SITE DISTURBANCE EFFECTS ON A CLAY SOIL UNDER PINUS RADIATA — ROOT BIOMASS, MYCORRHIZAL COLONISATION, ^{15}AMMONIUM UPTAKE, AND FOLIAR NUTRIENT LEVELS

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ABSTRACT

Timber harvesting can result in adverse physical, chemical, and biological alterations to soil. The objective of this study was to examine the effects of site disturbance to determine the extent and duration of possible harvesting impacts on soil chemical and biological properties, including fine roots and mycorrhizas of *Pinus radiata* D.Don. The disturbance study was located in the North Island of New Zealand and was examined 9 years after organic matter and compaction treatments were installed. Treatments included undisturbed control plots, O horizon removed with no compaction, and O and A horizons removed with heavy compaction. Soil was examined for soil solution nitrogen, extractable nitrogen, fine root biomass, mycorrhizal root tips, and specific mycorrhizal root tip ^{15}ammonium uptake rates. Results showed that total fine root biomass was reduced with loss of both organic-rich soil horizons and compaction to approximately one-third of that in the control treatment, but that mycorrhizal infection rates were higher (averaging over 60%). With removal of only the O horizon, the largest effect was simply the loss of rooting volume and the roots that would normally occur in this horizon, with little reduction in root biomass or change in mycorrhizal infection rates in the mineral horizons. Specific mycorrhizal root uptake rates of ^{15}ammonium did not appear to have been changed by the most severe disturbance treatment. However, the unaltered uptake rate may be due to the predominant mycorrhizal morphotype found in the most-

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severe treatment which was different from the dominant morphotype found in the two less-severe treatments. Reduced fine root biomass of the severe disturbance treatment correlated with reduced tree growth and foliar nitrogen.

Keywords: mycorrhizal colonisation; fine roots; foliar nutrients; forest recovery; soil compaction; timber harvesting.

INTRODUCTION

Timber harvesting can physically disturb soil resulting in removal of litter and mineral soil, or compaction. As vegetative cover may be removed during harvesting, a variety of physical, biological, and chemical changes in soil properties can occur in addition to the direct effects caused by physically disrupting the soil. Combined harvesting and disturbance effects can include numerous soil physical changes. The microclimate, such as soil temperature, can be affected (Fowler & Anderson 1987; Skinner *et al.* 1989; Spittlehouse & Strathers 1990), soil structure may be lost or altered, porosity can change, soil horizons may be mixed or removed (Swanston 1974; Clayton 1981), water infiltration can be reduced, and soil may be compacted (Kemper *et al.* 1971; Parish 1971; Froehlich 1979). Harvesting can create a poor rooting environment, increasing soil resistance to root penetration (Skinner *et al.* 1989). Likewise, harvesting and disturbance can change soil chemical properties including soil solution concentrations, nutrient capitals (Vitousek *et al.* 1992; Zabowski *et al.* 1996; Johnson & Todd 1998), weathering (Zabowski *et al.* 1994), and quantity and quality of organic carbon (Black & Harden 1995; Pennock & van Kessel 1997). Dyck & Skinner (1990) concluded that excessive soil disturbance is one major factor in the loss of soil quality and potentially can cause a decline in productivity of both high- and low-quality *Pinus radiata* sites in New Zealand.

If harvesting practices adversely affect soil biology and chemistry, then nutrient availability and acquisition may be affected through either reduced soil nutrient supply or decreased capabilities of the plants to access soil supplies, both of which will ultimately affect productivity. Timber harvesting may alter soil biota and the processes mediated by them either directly (physical damage to biota from harvesting) or indirectly through the alteration of the soil environment. It can be instructive to study forest soils and forests during recovery after timber harvesting to determine how essential soil biota might be influenced, as indicated by direct measures (e.g., counts — Ingham & Thies 1996) or indirect measures such as decomposition rates and release of carbon dioxide (Fernandez *et al.* 1993; Marra & Edmonds 1996; Lytle & Cronan 1998).

A few studies report how ectomycorrhizas are affected by timber harvesting and disturbance even though this symbiont has been shown to influence nutrient (especially nitrogen) and carbon physiology (Rygiewicz & Anderson 1994; Smith & Read 1997), weathering release of soil nutrients (Mojallali & Weed 1978; Jongmans *et al.* 1997), and soil solution nutrients (Knight *et al.* 1989). Loss of ectomycorrhizas and reductions in tree growth have been linked to high levels of soil disturbance, or removal of organic horizons (*see* review by Jurgensen *et al.* 1997). Exceptions to this general pattern have been found, e.g., numbers of mycorrhizal root tips on western white pine (*Pinus monticola* Dougl. ex D. Don) did not change due to removal of organic matter or soil compaction (Page-Dumroese *et al.* 1998). However, in this study, a compensatory response of the pine seedlings was found; proportions of mycorrhizal root tips increased because the numbers

of nonmycorrhizal root tips significantly declined due to disturbance treatments. Root biomass of *Acacia mangium* Willd. plantation trees decreased as soil depth increased in plots following both manual and tractor-hauling removal of the precedent rainforest trees (Högberg & Wester 1998). Differences in root biomass between treatments were not significant when data were pooled for the entire treatment plots, but when samples taken within and outside tractor tracks were compared root biomass, mycorrhizal colonisation, and root nodulation rates were significantly decreased in the tractor tracks. The authors attempted to determine if harvesting practices reduced nitrogen fixation rates using natural abundance values of ^{15}nitrogen. It is unfortunate that small and inconsistent differences in ^{15}nitrogen values between non-nitrogen-fixing reference species and *A. mangium* were found and this precluded making the assessments.

