AN ABSTRACT OF THE THESIS

Susan L. Borchers for the degree of Master of Science in the Department of Forest Science presented on December 16, 1988.

Title: Growth And Mycorrhiza Formation Of Douglas-fir Seedlings Grown In Soils Collected At Different Distances From Hardwoods Pioneering Southwest Oregon Clearcuts

Abstract approved: Signature redacted for privacy.

David A. Perry

A greenhouse bioassay was used to compare the effects of soils collected at different distances from hardwood species on the growth, mycorrhiza formation, and foliar nutrient concentrations of Douglas-fir seedlings. Soil nutrient concentrations and bulk densities were also determined. Soils were collected from two southwestern Oregon sites that had been clearcut and broadcast burned 5 years previously. The sites, poorly stocked with conifer reproduction, were occupied primarily by grasses, forbs, and scattered individuals of tanoak (Lithocarpus densiflora (Hook. and Arn.) Rehd.), Pacific madrone (Arbutus menziesii Pursh), and canyon live oak (Quercus chrysolepis Liebm.). Five-month-old seedlings grown in media containing mineral soil collected beneath hardwood crowns had an average 70% greater height, 2.2 times greater weight (roots plus shoots)

and almost 2 times more total and mycorrhizal root-tips than seedlings grown in media containing soil collected farther than 4 m from a hardwood. Rhizopogon sp. and Cenococcum geophilum dominated on seedlings grown in hardood soils and an unidentified brown mycorrhiza on seedlings grown in open-area soils. The "hardwood effect" did not vary among the three hardwood species or between the two sites. A study of soils collected at various distances from hardwoods indicated that the effect extended between 2 and 3 m. Average foliar nitrogen was higher for seedlings grown in hardwood soils, but differences were not statistically significant. Differences in other foliar nutrients of seedlings grown on soils from beneath the three hardwood species were inconsistent. There were no consistent differences in soil nutrient concentrations; however, rates of mineralizable nitrogen (anaerobic) were from 2 to nearly 6 times higher in hardwood than in open-area soils, and soil pH was higher. Results suggest that the pioneering hardwoods strongly influence soil biological activity in these clearcuts and impose one or more soil patterns that favor establishment and growth of conifer seedlings.

Growth And Mycorrhiza Formation Of Douglas-fir Seedlings Grown In Soils Collected At Different Distances From Hardwoods Pioneering Southwest-Oregon Clearcuts

by

Susan L. Borchers

A THESIS

submitted to

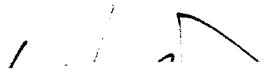
Oregon State University

in partial fulfillment of
the requirements for the
degree of
Master of Science

Completed December 16, 1988

Commencement June 1989

APPROVED:



Signature redacted for privacy.

Professor of Forest Science in charge of major

Signature redacted for privacy.

Head of Department of Forest Science

Signature redacted for privacy.

Dean of Graduate School

Date thesis is presented December 16, 1988

ACKNOWLEDGEMENTS

I sincerely thank Greg Koerper for the assistance in soil analyses, Deborah Parrish for field sampling and Boone Kauffman, Randy Molina and Jeff Borchers for review of this thesis. Special thanks goes to Dick Brainerd both for professional and personal support during my work. This work would not have been possible without the guidance and knowledge from Dave Perry, my major professor. And last but not least all my love and admiration goes to my best friend and husband Jeff.

I dedicate this thesis to my grandparents:

Ora Maryann Akers
William Akers
Albert Fleming

Odessa Adaline Boudreau
Walter James Boudreau Sr.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

Growth And Mycorrhiza Formation Of Douglas-fir Seedlings Grown In Soils Collected At Different Distances From Hardwoods Pioneering Southwest Oregon Clearcuts

INTRODUCTION

In hot, droughty forest environments of southwestern Oregon, where logging is usually followed by broadcast burning, hardwoods often occupy clearcuts. Research in recent years has indicated the detrimental effect of competing hardwoods on the growth and survival of young conifers (Radosevich et al. 1976; Newton 1981; Roy 1981; Tesch and Hobbs 1985). As a result, much effort has gone into developing methods to eradicate hardwoods.

Although competition is a major concern to foresters, early successional hardwoods can also benefit conifer seedlings. In southwestern Oregon, conifer seedlings commonly associated with madrone (Arbutus menziesii Pursh) and manzanita (Arctostaphylos viscida Parry) benefit from high levels of mycorrhizal inoculum (Amaranthus and Perry in press). Perry et al. (1987) suggest that seedlings planted with well-developed mycorrhizae may capture resources early and be more likely to survive in harsh environments.

Increasing evidence based on field observation, isolation studies, and synthesis tests indicates that madrone and manzanita form mycorrhizae with a wide range of mycorrhizal fungi that include species associated with conifers (Zak 1974; Largent et al. 1980; Molina and Trappe

1982a; Amaranthus and Perry in press). Early successional hardwoods may host some of the same species of mycorrhizal fungi as Douglas-fir seedlings, thereby acting as reservoirs of fungal inoculum during seedling establishment. Studies also have found more moisture, nutrients, and accumulation of litter, and more favorable temperatures for conifer seedlings survival beneath hardwood shrubs than in open areas (Youngberg 1966; Zavitkowski and Newton 1968; Tiedemann and Klemmedson 1973). On harsh sites in southwestern Oregon, Minore (1986) has measured higher soil moisture and lower soil temperatures beneath sprout clumps of hardwoods. However, nutrients in forest soils beneath hardwoods have not yet been reported.

This study focuses on greenhouse work with seedlings of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) inoculated with soil collected beneath and at various distances from hardwoods species that are common pioneers in southwestern Oregon clearcuts: tanoak (Lithocarpus densiflora (Hook. and Arn.) Rehd.); Pacific madrone (Arbutus menziesii Pursh); and canyon live oak (Quercus chrysolepis Liebm.). Our objective was to determine if Douglas-fir seedlings grown in soil collected beneath hardwoods sprouting in clearcuts differ in growth, mycorrhizal formation, or nutrient status from those grown in soil collected from adjacent open areas. In addition to the

greenhouse bioassay, soils collected beneath hardwoods and in open areas were examined for nutrient content, pH, litter depth, soil moisture, and bulk density.

METHODS

Study sites

Two sites were chosen within the Galice Ranger District, Siskiyou National Forest, in the mixed-conifer zone (Franklin and Dyrness 1973). The region is characterized by hot, dry summers and mild, wet winters, with annual precipitation (140-215 cm) occurring mostly from October through March. The study sites (1 and 2) occupy a relatively uniform southwesterly facing slope (45%) with elevations from 636 to 727 m. Each site was a broadcast burned 5-year-old clearcut having a moderate cover (about 30%) of tanoak, Pacific madrone, and canyon live oak. Tanoak and Pacific madrone were an average 2.5 m tall; canyon live oak was seldom over 1 m tall. Areas between the scattered hardwoods were occupied by herbs and grasses, primarily western fescue (Festuca occidentalis Hook.). Soils are shallow and skeletal, derived from meta-sedimentary parent material. Soil surface layers are gravelly loams and sandy loams with rock volume ranging from 40% to 60% (Stearns-Smith and Hann 1986).

