

AN ABSTRACT OF THE THESIS OF

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Title: Mycorrhiza Formation and Diversity in Undisturbed
Forest and Clearcut and Burned Areas in Three
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Abstract approved:

Signature redacted for privacy.


David A. Perry

A greenhouse bioassay was used to compare ectomycorrhiza formation and diversity in soils from undisturbed and clearcut and burned areas in moist mesic, moist montane and dry montane forest types representing a gradient of environmental harshness. It was hypothesized that mycorrhiza diversity decreases with increasing environmental harshness and that stability of mycorrhiza formation following clearcutting and burning is positively related to mycorrhiza diversity.

Soils were collected from three forest/clearcut pairs in each forest type. Clearcut and burned areas were well-stocked with both planted and naturally seeded conifers. The field soils were used to inoculate

greenhouse planting media in which Douglas-fir and ponderosa pine seedlings were grown. Douglas-fir seedlings were grown in moist mesic and moist montane soils and ponderosa pine seedlings were grown in dry montane soils. Numbers of mycorrhizal root tips and short roots by mycorrhiza type were determined and used to calculate percent mycorrhizal colonization, mycorrhiza type proportions, diversity indices, and branching indices.

For undisturbed forest soils, percent mycorrhizal colonization and diversity index of root tips increased across the gradient from the moist mesic to the dry montane sites. Numbers of total and mycorrhizal root tips were significantly higher in undisturbed soils from the dry montane type but did not differ between undisturbed moist montane and moist mesic soils. Greater numbers of total and mycorrhizal root tips in the dry montane soils may be partially due to the tendency of ponderosa pine roots to branch more than those of Douglas-fir. Two mycorrhiza types, Rhizopogon sp. and an unidentified brown type, dominated all soils and were usually accompanied by several minor types, each of which seldom comprised more than 5% of the mycorrhizal root tips.

When clearcut and burned soils were compared with undisturbed forest soils within each forest type, percent

mycorrhizal colonization was higher in clearcut than in undisturbed soils from both the moist mesic and the dry montane types. Numbers of mycorrhizal root tips were higher in clearcut soils from the moist mesic and the dry montane types while numbers of total root tips were higher in clearcut soils from the dry montane type only. Mycorrhizal diversity was consistently lower in clearcut soils from all forest types but in no case was the difference in diversity between forest and clearcut significant. Type composition differed between forest and clearcut soils from the dry montane type but not from the moist mesic or the moist montane types.

Mycorrhiza diversity and overall stability of mycorrhiza formation following clearcutting and burning. Mycorrhiza formation was significantly higher in clearcut than in forest soils at the sites with both the highest and lowest mycorrhiza diversity.

Mycorrhiza Formation and Diversity
in Undisturbed Forest and Clearcut and Burned Areas
in Three Forest Types in Oregon

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Richard E. Brainerd

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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~~

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MYCORRHIZA FORMATION AND DIVERSITY
IN UNDISTURBED FOREST AND CLEARCUT AND BURNED AREAS
IN THREE FOREST TYPES IN OREGON

INTRODUCTION

Ectomycorrhizae benefit conifers in numerous ways (Marx and Krupa 1978) and probably are required for their survival in nature (Harley 1969). Similarly, ectomycorrhizal fungi do not persist long without host plants to supply carbohydrates (HacsKaylo 1973, Harvey et al. 1980). The amount and types of ectomycorrhizae that develop on tree roots are influenced by soil properties (Slankis 1974, Alvarez et al. 1979, Parke et al. 1983b, Perry et al. 1987) that in turn are influenced by other environmental conditions. Previous studies indicate that ectomycorrhiza diversity is lower in harsher environments (Pilz and Perry 1984, Perry et al. 1982).

Successful establishment of conifer seedlings after forest harvesting depends on adequate levels of residual ectomycorrhiza inoculum (Parke et al. 1984, Amaranthus and Perry 1987). Previous studies in a variety of environments have shown that ectomycorrhiza formation following clearcutting and slash burning may decrease (Wright and Tarrant 1958, Wright 1971, Harvey et al. 1980a, Perry et al. 1982, Parke et al. 1984, Amaranthus and Perry 1987), increase (Amaranthus and Perry 1987), or remain unchanged (Parke et al. 1983b, Pilz and Perry

1984). Little is known of how disturbance affects ectomycorrhiza diversity in different environments, though clearcutting and burning caused significant shifts in ectomycorrhiza type proportions in one study in the western Cascades of Oregon (Schoenberger and Perry 1982).

The effects of disturbance on ectomycorrhiza formation and diversity have been examined in a range of environments, but lack of a standard methodology and differences in the time since disturbance make the results from different environments difficult to compare.

The purposes of this study were 1) to determine levels of ectomycorrhiza formation and diversity in soils from three undisturbed forest types representing a gradient of environmental harshness, and 2) to examine the effect of clearcutting and burning on ectomycorrhiza formation and diversity in the three forest types. We hypothesized that 1) ectomycorrhiza diversity decreases with increasing environmental harshness, and 2) level of ectomycorrhiza formation following clearcutting and burning is positively correlated with higher ectomycorrhiza diversity. The study was conducted as a greenhouse bioassay, using field soils as inocula for tree seedlings grown under controlled conditions.

STUDY SITES

The study sites are located in three forest types, moist mesic, moist montane and dry montane, along a moisture/temperature/elevation gradient in western Oregon. The moist mesic sites (elev. 360-410 m) are in the Oregon Coast Range, 60 km west of Eugene, Oregon, in the Mapleton District of the Siuslaw National Forest. The sites are in the Tsuga heterophylla Zone, with Pseudotsuga menziesii the dominant tree species in most stands (Franklin and Dyrness 1973). Soils are Typic Dystrochrepts and Typic Haplumbrepts underlain by sandstone parent material (Badura et al. 1974). Slopes are steep, averaging 68%, with extremes greater than 90%. Mean annual precipitation at the nearest weather station (10 km) is 2344 mm, 91 percent falling from October to May (personal communication, Mapleton Ranger District). Mean annual temperature at a Coast Range weather station 42 km to the north is 11.6°C (Redmond 1987).

The moist montane sites (elev. 1035-1100 m) are on the west slope of the Cascade Range 80 km east of Eugene, Oregon, in the McKenzie District of the Willamette National Forest. These sites are in the Tsuga heterophylla Zone and are dominated by stands of Pseudotsuga menziesii (Franklin and Dyrness 1973). Soils are Dystric Cryochrepts underlain by breccias and tuffaceous materials, and Entic Cryandeps underlain by

andesites and basalts (Legard and Meyer 1973). Slopes are moderately steep, averaging 41%. Mean precipitation at the nearest weather station (12 km) is 1765 mm, with 90 percent falling from October to May, and mean annual temperature is 10.3°C (NOAA 1961-1987).

The dry montane sites (elev. 1475-1615 m) are on the east slope of the Cascade Range 30 km northwest of Bend, Oregon, in the Sisters District of the Deschutes National Forest. They occur within the Abies grandis Zone and are dominated by stands of Pinus ponderosa (Franklin and Dyrness 1973). Soils are Entic Cryandeps derived from sandy volcanic ash deposited over buried soils formed from glacial till (Larsen 1976). Depth to buried soil ranges from 38 to 91 cm. Slopes are gentle, averaging 16%. Mean annual precipitation at the nearest weather station (16 km) is 362 mm, with 87 percent falling from October to May, and mean annual temperature is 7.4°C (NOAA 1961-1987).

METHODS

Field Procedures

Three pairs of undisturbed forest and adjacent three- to six-year-old clearcut and burn sites were selected within each forest type. The clearcuts are generally well-stocked with both planted and natural conifer regeneration. Sampling was conducted in May and June of 1986. Ten plots were located randomly along a transect through each site. At each plot, mineral soil was collected from two depths, 0-10 cm and 10-30 cm, from four points located two meters uphill, downhill, and to each side of plot center. Plot samples were composited by soil depth and stored at 4°C for later use as inocula in greenhouse experiments. To avoid contamination between samples, sampling equipment was sterilized with isopropyl alcohol between soil depths and plots. Additional soil samples were taken from odd-numbered plots for determination of N, P, and C content, pH and bulk density. Soil analysis methods and results, and the effects of disturbance on soil properties for these sites are reported in Brainerd and Perry (In preparation). A summary of soil chemical properties is given in Table 1.

