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Species effects of *Ceanothus velutinus* versus *Pseudotsuga menziesii*, Douglas-fir, on soil phosphorus and nitrogen properties in the Oregon cascades

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Abstract

Many authors have hypothesized that nitrogen-fixing species, as a functional group, would express different controls on soil properties and ecosystem development than non-nitrogen-fixing species. Although nitrogen (N) accretion under nitrogen-fixing tree species has been well studied, the effect of nitrogen-fixing species on other soil nutrients, such as phosphorus (P), has received less attention. We studied differences in soil phosphorus and nitrogen properties beneath *Ceanothus velutinus* (Ceanothus), a nitrogen-fixing species, and *Psuedotsuga menziesii* (Douglas-fir), a non-fixing species, in a high elevation successional watershed in the H.J. Andrews Experimental Forest in Oregon. Total P was 20% greater in Douglas-fir soils than Ceanothus soils in surface horizons, but there was no significant difference in deeper soil horizons. Surface soils (5 and 15 cm) under Douglas-fir generally had higher concentrations of specific P fractions than surface soils under Ceanothus, but this difference either disappeared or was not as apparent at greater soil depths (30 and 60 cm). Total nitrogen, and extractable ammonium and nitrate were greater in surface soils under Ceanothus than under Douglas-fir. δ^{15}N values of leaves and litter differed between Ceanothus and Douglas-fir (p-value = 0.0001 and 0.03, respectively), but the δ^{15}N of bulk soil and KCl extracted nitrate and ammonium did not differ. Soil enzyme activities suggested greater mineralization of organic P (phosphatase activity) under Ceanothus in summer, but not in fall, while no significant differences in general decomposition (β-glucosidase activity) were found in soils between the two species.

Keywords: Phosphorus fractions; Nitrogen-fixation; Soil enzymes; δ^{15}N natural abundance; Ceanothus; Douglas-fir

1. Introduction

Tree species can influence the size and distribution of nutrient pools across soil horizons, and soils often differ under different types of vegetation (Binkley, 1994; Van Breemen and Finzi, 1994;Berendse, 1998). Trees may affect soils through soil solution uptake, root production and turnover, mycorrhizal activity, organic compound exudation, and the quantity and quality of litter produced for decomposition (Angers and Caron, 1998). Tree species might also differ in their influence on soil biologic activity, such as the presence of mycorrhizae or the composition of microbial communities, that in turn may affect soil chemistry

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(Binkley, 1994; Saetre et al., 1999). Furthermore, some plants have the ability to modify the rhizosphere to access previously unavailable nutrients, such as phosphorus (P) (Ae et al., 1990; Ae and Otani, 1997; Jones, 1998).

Many authors have hypothesized that nitrogen-fixing species, as a functional group, would express different controls on soil properties and ecosystem development than non-nitrogen-fixing species (Van Breemen and Finzi, 1998). Nitrogen (N) accretion from symbiotic nitrogen fixation in early successional ecosystems can range up to 160 kg ha^{-1} per year (Boring et al., 1988). Indeed, many authors have found that nitrogen-fixing species can significantly increase soil N levels; e.g. *Alnus rubra* Bong., red alder, can accrete up to 130 kg N ha^{-1} per year (Binkley, 1992), while Ceanothus spp. can accrete up to 101 kg N ha^{-1} per year (Youngberg and Wollum, 1976; Binkley, 1982; Conard et al., 1985; McNabb and Cromack, 1983). In contrast, Walker (1993) found no correlation between the presence of nitrogen-fixing species and total N accumulation in surface soil in a review of primary succession studies. Cromack et al. (1999) found no correlation between red alder basal area and the amount of soil N in a coastal Oregon Douglas-fir plantation.

Besides N accretion and N-related properties, nitrogen-fixing plants may affect other soil properties including soil pH (Binkley and Sollins, 1990), enzyme activity (Giardina et al., 1995; Zou et al., 1995), carbon accumulation (Cole et al., 1995), soil phosphorus fractions and P cycling (Giardina et al., 1995; Compton and Cole, 1998; Binkley et al., 2000). Nitrogen-fixing species have high P requirements, which are essential for the high levels required during N-fixation (Griffith, 1978; Spent, 1988; Gressel et al., 1996), and therefore lower available soil P concentrations may result under nitrogen-fixing species than under non-fixing species. This high requirement for P, in effect, closely links the N and P cycles in soils (Cole and Heil, 1981). Due to this greater P demand, terrestrial nitrogen-fixing species are believed to cycle P at faster rates than non-fixing species. However, a consistent pattern of nitrogen-fixing species increasing or decreasing available soil P has not been established.

