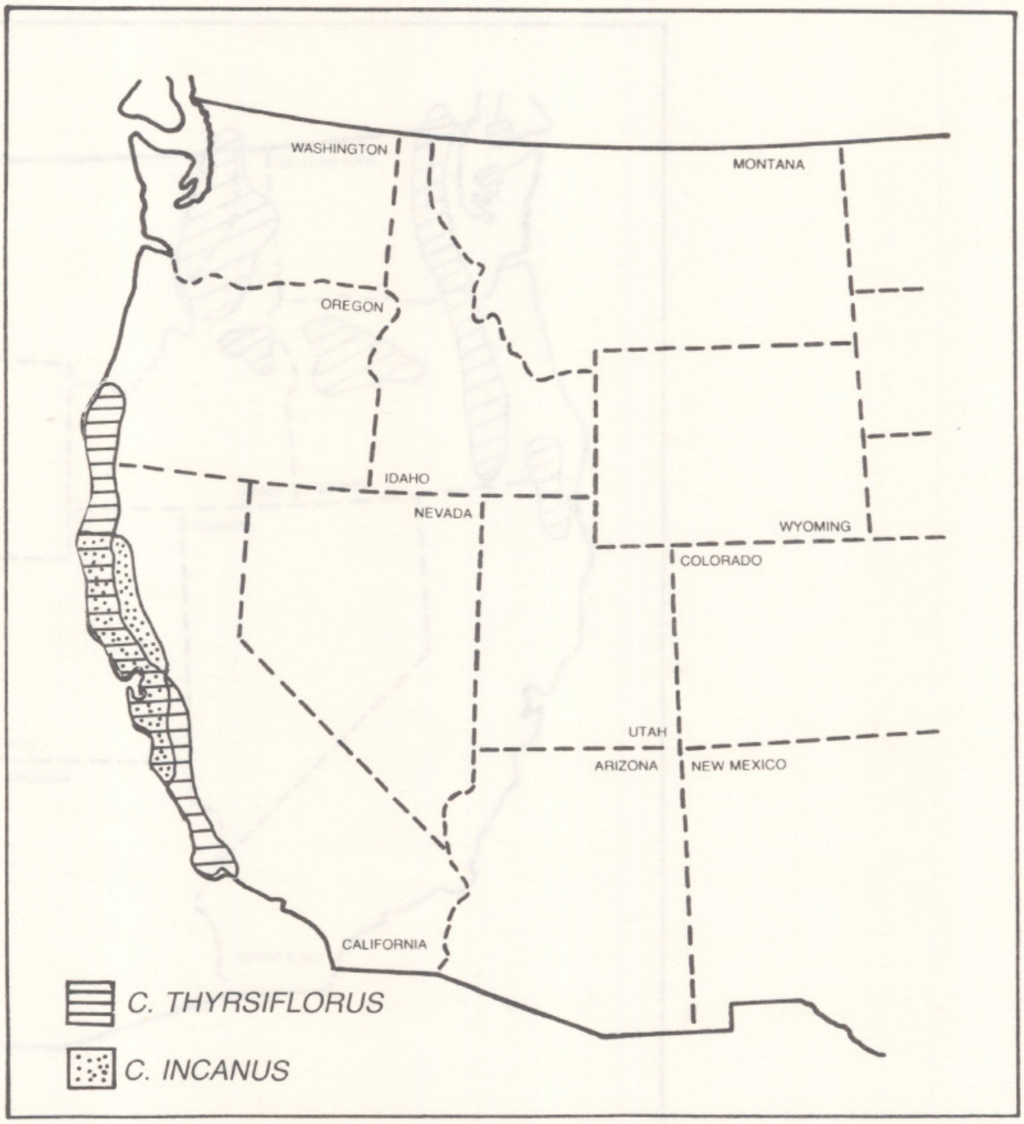

Figure 6.—Distribution of *Ceanothus thyrsiflorus* and *C. incanus*. Information from McMinn (1942), Munz and Keck (1973), and Sampson and Jesperson (1963).

Ceanothus thyrsiflorus (blueblossom, fig. 6) occurs in southern Oregon and northern California coastal regions on both forest and chaparral sites. *Ceanothus incanus* (fig. 6) is often associated with coast redwood. It occurs in coast redwood and mixed evergreen forests along the northern California coast.

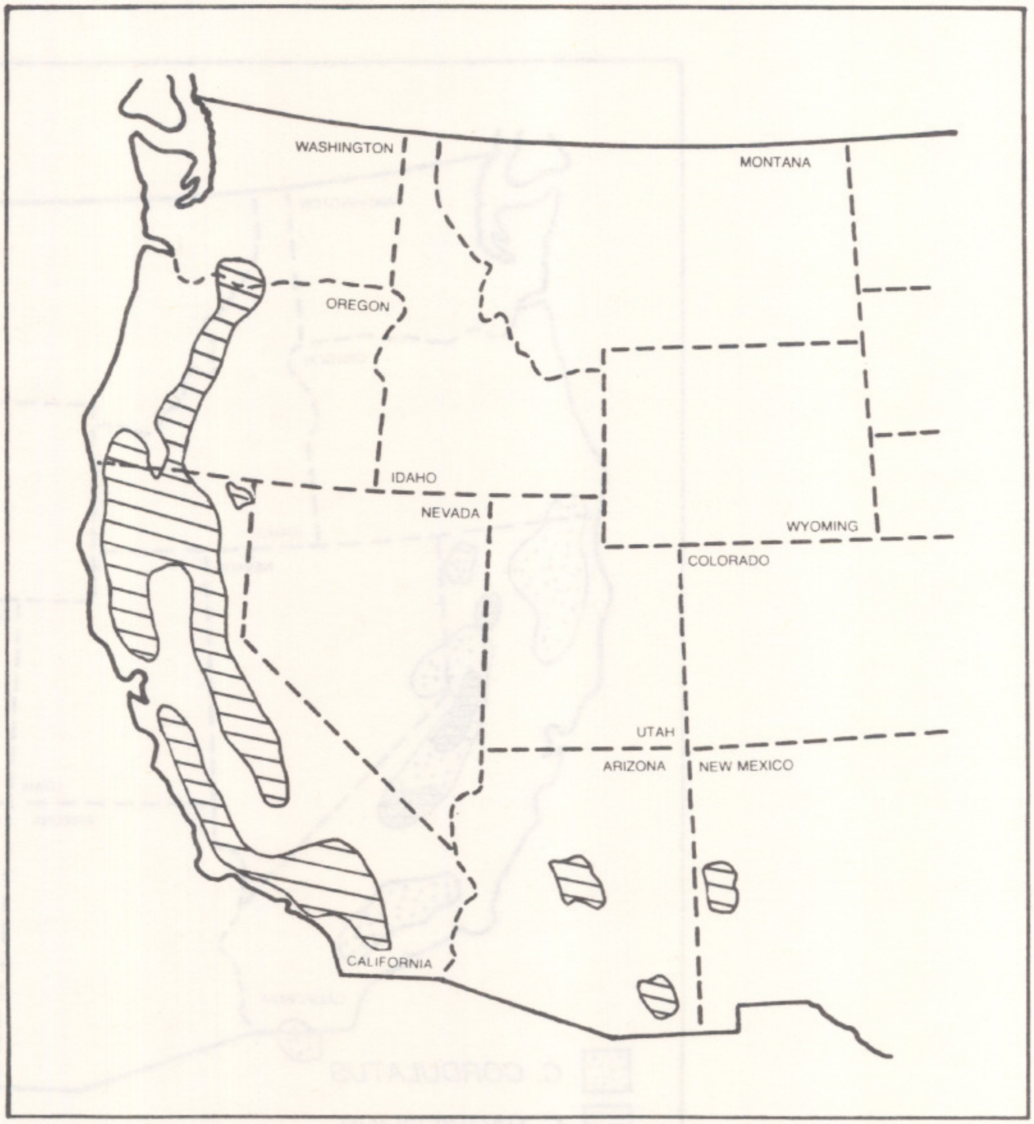

Figure 7.—Distribution of *Ceanothus integerrimus.* Information from McMinn (1942), Hitchcock and Cronquist (1961), Sampson and Jesperson (1963), and personal observations of the authors.

Ceanothus integerrimus (deerbrush, fig. 7) is widely distributed both geographically and ecologically and occurs from the dry ponderosa pine forests into the western hemlock and white fir zones. It is also associated with Coulter pine at lower elevations in southern California. Gratkowski (1961a) identified *C. integerrimus* as a major brush species in the Umpqua, Rogue, and Cascade regions of southern Oregon. It is also found in chaparral of the southern Rocky Mountains. Will Moir[2] notes that this species can occur in chaparral and in riparian forests in Arizona and southwestern New Mexico. Cronemiller (1959) indicates that it can form dense stands, it can sprout, and it can be eliminated with repeated disturbance. According to the Range Plant Handbook (USDA Forest Service 1937), it is "one of the most valuable western browse plants."

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[2] Personal communication, Will Moir, USDA Forest Service, Southwestern Region, Albuquerque, NM 87102.

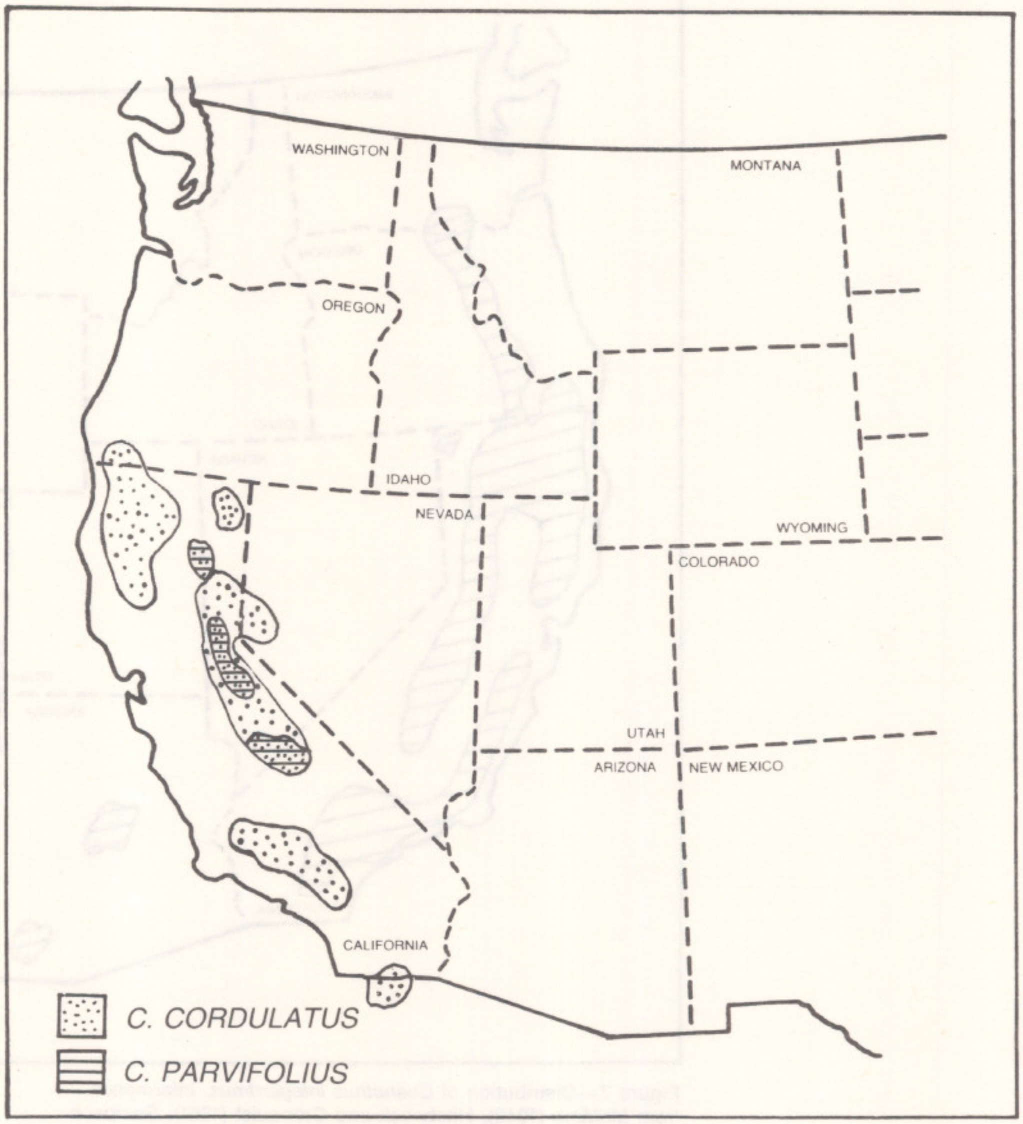

Figure 8.—Distribution of *Ceanothus cordulatus* and *C. parvifolius.* Information from McMinn (1942), and Sampson and Jesperson (1963).

Two California species are *Ceanothus cordulatus* (mountain whitethorn) and *Ceanothus parvifolius* (fig. 8). *C. cordulatus* is widespread geographically; it occurs from southern Oregon to Baja California and ranges from ponderosa pine forests into the red fir zones. Commonly associated with Jeffrey pine and ponderosa pine, this species increases with disturbance and forms very dense and difficult-to-penetrate brushfields. It also is persistent in the open forests on the midslopes of the Sierra Nevada and transverse ranges in California. *C. parvifolius* is similar but it lacks thorns and has a more limited range.