Bioassay Procedures

Greenhouse planting media consisted of one part field soil, sieved to 4 mm, mixed with one part each

steam-pasteurized (30 min. at 76°C) peat and vermiculite. Douglas-fir and ponderosa pine seeds were obtained from the same seed zones and elevations as the field soil samples (Oregon seed zone 062 and 472 for moist mesic and moist montane Douglas-fir, respectively, and 675 for dry montane ponderosa pine). The seeds were successively soaked in tap water, Tween surfactant, 30% H₂O₂, and distilled water to surface sterilize the seeds and stimulate germination (Trappe 1961). Three seeds were planted in each of 2520 150 cc Ray Leach Super Cell seedling tubes. Douglas-fir seeds were planted in Mapleton and McKenzie soils and ponderosa pine seeds were planted in Sisters soils. The use of different tree species admittedly limits the scope of comparisons that can be made among forest types, but we felt that it was more important to use the same species in the bioassay as occur naturally on the sites from which the soil inocula were taken, than to use an offsite species that might not have the same affinity for the mycorrhiza types present in the soil inocula.

All seeds were covered with 1 cm of crushed quartz to reduce soil splash between tubes. For each soil depth of each plot, seven tubes were planted including two extras to allow for planting failure and periodic assessment of mycorrhiza development. Tubes containing soil from a single plot constituted one row in seedling

racks. Clear Mylar sheets separated the rows to further minimize splash contamination. Racks were arranged randomly on greenhouse benches and rotated biweekly to minimize local greenhouse effects. After germination and establishment, seedlings were thinned to one per tube and grown under 18 hour daylengths and light supplemented by florescent tubes to a midday average of 210 μ E.

Greenhouse temperature was maintained at 21°C during the day and 15°C at night. Seedlings were misted daily until established, then watered once or twice weekly as needed to keep the planting media moist. During the growing period, each seedling received two fertilizer applications (once in each of the third and fourth months) consisting of 35 mg each of N, P and K. After 5 months, the seedlings were removed from the greenhouse and stored intact in their tubes at 2°C pending biomass measurement and examination of roots. Douglas-fir seedlings were examined within two weeks, and ponderosa pine seedlings within four weeks, of the date they were placed in cold storage.

Five of the seven seedlings for each soil depth of each plot were randomly selected and the planting medium was carefully washed from the roots. Three 1 cm transverse sections were subsampled from random locations within the top, middle, and bottom thirds of each root system, lumped with the other subsamples from the same

plot and soil depth, and examined at 2-5 power under a binocular dissecting scope. The number of mycorrhizal short roots and root tips by mycorrhiza type (see Table 2 for type descriptions), and the number of non-mycorrhizal short roots, were recorded. When mycorrhizal status was doubtful, thin sections or squash mounts of short roots were made and examined under a compound microscope for the presence of a mantle and Hartig net. Roots, and root subsamples were separately oven-dried and weighed.

The raw root count data were used to calculate percent mycorrhizal colonization, mycorrhiza type proportions, and a diversity index of mycorrhiza types for short roots and tips. The diversity index was calculated as $-\sum p_j \ln p_j$ (Pielou 1969) where p_j equals the proportion of the j th mycorrhiza type for a given plot and soil depth. A branching index was computed as the quotient of mycorrhizal tips divided by mycorrhizal short roots. Total and mycorrhizal short roots and tips per seedling were each computed by multiplying the number of short roots or tips sampled by the ratio of the total biomass of the sampled root systems to the biomass of the root sample, and dividing by the number of trees from which the sample was taken.

Statistical Analysis

Analyses of variance (ANOVA) were performed at two levels. Comparisons of undisturbed forest means among

the three forest types were made using a completely randomized design with subsampling, replicated three times within each geocode, and with plots comprising subsamples. An ANOVA was performed for each soil depth.

Comparison of undisturbed forest and clearcut and burned areas within each forest type were conducted as complete block designs with subsampling, each block composed of one forest/clearcut pair, and plots comprising the subsamples. A separate ANOVA was performed for each soil depth of each forest type. A similar design was used to compare soil depths within each disturbance class, with soil depth as the treatment. In this case, a separate ANOVA was performed for each disturbance class in each forest type.

Normal probability plots of residuals were made and data were transformed when necessary to assure normal distributions and constant variance. For comparisons among undisturbed forest types, the square root transformation was applied to the 0-10 cm mycorrhizal short root data. Mycorrhizal tip data were transformed by taking the natural log for the 0-10 cm soil depth, and by taking the square root for the 10-30 cm depth. Total tip data were log transformed for the 10-30 cm depth. For comparisons between undisturbed forest and clearcut and burned areas, mycorrhizal tips were transformed as the natural log for 0-10 cm depth for McKenzie, and as the square

root for the 10-30 cm depth for Mapleton. For Sisters the logit transformation was used to stabilize variance of percent colonization data for both soil depths. Branching index was log transformed for the 0-10 cm depth for Mapleton, both soil depths for McKenzie, and for the 10-30 cm depth for Sisters. No transformations were necessary for comparisons between soil depths. When significant differences were detected by the ANOVA, individual means were compared using Fisher's protected LSD.

Composition of mycorrhiza types on seedling roots was compared between disturbance classes and between soil depths. Minor types were grouped and treated as a single type for this purpose. Since the proportions of different types on a root system are correlated, it was necessary to test for differences using Hotelling's T^2 (Mardia, et al. 1979). Through matrix manipulation the correlated variables (mycorrhiza type proportions) were transformed into new, independent variables for which the test statistic was calculated.

RESULTS

Undisturbed Forest

The proportion of root tips colonized by mycorrhizal fungi increased across the gradient from west (moist mesic) to east (dry montane) (Fig. 1A). Seedlings grown in Mapleton soils had significantly lower ($p < 0.05$) percent colonization of root tips (47% in 0-10 cm soils and 51% in 10-30 cm soils) than McKenzie or Sisters. Percent colonization of seedlings inoculated with soils from the 0-10 cm depth averaged 68% and 75% for McKenzie and Sisters, respectively (significant at $p = 0.0575$), and 63% and 79% for the 10-30 cm depth (significant at $p < 0.05$). Patterns were similar when colonization of short roots, rather than root tips was examined (Table 3), but while significantly lower short root colonization occurred in Mapleton soils than in McKenzie or Sisters soils ($p < 0.05$), no differences were detected between McKenzie and Sisters at either soil depth. There were no significant differences in percent colonization of root tips or short roots between depths of undisturbed soils from any forest type.

For both soil depths, numbers of both total and mycorrhizal root tips did not differ between Mapleton and McKenzie soils, but were significantly higher ($p < 0.05$) in Sisters soils (Figs. 1B and 1C). This was partially due to a significantly greater branching index ($p < 0.05$) in

Sisters soils, i.e., more tips per short root, which was probably a tree species rather than a site effect. In our experience, ponderosa pine short roots tend to branch more than those of Douglas-fir. As with tips, however, numbers of mycorrhizal short roots in Sisters soils from both soil depths were significantly higher ($p < 0.05$) than in soils from Mapleton or McKenzie (Table 3). Total short roots in 0-10 cm soils differed significantly ($p < 0.05$) between Sisters and McKenzie, but not between Mapleton and either Sisters or McKenzie. For the 10-30 cm depth, numbers of total short roots in Sisters soils were significantly higher ($p < 0.05$) than in Mapleton or McKenzie soils.