Soil collection and preparation

In June 1986, soil samples were collected for two greenhouse bioassays. For the first, referred to here as the "Hardwood-area/open-area study," we collected mineral soil from sites 1 and 2 beneath 10 tanoak, 10 Pacific

madrone, and 10 canyon live oak individuals per site, and from 10 open areas >4 m from an individual hardwood. Around and beneath the crown of each hardwood, four mineral-soil samples were taken to 10-cm depth at 90-degree intervals and composited to make one sample per hardwood. In the open plots (radius about 30 cm), mineral soil was collected to 10-cm depth in four quadrants at right angles from plot center and composited to make one sample per plot. To reduce contamination, sampling tools were washed with 10% bleach solution between each replication.

A second study, referred to here as the "distance study," was established at site 2. Mineral soil was collected at <1, 1-2,and 3-4 m from the base of three additional hardwoods: one tanoak, one canyon live oak, and one golden chinquapin (Chrysolepis chrysophylla (Dougl.) DC.). Soil-collection points were selected semi-randomly with the constraint that they fall within one of the three distance ranges from the hardwood of interest. Data for two more ranges, 4-5 m and >5 m, were drawn from site-2 open-area soils of the hardwood-area/open-area study. (These are the only soils common to studies 1 and 2.) Once a point was selected, its horizontal distance from the hardwood was measured with a logger's tape. Three sampling points were .pa established for each distance range. Soil was collected and composited as open plots in the hardwood-area/open-area study.

Soil samples of both studies were processed in the same

way: placed in plastic bags, marked, set on ice in a cooler, and transported to the laboratory, where each composite sample was immediately sieved to 4 mm and mixed (2:1:1 by volume) with peat and vermiculite previously pasteurized 1 h at 70/C. A portion of the soil-peat-vermiculite mixture was pasteurized at 70/C for 1 h for use in the greenhouse study as a control to monitor greenhouse contamination by mycorrhizal fungi (primarily the common contaminant Thelephora terrestris).

Greenhouse study design and procedure

The two greenhouse studies corresponded to the two soil-collection patterns. The hardwood-area/open-area study included soils of both sites from directly beneath each of the three hardwood species (tanoak, Pacific madrone, and canyon live oak) from open areas >4 m from the nearest hardwood. The distance study included soils from site 2 only and compared soils collected at various distances from a hardwood, without attempting to distinguish effects related to species.

Douglas-fir seeds of both studies were planted in plastic pots (10 liter; 24 cm diameter) filled with the soil-peat-vermiculite mixture. Seeds were surface-sterilized 1 h in 30% hydrogen peroxide, then rinsed and refrigerated 24 h at 5/C. Fifteen seeds were planted per pot. The soil surface was covered with about 1 cm of chicken grit to reduce contamination by water splash and

airborne spores. Each composite sample for a single hardwood area, open area, or distance range was represented by one pot, the hardwood-area/open-area study having a total of 80 pots (4 soil sources x 10 replications of each source x 2 sites), the distance study a total of 15 (5 distance ranges x 3 replications for each range). Seeds were also planted in the pasteurized control mix of clearcut soil, peat, and vermiculite, 10 additional pots per site.

Seedlings were grown in the greenhouse under high-intensity lamps (12,000 lux; 18-h light cycle) with temperatures ranging from 24/C (day) to 18/C (night). Pots were randomly arranged on a greenhouse bench, watered lightly with a fine mist daily, and randomly relocated very 2 weeks to reduce environmental differences. After 6 weeks, seedlings were thinned to 10 per pot. At 12 weeks, each pot received 40 ml (2.5 g/l) of fertilizer (20-20-20).

Seedling analysis

After 5 months, seedlings were harvested and measured for diameter and shoot and root lengths. Roots were severed from the shoots at the soil line, gently washed under running distilled water, and examined for mycorrhizae. The total number of short roots and root tips on each seedling was recorded and identified as mycorrhizal or nonmycorrhizal. ("Short roots" are defined here as the small rootlets extending laterally from the main root stem and "root tips" as the portion originating from the end of a

short root and branching outward.) When not obvious, the mycorrhizal condition was determined by examining cross-sections and squash mounts of root tips for Hartig net formation. Mycorrhizal tips were classified by color, texture, branching, and chemical reaction (KOH and $FeSO_4$), and form (Zak 1971). Shoots and roots were oven-dried at 70/C and weighed separately.

Oven-dried foliage was removed from twigs and ground to 40 mesh in a Wiley mill. Foliage for nutrient analyses was chosen from 12 pots in the hardwood-area/open-area study to represent three replicates of each hardwood species and three replicates of open-area soil. Nitrogen (N) and phosphorus (P) were determined by Kjeldahl digestion (Bremner and Mulvaney 1982) and an Alpchem autoanalyzer. Potassium (K), calcium (Ca), iron (Fe), magnesium (Mg), manganese (Mn), and zinc (Zn) concentrations were determined on a perchloric acid digest by atomic absorption spectrophotometry (Johnson and Ulrich 1959). Sulfur (S) concentrations were obtained by the turbidimetric method described by Tabatabai and Bremner (1970).

Soil analysis

Soil samples for nutrient analyses were collected 24 June 1986 and 17 June 1987 at site 2. In the first year, subsamples of soil were collected from the same 12 points represented by the 12 pots selected for foliage analyses. Soils were analyzed within 2 weeks for mineralizable N determined by the anaerobic-incubation technique of Keeney and Bremner (1966); total N was determined by the Kjeldahl digestion method. Exchangeable K, Ca, and Mg were determined by the ammonium acetate method (Knudsen et al. 1982), zinc and Mn by the DTPA method (Lindsay and Norvell 1969 [1978?]), sulfur by the methylene blue method (Johnson and Nishita 1952), and soluble Fe by water-extraction (Soil Testing Lab, Oregon State University, personal communication). Atomic absorption spectrophotometry was used to measure all cations.

In addition, subsamples of soil were used to determine pH and moisture content. Soil pH was measured with a glass electrode pH meter in a 1:2 mixture of soil and water. Subsamples of soil (40 g) were weighed, oven-dried 48 h at 105/C, then reweighed to determine the percentage of soil moisture, based on oven-dry weight. Bulk density of soil from the 12 sample points was determined by placing a template on the soil surface and excavating a known volume of soil. Samples were placed in plastic bags, marked, and transported to the laboratory for processing. Bulk-density samples were weighed, oven-dried 4 days at 105/C, and

reweighed. Bulk density was calculated by taking the ratio of the weight of oven-dry soil to the volume of soil.

