

Ecological Significance of Nitrogen Fixation by Actinorhizal Shrubs in Interior Forests of California and Oregon¹

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Abstract

Biological nitrogen fixation (BNF) is vital to the terrestrial nitrogen (N) budget, balancing N losses from denitrification and providing N for organism growth and maintenance. Limited information exists, however, to verify the importance of BNF by actinorhizal shrubs in moisture- and nutrient-limited forests of the interior west. A series of studies are presented that evaluate BNF by actinorhizal shrubs in central Oregon and northeastern California ponderosa pine forests and examine the effects of several forest management practices on shrub growth and potential N fixation. Nitrogen fixation rates were determined for *Ceanothus velutinus* (snowbrush) and *Purshia tridentata* (bitterbrush) in central Oregon by ¹⁵N isotope dilution methods and for *Purshia* and *C. prostratus* (mahala mat) in northeast California by ¹⁵N natural abundance. Both *C. velutinus* and *Purshia* were efficient N fixers in the ponderosa pine understory of central Oregon; about 85 percent of their total plant N was derived from fixation. *Ceanothus velutinus* fixed an average of 10 kg N ha⁻¹ annually at sites with low to moderate shrub cover. Although this rate is substantially lower than that reported for *C. velutinus* shrub fields on the western slopes of the Cascades, it would provide enough N to offset losses from periodic prescribed fire or harvesting. *Purshia* fixed about 1 kg N ha⁻¹ yr⁻¹ or less as an understory species at sites in Oregon and California and showed little or no stimulation from several management treatments, including overstory removal, organic residue removal, prescribed fire, and fertilization. *Ceanothus prostratus* also fixed less than 1 kg N ha⁻¹ yr⁻¹ at the California site. Of the three species, only *C. velutinus* produces biomass and, consequently, fixes sufficient N to replace N lost during perturbation.

Introduction

Terrestrial ecosystems gain an estimated 130-170 million metric tons of nitrogen (N) annually from biological nitrogen fixation (BNF) (Galloway and others 1995), with about 40 million metric tons, or 23-31 percent of the total, attributed to forested ecosystems (Burns and Hardy 1975). Although these estimates are admittedly crude, they underscore both the magnitude and the significance of BNF to the global N budget. At the forest stand level, high rates of BNF are most often reported for actinorhizal and leguminous plants which fix N in symbiosis with soil prokaryotes. Examples include *Alnus rubra* (red alder), 130 kg N ha⁻¹ yr⁻¹ (Binkley 1981); *Casuarina equisetifolia*, 12-85 kg N ha⁻¹ yr⁻¹ (Diem and Dommergues 1990); and *Ceanothus velutinus* (snowbrush), 20-100 kg N ha⁻¹ yr⁻¹ (McNabb and Cromack 1983, Youngberg and Wollum 1976, Zavitkovski and Newton 1968). By comparison, asymbiotic N fixation by free-living soil prokaryotes typically contributes 1 kg N ha⁻¹ yr⁻¹ or less in forest ecosystems (Jurgensen and others 1992), whereas associative N

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fixation, although controversial, has been suggested to fix up to 50 kg N ha⁻¹ yr⁻¹ in the rhizosphere of conifer roots (Bormann and others 1993).

Not satisfied with the intrinsic rates of N fixation, soil and plant biologists have long had the goal to enhance BNF through better understanding of its biochemistry, physiology, and ecology. Unfortunately, what can be described by a simple chemical equation, the conversion of atmospheric N to ammonium by the enzyme complex *nitrogenase*, belies a complexity and elegance that is often frustrating to the scientific community. Although a wealth of knowledge has been gained in the study of BNF, translation of this knowledge to on-the-ground improvements has been slow, particularly in temperate agricultural ecosystems. It is important to ask, therefore, whether similar obstacles should be expected in forested ecosystems. Have we as a scientific community set our expectations of BNF too high?

If BNF is indeed besieged by predictions or unrealistic expectations, they are a likely indication that the long-standing goal of providing sizable improvements in N yield has been overemphasized. Instead of asking how much additional N can be fixed by advances in breeding programs, inoculum technology, or other scientific improvements, a more apropos question is to first ask how much added N is required by forested ecosystems. For example, if providing sufficient N for tree growth is required, then, as suggested by Turvey and Smethurst (1983), “initial fixation rates should be between 50 and 100 kg ha⁻¹ yr⁻¹.” An alternative approach is to provide sufficient N input from BNF to meet the needs of long-term ecosystem sustainability. The value of such an approach is subtle, yet would be of considerable importance if BNF could replace N losses from prescribed fire, wildfire, denitrification, or harvesting. For example, use of prescribed fire to reduce fuel buildup can result in N losses of between 50 and 150 kg ha⁻¹ in central Oregon pine forests (Landsberg 1993, Monleon and Cromack 1996, Simon 1990). Assuming a prescribed-fire program with a mean return interval of 15 years, complete replacement of N losses would be met by N fixation rates between 3 and 10 kg ha⁻¹ yr⁻¹. This example accentuates a proclivity to become entranced by high rates of N fixation without first taking into consideration the basic needs of an ecosystem.

Nitrogen fixation by actinorhizal shrubs is a viable means to replace N lost by perturbation in pine forests. Actinorhizal plants fix N in symbiosis with members of the genus *Frankia*, a soil actinomycete, and are common in the understory of pine and mixed conifer forests of central Oregon and northeastern California (Benson and Silvester 1993, Schwintzer and Tjepkema 1990). These N-fixing plants are early seral, establishing after natural or anthropogenic disturbances, and often persist until shaded by overstory trees. In addition to providing fixed N, actinorhizal shrubs are acknowledged for their importance as wildlife browse species (Conard and others 1985, Guenther and others 1993), erosion control (Conard and others 1985), and improvement of soil quality (Busse and others 1996, Dyrness and Youngberg 1966, Johnson 1995). Johnson (1995) found that stands of *C. velutinus* in the eastern Sierra Nevada had higher levels of soil carbon (C) and N compared to adjacent Jeffrey pine stands. Higher levels of C and N have also been reported in central Oregon soils when actinorhizal shrubs are present in the understory of ponderosa pine stands (Busse and others 1996).

