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Soil Compaction and Organic Matter Affect Conifer Seedling Nonmycorrhizal and Ectomycorrhizal Root Tip Abundance and Diversity

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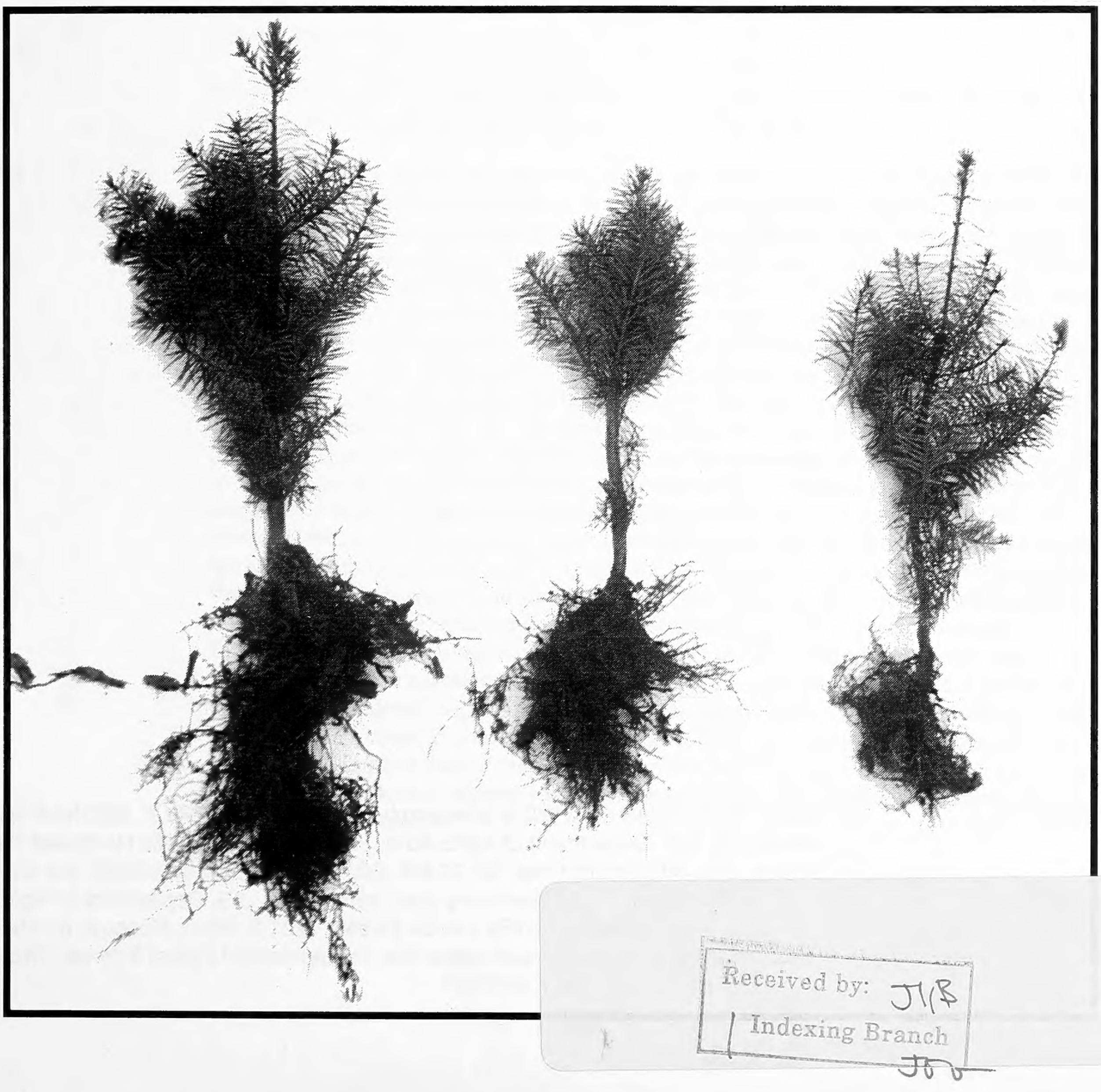