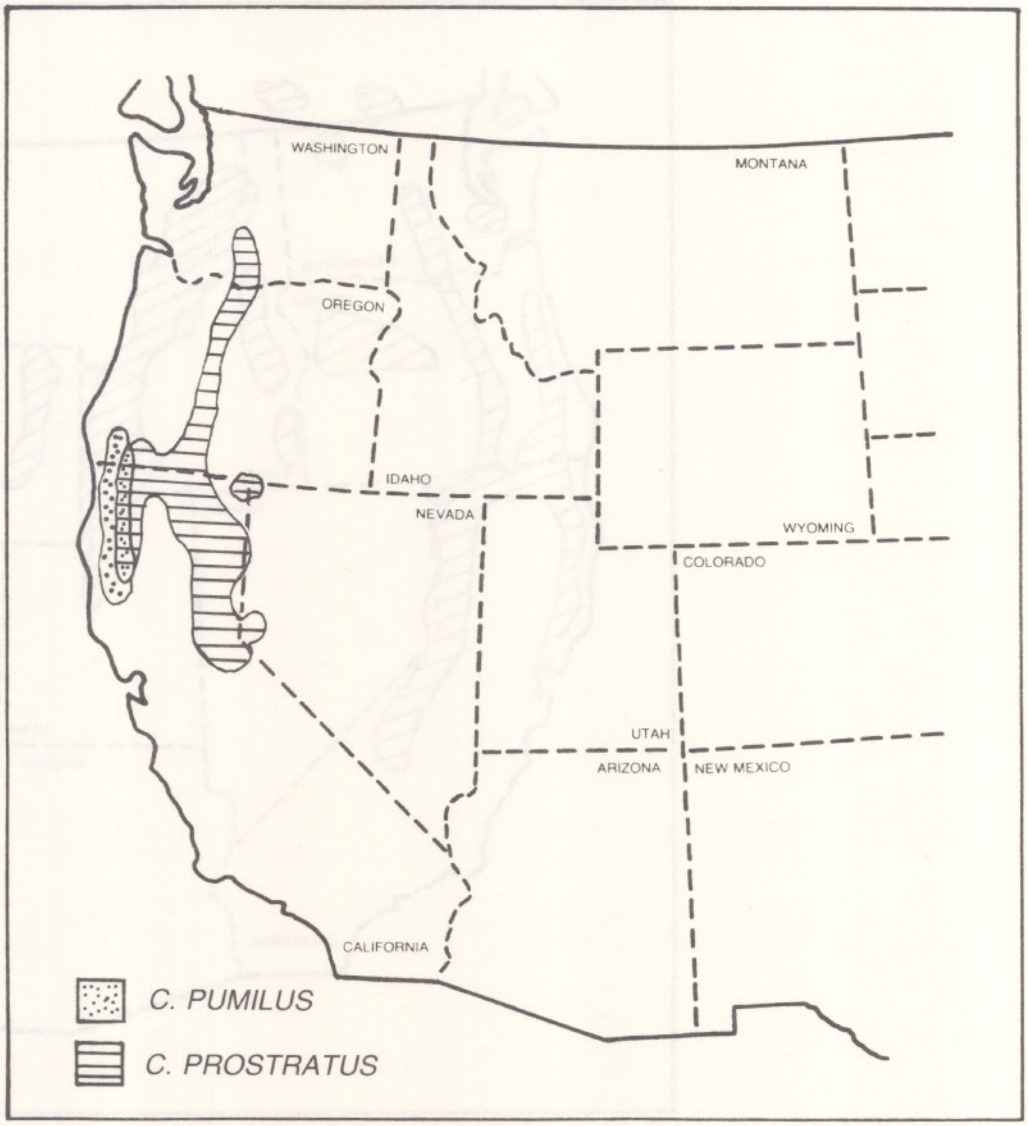

Figure 9.—Distribution of *Ceanothus prostratus* and *C. pumilus.* Based on information from McMinn (1942), Hitchcock and Cronquist (1961), and Munz and Keck (1973).

Two that form mats are *Ceanothus prostratus* (squaw carpet) and *Ceanothus pumilis* (fig. 9). *C. prostratus* has a wide elevational range and occurs on dry, lithosolic sites. It is common in Jeffrey pine and ponderosa pine forests in the southern Cascade Range and in the Sierra Nevada. *C. pumilis* is primarily a serpentine species found in association with Jeffrey pine.

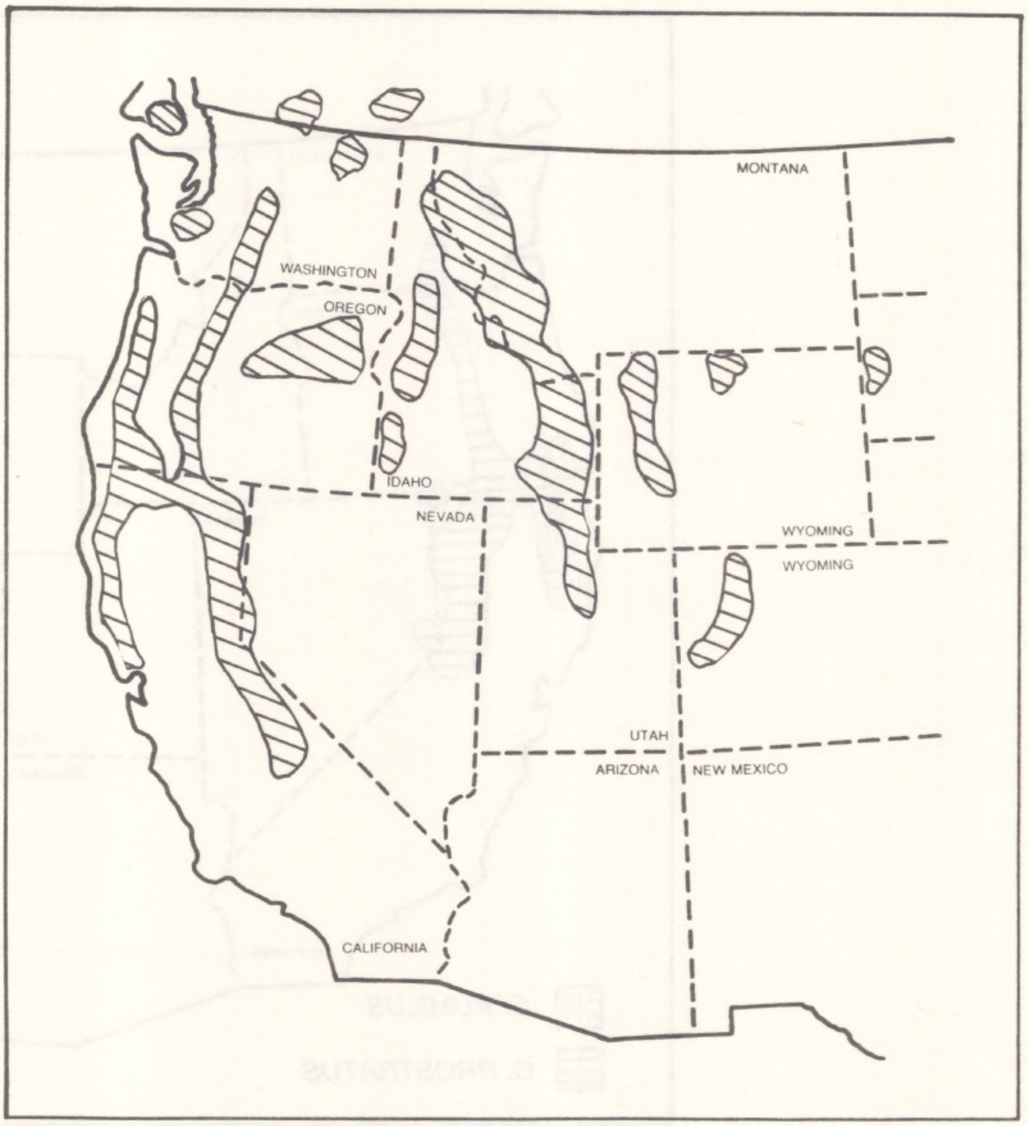

Figure 10.—Distribution of *Ceanothus velutinus.* Information from McMinn (1942), Mueggler and Campbell (1982), and Youngblood and Mueggler (1981).

Ceanothus velutinus (fig. 10), one of the most important forest species, has two widespread varieties--snowbrush (var. *velutinus*) and varnishleaf (var. *laevigatus*). *C. velutinus* is widespread geographically and grows in a wide variety of habitats. In California, it occurs in mixed evergreen, red fir, white fir, mixed conifer, Jeffrey pine, and ponderosa pine forests. In Oregon, it is found in mixed conifer, mixed evergreen, western hemlock, and lower Pacific silver fir zones. In the interior Rocky Mountain region, it is found in ponderosa pine, Douglas-fir, mixed conifer, and lower subalpine zones. *C. velutinus* is important in brushfield formation. On sites where it develops best it is seral—a successional species that reproduces through persistent seed that is perhaps three or four centuries old. It is eliminated as a shrub when the canopy closes. It can persist in mature forests on some sites, however, such as the decomposed granitic habitats in eastern Montana, which belong to the Douglas-fir series.

Ceanothus velutinus is the most extensively studied of the forest *Ceanothus* species. The studies include investigations of the ecological role, autecology, role in nitrogen cycling, and competitive abilities of the species. Wahlenberg (1930) investigated the vigor and mortality of ponderosa pine seedlings planted in, at the edge of, or outside *C. velutinus* clumps or bushes. Fire stimulates germination and sprouting but is not absolutely required for *C. velutinus* to reproduce. Halpern's data (unpublished) from the H. J. Andrews Experimental Forest, Willamette National Forest, show that *C. velutinus* may occur on sites that are disturbed but not burned. It develops more rapidly and more completely on sites that are burned, but occasional seeds can germinate on sites that are not burned. *C. sanguineus* is even less dependent on fire than is *C. velutinus* and it can develop into good stands on unburned sites.

Conclusions

Ceanothus species are tolerant of stress but intolerant of shade, are capable of nitrogen fixation, can reproduce from persistent seeds that require heat to germinate, have a limited ability or no ability to sprout, and require moderate disturbance to reproduce.

Ceanothus is a very important genus as a food source for wildlife. The Range Plant Handbook (USDA Forest Service 1937) describes *C. sanguineus, C. thyrsiflorus,* and *C. fendleri* as being some of the most important browse species in their respective ranges.

Ceanothus is important in site amelioration. The genus does have nitrogen-fixing and other soil-building attributes. It is tolerant of severe sites, and it can play a soil-building role on these sites.

Ceanothus species, especially those such as *C. prostratus* that form mats, are important in erosion prevention. Several species have root systems that can help to prevent mass soil movements.

Ceanothus species (in particular *C. prostratus* and *C. integerrimus*) have been mentioned as nurse crops. In dense *Ceanothus* thickets, however, some species *(C. velutinus, C. integerrimus, C. cordulatus,* and *C. cuneatus)* are regarded as very strong competitors that can retard the establishment and growth of conifers.

The roles and the controversies surrounding *Ceanothus* species provide several researchable problems. Quantitative data are needed on the actual roles that *Ceanothus* plays on various sites. There is a need for better predictive information on *Ceanothus.* For example, where will *Ceanothus* occur? What role does *Ceanothus* play in nitrogen fixation on a specific site? How serious are *Ceanothus* species as competitors? How important is *Ceanothus* competition over the rotation of a conifer forest? Do the positive contributions made by *Ceanothus* to a forest system offset its competitive impact on conifers?

3. Autecology and Synecology of *Ceanothus* [1]

Autecology

Seed Production, Germination, and Survival

Seed production.—*Ceanothus* species that have been studied appear to be prolific seed-producers. Although no published data are available on the age when seed production begins, field observations indicate that *C. integerrimus* begins to produce seed at about 4 years of age and *C. velutinus* begins seed production after 6 to 10 years in northern California.[2] Even less information is available for sprouts. Sprouts of *C. velutinus* can produce prolific seed crops 8 years following cutting.[3] In general, sprouts of most species begin to produce at least some seed after 3 to 6 years.

More is known about numbers of seeds produced. Estimates for various *Ceanothus* species of numbers of seeds stored in the duff range from 4.6 x 10^6 viable seeds per hectare (1.9 x 10^6/acre) for *C. cordulatus* and *C. parvifolius* combined in California (Quick 1956) to 2.5 x 10^5 seeds per hectare (1 x 10^5/acre) for *C. velutinus* in Oregon (Gratkowski 1962). Three hundred seventy-five thousand germinated seedlings per hectare (150,000/acre) and 150,000 to 600,000 germinated seedlings per hectare (60,000 to 240,000/acre) have been reported for *C. integerrimus* in California (Quick 1956) and *C. sanguineus* in Idaho (Hickey and Leege 1970), respectively.

The generally large seed reservoir in the soil where *Ceanothus* plants are abundant apparently represents only a small percentage of the seed produced annually. Based on 5 years of sampling, seed production by *C. greggii* and *C. leucodermis* on chaparral sites in southern California varied greatly from year to year, with production ranging from 47,000 to 29.2 x 10^6 seeds per hectare (18,800 to 11.6 x 10^6/acre) for *C. leucodermis* and from 0 to 170 x 10^6 seeds per hectare (68 x 10^6/acre) for *C. greggii* (Keeley 1977b). Seed production of mature *Ceanothus* plants may vary greatly from year to year as a function of the carbon stored by plants in the previous year's and the current year's precipitation. In chaparral species, a significant percentage (90 to 99 percent) of the annual seed production is eaten by rodents, with a small percentage consumed by birds and harvester ants.[4]

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[1] Participants in this discussion group were: Tom Beebe, Ray Boyd, Paul Dunn, Dick Fredricksen, Charles Halpern, Ed Harshman, Miles Hemstrom, Howard Horowitz, Annabelle Jaramillo, Bruce Kelpsas, Paul Lauterbach, Phil McDonald, Don Minore, Doug Robin, Bob Sanders, Bill Stein, and Howard Weatherly. Discussion Leaders were Tom Atzet and John Tappeiner.