Although actinorhizal shrubs are common to the dry, pine forests of central Oregon and northeastern California, little is known of their contribution to the N budget. The objectives of my research were to compare rates of N fixation by *Purshia*, *C. velutinus*, and *C. prostratus* in these forests and to evaluate their response

to a variety of forest management practices. The ecological importance of BNF by these species is discussed in the context of managing understory vegetation for a variety of uses, including wildlife habitat, timber production, and soil productivity.

Materials and Methods

Actinorhizal Species

More than 200 actinorhizal species representing 8 plant families are known (Berry 1994). The following species were selected for study on the basis of their relative abundance in pine forests of central Oregon and northeastern California:

- *Purshia*, or bitterbrush, a member of the *Rosaceae* family, is found throughout pine forests and rangelands of the interior west of North America. Its geographical distribution, estimated at 138 million hectares (Hormay 1943), extends from southern British Columbia to New Mexico, and includes all 11 western states. Noted characteristics include its high value as a wildlife browse (Guenther and others 1993), intolerance to fire (Driscoll 1963, Hormay 1943), and extensive phenotypic variation (Klemmedson 1979). Nodulation was first identified by Wagle and Vlamis (1961), and ability to fix N was confirmed several years later (Webster and others 1967). Current knowledge of the N-fixing capacity of *Purshia* under natural conditions is limited. Dalton and Zobel (1977) estimated annual rates well under 1 kg N ha⁻¹ in central Oregon pine forests and attributed this, in part, to low nodulation rates resulting from restrictive soil temperature and moisture.
- *C. velutinus*, or snowbrush, a member of the *Rhamnaceae* family, is also widespread in the western states and can flourish in a variety of forested habitats (see Conard and others 1985 for a review of the genus *Ceanothus*). It is a fast-growing, seral species capable of seed germination, even after several hundred years of dormancy (Conard and others 1985), and is fire tolerant with rapid resprouting typical after fire. The N-fixing ability is well characterized for pure stands of *C. velutinus*. Studies from shrub fields on the western slopes of the Cascade Range in Oregon estimate annual rates of fixation as high as 100 kg N ha⁻¹ yr⁻¹ (Binkley and others 1982, McNabb and Cromack 1983, Youngberg and Wollum 1976). On a drier site in central Oregon, fully stocked *C. velutinus* contributed an estimated 71 kg N ha⁻¹ yr⁻¹ (Youngberg and Wollum 1976).
- *C. prostratus* is a mat-forming species found on dry sites in pine forests in the Sierra Nevada and southern Cascade Range and is credited as a valuable species for erosion control (Conard and others 1985). Nitrogen fixation by *C. prostratus* was first identified by Delwiche and others (1965), yet no additional information exists with regard to its N-fixing ability in field conditions.

Measurement of BNF

Measurement of N fixation is problematic; the lack of a simple and accurate method to determine annual rates continues to be a limitation. Several methods have been used, including ¹⁵N isotope dilution, ¹⁵N natural abundance, acetylene reduction, N accretion, and N difference, each with their own assumptions and inaccuracies. Of

these, the ^{15}N stable-isotope methods are currently considered to have the least drawbacks for the quantitative measurement of BNF (Warembourg 1993). Their advantages rest in the ability to measure BNF cumulatively over one or more growing seasons, the high degree of precision of stable isotopes, and the capability of assessing the relative efficiency of N fixation, or the proportion of plant N derived from fixation (Ndff). Stable-isotope methods are not without their limitations, however. Several assumptions, which primarily involve the selection of the reference plant, must be satisfied to ensure an accurate measurement of BNF. Reference plants are required in order to estimate the relative proportion of plant N derived from fixation versus soil N uptake. They must have a similar rooting profile, timing of N uptake, and internal isotopic discrimination as N-fixing plants. Finding an appropriate reference plant, unless non-nodulating isolines are available, is a difficult task at best.

I used ^{15}N isotope dilution to measure BNF in central Oregon and ^{15}N natural abundance to measure BNF in northeastern California as summarized below.

Quantification of BNF by *C. velutinus* and *Purshia* in Central Oregon Ponderosa Pine Stands

Rates of N fixation by *C. velutinus* and *Purshia* were quantified at three sites on the eastern slope of the central Oregon Cascades, along a north-south transect of the Deschutes National Forest. Site characteristics are listed in *table 1*. Criteria for site selection were to provide: (i) 20 to 60 percent ground cover of *C. velutinus* in the understory of ponderosa pine and (ii) a range of ponderosa pine stand ages. Although occupancy by *Purshia* was not one of the original criteria, the species was included in this experiment given its presence at two of the sites.

Table 1—Site characteristics for the ^{15}N -isotope-dilution study in central Oregon.