Significantly higher ($p < 0.05$) numbers of mycorrhizal tips formed in 0-10 cm soils than in 10-30 cm soils from undisturbed forest at McKenzie, but no soil depth effect was detected in Mapleton or Sisters soils. Total root tips and short roots, and mycorrhizal short roots did not differ between depths of undisturbed soils from any forest type.

In contrast to our hypothesis, mycorrhiza diversity, like percent colonization, generally increased from the moist mesic to the dry montane forest type (Fig. 1D). Diversity indices for mycorrhizal tips differed significantly among all three forest types in both soil depths ($p < 0.06$ for 0-10 cm and $p < 0.05$ for 10-30 cm). For the 0-

10 cm depth, the diversity index of short roots was significantly lower in Mapleton soils but did not differ between McKenzie and Sisters. Short root diversity indices differed among all forest types in 10-30 cm soils. Diversity indices of short roots and tips did not differ between soil depths for any forest type.

Two mycorrhiza types, Rhizopogon sp. and an unidentified brown type, dominated in all soils and were usually accompanied by several minor types (Table 2). Each minor type rarely comprised more than 5% of the mycorrhizal root tips on a seedling.

Effects of Clearcutting and Burning

Results from the comparisons between undisturbed forest and clearcut and burned areas are presented in Figures 2A-D and 3A-D for the 0-10 cm and 10-30 cm soil depths, respectively. Total root tip formation differed between seedlings inoculated with forest and clearcut soils only for 0-10 cm soils from Sisters, where seedlings grown in clearcut soils formed significantly greater ($p < 0.05$) numbers of root tips. Percent mycorrhizal colonization of root tips, however, was higher in clearcut than in forest soils from both depths at Mapleton, and from the surface layer (0-10 cm) at Sisters. Numbers of mycorrhizal root tips were significantly higher in clearcut soils from the 10-30 cm layer at Mapleton ($p < 0.05$), and from the 0-10 cm layer at

Sisters ($p < 0.01$). For short roots, differences between forest and clearcut were detected only for percent mycorrhizal colonization, which was higher at $p = 0.064$ on seedlings grown in 0-10 cm soils from Mapleton (Table 3). Total short roots, mycorrhizal short roots, and short root mycorrhiza diversity did not differ significantly between forest and clearcut in soils from any forest type. Branching indices (Table 3) differed significantly ($p = 0.014$) only in 0-10 cm soils from Sisters but tended to be higher in clearcut than in forest soils from all forest types and soil depths.

Root tip formation and mycorrhiza diversity differed significantly between clearcut soil depths only in soils from Sisters. Numbers of total and mycorrhizal root tips were higher ($p < 0.02$ and $p < 0.01$ for total and mycorrhizal, respectively) in 0-10 cm than in 10-30 cm soils, while diversity index was higher ($p < 0.01$) in 10-30 cm soils.

In soils from each forest type, Rhizopogon sp. formed a higher average proportion of mycorrhizal tips in clearcut than in undisturbed forest soil (Fig. 4A and 4B). However, for mycorrhizal tips, the proportions of different types differed significantly ($p < 0.01$) between forest and clearcut soils only from Sisters ($T^2 = 11.332$ and 5.084 for 0-10 cm and 10-30 cm depths, respectively). Similarly, when calculated on the basis of short roots rather than tips, type composition differed significantly

only between forest and clearcut soils from Sisters ($T^2=17.153$, $p<0.01$ and $T^2=4.670$, $p<0.05$, for 0-10 cm and 10-30 cm depths, respectively). Differences in type proportions of tips at Sisters are partially due to greater branching of Rhizopogon sp. Branching indices of Rhizopogon sp. were significantly higher in clearcut soils from Sisters ($p=0.006$ and 0.067 for 0-10 cm and 10-30 cm soil depths, respectively), and did not differ between forest and clearcut soils from the other forest types. The branching indices of the brown type and the minor type did not differ significantly between forest and clearcut soils from any forest type. The higher proportions of Rhizopogon sp. tips were accompanied by consistently lower average mycorrhiza diversity indices in clearcut soils from all forest types, but in no case was the difference in diversity index between forest and clearcut significant. Type proportions of mycorrhizal tips differed significantly ($T^2=4.865$, $p<0.05$) between soil depths only in the clearcut soils from Sisters. Although Rhizopogon sp. colonized the majority of tips at both soil depths, a greater proportion of tips were colonized by Rhizopogon sp. in surface soils from Sisters clearcuts. When calculated on the basis of short roots, significant differences in type composition between soil depths were observed in clearcut soils from McKenzie ($T^2=3.584$, $p<0.05$) and Sisters ($T^2=5.443$, $p<0.01$). The

differences appear to be mainly due to a higher proportion of short roots colonized by the brown type relative to Rhizopogon sp. and the minor types at the 10-30 cm depth.

Contrary to our hypothesis, there was no correlation between mycorrhiza diversity for a forest type and overall stability of mycorrhiza formation following clearcutting and burning. Mycorrhiza formation was significantly higher in clearcut than in forest soils at the sites with both the highest (Sisters) and lowest (Mapleton) mycorrhiza diversity.

DISCUSSION

Undisturbed Forest

Percent mycorrhizal colonization and mycorrhiza diversity of seedlings grown in undisturbed forest soils increased from moist mesic to moist montane to dry montane forest. The numbers of mycorrhizal and total root tips were also highest in soils from the ponderosa pine forests at Sisters, but did not differ between the coastal and montane Douglas-fir sites. The forest types investigated in this study display a range of nutrient levels, moisture availability, temperature, frequency of disturbance, and overall productivity. Characteristics of mycorrhiza formation in undisturbed soils reflect both the environmental gradient and the different tree species represented by the three forest types.

Mycorrhiza formation is closely tied to environmental conditions (nutrients, moisture, temperature), host physiology, soil microorganisms and the availability of viable inocula (Slankis 1974, Perry et al. 1987). Environmental conditions provide the framework within which plant and fungus interact. On sites where soil nutrient and moisture availability are high -- such as in the coastal Douglas-fir forests -- the cost of maintaining large numbers of mycorrhizal roots and their associated fungal mycelia may outweigh the advantages of increased nutrient and water uptake provided by fungal symbionts,

resulting in lower rates of mycorrhizal colonization (Slankis 1974).

Mycorrhizae are likely to be more important to trees at Sisters, where moisture and nutrients are limiting and where a short growing season requires very efficient use of resources by the plant. In addition, fire in the ponderosa pine type is much more frequent, though of lower intensity, than for the two Douglas-fir forest types (Martin 1982), and probably results in periodic mineralization of biomass-bound nutrients (DeBano and Conrad 1978) including nitrogen (Wells 1971). Mycorrhizae may help to rapidly absorb pulses of nutrients released by fire.

In general, high levels of nitrogen and phosphorus inhibit mycorrhiza formation (Hatch 1937, HacsKaylo 1973, Slankis 1974). Nutrient deficiency may predispose the host plant physiologically to mycorrhizal colonization (Harley 1969), or better enable the mycorrhizal fungus to "impose the symbiotic relationship on the host plant" (Slankis 1974). In field trials, Menge et al. (1977) related decreased overall mycorrhiza formation to applications of nitrogen fertilizer, but found that the effect could be negative, positive or neutral depending on mycorrhiza type. Schoenberger and Perry (1982), in bioassays using forest soils from the western Oregon Cascades, found a positive correlation between the forma-

tion of mycorrhizal tips and soil nitrogen, phosphorus, and carbon. Since soil nitrogen, phosphorus and carbon are all closely related to soil organic matter, it is difficult to say whether mycorrhiza response is due to the actual nutrient levels, or to levels of organic matter, which also play a role in mycorrhiza formation (Harvey et al. 1976). In this study, soil nitrogen and carbon levels exhibited an inverse relationship with mycorrhiza formation, decreasing consistently from Mapleton to Sisters (Table 1).