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Abstract

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Three levels of organic matter removal (bole only; bole and crowns; and bole, crowns, and forest floor) and three levels of mechanical soil compaction (no compaction, moderate compaction, and severe soil compaction) were studied as they influence Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don) seedlings following outplanting. Moderate and severe soil compaction significantly reduced nonmycorrhizal root tip abundance on both Douglas-fir and western white pine seedlings ($p \leq 0.05$). Ectomycorrhizal root tip abundance was significantly reduced on Douglas-fir seedlings in severely compacted areas with bole and crowns and bole, crowns, and forest floor removed. Ectomycorrhizal diversity also was significantly reduced on Douglas-fir seedlings in all severely compacted areas.

Keywords: Douglas-fir, ectomycorrhizae, forest harvest, organic matter, reforestation, root tips, soil compaction, bulk density, western white pine.

Summary

Intensive forest harvest and soil compaction are widespread across inland forests of the Pacific Northwestern United States; both have potential to affect forest soil productivity through changing organic matter levels and soil bulk density. This study evaluates these effects on nonmycorrhizal and ectomycorrhizal root tip abundance and diversity on first-year outplanted conifer seedlings. Seedlings were grown in ash-influenced forest soils in northern Idaho. Three levels of organic matter removal (bole only [OM1]; bole and crowns [OM2]; and bole, crowns, and forest floor [OM3]) and three levels of mechanical soil compaction (no compaction [C1], moderate compaction [C2], and severe soil compaction [C3]) were studied as they influence Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don) seedlings following outplanting. Soil bulk density averaged over three soil depths was significantly greater for C2 and C3 compared to C1-treated areas for nearly all soil depths and organic matter treatments. Treatments C2 and C3 significantly reduced nonmycorrhizal root tip abundance on both Douglas-fir and western white pine seedlings ($p \leq 0.05$). Ectomycorrhizal root tip abundance was significantly reduced on Douglas-fir seedlings in C3-treated areas with OM2 and OM3 removal. Ectomycorrhizal diversity also was significantly reduced on Douglas-fir seedlings in all C3-treated areas. Ectomycorrhizal root tip abundance and diversity were not significantly reduced on western white pine seedlings by any treatment. Observed reduction in root tips in C2- and C3-treated areas suggest a loss the ability of establishing seedings to capture site resources and adapt to changing conditions, at least in the first year. This experimental site is designated as part of the Forest Service's National Long-Term Soil Productivity study of the impacts of organic matter depletion and soil compaction on stand development and soil productivity.

Contents

Introduction

Ectomycorrhizal fungi profoundly affect forest ecosystems by mediating nutrient and water uptake, protecting against pathogens and environmental extremes, and maintaining soil structure and forest food webs. Most conifers form ectomycorrhizae (literally, "fungus roots") with these symbiotic fungi and require the relationship to survive and grow. Ectomycorrhizal mycelia are extensions of root system and more effective in nutrient and water absorption than roots themselves. Nutrients and water absorbed by the mycelia are transported to the plant; in return, the ectomycorrhizal fungus receives essential sugars from the plant to fuel its activities. A typical forest site generally contains many ectomycorrhiza-forming fungal species (Eberhart and others, in press), and populations can be reduced or shift following disturbance (Amaranthus and Trappe 1993, Perry and Rose 1983, Pilz and Perry 1984). The ability of seedlings to rapidly form root tips and mycorrhizae is critical for seedling establishment on harsh sites (Amaranthus and Perry 1987, Amaranthus and others 1989).

Timber harvest and soil compaction can alter forest soil productivity by reducing organic matter. Ectomycorrhizae predominate in the organic soil layers (Harvey and others 1976, 1979, 1986; Trappe and Fogel 1977). Harvey and others (1976) found up to 95 percent of the active ectomycorrhizae in humus and decaying wood in a mature Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forest. Ectomycorrhizal diversity also may be tied to the diversity of organic matter on the forest floor. Some ectomycorrhizal fungi predominate in fallen trees (Amaranthus and others 1994). In periods of adequate moisture, the humus may support the highest level of ectomycorrhizal activity, but during drought decayed wood in soil may become the most active site (Harvey and others 1979). Following drought and wildfire in southern Oregon and northern California, decaying wood contained 25 times more moisture than mineral soil and was a center of ectomycorrhizal activity for recovering vegetation (Amaranthus and others 1989).