	Swede Ridge	Walker	Mt. Jeff
Elevation (m)	1520	1470	1950
Annual precipitation (cm)	53	38	89
Site index (m)	33	23	29
Stand age in 1991 (yr)	48	125	26
<i>C. velutinus</i> cover (pct)	23	31	59
<i>Purshia</i> cover (pct)	15	9	0

The Mt. Jeff site is about 60 km north of Bend, Oregon, on the eastern flank of the Mt. Jefferson Wilderness. *Ceanothus velutinus* established after a wildfire in 1954. The site was planted to ponderosa pine in 1963 and sprayed with 2,4-D ([2,4-dichlorophenoxy] acetic acid) to delay growth of competing vegetation. The understory is dominated by *C. velutinus* and *Arctostaphylos patula* (greenleaf manzanita). The Swede Ridge site is a ponderosa pine/ *Purshia*-*C. velutinus*/*Stipa occidentalis* (needlegrass) plant community (Volland 1985) about 18 km southwest of Bend, Oregon. The area was logged between 1920 and 1940, and an even-aged pine stand has regenerated in the exclusion of fire. The Walker site is a mixed-

conifer/*C. velutinus*-*Castanopsis chrysophylla* (golden chinkapin) plant community about 77 km south of Bend, at the base of Walker Mountain. Understory shrubs at Walker resprouted or germinated from seed following a moderate-intensity prescribed fire in 1976. Soils at the three sites are Cryandepts, with pumice and ash parent material derived primarily from the eruption of Mt. Mazama (Crater Lake) about 7,000 years ago.

Four 25-m² replicate plots were installed at each site. Aqueous ¹⁵N-ammonium sulfate (10 percent atom excess) was applied to the surface of the mineral soil at a rate of 5 kg ha⁻¹ in late summer 1989 and again in April 1990 immediately after snow melt. Forest floor material was carefully removed from each plot immediately before application of ¹⁵N and replaced after 48 h. Actively growing foliage and stems were sampled monthly from actinorhizal and reference plants beginning in May 1990, and ¹⁵N/¹⁴N and total N concentration was determined by the Stable Isotope Research Unit, Oregon State University. Thirty-one *C. velutinus* and 53 *Purshia* plants were compared. Species tested for applicability as reference plants included *Arctostaphylos*, *Ribes cereum*, and *Carex rossii*. *Arctostaphylos* was eventually chosen as the reference plant on the basis of similarity in rooting profile and synchronicity of N uptake with respect to the actinorhizal shrubs.

The relative contribution of atmospheric N to the actinorhizal plants was calculated by the equation:

$$\text{Ndff} = ([\delta^{15}\text{N}_r - \delta^{15}\text{N}_a] / \delta^{15}\text{N}_r) \times 100 \quad (1)$$

where Ndff is the percentage of plant N derived from atmospheric N; $\delta^{15}\text{N}_r$ is the per mil ¹⁵N excess of the reference plant; and $\delta^{15}\text{N}_a$ is the per mil ¹⁵N excess of the actinorhizal plant. Equation (2) was used to determine total N fixed:

$$\text{Total N fixed (kg ha}^{-1}\text{)} = (\text{Ndff}) \times (\text{plant biomass}) \times (\text{plant N concentration}) \quad (2)$$

Plant biomass was determined by destructively sampling each plant within the study plots after the last sampling date in 1991. Plants were excavated for both above- and below-ground biomass. Because of the extensive rooting system of *C. velutinus* and the amount of labor required to exhume all of its fine roots, only roots >1 cm in diameter were sampled. Although omitting fine roots of *C. velutinus* led to an underestimation of plant biomass, it was considered well under a detectable range of error for total biomass. Age of each shrub was also determined by counting annual rings in order to convert total N fixed to an average annual rate.

Quantification of BNF by *Purshia* and *C. prostratus* in Northeastern California Pine Stands

Nitrogen fixation by *Purshia* and *C. prostratus* was measured by the ¹⁵N-natural abundance method (Shearer and Kohl 1993) at Blacks Mountain Experimental Forest on the Lassen National Forest in northeastern California. The study area was part of a larger experiment, installed in the late 1930's through the early 1940's, designed to test the effect of harvest intensity on stand growth (Dolph and others 1995). Five levels of harvesting (100, 85, 50, 20, and 0 percent overstory removal) were compared in the original study. Two of these treatments were selected in the present study: 85 and 0 percent removal. Three replicate plots (8.2 ha) of each treatment were arranged in a randomized complete block design.

Blacks Mountain is located in the eastside pine type (Society of American Foresters forest cover type 237; Barrett and others 1980) and has an overstory dominated by mixed-age ponderosa pine and Jeffrey pine. Dominant understory plants include *C. prostratus*, *Purshia*, *Arctostaphylos*, *Artemesia tridentata*, and *Festuca idahoensis*. The climate is characterized by warm, dry summers and cold, wet winters, and the mean annual precipitation is about 50 cm. The soil is a loamy-skeletal, mixed, mesic Typic Argixeroll, about 1 m deep above basalt bedrock.

Foliage from five plants per species (*Purshia*, *C. prostratus*, *Arctostaphylos*) was collected at nine randomly selected subplots (0.05 ha) per treatment, for a total of 90 samples of each species. *Arctostaphylos patula* was chosen as the reference plant based on the results from the ^{15}N isotope dilution study. Plants were sampled in early November, and every attempt was made to sample species in proximity to each other in order to reduce potential variation in natural ^{15}N abundance. Nitrogen fixation was calculated by equations (1) and (2).

Predictive equations of plant biomass, based on canopy size, were developed in order to avoid destructive sampling. Fifty-four *C. prostratus* plants were measured for crown length and width (cm) and excavated for above- and below-ground dry weight determination. *Ceanothus prostratus* biomass (g plant^{-1}) was predicted by the equation ($r^2 = 0.89$):

$$\ln(\text{biomass}) = -5.3 + 2.54 (\ln [\text{mean crown length}]) \quad (3)$$

Purshia biomass was estimated by the ratio of mean crown length to biomass for 72 plants. Mean crown length (cm) of each shrub within the 0.05-ha subplots was measured, and total plant biomass per area was calculated using the predictive equations. The ages of 10 randomly selected shrubs per species were also determined to convert total N fixed to average annual N fixation.