Differences in soil P supply may result from biological or geochemical processes at different depths (Lajtha and Schlesinger, 1988; Frossard et al., 1995). In surface soils, mycorrhizal symbionts and other microorganisms closely couple decomposition and uptake processes, thus contributing to surface soil P retention. Biological controls on P availability include root growth patterns, amounts and quality of detrital inputs, extracellular enzyme activity, production of organic chelates, and mycorrhizal activity (Binkley, 1992; Zou et al., 1995). In lower soil horizons, decreased root and microorganism density may lower the potential for biological interception of soil solution P (Wood et al., 1984). However, lower soil horizons, such as the B horizon, may have increased geochemical buffers which regulate soil solution P at low levels. Aluminum and iron hydroxides tightly control P retention by fixation, and thus very little P is lost to deeper horizons by leaching. Additional geochemical controls on P availability include surface adsorption–desorption on organic matter, soil acidification (Binkley and Sollins, 1990; Frossard et al., 1995), and dissolution and precipitation of minerals (Gobran et al., 1998).

Although nitrogen-fixing species may influence the biological and geochemical soil P controls differently than non-fixing species, few studies have looked at species effects on soil biological or geochemical P sinks (Compton and Cole, 1998). Nitrogen-fixing species have been shown to increase soil acidity in some studies, which may increase the lability of soil P. Recent studies on red alder have shown that the process of nitrogen-fixation can acidify soil (Binkley and Sollins, 1990), decrease soil P and base cation content, and increase soil organic matter (Cole et al., 1995). Decreasing soil pH converts primary phosphate minerals into secondary Fe and Al-phosphate minerals (Lajtha and Schlesinger, 1988), while maximum P availability occurs at intermediate pH values. Yet in Nevada, Johnson (1995) found that the nitrogen-fixing species Ceanothus did not acidify soil, decrease base-saturation or lower extractable P. Although *Ceanothus velutinus* is the primary nitrogen fixer in the higher elevation xeric sites in the PACIFIC NORTHWEST (PNW), few studies have looked at the effect of this species on available soil P.

Nitrogen-fixing species may not only affect the total amount and availability of N, but may also affect the isotopic composition of soil N. The mean $\delta^{15}N$ of nitrogen-fixing species' foliage has been shown to be

significantly lower than the mean of non-fixing species, who derive their N from the soil (Kohl and Shearer, 1980; Vitousek et al., 1989). Isotopic signals from nitrogen-fixing plants reflect the atmospheric ^{15}N abundance, while leaves from plants that rely on soil N are more enriched in ^{15}N (Shearer et al., 1980; Lajtha and Marshall, 1994; Handley and Scrimgeour, 1997; Högberg, 1997).

It has been hypothesized that the $\delta^{15}N$ signal from a nitrogen-fixing species could be used to trace atmospherically derived N through soil N pools beginning with leaf litter. In an experiment to test this hypothesis, Binkley et al. (1985) concluded that ^{15}N isotopes are not a simple method of tracing alder fixed-N in the soil. Yet his study was at the stand-level scale and the $\delta^{15}N$ values varied inconsistently from stand to stand. Lajtha and Schlesinger (1986) suggested that, although the $\delta^{15}N$ value of the desert shrub *Prosopis* is unique, the values could be lost upon entering the general soil pool. However, as Lajtha and Schlesinger (1986) concluded, the distance from a nitrogen-fixing tree or shrub may influence the $\delta^{15}N$ of the soil.

Most previous studies examining the effects of nitrogen-fixers on soil biogeochemistry have been at the stand level, e.g. comparing the difference between a conifer stand, a pure nitrogen-fixer stand, or a mixed stand. However, such studies may be inherently problematic: there may be differences in stocking density, site characteristics, or soils among stands that make these results difficult to interpret (Compton and Cole, 1998). Indeed, Kohl et al. (1981) have shown that there is a large site-to-site variation in $\delta^{15}N$ values, and to date, no ^{15}N studies have been conducted on nitrogen-fixing trees at the single tree scale to test the above hypothesis.

The overall objective of this study was to determine if *C. velutinus*, as a nitrogen-fixing species, has different effects on soil nutrient availability than a non-fixing species, Douglas-fir. This study was conducted within a single stand to reduce variation in abiotic factors, and possible inter-stand variation. Specific objectives were to characterize soil P, and to examine relationships between species for soil P, N, and soil phosphatase and β-glucosidase activities. We hypothesized that the nitrogen-fixing species, Ceanothus, would decrease soil P concentrations due to the increased demand for P by nitrogen-fixation and therefore soils beneath Ceanothus would have lower labile P concentrations than Douglas-fir. This difference would be evident in surface soils where biological mechanisms control P, but not at depth where geochemical mechanisms would dominate.

