AN ABSTRACT OF THE THESIS OF

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Title: ECTOMYCORRHIZAL POPULATIONS ON A CHRONOSEQUENCE OF DISTURBED AREAS IN THE CENTRAL CASCADES

Abstract approved: Professor David Anthony Perry

A greenhouse bioassay was used to investigate effects of natural and manmade disturbances on native ectomycorrhizal populations of Douglas-fir and western hemlock on a steep southeast slope in the west central Cascade Mountains. Total and mycorrhizal root tips were counted on seedlings grown in soils collected from (a) two 100+ year old forests, (b) a 36-40 year old forest established after wildfire, (c) a recent clearcut in which residue had not been burned, (d) a recent clearcut which had been broadcast burned, and (e) a 20 year old Douglas-fir plantation.

With Douglas-fir, the greatest number of total and ectomycorrhizal root tips were produced on seedlings grown in soils from the unburned clearcut. The least number of tips were produced in soils from the plantation and one of the old forests. The natural burn, the other old forest, and clearcut and burn plots were intermediate in total and mycorrhizal root production.

The pattern of root tip formation on western hemlock was quite different. Plots with no recent burn history (the clearcut with no

burn, the natural burn, and the two old growth forests) produced equivalent numbers of total and mycorrhizal root tips. Total root and mycorrhizal tip formation was depressed in soils from the clearcut and burn and from the young plantation.

Soil variables measured, particularly nitrogen, carbon, and moisture, were highly correlated with both root dry weight and total mycorrhizal tips of Douglas-fir and western hemlock and occurrence of Cenococcum geophilum Fr., a mycorrhizal fungus common to both seedling species. Differences among soils of the disturbance units obscured the relationship between root size, root tip numbers, and mycorrhizae. Data from the greenhouse bioassay, however, particularly regarding occurrence of Cenococcum, and the litter experiment indicated that differences in these parameters were at least in part due to differences in mycorrhizal response. Differential responses of Douglas-fir and western hemlock species also suggested that the mycorrhizal fungi, save for Cenococcum, were different for each seedling species.

"Whatever theories may be proposed within the unsolved realm of mycorrhiza, it seems necessary to demand one thing: our conclusions must be ecologically reasonable."

E. Bjorkman 1970
Plant & Soil 32:589-610

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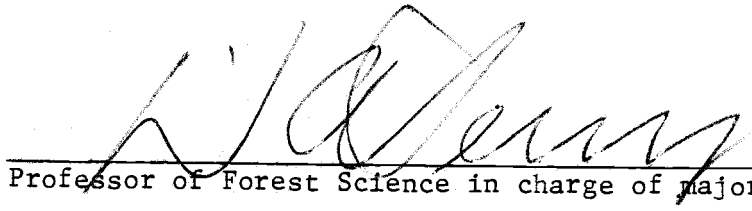

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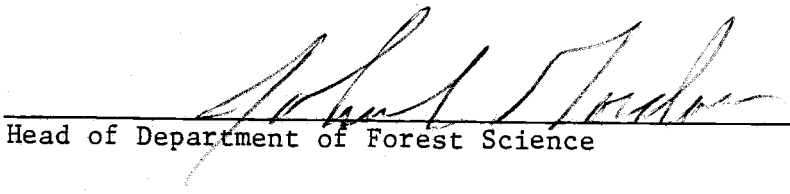

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INTRODUCTION

Recent years have seen an increasing concern over man's impacts on nutrient cycling and productivity of forest ecosystems (Leaf, 1979). The effects of disturbance on mycorrhizae, the fungus-root relationship prominent in the movement of nutrients from soil to plant, are poorly understood.

The necessity of mycorrhizae to conifer growth and survival is well-documented (Harley, 1969; Marks et al., 1973; Meyer, 1974). Nutrient absorption, drought resistance, and protection of roots from pathogens are among the more important aspects known to be influenced by the symbiosis (Voight, 1971; Zak, 1964; Marx, 1972; Duddridge et al., 1980). In undisturbed forests, mycorrhizal fungi are ubiquitous (Meyer, 1973; Mikola, 1970; Wilde, 1954). Some mycorrhizae are specific involving only one fungal species and host, while others are general, with many species of fungi being capable of forming mycorrhizae with a particular host and vice-versa (Trappe, 1962). Trappe (1977) has estimated that as many as 2,000 species of fungi may be capable of forming mycorrhizae with Douglas-fir alone. Species of mycorrhizal fungi, however, differ greatly in ability to influence growth and survival of the host (Benecke and Gobl, 1974; Rayner and Levisohn, 1941; Marx and Bryan, 1971; Bowen and Theodorou, 1967).

Benecke and Gobl (1974) noted in their study with Pinus mugo that mycorrhizae established in the nursery failed to develop further once

outplanted and, in time, were completely replaced by mycorrhizae formed by fungi native to the site. Lamb and Richards (1971) found the most beneficial mycorrhizae for slash and radiata pine seedlings were formed with fungi originally isolated from their respective hosts. Although growth responses due to mycorrhizal inoculation were observed at one site in their study, Theodorou and Bowen (1970) observed little to no growth response with inoculated seedlings that were outplanted to a site containing a more efficient native population of mycorrhizal fungi. Marx et al. (1977) found seedlings that were initially dominated by the nursery-inoculated fungus, Pisolithus tinctorius, were in time after outplanting invaded by mycorrhizal fungi native to the site. Maser et al. (1978) have hypothesized "that fungi endemic to nurseries will not function effectively at all sites and must be replaced by fungi native to a site if a plantation is to thrive".

Considering both the biological uncertainties and the added cost involved in inoculation programs, it seems important to maintain native populations of ectomycorrhizal fungi for future mycorrhiza formation. Of primary importance, then, is the question of how mycorrhizal fungi are affected by the direct or indirect effects of host removal. How long can an area remain "hostless" before inoculum becomes inadequate to insure rapid and successful mycorrhizal formation? The saprophytic capabilities of many mycorrhizal fungi are unknown or are rated low (Harley, 1969; Rayner, 1927). What happens when a site is not only cleared of host species but is also treated with some method of site preparation such as slash burning or scarification? Studies

with field planted seedlings have shown fire to delay mycorrhizal development for one to two years (Mikola et al., 1964; Wright and Tarrant, 1958). Fire, though not responsible for elimination of mycorrhizae from seedlings, did reduce numbers of mycorrhizae formed and increase soil depth at which initial mycorrhizal development occurred. Perry et al. (1981) showed that both total and mycorrhizal root tips are reduced for up to 16 years following harvest of lodgepole pine in Montana. In contrast, Greco (1978), dealing with methods of site preparation on a harvested Douglas-fir site in Washington, found that bareroot seedlings planted in burned and scarified areas possessed more mycorrhizae than those grown in non-scarified areas.

Depending on their specific life strategies, some mycorrhizal fungi may survive and proliferate on a disturbed site while others will be eliminated. Because mycorrhizal fungi differ in benefits to the host, it is important to find out whether site disturbances shift the types of mycorrhizae present. Robinson (1971), concerned with declining productivity of Pinus patula in some second rotation sites, found that successive rotations were marked by a shift in the type of mycorrhizae formed. He hypothesized that it was the shift to less "efficient" species of fungi that was in part causing the decline in productivity. Wright (1963) found that conditions considered suboptimal for development of many mycorrhizal fungi favored Cenococcum geophilum, a mycorrhizal fungus that has been shown in some cases to be less favorable for root growth (Marx et al., 1978; Theodorou and Bowen, 1970) and a slower former of mycorrhizae than some other fungal species (Munson, 1980).

Many of the studies mentioned above have used field-planted seedlings to investigate effects of various disturbances on mycorrhiza development. Disturbances create different environmental conditions such as the amount of sunlight reaching the soil surface in a clearcut versus undisturbed sites. This has been shown to affect seedling growth (Brix, 1967) and thus the disturbance may affect both the amount of mycorrhizal propagules present in the soil and the ability of the host and/or fungus to form the association (Hacskaylo and Snow, 1959). By testing soils in a greenhouse, soil moisture, light, and temperature may be controlled; thus restricting comparisons among treatments to the presence of inocula or other soil factors which directly or indirectly influence mycorrhizal formation. This type of controlled testing is especially important if disturbed soils are to be compared to soils with an undisturbed cover.