Determining if nutrient uptake by roots in compacted soil is altered has received little attention. As summarised by Shierlaw & Alston (1984) for cereal crops and phosphorus, increased ion movement to roots by diffusion in compacted soil is countered by restricted root growth, generally resulting in less acquisition of phosphorus in compacted soil than in non-compacted soil. If only a portion of the soil volume occupied by roots is compacted, then compensatory processes (e.g., enhanced root growth and nutrient uptake rates) may occur in the non-compacted areas. Therefore, relative to non-compacted soil, nutrient uptake rates and total foliar amounts of nutrients for plants grown in compacted soil are not necessarily diminished, but the areas in the soil from which nutrients are acquired may vary. Shierlaw & Alston (1984), studying annual ryegrass (*Lolium rigidum* Gaud.) and maize (*Zea mays* L.), found greater uptake of phosphorus per unit length of root for both species in the compacted areas of soil than in non-compacted regions.

To determine the extent and duration of timber harvesting disturbances on aspects of below-ground productivity and function, a soil disturbance study located on the North Island of New Zealand was examined for extended effects on soil chemical and biological properties. Zabowski *et al*. (1996) previously reported on changes in soil solutions and mineral stability at this site. In this paper we report on how fine roots and mycorrhizas, available soil nitrogen, specific rates of ammonium uptake, and foliar nutrient levels varied 9 years after the disturbance treatments were imposed. Seedling and sapling development can be good indicators of longer-term effects of soil compaction (Mitchell *et al*. 1982), and negative effects of compaction on tree growth have been found up to 45 years after the soil was disturbed (Froehlich *et al*. 1985). We measured densities of fine roots and mycorrhizas at various soil depths, the proportion of fine root tips colonised by mycorrhizal fungi, ^{15}ammonium uptake by the predominant mycorrhizal morphotype, soil extractable and soil solution nitrogen, and selected foliar nutrients.

MATERIALS AND METHODS

Soil Disturbance Treatments

The Maramarua soil disturbance study was established in 1981 in the Waikato Forest located in the North Island of New Zealand near the Firth of Thames and has been described previously (Skinner *et al*. 1989). The site was converted from native forest to *P. radiata* in 1930. First-rotation *P. radiata* was harvested in 1981 using a cable-hauler system to minimise soil disturbance. Five soil disturbance treatments ranging from minimal to severe

were installed with five replicate 0.06-ha plots in a randomised block design (Skinner *et al.* 1989). The site was replanted in *P. radiata* after treatments were installed.

The soil was a clayey, kaolinitic, mesic Typic Hapludult developed from highly-weathered greywacke (Zabowski *et al.* 1996). Undisturbed soil horizons consisted of O (ranging from 3 to 1 cm deep), A (averaging 9 cm), Bt1/A (41 cm), Bt2 (55 cm), Bt3 (60 cm), and BC (>20 cm) (*see* Zabowski *et al.* 1996 for a complete description).

In 1990, we re-examined three of the five treatments: no disturbance (UN), and two disturbance treatments simulating levels of organic matter loss [O horizon removed (OR), and O and A horizons removed followed by high compaction from eight passes of a loader (OARHC)]. A persistent platey structure (2–4 cm thick) was evident in the surface of the Bt1/A horizon.

Mass of Roots and Mycorrhizas, and Root Colonisation by Mycorrhizal Fungi

Roots were sampled by taking two, 3-cm-diameter, soil cores per plot (five plots per treatment, 10 cores per treatment, 30 cores total). Using preliminary sample cores, no uniform pattern was found between mass of roots and distance from tree trunks (one-quarter, one-half, and full tree height). Therefore, one soil core was taken at one-half tree height from under each of two trees randomly selected in each plot. The Oa horizon was included in cores when present and horizon depths were noted. Cores were immediately placed in plastic tubes and stored in a cooler until they were brought to the lab. Cores in tubes were stored at 4°C until processed (within 48 h of removal from the field).

Cores were separated into 5-cm segments by depth within each organic or mineral horizon, and the total thickness of each horizon was also noted. Soil segments were placed in distilled water in plastic bottles and incubated overnight. Soil samples were gently shaken until roots and mycorrhizas became dislodged from soil. Slurries were washed over a series of sieves with mesh sizes of 5, 2, and 0.05 mm. Washed and sieved material was examined under a stereomicroscope and coniferous fine roots (< 2 mm diameter) and mycorrhizas were removed from all other material. Recovered material was oven dried (75°C) and then weighed.

Colonisation by fungi was evaluated on all fine root tips collected, using a stereomicroscope. Washed roots were stained following a 0.05% trypan blue/lactoglycerol procedure modified from the trypan blue/acidic glycerol method of Koske & Gemma (1989). Prior to clearing roots with potassium hydroxide and then staining them, dried root samples were rehydrated in 50% ethanol (R.M.C.Muchovej, pers. comm.).

Mass of roots and mycorrhizas, total numbers of root tips, and mycorrhizal colonisation rates of root tips determined for each segment of the soil cores were determined. These values were used to calculate fine root and mycorrhizal root tip densities (mass per unit volume soil), numbers of total fine root tips per unit volume of soil, and mycorrhizal root tip colonisation rates per unit volume of soil for each 5 cm depth in each organic and mineral horizon. A single-factor analysis of variance was used to compare fine root densities and total number of root tips by horizon. No statistical comparisons were made with the 5-cm depth increments due to the high variability between replicates and within horizons.