Changes in mycorrhiza formation, whether in response to soil nutrients or some other factor, may be mediated directly by availability of inocula and physiological root-fungus responses, or indirectly through action of plant-produced allelochemicals on mycorrhizal fungi. Foliage chemical properties have been shown to vary with soil chemistry (Smith et al. 1981), as well as with species, and the chemical properties of litter and soil organic components may vary accordingly in the forest types examined in this study. Research indicates that responses to litter and soil organic matter range from stimulation to suppression of mycorrhiza formation. Harvey et al. (1976) found most ectomycorrhizae in a Douglas-fir/larch forest to be associated with soil organic fractions, and proliferation of mycorrhizae in organic layers has been observed since the late 1800s

(see Hatch 1937). However, Alvarez et al. (1979) found reduced mycorrhiza formation on white fir seedlings grown in mineral soil with vs. without an organic layer, although a greater diversity of types was found on seedlings grown in soils with organic layers. They suggest that toxic substances in the organic layers suppressed overall mycorrhiza formation, but that mycorrhizal fungi may be differentially susceptible to such substances. Mycorrhiza formation was inhibited on Pinus radiata by aqueous extracts of older P. radiata roots (Chu-Chou 1978), and on Douglas-fir by leachates of litter from one stand of old growth Douglas-fir in the western Cascades, but not from another (Schoenberger and Perry 1982). Rose et al. (1983) noted variable responses of different mycorrhiza types to different levels and types of litter leachates. Differential response to litter and other organic matter leachates may be related to the successional roles of different mycorrhizal fungi following disturbance, and probably varies depending on environment and community composition (Perry and Choquette 1987).

In this study, Rhizopogon sp. and the brown type dominated on seedlings grown in undisturbed soils from all forest types, with minor types comprising a third component. We hypothesized that mycorrhiza diversity would decrease as environmental harshness increased. The results indicate just the opposite. While more mycor-

rhiza types occurred on seedlings grown in undisturbed soils from Mapleton and McKenzie (10 and 11 types, respectively, vs. 8 types for Sisters), Sisters seedlings had a higher average number of types per seedling and more evenness in the proportions of types, hence greater diversity. Previous greenhouse bioassays by Perry et al. (1982) detected a single mycorrhiza type in Montana lodgepole pine forest soils (high environmental harshness), but Pilz and Perry (1984) found 12 types in western Cascades Douglas-fir soils (low environmental harshness). Pilz and Perry (1984) noted that while there is a good relationship between proportions of major types occurring in a greenhouse bioassay and those occurring in the field, the relationship breaks down for minor types, hence the greenhouse bioassay used in this study probably does not reflect the potential importance of these types.

Trees may gain at least two advantages from higher mycorrhiza diversity under unfavorable environmental conditions. First, different fungal species may be specialized to cope with different environmental stresses and to exploit different microenvironments. Such specialization may be more effective in continental environments, such as Sisters, where both soil moisture and fertility are low and temperature extremes are large. Second, mycorrhiza diversity may help to buffer the soil system against disturbances such as forest fires. With

natural fire frequencies of 20 years or less (Sisters), mycorrhiza types that are adapted to survive in the disturbed system can absorb disturbance-caused pulses of nutrients, helping to keep them on site.

Effects of Clearcutting and Burning

Clearcut harvesting and slash burning have the potential to impact many of the soil and environmental conditions that affect mycorrhiza formation, and it seems reasonable to expect such impacts to be shaped by the environment in which they occur. We hypothesized that mycorrhiza formation would be lower in clearcut and burned soils than in undisturbed forest soils, and that the reduction would be greatest in the harshest environment. This hypothesis, however, is not supported by results of this study. Mycorrhiza formation was higher in soils from clearcut than in soils from forest for the moist mesic and the dry montane forest types, respectively the least and the most harsh environments examined. For the moist mesic type, higher percent colonization occurred in clearcut soils from both soil depths and absolute numbers of mycorrhizal tips were higher in clearcut than in forest soils at the 10-30 cm depth. Since total root tips did not differ between disturbed and undisturbed soils, fewer nonmycorrhizal roots formed in clearcut soils. For the dry montane type, the effects of clearcutting and burning were

detected only in the surface soil layers. Percent colonization, numbers of mycorrhizal tips and numbers of total root tips were all higher in clearcut than in forest soils from the 0-10 cm depth, while numbers of nonmycorrhizal root tips did not differ. Thus, seedlings grown in clearcut soils from both the moist mesic and the dry montane forest types allocated more carbon to mycorrhizal root tips than seedlings grown in soils from undisturbed forest.

Mycorrhiza type composition of tips differed between clearcut and forest only in soils from the dry montane forest type, where Rhizopogon sp. formed a larger proportion of mycorrhizal tips in clearcut than in forest soils. Diversity of mycorrhiza types was not significantly different in clearcut vs. forest soils from any forest type but the mean diversity index was lower in clearcut soils from every soil depth and forest type. Higher proportions of Rhizopogon sp. tips in clearcut soils reduced evenness in type composition resulting in lower average diversity indices.

A look at short roots rather than tips is revealing. Aside from higher percent colonization in 0-10 cm soils from Mapleton (significant at $p=0.064$), neither percent colonization of short roots nor numbers of mycorrhizal or total short roots differed significantly between forest and clearcut soils from any forest type or soil depth.

Thus, in those clearcut soils where mycorrhiza tip formation was higher than in forest, greater branching rather than higher numbers of mycorrhizal short roots accounts for the differences. Examination of the branching indices for the different mycorrhiza types indicates that greater branching in clearcut relative to forest soils occurred almost exclusively in Rhizopogon sp., although differences were significant only at Sisters. Since Rhizopogon sp. also constituted large proportions of mycorrhizal short roots in all soils, higher mycorrhizal tip formation in clearcut soils may be driven by the greater branching of this type. The trend toward lower mycorrhizal tip diversity indices in clearcut soils appears to be at least partially a result of the proliferation of Rhizopogon sp. root tips through increased branching. At Sisters, however, a similar trend was noted for mycorrhizal diversity of short roots, suggesting that the differences were not entirely due to greater branching of short roots.

Previous work has shown that the effects of clear-cutting and slash burning on mycorrhiza formation vary with site, tree species, length of time since the disturbance and whether or not the disturbed area was reforested. Numerous studies, utilizing field and greenhouse bioassay techniques, have reported reduced mycorrhiza formation resulting from clearcutting and burning (Wright

and Tarrant 1958, Wright 1971, Harvey et al. 1980a, Perry et al. 1982, Parke et al. 1984, Amaranthus et al. 1987). Others have shown either no effect (Parke et al. 1983b, Pilz and Perry 1984) or stimulation of mycorrhiza formation (Schoenberger and Perry 1982, Amaranthus and Perry 1987). Schoenberger and Perry (1982) observed greater mycorrhiza formation in soils from an unburned clearcut than from either undisturbed forest or a burned clearcut. Different measures of mycorrhiza activity may produce contradictory results. Mikola et al. (1964) detected lower percent colonization but greater numbers of mycorrhizal root tips on pine seedlings grown in severely burned vs. unburned or lightly burned soils. Few studies have examined the effects of clearcutting and burning on mycorrhiza diversity or on mycorrhiza type composition. Significant shifts in mycorrhiza types with clearcutting and burning in the western Cascades were observed by Schoenberger and Perry (1982) and Pilz and Perry (1984). In the former study, the shift was in the proportions of dominant types present in both clearcut and forest soils, while in the latter, it was mainly due to the occurrence of a greater proportion of uncommon types in undisturbed forest soils.

Time since disturbance and rapidity of host plant regeneration are important determinants of mycorrhizal inoculum levels (Parke 1982, Amaranthus and Perry 1987,

Perry et al. 1987). All the clearcuts examined in this study were regenerated quickly after burning and were well-stocked at the time of sampling. Plentiful inoculum likely existed at the time of planting and would have been maintained by successful colonization of both planted and natural seedlings. Amaranthus and Perry (1987) showed that soils from a well-stocked clearcut that had been burned could stimulate mycorrhiza formation on seedlings planted in an eight year-old unregenerated clearcut.