We further hypothesized that there should be an enriched Ceanothus $\delta^{15}N$ isotopic signal that could be used to distinguish nitrogen fixation-N from soil N, and that this difference would be evident in the surface soil N pools. We hypothesized that the pH of the soils would be lower under the Ceanothus due to nitrogen fixation. We also hypothesized that phosphatase activity would be greater under Ceanothus, because Ceanothus may have an increased need for organic forms of soil P. Enzymes catalyze the rate limiting steps of nutrient cycling and often begin the transformation of organic forms of nutrients into available inorganic forms; and therefore phosphatase activity can be used as an indicator of P availability in soils. We also hypothesized that β-glucosidase enzyme activity would also be greater under Ceanothus than Douglas-fir, because decomposition of N-rich Ceanothus litter may be faster than N-poor Douglas-fir litter.

2. Methods and materials

2.1. Site description

The study site is located in Watersheds 6 and 7 at the H.J. Andrews Experimental Forest in the Cascade Mountains of western Oregon. Although delineated as two watersheds, the site is one contiguous stand of Douglas-fir and Ceanothus. Soils are frigid Andic Dystrudepts, derived from volcanic ash and pumice, deep, and well-drained with a 35% southern slope. The climate is quasi-Mediterranean with cool, wet winters and warm, dry summers. Precipitation averages 2500 mm per year, and mean January and July temperatures are 2 and 11°C, respectively. The stand was clear-cut and burned under low intensity in 1974, and planted with Douglas-fir in 1975 and 1976. Ceanothus germinated from the soil seed bank after fire (Binkley et al., 1982) and are now beginning to be overtopped by the Douglas-fir canopy.

2.2. Field sampling

Field sampling consisted of randomly placed transects from the road into the stand. Soil pits were dug

under 12 Ceanothus and 12 Douglas-fir trees on the transects, which were selected based on the criteria that the litter beneath the tree was specific to that species and did not overlap with the opposite species. Soil was collected at four discrete depths (5, 15, 30 and 60 cm) for P fractionation in August 1996. Samples for enzyme analysis and N analysis were collected from 0 to 5 cm beneath 10 Ceanothus and 10 Douglas-fir in August 1998, and at two depths (5 and 15 cm) in November 1998.

2.2.1. Chemical analysis

Soil samples were analyzed for phosphorus using a modified Hedley fractionation, which separates P into fractions based on their biological availability (Hedley et al., 1982; Tiessen et al., 1983; Lajtha and Schlesinger, 1988). Labile phosphorus in soil solution was removed using an anion exchange resin. Adsorbed labile P was extracted with a 0.5 M sodium bicarbonate solution. Amorphous, crystalline aluminum and iron phosphate P was extracted with NaOH. This fraction can also contain organic phosphorus associated with humic and fulvic acids, and is therefore separated into organic and inorganic fractions. The NaOH P_o fraction was calculated by subtracting NaOH P_i from total NaOH P after digestion. Insoluble calcium bound phosphorus was extracted with HCl. Residual P was analyzed by H_2SO_4–H_2O_2 digestion (Lowther, 1980), or by $LiBO_4$ fusion (Thompson and Walsh, 1983). Total soil P was measured on 16 replicate samples by fusion to compare with the sum of the Hedley fractions. All samples were analyzed on an Orion Scientific AC 100 Autoanalyzer using the ascorbic acid method for *ortho*-P (Lennox, 1979).

Soil enzyme assays were adopted from Caldwell et al. (1999) using 5 g (surface) soil slurried with 25 ml deionized water. Phosphatase assays were incubated for 1 h and β-glucosidase assays for 3 h. Results were calculated as umol *p*-nitrophenol released per gram dry weight per hour.

Surface mineral soils collected in summer and fall of 1998 were analyzed for total nitrogen after H_2SO_4–H_2O_2 digestion (Lowther, 1980), and for NO_3^--N and NH_4^+-N after 1 M KCl extraction.

Soil, litter, and leaves from Ceanothus and Douglas-fir were sent to the Boston University Stable Isotope Lab for analysis of $\delta^{15}N$. Additional soil samples were extracted in 2 M KCl and analyzed for $\delta^{15}N$ as NO_3^--N and NH_4^+-N (Sorenson and Jensen, 1991; Stark and Hart, 1996; Sigman et al., 1997).

Soil pH was analyzed in 0.01 M $CaCl_2$ (McLean, 1982). Soil organic matter was estimated by loss on ignition (Lim and Jackson, 1982).