[2] Personal communication, P. McDonald, Pacific Southwest Forest and Range Experiment Station, 2400 Washington, Avenue, Redding, CA 96001.

[3] Personal communication, S. Conard.

[4] Personal communication, R. Quinn, California Polytechnic University, San Luis Obispo, CA 93407.

Conclusions drawn from the discussion of seed production by *Ceanothus* were:

1. In years of high seed production, *Ceanothus* species are capable of producing more seeds in a single year than are stored in the soil.

2. The number of seeds in the soil can be expected to vary from year to year as a function of both seeds produced and seeds utilized by consumers.

3. Substantial seed reservoirs exist in the soil in areas that have been dominated by *Ceanothus* species.

Seed longevity.—Seeds of *Ceanothus* species are thought to be long-lived. Gratkowski (1962) reports viable *C. velutinus* seeds in the duff of conifer stands over 200 years old. The only direct information on longevity, however, comes from work by Quick and Quick (1961) who obtained excellent germination in *Ceanothus* seeds known to be 9 to 24 years old. More studies in this area are needed.

Seed dissemination.—Because the seeds of *Ceanothus* species are generally small (2-4 millimeters (0.08-0.16 in) long), smooth, hard, and round, they tend to stay where they fall, gradually filtering into the duff and soil, unless they are carried off by small animals (rodents, birds, ants).

When *Ceanothus* seeds ripen, they are forcibly ejected from the pods. One chaparral species, *C. crassifolius*, has been observed to shoot seeds an average of 3 meters (10 ft).[5]

Seed germination.—Laboratory studies of treatments to stimulate germination of *Ceanothus* species were summarized by Reed (1974). The ability of the seeds to remain viable for years under field conditions is a function of a strong seedcoat dormancy. As the seeds dehydrate, their hilar fissures act as one-way valves and prevent moisture from being imbibed. In nature, dormancy is broken when the hilum is fractured (Gratkowski 1962). Fire is the most common agent stimulating germination, although high soil temperatures caused by solar radiation and mechanical abrasion may also be factors. Laboratory studies have shown that either soaking in hot water at 80 to 90 °C (176 to 194 °F) or dipping in boiling water for as little as 10 to 30 seconds to as much as 5 minutes will stimulate germination of many *Ceanothus* species. Various combinations of immersion of seeds in sulfuric acid and soaking them in gibberellin or in thiourea will also stimulate germination. Cold, moist stratification normally increases germination significantly following hot water or other heat treatments (Gratkowski 1973). At least one chaparral species *(C. crassifolius)* averages about 15 percent germination if it is placed in water at 70 °C (160 °F) and left in the same water at room temperature, suggesting that cold stratification is not required for all species. Even in this species, though, germination is enhanced considerably by cold stratification (M. Poth, unpublished data). In dry soils, temperatures of 120 to 140 °C (248 to 284 °F) are normally lethal to *Ceanothus* seeds.

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[5] Personal communication, P. Dunn, Forest Fire Laboratory,
4955 Canyon Crest Drive, Riverside, CA 92507.

In field situations, autumn slash burnings have produced four times as many *C. sanguineus* germinants as have spring burns, presumably because of the hotter temperatures common in autumn burns and the cold, wet stratification that follows with winter weather. Germination following spring burns is often delayed until the following spring (Leege 1968). On two experimental watersheds in the H. J. Andrews Experimental Forest, Willamette National Forest, in western Oregon, the highest crown covers of both *C. sanguineus* and *C. velutinus* occur in the most heavily burned areas (C. Halpern, unpublished data). Chaparral studies have shown that soil temperatures in hot or moderate fires may reach 150 °C (302 °F) —a lethal temperature—down to 2.5 centimeters (1 in) in dry soils (DeBano and others 1977).

Seedling survival.—Although large numbers of seeds of *Ceanothus* species typically germinate after fire, mortality is high, especially in the first few years following germination. For example, in the Sierra Nevada, *C. integerrimus* decreased from 750,000 seedlings per hectare (300,000/acre) in the first year to 25,000 per hectare (10,000/acre) after 10 years; 6,250 (2,500/acre) after 20 years; and less than 1,250 per hectare (500/acre) after 30 years (Cronemiller 1959). Rapid early mortality has also been observed from *C. velutinus, C. sanguineus, C. cuneatus,* and *C. megacarpus* on some sites. In pure stands, however, densities of these species appear to level off after 5 or 6 years. Density of 5-year-old *C. velutinus* in the mixed species shrub community near Mount Shasta, California, ranges from 2,250 to 3,750 per hectare (900 to 1,500/acre) (P. McDonald, unpublished data). Schlesinger and others (1982) report decreases in *C. megacarpus* seedlings on sites from 101,250 per hectare (40,500/acre) at age 1 to 20,250 per hectare (8,100/acre) at age 20.

Because *Ceanothus* species are generally intolerant of shading, they begin to die out after conifers grow through the shrub canopy (approximately 10 years on some *C. velutinus* sites in Oregon; considerably longer on some sites in the Sierra Nevada). Only a small percentage of the viable seeds in the soil germinate after a typical fire. Because of large numbers of seeds in the soil, even relatively low germination is sufficient to produce high densities of *Ceanothus* shrubs.

Plant Growth and Stand Development

Seedlings.—Both varieties of *C. velutinus* (var. *laevigatus* and var. *velutinus*), as well as other *Ceanothus* species, exhibit sigmoidal height growth. Height growth is slow until age 4 or 5 years in var. *velutinus* and until age 3 years in var. *laevigatus* and then is rapid until about age 10 years when it begins to level off. A typical *C. velutinus* var. *velutinus* stand in Oregon or California reaches a height of 0.6 to 2.5 meters (2 to 8 ft) after 10 years. Stand height sometimes decreases between age 15 and 50 as older stems collapse. Maximum stand height depends on site characteristics. In the Cascade Range (McKenzie Ranger District, Willamette National Forest), the number of *C. velutinus* plants decreased from 3,700 at age 4 years to less than 400 at age 12 years (E. Harshman, unpublished data). The data showed a rapid exponential decline in numbers required for full cover until about age 8 or 9 years, when the decline became more gradual as shrubs approached maximum size. Little site-specific information is available, however. In one study in the northern Sierra Nevada, *C. integerrimus* was reported to grow 7 to 11 centimeters (3 to 4 in) the first year, and 20 (8), 30 (12), and 36 centimeters (14 in) in years 2, 3, and 4, respectively. Total height growth after 5 years ranged from 0.8 to 1.3 meters (2.5 to 4.3 ft). This species begins to spread out rapidly, horizontally and vertically, in the third year (P. McDonald, unpublished data). Cronemiller (1959) reported similar growth data from the Stanislaus National Forest in the Sierra Nevada. As with *C. velutinus,* growth varies considerably from one site to another.

Sprouts.—Although many *Ceanothus* species are vigorous sprouters following top removal, few data are available on the growth rates of sprouting shrubs. Sprout growth of 51 to 65 centimeters (20 to 25 in) after 1 year and 1.0 to 2.1 meters (3 to 7 ft) after 5 years have been observed for *C. velutinus.*[6] *C. integerrimus* sprouts grew 75 centimeters (30 in) in the first year after burning on one site (Cronemiller 1959). Sprout growth rates also vary from site to site.

The ability to sprout may also be a function of the age and vigor of the plant when cut. In one study in the Cascade Range, when *C. velutinus* plants were cut, the percentage of sprouting plants decreased from 100 percent for 5-year-old plants to 50 percent for 11-year-old plants. Almost no sprouting was observed on 13-year-old plants (R. Sanders, unpublished data). In the Sierra Nevada, however, vigorous sprouting was observed following cutting of 35- to 50-year-old *C. velutinus* (Conard and Radosevich 1982a). Again, these patterns vary from site to site.

Productivity.—The interest in *Ceanothus* species as browse for big game has led to several studies of annual stem growth and biomass production. Leege and Hickey (1975) report average annual twig growth for 32- to 36-year-old *C. sanguineus* plants in Idaho ranging from 23.6 to 30.5 centimeters (9.3 to 12 in). Annual growth was significantly correlated with May to August precipitation totals and was higher on south than on east or west aspects. They also observed substantial twig dieback, especially on older plants, during periods of severe winter temperature fluctuations. Winter twig dieback was also reported by Young and others (1948) for *C. sanguineus* in northern Idaho and by Stickney (1965) on *C. velutinus* in Montana. Winter desiccation of foliage is a common occurrence on *C. velutinus* in the Cascade Range in Oregon and in the Sierra Nevada.[7] Little is known about how this dieback may affect either annual or long-term productivity.

Kie (unpublished data) has recently developed models relating annual production of twigs and foliage by *C. integerrimus* and *C. cordulatus* to measures of shrub volume and to overstory crown closure in the southern Sierra Nevada. Published models are available that relate *C. integerrimus* browse production to stem diameters (Bartolome and Kosco 1982) and *C. cordulatus* browse production to canopy area of shrubs (Eberlein 1982).

Biomass and nutrient cycling.—Most available biomass and nutrient cycling data are for *C. velutinus.* This species accumulates biomass rapidly. Martin and others (1981) report aboveground biomass values of 36 metric tons per hectare (16.2 t/acre). Zavitkovski and Newton (1968) and Youngberg and Wollum (1976) report accumulation rates of 4 000-5 000 kilograms per hectare per year (3,560-4,450 lb/acre) for the first 10-15 years with slower rates at later stages. *C. velutinus*

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[6] Personal observation, S. Conard.

[7] Personal observation, S. Conard.

biomass is high in nitrogen, and stands older than 10 years may contain more than 500 kilograms per hectare (445 lb/acre) of nitrogen. The forest floor may contain an additional 300 kilograms per hectare (267 lb/acre) of nitrogen. Nitrogen cycling in aboveground litterfall is even more striking. Zavitkovski and Newton (1968) measured an average of 90 kilograms per hectare (80 lb/acre) per year in *C. velutinus* ecosystems. This rate of nitrogen recycling in litterfall exceeds other temperate forest ecosystems except those containing nitrogen-fixing plants such as *Alnus.*

C. megacarpus is also a prodigious biomass producer and nitrogen cycler. Schlesinger and others (1982) recorded biomass accumulation rates of 3 000 kilograms per hectare (2,670 lb/acre) per year over 20 years. A 22-year-old stand contained 480 kilograms per hectare (427 lb/acre) in biomass, 200 kilograms per hectare (178 lb/acre) in the forest floor, and 70 kilograms per hectare (62 lb/ac) in annual litterfall. The values for this chaparral species are similar to those noted previously for montane *C. velutinus* and much greater than average for nonnitrogen-fixing chaparral species.

Root distribution.—Root systems of *Ceanothus* vary considerably from species to species. Most species are deep rooted with a large number of fine roots near the soil surface. A species with shallow roots is *C. greggii,* a chaparral species that has over 90 percent of its roots in the top 30 to 40 centimeters (12 to 16 in) of soil (Kummerow and others 1977, Miller and Ng 1977) and a root-to-shoot biomass ratio of 0.25 to 0.39 (Miller and Ng 1977). Roots of *C. greggii* var. *vestitus,* on the other hand, have been found down to 4 meters (13 ft) in chaparral (Hellmers and others 1955). *C. prostratus* roots may extend down to 1.5 meters (5 ft) and may even penetrate the C soil horizon (Tappeiner and Helms 1971).

C. velutinus roots extend to depths of 1.8 to 2.4 meters (6 to 8 ft) and extend laterally well past the crown of the plant. In southwestern Oregon, *C. cuneatus* seedlings had roots averaging 20 centimeters (8 in) in length after one growing season (Gratkowski 1961b). Maximum length of roots was reported for *C. leucodermis* in southern California by Hellmers and others (1955). This species had a maximum rooting depth of 6.4 meters (21 ft), and the lateral extent of the roots was approximately 2.3 times that of the aerial parts.

Longevity.—Compared to other genera of shrubs, *Ceanothus* are short lived. This may be because these species are eventually shaded out by overtopping vegetation; overtopping begins to occur at 10 to 75 years on sites where conifers are present. Individual 40-year-old plants of *C. velutinus* and *C. integerrimus* have been observed (Cronemiller 1959). In the Sierra Nevada, vigorous *C. velutinus* were still present in a brushfield that had resulted from a fire 50 years earlier (Conard and Radosevich 1982a). In the Cascade Range, however, mature *C. velutinus* are often subjected to heavy injury to root crowns from snow (Zavitkovski and Newton 1968), which can lead to senescence of stands. The functional life span of *C. velutinus* on many sites in the Cascades is believed to be between 20 and 40 years before shading by conifers and snow damage begin to decrease its vigor. Observations in the Rocky Mountains have suggested that periodic fire is necessary to maintain the vigor of *C. sanguineus.* Without fire, plants of *C. sanguineus* may be replaced by other shrub species, such as *Holodiscus* or *Prunus.*

Table 1--Browse value and protein content of *Ceanothus* foliage

Species	Browse value[1]			
	Deer	Cattle	Sheep	Crude protein
				Percent
C. cordulatus	1-2	4	3	6-15
C. cuneatus	3	4	2-3	8-15
C. integerrimus	1-2	2-3	1-2	12-20
C. prostratus	2-3	5	4-5	5-10
C. thyrsiflorus	2-4	3-4	2-3	--
C. velutinus	3	5	4	up to 17

[1] Browse value: 5 = useless, 4 = poor, 3 = fair, 2 = good, 1 = excellent. Source: Sampson and Jespersen 1963.