Soil and Foliar Analysis

Soil samples were collected from the O, A, and Bt1/A horizons, air-dried, and sieved to < 2 mm. Air-dried sieved soil was assessed for extractable nitrogen by standard 2 M KCl extraction (Keeney & Wilson 1982). Soil solutions were collected from fresh soil samples using centrifugation with double-bottomed centrifuge cups following procedures by Zabowski *et al*. (1996). Centrifuged solutions were filtered to 0.2 mm using disposable syringe filters. Concentrations of ammonium and nitrate in extracts and soil solutions were determined by autoanalyser and ion chromatograph, respectively. Soil pH was measured in water (1:5), and soil organic matter was determined by loss on ignition.

Foliar analysis was done using samples of current-year, fully-expanded needles and 1-year-old needles on second-order lateral branches which were collected in 1989 from 10 trees per plot in each treatment. Samples were oven-dried (80°C), ground to a fine powder, and analysed for nitrogen and phosphorus by the methods of Nicholson (1984).

Uptake of ^{15}Ammonium by Mycorrhizal P. radiata Roots

Specific rates of ammonium uptake were assessed in an experiment conducted in the field using freshly harvested mycorrhizal pine roots. Samples were collected by gently removing soil and mycorrhizal roots from the upper 15 cm of mineral soil with a hand trowel, at a distance from the trunk equivalent to one-half tree height, from beneath four randomly-selected trees per plot. The predominant mycorrhizal morphotype was immediately hand-sorted by visual inspection. All phases of the uptake experiment were conducted using a complete, dilute, nutrient solution (Rygiewicz *et al*. 1984). Firstly, mycorrhizal tips were washed once for 15 min at 15°C in a nitrogen-free formulation of the dilute nutrient solution. An uptake period (45 min at 15°C) followed, using a solution containing 0.35 m$\underline{M}$ $(^{15}NH_4)_2SO_4$. Tips were desorbed in a solution containing 0.7 m$\underline{M}$ $(^{14}NH_4)_2SO_4$. Periodically, solutions with roots were shaken gently by hand. Desorbed tips were kept on ice until they could be returned to the lab and frozen (within 6 hours). Uptake of ammonium was determined using ^{15}nitrogen enrichment of samples determined by isotope ratio mass spectroscopy following oxidation of nitrogen in the sample (Isotope Services Inc., Los Alamos, NM, USA).

Single-factor analyses of variance, using the three disturbance treatments as levels of the factor, were done on the dependent variables.

RESULTS

Fine Roots and Mycorrhizal Root Tips

Average densities of fine roots and putative mycorrhizas for the soil profile sampled were greatest in the Oa and A horizons of the UN (undisturbed soil) treatment (Fig. 1a). Densities in the A horizon of the OR (O horizon removed) treatment were approximately two-thirds that of the values calculated for the A horizon in the UN treatment. Nevertheless, single-factor analysis of variance showed that there was no statistical difference in root density between treatments in the A horizon ($p = 0.31$), undoubtedly due to the high variability in the UN treatment. In the Bt1/A horizon, there was a small and consistent trend ($p = 0.69$) of decreased fine root and mycorrhizal root tip densities with increased soil disturbance (UN>OR>OARHC), with the OARHC treatment (Oa and A horizon removed