In the second year, soil was collected from beneath and at various distances from the same hardwoods as before in order to determine change in mineralizable N with distance. Four transects (150 cm long) were established at right angles directly beneath a given hardwood and extending into an adjacent open area. Mineral soil was collected to 10-cm depth at distances of 20, 40, 60, 100, and 150 cm along each transect. Four soil samples for each distance were composited to make one sample per distance for each hardwood. Samples were placed in plastic bags, marked, set on ice in a cooler, and transported to the laboratory for processing the following day. The composited samples were sieved through a 4 mm sieve, placed in marked bottles, and processed immediately by the anaerobic-incubation procedure described previously.

Statistical analysis

Both studies were arranged in a completely randomized design. Data for seedlings from both were subjected to analysis of variance (ANOVA) for differences among growth variables and mycorrhiza formation. Hardwood-area/open-area data for site 1 was analyzed separately from data for .pa site 2, and mean values for each hardwood-area were compared to mean values for open-area soils by means of Fisher's protected LSD.

In the distance study, ANOVA was used to compare data for the five distance classes (three replicates per class). Fisher's protected LSD was used to compare means of the four most distant classes with means for <1 m distance.

Data for foliage and soil nutrients from the hardwood-area/open-area study (site 2) were also subjected to ANOVA. Fisher's protected LSD was used to compare means for each hardwood-area with those for open-area soil, and means for second-year mineralizable N for each range of distance from a given hardwood with means for the 20-cm distance.

RESULTS

Seedling size and mycorrhiza formation

In the hardwood-area/open-area study on both sites, seedlings grown in soils collected beneath hardwoods were significantly taller and heavier and formed more total mycorrhizal root-tips than those grown in open soils (Table 1, Fig. 1). Figure 3 (top) shows randomly selected pots for each soil. Root length did not differ between hardwood and open soils, nor did the percentage of total mycorrhizal root tips (>90% in all cases). Mean values for seedling size and numbers of mycorrhizae varied little among the three hardwood species.

The distance study on site 2 showed that the "hardwood effect" extended between 2 and 3 m from hardwoods (Table 2, fig. 2). Figure 3 (bottom) shows randomly selected pots for each distance. Seedling growth and total mycorrhizal tips declined with distance from hardwoods. Root lengths and percentage of total root tips (nonmycorrhizal and mycorrhizal) did not differ among distance ranges.

Mycorrhiza types

In both the hardwood-area/open-area study and the distance study, we found five mycorrhizal types. Rhizopogon sp. and Cenococcum geophilum sp. were identified because of their distinctive color and morphology; three other types were classified by the procedure described by Zak (1971).

One mycorrhiza type, found on control seedlings (in pasteurized soil), we believe to be the greenhouse contaminant (Thelephora terrestris (Marx and Bryant 1970).

In our study, mycorrhizae formed by Rhizopogon sp., some of the most important mycorrhizal fungi of Douglas-fir (Zak 1971), were single branching in the upper layer of the root and covered by a thin, loose, outer veil of mycelium. The tips were silvery white and originated on the sides of the main root stem and from a single short root. White rhizomorphs extended along the roots and branched abundantly into the surrounding soil. More Rhizopogon were found on seedlings grown in soil collected beneath hardwoods than in the open soil of both sites (Fig. 1). As with growth, the sharpest decline of Rhizopogon occurred between the 1-2 m and 3-4 m distance ranges (Fig. 2).

Cenococcum geophilum, a common mycobiont of Douglas-fir, manzanita, madrone, and oak (Zak 1974; Mejstrik and Hadac 1975; Largent et al. 1980; Beckjord and McIntosh 1984) characterized by a jet black mantle, coarse black hyphae, and the absence of rhizomorphs (Melin 1927; Hatch 1934; Trappe 1969) was found in highest concentrations on the root just beneath the soil. For both sites, seedlings grown in soil collected beneath hardwoods had more C. geophilum mycorrhizal root tips than seedlings grown in soil collected in the open (Fig. 1). In the distance study, C. geophilum

was less common on seedlings grown in soil collected 3 m or more from a hardwood, with the sharpest drop occurring between the 1-2 m and 3-4k m ranges (Fig. 2).

Like others observing Douglas-fir seedlings in the greenhouse and field (Shoenberger and Perry 1982; Pilz and Perry 1984; Amaranthus and Perry 1987; J.G. Borchers and D.A. Perry, unpublished; R. Brainerd and D.A. Perry, unpublished), we observed a brown mycorrhiza with pyramidally pinnate branching and a golden-brown swollen mantle. In the hardwood/open-area study, these brown mycorrhizae comprised a much higher proportion of total mycorrhizal tips on seedlings of both sites grown in open soils than on those grown in hardwood soils (Fig. 1). But in the distance study, their numbers differed only slightly (Fig. 2).

C. geophilum replacing the brown mycorrhizae (ceno + brown) on seedlings in both studies (Fig. 1) had a well-developed swollen mantle, a golden-brown tip, and coarse black hyphae. In both sites, the number of ceno + brown mycorrhizal root tips were greater on seedlings grown in hardwood soils than on seedlings grown in the open soils. There was a distinct decline of such tips between the 1-2 m and 3-4 m distance ranges (Fig. 2).

An unbranched, black mycorrhiza with dark-brown-to-black smooth mantle and, when present, transparent white hyphae--similar to a black type found on Douglas-fir roots by Chu-Chou and Grace (1980)--was observed primarily on the

bottom half of the root system. Black mycorrhizal root tips occurred more often on seedlings grown in soils collected in the open than on seedlings grown in soils from beneath hardwoods (Fig. 1). The numbers increased between 1-2 m and 3-4 m (Fig. 2).

Fruiting bodies of Thelephora terrestris, a common ectomycorrhizal contaminant in greenhouses (Marx and Bryant 1970), were found at the base and top of the control pots. The mycorrhizae were white to tan, cruciform and swollen with a thin mantle and smooth, white hyphae. Control seedlings were free of all other mycorrhiza types.

Foliar nutrients

Foliar nutrient concentrations of seedlings grown in hardwood and open soils showed few significant differences and were frequently inconsistent among the three hardwood species tested (Table 3). Seedlings grown in soils from beneath Pacific madrone had higher K, Ca, Mg, and Fr. Those grown in soils from beneath canyon live oak also had higher Fe, but lower Mg, Mn, and Zn and a higher Ca/Mg ratio ($p = 0.05$) than those grown in the open (2.4:1). Seedlings from all hardwood-area soils had higher Fe/Mn ratios than seedlings grown in open-area soils ($p = 0.05$). Except for the Fe/Mn ratio, there were no significant differences between seedlings grown in tanoak and open soils.

Average values for some foliar nutrient concentrations of seedlings grown in hardwood-area and open-area soils differed consistently but insignificantly. Average N and Ca concentrations were higher for seedlings grown in the hardwood-area soils, but P concentrations were lower.