Biotic agents.—*Ceanothus* foliage, twigs, and seeds are an important food source for wildlife and domestic grazers. The foliage of *Ceanothus* is high in protein and can be an attractive spring and summer forage for deer, elk, cattle, and sheep. Management to favor production of *Ceanothus* for browse is common on big game ranges (Hickey and Leege 1970, Leege 1979). Palatability and protein content of several major *Ceanothus* species that occur in California are summarized in table 1. One species that is heavily browsed by elk and deer is *C. sanguineus.* On five sites in Idaho, 25 to 80 percent of the annual growth was removed by elk (McCulloch 1955); deer use of this species can reach similar levels (Thilenius and Hungerford 1967). *C. sanguineus* and *C. integerrimus* are preferred over *C. velutinus* as browse. Snowshoe hare are also heavy browsers of *Ceanothus sanguineus* on some sites (Asherin 1974). Rodents (with an assist from birds and ants) may eat as much as 99 percent of the annual seed crop of *Ceanothus* on chaparral sites.[8] Predation could have profound effects on *Ceanothus* establishment after disturbance if similar seed predation occurs on forest sites.

A large number of biotic agents, such as birds, insects, mammals, and fungi, have been shown to affect *Ceanothus* species. Birds often act as seed dispersal agents. Several insect species heavily infest seeds of *Ceanothus* species in some years and can cause substantial loss of viable seeds. Reductions of 9 to 27 percent in seed production were reported for *C. sanguineus* and 80 percent for *C. greggii* following infestations by wasps, weevils, and caterpillars (Bugbee 1971, Furniss and others 1978). The California tortoise shell butterfly can severely defoliate both *C. velutinus* and *C. integerrimus.*[9] [10] Although no quantitative data are available, plants seem to recover within a few weeks from severe infestations.

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[8] Personal communication, R. Quinn, California Polytechnic University, San Luis Obispo, CA. 93407

[9] Personal communication, A. Shapiro, University of California, Davis, CA 95616.

[10] Personal communication, P. McDonald, Pacific Southwest Forest and Range Experiment Station, 2400 Washington Avenue, Redding, CA 96001.

Fungi may be another important biotic agent that affects *Ceanothus* species on forest sites. *Armillaria mellea* parasitizes *C. velutinus* by girdling roots mechanically with rhizomorphs (Tarry 1968). Because this fungus is not host specific, infections in *Ceanothus* stands could provide a source for attack of conifers growing on the same site. The *Cytosporina* state of the fungus *Eutypa armeniacae* has been reported to cause stem dieback of several *Ceanothus* species (Moller and others 1971a, b).

Effects of some of these biotic agents might be confused with foliage or twig dieback caused by winter injury, as discussed earlier. Additional information on how these biotic agents affect *Ceanothus* species and their associates would be useful to those managing growth and distribution of *Ceanothus* species in forest systems.

Synecology

Ceanothus species occur over a wide geographic area and have a large number of associates in many plant communities. Much of the known information on distribution patterns of individual species was presented earlier. Little quantitative information on productivity, community ecology, and successional relationships of *Ceanothus* species in forest ecosystems is available.

The distribution of sprouting and nonsprouting species of *Ceanothus* appears to be related to frequency of fires. Nonsprouting species are more common than sprouting species, and more sprouting species occur in the Sierra Nevada, where lightning-caused fires are more frequent, than at low elevations. Keeley (1977a) discusses potential evolutionary reasons for these differences.

Information describing forested plant communities in which the major *Ceanothus* species occur has been reported for Oregon and Washington (Franklin and Dyrness 1973), the west side of the Cascade Range in Oregon (Hemstrom and others 1982), northeastern Washington (Daubenmire 1953), Montana (Pfister and others 1977), and California (Barbour and Major 1977).

Seral status of *Ceanothus* species.—Although few data on specific seral sequences are available (Conard and Radosevich 1982b), *Ceanothus* species are generally considered pioneers because of their fire-dependent reproductive strategies. Where they are not shaded out by taller shrubs or trees, however, some species can persist as a long-term, semipermanent component of the vegetation. Observations suggest that *C. cuneatus* may form a climax vegetation type on some sites in southwestern Oregon and that *C. velutinus* is part of the climax vegetation in open ponderosa pine woodlands on the east side of the Cascade Range.

Ceanothus species as indicators of site productivity for conifers.—Based largely on the field experience of the participants in this session, several relationships between site quality and the species of *Ceanothus* present are suggested and summarized:

Location	*Ceanothus* species according to site quality
	Best sites (wet) → Worst sites (dry)
Southwestern Oregon	*velutinus* → *integerrimus* → *prostratus* → *cuneatus* → *pumilis*
Idaho	*sanguineus* → *velutinus*
Eastern Washington	*velutinus* → *sanguineus*
Sierra Nevada (California)	*diversifolius* → *integerrimus* → *prostratus* → *lemmoni* → *cuneatus*
Northern California	*integerrimus* → *prostratus* → *lemmonii* → *cuneatus*

Intuition has led to different conclusions from one region to another. This discussion group concluded that good information on correlations among distribution of *Ceanothus* species and site quality, moisture availability, and temperature are sorely lacking.

Research Needs

The following needs were identified for future research on the autecology and synecology of *Ceanothus* species:

1. Quantifying optimum and extreme values of environmental factors such as site quality, elevation, aspect, plant moisture stress, and degree days for growth and establishment of each species of *Ceanothus.*

2. Quantifying interactions among *Ceanothus* species and their associates in the major (forest) plant communities where they occur.

3. Defining the autecological characteristics of individual species. Some of the most critical are: age at onset of seed production (for seedlings and sprouts), longevity of plants, duration of viable seed in the soil, influence of shrub age on sprouting capacity, and rates of shrub growth and canopy development.

4. Interactions Between *Ceanothus* Species and the Soil System[1]

Ceanothus is one of the most widespread genera of nodulated, nonleguminous, nitrogen-fixing plants in North America. Many of the nitrogen-fixing species in this genus occur in the western United States and are integral components of forest ecosystems (Youngberg and Wollum 1976, Zavitkovski and Newton 1968). Nitrogen (N) fixation occurs in nodules that range from simple lobes or clusters a few millimeters across, which are white when fresh, to large, brown lobes 21 centimeters (8 in) across (Bond 1963, Furman 1959, Gardner 1976). Fixation of atmospheric dinitrogen (N_2) has been reported in the field and confirmed in the laboratory (Delwiche and others 1965, McNabb and Geist 1979, Russell and Evans 1966).

In 1890, Beal described hyphae and swollen structures inside nodules of *Ceanothus*. More recently, Furman (1959) and Kummerow and others (1978a) detail the filamentous nature of the nitrogen-fixing endophyte. Isolation and culture techniques for *Frankia* have been developed (Lalonde 1979), and the endophytes have been isolated and cultured for *C. americanus* by D. Baker and for *C. crassifolius* and *C. oliganthus* by M. Poth.[2] It is known from microscopic observations and from inferences drawn from cultures of the alder endophyte that the microorganism is filamentous and encapsulated by a host membrane (Lalonde and Knowles 1975). The filaments terminate in swollen tips or vesicles that appear to be the site of N_2 fixation (Kummerow and others 1978a).

Although all *Ceanothus* species tested to date are capable of fixing N_2 if a suitable inoculum of the endophyte is present (Delwiche and others 1965), little is known about host-specificity and environmental influences. In the field, both the degree of nodulation and the rate of N_2 fixation (or accretion) vary greatly among species and among sites (McNabb and Geist 1979, Youngberg and Wollum 1971). Possible causes for these observed variations include inherent differences among species of host and endophyte, physical and biological site factors, environmental conditions, and variability in assessment and measurement methods and research designs.

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[1] Participants in this discussion group were: Ray Armstrong, Dick Fredricksen, Martin Jurgensen, Logan Norris, Dan Binkley, John Marshall, Dave McNabb, Dave Perry, Harold Evans, Bill Schlesinger, and Jim Boyle. The discussion leaders were Sharon Rose and Kermit Cromack.

[2] Personal communication, M. Poth, Forest Fire Laboratory, 4955 Canyon Crest Drive, Riverside, CA 92507.

Factors Affecting Nodulation and N_2 Fixation.--Chemical, physical, and biological characteristics of the soil will affect both the infectivity and effectivity of the N_2-fixing endophyte and will influence the rate of N_2 fixation.

High levels of ammonium nitrogen in the soil decrease N_2-fixation rates of *C. velutinus* in laboratory conditions (Rodriguez-Barrueco and others 1970), but this has not yet been tested experimentally in the field. The suppression of N_2 fixation by high soil N levels is widespread in both the legumes and other families of N_2-fixing host plants (Rodriguez-Barrueco and others 1970). Other macronutrients known to influence nodulation and N_2 fixation in *C. velutinus* include calcium, phosphorus, and sulfur (Scott 1973). Evidence for the broad applicability of these results to other *Ceanothus* species comes from work on free-living microorganisms and legumes. Calcium is required by most free-living N_2-fixing microorganisms and is essential for fixation in leguminous hosts.[3] A deficiency in phosphorus may inhibit nodulation, and a low soil pH has been shown to decrease the effectiveness of the legume endophyte (see footnote 3). The micronutrients molybdenum, cobalt, and nickel are necessary for N_2 fixation in legumes and may be required as well by nonleguminous plants (Silvester 1977). Nickel is essential for the synthesis of hydrogenase in *Rhizobium japonicum* and presumably is required for this enzyme to function in nonleguminous plants (see footnote 3). High levels of aluminum and manganese may be toxic to either the endophyte or host.

Environmental extremes may influence both the endophyte and the host and will directly affect N_2 fixation. Variables such as soil temperature, soil moisture, and light affect physiological processes in *C. velutinus* (McNabb and Cromack 1983, Wollum and Youngberg 1969). Soil temperature affects both the number and size of nodules formed on *C. velutinus* (Wollum and Youngberg 1969). Nitrogen-fixation rates in *C. velutinus* can decrease following decreases in soil temperature, soil moisture, and light (McNabb and Cromack 1983). Kummerow and others (1978a) found fewer healthy nodules on *Ceanothus* plants when the soil was dry than when the soil was moist. Wollum and Youngberg (1969) found maximum nodulation on *C. velutinus* when the soil temperature was 23-26 °C (73-79 °F).

Age of seedlings, site preparation, and disturbance also affect nodulation and N_2 fixation. Kummerow and others (1978a) found nodules on only 4 of 100 6- to 8-month-old *Ceanothus tomentosus* seedlings that had germinated following a fire in the Tecate Mountains, although they did find nodules consistently on 5- to 10-year-old shrubs of *C. greggii*. Youngberg (1966), however, notes maximum nodulation following logging and burning, provided the age of the timber is 100 years or less. He attributes high nodulation to increased light intensity on the site following logging and to heat scarification of *Ceanothus* seeds by fire. He also hypothesizes that poor nodulation on older sites could result from a lack of the endophyte when a site had been dominated by conifers for many years. Nodulation and the general health of the plants declined after several years, probably because of canopy closure and the intolerance of *Ceanothus* to shade.

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[3] Personal communication, H. Evans, Botany Department, Oregon State University, Corvallis, OR 97331.

Photosynthates produced by the host and transported to the roots supply the necessary carbohydrates to the nodular endophyte (Paul and Kucy 1981). Rodriguez-Barrueco and others (1970) suggest that when N is added to the soil in the form of fertilizer, the host plant grows faster and utilizes surplus carbohydrates, thus denying a carbon supply to the endophyte and reducing N_2 fixation. Youngberg (1966) states that *C. velutinus* produces less photosynthate under shade conditions and, consequently, has fewer nodules and lower N_2 fixation.

Soil chemistry, including such factors as cation exchange capacity, base saturation, organic matter content, and ion concentrations, influences the endophyte as it lives in the soil and directly influences the growth of the host plant and degree of nodulation (Scott 1973). White (1967) notes an absence of nodules on *C. cuneatus* roots in plants growing in serpentine soil. This may be because of ion imbalance, especially of calcium, magnesium, nickel, and chromium. It is not known if the ions affect the populations of the endophyte or the actual nodulation process.

Nodulated *Ceanothus* plants are also commonly mycorrhizal. It has been demonstrated that when legumes are mycorrhizal there is an increase in nodulation and N_2 fixation (Carling and others 1978). Rose and Youngberg (1981) found a similar synergism in *C. velutinus.* Nodulated *Ceanothus* with mycorrhizal fungal partners produced three times more nodular tissue and fixed about twice as much N_2 per plant as did nodulated plants without mycorrhizae. Increased N_2 fixation both in legumes and actinorryhizal plants is attributed to increased nutrient uptake and healthier plants producing more photosynthates than nonmycorrhizal nodulated plants (Carling and others 1978, Gardner and others 1984, Rose and Youngberg 1981).

Methods for Measuring N_2 Fixation

The methods for measuring N_2 fixation in both the field and laboratory include acetylene reduction, natural isotope (^{15}N) tracer studies, isotope (^{15}N) enrichment studies, N-accretion studies, and analysis of N-transport products in xylem sap. Each of these methods has a bias and built-in assumptions that may or may not be valid for an individual study and may account for much of the variation in reported N_2-fixation rates and N accumulation.

Sources of errors in determining N_2-fixation rates arise from taking too few samples and from making wide extrapolations from one sample at one time. The difficulty of estimating nodule biomass accurately, seasonal variations in nodule biomass, short-term variations in nodule efficiency and activity (due to changing environmental conditions), and differences among sites add to the problem of accurately quantifying N_2-fixation rates.

Rates of N_2 fixation vary by *Ceanothus* species, site, age of the plants, season, and light regime (McNabb and Cromack 1983, McNabb and Geist 1979). Some of the rates of N_2 fixation (or accretion) that have been estimated in field studies are summarized in table 1.