2.2.2. Statistical analysis

All statistical analyses of data were performed using SAS (SAS Institute, Cary, NC, 1996). A Student's *t*-test was used to compare the differences in soil pH, NO_3^-, NH_4^+, phosphatase activity, β-glucosidase activity, and $\delta^{15}N$ isotope values between Ceanothus and Douglas-fir soils. Although correlation exists between depths, examining the data at each depth individually still results in a valid test. Therefore, P fractions were also analyzed by *t*-tests. All hypotheses were tested at $\alpha = 0.05$.

3. Results

The sum of the Hedley P fractions and total P by the fusion method were highly correlated ($R^2 = 0.91$) suggesting that sample extraction efficiency and accuracy remained relatively constant between the two techniques. Total P was highest in the surface soils and decreased with depth ranging from 518 to 1961 μg P g^{-1} in soils under Ceanothus, and from 622 to 3308 μg P g^{-1} in soils under Douglas-fir. Total soil P was 22% greater in Douglas-fir soils at 5 cm ($p = 0.05$) and 26% greater at 15 cm ($p = 0.04$). Although there were no significant differences in total P between the two species deeper in the soil profile, the mean soil concentration of total P under Douglas-fir was higher than Ceanothus at 30 and 60 cm (Fig. 1a–h).

In general, each phosphorus fraction was higher for Douglas-fir soils than for Ceanothus soils, while the mean concentration of the P fractions generally decreased with depth for both species. Resin P was significantly lower in Ceanothus soils than Douglas-fir soils at 5 cm ($p = 0.006$), and marginally lower at 15 cm ($p = 0.07$) and 60 cm ($p = 0.07$). There were no significant differences between Ceanothus soils and Douglas-fir soils at 30 cm ($p = 0.16$).

Bicarbonate P was lower in Ceanothus soils than Douglas-fir soils at 5 cm ($p = 0.07$), but was more