Timber harvesting can also reduce site productivity by compacting soils. The inland Pacific Northwest has large areas of productive forests on volcanic ash soils (Geist and others 1989) prone to compaction because they have a low volume weight (weight-to-volume ratio) and relatively few coarse fragments in the soil profile (Geist and Cochran 1991). Froehlich and others (1985) found that seedling height growth declines as soil bulk density increases. They also concluded that the effects of compaction can last up to 45 years. Soil compaction in a central Oregon clearcut caused a significant decline in seedling growth after 5 years (Cochran and Brock 1985). Soil compaction degrades soil structure and restricts movement of oxygen and water through the soil, and flushing out of carbon dioxide and populations of ectomycorrhizal fungi may be adversely altered as a result. In addition, compaction reduces the pore space for root penetration and production of feeder rootlets where mycorrhizae form.

Sustaining forest productivity requires understanding the complex interactions among soils, roots, and mycorrhizae. A previous study in northern Idaho indicates harvesting and site preparation increases soil bulk density (Page-Dumroese 1993). The objectives of this study were to investigate nonmycorrhizal and ectomycorrhizal root tip abundance and diversity on Douglas-fir and western white pine (*Pinus monticola* Dougl. ex D. Don) seedlings following three levels of organic matter removal and three levels of soil compaction on volcanic ash soil.

Methods

The Study Site

This study was conducted on a bench adjoining the Priest River at the Priest River Experimental Forest, Priest River, Idaho, at latitude 48° 21' 06.3417" N., longitude 116° 50' 22.9822" W., and elevation 725 meters. This experimental site is a designated part of the USDA Forest Service's National Long-Term Site Productivity study. The study area receives about 83.8 centimeters of precipitation annually, 80 percent of which is as snow, with a mean annual temperature of 6.6 °C (Wellner 1976). The habitat type is classified as *Tsuga heterophylla/Clintonia uniflora* (Cooper and others 1991a, 1991b). The soil has a silt loam surface layer 28 to 38 centimeters thick derived from Mount Mazama volcanic ash. The subsoil, 50 to 75 centimeters thick, is a silty clay loam derived from glacial lacustrine (lake) sediments. These are underlain at depths of 60 to 100 centimeters by gravely to very gravely sands and sandy loams deposited by alluvial processes. The soil is a medial, frigid Ochreptic Fragixeralf (Mission series). Before harvest, the site consisted of a well-stocked stand of about 90-year-old western white pine, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir, and western larch (*Larix occidentalis* Nutt.). About 40 years ago some western white pine was selectively harvested, creating one skid trail. This skid trail became part of the buffer around the treatment plots.

Study Installation and Treatments

The study site was divided into nine 0.8-hectare plots surrounded by a 200-meter buffer. Trees were directionally felled and skidded along a central skid trail or from the plot boundaries to prevent compaction during harvesting. The treatments were a three-by-three factorial design of three levels of residual organic matter and three levels of soil compaction, yielding nine types of treatments. Organic matter treatments were (1) bole only removal (OM1) in which the limbs were lopped on the plot before skidding; (2) bole and crown removal (OM2) in which the entire tree was removed from the plot; and (3) bole and crown removal and surface organic matter displacement (OM3) in which entire trees were removed and slash and surface organic matter were removed from the plot. Soil compaction levels consisted of none (C1), in which no mechanical equipment operated on the plot during harvesting or soil compaction; moderate (C2), in which a Grappler log carrier passed over the plots twice; and severe (C3), in which D-6 Caterpillar tractor passed over the plots four times.[1] For C2 and C3 treatments with OM1 and OM2 levels of surface organic matter removal, debris were removed into the buffers with the first equipment pass to prevent organic and mineral components from being mixed. The organic matter was then evenly redistributed on the plots. In each 0.8-hectare plot, 16 locations were established on a 20-meter grid. At each location, bulk density samples were taken with a core sampler. Samples were taken at 0 to 10 centimeters, 10 to 20 centimeters, and 20 to 30 centimeters to determine soil bulk density (table 1). Soil moisture during soil compaction averaged 25 percent.