Soil physical and chemical properties

Soil from beneath hardwoods had lower bulk density and higher moisture content, pH, and mineralizable N (anaerobic) than soils from open areas (Table 4). For the most part, the variables differed little among soils from beneath the three hardwood species, mineralizable N being an exception. In 1986, mineralizable N in soils under canyon live oak was well over 2 times greater than in soils under other hardwoods and 4 times greater than in soils from open areas. In the following year, it was highest beneath Pacific madrone, which is not surprising considering that mineralizable N can vary according to season and year of sampling (Gosz and White 1986). Mineralizable nitrogen declined steadily with distance from all hardwoods in 1987 (Fig. 4).

Soil nutrient concentrations in this study were in the same range reported by Heilman (1981) for Douglas-fir sites in southwestern Oregon. Like foliar nutrient concentrations, soil nutrient concentrations did not differ consistently between hardwood-area and open-area samples. Canyon live oak soils were higher in total N, while Mg

concentration was higher in Pacific madrone and tanoak soils (Table 5). Average Ca concentrations were higher in all hardwood-area soils than in open-area soils; however, values were highly variable (especially beneath Pacific madrone) and differences were not statistically significant. Soil micronutrients varied beneath hardwood species: Zn concentration was highest beneath tanoak and Mn highest beneath Pacific madrone. Canyon live oak and tanoak soils were significantly lower in sulfate than were open-area soils, and iron concentrations tended to be lower in hardwood-area than in open-area soils. However, the difference in bulk density was such that nutrients having greater concentration beneath hardwoods 3were not necessarily present in greater amounts.

DISCUSSION

Enhanced growth of Douglas-fir seedlings in hardwood-area soil may be due to a combination of rapid mycorrhiza formation, differences in mycorrhiza types and perhaps other soil microorganisms, and greater nutrient availability. Like Douglas-fir, the three hardwood species tested are ectomycorrhizal (Zak 1976; Largent et al. 1980; Molina and Trappe 1982a). Rhizopogon sp. and Cenococcum geophilum were most frequent on seedlings grown in hardwood-area soils, the brown and black mycorrhizae most frequent on seedlings grown in open-area soils. In the field, we observed C. geophilum on roots of tanoak and canyon live oak, and we found a mycorrhiza with the morphology and color of a Rhizopogon sp. on Pacific madrone and tanoak (S.L. Borchers and D.A. Perry, unpublished). Mycelial fans radiating from the extensive root system of hardwoods may have high potential to inoculate, rapidily reaching neighboring Douglas-fir roots and inducing infection (Wilcox 1983; Read 1987).

Hardwoods also may markedly influence the type of mycorrhiza through effects on the soil environment. Soils beneath all three species had greater accumulations of litter, higher pH and soil moisture, and lower bulk density than soils in open areas. Previous studies have indicated that the proportion of ectomycorrhizal types forming on seedlings is sensitive to environmental conditions (Mikola and Laiho 1962; Theodorou and Bowen 1970; Skinner and Bowen 1974; Schoenberger and Perry 1982; Parke et al. 1983; Pilz

and Perry 1984). In the mixed conifer zone of southwestern Oregon, soil temperature may be an important factor in the survival of native ectomycorrhizal fungi (Parke et al. 1983).

The inconsistent patterns of foliar nutrient concentrations for seedlings grown in the various soils may be due to insufficient sampling. A more comprehensive sampling could determine differences, if any. Of the nine foliar nutrients analyzed, N, Ca, and Fe were consistently higher for seedlings grown in hardwood-area soils. High foliar Fe levels may be related to various biologically produced chelating agents (Powell et al. 1980; Perry et al. 1984; Reid et al. 1984) in hardwood rhizospheres. Among the most important are the siderophores produced by various bacteria and fungi, including mycorrhizal fungi. In southwestern Oregon, siderophore concentrations were found to be lower in clearcut soils than in those of adjacent forest soils (Perry et al. 1984). Hardwoods sprouting after clearcutting may have an important role in stabilizing rhizosphere organisms.

Except for relatively high rates of mineralizable N and concentrations of Mn, there were no consistent nutrient patterns in soils from beneath the three hardwood species. Anaerobic mineralizable N correlates with total microbial biomass (Myrold 1987); however, soils beneath the hardwoods had not only more total microbial biomass than those in the open but different types of microbes as well. C.Y. Li

(unpublished) isolated 10 times more actinomycete colonies (Streptomyces sp.) from open-area soils than from hardwood-area soils. In pure culture, some actinomycete colonies have been found to inhibit growth of mycorrhizal fungi (Perry and Rose 1983; Freidman et al. 1987). Interestingly, adverse effects of streptomycin on plants can be reversed by Mn (Rosen 1954; Gray 1955), which occurs in relatively high levels beneath hardwoods.

More research is needed to determine the role of early successional hardwoods in the biology of southwestern Oregon soil. Our data show that, on these clearcuts, pioneering hardwoods enhance soil biological activity and N cycling. The enhancement may be a result of lower bulk density, increased pH and soil water, and a substrate of root exudates and root and leaf litter (Richards 1987). Greater numbers of Rhizopogon sp. and C. geophilum mycorrhizae in hardwood soils may be an indirect effect of the altered soil environment or a direct effect of transfer between hardwood and conifer roots.

Of course, seedling growth in the greenhouse bioassay cannot be directly extrapolated to field conditions in which hardwoods may compete with conifer seedlings for light and water. But results of this study point to the need for detailed work on the possible benefit of hardwoods to conifer performance. Although a dense hardwood cover on clearcuts is probably undesirable, some cover maybe preferable to none at all.

BIBLIOGRAPHY

AMARANTHUS, M.A., and PERRY, D.A. 1987. Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. Can. J. For. Res. 17: 944-950.

BECKJORD, P.R., and McINTOSH, M.S. 1984. Growth and fungal persistence of Quercus rubra inoculated with ectomycorrhizal fungi and planted on a clear-cutting and strip mine. Can. J. Bot. 62:1571-1574.

BREMNER, J.M., and MULVANEY, C.S. 1982. Total nitrogen. In Methods of soil analysis, Part 2. Edited by A.L. Page. American Society of Agronomy, Madison, WI. pp. 595-624.

CHU-CHOU, M., and GRACE, L.J. 1980. Mycorrhizal fungi of Pseudotsuga menziesii in the north island of New Zealand. Soil Biol. Biochem. 13:247-249.

FRANKLIN, J.F. AND DYRNESS, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.

FREIDMAN, J., HUTCHINS, A.S., and PERRY, D.A. 1987. Phytotoxic actinomycetes and their possible role in regeneration failure of Douglas-fir in the Siskiyou Mountains of southwest Oregon. In 42nd Northwest Regional Meeting, American Chemical Society. Western Washington University, Bellingham, WA.

GOSZ, J.R., and WHITE, C.S. 1986. Seasonal and annual variation in nitrogen mineralization and nitrification along an elevational gradient in New Mexico. Biogeochemistry, 2:281-297.