The participants in this session discussed at length the most important methods for measuring N_2 fixation and changes in soil N levels in laboratory and field studies. This discussion focused on the appropriate or potential uses, the assumptions required for drawing conclusions, and the potential sources of error for each method. A brief description of each method and a summary of the points brought up in the discussions follow:

Table 1--Estimated rates of N accretion or N_2 fixation on forest and chaparral sites in the Western United States

Ceanothus species and location	Accretion or fixation	Stand age	Source	Method
	kg/ha/yr	years		
Ceanothus velutinus, H. J. Andrews Experimental Forest, Oregon	[1] 42-48 [2] 95-100	0 and 12	Binkley and others 1982	chronosequence
C. velutinus, H. J. Andrews Experimental Forest, Oregon	[3] 101	17	McNabb & Cromack 1983	acetylene reduction
C. velutinus, Cascade Range, Oregon	[1] 56 [2] 84	0-15	Youngberg and others 1979	accretion
C. velutinus, Cascade Range, Oregon	[1][4] < 0-40 [1][4] < 0-46 (96)	2-33	Binkley unpublished data, Zavitkovski and Newton 1968	chronosequence; accretion
C. velutinus, Cascade Range, Oregon	[2] 72-108	0-10	Youngberg and Wollum 1976	accretion
C. sanguineus, Vancouver Island, British Columbia	[1] 24-50 [2] 45-80	10	Binkley and Husted 1983	accretion, based on spatial variation
C. greggii var. *perplexans*, San Diego County, California	[3] 0.1	25	Kummerow and others 1978	acetylene reduction
C. crassifolius, San Dimas Experimental Forest, Southern California	[1] 28 [2] 76	0-13	Zinke 1969	accretion

[1] Soil N accretion.

[2] Ecosystem N accretion (soil, litter, biomass).

[3] N_2 fixation in field.

[4] Highest number is average over first 10 years.

1. Acetylene reduction.—In the acetylene reduction method, nodule tissue is incubated in an acetylene-enriched atmosphere, and the amount of ethylene evolved is assayed as an indirect measure of nitrogenase activity in the nodules (Postgate 1972). The efficiency of the reduction reaction may sometimes be considerably less than the theoretical ratio of 0.3 moles of N production for each mole of ethylene evolved (Bergersen 1980, Hardy and others 1968). Additional sources of error occur when this method is used to estimate seasonal or annual N_2-fixation rates per unit area in the field. To develop reasonable estimates using this approach, investigators need estimates of the current age, structure, and vigor of the stand. By measuring levels of environmental regulating factors such as light and moisture in the field, laboratory data on responses of fixation (acetylene reduction) to environmental conditions can be incorporated into these models.

2. Accretion.—Estimates of soil N accretion over time can be made by successive measurements of soil N levels on one or more sites (Youngberg and Wollum 1976) or in experimental plots in stands of pure species composition (Zinke 1969). Many years are obviously required to obtain meaningful results with this approach, and the accuracy of estimates relies heavily on the accuracy of initial estimates of N pools and soil N.

3. Chronosequence.—Another method for studying accumulation of soil N over time is to measure the soil N levels on sites with a range of ages following the establishment of *Ceanothus* (Binkley and others 1982, Zavitkovski and Newton 1968). In this approach, the assumptions must be made that (1) baseline levels of soil N are the same on all sites and (2) historical patterns of N_2 fixation have been the same on all sites. Even if sites are selected very carefully, differences in site characteristics (such as micronutrient levels) and in patterns of vegetation development or of nodulation are likely to make these assumptions questionable. Violation of these two assumptions can introduce substantial error into estimates of N accumulation made by this method.

It is important, furthermore, to recognize that both chronosequence and accretion studies yield only estimates of changes in soil N levels over time, not rates of current or past N_2 fixation. These methods do not generally take into account N losses caused by plant uptake, leaching, and denitrification, nor do they allow compartmentalization of input sources such as rainfall, lightning, and nitrification. Therefore, estimates of N balance made by these methods do not represent fixation rates unless corrections can be made for other inputs and outputs of N in the ecosystem. If inputs and outputs can be quantified independently these methods might allow N_2 fixation to be estimated with reasonable accuracy.

4. Natural isotope distribution.—In most soils, the ratio of ^{15}N to ^{14}N is higher than it is in the atmosphere. The basis for the natural isotope discrimination method for estimating N_2 fixation is that the ratio of these isotopes in plant tissues should reflect the source of the plant's N. A plant that obtains most of its nitrogen through nodular fixation of N_2 therefore, has a ratio close to that in the atmosphere, whereas plants that do not fix N_2 have ratios closer to that in the soil. Theoretically, the ratio, ^{15}N:^{14}N (expressed commonly as atom percent excess of ^{15}N), can be partitioned to yield an estimate of what proportion of a plant's N has been derived from the atmosphere (Bergersen 1980, Delwiche and others 1979, Silvester 1983).

This method permits the investigator to follow N through an ecosystem or through a plant. A potential problem with this approach is that the within-pool variation in various ecosystem components (such as soil and plant tissue) may be high enough to make detection of differences among species, among ecosystem components, or among treatments difficult. The advantages of this method for ecosystem studies are that it gives integrated values of N_2 fixation over time, it can be used where nodules are difficult to locate or to excavate, and measurements are made on easily obtained materials (leaves, stems, soil). The method has been used successfully to estimate N_2 fixation by mesquite and other species in desert ecosystems (Shearer and others 1983) and to detect differences in the atom percent excess of ^{15}N between presumed N_2-fixing and nonfixing plants in a wide range of northern California ecosystems (Virginia and Delwiche 1982).

5. ^{15}N isotope enrichment.—In this method, the nodules or roots are placed in an atmosphere that has been enriched in known amounts with $^{15}N_2$ (Bergersen 1980, Silvester 1983). The atom percent excess of ^{15}N in the samples (plants, nodules, roots) following treatment can provide an estimate of the amount of N_2 fixed during the incubation period and (for whole plants) of the distribution and biochemical fate of that N within the plant. This method allows direct comparisons to be made among fixing and nonfixing plants. Disadvantages include the high costs of isotopic N and of chemical analysis. The same problems of high within-pool variability that were discussed before can occur, especially in field studies, and laboratory studies require disturbance of living plant material as well as its monitoring in a somewhat unnatural environment. Despite potential shortcomings, this technique has provided extremely useful information in a large number of studies. It was used by Delwiche and others (1965) to estimate rates of N_2 fixation for 12 *Ceanothus* species that occur on forest and chaparral sites in California.

6. Xylem sap.—In both legumes and nonlegumes, certain N-transport compounds found in the xylem serve primarily as carriers for symbiotically fixed N, while other compounds are carriers for N obtained from the soil solution (Dixon and Wheeler 1983, Pate 1980). In soybeans, for example, the abundance of ureides (relative to that of nitrate-N) in xylem sap decreased from 94 percent to 9 percent as the proportion of plant N derived from N_2 fixation decreased from 100 percent to 1 percent (Herridge 1982). In this same study, a positive relationship was apparent between the concentration of ureides in the xylem and the rate of N_2 fixation measured by acetylene reduction. The major transport compounds for symbiotically fixed nitrogen are species specific (Pate 1980). Citrulline appears to dominate in alder and asparagine in *Ceanothus* (Dixon and Wheeler 1983). Relationships could theoretically be determined between rates of N_2 fixation and concentrations of N-transport compounds in the xylem by obtaining independent estimates of N_2 fixation using acetylene reduction or ^{15}N enrichment techniques. Although this approach is still in the early stages of development, it shows particular promise for studies of deep-rooted woody species such as *Ceanothus,* because it has potential for permitting N_2 fixation to be estimated without access to the rooting zone of the plants.

Additional details, and a wealth of references, on methods of evaluating N_2 fixation can be found in Bergersen (1980) and in Silvester (1983).

Research Needs

The following needs for future research on interaction between *Ceanothus* species and the soil system were identified:

1. Identify the factors that influence nodule establishment and development.
    - a. Determine factors that influence the presence and efficacy of the endophyte.
    - b. Quantify the influence of microenvironmental parameters (such as water, light, temperature).
    - c. Quantify the influence of soil chemistry characteristics, such as soil pH, calcium, and micronutrient levels.
2. Identify the factors that limit N_2-fixation rates.
    - a. Determine the importance of genotypic variability of hosts and endophytes.
    - b. Measure effects of factors such as soil moisture, soil temperature, plant moisture stress, light, and photosynthetic rates.
3. Identify the factors that affect N-cycling rates.
    - a. Determine whether or not non-N_2-fixing plants cycle as much N in litterfall as do plants that fix N_2.
    - b. Determine the importance of abiotic factors and site characteristics in regulating N cycling.
    - c. Determine the influence of *Ceanothus* on pathways and rates of N cycling.
4. Quantify the changes in soil organic matter that accompany N accretion, and determine the effects of soil organic matter on soil moisture infiltration, moisture retention, soil aggregation, soil aeration, and overall soil structure.
5. Investigate litter decomposition patterns.
    - a. Quantify rates.
    - b. Determine the roles of microorganisms and of macrofauna, such as earthworms, in these patterns.

5. Physiological Ecology of *Ceanothus* and Associated Conifer Species[1]

The presence of *Ceanothus* on a site can affect many aspects of the conifer growth environment other than nitrogen availability and nutrient cycling. Effects of *Ceanothus* on environmental factors—such as light, water, and temperature—as well as production of allelopathic substances can potentially affect the growth and survival of associated conifers. The relative abilities of conifers and *Ceanothus* species to exploit resources and to tolerate resource depletion are determining factors in dynamic interactions in the vegetation. This section considers effects of *Ceanothus* on environmental factors, effects of environmental conditions on conifers and *Ceanothus* species, and the implications of these effects for shrub-conifer interactions.

Effects of *Ceanothus* on the Conifer Growth Environment

Light.—Many *Ceanothus* species have dense canopies. Few data are available, however, on the actual light levels under *Ceanothus* canopies. Petersen (1980) used ozalid paper and measured 30 percent of full sunlight (integrated over the whole day) at the bottom of the live canopy in 5- to 10-year-old *C. velutinus* stands in the Cascade Range. Conard and Radosevich (1982a) report 7 percent of full sunlight at midday at the soil surface under 35- and 50-year-old *C. velutinus* in the Sierra Nevada. McPherson and Muller (1967) used a hand-held light meter to find values of 200 to 4,000 foot-candles under *C. cuneatus* canopies in Santa Barbara County, California.

Soil temperature.—Soil-surface temperatures in summer under *C. velutinus* canopies in the Cascade Range were 11 to 33 °C (20 to 60 °F) lower than temperatures in adjacent unshaded areas (Scott 1969, Youngberg 1966). The average soil-surface temperatures in August as measured in open areas by Scott (1969) frequently exceeded 65 °C (150 °F). Temperatures this high have been reported to cause substantial seedling mortality in many conifer species (Hare 1961, Silen 1960) and could be expected to inhibit survival of natural germinants in unshaded microsites.

Midsummer soil temperatures at the 15- and 45-centimeter (6- to 18-in) depths in areas where *C. velutinus* and *Arctostaphylos patula* had been removed were generally 1 to 4 °C (1.8 to 7.2 °F) higher than temperatures where the shrubs had not been removed (S. Conard, unpublished data). Mean temperatures in late July at the 15-centimeter (6-in) depth in this study were 17 °C (63 °F) in the open and 15 °C (60 °F) under the canopy.

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[1] Participants in this discussion group were: Ned Dimock, Ivend Holen, Denis Lavender, Bill Lopushinsky, Dave McNabb, Pete Owston, Terry Petersen, Greg Prull, Steven Radosevich, Bob Tinnin, Bob Wagner, Jack Walstad, and Diane White. The discussion leader was Susan Conard.

Although high soil-surface temperatures may inhibit survival of conifer germinants, there is no evidence that they have negative effects on planted seedlings. Two potential benefits to conifers from slightly higher temperatures in the rooting zone are that root growth could begin earlier in the spring in open areas and that higher soil temperature could enhance the ability of roots to remove water from the soil. These benefits could be compounded by the soil where shrubs have been removed having substantially more soil moisture below the top 15 centimeters (6 in) than the soil where shrubs are present.

Little or no information is available on the influence of other *Ceanothus* species on soil temperatures or on the relative ecological importance of small differences in rooting-zone temperature on conifer growth. Without additional research, it is impossible to determine the ecological importance of small temperature differences in the rooting zone of planted or naturally established conifers. Routine installation of thermocouples or thermistors in experiments measuring soil moisture with moisture blocks could provide a great deal of soil temperature information at low cost.

Air temperature.—Conard and Radosevich (1982a) observed higher air temperatures inside live *Ceanothus* canopies than in open areas. They consistently observed minimum temperatures 2 to 3 °C (3 to 5 °F) lower and maximum temperatures 2 to 3 °C (3 to 5 °F) higher under a *C. velutinus* canopy than at the same height outside the canopy or at the same height (50 cm; 20 in) in the open. This relationship is probably a function of reradiation from stems and a lack of air mixing within the canopy. The relationship is probably dependent on canopy structure and would not be expected to be true for all species of *Ceanothus*. Further research is needed to: (1) determine how common these effects are within shrub canopies, (2) evaluate the effects of factors such as time of year and aspect, and (3) determine what influence (if any) such temperature differences might have on conifer growth or survival.