Formation of mycorrhizae is influenced by soil nitrogen, phosphorus, carbon and pH (Slankis 1974). Clearcutting and particularly slash burning can profoundly affect these properties. Carbon and nitrogen of the forest floor and surface soil layers are highly susceptible to volatilization, especially by slash fires of high intensity (Feller and Kimmins 1984). Soil phosphorus may increase from ash inputs (Wells 1971) or decrease from losses in fly ash (Feller et al. 1983) or increased leaching (Fredriksen 1971) and erosion (Bennett 1982) following the burn, and cations deposited in ash are likely to cause increases in pH (Isaac and Hopkins 1937, Wells 1971). Soil chemical properties differed significantly between undisturbed and clearcut soils from all three forest types. In comparison with undisturbed forest soils, clearcut soils had significantly lower N,

and C in the moist mesic type, significantly lower P in the moist montane type and significantly higher N in the dry montane type.

Overall mycorrhiza formation and proportions of mycorrhiza types in clearcuts were correlated with different soil chemical properties in each forest type (Brainerd and Perry, unpublished data). In the moist mesic type, overall mycorrhiza formation and numbers of Rhizopogon sp. tips correlated negatively with the ratio of N to P in the soil, and numbers of tips of the brown type correlated positively with C:N ratio. In moist montane soils, overall mycorrhiza formation was correlated positively with levels of C, N, and P. Rhizopogon sp. tips were positively correlated with C, N, P, and pH, while minor type tips correlated positively with C:N ratio and negatively with N and P. In dry montane soils, mycorrhiza formation was correlated negatively with soil N, and positively with pH. Brown type tips correlated negatively with soil C and N:P ratio, and minor type tips were positively correlated with pH.

That mycorrhiza formation is keyed to different nutrients or ratios of nutrients is probably a reflection of the differing nutrient status existing in each forest type. At Mapleton, N may be limiting mycorrhizae by its abundance. With significant losses of N apparently occurring with clearcutting and burning, nutrient ratios

may move into ranges more favorable for mycorrhiza development. Very localized surface effects may take on greater importance at Sisters where intensity of slash burns may be lower because of gentler slopes and lighter fuels. Losses of nutrients and organic matter that occur in the top few centimeters of soil may be undetectable by our soil sampling methods, yet may have significant effects on mycorrhiza formation.

Response of mycorrhizae to clearcutting and burning may also be related to removal of allelopathic effects that existed in the undisturbed soil. Rose et al. (1983) found that while low concentrations of litter leachates stimulated the growth of mycorrhizal fungi *in vitro*, the effect of high leachate concentrations could be stimulatory, inhibitory, or neutral depending on both the fungal species and the source of the litter. In that study, litter leachates were inhibitory to Rhizopogon sp. mycorrhizae on greenhouse-grown Douglas-fir, but had no significant effect on brown type mycorrhizae, reducing the proportion of Rhizopogon sp. mycorrhizae. Mycorrhiza formation on Douglas-fir was reduced by litter leachates from a Douglas-fir forest (Schoenberger and Perry 1982), mainly due to the effects of the leachate on Rhizopogon sp. These studies suggest that Rhizopogon sp. may be selectively suppressed relative to other mycorrhiza types in maturing forest stands. Removal of the forest floor

by harvesting and burning may effectively remove allelopathic limits and allow increased development of Rhizopogon sp.

While the exact cause of the stimulation of Rhizopogon sp. formation in clearcuts remains unidentified, and may vary depending on plant community and environment, the dominance of this type in disturbed soils suggests that it is important in early stages of succession to assure rapid reestablishment and growth of coniferous regeneration. Other types, such as the brown mycorrhiza, may gain importance later in succession as nutrient capital is fixed in biomass and as litter alters the chemistry of the forest floor and surface soil layers.

The results of this study support the hypothesis that mycorrhizal fungi become increasingly important to trees as water and/or nutrients become more limiting. Undisturbed soils from Sisters, the forest type lowest in nutrients and moisture, supported the highest levels of mycorrhiza formation. The increase in mycorrhiza formation with clearcutting at Mapleton was associated with a significant loss of soil nitrogen and tree seedlings grown in soils from this type responded by allocating more energy to mycorrhizal roots. Mycorrhizae may serve as a safety net, providing seedlings with a steady nutrient supply despite periodic losses due to

disturbance. This study contrasts with others that have shown that clearcutting and burning reduce mycorrhiza formation. Our results indicate no negative effect of these harvest practices on mycorrhiza formation. On the contrary, it appears that we observed the healthy response of forest systems adapted to periodic disturbance. The clearcut sites investigated were well-stocked with conifer seedlings. A similar response would not be expected in clearcuts that were not promptly reforested, or otherwise occupied by noncrop plant species capable of supporting ectomycorrhizal fungi (Amaranthus and Perry 1987 and in press, Perry et al. 1987, Borchers and Perry, submitted).

Table 1. Soil chemical properties of undisturbed and disturbed soils in each forest type.¹

Forest Type	DC ²	N (%)	P (%)	C (%)	C:N	N:P	pH
Moist Mesic	UF	0.278a ³ (0.018) ⁴	0.057a (0.003)	6.291a (0.259)	23.35a (1.82)	4.90a (0.27)	5.1a (0.1)
	CCB	0.161b (0.019)	0.046a (0.003)	4.282b (0.269)	26.18a (1.89)	3.55b (0.28)	5.2a (0.2)
Moist Montane	UF	0.135a (0.016)	0.177a (0.007)	3.963a (0.261)	30.85a (2.55)	0.79a (0.08)	6.0a (0.3)
	CCB	0.142a (0.017)	0.122b (0.007)	3.888a (0.280)	28.84a (2.74)	1.19b (0.08)	6.1a (0.3)
Dry Montane	UF	0.057a (0.003)	0.081a (0.003)	1.855a (0.235)	33.05a (2.74)	0.71a (0.07)	6.4a (0.2)
	CCB	0.077b (0.003)	0.087a (0.003)	2.175a (0.227)	29.11a (2.65)	0.88a (0.08)	6.4a (0.2)

¹From Brainerd and Perry, in manuscript.

²Disturbance classes (DC): UF = undisturbed forest; CCB = clearcut and burned.

³For a given forest type, means in the same column followed by different letters are significantly different ($p=0.05$) by Fisher's protected LSD.

⁴Numbers in parentheses are \pm standard error.

Table 2. Ectomycorrhiza type characteristics.

Type no.	Tree sp.	ID ¹	Mantle		Form		Attached mycelium	
			Color	Texture	Tips	Branching	Hyphae	Rhizomorphs
1	DF, PP	<u>Rhizopogon</u> sp.	White to pink to brown to black	Velvety, cottony	Straight, swollen, club-shaped	Single to pinnate to clustered tuberculate	Thick brown mat enclosing clusters	Thick, branched, abundant, white to brown to black
2	DF, PP	<u>Cenococcum</u> sp.	Black	Granular to crusty	Straight, swollen club-shaped	Single to dichotomous	Black, stiff bristly	Absent
3	DF, PP	Brown type	Golden brown, dark hairs interspersed	Smooth	Elongate, often curved	Usually single, pinnate, irregular	Clear to white, sparse	Absent
4	DF	Unknown minor type	Black under clear surface hyphae	Granular to felty	Elongate	Single	Absent	Absent
5	PP	Unknown minor type	Rust orange to brown, w/ white patches	Crusty to fuzzy	Short, stout, club-shaped	Dichotomous to irregularly clustered	Fuzzy orange mat	Thick, white to orange, abundant

¹All types except type 1 and type 3 were grouped into a single "minors" type.

Table 2. (Cont.) Ectomycorrhiza type characteristics.