Seedling Measurements

Each organic matter-soil compaction treatment was planted with local seed source of 1-year-old containerized inland Douglas-fir or western white pine seedlings at 2-meter spacing in May 1992. On June 1, 1993, three live Douglas-fir and western white pine seedlings per treatment were randomly selected. Root systems of these seedlings were excavated with a tile spade in a trench beyond the width and depth of the existing root system. Seedlings were refrigerated and taken to the laboratory for analysis of root and ectomycorrhizal tips. Entire roots systems were gently washed free of soil and extraneous material and subsampled in three cross-sections, 2.5 centimeters broad, in upper, middle and lower positions, generally occurring 5 to 10 centimeters, 15 to 20 centimeters, and 25 to 30 centimeters below the root collar. All active tips were tallied as nonmycorrhizal or ectomycorrhizal from characteristics observed through a stereo microscope (2× by 5×

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[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 1—Soil bulk density at 3 soil depths in areas receiving 3 levels of compaction and organic matter removal on volcanic ash soil in northern Idaho

Treatment	Depth (cm)		
	0-10[a]	10-20	20-30
		Gram/cm^3	
No soil compaction (C1):			
Bole only (OM1)	0.49a	0.71a	0.73a
Bole and crown (OM2)	.50a	.68a	.70a
Bole, crown and forest floor (OM3)	.61a	.76ab	.75a
Moderate soil compaction (C2):			
Bole only (OM1)	.71b	.82b	.84b
Bole and crown (OM2)	.70b	.78b	.83b
Bole, crown and forest floor (OM3)	.78bc	.81b	.82b
Moderate soil compaction (C2):			
Bole only (OM1)	.71b	.71a	.84bc
Bole and crown (OM2)	.74b	.85b	.86bc
Bole, crown and forest floor (OM3)	.84c	.85b	.91c

[a] Within a column different letters indicate significant differences between treatments ($p \leq 0.05$).

magnification). Root tips with root hairs, clear, translucent tips, and a lack of hyphal mantle were recorded as nonmycorrhizal. Root tips were judged to be ectomycorrhizal if mantled by hyphae; previous examination of Douglas-fir and western white pine root tips had shown that mantled rootlets always had the Hartig nets typical of ectomycorrhizae. Differentiation of ectomycorrhizal types was based on mantle structure, color, surface appearance, branching morphology, degree of swelling, length, and characteristics of rhizomorphs and emanating hyphae.

Statistical Analyses

The experimental design was a completely randomized block design. ANOVA was selected as the primary analysis technique. ANOVAS were performed separately for each species and variable. Means comparisons were calculated by using Fisher's LSD. Residuals from the performed ANOVAS were examined by using stem-and-leaf plots, normal probability plots, tests that the residuals come from normal distributions, and plots of residuals versus predicted values. In Douglas-fir, the hypothesis that the residuals came from a normal distribution was rejected only at a type I error rate of 0.05 for ectomycorrhizal types data ($p=0.04$). The null hypothesis was not rejected for any other variable in Douglas-fir or western white pine.

Results

Soil bulk density following C2 and C3 treatments was significantly higher compared to C1 treatments for nearly all soil depths and organic matter treatments (table 1). The average soil bulk density increased 20 and 23 percent, respectively, with C2 and C3 treatments compared C1 treatments for all organic matter treatments and soil depths. Much of the increase in soil bulk density occurred with just two passes of the Grappler log carrier (C2). Additional passes with the D-6 Caterpillar tractor (C3) failed to result in large additional increases in soil bulk density.

Table 2—The effects of soil compaction and organic matter removal on mean number of Douglas-fir and western white pine nonmycorrhizal root tips 1 year after outplanting

Treatment	Mean no. nonmycorrhizal root tips[a]	
	Douglas-fir	Western white pine
No soil compaction (C1):		
Bole only (OM1)	50a	77a
Bole and crown (OM2)	46a	92a
Bole, crown and forest floor (OM3)	45a	91a
Moderate soil compaction (C2):		
Bole only (OM1)	28b	34b
Bole and crown (OM2)	34b	39b
Bole, crown and forest floor (OM3)	23c	54b
Severe soil compaction (C2):		
Bole only (OM1)	15c	28b
Bole and crown (OM2)	21bc	24b
Bole, crown and forest floor (OM3)	18bc	30b

[a] Within a column, different letters indicate significant differences among treatments ($p \leq 0.05$).