Soil moisture.—Several studies have measured soil moisture under *C. velutinus* canopies and compared it to soil moisture in areas where shrubs were removed or where shrubs were absent. Soil moisture in the top 15 centimeters (6 in) remained higher throughout the season under *C. velutinus* canopies than in the open (Scott 1969, Youngberg 1966). In these studies, however, "open" areas had dense covers of grasses and other herbaceous vegetation that typically have shallow rooting systems as compared to shrub species. Petersen (1980) created open areas in *C. velutinus* brushfields by removing shrubs and herbaceous vegetation with herbicides. In his study, soil moisture at 10 centimeters (4 in) was depleted more rapidly by shrubs than by herbaceous vegetation on one site. On another site, soil moisture depletion by shrubs and herbaceous vegetation at 10 centimeters was comparable. At 40 centimeters (16 in), shrubs depleted soil moisture more rapidly than did herbs on both sites. On one site, soil water potentials under herbaceous vegetation reached a minimum of about -8 bars for the season; water potentials under shrubs had decreased to less than -15 bars by late July. At 100 centimeters (39 in), soil water potential stayed greater than about -2 bars under herbaceous vegetation and was decreased to -15 bars by mid-July to mid-August where shrubs were present. Soil moisture showed no seasonal decrease at any depth where measurements were made if both shrubs and herbs were controlled.

Conard and Radosevich (1982a) report similar responses in soil moisture levels under *C. velutinus* canopies and in treatments where shrubs were removed in the Sierra Nevada. Scott (1969) also reports substantially lower minimum soil water potentials under *C. velutinus* (about -12 bars) than in the open under herbaceous vegetation (about -8 bars) at a 70-centimeter (24-in) depth. *C. prostratus* has also been shown to deplete soil moisture to approximately -15 bars by late summer at depths from near the surface to 45 centimeters (18 in) (Tappeiner and Helms 1971).

Although specific information on many *Ceanothus* species is lacking, the data presented above for *C. velutinus* and *C. prostratus* suggest that these species growing on forest sites can decrease soil water potentials to near -15 bars by late summer in the rooting zone of young conifers. Comparisons with areas where *Ceanothus* is not present must be made carefully as results can vary widely depending on what other vegetation is present on the site or on whether soil conditions in areas being sampled are comparable.

Humidity.—The presence of transpiring *Ceanothus* crowns causes substantial local increases in humidity and decreases in wind velocity. The net result of these effects is a decrease in evaporative demand. Conard and Radosevich (1982a) and Petersen (1980) document 120- to 180-percent increases in evaporation rates (measured with Piché evaporimeters) on *C. velutinus* sites when either shrubs or shrubs and herbs had been removed. The participants were aware of no similar studies on other *Ceanothus* species.

Allelopathy.—Tinnin and Kirkpatrick (in press) evaluate the allelopathic potential of water extracts of recent litterfall from several important shrub species in southwestern Oregon. In laboratory bioassays, *C. integerrimus* and *C. velutinus* reduced growth of *Cucurbita* by 30 percent and 60 percent, respectively. *Ceanothus velutinus* extracts also reduced root elongation of Douglas-fir germinants. Experiments in natural soils are in progress. Conard (1985) found that water extracts of fresh *C. velutinus* foliage also cause significant inhibition of radicle elongation in white fir germinants.

Rose and others (1983) found that water-soluble extracts of *C. velutinus* litter had varied effects on the growth of several mycorrhizal fungi that are found on conifers. All concentrations (parts per thousand, per hundred, per ten) stimulated the growth of *Cenococcum geophilum*. High concentrations (parts per ten) of extract inhibited the growth of *Laccaria laccata*. *C. velutinus* litter leachate also reduced mycorrhizal formation on Douglas-fir seedlings.

No studies to date have demonstrated the allelopathic effects of *Ceanothus* species on conifers in the field. Because of the observed effects on root growth and mycorrhizal formation in laboratory studies, allelopathy might be expected to be most important in situations where water or minerals are limiting and where the inhibition of root elongation significantly decreases efficiency of water or mineral uptake.

Effects of Environmental Conditions on Conifer Growth

The effects of *Ceanothus* on conifer growth are a function of how well the conifers are able to establish, survive, and grow under the modified environmental conditions established by *Ceanothus* and of how well the conifers can compete for potentially limiting resources such as light and water.

Factors that can affect growth of conifer species include the photosynthetic surface area of individual plants and the photosynthetic efficiency of the tissues. Under potentially limiting environmental conditions, responses of photosynthesis to light, temperature, and water availability can greatly influence seasonal growth in the field. Relative growth rates can provide valuable information about responses to different environmental conditions.

Light.—Although most conifers do not require full sunlight for maximum photosynthesis of individual branches or of seedlings, the light saturation level of a mature tree can vary considerably as a function of crown structure. Most pine species, however, require close to full sunlight for maximum photosynthesis. Light requirements that have been reported for maximum photosynthesis of conifers range from about 2,000 to 2,500 foot-candles ($\sim$400 to 500 μE m^{-2} sec^{-1}) for seedlings of Douglas-fir and western hemlock (Brix 1967, Krueger and Ferrell 1965, Krueger and Ruth 1969). In contrast, light saturation is around 1 000 μE m^{-2} sec^{-1} for individual fascicles of ponderosa pine (Coyne and Bingham 1982), and 3,500 and $>$9,500 foot-candles (about 700 and $>$1 900 μE m^{-2} sec^{-1}), respectively, for needles and seedlings of loblolly pine (Kramer and Kozlowski 1979).

Minimum light requirements for establishment and survival are considerably lower, although little quantitative information is available (Atzet and Waring 1970). Light requirements may be particularly important when the requirements of the conifer species differ from those of associated noncrop species with which they are competing. For example, Conard and Radosevich (1981) found that white fir reached 90 percent of maximum photosynthesis at 0.53 mmol m^{-2} sec^{1} (1 mmol $=10^3$ μE). compared with 0.71 mmol m^{-2} sec^{-1} for *Ceanothus velutinus*. This difference in light requirements fits in well with the ability of white fir to survive under the shrub canopy and eventually to overtop and shade out the *Ceanothus*.

Several authors (Baker 1949, Minore 1979, Waring 1970) have ranked the shade tolerance of conifers. Of the western conifers, western hemlock and western redcedar are among the most shade tolerant, most true firs are intermediate, and pines have relatively low shade tolerance. Despite ranges in tolerance (ability to survive and grow at low light levels), both greenhouse and field studies suggest that growth of a wide range of conifer species increases with increasing light up to 70 to 100 percent of full sunlight. Species studied in the field (Emmingham and Waring 1973) have included Douglas-fir, white fir, and red fir.

With field studies it is difficult to separate effects of light level on photosynthesis and growth from effects of factors such as water availability. In greenhouse studies on Douglas-fir, incense-cedar, Port-Orford-cedar, ponderosa pine, Jeffrey pine, Monterey pine, and tamarack, only growth of Port-Orford-cedar, Jeffrey pine, and Douglas-fir showed clear evidence of light saturation—at about 65 to 70 percent of full sun (Baker 1945).

It is frequently difficult to extrapolate lab results to field situations where adaptations of foliage to light may vary and environmental factors such as temperature and water stress may limit photosynthesis. Even under field conditions where light may be expected to limit photosynthesis, other limiting factors may be more important. For example, increasing available soil moisture may stimulate photosynthesis and growth, while increasing light availability may have little or no effect if water remains limiting. In terms of management, the *most* limiting factor or factors must be identified and ameliorated for a substantial growth response to occur. In the absence of other limiting factors, however, we would expect conifer saplings to show significant increases in growth anytime light is increased from low levels (less than 50 percent full sun) to almost full sunlight.

The light levels a seedling has experienced previously will also precondition it and will affect its response to manipulation of light intensity. Reduced light decreases canopy volume and vigor and alters the structure, photosynthetic efficiency, and responses of the photosynthetic apparatus and stomata to low light intensities. Because of these changes, suppressed conifers may require a period of adaptation following sudden exposure to full sun, primarily because shade leaves have poorer ability to control water loss than do sun leaves. Sudden exposure may result in mortality, nearly total loss of current needles, or severe reduction in height and diameter growth for one or more years. Plants that survive can be expected to recover once a full complement of sun-adapted foliage is developed. Responses of this type have been observed for western hemlock (Keller and Tregunna 1976), white fir (Conard and Radosevich 1982a), and Douglas-fir (Petersen 1980). The severity of exposure shock will vary among species and within species among habitats. Assuming that exposed plants survive, then long-term growth response to overstory removal should be positive.

The decreased radiation load and higher relative humidity under shrub canopies appear to aid the establishment of seedling conifers in both *C. prostratus* (Tappeiner and Helms 1971) and *C. cordulatus* (S. Radosevich, unpublished data). Based on the effects of *C. velutinus* on evaporative demand and light intensity, similar factors might explain differences in natural seedling densities of Douglas-fir that have been observed under and outside *C. velutinus* canopies (See section 5 for additional detail on these studies).

Soil moisture.—Both field and laboratory studies have shown that soil water potentials between -1 and -5 bars are sufficient to limit photosynthesis in many conifer species (Havranek and Benecke 1978, Zavitkovski and Ferrell 1970). In a laboratory study of five western conifers (Lopushinsky and Klock 1974), transpiration rates decreased to 50 percent of maximum at soil water potentials ranging from -4 to -8 bars. At -10 bars, transpiration rates of grand fir and ponderosa pine were about 35 and 12 percent of maximum values, respectively. At high vapor pressure deficits between leaf and air, stomata will close at even higher soil water potentials than indicated by these studies.

Because *Ceanothus* species can decrease soil moisture to below these levels by midsummer, conifers growing with *Ceanothus* can be expected to have transpiration and photosynthesis rates below their potential maxima for some of the growing season on many sites. Low soil and plant water potentials would also be expected to reduce conifer root growth.

Physiological Responses of *Ceanothus* Species to Environmental Conditions

In general, *Ceanothus* species maintain high stomatal conductances and high photosynthesis rates at substantially lower plant and soil water potentials than do associated conifers. Photosynthesis rates of *C. integerrimus, C. cordulatus,* and *C. velutinus* were near their seasonal maxima at plant water potentials at least as low as -25 to -30 bars, -24 bars, and -20 bars, respectively, in a study in the central Sierra Nevada (Lanini 1980). Conard and Radosevich (1981) found that photosynthesis and leaf conductance of *C. velutinus* remain at maximum rates even in late summer at the lowest plant water potentials observed (-18 bars). Other studies (Marshall and Waring 1984) have found that *C. velutinus* in the Oregon Cascade Range has extremely high stomatal conductances and poor stomatal control. Stomatal closure has been reported to occur at leaf water potentials of -30 and -20 bars for *C. thyrsiflorus* and *C. incanus,* respectively (Barnes 1981). These species all occur in forest habitats. For *Ceanothus* species of drier chaparral habitats, tolerance to low water potentials may be even greater. Stomatal closure has been reported at water potentials of -55, -45, and -55 to -60 bars for *C. ferrisae, C. ramulosus,* and *C. greggii,* respectively (Barnes 1981, Poole and Miller 1975).

Ceanothus species in general are capable of maintaining high photosynthesis and transpiration rates under conditions when photosynthesis of conifers will be severely limited. This is demonstrated by Conard and Radosevich (1981) for *C. velutinus* growing with white fir in the Sierra Nevada. Copeland (1932) estimates that *C. velutinus* and *C. cordulatus* in the northern Sierra Nevada transpire approximately 0.6 meters (2 ft) of water per unit leaf area over the growing season. He estimates that transpiration of *Castanopsis sempervirens, Quercus vaccinifolia,* and *Q. kelloggii* was about half that of the two *Ceanothus* species. *Ceanothus* species also have a high light requirement for maximum growth (Schlesinger and others 1982) and photosynthesis (Conard and Radosevich 1981). This characteristic might be expected for early seral species.

Conclusions.—*Ceanothus* species can decrease light intensities to levels well below those required for maximum growth of conifers. Thus, one would expect reduced growth of conifers under *Ceanothus* canopies even in the absence of other limiting factors. On many sites where *Ceanothus* and conifers are growing together, however, soil moisture depletion is probably the major factor limiting conifer photosynthesis except, perhaps, during the early part of the growing season. *Ceanothus* may have a competitive advantage because it can absorb water from relatively dry soil. In spite of high internal water stress, *Ceanothus* can maintain open stomata and continue photosynthesis. Conifers are less able to do so. The result is that *Ceanothus* species have the potential to compete strongly with conifers and to reduce conifer growth.

Levitt (1980) suggests that at high stress, users tend to revert to conserver strategies. It appears that stress levels in forest systems are rarely high enough to induce this for *Ceanothus.* Even if it does occur, little benefit could be expected to accrue to the less tolerant conifers.

The potential benefits to conifers from N_2 fixation by *Ceanothus* species are discussed in section 4. These and other benefits (such as amelioration in seedling environment and improved wildlife habitats) will need to be balanced against potential growth losses in making management decisions. The duration of conifer growth suppression could vary widely from site to site depending how long it takes for conifers to achieve dominance and begin to suppress associated *Ceanothus.*

Research Needs

This discussion group identified 12 areas where further research is needed:

1. Effects of canopy structure of different *Ceanothus* species on environmental factors such as light penetration, soil and air temperatures, humidity, and surface soil moisture need to be determined, and influences of season, aspect, and slope need further study.

2. Descriptions are needed of the development over time of vertical and horizontal structure of *Ceanothus* canopies (individual shrubs and communities) including biomass and leaf area.

3. Patterns of light distribution under canopies need to be quantified using techniques such as fisheye lens photography, quantum (PAR) sensors, or correlations with canopy structure, biomass, leaf area, and canopy volumes.

4. Studies are required on the effects of light levels, such as those found under *Ceanothus* canopies, on the productivity of conifers at various stages of community development.

5. Importance of the allelopathic potential of *Ceanothus* species in field situations, including the influence on conifer growth and rates of N_2 fixation, should be investigated further.

6. Effects of environmental modification by *Ceanothus* species on their own ability to fix N_2 need to be quantified. There is some evidence that dense stands of *C. velutinus* may reduce soil moisture to levels that inhibit symbiotic N_2 fixation. This topic was discussed in more detail in section 4. Effects of canopy structure and distribution on factors such as soil temperature might also be important here.