It was the objective of this study to determine via a greenhouse bioassay the degree to which ectomycorrhizal fungi of Douglas-fir and western hemlock were affected by different types of site disturbance, and over what period of time the effects of disturbance might persist.

STUDY AREA

We chose sites on which reforestation might be difficult - southern exposure, steep slopes, highly erodible soils. Under these conditions, the presence of mycorrhizae may be critical for seedling survival and growth. All study units (treatments) were on a steep southeast slope approximately 2 kilometers wide in the west central Cascades near Blue River, Oregon (latitude 44° 10'N, longitude 122° 20'W), at 2,000 ft (610 m) elevation. The site represented a dry Douglas-fir/western hemlock community (Dyrness et al., 1974). Despite reasonable uniformity in aspect and slope, there was some variation among treatment areas in Douglas-fir site class, which is an index of site quality (I high, IV low - McArdle et al., 1961) (Table I). The predisturbance forest consisted of an overmature stand of Douglas-fir (250+ yrs) with smaller components of western hemlock (100+ yrs), western red cedar (Thuja plicata Donn.), and a small component of bigleaf maple (Acer macrophyllum Pursh), chinkapin (Castanopsis chrysophylla (Dougl.) A.DC.), and Pacific madrone (Arbutus menziesii Pursh.).

The area is characterized by cool, wet winters (mean temperature 2.3°C) during which the major portion of the precipitation (mean precipitation 2,300 mm/yr) falls; and hot dry summers (mean temperature 20.6°C) (Rothacher et al., 1967). Soils are shallow, rocky, unstable clay-loams with low fertility and moisture holding capacity. Parent material is colluvium and residuum derived from breccia and andesitic bedrock (Legard and Meyer, 1973). A decription of each treatment unit follows:

Plot Descriptions

Clearcut-no burn (CC): The site was clearcut and cablelogged in March 1977. Post-disturbance vegetation consisted of scattered shrubs [vinemaple (Acer circinatum Pursh), hazel (Corylus cornuta Californica (A.DC.) Sharp), Oregon grape (Berberis nervosa Pursh), trailing blackberry (Rubus ursinus (Dougl.) Brown), and chinkapin starting to invade the area. A sparse herb layer was present consisting mainly of assorted grasses, bedstraw (Galium oreganum Britt.), fireweed (Epilobium angustifolium L.), and modest whipplea (Whipplea modesta Torr.). Due to steepness of the slopes and nature of the soils here, local debris slides have caused incorporation of much of the organic residue into the mineral layer, retarding the development of a litter layer.

Natural burn-revegetated (NB): The site, burned by wildfire, supported a 36-40 year old Douglas-fir overstory. The understory was composed of regenerating conifers of western hemlock and western red cedar, bigleaf maple, and chinkapin. Hazel, Oregon grape, salal (Gaultheria shallon Pursh), rhododendron (Rhododendron macrophyllum G. Don), and vine maple occur under crown openings. A small to moderately developed herb layers was present and consisted of Prince's pine (Chimaphila umbellata (L.) Bart.), modest whipplea, twisted stalk (Disporium smithii (Hook.) Piper), and sword fern (Polystichum munitum (Kaulf.) Presl.). A litter-moss layer and a buildup of above ground woody residue were present.

Old-growth one (OG1): The site, originally selected as one of two plots to constitute the undisturbed plot (OG2 was located at the opposite lower corner of the study area), was a mature stand of Douglas-fir (250+ yr old) and western hemlock (100+ yr old). A number of younger (100-150 yr old) Douglas-fir suggested that this site had experienced some type of disturbance, most likely wildfire. The age distribution difference between OG1 and OG2 and the near ridgetop position of OG1 had created a more open stand in OG1, so the two were treated separately. Some regeneration of Douglas-fir, western hemlock, and western red cedar had occurred. A moderate to strong shrub layer dominated by rhododendron, vine maple, Oregon grape, and salal was present with an herb layer dominated by beargrass (Xerophyllum tenex). Both above and below ground woody residue at various stages of decay and a litter-moss layer was present.

Clearcut-burn (CB): The site, clearcut along with CC in March 1977, was burned in March-April of 1978. By October, 1978, vegetation was recolonizing the area. Vine maple, rhododendron, salal and Oregon grape constituted the sparse shrub layer. A few herbs, dominated by thistel (Cirsium arvense (L.) Scop.) were scattered throughout the plot. No litter or moss layer had yet been established. The soil surface was covered with a dark ash layer. Charred woody debris was present.

Young-growth plantation (YG): The site was logged in 1958, burned in 1959, and planted with 2-0 Douglas-fir in 1960. The unit was precommercially thinned in September 1978 to 232 trees per acre. The existing overstory was a pure stand of Douglas-fir. The shrub layer was composed of hazel, rhododendron, Oregon grape, and salal, which along with a weakly developed herb layer composed of beargrass, sword fern, bracken fern (Pteridium aquilinum Underw.), and modest whipplea, was evenly distributed throughout the stand. The litter layer was small to nonexistent. Slash from thinning remained on the plot.

Old-growth two (OG2); The site was a mature stand of 150-250+ year old Douglas-fir and 100+ year old western hemlock. Western hemlock regeneration predominated more here than OG1. Western red cedar is present to a lesser extent. A well-developed shrub stratum was present, dominated by rhododendron and salal. Beargrass and a few miscellaneous herbs composed the sparse herb layer. A well developed litter and moss layer was present.

To further characterize treatment units several field measurements were taken. Litter depths were determined for each sample point at the time the soils were collected. Percent light reaching the soil surface was determined by the Ozalid paper method described by Friend (1961). Soil samples were collected at each point once a month from April until October for gravimetric soil moisture determinations and, at the same time, soil temperatures were determined at 2 and 10 cm with a bimetal thermometer. Soil pH was determined with a 1:2 soil

to water mix. Total soil nitrogen, nitrate, and total cations were analyzed by the Forestry Sciences Lab, Corvallis, Oregon, using standard laboratory procedures. Mineralizable nitrogen was determined by the anaerobic-incubation technique of Keeney and Bremner (1966). Organic matter (% carbon) was determined by a modified Walkley-Black Method (Jackson, 1958).

MATERIALS AND METHODS

Greenhouse Bioassay

Ten points were randomly located within the central portion of each treatment unit (five points each in the old growth stands). During the first week of October 1978 four soil samples were collected to a depth of 10 centimeters around each point. A 70% ethyl alcohol wash was used on all collecting tools to reduce contamination between points. Soil samples were transported to the laboratory and processed within 24 hours of collection. The four samples from each point were combined and put through a 2 mm sieve to eliminate debris and rocks. Care was taken to gently crumble as much of the material as possible through the sieve. The sieve was sterilized with an ethyl alcohol dip between processing of composite sample to avoid contamination.

For the greenhouse bioassay, two parts sieved forest soil were mixed with one part each of steam-sterilized peat and vermiculite. This mix was necessary as the sieved soil tended to be compacted in the containers when watered. For each soil collection point, twelve pine-cell sized Ray leach tubes, sterilized in a weak sodium hypochlorite solution, were filled with the soil mix. Six tubes were planted with seeds of Douglas-fir and six with western hemlock. Tree seed were selected from an appropriate seed zone and lot, and before planting were surface sterilized for 15 minutes in a 30% hydrogen perioxide solution then rinsed several times in sterile distilled water. A small cover of chicken grit was added to the top of each tube to reduce contamination by water splash. Several blanks,

consisting of only steam-sterilized peat and vermiculite mix, were planted to test for possible airborne or seed contamination by mycorrhizal fungi.

Tubes were located randomly within standard tube racks. The racks were randomly located on the greenhouse bench and rotated weekly to reduce environmental differences in the greenhouse. As seedlings emerged, tubes were weeded to one seedling each.