GRAY, R.A. 1955. Inhibition of root growth by streptomycin and reversal of the inhibition by manganese. Am. J. Bot. 42:327-331.

HATCH, A.B. 1934. A jet-black mycelium forming ectotrophic mycorrhizae. Svensk. Bot. Tidskr. 28:369-383.

HEILMAN, P. 1981. Minerals, chemical properties, and fertility of forest soils. In Forest soils of Douglas-fir region. Washington State University Cooperative Extension Service, Pullman, WA. pp. 121-136.

JOHNSON, C.M., and NISHITA, H. 1952. Microestimation of sulfur in plant materials, soils, and irrigation waters. Anal. Chem. 26:736-742.

JOHNSON, C.M., and ULRICH, R. 1959. Analytical methods for use in plant analysis. Calif. Agric. Exp. Stn. Bull. 766.

KNUDSEN, D., PETERSON, G.A., and PRATT, P.F. 1982. Lithium, sodium, and potassium. In Methods of soil analysis, Part 2. Edited by A.L. Page. American Society of Agronomy, Madison, WI. pp. 225-246. .pa

LARGENT, D.L., SUGIHARA, N., and WISHNER, C. 1980. Occurrence of mycorrhizae on ericaceous and pyrolaceous shrubs and subshrubs in northern California. Can. J. Bot. 58:2274-2279. .pa

LINDSAY, W.L., and NORVELL, W.A. 1978. Development of a DTPA test for zinc, iron, manganese, and copper. Soil Sci. Soc. Am. J. 42:421-428.

KEENEY, D.R., and BREMNER, J.M. 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. Agron. J. 58:498-503.

MARX, D.H., and BRYANT, W.C. 1970. Pure culture synthesis of ectomycorrhizae by Thelephora terrestris and Pisolithus tinctorius on different conifer hosts. Can. J. Bot. 48:639-643.

MEJSTRIK, V.K., and HADAC, H. 1975. Mycorrhizas of Arctostaphylos uva ursi. Pedobiologia, 15:336-342.

MELIN, E. 1927. Mykorhizans utbildning hos tallplantat i olike rohumusformer. Statens Skogsforsokanst Medd. 23:433-494.

MIKOLA, P., and LAIHO, O. 1962. Mycorrhizal relations in the raw humus layer of northern spruce forests. Commun. Inst. For. Fenn. 55.

MINORE, D. 1986. Effects of madrone, chinkapin, and tanoak sprouts on light intensity, soil moisture, and soil temperature. Can. J. For. Res. 16:654-658.

MOLINA, R. and TRAPPE, J.M. 1982a. Lack of mycorrhizal specificity by the ericaceous hosts Arbutus menziesii and Arctostaphylos uva-ursi. New Phytol. 90:495-509.

MOLINA, R. and TRAPPE, J.M. 1982b. Patterns of ectomycorrhizal host specificiy and potential among Pacific Northwest conifers and fungi. For. Sci. 28:423-458.

MYROLD, D.D. 1987. Relationship between microbial biomass nitrogen and a nitrogen availability index. Soil Sci. Soc. Am. J. 51:1047-1049.

NEWTON, M. 1981. Ecological principles of weed control in forestry. In Weed control in forest management. Proceedings, 1981 J.S. Wright Forestry Conference, Purdue University, West Lafayette, IN. pp. 14-25.

PARKE, J.L., LINDERMAN, R.G., and TRAPPE, J.M. 1983. Effect of root zone temperature on ectomycorrhiza and vesicular-arbuscular mycorrhiza formation in disturbed and undisturbed forest soils of southwest Oregon. Can. J. For. Res. 13:657-665.

PERRY, D.A., MOLINA, R., and AMARANTHUS, M.A. 1987. Mycorrhizae, mycorrhizospheres, and reforestation: current knowledge and research needs. Can. J. For. Res. 17:929-940.

PERRY, D.A., and ROSE, S.L. 1983. Soil biology and forest productivity: opportunities and constraints. In IUFRO symposium on forest site and continuous productivity. Edited by R. Ballard and S.P. Gessel. USDA For. Serv. Gen. Tech. Rep. PNW-163. pp. 229-238.

PERRY, D.A., ROSE, S.L., PILZ, D., and SCHOENBERGER, M.M. 1984. Reduction of natural ferric iron chelators in disturbed forest soils. Soil Sci. Am. J. 48:379-382.

PILZ, D.P., and PERRY, D.A. 1984. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can. J. For. Res. 14:94-100. .pa

POWELL, P.E., CLINE, G.R., REID, C.P.P., and SZANISZLO, P.J. 1980. Occurrence of hydroxamate siderophore iron chelators in soils. Nature (London), 287:833-834.

RADOSEVICH, S.R., PASSOF, P.C., and LEONARD, O.A. 1976. Douglas-fir release from tanoak and Pacific madrone competition. Weed Sci. 24:144-145.

READ, D.J. 1987. Development and function of mycorrhizal hyphae in soil. In Mycorrhizae in the next decade. Practical applications and research priorities. Edited by D.M. Sylvia, L.L. Hung, and J.H. Graham. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL. pp. 178-180.

REID, R.K., REID, C.P.P., POWELL, P.E., and SZANISZLO, P.J. 1984. Comparison of siderophore concentrations in aqueous extracts of rhizosphere and adjacent bulk soils. Pedobiologia, 26:263-266.

RICHARDS, B.N. 1987. Pattern and process in the soil ecosystem. In The microbiology of terrestrial ecosystems. John Wiley and Sons, Inc., New York. pp. 79-117.

ROSEN, W.G. 1954. Plant growth inhibition by streptomycin and its prevention by Manganese. Soc. Exp. Biol. Med. 85:385-388.

ROY, D.F. 1981. Effects of competing vegetation on conifer performance. In Forest vegetation workshop, March 3-5, 1981, Corvallis, OR.

SCHOENBERGER, M.M., and PERRY, D.A. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings: a greenhouse bioassay. Can. J. For. Res. 12:343-353.

SKINNER, M.F., and BOWEN, G.D. 1974. The penetration of soil by mycelial strands of ectomycorrhizal fungi. Soil Biol. Biochem. 6:57-61.

STEARNS-SMITH, S.C., and HANN, D.W. 1986. Forest soil associations of southwestern Oregon. FRL Map. Forest Research Laboratory, Oregon State University, Corvallis, OR.

TABATABAI, M.A. and BREMNER, J.M. 1970. A simple turbidimetric method of determining total sulfur in plant materials. Agron. J. 62:805-806.

TESCH, S.D., and HOBBS, S.D. 1985. Sprouting brush is tough competition for planted Douglas-fir seedlings in southwestern Oregon. In Proc., 7th Annual Forest Vegetation Management Conference, Nov. 6-7, 1984, Eureka, CA.