7. Correlations should be developed that would permit information on photosynthesis and plant water potential of *Ceanothus* species to be used to estimate or predict N_2-fixation rates under varying enviromental conditions.

8. More information is needed on water utilization by both *Ceanothus* and conifer species and on distribution of roots horizontally and by depth. Seasonal patterns of water use at different depths can provide a better understanding of the degree of synchrony of water demands by shrubs and conifers and how this affects the intensity of competition. Better information on root distribution could aid greatly in interpreting studies that are concerned with soil moisture depletion, plant-water relations, and shrub-conifer interactions.

9. Relationships need to be established between canopy volume, biomass, leaf area, and spatial distribution of *Ceanothus* species and their effects on soil moisture regimes.

10. More field data are needed on relationships between environmental moisture deficit, plant moisture stress, photosynthesis, and productivity for conifer species, including effects of water stress in the field on the initiation of conifer dormancy. Information on young planted seedlings of the major commercial species would be particularly beneficial when combined with information from items 1, 2, and 9.

11. Additional research is needed on the relative strength of interspecific competition between *Ceanothus* and conifer species and intraspecific competition among conifers in various situations. These topics are discussed more thoroughly in section 6.

12. A great deal of research relevant to the physiological ecology of *Ceanothus* species in forest habitats has centered on *C. velutinus.* More information on other common forest species such as *C. integerrimus, C. cordulatus, C. prostratus, C. sanguineus,* and *C. thyrsiflorus* would be extremely valuable.

6. Effects of *Ceanothus* on Forest Productivity and Conifer Growth[1]

Effects of *Ceanothus* on Conifer Establishment

In many ways, this discussion was the focus of the workshop. The discussion provided a forum for integrating some of the basic information presented at earlier sessions, and studies that have attempted to quantify responses of conifers in relation to the presence of *Ceanothus* species were discussed . The major topics were the effects of *Ceanothus* on (1) conifer establishment, (2) early growth of conifers, and (3) site quality.

Several studies have documented better initial establishment of conifer species under *Ceanothus* canopies than in the open. Scott (1969) reports 53-percent stocking of Douglas-fir in *C. velutinus* clumps in the Cascade Range in Oregon, as compared to 36-percent stocking in open areas on the same site. Dyrness and Youngberg (1966), working in an area where canopy coverage of *C. velutinus* was 33 percent, found that 66 percent of the ponderosa pine seedlings on the site are associated with *Ceanothus* clumps. Tappeiner and Helms (1971) report better survival of Douglas-fir and white fir natural regeneration in *C. prostratus* mats than in several other microsites in the Sierra Nevada; Lanini (unpublished data) observed improved survival of planted ponderosa pine, sugar pine, and Douglas-fir seedlings in association with *C. cordulatus* and other shrub species. Show (1924) also reports improved survival of planted ponderosa pine, sugar pine, and giant sequoia as shading by brush increased (in mixed brushfields containing *Ceanothus velutinus, Arctostaphylos patula,* and *Castanopsis sempervirens*). Show concludes that the benefits of shading are greatest on poor sites, in dry years, and with small planting stock. Wahlenberg (1930) reports first season survival of 89 percent for planted ponderosa pine under *C. velutinus* canopies and 53 percent in the open in the Rocky Mountains in Montana. He attributes this, in part, to higher humidity, lower evaporative demand, cooler soil temperatures, and higher surface soil moisture under the shrub canopies.

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[1] All workshop participants were members of this discussion group. Discussion leader was Bill Stein.

In the only experimental study we are aware of, Zavitkovski and others (1969) planted seedlings of four conifer species under live *C. velutinus,* under dead *C. velutinus,* in openings, and on freshly burned areas. All species survived best in freshly burned areas. Survival in the other three treatments was equal for ponderosa pine and Douglas-fir. Western hemlock had its lowest survival in openings, and noble fir survival was lowest under live and dead *Ceanothus.* Clearly, different species can be expected to respond differently to the presence of *Ceanothus.* These studies suggest that where *Ceanothus* benefits conifer survival, results may apply both to natural regeneration and to planted seedlings.

Causes for the observed effects of *Ceanothus* species on initial survival may vary. As discussed in a previous section, summer soil temperatures and evaporative demand are frequently lower under *Ceanothus* canopies than in the open. There is also evidence that surface soil moisture remains higher underneath the canopy than where *Ceanothus* is absent (herbaceous vegetation is usually present in the latter areas). These factors are discussed more fully in section 5. Shrubs may provide protection from browsing on some sites, although there have also been reports of increased rabbit damage under *Ceanothus* canopies (Zavitkovski and others 1969). Most reports discussed in this section were based on sample measurements rather than on controlled experiments, so causal relationships can only be postulated. Effects of brush on survival may be confounded in some of these studies with microsite differences between areas where shrubs established initially and areas where shrub establishment was poor ("open" areas).

There is a lack of studies in which the effects of *Ceanothus* on the conifer environment have been specifically characterized and isolated from possible confounding factors. Some of the factors that need to be considered in design of research on this topic are:

1. Effects of different levels (densities, sizes, cover) of *Ceanothus* need to be evaluated on comparable microsites. This requires a replicated, randomized design where levels of *Ceanothus* are manipulated experimentally.

2. Animal damage and other sources of injury (for example, frost and winter desiccation) should be documented.

3. Mechanical damage, such as that from snow, wind, or falling debris, should be documented if it occurs.

Effects of *Ceanothus* on Early Growth of Conifers

There are two categories of research that have been conducted on the effect of *Ceanothus* on early growth of conifers. The first involved studies in which the structure of *Ceanothus* stands was manipulated experimentally. The second group of studies measured conifer growth relative to varying levels or ages of naturally established, undisturbed *Ceanothus.* These two types of studies were further divided into those dealing with planted conifers and those concerned with natural regeneration.

Experimental Studies

Several studies have demonstrated dramatic increases in height, diameter, and volume growth of conifers following release from *C. velutinus.* One of the earliest (Gratkowski and Lauterbach 1974) shows 6-year height growth in Douglas-fir to be 170 to 255 percent that of untreated controls following aerial spraying of *C. velutinus* var. *laevigatus.* Petersen and Newton (1982) measured 3-year responses of 5- and 10-year-old Douglas-fir following control of *C. velutinus* or of both *Ceanothus* and herbaceous vegetation. Volume growth of 5-year-old trees was 258 and 415 percent of controls, respectively, where shrubs only or shrubs and herbs were controlled. Results for 10-year-old trees were similar but less striking. Differences among treatments in the study by Petersen and Newton were still accelerating as of the last measurements.

Studies by Weyerhauser Company in the Cascade Range in Oregon demonstrated similar increases in height and diameter growth following release of Douglas-fir from *C. velutinus* (Lauterbach 1967). Conard and Radosevich (1982a) report increases of 140 to 200 percent in white fir height growth relative to untreated controls 4 years after release from *C. velutinus.* The largest growth response was observed when shrubs were controlled and the conifers were artificially shaded for several years. Substantial growth check was observed in many released trees that were not shaded. Eight-year cumulative height growth of released trees in the Conard and Radosevich study is 200 percent of controls, and growth of released trees is continuing to increase faster than growth of the untreated controls (S. Conard, unpublished data). Sanders (unpublished data) also reported greater height growth for unreleased trees than for released trees 1 year after manual release from *C. velutinus.* By the second year, released trees on 6 out of 7 sites were growing at prerelease rates, and after 4 years, released trees on all sites were growing significantly better than unreleased trees.

In a study evaluating release of lodgepole pine from *Ceanothus,* no growth response was observed 2 years after treatment (R. Boyd, unpublished data). Other studies have shown, however, that growth reduction can occur for 1 or 2 years following treatment, so a delayed response may well occur.

Only one study was discussed in which effects of site preparation methods on growth of planted conifer seedlings are evaluated. This was a study described earlier, where Zavitkovski and others (1969) planted seedlings in four site preparation treatments. For all four conifer species planted in these experiments, height growth was reduced if the species were planted in *C. velutinus* stands over 10 years old. This corresponds to the age at which *C. velutinus* achieves maximum biomass. Based on 2-year height growth measurements, the effects of other treatments were inconclusive, except that ponderosa pine height growth was highest in fresh clearcuttings.

Height growth of naturally established seedlings was substantially greater in the fresh clearcutting than under live *C. velutinus;* growth increases were 44 percent, 66 percent, 116 percent, and 124 percent for western hemlock, Douglas-fir, ponderosa pine, and noble fir, respectively (Zavitkovski and others 1969). These values suggest that planted seedlings may experience planting check for the first two seasons following planting. It is unfortunate that longer term data are not available for these study sites. Height and diameter growth measurements on conifers 5 and 10 years following treatments could provide valuable information.

The participants were aware of several current research projects in which effects of *Ceanothus* species on survival or growth of conifers are being investigated:

1. A series of administrative studies by the USDA Forest Service in California, Idaho, and Oregon are comparing effects of various chemical and manual site preparation and release treatments on conifer growth, and survival and vegetation development on sites where *Ceanothus* species occur. The principal scientists are W. Stein and E. Dimock II, Pacific Northwest Forest and Range Experiment Station; P. McDonald, Pacific Southwest Forest and Range Experiment Station; and R. Boyd, Intermountain Forest and Range Experiment Station.

2. An intensive study is being conducted through Oregon State University in the H.J. Andrews Experimental Forest, Willamette National Forest, to investigate the long-term effects of *C. velutinus,* at several densities, on conifer growth and on soil properties. This research is being conducted by P. Sollins, Oregon State University.

3. A comparison of several release treatments on *C. velutinus*-dominated sites in western Idaho is being conducted through the Coordinated Research on Alternative Forestry Techniques and Systems (CRAFTS) program under the direction of S. Radosevich, Oregon State University.

4. Several studies on conifer release have been started by scientists at Weyerhaeuser Company, Champion International, and Groundwork, Inc.

Sampling Studies

Several researchers have reported greater height growth of young Douglas-fir under or at the edge of *C. velutinus* canopies than in open areas between shrubs (Horowitz 1980, 1982; R. Sanders, unpublished data; Scott 1969). The most dramatic results are those of Scott (1969), who reports Douglas-fir heights after 9 years of 1.6, 1.2, and 0.8 meters (5.2, 3.9, 2.6 ft) under shrub canopies, at the edge of canopies, and in the open, respectively. Horowitz (1980, 1982) conducted a similar study on sites with *C. velutinus* in the hemlock and true fir zones in the Cascade Range. He reports slightly to significantly greater height growth by Douglas-fir in edge positions than by those either inside or outside shrub canopies on 60 percent of his hemlock-zone study sites. Growth was greatest in the outside position on 30 percent of the study sites. In the true fir zone, where *C. velutinus* was less abundant, conifer height growth decreased 40 percent from outside to inside shrub canopies, and growth in the edge position was intermediate. In this study, no correlation was observed between shrub cover and conifer growth.

Horowitz (1982) measured conifer and shrub growth on forest sites proposed for aerial release treatments of 2,4,5-T in the Willamette National Forest. Mean crop tree growth was not significantly correlated with the presence or absence of shrub species, although mean growth was correlated with site factors such as elevation and aspect. Five years after herbicide treatment of some of the sites, measurements of crop tree height, leader length, and diameter were not significantly different from those on comparable untreated sites (Horowitz, unpublished data).

Although these studies provide information on the relative growth of conifers in natural situations with and without *Ceanothus,* they do not address the question of how conifer growth might be affected by reduction or removal of *Ceanothus.* Many factors, other than the direct influence of *Ceanothus* on growth, may influence results in nonmanipulative studies such as these and make results difficult to interpret. The open environment may be particularly stressful for young conifers if they are growing within the active rooting zone of shrubs, or if water-using herbs are present. In addition, shrub regeneration may have occurred preferentially in favorable microsites, and confounding factors such as increased or decreased animal damage in shrub canopies can influence results.

Effects of *Ceanothus* on Site Quality

Much of the information available on this topic has already been discussed in section 4 so will not be repeated here. There have been few direct measurements of the effect on associated conifers of nitrogen added to the soil by *Ceanothus* species. Youngberg and others (1979), however, report significantly higher levels of foliar N in July in Douglas-fir seedlings growing under *C. velutinus* (1.56 percent N) than in seedlings growing in the open (1.15 percent N) or at the edge of *Ceanothus* canopies (1.32 percent N). They consider 1.2 percent N in foliage to be the minimum for "adequate growth."

A recent study by Binkley and Husted (1983) reports similar results for seedlings associated with *C. sanguineus.* In that study, foliar N levels correlated well with levels of available N in the soil. Binkley and Husted also found higher levels of calcium and magnesium both under the shrub canopies and in the foliage of Douglas-fir growing under the canopies as compared to areas where *Ceanothus* was absent. These studies suggest that, at least on some sites, the presence of *Ceanothus* species can improve the mineral nutrition of associated conifers. Information is lacking on how these differences may affect growth and on what types of sites we can expect to show these types of responses.

There are many areas in the Cascade Range where soil N levels are quite high and rainfall input of N is probably on the order of 2 to 3 kilograms per hectare (2.7 lb/acre) per year. Although this adds up to a large amount of N over several hundred years, it is probably insufficient to maintain long-term productivity with short rotations and frequent slash fires.

Conclusion

Several general observations came out of this session. First, we do not have sufficient data to permit accurate predictions of the effect that management of *Ceanothus* species will have on long-term site productivity, even for sites where *C. velutinus* is dominant. There is considerably less information on other *Ceanothus* species. Second, we have a poor understanding of the tradeoffs involved in controlling *Ceanothus.* Can reduced conifer growth attributed to competition from *Ceanothus* be balanced by long-term nutritional benefits? Although this is a reasonable hypothesis, it has not yet been tested thoroughly. Because of the effects of water stress on N_2 fixation, that maximum (or near maximum) levels of nutrient addition might be achieved at well below maximum cover of *Ceanothus.* Third, both sampling and experimental studies can add to the understanding of *Ceanothus*-conifer interactions. Whenever possible, information from sampling studies should be verified by well-designed experimental studies. Fourth, the *Ceanothus*-conifer systems are extremely complex: Researchers should be aware of this and avoid simplistic, single-factor interpretations.