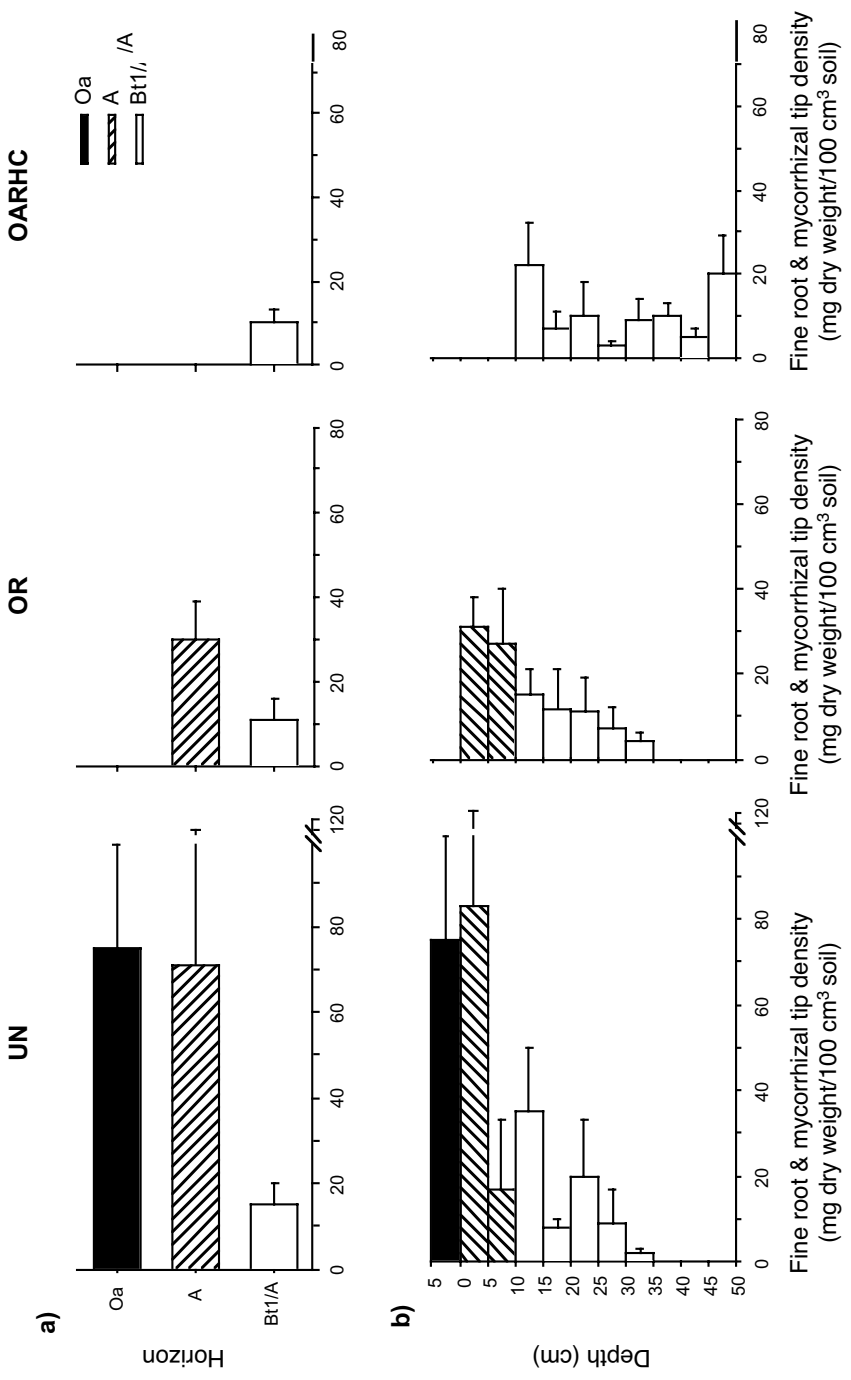

FIG. 1–Mean and standard error of mass of oven-dried fine roots (<2 mm) including ectomycorrhizal and nonmycorrhizal root tips/100 cm^3 soil (root density) in undisturbed soil (UN), O horizon removed (OR), and O and A horizon removed followed by compaction (OARHC). Total mass of fine roots is shown by horizon in (a), and by 5-cm depth increments in (b).

following by high compaction) having the lowest density. However, when fine root and mycorrhizal tip densities were summed over all horizons, there was a significant difference between treatments ($p = 0.03$) showing the overall effect of soil loss.

Changes in densities of fine roots and mycorrhizal tips with increasing depth were not consistent among the three soil disturbance treatments (Fig. 1b). The overall pattern for the UN and OR treatments was decreasing densities as depth increased, with relatively larger changes in density values occurring at horizon boundaries (cf. Fig. 1a and 1b). However, there might not be significant differences in density values between any two adjacent 5-cm segments within a horizon. The lack of a difference in densities between the Oa and A horizons of the UN treatment (Fig. 1a) appeared to result from within-horizon variation in density values for the A horizon. The upper 5-cm segment of the A horizon had density values similar to those of the Oa horizon, while the lower 5-cm segment had a density value lower than that for either of the upper 5-cm segments. For the OR treatment, within-horizon changes in density values were not apparent in the A horizon. A slight decrease in density was apparent at the boundary between the Oa and A horizons, but the greater effect on lower root densities in the Bt1/A horizon than in the A horizon was the decrease in density values at the lower depths of the Bt1/A horizon. Unlike the overall decreasing pattern of root density as depth increased found for the UN and OR treatments, density in the OARHC treatment was initially higher at the surface of the Bt1/A horizon, decreased at the intermediate horizon depths, and appeared to increase in the deepest 5-cm segment. Interestingly, the upper 5-cm segment of Bt1/A soil, where the platey structure from compaction was evident, had a fine root and mycorrhizal tip density similar to that of the 45–50 cm depth.

When total numbers of root tips (both mycorrhizal and nonmycorrhizal) are considered (Fig. 2), treatment effects are different from those found for root tip densities. Although the summation of total fine root tips (O + A + Bt1/A) by treatment was not significantly higher (single-factor ANOVA, $p = 0.39$), total fine root tips in the Bt1/A horizon were significantly different (single-factor ANOVA, $p = 0.02$). Total numbers of root tips in the Bt1/A horizon of the OARHC were similar to those of the Oa and A horizons of UN, and much greater than the values for the Bt1/A horizon of either UN or OR treatments (Fig. 2a). In fact, the smallest mean numbers of tips in the A and Bt1/A horizons occurred in OR, not in the most severe soil disturbance treatment, although the numbers of tips in OR were not significantly different from those in UN. Thus, as both the smallest root biomass and the greatest numbers of root tips occurred in the OARHC treatment, this indicates roots in this soil were generally smaller and/or more branched. The predominant mycorrhizal morphotype in UN and OR treatment soil was similar in colour (white mantle), whereas the morphotype in OARHC was a dull yellow/brown.

Mean numbers of fine root tips among horizons were generally lower in deeper horizons than in upper horizons of the same treatment. Within the A and Bt1/A horizons, tip numbers generally decreased in each deeper 5-cm segment of the soil core (Fig. 2b). Although the mass of fine and mycorrhizal roots tended to be unaffected by depth with compaction, the numbers of tips were greater in the upper Bt1/A than in the lower depth increments.