THEODOROU, J., and BOWEN, D. 1970. Mycorrhizal responses of radiata pine in experiments with different fungi. Aust. For. 34:183-191.

TIEDEMANN, A.R., and KLEMMEDSON, J.O. 1973. Nutrient availability in desert grassland soils under mesquite (Prosopis juliflora) trees and adjacent open areas. Soil Sci. Soc. Am. Proc. 37:107-111.

TRAPPE, J.M. 1969. Studies on Cenococcum graniforme. I. An efficient method for isolation from sclerotia. Can. J. Bot. 47:1389-1390.

WILCOX, H.E. 1983. Fungal parasitism of woody plant roots from mycorrhizal relationships to plant disease. Annu. Rev. Phytopathol. 21:221-242.

YOUNGBERG, C.T. 1966. Silvicultural benefits from brush. In Proc. Soc. Am. For. 1965. pp. 55-59.

ZAK, B. 1971. Characterization and classification of mycorrhizae of Douglas-fir. II. Pseudotsuga menziesii + Rhizopogon vinicolor. Can. J. Bot. 49:1079-1084.

ZAK, B. 1974. Ectendomycorrhiza of Pacific madrone (Arbutus menziesii). Trans. Br. Mycol. Soc. 62:202-205.

ZAK, B. 1976. Pure culture synthesis of Pacific madrone ectendomycorrhizae. Mycologia, 68:362-369.

ZAVITKOVSKI, J., and NEWTON, M. 1968. Ecological importance of snowbrush Ceanothus velutinus in the Oregon Cascades. Ecology, 49:1134-1145.

APPENDICES

FIGURE 1

Mycorrhizal root tips of 5-month-old Douglas-fir seedlings grown in soil collected beneath hardwoods and in open areas on site 1 (S1) and site 2 (S2).

Standard errors are shown in parenthesis. Hardwoods soils are compared with open soils using Fisher's protected LSD. Significance (0.05) is indicated by asterisks: * = 0.05.

FIGURE 1

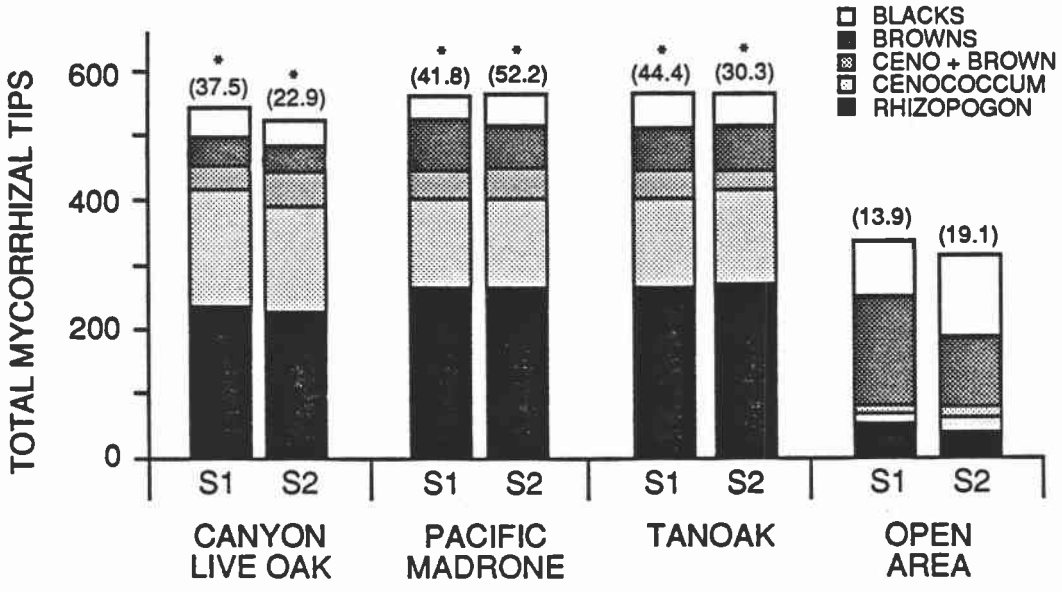

TOTAL MYCORRHIZAL TIPS
600
400
200
0
BLACKS
BROWNS
CENO + BROWN
CENOCOCCUM
RHIZOPOGON
(37.5)
(22.9)
(41.8)
(52.2)
(44.4)
(30.3)
(13.9)
(19.1)
S1
S2
CANYON LIVE OAK
PACIFIC MADRONE
TANOAK
OPEN AREA

Figure 2

Mycorrhizal root tipes of 5-month-old Douglas-fir seedlings grown in soil collected at different distances from hardwoods on site 2.

Standard errors are shown in parenthesis. Means for each distance range are compared to those <1 m from a hardwood using Fisher's protected LSD. Ssignificance (0.05) is indicated by asterisks: * = 0.05.

FIGURE 2

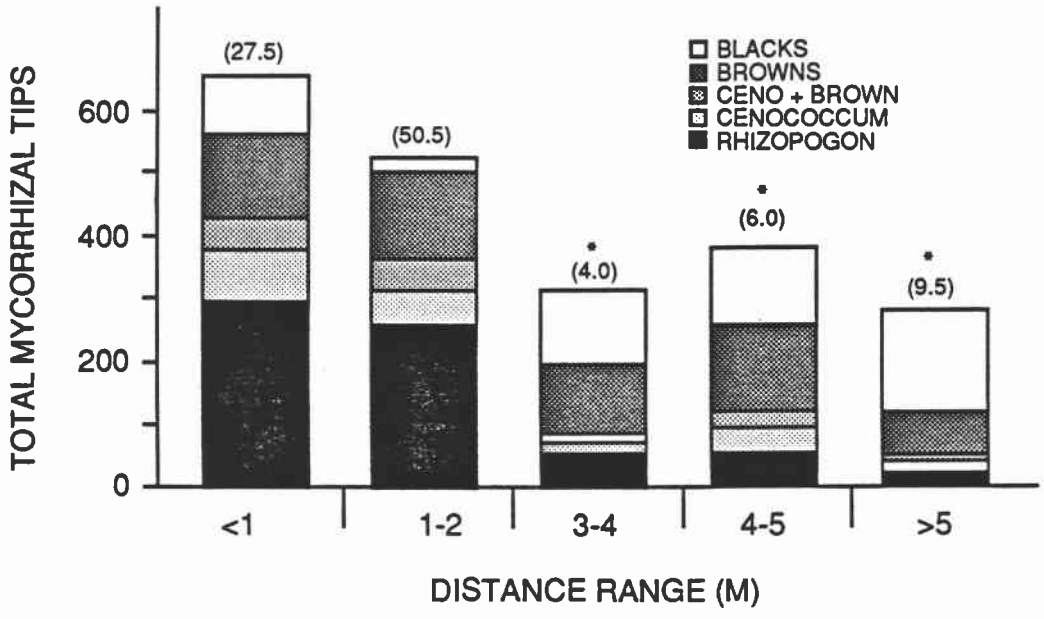
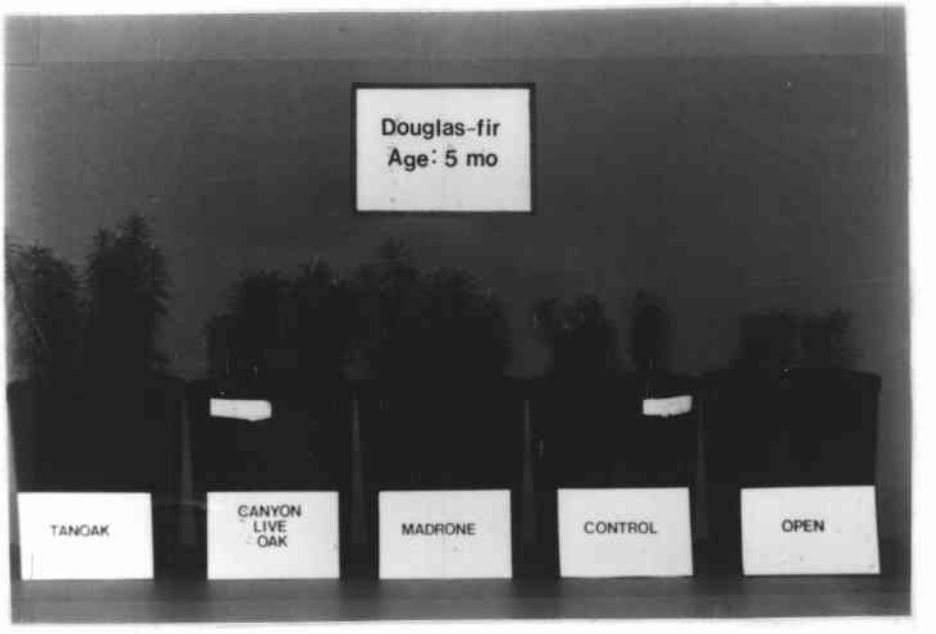