The mean number of nonmycorrhizal root tips of both Douglas-fir and western white pine seedlings were significantly reduced in C2 and C3 compared to C1 treatments (table 2). Reductions in nonmycorrhizal root tips were dramatic, 40 and 51 percent for Douglas-fir and western white pine, respectively, in C2 treatments. In C3 treatments, reductions in nonmycorrhizal root tips were 62 and 78 percent for Douglas-fir and western white pine, respectively. Organic matter removal-treatments did not significantly reduce the number of nonmycorrhizal root tips for either conifer species.

Compared to C1 treatments, the mean number of ectomycorrhizal root tips was significantly reduced on Douglas-fir seedlings receiving C3 treatments with OM2 and OM3 removal (table 3). Ectomycorrhizal root tips were reduced over 60 percent for Douglas-fir in areas receiving these treatment combinations. The number of ectomycorrhizal root tips on western white pine seedlings was not significantly affected by any soil compaction or organic matter removal treatment; however, ectomycorrhizal root tips were significantly higher as a percentage of total root tips in C3 compared to C1 treatments and reflected the dramatic decline in the number of nonmycorrhizal root tips. For Douglas-fir, ectomycorrhizal root tips were significantly higher as a percentage of total root tips in the C3 and OM1 treatment combination compared to C1 treatments.

Compared to C1, the mean number of ectomycorrhizal types per seedling was significantly reduced for Douglas-fir in C3 and all organic matter removal-treatment combinations (table 4). Average number of ectomycorrhizal types per Douglas-fir seedling was reduced from 2.7 to 1. The average number of ectomycorrhizal types on western white pine seedlings was not significantly affected by any soil compaction or organic matter removal treatment. Twenty-six ectomycorrhizal morphological types were detected on seedling root systems (table 5). One year after outplanting, 15 types were present on Douglas-fir and 19 types on western white pine seedlings. Mycorrhizae were largely specific to individual host plants; only eight types occurred on both Douglas-fir and western white pine.

Table 3—The effects of soil compaction and organic matter removal on mean number of Douglas-fir and western white pine ectomycorrhizal (EM) root tips and ectomycorrihzal root tips as a percentage of total seedling root tips 1 year after outplanting

	Douglas-fir[a]		Western white pine[a]	
Treatment	No. EM	Percent EM	No. EM	Percent EM
No soil compaction (C1):				
Bole only (OM1)	70a	58a	85a	52a
Bole and crown (OM2)	91a	66a	131a	59a
Bole, crown and forest floor (OM3)	74a	57a	100a	52a
Moderate soil compaction (C2):				
Bole only (OM1)	65a	70a	124a	78b
Bole and crown (OM2)	55a	62a	85a	69ab
Bole, crown and forest floor (OM3)	61a	73ab	130a	71ab
Severe soil compaction:				
Bole only (OM1)	62a	80b	82a	75b
Bole and crown (OM2)	32b	60a	102a	81b
Bole, crown and forest floor (OM3)	29b	62a	81a	73b

[a] Within a column, different letters indicate significant differences among treatments ($p \leq 0.05$).

Table 4—The effects of soil compaction and organic matter removal on mean number of Douglas-fir and western white pine ectomycorrhizal types 1 year after outplanting

	Mean no. nonmycorrhizal root tips[a]	
Treatment	Douglas-fir	Western white pine
No soil compaction (C1):		
Bole only (OM1)	2.7a	3.7a
Bole and crown (OM2)	2.7a	3.3a
Bole, crown and forest floor (OM3)	2.7a	3.3a
Moderate soil compaction (C2):		
Bole only (OM1)	2.0ab	3.3a
Bole and crown (OM2)	2.0ab	3 7a
Bole, crown and forest floor (OM3)	2.0ab	3.3a
Severe soil compaction (C2):		
Bole only (OM1)	1.0a	3.3a
Bole and crown (OM2)	1.0b	3.7a
Bole, crown and forest floor (OM3)	1.0b	3.3a

[a] Within a column, different letters indicate significant differences among treatments ($p \leq 0.05$).