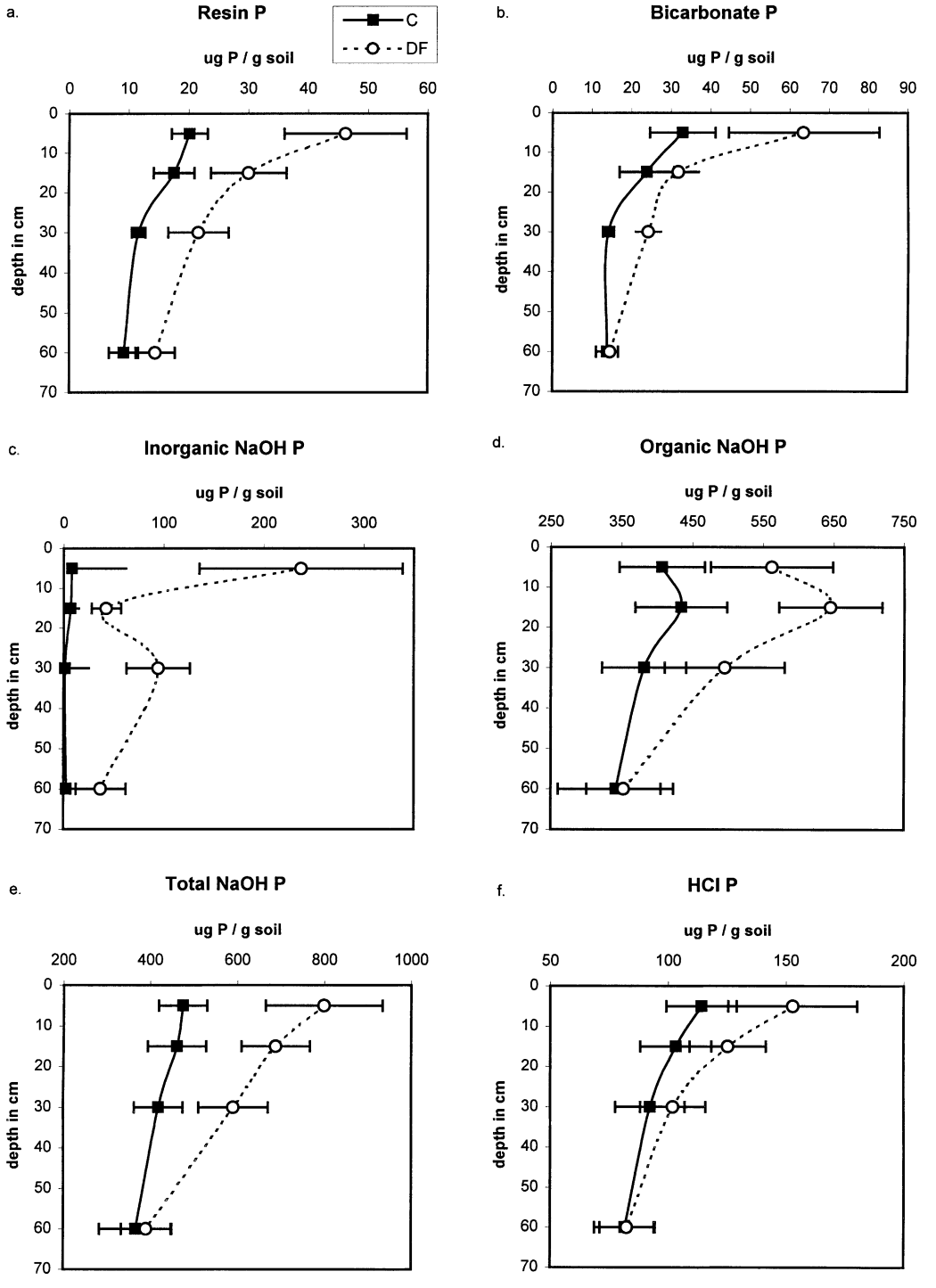

Fig. 1. Mean soil phosphorus concentrations in ug P g^{-1} air-dry soil from four depths under Douglas-fir and Ceanothus ($n = 12$) for each Hedley fraction (a–g) and total P (h).

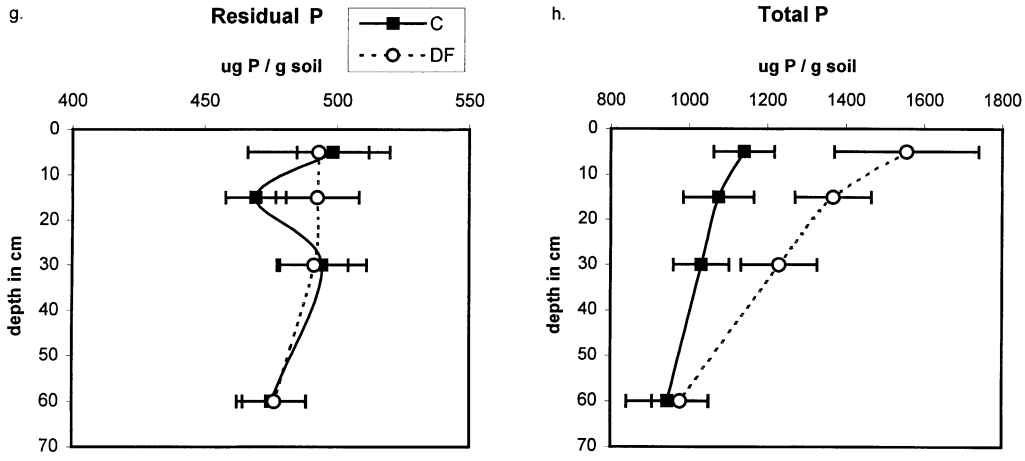

Fig. 1. (*Continued*)

clearly lower at 30 cm ($p = 0.02$). There were no significant species differences at 15 cm ($p = 0.16$) and 60 cm ($p = 0.22$).

NaOH P_i was significantly greater in soil under Douglas-fir than soil under Ceanothus at 5 cm ($p = 0.045$) and marginally greater at 30 cm ($p = 0.08$). There was no difference between species at 60 cm ($p = 0.71$). NaOH P_o was significantly greater for Douglas-fir than for Ceanothus only at 15 cm depth ($p = 0.04$).

Total NaOH P was significantly higher under Douglas-fir than Ceanothus at 5 cm ($p = 0.04$) and at 15 cm ($p = 0.04$), marginally higher at 30 cm ($p = 0.09$), and not significantly different between the two species at 60 cm ($p = 0.81$). Residual and HCl P fractions were not significantly different between Ceanothus and Douglas-fir soils at any depth, although the trend of more P under Douglas-fir remained constant.

Phosphatase activity was marginally greater in soils under Ceanothus ($p = 0.09$) (Table 1). There were no differences in phosphatase activity between Ceanothus and Douglas-fir soils in fall ($p = 0.8862$). No difference was found in β-glucosidase activity for either summer or fall ($p = 0.16$ and 0.44, respectively). There were no significant pH differences between soils for these species.