Mean colonisation of root tips by mycorrhizal fungi was generally similar among horizons for the UN and OR treatments (Fig. 3a). Percentages of mycorrhizal tips were not significantly different among treatments in the Bt1/A horizon, although average colonisation

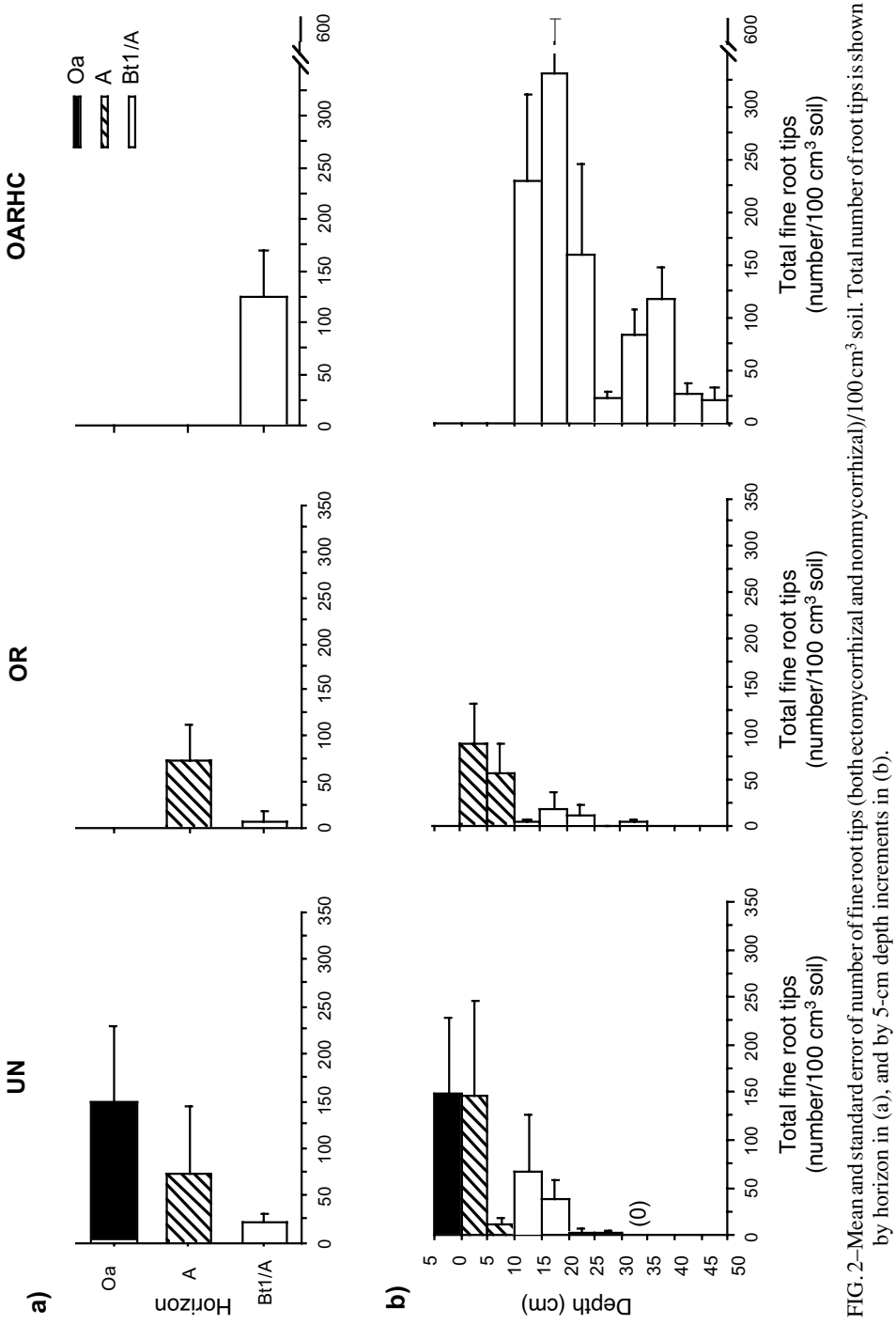

FIG. 2–Mean and standard error of number of fine root tips (both ectomycorrhizal and nonmycorrhizal)/100 cm^3 soil. Total number of root tips is shown by horizon in (a), and by 5-cm depth increments in (b).