Table 5—Ectomycorrhizal morphological types on Douglas-fir (DF) and western white pine (WWP) seedlings after outplanting

Type	Host	Description of types
1	DF/WWP	Creamish to pale brown when young. Dark brown to blackish when old. Up to 10 millimeters long. Abundant brown hyphae surrounding the mantle. Rhizomorphs dark brown to blackish, long and branched. Granules of brown pigments stuck to the hyphae. Knobby appearance in the septa. No clamp connections.
2	WWP	Short, up to 2 millimeters. Brown. Many yellowish hyphae surrounding the mantle. Slender yellow rhizomorphs. Inner mantle is a net synenchyma, yellowish-walled hyphae. Clamp connections present.
3	DF	Pinnate. Long, up to 8 millimeters. Brown and shiny. No hyphae surrounding the mantle. Inner mantle a synenchyma. Lactarius-like type.
4	WWP	Pale orange-brown or buff. Short branched, up to 3 millimeters. Fluffy when young. No rhizomorphs or masses of hyphae arround the tips. Inner mantle a synenchyma. No clamp connections.
5	WWP	Brown. Irregular pattern of branched tips. 1-2 millimeters. No rhizomorphs. Inner mantle a synenchyma. Clamp connections present in the outer hyphae. Branched thick-walled outer hyphae.
6	WWP	Brown. Short branched. Up to 2 millimeters. No rhizomorphs. Clamp connections. Compact mantle. Emanating tips of hyphae (cyctsidia-like) in some areas. Inner mantle a synenchyma.
7	DF	Long, up to 10 millimeters. Blackish and woody appearance. No rhizomorph. No hyphae surrounding the mantle. Compact mantle. Synenchyma. Thick-walled hyphae. No clamp connections.
8	WWP	Short. Branched (bifurcate), up to 2 millimeters. Dark brown to black. Some brown hyphae on the surroundings. No rhizomorphs. Brown thick-walled hyphae. Compact mantle a synenchyma. Clamp connections. Short hyphae tips at the surface.
9	DF	Long. Pale brown to brown. Up to 3 millimeters. No rhizomorphs. Thin-walled hyaline. Clamp connections. Prosenchyma.
10	DF/WWP	Buff to pale brown. Pinnate. Up to 7 millimeters. No rhizomorphs. No clamps. Setae on the mantle surface resembling cystidia. Synenchyma.
11	WWP	Short, branched. Brown and woody appearance. Up to 2 millimeters. Hyaline hypahe surrounding the mantle. Clamp connections. No rhizomorphs.
12	DF/WWP	Branched (bifurcate). Buff to pale brown. Up to 2 millimeters. Synenchyma. No clamp connections. No rhizomorphs.
13	DF/WWP	*Cenococcum geophilum*
14	WWP	Short, branched. Pale brown-yellowish. Up to 2 millimeters. No rhizomorphs. No hyphae around the mantle. Synenchyma. Clamp connections.
15	DF	Straight to slightly pinnate, up to 3 millimeters. Orangish brown. Tapered tips. No rhizomorphs. Some hyphae arround the mantle. Synenchyma. Clamp connections.

Table 5—(Continued)