Total N was greater in soil under Ceanothus, 2.60 mg g^{-1}, than in soil under Douglas-fir, 1.99 mg g^{-1} ($p = 0.0283$). Ceanothus litter was higher in total N, 17.94 mg g^{-1}, than Douglas-fir litter, 5.34 mg g^{-1} ($p = 0.0001$). Extractable NO_3^--N was significantly greater under Ceanothus soils in the summer ($p = 0.0355$) although extractable NH_4^+-N

Table 1
Mean β-glucosidase and phosphatase enzyme activity in μmol g^{-1} soil ($n = 10$)[a]

	Ceanothus (umol g^{-1} h^{-1})	Douglas-fir (umol g^{-1} h^{-1})	*p*-value
Summer 1998			
Phosphatase	14.47 (2.60)	8.89 (1.75)	0.09
β-Glucosidase	5.29 (0.69)	3.93 (0.64)	0.17
Organic matter	0.40 (0.03)	0.42 (0.05)	0.69
Fall 1998			
Phosphatase	15.37 (3.32)	15.90 (1.61)	0.89
β-Glucosidase	4.03 (0.45)	3.59 (0.36)	0.44

[a] S.E. are given in parentheses. *p*-values are from a *t*-test for a difference between species.

Table 2
Mean NO_3^--N and NH_4^+-N concentrations in KCl extracts for Ceanothus and Douglas-fir soils ($n = 10$)[a]

	Depth (cm)	Ceanothus (mg N g^{-1} soil)	Douglas-fir (mg N g^{-1} soil)	p-value
Summer 1998				
NO_3^--N	5	1.59 (0.13)	1.22 (0.10)	0.04
NH_4^+-N	5	22.70 (3.44)	15.53 (1.38)	0.08
Fall 1998				
NO_3^--N	5	5.72 (0.54)	5.24 (0.57)	0.55
NH_4^+-N	5	8.04 (1.13)	4.18 (0.88)	0.01
NO_3^--N	15	5.60 (0.39)	3.92 (0.56)	0.02
NH_4^+-N	15	2.99 (0.38)	1.74 (0.80)	0.02

[a] S.E. are given in parentheses. p-values are from a t-test for a difference between species.

Table 3
Mean delta ^{15}N values for Ceanothus and Douglas-fir leaves, litter and soil ($n = 10$)[a]

	Ceanothus	Douglas-fir	p-value
Leaf ^{15}N	−0.327 (0.05)	−4.17 (0.22)	0.0001
Litter ^{15}N	−0.86 (0.17)	−1.57 (0.24)	0.03
Soil ^{15}N	3.845 (0.68)	3.915 (0.36)	0.93
NH_4^+ ^{15}N in KCl extract	4.7 (0.44)	6.31 (0.56)	0.04
NO_3^- ^{15}N in KCl extract	−2.212 (0.76)	−0.168 (0.40)	0.03

[a] S.E. are given in parentheses. p-values are from a t-test for a difference between species.

was only marginally greater under Ceanothus ($p = 0.08$) (Table 2). NH_4^+-N was significantly greater in soil under Ceanothus in the fall ($p = 0.015$), although there was no species difference for NO_3^--N ($p = 0.55$). There was a significant seasonal difference for NO_3^--N ($p = 0.0001$) and for NH_4^+-N ($p = 0.0001$) in soils. For both species' soils, NO_3^--N was lower in the summer than in the fall, while NH_4^+-N was lower in the fall than in the summer.

Although the $\delta^{15}N$ of Ceanothus leaves (−0.327) and litter (−0.86) were significantly higher than Douglas-fir needles (−4.17, $p < 0.0001$) and litter (−1.57, $p = 0.025$), total soil $\delta^{15}N$ did not differ between species ($p = 0.92$) (Table 3). KCl-extracted $\delta^{15}N$ of NH_4^+-N values were significantly lower for the Ceanothus soil than for the Douglas-fir soil ($p = 0.04$). The $\delta^{15}N$ of KCl-extracted NO_3^--N was significantly lower in Ceanothus soils than in Douglas-fir soils ($p = 0.0325$). No correlation was found between extractable levels of NH_4^+ or NO_3^- and $\delta^{15}N$.

4. Discussion

4.1. Soil P

Wood et al., 1984 suggested that biological activity controls the retention of P in surface soils, while geochemical activity controls the retention of P in lower soil horizons. Our results are consistent with Wood's hypothesis. We found no significant differences between species for residual or HCl P fractions at any depths, suggesting that these fractions are under geochemical rather than biological control. We found significant differences between species for total P, resin P, and bicarbonate P at shallow soil depths, but not in lower soil horizons, which suggests that biological activity is more prevalent in the surface soil horizons and that Ceanothus may affect soil differently than Douglas-fir.