Type Tree no. sp.	ID	Mantle		Form		Attached mycelium		
		Color	Texture	Tips	Branching	Hyphae	Rhizomorphs	
6	DF	Unknown minor type	Shiny sulfur yellow	Smooth	Short, very swollen	Single	White fuzz, brown hairs near base	Small, purple- brown, limited to area near base
7	DF PP	Unknown minor type	White to golden brown	Smooth	Elongate, curved	Single	White, wefty, may be tufted	Yellow, with weftiness, braid- ed appearance
8	PP	Unknown minor type	Dark brown	Crusty, pitted	Short and irregular to straight	Single to dichotomous to irregular	Sparse reddish hairs	Absent
9	DF	Unknown minor type	Yellow under layer of black hyphae	Felty	Elongate, curved	Single	Long, clear, projecting	Absent
10	PP	Unknown minor type	Yellow with black patches	Smooth	Elongate, straight, swollen	Usually single to irregular	Absent	Absent

Table 2. (Cont.) Ectomycorrhiza type characteristics.

Type Tree no. sp.	ID	Mantle		Form		Attached mycelium		
		Color	Texture	Tips	Branching	Hyphae	Rhizomorphs	
11	DF PP	Unknown minor type	Purple-black	Granular to velvety	Short, swollen	Usually single to dichotomous	White, wefty, tufted	Absent
12	DF	Unknown minor type	Reddish to dark reddish brown	Velvety to crusty	Short, swollen	Pinnate to irregularly clustered	White layer of fuzz	Absent
13	DF	Unknown minor type	Gold, surface hyphae light blue	Smooth to fine- ly fuzzy	Short to long, swol- len, curved	Single to pinnate to irregular	Light blue, very fine, wefty	Absent
14	DF PP	<u>Tuber</u> <u>calif-</u> <u>ornicum</u>	Yellow brown	Smooth to granular	Short to long, swol- len, curved	Single to dichotomous to irregular	Clear, thin, pointed sur- face hyphae	Absent

Table 3. Short root characteristics of seedlings grown in undisturbed and disturbed soils from each forest type.

Forest Type	DC ¹	Percent Colonization		Mycorrhizal Short Roots		Total Short Roots		Diversity Index		Branching Index	
		0-10 ²	10-30	0-10	10-30	0-10	10-30	0-10	10-30	0-10	10-30
Moist Mesic	UF	37.1ax ³	42.4ax	1358.2ax	1372.8ax	3634.5axy	3038.9ax	0.661ax	0.609ax	1.57ax	1.47ax
	CCB	50.3a (2.5) ⁴	49.5a (2.1)	1493.5a (107.9)	1479.4a (85.0)	3038.9a (174.2)	3005.0a (88.5)	0.590a (0.087)	0.551a (0.043)	1.96a (0.21)	1.61a (0.11)
Moist Montane	UF	60.6ay	56.8ay	1865.0ax	1650.6ax	3121.5ax	2931.9ax	0.979ay	0.751ay	1.52ax	1.35ax
	CCB	57.0a (4.1)	49.9a (3.6)	1624.2a (169.1)	1373.6a (146.8)	2897.9a (396.6)	2748.7a (130.6)	0.858a (0.086)	0.723a (0.073)	1.57a (0.08)	1.39a (0.03)
Dry Montane	UF	62.0ay	64.1ay	2735.0ay	2589.4ay	4419.1ay	4015.2ay	1.133ay	1.113az	2.04ay	2.29ay
	CCB	63.9a (0.6)	68.9a (2.1)	2653.9a (49.6)	2650.2a (102.1)	4226.3a (143.9)	3868.1a (75.8)	0.982a (0.133)	1.115a (0.017)	2.82b (0.07)	2.55a (0.19)

¹Disturbance classes (DC): UF=undisturbed forest; CCB=clearcut and burned.

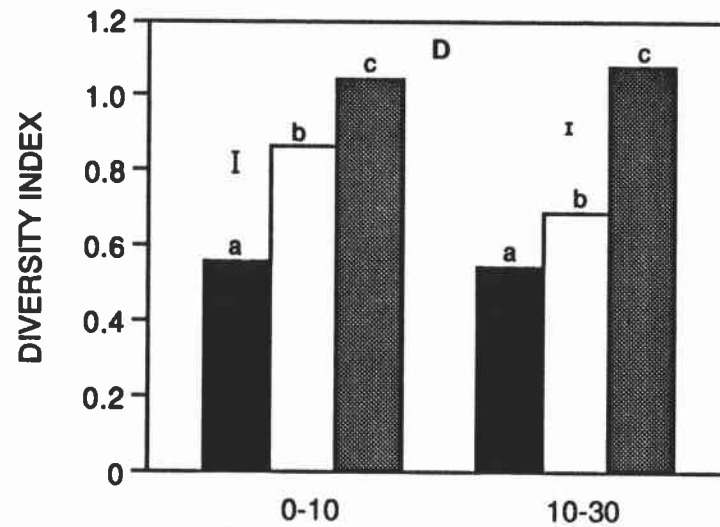
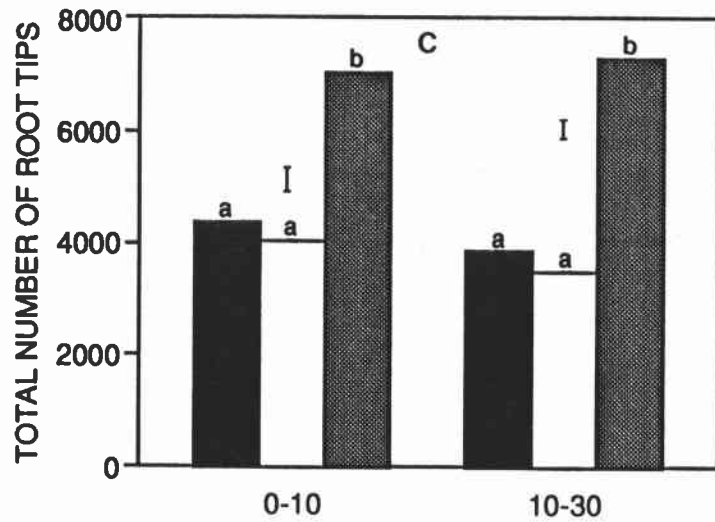
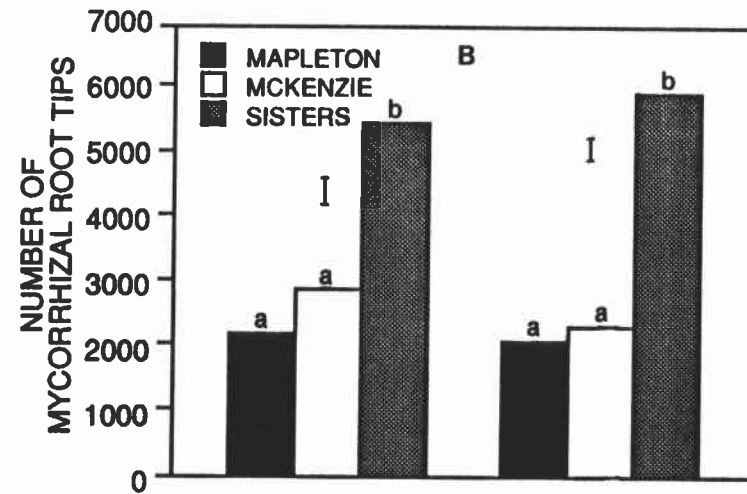
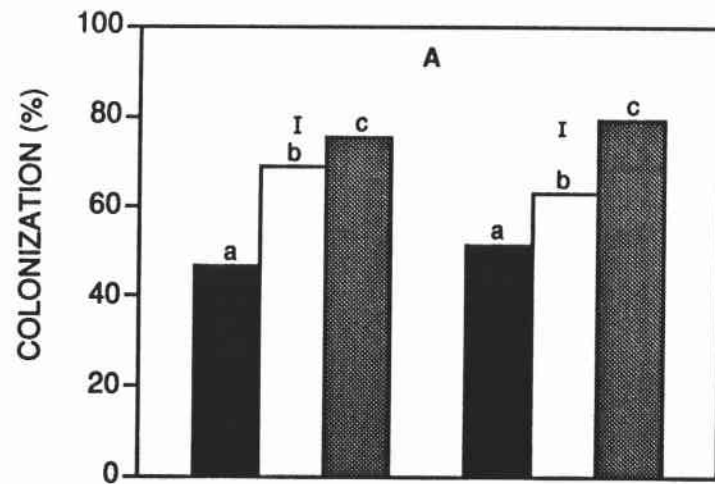
²Soil depths in centimeters.