Type	Host	Description of types
16	DF	Long, up to 6 millimeters. Brown. No rhizomorphs. Compacted mantle. Synechyma.
17	DF/WWP	Pinnate, up to 7 millimeters. Buff. No rhizomorphs. Synechyma. Setaecyctidia-like on the surface of the mantle. Setae are thicker. Similar to B5, but this is more slender and brownish color.
18	DF/WWP	Brown to dark brown. Short, up to 2 millimeters. Branched (bifurcate). No rhizomorphs. No hyphae around the mantle. Dark-brown thick-walled hyphae. No clamp connections. (E-strain).
19	DF/WWP	Cenococcum-like. Up to 2 millimeters. Blackish. No hypae emanating like in Cenococcum. No rhizomorphs. No clamp connections. Greenish to blackish thick-walled hyphae. Synenchyma to interwoven hyphae.
20	WWP	Short, up to 2 millimeters. Brownish with whiteish mantle. Brownish rhizomorphs. No clamp connections. Synechyma.
21	WWP	Short, up to 2 millimeters. Bifurcate. Dark brownish tinted purplish to vinaceous. Fussy or felty. Rhizomorphs (brownish) of slender bifurcate setae-like brownish hyphae. Synenchyma. No clamp connections. Many pinkish to purplish pigments in KOH.[a]
22	DF	Short, up to 2 millimeters. Brown. clusters. No rhizomorphs. Synechyma. No clamp connections.
23	WWP	Only a few tips. Bifurcate, short, up to 2 millimeters. Purplish to vianceous, felty. Synechyma. Many brownish pigments in KOH. No clamp connections.
24	WWP	Greenish tints. Up to 3 millimeters. Bifurcate. No rhizomorphs. Regular Synechyma to stellate. Thick-walled brown hyphae.
25	DF	Bifurcate, up to 2 millimeters. Brown. No rhizomorphs. Clamp connections. Prosenchyma. Brown to orangish brown thick-walled hyphae.
26	DF/WWP	Long, up to 5 millimeters. Orangish brown. Pale brown at the young tips. No hyphae surrounding the mantle. No rhizomorphs. Inner mantle is an irregular synenchyma, occassionally brown, thick-walled hyphae on the mantle.

[a] KOH = potassium hydroxide.

Discussion

The reduction in numbers of nonmycorrhizal root tips for both Douglas-fir and western white pine seedlings in moderate and severe soil compaction is likely a result of the increased soil density. Soil compaction increases were significant at all three soil depths, and nonmycorrhizal root tips of Douglas-fir and western white pine seedlings were distributed throughout. Even after the C3 treatment, the average bulk density was still lower than that of many coarse-textured soils in the inland Pacific Northwest. This study indicated, however, that an approximately 20-percent increase in soil bulk density during soil compaction treatments can significantly reduce nonmycorrhizal root tip numbers on Douglas-fir and western white pine seedlings even though final bulk densities remained below 1.0 grams per cubic centimeter. The dramatic decline in nonmycorrhizal roots with C2 and C3 treatments decreases the ability of seedlings to capture site resources and may adversely affect reforestation success, especially on sites where the period for seedling establishment is limited.

Large increases in bulk density have been reported with the first vehicle pass over the soil (Gent and others 1984, Kroger and others 1984, Miles and others 1981, Reisinger and others 1988). In our study, average soil bulk density increased an average of 20 percent down to 30 centimeters after just two passes of the Grappler (C2). Soil compaction can persist for decades on some volcanic ash soils (Froehlich and others 1985). The degree of compaction depends on many factors, such as soil texture, moisture, structure, number of machine passes, and loading and operator skills (Geist and Cochran 1991). Loosening of compacted soils is slow on many sites in the inland Pacific Northwest because deep snow cover early in winter limits frost action, and low soil clay content limits shrink-swell potential. Therefore, compaction within the soil profile may remain high for many decades, especially at lower depths. Our study indicated nonmycorrhizal roots are most adversely affected in the first-year.

Not removing woody residue and surface organic matter on the site helps protects mineral soil from detrimental compaction (Page-Dumroese 1993); it also reduces erosion (Gilmour 1977, Rice and Datzman 1981), maintains soil nutrition (Page-Dumroese and others 1991), and soil microbe populations (Jurgensen and others 1991). This study indicates that leaving woody residue and surface organic matter (OM1) also helps maintain the production of ectomycorrhizal root tips on Douglas-fir in C3 areas. During seedling harvest, we observed that in compacted areas numbers of ectomycorrhizal root tips was greatest on seedling root systems within uncompacted, highly decomposed coarse woody debris. The diversity of Douglas-fir ectomycorrhizal types was still reduced, however, with C3 treatments in combination with all organic matter removal treatments (table 4).