Response of *Purshia* to Forest Management Practices

A logical progression after the measurement of BNF is to ascertain the effect of forest management practices on actinorhizal plant growth. To address this effect, results are presented from the “Black Bark” study in central Oregon. The study was designed to test the effect of several types of organic-residue treatments on ponderosa pine ecosystem processes. Sixteen treatments, arranged in 4 x 4 factorial treatment design, were replicated at three sites on the Deschutes National Forest, including the Swede Ridge site from the ^{15}N isotope dilution study (see Monleon and Cromack 1996 for location and stand characteristics of the other two sites). The treatments included four levels of organic matter removal after thinning: (1) whole tree removal; (2) bole removal only; (3) no removal; and (4) no thinning, in combination with four silvicultural treatments: prescribed fire; fertilization; prescribed fire + fertilization; and no treatment (control). Plots receiving prescribed fire were burned in spring 1991, and fertilizer (200 kg N ha^{-1} , $100 \text{ kg phosphorus [P] ha}^{-1}$, $33 \text{ kg sulfur [S] ha}^{-1}$) was applied in fall 1991.

A nondestructive sampling protocol was used to predict *Purshia* biomass. Fifty plants per site, encompassing a range of shrub sizes, were collected adjacent to the experimental plots and measured for mean crown length (cm) and biomass (g plant^{-1}). The resulting regression equation was:

$$\ln(\text{biomass}) = -161 + 0.115 (\ln [\text{mean crown length}]) \quad (4)$$

with $r^2 = 0.93$. Canopy size of each shrub within three 0.01-ha subplots was measured in every plot at the end of the third growing season after treatment, and biomass was estimated using the regression equation. Total N fixed was then calculated using values for Ndff and N concentration from the Swede Ridge site as determined in the ^{15}N isotope dilution study.

Results and Discussion

BNF by C. velutinus and Purshia in Central Oregon

Plant N derived from fixation averaged 87 percent for *C. velutinus* and 83 percent for *Purshia* at the combined sites in 1990. Differences in Ndff between sites were not significant for either species ($\alpha = 0.05$), indicating a high N-fixing efficiency regardless of the level of shrub coverage or stand age. The Ndff of the young pine stand at Mt. Jeff, with 59 percent *C. velutinus* coverage, was only nominally lower than the Ndff of Swede Ridge (80 vs. 91 percent, respectively), which is a dense pine stand with only 23 percent *C. velutinus* coverage. Results for *C. velutinus* and *Purshia* compare favorably with those for other actinorhizal species. Previous studies, although limited to actinorhizal trees, have reported Ndff values of 68 to 100 percent for *Alnus glutinosa* (Beaupied and others 1990, Cote and Camire 1984, Domenach and others 1989) and 48 to 67 percent for *Casuarina equisetifolia* (Gauthier and others 1985, Parrotta and others 1994). From a practical standpoint, the Ndff values indicate that N fixation is not a limiting process in the growth of these shrubs in central Oregon pine ecosystems and that little opportunity (or need) exists to improve their N-fixing efficiency. Development of selected *Frankia* inoculum for outplanting of nursery-grown stock, therefore, would likely have minimal or no impact on BNF and plant growth rates.

Percentage Ndff was plotted as a function of shrub age in order to determine the optimum plant age for *nitrogenase* activity (fig. 1). If a peak age (followed by a decline in activity) could be identified, it would provide forest managers with a target period in which to regenerate shrubs by low-intensity underburning or other silvicultural methods. *Ceanothus velutinus* had consistently high values of Ndff for plants between 8 to 22 years old. *Purshia* also failed to show a clear change in Ndff with increasing plant age from 8 to 45 years, yet had considerably more variation in Ndff compared to *C. velutinus*. This variation was possibly due to inconsistent nodulation attributed to *Purshia* (Dalton and Zobell 1977, Righetti and Munns 1982, Righetti and others 1986). Evidently, ability to fix N does not decline for either species with increasing age.

Total N fixed by *C. velutinus* was significantly different between sites ($\alpha = 0.05$), ranging from 83 to 246 kg ha⁻¹ (table 2). The highest level was found at Mt. Jeff, which has shrub coverage between 2- and 2.5-fold greater than the other sites. Annual N fixation followed the same trend: the rate increased as a function of *C. velutinus* coverage, from a low at Swede Ridge to its highest rate at Mt. Jeff. It is important to note, however, that the annual rate of 10 kg ha⁻¹ yr⁻¹ is a linear average for the life of the stand. The extent to which this overestimates the annual rate of a young *C. velutinus* stand and underestimates the annual rate of a stand at its peak age of growth is unclear and requires further attention. Youngberg and Wollum (1976) found *C. velutinus* plants well nodulated in the first growing season after wildfire and salvage logging in central Oregon. The maximum level of N accretion did not occur, however, until the seventh growing season after disturbance. Failure to account for

the loss of plant biomass from root mortality and leaf fall in the present study also resulted in an underestimation of annual N fixation. Production and turnover of fine root biomass can account for a large percentage of net primary productivity of conifer forests (Fogel 1990, Grier and others 1981, Ruess and others 1996), although limited information suggests that annual root production and turnover are less prolific for shrubs than for other vegetation lifeforms (Aerts and others 1992, Persson 1979). Leaf fall would not be expected to have a major impact on the estimation of N fixation because *C. velutinus* is an evergreen shrub that typically does not lose a large percentage of its foliage in central Oregon except during winters with low snowfall.