Douglas-fir and western hemlock seedlings were allowed to grow 4 1/2 and 6 months, respectively, with natural daylengths extended to 16 hours by high intensity sodium vapor lamps, and watered with an overhead mist system. At harvest time, seedlings were removed from the tubes and the roots were gently cleaned under running water. Shoot and root lengths were measured at this time. The entire root system of each seedling was then removed for root tip and mycorrhizal examination. Total root and mycorrhizal tips were counted with the aid of a stereomicroscope (10 to 70x). Squash mounts and thin sections were used as needed to verify mycorrhizal status. As the seedlings were quite young at the time of harvest, all tips appeared active according to the criteria used by Harvey et al. (1976), and, as such, all counts represent that of active tips. The root tips were further classified by mycorrhizal type based on visual morphological differences, i.e. color, texture and branching patterns. Due to the short duration of this study, isolation, culture, and/or identification of the fungal symbionts were not undertaken. A short description of the mycorrhizal types follows:

Mycorrhizal Types Observed on Douglas-fir:

D1: Black and White Mycorrhiza: The sheath was black and white with white predominating. White to buff colored fibrous rhizomorphs were abundant. Individual elements were club-like, often occurring in clusters. In paraffin thin sections, the mantle was very conspicuous (50-107 μm) and dense with an outer peridium-like layer sometimes present. The Hartig net was well developed with no apparent intracellular penetrations. These characteristics plus the tendency for the sheath to turn pink when bruised suggested this mycorrhizae to be formed by a species of Rhizopogon (Dr. James Trappe, personal communication).

D2: Black Mycorrhiza: The sheath was black with black, stiff, hair-like hyphae extending from the club-like element. The symbiont was Cenococcum geophilum Fr.

D3: Smooth Pale Mycorrhiza: The sheath appeared smooth and yellowish-brown to tan under the stereomicroscope. The mycorrhizae were present as single, straight to slightly swollen, to pinnately branched structures. Thin sections revealed a complete but thin mantle with a well developed Hartig net.

D4: Brown Slender Mycorrhiza: These appered as unswollen to only slightly swollen light brown root tips devoid of root hairs. Although this is characteristic of uninfected Douglas-fir short roots (Bogar and Smith, 1965), squash mounts did reveal some tips to possess a discernible mantel and Hartig net. Thin

sections varied from suberized roots with a collapsed cortical region to mycorrhizae with a tightly appressed mantle and a Hargit net one to three tiers cells deep. As a majority of squash mounts did show some hyphal presence, the tips with this appearance were counted as mycorrhizal.

D5: Yellow Brown Mycorrhiza: This mycorrhiza resembled D3 but was darker and appeared more as alternating knobs projecting off a lateral root than as the branched structures of D3. Thin sections revealed a sparse to spotty mantle development with a well developed Hartig net.

Mycorrhizal Types Observed on Western Hemlock[1]:

H1: Black Mycorrhiza: This mycorrhiza followed the description of D2, and was formed by Cenococcum geophilum Fr.

H2: Red Brown Mycorrhiza: The sheath was smooth and a consistent reddish brown in color. The mycorrhizae were single slightly clavate structures, usually 3-5 mm in length. No extending hyphae or rhizomorphs were present. Hand sections revealed a well developed Hartig net.

H3: White Cottony Mycorrhiza: The sheath was brownish yellow to white, fibrous and cottony. Extending hyphae were white, rhizomorphic, and abundant. The mycorrhizae occurred as a

[1]As these types were visually distinct from one another, thin sections were not made.

single somewhat curved digitate structure. Hand sections revealed a well developed Hartig net.

H4: Smooth Brown Mycorrhiza: The sheath was light brown to beige and usually smooth. The mycorrhizae appeared singly as slightly clavate digitate structures somewhat like H2 but not as swollen. Squash mounts and hand cross sections revealed a small tightly appressed mantle and presence of a Hartig net.

H5: Pearly Smooth Mycorrhiza: The sheath was smooth with a pearly sheen ranging from white to beige to very light purple. The mycorrhizae were single or coralloid. Squash mounts and hand cross sections revealed a well developed mantle and Hartig net. These characteristics suggested the fungus might probably be haccaris laccata.

Litter Study

Mycorrhizal differences between the two old growth plots (OG1 and OG2) possibly attributable to litter differences was studied. Litter was collected from five points each in OG1 and OG2 and processed as described in the greenhouse bioassay. The material was hand crumbled. Large sticks and debris were removed. Ray leach tubes were filled with mix of forest soil and a 1:1 steam-sterilized peat and vermiculite. Soils from CC were used as the common forest soil (≡ mycorrhizal inoculum). The tubes were sown with seeds of Douglas-fir as described previously. Treatments consisted of (1) placement of litter on top of one set of seedlings and (2) application of a litter

leachate on the other. Leachate was prepared by grinding litter material in a Wiley-mill (20 mesh), putting 25 ml of the ground material in a jar with 100 ml sterile distilled water, putting the material on a shaker for 1 hour, and then filtering. Leachate was prepared and 5 mls of fresh leachate applied weekly. Five seedlings were planted per point per treatment giving one hundred total seedlings for the experiment. Control seedlings were planted in steam-sterilized peat and vermiculite to test for greenhouse contamination. The experiment was set up and run in the greenhouse as previously described, were harvested at 4 1/2 months, and processed as in the previous experiment.

Statistical Analysis

Seedling data were expressed as average value per seedling per disturbance unit.

Analyses of variance were made on all data and differences among means were evaluated with Fisher's Protected L.S.D. ($P = 0.05$) (Ott, 1977). The relationship between soil and seedling variables were investigated by correlation and regression (Steele and Torrie, 1960).

RESULTS

Root Tip Analysis

Seedlings used as controls were devoid of mycorrhizae indicating the mycorrhizae formed on the test seedlings were from the forest soil inoculum and not due to greenhouse, soil mix, or seed contamination. All disturbance units produced seedlings with at least some mycorrhizae (Tables IV and V). Although disturbance never completely eliminated mycorrhizal inoculum from the site, the units definitely differed in quantity and quality of mycorrhizae present (Figures IA and IB) and in behavior of the two tree species.

Douglas-fir

Total root tips varied from 66.2 to 108.0 tips per seedling (Table IV), with the clearcut-no burn (CC) having significantly greater number of tips ($P = 0.05$) than other units. Mycorrhizal tips ranged from 33.9 to 73.9 tips per seedling, with C again having significantly greater numbers ($P = 0.05$) than other units. Young growth (YG) soils produced seedlings with significantly lower numbers of total root tips than CC and OG1 and significantly lower mycorrhizal root tips than CC, NB, OG1, and CB.

Differences in numbers of mycorrhizal tips among treatment units was accompanied by a shift in total tip numbers and overall percentages of each type of mycorrhizae (Figures IA and IIA). Contingency table analysis (Steele and Torrie, 1960) showed significant interaction between mycorrhizal types and treatment ($\chi^2 = 36.28$, $P = 0.025$).

Western Hemlock

Old growth one (OG1) soils produced seedlings with significantly greater number of total root and mycorrhizal tips than YG and OG2 (Table V). The least amount of both total root and mycorrhizal tips were produced in the clearcut-burn (CB) soils, although these differences were not significantly different from several of the other plots. As seen in Douglas-fir, there was significant interaction between mycorrhizal type and disturbance type ($\chi^2 = 65.66$, $P = 0.005$) (Figures IB and IIB). Type H3 occurred in very small numbers and was left out of the graphs. Soils from plots with relatively recent fire histories (CB and YG) produced significantly ($P = 0.05$) fewer total root and mycorrhizal tips. Contingency table analyses showed this to be associated with lower than expected numbers of Cenococcum geophilum (H1) tips.

Seedling Growth

Douglas-fir

Although shoot dry weight did not differ significantly among the plots, root dry weights ranged from 45.8 to 69.7 mg, significantly greatest in CC and OG1 (Table IV). In comparing the unburned (CC) and burned (CB) clearcuts, consistently larger and heavier root systems were produced in CC. Of note are the differences in seedling measurements between the two old growth plots, with OG1 producing the larger, heavier root system than OG2.