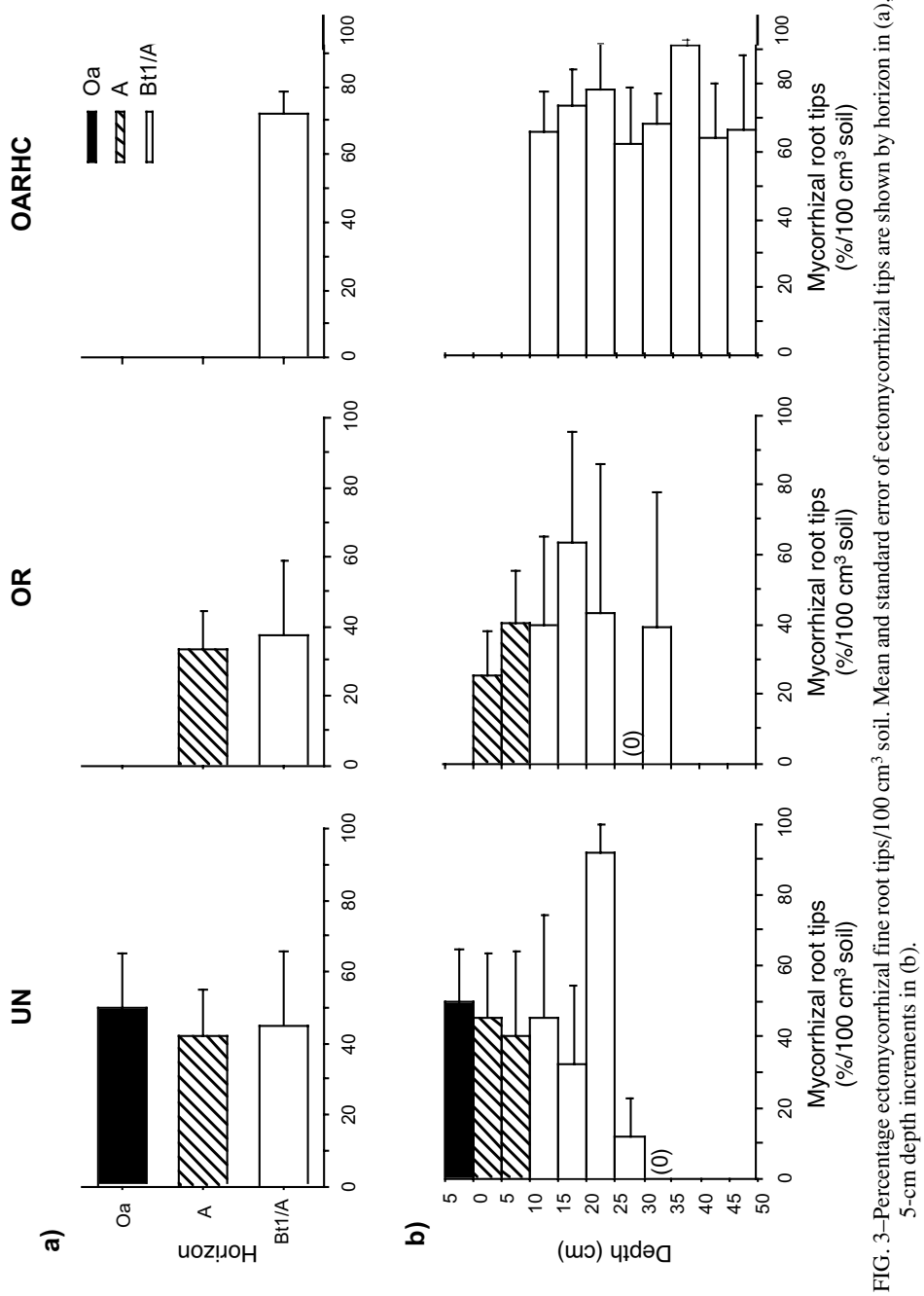

FIG. 3–Percentage ectomycorrhizal fine root tips/100 cm^3 soil. Mean and standard error of ectomycorrhizal tips are shown by horizon in (a), and by 5-cm depth increments in (b).

rate was somewhat higher in the treatment with compaction. Surprisingly, there was no apparent trend of decreasing rates of mycorrhizal fungal colonisation by depth either among horizons or within horizons (Fig. 3b). Colonisation in the Bt1/A was more variable with depth in the UN and OR treatments, whereas it was consistently above 60% in the OARHC treatment.

^{15}Nitrogen Uptake and Soil Nutrients

Mycorrhizas in the OR treatment absorbed ^{15}ammonium at the fastest rate (15.9 $\pm$ 0.66 μMol ^{15}N/g dry wt · h). Lower but similar rates occurred in the mycorrhizas of the UN and OARHC treatments (14.2 $\pm$ 0.81 and 14.4 $\pm$ 0.65 μMol ^{15}N/g dry wt · h, respectively); uptake rates were not significantly different. Root tips were smaller in the OARHC treatment (Fig. 1 and 2), and so total nitrogen uptake per mycorrhizal tip actually may be lower in this treatment. Despite the similar uptake rates by mycorrhizas in the UN and OARHC treatments, the predominant mycorrhizal morphotype in each treatment appeared different (white *vs* yellow/brown mantle).

Potassium chloride-extractable ammonium and nitrate were greatest in the Oa horizon (Table 1), and lowest in the Bt1/A horizon. Treatment effects were not significant within horizons. Removal of the O horizon did not affect concentrations of either ammonium or nitrate in the mineral soil. Nevertheless, removal of the O and A horizons removes much of the available soil nitrogen. As with the extractable nitrogen, soil solution ammonium and nitrate concentrations were also highest in the O horizon. Soil solution ammonium and nitrate in the mineral soil were not significantly different by treatments.

Soil pH was lowest in the Oa horizon and increased to similar values in mineral horizons among all treatments. The soil pH at Maramarua is typical of values under *P. radiata* on Ultisols of New Zealand (New Zealand Soil Bureau 1954). Soil pH does not appear likely to have affected the mycorrhizas or the uptake rates. Soil organic matter content was highest in the Oa horizon. In the UN and OR treatments, percentage organic matter decreased with depth. Nine years after the soil disturbance treatments were imposed, a slight increase in organic matter was found in the Bt1/A horizon of the OARHC treatment compared with the same horizon of the other treatments.

Foliar Nutrients

Established satisfactory foliar nutrient levels for *P. radiata* are: N $\geq$1.5%, P $\geq$0.11%, K $\geq$0.5%, Ca $\geq$0.1%, Mg $\geq$0.08% (Will 1985). Foliar analysis of *P. radiata* showed that all nutrients except nitrogen appeared to be in adequate supply (Table 2). Concentrations of nitrogen, phosphorus, potassium, and magnesium in current-year foliage were similar to or higher than in 1-year-old foliage, while comparable calcium concentrations were lower. When comparisons are made between treatments, it is evident that foliar nitrogen and potassium concentrations were reduced in the OARHC treatment, and only potassium appeared to have been affected by the OR treatment.