Research Needs

It was generally agreed that many of the past studies on effects of *Ceanothus* species on conifer growth have serious flaws that should be corrected wherever possible in future research. Some of the major recommendations of participants in this regard were:

1. Studies should be designed to avoid confounding of factors such as microsite differences.

2. Sufficient time should be allowed for responses to occur before publication of results. Because of initial growth check following planting or resulting from release treatments, growth responses may not be observed until 3 to 5 years after treatment on many sites. Studies should be designed with at least a 5- to 10-year time frame.

3. Height and diameter measurements should be standard practice. Diameter growth frequently responds more rapidly to treatments than height growth. Furthermore, factors such as shading and moisture stress can alter height-to-diameter relationships dramatically.

4. Effects of treatments on shrub growth, distribution, and canopy volume should also be evaluated. This information is critical for comparing results of different studies, for developing models to predict growth benefits, and to determine where and when these benefits can be expected.

5. Close attention should be paid to the quality and source of planting stock and to careful handling and planting of seedlings.

6. Clear distinction should be made between studies evaluating responses of natural regeneration and those involving planted seedlings.

7. Effects of factors such as animal damage, insect infestation, mechanical damage, and frost injury should be recorded and quantified. For example, in a recent manipulative study in *C. velutinus* brushfields, Perry[2/] observed substantial aphid infestations on Douglas-fir saplings when surrounding shrubs were removed.

[2/] Personal communication, D. Perry, Forest Science Department, Oregon State University, Corvallis, OR 97331.

7. Research Priorities[1]

Six major areas of needed research were identified: (1) autecology and physiological ecology of *Ceanothus* species, (2) interactions between *Ceanothus* and conifers, (3) development of computer simulation models, (4) synthesis of information that can be obtained from stand sampling, (5) interactions between *Ceanothus* and wildlife, and (6) standardization of study methods and nomenclature. Technology transfer is also needed. Research in the first two areas was ranked as high priority by all three study groups. The importance of summarizing pertinent research information in forms useful to land managers was also discussed, and suggestions were made for implementation. In all research areas, participants stressed the need to obtain more information (1) on species other than *C. velutinus* and (2) from geographic areas outside the Pacific Northwest. There was also general concern expressed over the need for well-designed, replicated studies that can serve multiple purposes. There is a need for long-term studies that will produce information concerning conclusions about the effects of *Ceanothus* over one or more rotations.

Autecology and physiological ecology of *Ceanothus* species:

1. Investigate requirements for and effects of *Ceanothus* establishment—seed longevity, dormancy, germination requirements, effects of fire intensity, seed production and storage, planting of *Ceanothus,* reproductive strategies (seed vs. sprout), and effects of age, size, and site characteristics on sprouting.

2. Study productivity—determine growth rates, biomass production, site occupancy, canopy structure and densities, seasonal growth patterns (phenology), carbon balance and allocation patterns, and develop predictive models.

3. Conduct detailed field research on nitrogen dynamics—nutrient cycling, nitrogen fixation, and effects of environmental conditions (water, light, temperature, biotic interactions, micronutrients, and pH) and of endophyte characteristics.

4. Conduct field investigations of patterns of water use and water relations of *Ceanothus* species, especially for species other than *C. velutinus.*

5. Investigate effects of *Ceanothus* on erosion prevention and slope stability.

Interactions between *Ceanothus* and conifers:

1. Identify existing long-term studies (at least 20 years) with adequate design or controls to permit comparisons of sites where *Ceanothus* is present with those where it has been removed. This could provide preliminary estimates of the long-term effects of potential management strategies for *Ceanothus*-conifer systems.

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[1] Participants were divided into three separate groups to identify research priorities. This section summarizes the conclusions of all three groups.

2. Establish long-term experiments to look at effects of absolute and relative densities of *Ceanothus* and conifers on growth, nutrients, and other factors. Both replacement series and Nelder designs are approaches that might be useful. Weigh positive and negative interactions (nitrogen fixation, browse value, moisture competition, and shading).

3. Initiate well-designed studies to evaluate positive and negative effects of release in plantations where *Ceanothus* is well established (for example, codominant or dominant).

4. Investigate interactions between conifers and vegetation that replace *Ceanothus* where *Ceanothus* is controlled. Look at effects of manipulation on seral sequences. Weigh benefits against negative interactions.

5. Investigate effects of timing on interactions; for example, how does the effect of a short rotation of *Ceanothus* followed by its removal and planting of conifers compare with the effect of growing the two species concurrently or eliminating *Ceanothus* entirely?

6. Monitor nutrients, physiology, and environmental conditions in the studies listed above.

Development of computer simulation models:

1. Test and integrate scientific concepts or assumptions and generate hypotheses.

2. Evaluate the importance of individual factors that influence interactions between *Ceanothus* species and conifers, such as competition for site resources, growth enhancement, or suppression.

3. Predict responses of *Ceanothus*-conifer association to individual factors, such as nitrogen fixation/accretion, site fertility, and management practices.

4. Facilitate information exchange and stimulate discussion among scientists, land managers, and others.

Synthesis of information from stand sampling:

1. Analyze existing stand examination data from a wide geographical area for possible use in acquiring site-specific information.

2. Integrate biological research data with stand examination data for possible use in management of the *Ceanothus*-conifer complex.

3. Corroborate research results on a broader scale.

The use of *Ceanothus* species by wildlife:

1. Develop guidelines for wildlife management where *Ceanothus* is abundant.

2. Conduct additional research on wildlife/*Ceanothus* interactions.

3. Investigate the effect of shelter, alternate food, and browse for wildlife on conifer establishment, survival, and growth.

Standardization of study methods and definitions:

1. Define terms and concepts for uniformity; for example, definitions of conifer suppression can incorporate such factors as the percentage of foliage that is above the photosynthetic compensation point (more practically, the percentage of foliage that is shaded), conifer development over a specific period of time, and height of conifer leaders.

2. Develop standardized, statistically sound study methods and designs that will allow comparison of results among experiments.

3. Develop interim guidelines for *Ceanothus* management based on current knowledge of the importance of *Ceanothus* as browse for game species, as a site stabilizer, as a nitrogen fixer, and as a competitor.

Technology transfer:

1. Publish a periodic newsletter describing current studies or research results. This can include a directory of individuals active in *Ceanothus* research and management. Encourage researchers to use existing periodicals (such as Forestry Research West, FIR Report, Forestry Update) for disseminating research information.

2. Develop monograph or book on the biology of *Ceanothus.*

3. Develop a comprehensive manual on the management of *Ceanothus* much like the silvics manual used by foresters.

Many of the research needs that are identified here overlap considerably, and with careful research design and coordination among researchers in different areas, information on many of these topics can be obtained from single experiments. Because of the large investment in time and energy required for large-scale field experiments, the consensus was that coordinated interdisciplinary efforts should be encouraged wherever possible.

8. Concluding Remarks[1]

Much scientifically and operationally useful information is known about *Ceanothus.* Everything about all 55 species in all conceivable environments will never be known. Thus, we must make an investment decision, or rather two:

1. What do we do with the information we have?

2. What new information should we seek, if any?

The answer to the first question is straightforward. The results of this workshop should not only be packaged into a proceedings, but distilled into a "how to" publication for people interested in managing or studying *Ceanothus.* This publication should be presented as widely as audience demand will allow. Thus, we could be reasonably sure what we know about *Ceanothus* will be used and not misused.

The answer to second question is trickier. If we invest in *Ceanothus,* we will not invest in some other dollar equivalent research. Consideration of what we are willing to give up to learn more about *Ceanothus* is a potential problem in obtaining financial support for *Ceanothus* research. I am willing to hypothesize that until we know something about true fir autecology, for example, or how to grow Douglas-fir on specific sites or to meet specific objectives, further research on *Ceanothus* should be defined by two criteria:

1. What hypotheses, leading to results generalizable beyond the genus *Ceanothus,* can be tested most efficiently using *Ceanothus* as a guinea pig?

2. What missing practical information about *Ceanothus* now prevents us from making effective and efficient management decisions?

By way of examples, more than concrete suggestions, I put forward two hypotheses for addressing the first criterion.

1. The general hypothesis that endophyte quantity and quality limit nodulation might be efficiently tested with *Ceanothus.* Nodulation in *Ceanothus* is spotty, but apparently ubiquitous. Testing will require several activities including isolation of the endophyte into pure culture and field experiments where endophyte populations are deliberately manipulated. Neither will be easy.

2. A second general hypothesis is that nitrogen-fixing species employ different evolutionary strategies in the occupation of territory than do nonnitrogen-fixing species. Comparisons of *Ceanothus* with similar but non-nodulating genera could shed light on this question.

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[1] This section prepared by John Gordon, Dean, School of Forestry, Yale University, New Haven, CT 06520.

To address the second criterion, additional practical information should be sought. Ideally, sensitivity analyses should be done to indicate returns from different kinds of environmental information such as that done for soils by Schöne (1983). Because it is unlikely that this will happen, I suggest:

1. Examine the consequences of control by observing the effects of complete and partial control over time on all values of management interest, including wildlife, soil erosion, and crop tree growth, in relation to probable future management systems.

2. Learn how nitrogen accretion occurs; the major need is to know relationships between the quantity and effectiveness of nodules and aboveground variables such as species composition and stem basal area.

3. Learn how variability at the species level can be used for specific management purposes through common garden studies that relate nitrogen fixation to growth rates and competitive effects.

By far, the highest priority for incremental effort is to capture, and to render usable by managers, the results of the last 2-1/2 days.

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Appendix 1: Scientific Names of Species Cited

Ceanothus Species

Ceanothus americanus L. (New Jersey Tea)
C. cordulatus Kell. (mountain whitethorn)
C. crassifolius Torr. (hoaryleaf ceanothus)
C. cuneatus (Hook.) Nutt. (buckbrush)
C. diversifolius Kell. (trailing ceanothus)
C. fendleri Gray (Fendler ceanothus)
C. greggii Gray (desert ceanothus)
C. greggii var. *perplexans* (Trel.) Jeps.
C. greggii var. *vestitus* (Greene) McMinn
C. incanus T. & G. (coast whitethorn)
C. integerrimus H. & A. (deerbrush)
C. lemmonii Parry (Lemmon ceanothus)
C. leucodermis Greene. (chaparral whitethorn)
C. megacarpus Nutt. (bigpod ceanothus)
C. oliganthus Nutt. in T. & G. (hairy ceanothus)
C. parvifolius (Wats.) Trel. (littleleaf ceanothus)
C. prostratus Benth. (squaw carpet)
C. pumilis Greene (dwarf ceanothus)
C. sanguineus Pursh. (redstem ceanothus)
C. thyrsiflorus Esch. (blueblossom)
C. tomentosus Parry
C. velutinus Dougl. (snowbrush)
C. velutinus var. *velutinus* Dougl. ex Hook. (snowbrush)
C. velutinus var. *laevigatus* (Hook.) T. & G. (varnishleaf)

Conifer Species

Abies amabilis Dougl. ex Forbes (Pacific silver fir)
A. concolor (Gord. & Glend.) Lindl. ex Hildebr. (white fir)
A. grandis (Dougl. ex D. Don) Lindl. (grand fir)
A. magnifica A. Murr. (California red fir)
A. procera Rehd. (noble fir)
Chamaecyparis lawsoniana (A. Murr.) Parl. (Port-Orford-cedar)
Larix laricina (Du Roi) K. Koch (tamarack)
Libocedrus decurrens Torr. (incense-cedar)
Picea sitchensis (Bong.) Carr. (Sitka spruce)
Pinus attenuata Lemm. (knobcone pine)
P. contorta Dougl. ex Loud. (lodgepole pine)
P. coulteri D. Don (Coulter pine)
P. jeffreyi Grev. & Balf. (Jeffrey pine)
P. lambertiana Dougl. (sugar pine)
P. ponderosa Dougl. ex Laws. (ponderosa pine)
P. radiata D. Don (Monterey pine)
P. sabiniana Dougl. (Digger pine)
P. taeda L. (loblolly pine)
Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir)

Sequoia sempervirens (D. Don) Endl. (coast redwood)
Sequoiadendron giganteum (Lindl.) Buchholz (giant sequoia)
Thuja plicata Donn ex D. Don (western redcedar)
Tsuga heterophylla (Raf.) Sarg. (western hemlock)

Other Species

Trees and shrubs:

Alnus Mill. (alder)
Arctostaphylos patula Greene (greenleaf manzanita)
Castanopsis sempervirens (Kell.) Dudl. (bush chinkapin)
Holodiscus Maxim. (ocean-spray)
Lithocarpus densiflorus (Hook. & Arn.) Rehd. (tanoak)
Prosopis glandulosa Torr. var *torreyana* (L. Benson) M.C. Johnst (mesquite)
Prunus L. (cherry, plum)
Quercus L. (oak)
Quercus vaccinifolia Kellogg (huckleberry oak)
Quercus kelloggii Newb. (California black oak)

Mycorrhizal and symbiotic fungi:

Armellaria mellea Vahl. ex Fr. (*Armellaria* root disease)
Cenococcum geophilum Fr. (*Cenococcum*)
Eutypa armeniacae Hansf. & Carter. (no common name)
Frankia spp. (*Frankia*)
Laccaria laccata (Scop. ex Fr.) Berk. & Br. (*Laccaria*)
Rhizobium japonicum

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