Western Hemlock

Growth response of western hemlock seedlings to the various disturbances differed from those observed by Douglas-fir (Table V). Seedlings from CC possessed the greatest shoot lengths. OG1, although not significantly different from CC in root length, did produce significantly smaller seedlings with regard to shoot length, shoot dry weight, and root dry weight. The young growth (YG) soils produced an overall smaller seedling in all four categories (shoot and root lengths and shoot and root dry weights). OG1's seedlings were larger and heavier than OG2 although this difference was not as great as that seen in Douglas-fir. Smaller seedling shoot and root lengths and dry weights were once again produced in CB and CC.

Environmental Characteristics of Disturbance Units

As would be expected, removal of all (clearcut units - CC and CB) or part (thinned young growth - YG) of the overstory resulted in a greater percentage of light reaching the soil surface than in plots with a well-developed overstory (NB, OG1, and OG2) (Table II). The methods of overstory removal greatly decreased depths of the litter layer both by physical removal of the litter layer and by eliminating the source (overstory) of new litter. The increase in light, along with the decrease in the amount of insulating litter, resulted in higher average (May through October) soil temperatures at both the 2 and 10 centimeter depths for CC, and CB, and YG. Soil moistures were lower for CB and YG, probably due to increased insolation and

increased soil temperatures. Soil moistures of CC were comparable to the developed overstory stands, NB, OG1, and OG2. Incorporation of woody and other organic debris into the surficial layers was probably responsible for the higher soil moisture in CC than CB and YG (see % carbon, Table III (Harvey et al., 1979)). Soil pH values did not differ significantly among disturbance units (average pH 5.11) despite disturbances ranging from old growths (OG's) to a recent burn (CB).

CC soils had more total and mineralizable nitrogen (N) and more calcium (Ca) than those from all other units, and more carbon (C) and phosphorous (P) than OG1, BC, and YG (Table III). Nitrate-nitrogen (NO_3) and potassium contents were greatest in CB as would be expected in a recent burn area, as was percent potassium (Austin and Baisinger, 1955).

Correlations Between Seedling Growth, Mycorrhizae, and Soil Variables

Root dry weight of Douglas-fir correlated positively with number of total root tips per seedling ($r = 0.65$, $P = 0.001$) and with number of mycorrhizal tips per seedling ($r = 0.58$, $P = 0.001$), as was root dry weights of western hemlock ($r = 0.59$, $P = 0.001$ and $r = 0.54$, $P = 0.001$ for total root mycorrhizal tips, respectively) (Table VI). Four of the Douglas-fir mycorrhizal types (D1, D2, D3, and D5) correlated significantly to root dry weight, whereas in western hemlock, only the occurrence of H1 - Cenococcum geophilum correlated significantly with root dry weight ($r = 0.54$, $P = 0.001$). In both seedling species, numbers of total root and mycorrhizal tips correlated highly to each other.

Both root dry weight and total mycorrhizal tips of Douglas-fir correlated positively with all measured N variables, C, P, and percent moisture (Tables VII and VIII). Western hemlock root weights correlated with essentially the same variables as Douglas-fir. However, mycorrhizal tips of the two seedling species responded differently. As in Douglas-fir, western hemlock mycorrhizal tips were positively correlated with N variables, C, P, and percent moisture. There was, however, a highly significant negative correlation between numbers of mycorrhizal tips on hemlock and both mean soil temperatures (2 and 10 centimeters) and sodium (Na).

Cenococcum geophilum, the only fungal type clearly associated with both seedling species had a much stronger correlation with seedling variables of western hemlock than in Douglas-fir (Table IX). Of note is the strong negative correlation between occurrence of Cenococcum and soil temperatures as also occurred between total mycorrhizal tips and Cenococcum with hemlock.

Effects of Litter Leachate on Tip Production in Douglas-fir

The method of litter application - application of litter on surface and application of litter as a leachate - did not produce any significant differences in Douglas-fir seedling variables. Seedling variables did differ significantly by litter site. Seedlings grown in CC soils that had litter applied from OG2 produced significantly fewer mycorrhizal tips than seedlings grown in the same soil but with litter applied from OG1 (Table X). This reduction in mycorrhizae was due to a significant reduction ($P = 0.01$) in mycorrhiza type D1 and was also

associated with a significant reduction ($P = 0.01$) of total root tips. These reductions correspond with those of Douglas-fir seedlings grown in OG2 soils when compared with OG1. pH did not differ between the two litter leachates, both averaged about 5.15.

Mycorrhizal type D3 was absent from both litter site treatments. Type D5 tips were quite low. Both types were present on Douglas-fir grown in CC soils in the greenhouse bioassay (Figure IA) with no litter leachate.

DISCUSSION

Although none of the disturbances completely eliminated mycorrhizal inoculum from the units alterations of unit characteristics resulted in changes in root weights, numbers of root and mycorrhizal tips, and amounts of mycorrhizal types. Douglas-fir and western hemlock responded differently to the disturbances with regard to these variables. Differential tree species behavior was associated with variation in response of different mycorrhizal types.

In the litter study, greater numbers of Douglas-fir mycorrhizal tips were related to a greater amount of D1. Diffeences in numbers of tips between seedlings grown in OG1 and OG2 soils appeared to be largely related to an apparent allelopathic response of D1 (tentatively identified as a Rhizopogon sp.) to OG2 litter. Reduction of western hemlock tip numbers in CB and YG soils was mostly related to fewer Cenococcum (H1) tips.

Many factors influence mycorrhiza formation (see the review by Slankis, 1974). Nitrogen is known to influence growth and branching pattern of conifer seedlings (Knight, 1973) and the percentage of active root tips (Giertych and Farrar, 1961). Thus differences in soil nutrients, such as nitrogen, may indirectly affect mycorrhizal formation by directly affecting the amount of root or "receptive surface". Data from CC soils which possessed the higher amounts of nutrients and which produced Douglas-fir seedlings with greater dry weights and numbers of root tips would seem to support this argument. Conversely, mycorrhizal fungi improve seedling vigor and produce

growth hormones (Slankis, 1971), both of which likely influence root growth and tip formation. Additionally, newly developing root tips may abort if not colonized by a mycorrhizal fungus (Wilcox, 1967). Behavior of Douglas-fir seedlings in CB and YG would seem to support this. Here YG, which produced seedlings with the least number of total root tips, mycorrhizal tips, and the least root dry weights; possessed similar amounts of nutrients as CB, yet CB produced seedlings with significantly greater mycorrhizal tips, total root tips, and root dry weight. Certainly in our study, no clear cause-effect relation can be demonstrated between root size, mycorrhizal numbers, and soil nutrient status. It seems likely that we have measured the integrated effect new environments created by various disturbances on the seedling, the fungus, and the symbiosis.

Variable behavior of the different mycorrhizal types between the two seedling species, and among the disturbances, suggests strongly that at least a portion of the response pattern which we observed was due to a mycorrhizal effect either directly on the fungus (i.e. reduction inocula) or on the capabilities of the host and fungus to form the symbiosis. The former is suggested by the significant correlations between mycorrhizal tips and soil temperature (western hemlock) and soil moisture (western hemlock and Douglas-fir), both of which were field measurements and thus could not directly influence formation of the symbiosis nor seedling growth in the greenhouse. They could, however, be symptomatic of soil factors not related to fungal inocula, which were carried into the greenhouse. Note that the primary correlation of soil temperature and moisture was with Cenococcum,

further evidence that both fungus, and seedlings are involved in the root patterns measured.