DISCUSSION

Soil disturbance clearly altered fine root and mycorrhizal root tip densities in surface soil, largely through the loss of the organic-rich Oa and A horizons — a prime habitat for

TABLE 1–Extractable nitrogen, nitrogen in soil solution, soil pH, and soil organic matter after soil disturbance treatments. Values are means (n = 5) with standard error in parentheses. Treatments are: UN (undisturbed), OR (O horizon removed), and OARHC (O and A horizons removed followed by high compaction).

Treatment	Horizon	KCl extractable (mg/kg)		Soil solution (m*M*/litre)		pH	Organic matter (kg/kg)
		NH_4^+	NO_3^-	NH_4^+	NO_3^-		
UN	Oa	53.6 (14.4)	0.04 (0.03)	108 (26)	0.09 (0.03)	4.27 (0.11)	88 (3.3)
	A	7.23 (2.34)	0.00 (0.00)	8.2 (7.2)	0.04 (0.02)	4.83 (0.05)	8.2 (0.8)
	Bt1/A	3.66 (1.47)	0.00 (0.00)	2.8 (2.8)	0.07 (0.03)	4.83 (0.09)	6.4 (0.6)
OR	A	5.87 (2.60)	trace	6.1 (2.6)	0.07 (0.03)	4.79 (0.04)	8.2 (0.4)
	Bt1/A	2.81 (1.54)	trace	3.3 (1.5)	0.03 (0.01)	4.77 (0.04)	6.3 (0.3)
OARHC	Bt1/A	3.3 (0.11)	0.00 (0.00)	0.6 (4.2)	0.05 (0.03)	4.82 (0.05)	7.3 (0.2)

TABLE 2–Foliar nutrient contents of current and 1-year-old *Pinus radiata* needles after soil disturbance treatments. Foliar samples were taken in 1989, 8 years after soil disturbance treatments were imposed. Data are means (n = 50) with standard errors in parentheses. Treatment codes are described in Table 1.

Treatment	Needle age	N	P	K	Ca	Mg
		g/kg				
UN	Current	12.4 (0.5)	1.3 (0.1)	9.8 (0.3)	1.8 (0.1)	1.3 (0.1)
	1-year-old	12.0 (0.4)	1.3 (0.1)	7.9 (1.2)	4.3 (0.2)	1.0 (0.1)
OR	Current	12.7 (0.4)	1.4 (0.1)	7.3 (1.2)	1.6 (0.1)	1.1 (0.04)
	1-year-old	11.6 (0.7)	1.3 (0.1)	7.5 (0.9)	4.0 (0.3)	0.8 (0.03)
OARHC	Current	11.1 (0.2)	1.1 (0.1)	6.6 (0.5)	1.8 (0.1)	1.2 (0.04)
	1-year-old	10.0 (0.3)	1.0 (0.1)	6.6 (0.9)	3.5 (0.3)	1.0 (0.1)

mycorrhizas. The highest fine root (including mycorrhizal tips) mass and numbers of root tips (Fig. 1 and 2) were found in the Oa and A horizons. Considering the top 35 cm of soil as a whole, it is apparent that there were fewer fine roots/mycorrhizas when any organic soil was removed as mean densities decreased from 35 to 15 and 12 mg/100 cm^3 soil in the UN, OR, and OARHC treatments respectively. Thus, loss of the O and A horizons is likely to reduce the total amount of fine root and mycorrhizal tip mass in the soil. Clearly, removal of either the O horizon, or the O and A horizons, was not compensated for by increased root production in the remaining surface soil horizon. However, the trend of greater total fine root and mycorrhizal tip numbers and mycorrhizal colonisation levels in the Bt1/A horizon of the compaction treatment may be possible compensatory responses. These changes in root and mycorrhizal tip development can result in increased absorptive surface area rather than an increase in root mass, especially since mycorrhizal numbers increased in the Bt1/A. Ares & Peinemann (1992) found decreased root densities of several coniferous tree species with depth, also a common pattern for *P. radiata* (Davis *et al.* 1983; *see* Nambiar & Sands 1992 for other reports), and that soil organic matter content provided the best correlation with root densities. Loss of nutrients due to removal of the topsoil was implicated to reduce growth of *Gmelina arborea* Roxb. and *Terminalia brassii* Exell. seedlings in forests of the Solomon Islands (Neumann 1987).

Besides habitat removal, another major effect of soil loss was decreased mass of roots and mycorrhizal tips in the remaining surface soil. When soil disturbance consisted of removing the forest floor (OR treatment), fine root densities and numbers were reduced by approximately half, with mycorrhizal fungal colonisation rates reduced by two-thirds in the top 5 cm of the A horizon. Considering the A horizon as a whole, tip numbers and percentages of mycorrhizal tips were reduced but not significantly, despite reduced fine root densities. This suggests a similar root/mycorrhizal morphology to the UN treatment (and also the mycorrhizal morphotype was similar), with possibly a slight increase in fine root size. Despite this similarity in morphology, ^{15}ammonium uptake rates were higher in the OR treatment. In addition, soil solution and soil extractable-ammonium were similar between the UN and OR treatments. Clearly this increased uptake rate compensated for reduced fine root and mycorrhizal tip densities as *P. radiata* foliar nitrogen concentrations did not show any extended alterations by the OR disturbance treatment. Nutrient foliar analyses (Table 2) indicate that even though calcium levels in current-year foliage were diminished, nitrogen (based on both needle-age classes) was the nutrient most likely limiting growth at the Maramarua site. So, the increased ^{15}ammonium uptake rates found in the OR treatment may reflect compensatory processes to mitigate the relatively greater nitrogen-limited condition of this treatment compared with the UN treatment. The *P. radiata* trees were measured at age 11, and mean aboveground tree volume was 0.45 m^3, 0.33 m^3, and 0.15 m^3 for the UN, OR, and OARHC treatments, respectively (Murphy *et al.* 1997). Tree volume in both disturbance treatments was less than in the UN treatment. However, volume was reduced in the OR treatment by less than half (26%) of the reduction measured in the OARHC treatment (67%).