TOTAL MYCORRHIZAL TIPS
600
400
200
0
(27.5)
(50.5)
(4.0)
(6.0)
(9.5)
BLACKS
BROWNS
CENO + BROWN
CENOCOCCUM
RHIZOPOGON
<1
1-2
3-4
4-5
>5
DISTANCE RANGE (M)

Figure 3

Randomly selected Douglas-fir seedlings grown 5 months in different soils. Top: soils collected beneath hardwoods and in the open >4 m from hardwoods. Control soil is pasteurized clearcut soil, peat, and vermiculite. Bottom: soils collected at different distances from hardwoods.

FIGURE 3


Douglas-fir
Age: 5 mo
TANOAK
CANYON LIVE OAK
MADRONE
CONTROL
OPEN

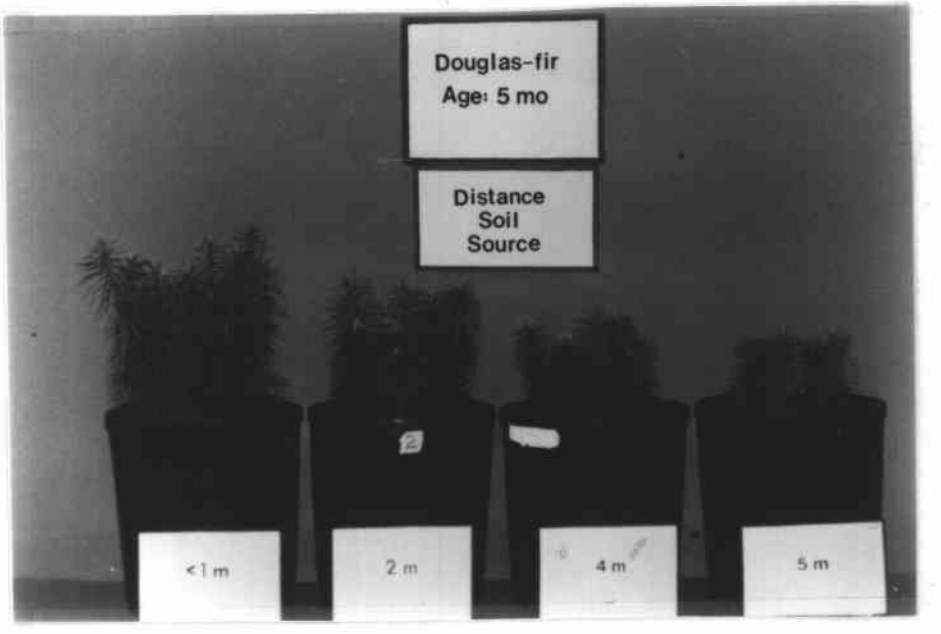

Douglas-fir
Age: 5 mo
Distance
Soil
Source
<1 m
2 m
4 m
5 m

Figure 4

Soil mineralizable N (anaerobic) at different distances from hardwoods.

Means for each distance range are compared to those <20 cm from a hardood using Fisher's protected LSD. Significance is indicated by asterisks: ** = 0.01; * = 0.05.

FIGURE 4

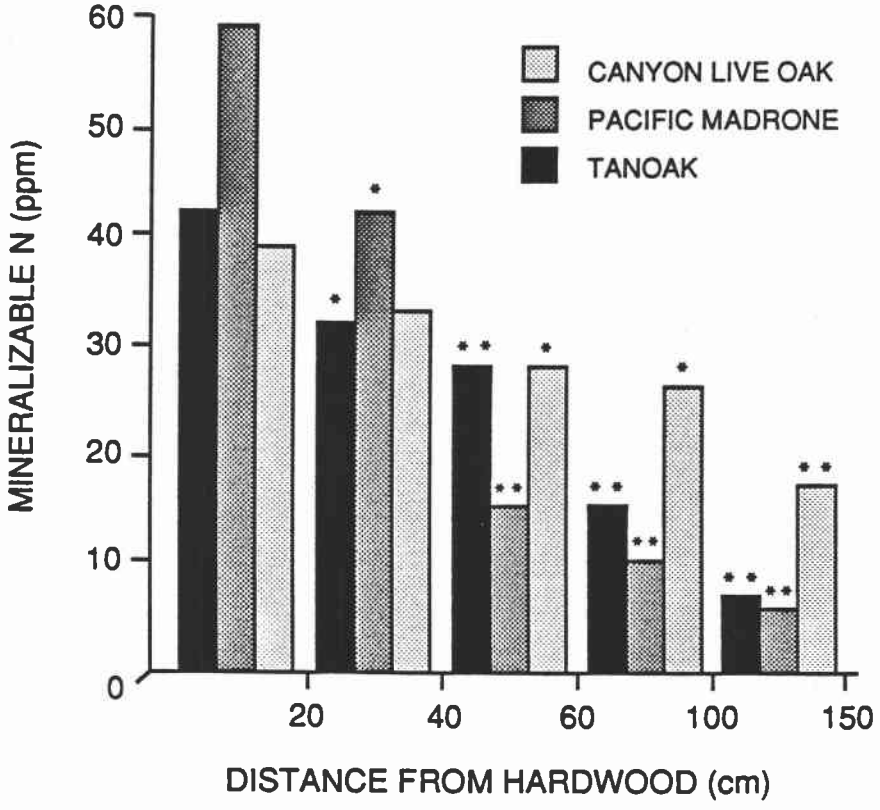

60
50
40
30
20
10
0
MINERALIZABLE N (ppm)
CANYON LIVE OAK
PACIFIC MADRONE
TANOAK
20
40
60
100
150
DISTANCE FROM HARDWOOD (cm)

Table 1

Shoot length, root length, dry weight, and percentage of mycorrhizae of 5-month-old Douglas-fir seedlings grown in soil collected for Hardwood-area/open-area study.