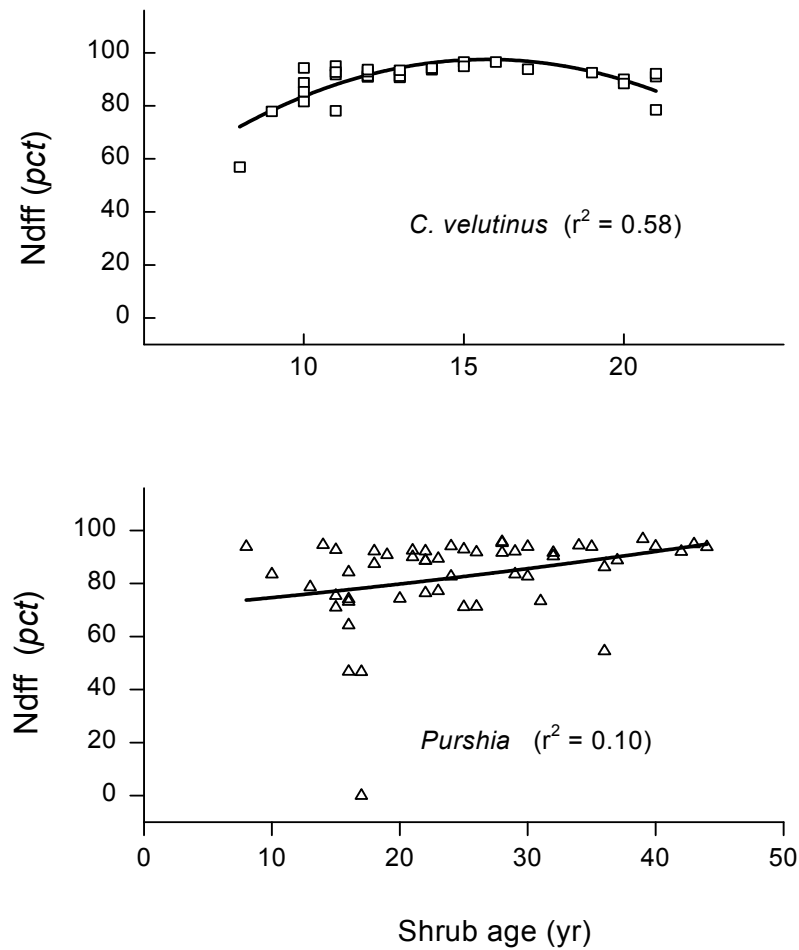


Figure 1—Percentage of plant N derived from N₂ fixation (Ndff) for shrubs of different ages.

Table 2—Nitrogen fixing characteristics of *C. velutinus* and *Purshia* at three ponderosa pine sites in central Oregon.

Site	Biomass ¹ Mg ha ⁻¹	Ndff ² pct	<i>C. velutinus</i>	
			Total N ₂ fixed ³ kg ha ⁻¹	Annual N ₂ fixed ⁴ kg ha ⁻¹ yr ⁻¹
Swede Ridge	7.8 (1.4) ⁵	91 (5)	83 (3)	4.0 (0.7)
Walker	11.8 (2.1)	90 (3)	165 (20)	11.1 (3.1)
Mt. Jeff	24.5 (2.8)	80 (7)	246 (26)	15.1 (1.8)
Average	14.7 (8.7)	87 (6)	165 (82)	10.1 (5.6)

Site	Biomass Mg ha ⁻¹	Ndff pct	<i>Purshia</i>	
			Total N ₂ fixed kg ha ⁻¹	Annual N ₂ fixed kg ha ⁻¹ yr ⁻¹
Swede Ridge	2.4 (0.6)	85 (12)	30 (4)	1.5 (0.4)
Walker	0.4 (0.4)	82 (10)	11 (5)	0.4 (0.3)
Mt. Jeff	---	---	---	---
Average	1.4 (1.4)	83 (2)	21 (14)	0.9 (0.8)

¹ Aboveground + belowground.

² Nitrogen derived from fixation.

³ Total N₂ fixed = (Biomass) x (Plant N concentration) x (Ndff).

⁴ Annual N₂ fixed = Σ total N fixed for each shrub within a plot, divided by its measured shrub age.

⁵ Values in parentheses are one standard deviation ($n = 4$).

The annual rate of N fixation was considerably lower for *Purshia* than for *C. velutinus* at Swede Ridge and Walker (table 2). The average rate of 1.1 kg ha⁻¹ yr⁻¹ is in general agreement with the conclusion of Dalton and Zobel (1977) that *Purshia* is a minor contributor to the total N economy in central Oregon pine stands. They estimated an annual rate of 0.057 kg ha⁻¹ yr⁻¹ at a ponderosa pine site in central Oregon, using the acetylene reduction method. The difference in annual rate between the two studies is not surprising given the differences in methods used and the inconsistent nodulation found in the earlier study. It should be emphasized that these findings are only relevant for *Purshia* in the understory of ponderosa pine, where low N fixation rates are most likely dictated by the slow growth rate of the shrub. This conclusion may not apply, however, throughout its entire range, particularly in nonforested lands where the faster growing, erect form of *Purshia* can be found.

Although the annual rates of N fixation for *C. velutinus* were as much as 18 times greater than those for *Purshia*, they were still substantially below the levels measured in the western Oregon Cascade Range (table 3). With one exception (Zavitkovski and Newton 1968), the previous studies have found up to 10-fold higher annual rates of N accretion in comparison with those in the present study. Several factors, including climatic differences, stand conditions, and methodology, can help

explain this discrepancy. For example, rainfall is considerably higher and temperature fluctuations less extreme west of the Cascade crest. The study site used by McNabb and Cromack (1983) received 250 cm of annual rainfall in comparison to an average of 60 cm for the three sites used in the present study. Growth rates and, consequently, BNF rates are higher in the wetter and milder climate west of the Cascade crest. Differences in stand conditions also contributed to the lower rate of BNF in central Oregon and are a reflection of the contrasting objectives of these studies. The earlier studies were conducted in *C. velutinus* shrub fields with the objective of predicting the maximum amount of N accretion on a disturbed site. By comparison, my objective was to measure the amount of N input by *C. velutinus* as a component of a ponderosa pine understory. Not only is plant coverage reduced from shading in the understory, but competition from overstory trees for limited site resources further reduces the potential for growth (Riegel and others 1992). Finally, caution must be used in comparing these studies because of the inconsistency of methods used to quantify N fixation. Correlation between acetylene reduction, N difference, and ^{15}N isotope dilution as measures of N fixation has never been made in forested ecosystems, and, therefore, their relative accuracy is unclear.