Loss of organic-rich soil horizons and surface compaction (OARHC) resulted in reduced mass of roots and mycorrhizal tips, but roots that were produced tended to be finer, as indicated by increased numbers of root tips compared to the Bt1/A horizon in undisturbed soil. Soil compaction frequently changes root morphology of species of angiosperms and

gymnosperms, e.g., thinner roots are formed with higher permeability due to increased hydrostatic pressure, and more root branching and cellular alterations can occur. However, there is considerable variability among species in which characteristics respond to the stress (Simmons & Pope 1987, 1988; Liang *et al*. 1999). The mycorrhizal fungal colonisation rates also increased throughout the remaining soil of the B horizon, and the predominant mycorrhizal morphotype was clearly different from that in the UN treatment. Thus, loss of topsoil and compaction of the surface resulted in slightly different effects on roots and mycorrhizas compared with only loss of forest floor; some of this may be specifically the result of decreased root penetrability. Abercrombie (1990) found roots of avocado (*Persea americana* Mill.) trees restricted to the topsoil in compacted soils, with only sporadic occurrence of roots below the compacted layers. Skinner & Bowen (1974) found reduced mycorrhizal mycelium in soils that had been compacted, and Skinner *et al*. (1989) found increased soil resistance in the top 20 cm of the B horizon in the OARHC treatment 1 year after disturbance. Working in south-east Asia, Högberg & Wester (1998) found reduced fine root biomass, mycorrhizal infection, and root nodulation of *Acacia mangium* under tractor tracks compared with other areas of the plantations not subjected to compaction. Also, organic matter was lost in the tractor tracks due to erosion of the topsoil. Perhaps smaller roots with more root tips may compensate for decreased soil penetrability by allowing greater utilisation of a restricted soil volume without extensive root exploration of the soil. Nevertheless, increased nitrogen uptake rates were not found in the OARHC treatment, and soil solution and extractable soil nitrogen were lower, indicating reduced availability of soil nitrogen (Tables 1 and 2). This lower nitrogen uptake rate was evident in the reduced foliar nitrogen concentrations and the vastly reduced volume of the trees; tree volume in the OARHC treatment was reduced by 67% compared with the UN treatment (see above in this section for results of Murphy *et al*. 1997). These results suggest that the compaction effects may outweigh the nutrient acquisition benefits imparted by mycorrhizas, as was also found by Simmons & Pope (1987). Our data for the two disturbance treatments are partially consistent with those of Nambiar & Sands (1992). They found reduced tree growth due to disturbance treatments [soil was either (1) physically disturbed and then back-filled into its original place, (2) compacted, or (3) compacted and then subsequently perforated in a grid pattern], but no treatment effects on foliar nutrient concentrations.

We found different types of the predominant mycorrhizas on the *P. radiata* trees among the disturbance treatments. Richness of species forming ectomycorrhizal tips was reduced on *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) seedlings, but not on *Pinus monticola* seedlings, after organic matter was removed or soil was compacted (Page-Dumroese *et al*. 1998). These authors did not report values for nitrogen uptake rates by roots, or for foliar nitrogen contents, to indicate if different process rates by the varied ectomycorrhizal fungal communities might have occurred among treatments. Species richness and diversity of ectomycorrhizal fungal types on two species of dipterocarp seedlings were affected by logging treatments evaluated in Malaysia (Lee *et al*. 1994). However, inconsistent patterns in these estimates of the ectomycorrhizal fungal community were found among the various logging practices investigated. Similar results were also found in a related study in Malaysian dipterocarp forests done by Watling *et al*. (1996). In the latter study, the authors also found no differences in ectomycorrhizal colonisation rates among logging treatments. Inconsistencies in responses may be related to the structures of the canopies of the residual forest (number, size and age of trees, size of gaps, etc.) and light

interception. Reduced photosynthetically-active photon flux densities at the understorey level in residual forests can decrease carbon acquisition and allocation by regenerating seedlings, thus reducing carbon available to sustain the mycorrhizal symbiosis (Gardingen *et al*. 1998). At the Maramarua site, we found trees of decreasing volume as the severity of the disturbance treatments increased.

In summary, it is evident that soil disturbance resulted in changes in both fine roots and mycorrhizal tips. With removal of only the forest floor, an increased nitrogen uptake rate partially compensated for reduced soil nitrogen availability and decreased fine root and mycorrhizal tip densities. With loss of both O and A horizons and compaction of the surface B horizon, there was a decrease in fine root densities and no difference in nitrogen uptake rates compared with the undisturbed soil. Nitrogen uptake rates and percentages of mycorrhizal tips appear to be less effective in compensating for the decreased fine root densities as foliar nitrogen and tree volumes remained reduced 9–11 years after disturbance treatments.

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