Standard errors are shown in parenthesis. Hardwood soils are compared with open soils using Fisher's protected LSD. Significance is indicated by asterisks: ** = 0.01 and * = 0.05.

TABLE 1

Hardwood/open study

Soil source	Shoot length (mm)	Root length (mm)	Dry weights Shoot (g)	Dry weights Root (g)	Percentage of root tips Nonmycorrhizal	Percentage of root tips Mycorrhizal
			-Site 1-			
Canyon live oak	233.00** (8.97)	338.40 (10.33)	11.24** (0.59)	9.28** (0.52)	5	95
Pacific madrone	237.40** (5.34)	339.80 (9.06)	11.38** (0.52)	8.88** (0.48)	3	97
Tanoak	258.62** (21.42)	331.75 (24.82)	10.28** (0.42)	8.72** (0.55)	5	95
Open	141.60 (4.71)	334.40 (8.81)	4.95 (0.28)	5.11 (0.24)	7	92
			-Site 2-			
Canyon live oak	228.00** (5.48)	337.90 15.47)	9.94** (0.47)	10.15** (0.62)	2	98
Pacific madrone	236.60** (5.95)	349.90 (8.87)	10.92** (0.58)	9.06** (0.20)	3	97
Tanoak	238.60** (6.49)	328.50 (8.20)	10.85** (0.29)	9.76** (0.24)	3	97
Open	140.83 (10.29)	333.50 (8.20)	3.18 (0.38)	4.92 (0.35)	7	93

Table 2

Shoot length, root length, dry weight, and percentage of mycorrhizae of 5-month-old Douglas-fir seedlings grown in soil collected for Distance study.

Standard errors are shown in parenthesis. Means for each distance range are compared to those <1 m from a hardwood using Fisher's protected LSD. Significance is indicated by asterisks: ** = 0.01; * = 0.05.

TABLE 2

Variable distance study

Distance range (m)	Shoot length (mm)	Root length (mm)	Dry Weights shoot (g)	Dry Weights root (g)	Percentage of root tips Nonmycorrhizal	Percentage of root tips Mycorrhizal
<1	242.50 (13.50)	311.50 (28.50)	6.24 (0.16)	9.68 (0.30)	3	97
1-2	243.00 (33.00)	334.50 (7.50)	6.68 (0.03)	10.32 (0.68)	2	98
3-4	164.00 ** (1.50)	350.00 (2.00)	3.41* (0.37)	5.13** (0.43)	7	93
4-5	137.00 ** (16.00)	330.00 (8.00)	2.94** (0.48)	5.08** (0.88)	5	95
>5	121.00 ** (19.00)	320.50 (78.50)	3.19* (1.28)	4.56** (0.82)	10	90

Table 3

Foliar nutrient concentrations for 5-month-old Douglas-fir seedlings grown in soil collected beneath hardwoods and in the open of site 2.

Standard errors are shown in parenthesis. Hardwood soils are compared with open soils using Fisher's protected LSD. Significance is indicated by asterisks: *** = 0.01; ** = 0.05; * = 0.10.

TABLE 3

Soil source	N %	P %	K %	S %	Ca %	Mg %	Fe ppm	Mn ppm	Zn ppm
Canyon live oak	0.96 (0.03)	0.24 (0.02)	0.84 (0.03)	0.11 (0.02)	0.22 (0.02)	0.09*** (0.00)	102* (7.31)	184** (8.54)	42*** (2.00)
Pacific madrone	1.08 (0.20)	0.23 (0.06)	1.05*** (0.04)	0.14 (0.02)	0.25 ** (0.03)	0.14** (0.003)	170*** (15.53)	613 (88.38)	53 (2.65)
Tanoak	1.10 (0.02)	0.26 (0.07)	0.99 (0.20)	0.12 (0.02)	0.21 (0.02)	0.11 (0.007)	99 (17.84)	330 (80.21)	45 (7.55)
Open	0.91 (0.04)	0.29 (0.05)	0.84 (0.11)	0.11 (0.03)	0.18 (0.02)	0.11 (0.01)	65 (7.51)	573 (183.3)	57 (5.46)

Table 4

Soil characteristics and chemical analysis from site 2.

Standard errors are shown in parenthesis. Hardwoods are compared with open soils. Significance is indicated by asterisks: *** = 0.01; ** = 0.05; * = 0.10.

TABLE 4

Soil source	Bulk density (g/cm^3)	Litter depth (cm)	Moisture content (%)	pH	Mineralizable N (ppm)	Total N (%)	Ca	Mg	K	SO^4	Zn	Fe	Mn
							--meq/100g--		----------ppm----------				
Canyon live oak	0.51*** (0.02)	1.4*** (0.03)	19.17*** (1.6)	5.3** (0.07)	52.67*** (1.76)	0.32** (0.05)	6.60 (1.34)	0.64 (0.07)	183 (7.67)	6.2** (0.32)	1.16 (0.22)	0.36* (0.12)	109 (15.51)
Pacific madrone	0.50*** (0.1)	1.8*** (0.09)	23.17*** (1.58)	5.3** (0.03)	20.33*** (1.20)	0.17 (0.007)	10.73 (4.84)	1.33*** (0.03)	205 (11.61)	8.3 (0.30)	0.45 (0.13)	0.76 (0.22)	263*** (54.70)
Tanoak	0.67*** (0.01)	1.6*** (0.06)	17.47** (3.08)	5.1** (0.01)	17.00** (0.58)	0.22 (0.02)	8.83 (0.89)	0.82* (0.01)	191 (6.93)	5.8*** (0.18)	1.84*** (0.32)	0.34* (0.09)	156 (15.62)
Open	0.96 (0.01)	0 (0)	9.47 (0.20)	4.5 (0.20)	11.67 (1.67)	0.18 (0.007)	4.88 (0.22)	0.59 (0.05)	182 (11.06)	7.6 (0.40)	1.00 (0.08)	1.06 (0.45)	87 (11.68)