Table 3—Summary of N_2 fixation by *C. velutinus*.

Location	Stand condition	Cover	N_2 fixation		Source
			Annual rate	Method	
		pct	$\text{kg ha}^{-1} \text{ yr}^{-1}$		
Western Oregon	Shrub field	19-86	0-20	N accretion	Zavitkovski and Newton 1968
Cascade Range	Shrub field	58	108	N accretion	Youngberg and Wollum 1976
	Shrub field	Not available	94-100	N accretion	Binkley and others 1982
	Shrub field	≈ 100	101	Acetylene reduction	McNabb and Cromack 1983
Central Oregon	Shrub field	70	72	N accretion	Youngberg and Wollum 1976
	Pine understory	23-59	10	^{15}N isotope dilution	This study

The N-fixing potential of *C. velutinus* and *Purshia* in central Oregon was estimated for a range of shrub coverages (fig. 2.). Total N fixed was calculated by multiplying aboveground biomass values measured at known coverages (Martin 1981) by the N concentration and Ndff values from the present study. All biomass

values were corrected to include an estimate of belowground biomass as determined at the Swede Ridge site (belowground biomass = 45 percent of total biomass for *C. velutinus* and 19 percent of total biomass for *Purshia*). Based on these estimates, *C. velutinus* fixes about three times more N than *Purshia* at given canopy coverage. For example, BNF at 60 percent shrub coverage is 20 kg ha⁻¹ yr⁻¹ for *C. velutinus* and 7 kg ha⁻¹ yr⁻¹ for *Purshia* for a stand age of 15 years. It should be noted, however, that it is uncommon to find *Purshia* coverage as high as 60 percent in pine understories. Seldom will it exceed 40 percent, which is equivalent to approximately 4.5 kg N fixed ha⁻¹ yr⁻¹.

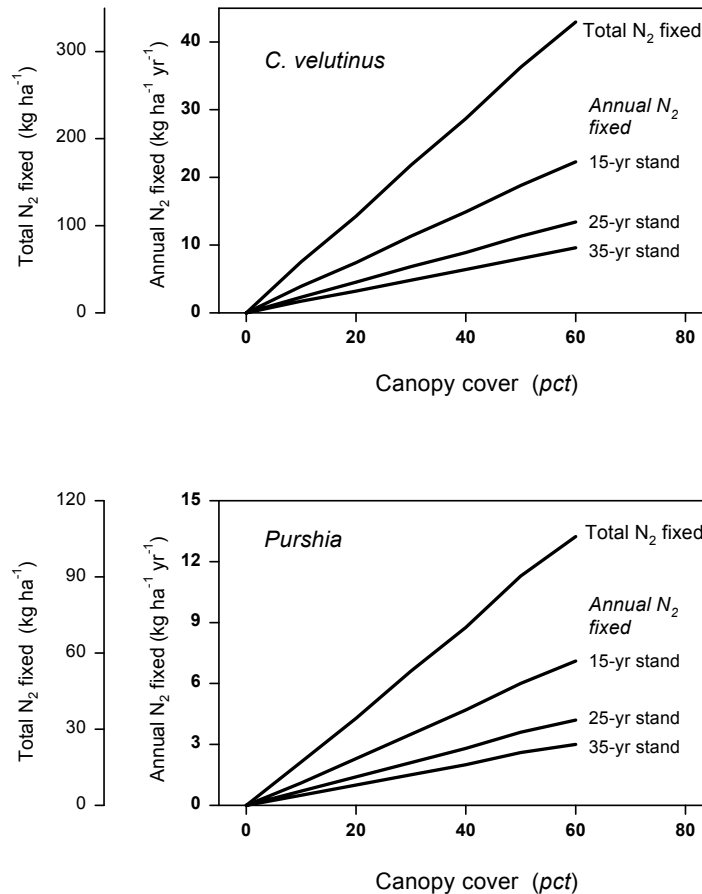


Figure 2—Nitrogen-fixing potential of *C. velutinus* and *Purshia* in the understory of central Oregon ponderosa pine stands.

BNF by *Purshia* and *C. prostratus* in Northeastern California

Preliminary results from the study at Blacks Mountain are presented in *table 4*. Shrub growth and N-fixing characteristics were compared after more than 50 years after harvesting (85 percent overstory removal) with an unharvested control. Neither species was capable of a long-term response to the more open conditions created by

harvesting. There were no significant effects of harvesting on shrub coverage, biomass, or N-fixing characteristics of either species ($\alpha = 0.05$). Average annual N fixation was well under $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for *Purshia* and *C. prostratus* in both harvested and control treatments.

Nitrogen fixation efficiency (Ndff) for *Purshia* was lower and more variable at Blacks Mountain than at central Oregon. Whether this is a reflection of site differences in infectivity and/or effectivity of indigenous *Frankia*, or, more simply, is due to differences in ^{15}N methodologies between the two studies is unknown. It is unlikely, however, that improving Ndff at Blacks Mountain by inoculating with selected *Frankia* strains would result in measurable increases in plant biomass due to the inherent slow growth of *Purshia* in pine understory.