Seedlings of the two tree species unquestionably have affinities for different types of fungi; the greater prevalence of Cenococcum on hemlock (Figure IBB), the strong negative correlation between Cenococcum geophilum and soil teperatures for both seedling species, and the strong negative correlation between total mycorrhizal tips and soil temperatures, suggest Cenococcum geophilum is a more significant mycorrhizal symbiont on hemlock than on Douglas-fir. Affinities, such as with Cenococcum with hemlock, seem closely related to the ecological role of the trees. In this study, Douglas-fir, a pioneer on disturbed sites, formed mycorrhizae which were not negatively affected, and may even be positively influenced by disturbance. Our litter study indicated in undisturbed sites where litter is allowed to build up, that one of the more important mycorrhizal types found in this study for Douglas-fir, D1, was adversely affected by litter application from OG2. We have not as yet determined why litter from OG2 exhibits this allelopathic response and OG1 litter does not. The near ridge-top position, and higher soil temperatures of OG1 may have reduced litter accumulation and increased decomposition of litter materials, both of which could result in lesser buildup of allelopathic substances. The greater amount of hemlock overstory and thus litter layer in OG2 may also be responsible.

It is of note, that Cenococcum (D2) was not affected by application of litter as was D1 but was affected by soil disturbances (i.e. clearcutting and burning) which affected soil temperature and moisture

in the field. If, indeed, Cenococcum geophilum is a more important symbiont on hemlock than Douglas-fir, this observation would be consistent with the late seral role of hemlock.

Only in the YG soils were seedling and mycorrhizal parameters of both Douglas-fir and western hemlock adversely affected. This was apparently related to a combination of high soil temperatures and low soil moistures, and, perhaps, was also due to other factors which we did not measure.

The story of how disturbances affected the mycorrhizae in this study is complex. In order to adequately relate effects of disturbance to amounts of native mycorrhizal fungi present for future mycorrhizal formation, further studies will be needed to determine whether disturbances affect amounts and kinds of inoculum present or abilities of host and symbiont to form the symbiosis. If it is a combination of the two, as seems likely, another method of field evaluation will be needed that can distinguish the two. The greenhouse bioassay was useful in this study in that it allowed comparisons to be made on the effects of a variety of forest ecosystem disturbances with regards to the behavior of two conifer seedling species and their respective mycorrhizae.

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Table I. Treatment unit characteristics.

Plots	History	Age since disturbance	Aspect	Slope	Site Class*
CC	Clearcut-no burn	1 yr	SE	76	IV
NB	Natural burn	36-40 yr	SE	64	IV
OG1	Old-growth I	--	SE	52	IV
CB	Clearcut & burn	1 yr	SE	63	II-III
YG	Young growth	20 yr	SE	52	III
OG2	Old-growth II	--	SE	34	II-III

*Data from TRI system.

Table II. Mean litter depth, soil temperature, moisture, pH and percent light of each treatment unit.

Plot	Litter depth (cm)	Soil Temperature[1] (C°) 2 cm	10 cm	Moisture[1] (%)	pH	% Light
CC	0.77	18.0	15.1	37.4	5.23	59.3
NB	3.72	15.1	12.9	37.8	5.08	4.0
OG1	2.33	16.3	13.2	31.7	5.42	2.9
CB	0.05	21.4	18.1	24.8	5.14	85.1
YG	0.72	17.4	15.2	24.4	5.20	24.4
OG2	3.25	15.0	12.2	44.5	4.58	2.2

[1]Average value of data collected monthly from May to October 1979.

Table III. Soil chemical analysis for each disturbance unit.

Plot	Nitrogen				%O.M.	%P	%Na	%K	%Ca	%Mg	C:N
	Minn N (ppm)	Total %N	NO_3 (ppm)	NH_3 (ppm)							
CC	41.10a[1]	0.36a	0.61b	22.80	14.64a	0.13a	0.044	0.094d	0.57a	0.546	41:1
±s.e.[2]	(±4.58)	(±0.05)	(±0.11)	(±2.13)	(±2.18)	(±0.01)	(±0.011)	(±0.007)	(±0.022)	(±0.050)	
NB	27.45b	0.25b	0.25b	19.60	12.13ab	0.11ab	0.029	0.084d	0.315b	0.400	49:1
	(±7.63)	(±0.06)	(±0.02)	(±5.12)	(±4.83)	(±0.01)	(±0.004)	(±0.005)	(±0.046)	(±0.044)	
OG1	12.78c	0.13bc	0.37b	14.67	6.00bc	0.08bc	0.016	0.063d	0.212c	0.397	46:1
	(±3.36)	(±0.01)	(±0.09)	(±0.67)	(±0.81)	(±0.01)	(±0.003)	(±0.002)	(±0.023)	(±0.036)	
CB	8.47c	0.11c	2.00a	14.80	3.67c	0.07c	0.027	0.310a	0.174c	0.304	33:1
	(±0.75)	(±0.01)	(±0.74)	(±1.62)	(±0.41)	(±0.01)	(±0.003)	(±0.015)	(±0.014)	(±0.015)	
YG	9.65c	0.12c	0.31b	14.60	3.62c	0.08bc	0.029	0.144c	0.229c	0.478	30:1
	(±1.08)	(±0.01)	(±0.03)	(±2.11)	(±0.30)	(±0.01)	(±0.002)	(±0.010)	(±0.021)	(±0.059)	
OG2	13.64bc	0.19bc	0.33b	17.00	7.51abc	0.11abc	0.027	0.244b	0.182c	0.406	40:1
	(±3.04)	(±0.02)	(±0.02)	(±4.00)	(±0.81)	(±0.02)	(±0.001)	(±0.020)	(±0.010)	(±0.008)	

[1]Values followed by similar letters are not significantly different (P = 0.05) as determined by a Fisher's Protected L.S.D. Those columns without letters were not significantly different from each other.

[2]±s.e. = ± standard error.

Table IV. Mean seedling values for Douglas-fir.[1]

	Shoot[2] length (mm)	Root length (mm)	Shoot dry wt (mg)	Root dry wt (mg)	No. total root tips	No. mycorrhizal root tips	No. non-mycorrhizal root tips	Percent mycorrhizal root tips[3]
CC	48.9a	175.5a	62.9	69.7a	108.0a	73.9a	34.0	69.0ab
s.e.[4]	(±1.05)	(±1.54)	(±1.9)	(±2.3)	(±5.13)	(±4.12)	(±3.30)	(±2.24)
NB	44.7b	164.0c	57.1	52.4c	78.7bc	48.0bc	30.7	57.8c
	(±1.04)	(±2.37)	(±2.1)	(±2.4)	(±6.20)	(±4.69)	(±3.08)	(±2.86)
OG1	45.9ab	174.2a	63.4	65.3ab	79.7bc	59.9b	19.9	74.6a
	(±1.40)	(±1.88)	(±3.2)	(±2.5)	(±5.93)	(±5.02)	(±1.69)	(±1.80)
CB	45.8b	170.7ab	60.2	59.8b	83.9b	52.3b	31.6	61.9bc
	(±0.91)	(±1.29)	(±2.0)	(±1.9)	(±2.97)	(±2.72)	(±2.31)	(±2.58)
YG	45.2b	164.4c	60.0	45.8d	66.2c	33.9d	32.3	49.4d
	(±0.92)	(±3.44)	(±2.3)	(±2.2)	(±3.51)	(±2.95)	(±2.81)	(±3.53)
OG2	44.0b	164.9bc	63.2	50.4cd	70.2bc	36.5cd	33.7	54.8cd
	(±1.39)	(±2.97)	(±3.7)	(±3.4)	(±6.38)	(±3.45)	(±5.37)	(±4.57)

[1]All values are expressed as average value per seedling.

[2]Values followed by similar letters are not significantly different (P = 0.05) as determined by a Fisher's Protected L.S.D. Those columns without letters contain values not significantly different from each other.

[3]Statistical differences determined on transformed data (arc sin $\sqrt{\%\ \text{mycorrhizal tips}}$). Values in tables are presented in untransformed form.

[4]s.e.: ± standard error.