The differences in soil P fraction concentrations between species may be influenced by soil biological activity. Microbial activity may increase soil weathering and thus play a role in P availability. Dissolution

of inorganic phosphates by organic acids or H^+ may stimulate weathering of adjacent minerals (Banfield et al., 1999). Several aliphatic acids such as oxalate and citrate are very effective in the dissolution of P-containing minerals, as well as in the mobilization of P held in humic-metal complexes (Frossard et al., 1995; Jones, 1998). Mycorrhizal fungi can secrete organic acids, which may dissolve insoluble P minerals or they may secrete phosphatases which hydrolyze P_o (Cromack et al., 1979; Frossard et al., 1995). Oxalic acid has been shown to react with Al and Fe in andesite, increasing soil weathering under Douglas-fir (Cromack et al., 1979). These reactions may have caused the distinct decrease in NaOH P_i in the rhizosphere under Douglas-fir (Fig. 1c). However, desorption and release of P by organic acids is soil dependent, and generally requires high concentrations of organic acids (Jones, 1998).

Because soil enzyme activities are sensitive to changes in soil properties, assays of microbial enzymes can be used as general measures of heterotrophic microbial activity (Sinsabaugh, 1994) and more specifically, as measures of nutrient cycling in the ecosystem (Bergstrom et al., 1998). We found marginally significant differences between Ceanothus and Douglas-fir for phosphatase activity, but not for β-glucosidase activity. Our results agree with Zou et al. (1995), who did find an increase in phosphatase activity in soils under both nitrogen-fixing alders in Oregon and *Albizia falcataria* in Hawaii, but concluded that the nitrogen-fixing species, *A. falcataria*, had little effect on soil P transformation rates. Giardina et al. (1995) found phosphatase activity to be three times greater in an alder-Douglas-fir stand than a pure Douglas-fir stand, and they suggested that the alder-Douglas-fir stand's higher enzyme activity may help to meet alder's high requirement for P. However, Giardina et al. (1995) also concluded that the correlation between resin P and phosphatase may be due to soil differences between stand types. Indeed, McGill and Cole (1981) found an inverse relationship between phosphatase activity and labile inorganic P. They concluded that the lack of consistent relationships between available P and phosphatase activity is perhaps due to the complexity of organic P polymers; additional enzymes may be needed to depolymerize the P_o before it is available for phosphatase.

Compton and Cole (1998) hypothesized that lower soil pH under nitrogen-fixing alder would increase the anion sorption capacity of the soil and therefore, more P_i would be adsorbed to Fe and Al hydrous oxides. Instead, they found that NaOH P_o was the largest pool under red alder and NaOH P_i was the largest pool under Douglas-fir. Our study found that for both species, NaOH P_o increased from 5 to 15 cm but then declined with increasing depth, while NaOH P_i decreased from depth 5 to 15 cm. The decrease in NaOH P_i is indicative of root uptake; the increase in NaOH P_o is not as easily explained, but might be indicative of root exudation or high microbial activity and/or microbe and root turnover.

Although both Douglas-fir and Ceanothus have mycorrhizal symbionts, one mycorrhizae may be more effective than another at finding and absorbing P in soil. Douglas-fir are known to have ectomycorrhizae, whereas Ceanothus have arbuscular mycorrhizae. Arbuscular mycorrhizae are not as effective as ectomycorrhizae in aggregate penetration (Cromack, personal communication). Although the Douglas-fir symbiont may be more effective in P acquisition, our results suggest that the Ceanothus and its symbiont were more efficient in mining soil P because the soil P concentration beneath Ceanothus was generally lower than the Douglas-fir. However, the difference in the total P between Ceanothus and Douglas-fir soil was 110 kg P ha^{-1} for the top 15 cm of the soil and could not be accounted for in Ceanothus biomass. We estimated the biomass of our stand by assuming that our stand is similar to a 17-year-old stand at 42 680 kg ha^{-1} measured by Cromack et al. (1979). Assuming a mean P concentration in biomass of 0.08%, the amount of P in Ceanothus biomass could only be 28.33 kg ha^{-1}.

Other possible explanations for the large difference in P from soil under Ceanothus compared to Douglas-fir include leaching of organic and inorganic P from the soil, dispersion of P-rich litter from Ceanothus through the area, non-random germination of Ceanothus in the field, or simply random field sampling error. Leaching of both organic and inorganic P from PNW soils are low (Compton and Cole, 1998). Although it is possible that Ceanothus preferentially germinated in low P microsites, this is highly unlikely at the scale and density of Ceanothus in the field. Ceanothus appears to germinate and grow in dense

stands until outcompeted by planted Douglas-fir, and because Douglas-fir in these stands are planted, it is unlikely that they were systematically planted in high P microsites. Field sampling errors may occur randomly. Therefore, we used retrospective power analysis to check the power of our statistics. Power is the probability of rejecting the null hypothesis if the null is false, while some alternative hypothesis is true. A retrospective power test using observed variances can evaluate whether the sample size and the α-level are sufficient to detect a meaningful significance given an observed level of variation (Thomas, 1997). Our power to detect a meaningful difference of 200 units (in our case 200 ug P g^{-1}) between species was 0.8, a value which indicates that our sample size was adequate to detect a statistical difference in total P between species amid a large amount of variation.