Table 4—Nitrogen-fixing characteristics of *Purshia* and *C. prostratus* at Blacks Mountain Experimental Forest.¹

Species	Overstory treatment	Above + belowground					
		Cover	Biomass	Biomass N	Ndff ²	Total N ₂ fixed ³	Annual N ₂ fixed ⁴
		pct	kg ha ⁻¹	kg ha ⁻¹	pct	kg ha ⁻¹	kg ha ⁻¹ yr ⁻¹
<i>Purshia</i>	0 pct removal	8.4 (4.1) ⁵	856 (665)	6.2 (4.9)	63 (42)	5.3 (5.0)	0.3 (0.3)
	85 pct removal	6.8 (4.3)	724 (697)	5.3 (4.5)	36 (22)	2.1 (1.7)	0.1 (0.1)
	Average	7.6 (1.1)	790 (93)	5.8 (0.6)	50 (19)	3.7 (2.3)	0.2 (0.1)
<i>C. prostratus</i>	0 pct removal	13.3 (9.2)	1588 (1162)	11.9 (8.7)	83	9.9 (7.3)	0.6 (0.4)
	85 pct removal	14.4 (6.6)	1968 (953)	14.7 (7.1)	83	12.2 (5.9)	0.7 (0.3)
	Average	13.8 (0.8)	1778 (269)	13.3 (2.0)	83	11.1 (1.6)	0.7 (0.1)

¹ Results are preliminary.

² Nitrogen derived from fixation.

³ Total N₂ fixed = (Biomass N) x (Ndff).

⁴ Annual N₂ fixed = (Total N₂ fixed)/(mean shrub age).

⁵ Values in parentheses are one standard deviation ($n = 3$).

The natural abundance method appears ineffective at estimating Ndff for *C. prostratus* even though all plants sampled for biomass determination were well nodulated. This species had a much higher percentage of fine roots in the upper 20 cm of mineral soil than *Arctostaphylos* had, which conflicted with the assumption that both the N-fixing plant and reference plant have the same rooting profile and access to the same pool of available N in the soil profile. As a result, total and annual

N fixation were calculated with the Ndff value determined for *C. velutinus* in central Oregon (83 percent). Using this value, in effect a “best case scenario” of N fixation, still resulted in a rate of less than 1 kg ha⁻¹ yr⁻¹. Low biomass production, even at a relatively high coverage, appears to be the controlling factor limiting N input from *C. prostratus*.

Effects of Forest Management Practices

The response of *Purshia* to organic residue removal, prescribed fire, and fertilization was measured after three growing seasons on the “Black Bark” Study in central Oregon. Results are presented in *table 5* for the main factors (organic residue and silvicultural treatment) only, as there were no significant interactions ($\alpha = 0.05$) between factors. *Purshia* biomass and cover were unresponsive to the combination of treatments. The only exception was a significant decline in both biomass and cover ($\alpha = 0.05$) after prescribed fire. Of the four organic-residue treatments, thinning with minimal soil disturbance (thin, no removal) had the greatest biomass and cover. Fertilization with N, P, and S resulted in a slight, nonsignificant ($\alpha = 0.05$) decline in biomass and cover. The inability of *Purshia* to respond to fertilization is in direct contrast to the response of the herbaceous layer. Total herbaceous biomass increased an average of 500 percent during the first three growing seasons (data not shown).

Table 5—Effect of organic residue removal, fertilization, and prescribed fire after overstory thinning on *Purshia* growth characteristics and estimated N₂ fixation.

Treatment ¹	Above-ground biomass Mg ha ⁻¹	Cover pct	Estimated N ₂ fixation kg ha ⁻¹ yr ⁻¹	New seedlings no. ha ⁻¹
Organic residue				
Whole-tree removal	0.78a ¹	7.5a	0.7a	741a
Bole-only removal	0.60a	6.6a	0.7a	924a
Thinning, no removal	1.00a	10.2a	1.1a	745a
No thinning	0.60a	5.5a	0.6a	488a
Silvicultural practice				
Control (no treatment)	1.60a	16.1a	1.6a	341b
Fertilize	1.21a	12.3a	1.2a	225b
Burn	0.10b	1.1b	0.1b	1328a
Burn + fertilize	0.05b	0.4b	0.2b	1004a

¹ For organic residue or silvicultural practice, means within a column followed by the same letter are not significantly different at the 0.05 level.

Annual N fixation was estimated using N concentrations and Ndff values determined previously at the Swede Ridge site. Prescribed fire was the only treatment that had a significant effect ($\alpha = 0.05$) on N fixation. The decline after burning was

nominal, however, considering the low average annual N fixation rate of $0.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for all treatments. No effects due to organic residue removal or fertilization were found. The inability of *Purshia* to respond to any of the treatments, in conjunction with its overall low N fixation rate, raises doubt as to the potential for using management options to improve the biomass production or N fixation rate of *Purshia*.

Purshia is generally known for its intolerance to fire (Driscoll 1963, Horsay 1943). Simon (1990) found greater resprouting after spring burning when the fire intensity was limited by high moisture content in the O horizon and recommended using a mosaic pattern of burning to maintain a viable population of *Purshia*. In the present study, only 11 percent (274 out of 2,496 plants) of the shrubs resprouted. Seed germination, by comparison, responded more favorably to prescribed fire; seedling number was significantly greater ($\alpha = 0.05$) on burned plots than on unburned plots (table 5). Continued monitoring of seedling survival is required to determine whether *Purshia* biomass and N fixation will eventually benefit from a single-entry prescribed burn.

Ecological Significance of N Fixation by Actinorhizal Shrubs

The rates of N fixation by *Ceanothus* and *Purshia* in central Oregon and northeastern California are low, especially when compared with other ecosystems or other actinorhizal species. The amount of N input, which reached a maximum of $15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for *C. velutinus*, should not come as a surprise, however, considering the adverse climate and fierce competition for moisture, nutrients, and light in ponderosa pine stands (Riegel and others 1992). Whether this observation diminishes the importance of these species as N fixers depends on the criteria used to assess ecosystem needs. Replenishing N lost during low-intensity prescribed fires, for example, can easily be met by the N fixation rate of *C. velutinus* (table 6). Coverage between 5 and 23 percent is sufficient to replace volatilized N for a fire-return interval of 15 years.