Table V. Mean seedling values for western hemlock.[1]

	Shoot[2] length (mm)	Root length (mm)	Shoot dry wt (mg)	Root dry wt (mg)	No. total root tips	No. mycorrhizal root tips	No. non-mycorrhizal root tips	Percent mycorrhizal root tips[3]
CC	36.7a	187.4a	29.5a	29.5a	105.6ab	74.8a	30.8a	72.9c
s.e.[4]	(±1.52)	(±2.61)	(±2.3)	(±1.7)	(±8.98)	(±5.87)	(±3.66)	(±1.4)
NB	28.8b	186.2a	19.0b	23.9b	90.2b	71.5a	18.6b	79.5a
	(±1.19)	(±0.98)	(±1.2)	(±0.9)	(±4.71)	(±3.79)	(±1.36)	(±1.0)
OG1	26.0bc	181.7ab	17.7bc	22.5bc	111.2a	82.8a	28.3a	74.4bc
	(±0.74)	(±3.02)	(±0.8)	(±1.1)	(±3.40)	(±3.06)	(±1.54)	(±1.3)
CB	25.6c	177.4bc	16.1bc	22.4c	71.1c	51.2b	19.9b	72.2c
	(±0.50)	(±2.52)	(±0.6)	(±0.6)	(±3.21)	(±2.37)	(±1.77)	(±1.7)
YG	23.5c	172.8c	12.9c	17.1c	71.8c	55.1b	16.7b	77.6ab
	(±0.42)	(±2.43)	(±0.3)	(±0.5)	(±3.14)	(±2.25)	(±1.22)	(±1.1)
OG2	24.0c	180.8ab	13.9c	19.4c	107.4b	79.1a	28.3a	74.1bc
	(±0.95)	(±4.03)	(±0.8)	(±1.0)	(±6.90)	(±5.61)	(±2.56)	(±1.9)

[1]All values are expressed as average value per seedling.

[2]Values followed by similar letters are not significantly different (P = 0.05) as determined by a Fisher's Protected L.S.D. Those columns without letters contain values not significantly different from each other.

[3]Statistical differences determined on transformed data (arc sin $\sqrt{\%\ \text{mycorrhizal tips}}$). Values in tables are presented in untransformed form.

[4]s.e.: ± standard error.

Table VI. Correlation matrix of seedling growth measurements and root tip counts for (a) Douglas-fir and (b) western hemlock seedlings.

Variable	1	2	3	4	5	6	7	8	9	10	11	12
(a) Douglas-fir[1]												
1. Shoot length (mm)												
2. Root length (mm)	N.S.[3]											
3. Shoot dry wt (gm)	0.55***	N.S.										
4. Root dry wt (gm)	0.40***	0.26***	0.61***									
5. # Non-mycorrhizal tips	0.19**	N.S.	0.33***	0.30***								
6. # Mycorrhizal tips	0.22***	0.21***	0.19**	0.58***	N.S.							
7. % Mycorrhizal tips	N.S.	0.25***	N.S.	0.30***	-0.61***	0.67***						
8. # D1	0.24***	0.17**	0.28***	0.41***	-0.18**	0.40***	0.47***					
9. # D2	N.S.	N.S.	N.S.	0.33***	0.27***	0.54***	0.13*	N.S.				
10. # D3	0.17**	N.S.	N.S.	0.19**	0.13*	0.39***	0.13*	-0.13*	0.20**			
11. # D4	N.S.	N.S.	0.12	N.S.	0.15*	N.S.	N.S.	-0.11	N.S.	N.S.		
12. # D5	N.S.	0.15*	N.S.	0.16*	-0.22***	0.56***	0.46***	N.S.	0.11	N.S.	-0.24***	
13. # Total root tips	0.29**	0.14*	0.35***	0.65***	0.57***	0.81***	0.19**	0.22***	0.60***	0.40***	0.13*	0.34***
(b) Western hemlock[2]												
1. Shoot length (mm)												
2. Root length (mm)	0.25***											
3. Shoot dry wt (gm)	0.89***	0.29***										
4. Root dry wt (gm)	0.77***	0.32***	0.87***									
5. # Non-mycorrhizal tips	0.48***	0.28***	0.62***	0.54***								
6. # Mycorrhizal tips	0.39***	0.27***	0.55***	0.54***	0.61***							
7. % Mycorrhizal tips	-0.20***	-0.11	-0.21***	-0.13*	-0.63***	0.11						
8. # H1	0.37***	0.24***	0.52***	0.54***	0.58***	0.81***	N.S.					
9. # H2	N.S.	N.S.	0.11	N.S.	N.S.	0.13*	0.13*	N.S.				
10. # H3	N.S.	N.S.	N.S.	N.S.	0.12*	0.12*	N.S.	0.13*	N.S.			
11. # H4	N.S.	N.S.	N.S.	N.S.	N.S.	0.22***	N.S.	-0.29***	-0.15*	N.S.		
12. # H5	N.S.	N.S.	N.S.	N.S.	N.S.	0.15*	0.20***	N.S.	N.S.	N.S.	-0.13*	
13. # Total root tips	0.47***	0.30***	0.63***	0.59***	0.82***	0.95***	-0.17**	0.80***	N.S.	0.13*	0.19***	N.S.

[1] n = 246 seedlings.

[2] n = 284 seedlings.

[3] Significant at 0.1%, 0.05%*, 0.01%**, 0.001%***level. N.S.= not significant.

Table VII.Linear correlations between root dry weight of Douglas-fir and western hemlock seedlings, and soil parameters.

Variable Y	Correlation Coefficient (r)[1]	
	Douglas-fir[2]	Western hemlock[3]
Mineralizable nitrogen (ppm)	0.32***	0.55***
Total nitrogen	0.25**	0.47***
Ammonia nitrogen	0.15*	0.45***
Nitrate nitrogen	0.16*	N.S.
Carbon	0.29***	0.49***
Sodium	N.S.	N.S.
Potassium	N.S.	-0.19*
Calcium	0.31***	0.50***
Magnesium	N.S.	N.S.
Phosphorus	0.20*	0.36***
pH	N.S.	N.S.
Litter layer depth (cm)	N.S.	N.S.
Soil temperature (2 cm)	N.S.	N.S.
Soil temperature (10 cm)	N.S.	N.S.
Moisture (%)	0.33***	0.47***

[1]Significant at the 0.1%, 0.05%*, 0.01%**, 0.001%*** level. N.S. = not significant.

[2]n = 126 seedlings.

[3]n = 141 seedlings.

TableVIII.Linear correlations between total mycorrhizal tips of Douglas-fir and western hemlock seedlings, and soil parameters.

Variable Y	Correlation Coefficient (r)[1]	
	Douglas-fir[2]	Western hemlock[3]
Mineralizable nitrogen (ppm)	0.47***	0.28***
Total nitrogen (%)	0.46***	0.24**
Ammonia nitrogen (%)	0.35***	0.31**
Nitrate nitrogen (%)	0.27**	N.S.
Carbon (%)	0.43***	0.30***
Sodium	0.17	-0.26**
Potassium	N.S.	-0.16
Calcium	0.42***	0.15
Magnesium	N.S.	N.S.
Phosphorus	0.35***	0.24*
pH	N.S.	-0.17*
Litter layer depth (cm)	N.S.	0.14
Soil temperature (2 cm)	N.S.	-0.35***
Soil temperature (10 cm)	N.S.	-0.40***
Moisture (%)	0.32***	0.49***

[1]Significant at 0.1%, 0.05%*, 0.01%**, 0.001*** level. N.S. = not significant.

[2]n = 126 seedlings.

[3]n = 141 seedlings.

Table IX. Linear correlations (r) between Cenococcum geophilum occurrence on Douglas-fir and western hemlock seedlings and seedling and soil parameters.