³Means in the same column followed by different letters are significantly different ($p < 0.05$) by Fisher's protected LSD. Differences between UF and CCB means within a given forest type are indicated by the letters a, b, and c. Differences among UF means across all forest types are indicated by the letters x, y, and z.

⁴Numbers in parentheses are \pm standard error.

Figure 1

Mycorrhizal and total root tip formation in undisturbed forest soils from 0-10 cm and 10-30 cm depths. Lower case letters indicate statistically significant differences between forest types within each soil depth ($p < 0.05$ unless otherwise noted): A) percent mycorrhiza colonization (for 0-10 cm depth, differences between Sisters and McKenzie significant at $p = 0.0575$), B) numbers of mycorrhizal root tips, C) total root tips, D) diversity index of mycorrhizal root tips.



SOIL DEPTH (cm)

Figure 2

Root tip characteristics in forest vs. clearcut soils from the 0-10 cm depth, for the three forest types.

Lower case letters indicate statistically significant differences between forest and clearcut soils within each forest type ($p < 0.05$): A) percent mycorrhiza colonization, B) numbers of mycorrhizal root tips, C) total root tips, D) diversity index of mycorrhizal root tips.

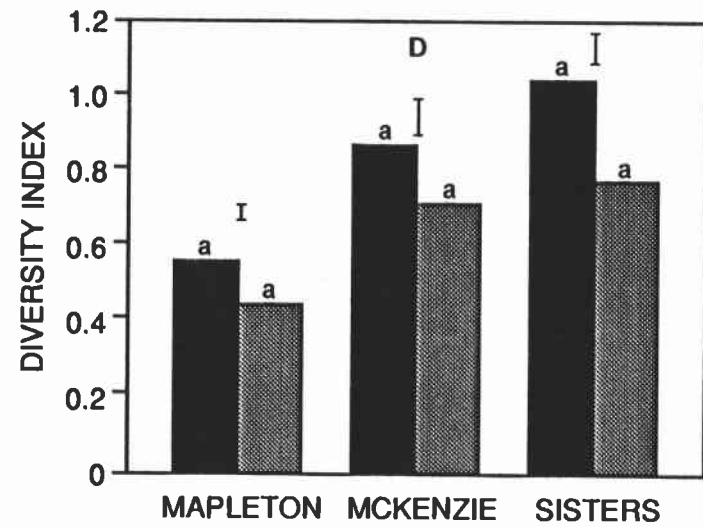
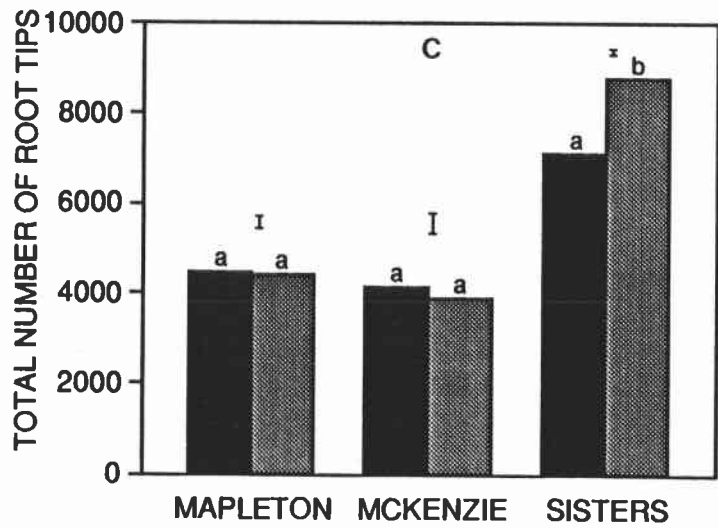
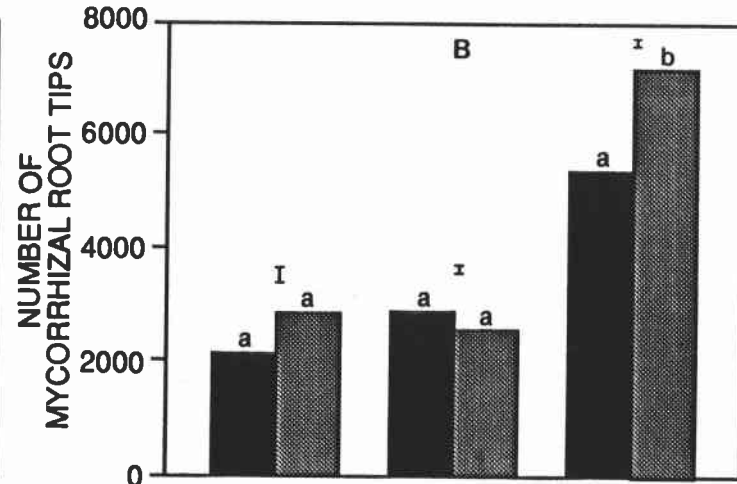
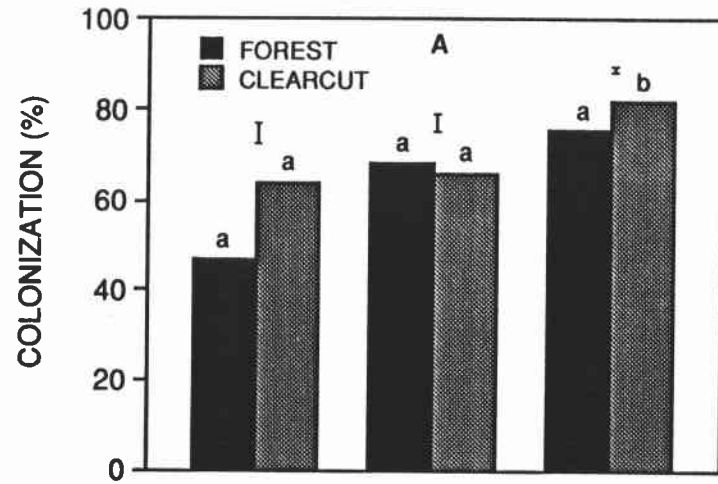


Figure 3

Root tip characteristics in forest vs. clearcut soils from the 10-30 cm depth, for the three forest types. Lower case letters indicate statistically significant differences between forest and clearcut soils within each forest type ($p < 0.05$): A) percent mycorrhiza colonization, B) numbers of mycorrhizal root tips, C) total root tips, D) diversity index of mycorrhizal root tips.