Reductions in nonmycorrhizal and ectomycorrhizal root tip abundance may be a factor in the observed growth reduction of commercial timber species after extensive site preparation and subsequent compaction. On well-drained soils in Oregon formed from Mount Jefferson ash (Cochran and Brock 1985), compaction reduced height of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) seedlings for 5 years after planting. Compaction or displacement of organic material significantly reduced one or more growth variables of 15- to 25-year-old lodgepole (*P. contorta* Dougl. ex Loud.) and ponderosa pine in north-central Idaho (Clayton and others 1987). Froehlich (1979) suggests that compaction may reduce seedling growth for several decades. This study indicates some conifer species seem to be more sensitive than others to soil compaction effects. Additional research is needed to determine why ectomycorrhizal root tip abundance and diversity were significantly reduced on Douglas-fir but not on western white pine seedlings.

Loss of large soil aggregates and surface organic matter with C3 in combination with OM2 and OM3 treatments may be a factor in the reduced ectomycorrhizal root tip abundance and diversity on Douglas-fir. Soil aggregates and soil organic matter are important legacies passed from old stands to new stands following natural disturbance. Large soil aggregates are sustained by roots and hyphae of ectomycorrhizal fungi from the previous stand and provide packages of ectomycorrhizal propagules that can be important in future ectomycorrhizal formation (Borchers and Perry 1992). Surface organic matter also contains abundant propagules in the form of ectomycorrhizal spores, sclerotia, and hyphae important to ectomycorrhizal formation. Much ectomycorrhizal activity in forest soils is centered in this organic fraction (Harvey and others 1986) and can be impacted by soil compaction and organic matter removal.

Eight of the twenty-six ectomycorrhizal morphological types were detected on both Douglas-fir and western white pine seedling root systems (table 5). The ability of the two conifer species to form with compatible mycorrhizae could influence plant community development in a number of ways. Forest ecosystems change over time in response to many factors such as fire, wind, floods, insects, pathogens, climate, and management. During periods of rapidly changing aboveground community structure and composition mycorrhizal compatibility can facilitate conifer establishment by providing a ready source of inoculum, nutrients, and water (Amaranthus and Perry 1989a, 1989b; Amaranthus and others 1990). Over the long-term, shared mycorrhizal compatibility may influence the ability of plants to migrate into new locations and may affect plant migrations during periods of rapid global climate change (Perry and others 1990).

Our study indicates Douglas-fir ectomycorrhizal type diversity declines with increases in soil bulk density. Healthy forests typically have a highly diverse ectomycorrhizal flora (Arnolds 1991; Fogel and Hunt 1983; Eberhart and others, in press), yet there is little information that examines the impacts of loss of ectomycorrhizal diversity. Because each ectomycorrhizal fungus has its own set of physiological characteristics (Trappe and Fogel 1977), none can be said to be strictly redundant to any other. Some may be active at cool or moist times of year, others at warm or dry times. Some may be particularly effective at extracting phosphorus or nitrogen from mineral soil, others more effective at releasing bound nutrients from organic matter. Some may thrive in coarse woody debris, others in humus or other substrate components. One can argue that this diversity equips both tree and forest to functionally adapt to changes in season, habitats, assaults by pollution, or climate change and may be linked to the ability of Douglas-fir and western white pine to grow well over decades and centuries. Effects of soil compaction in this study are first-year results only, monitoring is needed to assess impacts on root tip abundance, diversity, and vegetative response over the long-term.

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Three levels of organic matter removal (bole only; bole and crowns; and bole, crowns, and forest floor) and three levels of mechanical soil compaction (no compaction, moderate compaction, and severe soil compaction) were studied as they influence Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don) seedlings following outplanting. Moderate and severe soil compaction significantly reduced nonmycorrhizal root tip abundance on both Douglas-fir and western white pine seedlings ($p \leq 0.05$). Ectomycorrhizal root tip abundance was significantly reduced on Douglas-fir seedlings in severely compacted areas with bole and crowns and bole, crowns, and forest floor removed. Ectomycorrhizal diversity also was significantly reduced on Douglas-fir seedlings in all severely compacted areas.

Keywords: Douglas-fir, ectomycorrhizae, forest harvest, organic matter, reforestation, root tips, soil compaction, bulk density, western white pine.

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