Variable Y	Correlation Coefficient (r)[1] Douglas-fir[2]	Western hemlock[3]
Seedling Measurements[5]		
Shoot length (mm)	0.19*	0.55***
Root length (mm)	N.S.	0.26**
Shoot dry wt (gm)	N.S.	0.68***
Root dry wt (gm)	0.44***	0.68***
# Non-mycorrhizal root tips	0.37***	0.73***
# Mycorrhizal Type 1	N.S.	--
Type 2	--	N.S.
Type 3	0.27**	N.S.
Type 4	N.S.	-0.29***
Type 5	N.S.	N.S.
# Total mycorrhizal tips	0.50***	0.86***
# Total root tips	0.63***	0.86***
% Mycorrhizal tips	N.S.	N.S.
Soil Measurements		
Mineralizable nitrogen (ppm)	0.61***	0.43***
Total nitrogen (%)	0.50***	0.40***
Ammonia-nitrogen (%)	0.58***	0.46***
Nitrate-nitrogen (%)	N.S.	N.S.
Carbon (%)	0.63***	0.49***
Sodium (%)	N.S.	-0.15
Potassium (%)	-0.20*	-0.18*
Calcium (%)	0.38***	0.20*
Magnesium (%)	-0.17	-0.24**
Phosphorus (%)	0.49***	0.36***
pH	-0.32***	-0.39***
Litter layer depth (cm)	N.S.	0.24**
Soil temperature (2 cm)	-0.21*	-0.35***
Soil temperature (10 cm)	-0.26**	-0.42***
Soil moisture (%)	0.73***	0.67***

[1]Significant at 0.1%, 0.05%*, 0.01%**, 0.001%*** level. N.S. = not significant.

[2]n = 126 seedlings.

[3]n = 141 seedlings.

[4]See descriptions of mycorrhizal type in Materials and Methods.

[5]Seedlings measurements given as average value per seedling.

Table X. Significance levels for differences between effects of litter from OG1 and OG2 on seedling variables.

Seedling variables	Litter type[2]	Litter site[2]
Shoot length (mm)	0.20	0.07
Root length (mm)	0.71	0.09
Shoot dry weight (gm)	0.87	0.04
Root dry weight (gm)	0.34	0.05
# Total root tips	0.66	0.01
# Non-mycorrhizal tips	0.12	0.05
# Mycorrhizal tips	0.55	0.03
# D1[1]	0.39	0.01
# D2	0.49	0.76
# D3	--	--
# D4	0.81	0.73
# D5	0.65	0.44
% Mycorrhizal tips	0.10	0.84

[1]Mycorrhizal types observed on Douglas-fir (see Materials and Methods).

[2]Probability > |T| HO: Least square means 1 = least square means = 2. Where Litter type 1 = application of litter, 2 = application of litter leachate; and Litter site 1 = old growth one (OG1), 2 = old growth two (OG2).

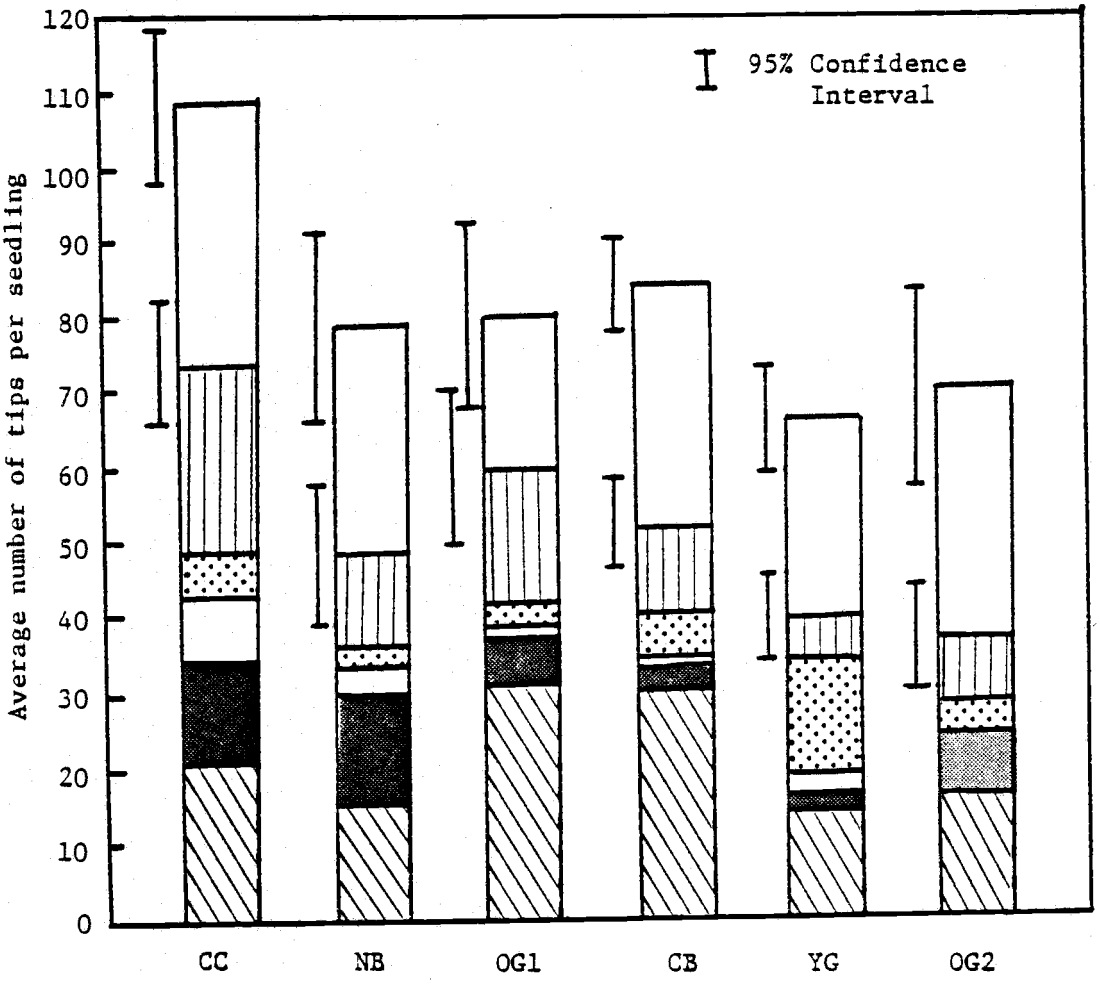

Figure 1A. Average total root, total mycorrhizal, and mycorrhizal type tips per seedling for Douglas-fir.

D1 D2 D3 D4 D5*

*Mycorrhizal types as described in Materials and Methods.