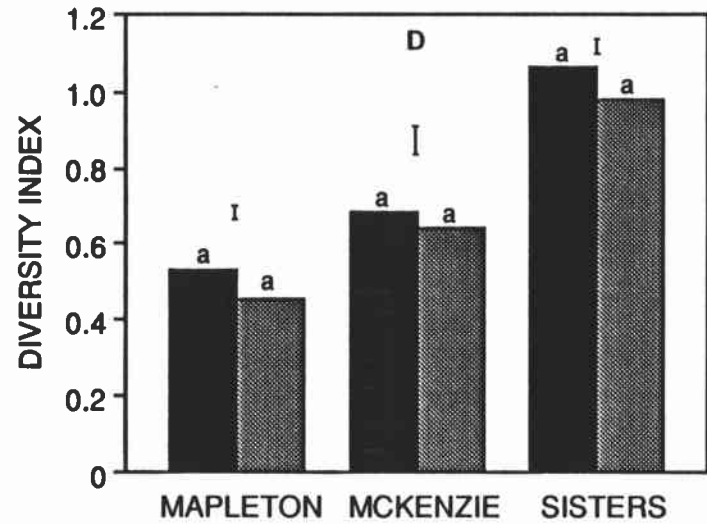
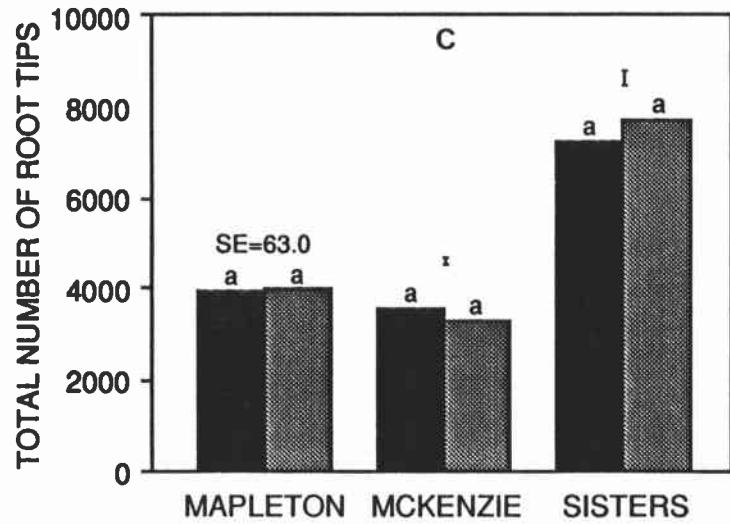
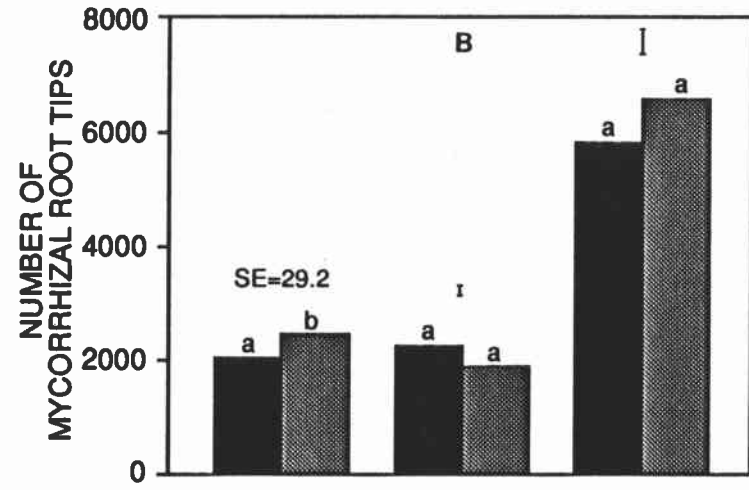
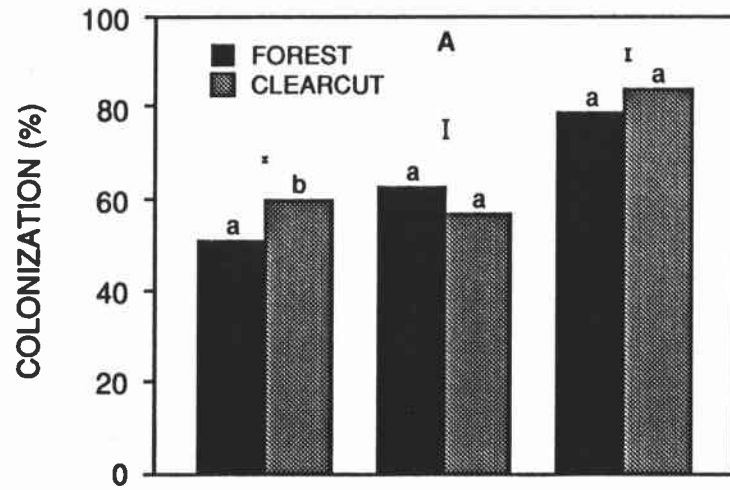
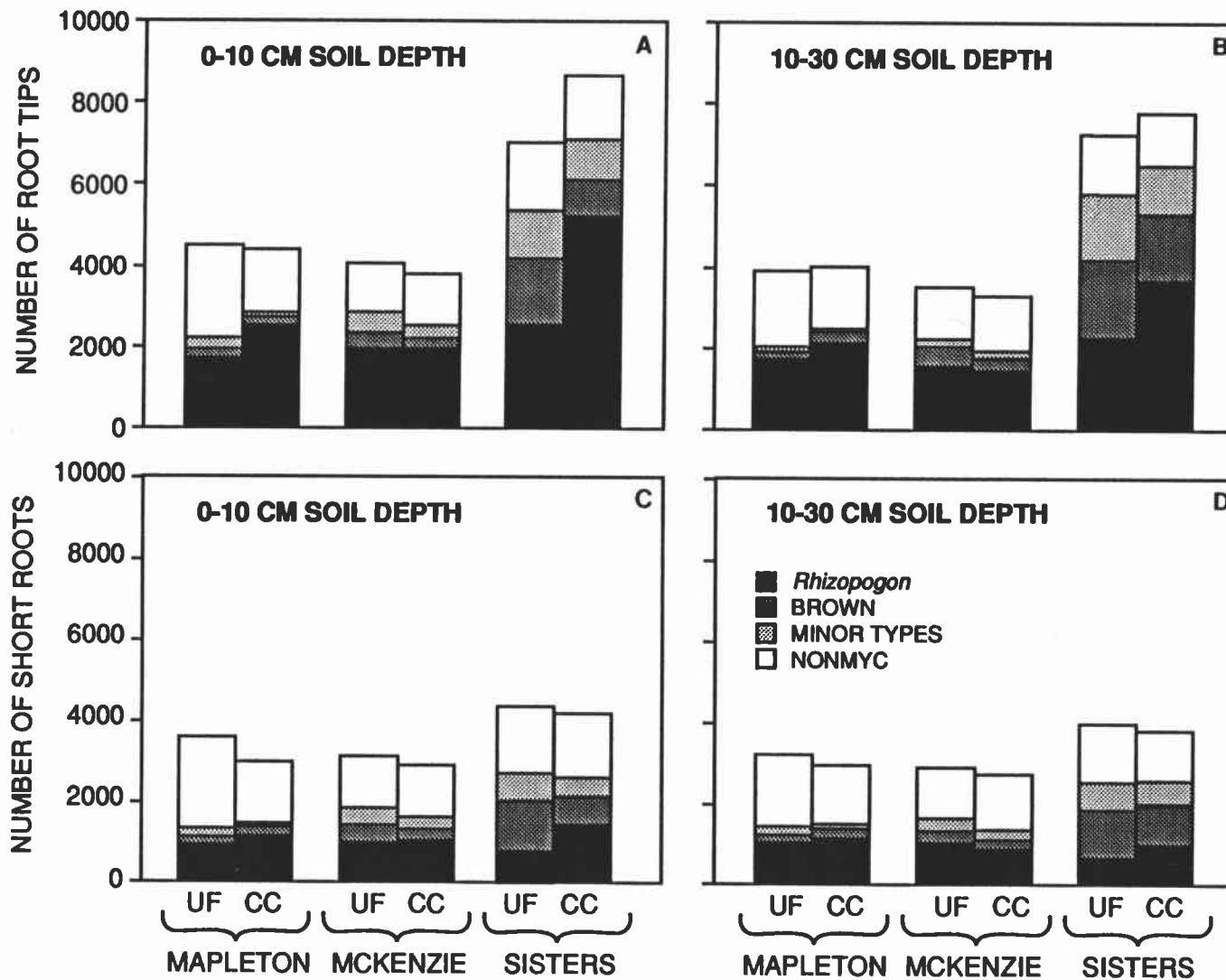


Figure 4

Root tip and short root type composition in forest and clearcut soils from the three forest types: A) root tips, 0-10 cm soil depth, B) root tips, 10-30 cm soil depth, C) short roots, 0-10 cm soil depth, D) short roots 10-30 cm soil depth.



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