Although understory plant biomass appears greater under Ceanothus as compared to Douglas-fir, it is unlikely that understory species alone could account for such a large P discrepancy. Furthermore, litter dispersion could account for only 8.89 kg P ha^{-1} over 9 years. This amount was calculated from 157 kg N ha^{-1} in litter (Youngberg and Wollum, 1976), and converted to P using a N:P value of 17.65 as found by in Valachovic (1998) for snowbrush. Further studies in a broad range of sites will be needed to test the robustness of our results and to elucidate the mechanisms behind the large difference in phosphorus under Douglas-fir as compared to Ceanothus.

4.2. Soil nitrogen

Previous work has shown that soil under nitrogen-fixing alder has a greater organic matter content and lower bulk density than under a non-nitrogen-fixing species (Tarrant and Miller, 1963; Binkley, 1994; Cole et al., 1995). Soil C has been shown to parallel N accumulation under alder (Cole et al., 1991). In contrast, we found no difference in soil organic matter content in soils under Douglas-fir versus those under Ceanothus, but we did find more available N under Ceanothus than Douglas-fir. This could be due to increased decomposition of Ceanothus litter, which is less recalcitrant than Douglas-fir needles, or it could be due to lower amounts of litterfall under Douglas-fir. In general, litter from the nitrogen-fixing species would tend to decompose faster than litter from a non-fixing species (Melillo et al., 1982).

Although many authors have attempted to use natural abundance $\delta^{15}N$ isotopes as tracers of biologically-fixed N in soils, in most cases it has been largely unsuccessful (Binkley et al., 1985; Lajtha and Marshall, 1994). Indeed, we found that the $\delta^{15}N$ in Ceanothus and Douglas-fir leaves were significantly different, with Ceanothus reflecting the atmospheric signal while the Douglas-fir needles were depleted. The differences in $\delta^{15}N$ ratios between species narrowed in leaf litter. Ceanothus litter values became more depleted while Douglas-fir values were slightly more enriched. This may occur in Ceanothus, perhaps, because the heavier isotope is discriminated against during N resorption before leaf senescence and abscission. No study has determined if fractionation occurs during N resorption.

Soil $\delta^{15}N$ values were approximately equal for Ceanothus and Douglas-fir (3.8 and 3.9‰, respectively) and are in the range (+5 to −12‰) commonly found in mineral soils (Nadelhoffer and Fry, 1994; Stevenson, 1994). Mineralization and immobilization discriminate against the heavier isotope, leaving it behind in residual organic matter (Lajtha and Marshall, 1994), and thus the atmospherically-derived ^{15}N signal can be obscured in soil organic matter. The $\delta^{15}N$ values of NH_4^+ became heavier still which is not as easily explained. These results do concur with Högberg (1990) who found that large additions of fertilizer N with a low $\delta^{15}N$ abundance increased the $\delta^{15}N$ values of the soil.

The $\delta^{15}N$ of available N became further convoluted in NO_3^-. Nitrification may discriminate against $^{15}NH_4^+$ and hence the soil nitrate became more depleted, but our values seemed extreme. Therefore, even at the single tree level, $\delta^{15}N$ isotopes were not able to trace N fixed by Ceanothus into the soil N pool as the signal was lost upon entry into the soil N pool. The progressive enrichment pattern found in this study and by Högberg et al. (1995) deserves more study.

5. Conclusion

Management concerns that N-fixing species decrease soil P availability and therefore, limit Douglas-fir growth, remain unanswered (Giardina et al., 1995).

Although some studies have found that alder, in a mixed stand, can lower P nutrition of Douglas-fir, other studies have found nitrogen-fixing species to have no affect on Douglas-fir nutrition (Binkley and Husted, 1983; Binkley et al., 1991). Results of most studies vary depending on the stand, soil, and species. For example, a mixed stand of Sitka alder contained more P than a mixed stand of red alder suggesting that P availability may be determined by site-specific interactions (Binkley, 1992).

The Hedley fractionation used in this study, is a static measure of pool size, and therefore does not include a true assessment of availability (flux). However, because plants may have different methods of acquiring P, e.g. mycorrhizae and organic acids, flux and bioavailability of P is not as easily measured as it is for N. Our study has shown that surface soils under individual Douglas-fir trees have more total P than soils under individual Ceanothus trees. Further study is necessary to clarify the spatial and temporal extent of a species effect in soil, i.e. how long does the nitrogen-fixer effect concentrations of available soil P and how far (in distance) from the tree does the effect extend?

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