A similar approach can be used to estimate the level of N input required to balance expected N losses from overstory harvesting. An estimated 189 kg N ha^{-1} are sequestered in 45-year-old stands of ponderosa pine in central Oregon (Little and Shainski 1995). Assuming that stands are harvested at 90 years and average N uptake between years 45 and 90 is double the rate of that during the first 45 years, then only $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ are needed to replace the harvested N. This rate can be supplied by a low to moderate coverage of *C. velutinus*. It is unlikely that N fixation by *Purshia* would be sufficient to replace N losses from either harvesting or prescribed fire; the canopy coverage requirements would be uncharacteristically high for *Purshia* in pine understories and would present an unwanted risk of potential wildfire damage.

Shrubs are often viewed as unwelcome competitors for site resources, and their role as a fuel ladder, increasing the potential damage from wildfire, is an added concern. Should *Purshia*, *C. velutinus*, and *C. prostratus* then be managed for their role as N fixers? Or, are the costs too high? The relatively low rate of N fixation by *Purshia* and *C. prostratus* would indicate, at first glance, little benefit to pine forests of central Oregon and northeastern California. These ecosystems acquire limited exogenous inputs of N, however. Estimates of N input from dry deposition are about $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Dalton and Zobel 1977). Consequently, about 50 percent of the annual N addition in these ecosystems is derived from N fixation by *Purshia* and *C.*

prostratus. Potential benefits to ecosystem N levels from managing *C. velutinus* are even more tangible. Nitrogen-fixation rates for *C. velutinus* found in this study are sufficient to replace ecosystem N losses due to periodic disturbance. Developing a balance, therefore, between the concerns of wildlife habitat, overstory competition, potential fire danger, and N fixation should be considered in the management of these species.

Table 6—Nitrogen fixation and canopy coverage requirements by actinorhizal shrubs to replace N lost from periodic disturbances.¹

Disturbance	Estimated N removed ²	N ₂ fixation required for N replacement ³	Shrub coverage required to replace N	
			<i>C. velutinus</i>	<i>Purshia</i>
	kg ha ⁻¹	kg ha ⁻¹ yr ⁻¹	————— pct —————	
Low-intensity prescribed fire	50-150	2-9	5-23	20-80
Overstory harvest	570	5	16	42

¹Coverage requirements were determined from figure 2 for a 15-yr-old shrub stand.

²Values for low-intensity prescribed fire from Simon (1990), Landsberg (1993), Monleon and Cromack (1996). Value for overstory harvest from Little and Shainski (1995).

³Assumes a 15-yr fire-return interval, a 90-yr rotation age for harvesting, and 1 kg ha⁻¹ yr⁻¹ supplied by atmospheric deposition.

It is well established that competition by shrubs for water, nutrients, and light can limit conifer growth in plantations (Conard and Radosevich 1982, Conard and Sparks 1993, Lanini and Radosevich 1986, McDonald and Fiddler 1993). Conventional wisdom suggests that control of understory shrubs is required to meet the objective of optimizing tree growth. The effects of shrub competition, however, can vary with site quality. Powers and Ferrell (1996) found that dry, nutrient-poor sites had the greatest reduction in ponderosa pine seedling growth due to competing shrubs, whereas sites with adequate rainfall and nutrient resources showed little inhibition in seedling growth. Furthermore, whether the competitive advantage provided by eliminating shrubs in young plantations lasts throughout an entire rotation is not clear. Oliver (1990) found that ponderosa pine growth was reduced by shrub competition for the initial 20 years after planting. Barrett (1982) found similar results at 20 years for naturally regenerated pine stands in central Oregon dominated by *C. velutinus*, *Purshia*, and *Arctostaphylos*. After 35 years, however, trees free of shrub competition were larger but had similar growth rates as trees grown with shrub competition (Busse and others 1996). In addition, indices of soil quality (total C, N, and microbial biomass) had increased after 35 years in the presence of shrubs. Long-term improvement of soil quality by actinorhizal shrubs (Binkley and others 1982, Busse and others 1996, Johnson 1995) could counterbalance the reductions in initial tree growth resulting from competition for site resources.

Conclusions

A series of studies were presented which evaluated BNF by actinorhizal shrubs in the understory of ponderosa pine forests. Results showed that *Purshia* and *C.*

velutinus are efficient N fixers, providing the majority of N required for their biomass production. Nevertheless, their annual N fixation rates are comparatively low, apparently controlled by the slow growth of shrubs in these moisture-limited forests. Only in the case of *C. velutinus*, which fixed an average of 10 kg ha⁻¹ yr⁻¹, was N fixation considered sufficient to offset N losses from perturbation. Maintaining low to moderate coverage of *C. velutinus* (between 5 and 23 percent) is adequate to replace N lost during prescribed fire or harvesting. These results contrast with previous studies from *C. velutinus* shrub fields in the western Oregon Cascades which showed N accretion rates of about 100 kg ha⁻¹ yr⁻¹. This discrepancy can be attributed to differences in climatic regime, stand conditions, and methods. The rate of N fixation in both *Purshia* and *C. prostratus* averaged 1 kg ha⁻¹ yr⁻¹ or less.

Actinorhizal plants serve numerous functions in forest ecosystems. They are valued for wildlife browse and habitat, erosion control, improvement of soil quality, and N fixation. They also compete for site resources and contribute to fuel loading and potential wildfire danger. Future work is needed to identify an appropriate balance between these factors in the management of understory shrubs.

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