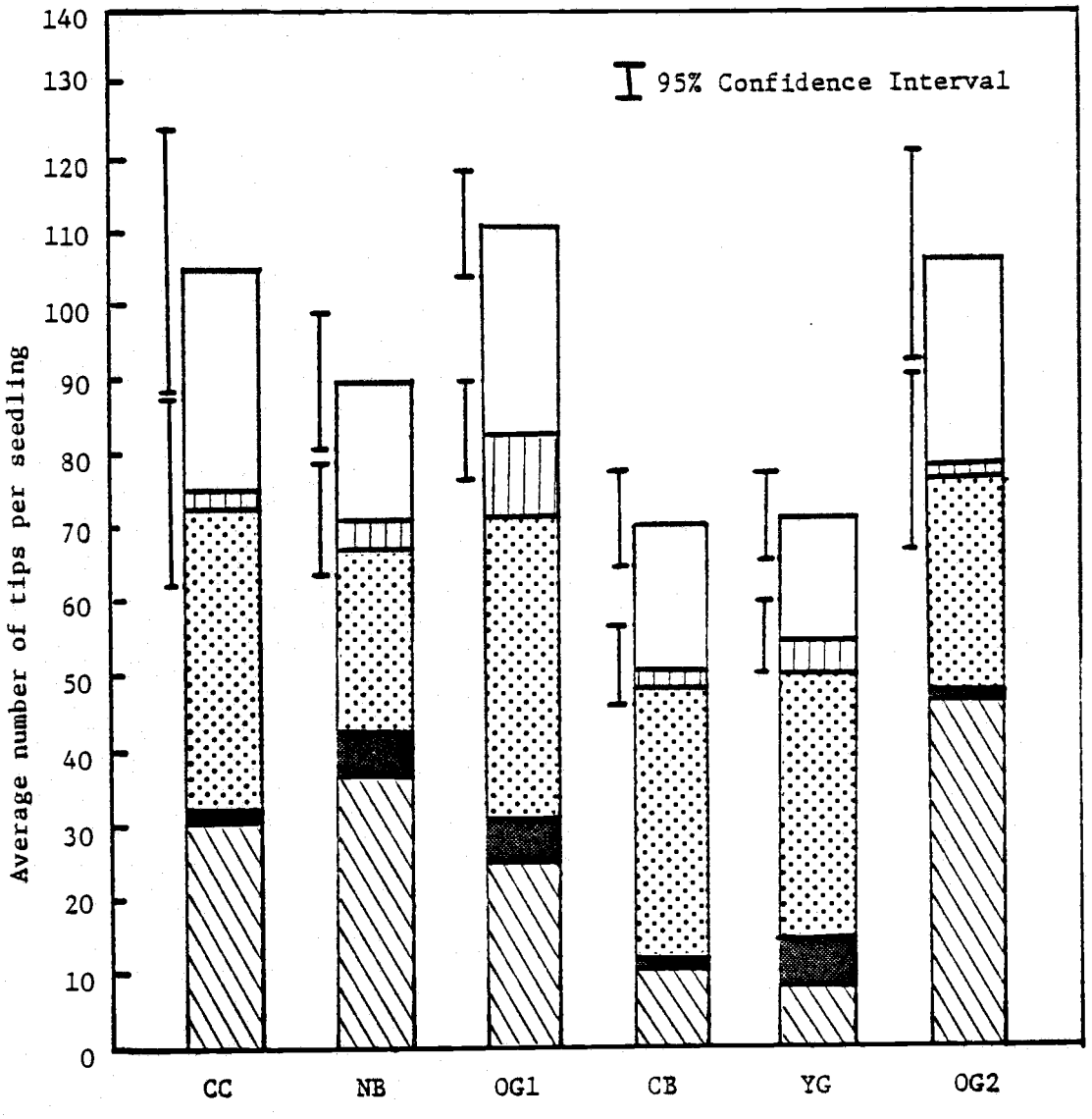

Figure IB. Average total root, total mycorrhizal, and mycorrhizal type tips per seedling for western hemlock.

*Mycorrhizal types as described in Materials and Methods.

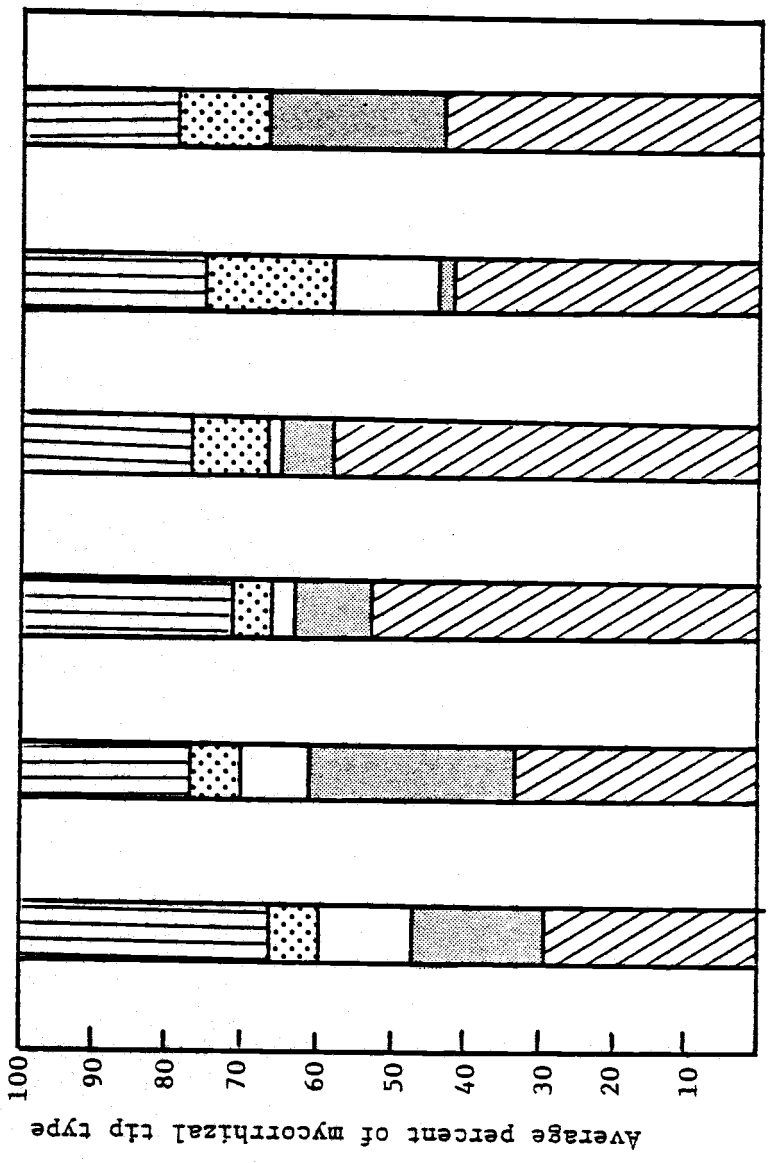

Figure IIA. Average percent of mycorrhizal tip types for Douglas-fir.

*Mycorrhizal types as described in Materials and Methods.

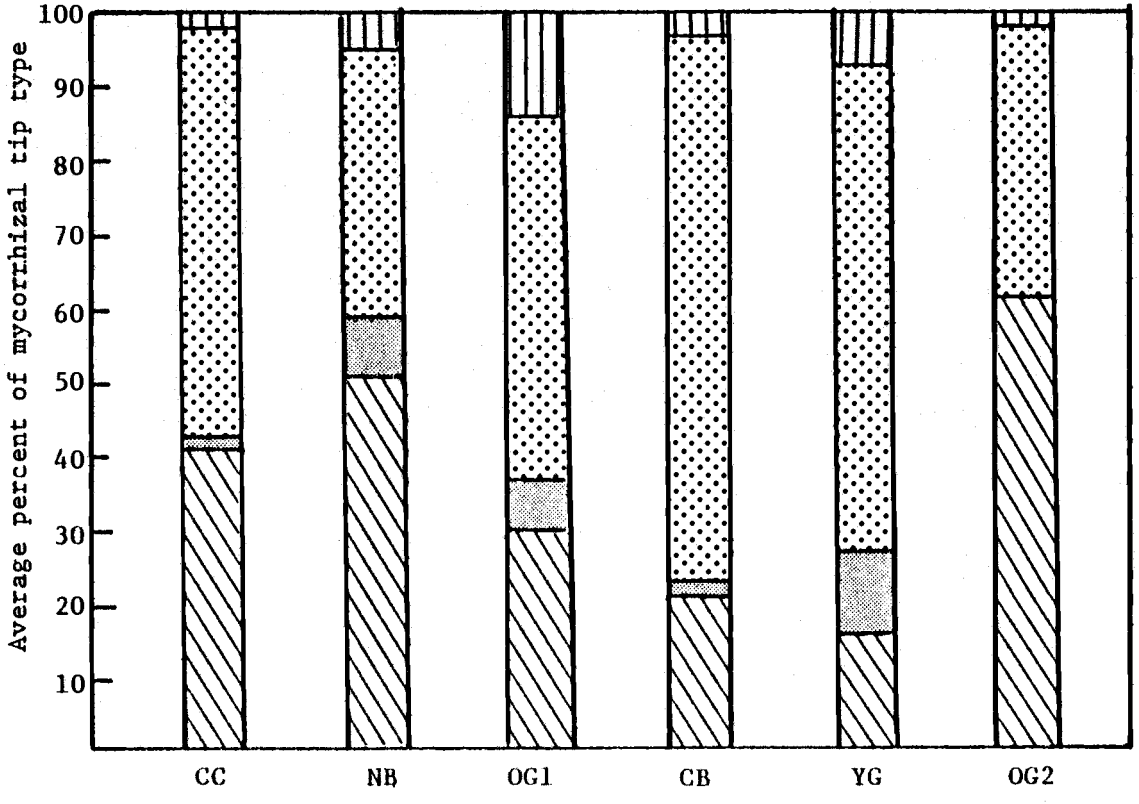

Figure IIB. Average percent of mycorrhizal tip types for western hemlock.

*Mycorrhizal types as described in Materials and Methods.