Effects of nitrogen fertilization on fine root and mycorrhizal biomass in a second growth Douglas-fir stand in western Washington

by

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Abstract

EFFECTS OF NITROGEN FERTILIZATION ON FINE ROOT AND MYCORRHIZAL BIOMASS IN A SECOND-GROWTH DOUGLAS-FIR STAND IN WESTERN WASHINGTON

by Rachel Friedman-Thomas

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Short-term effects of nitrogen fertilization on the below- and above-ground biomass of a second-growth Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco.) stand were estimated. Total fine root and mycorrhizal biomass in the plots treated with 448 kg N ha^{-1} decreased within four months following fertilization by 35% of the control plots. This decrease occurred mainly in the < 1 mm mycorrhizal root and < 5 mm angiosperm root categories. Another short-term response to nitrogen fertilization was shown for the conifer root tip biomass and density. The greatest change in conifer root tips was observed in the A horizon which showed the highest proportional increase in availability of mineral nitrogen. Fertilizer effects were also shown for the above-ground component with increases in new foliage and new twig biomass on fertilized plots. Results of this study pointed out the relationships between nutrient amendment and carbon allocation to roots and shoots four months after fertilization.

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Chapter 1

INTRODUCTION

Utilization of forest fertilizers began in response to the need to restore or augment the nutrient status of forest sites. While the practice was originally heralded as able to correct soil nutrient deficiencies and thus enhance site productivity, impacts on the total ecosystem were not understood. Scientists have since learned that the interaction between environmental factors, such as water availability, soil moisture holding capacity and nutrient availability may be more important in hindering site production than any single limiting nutrient.

Conflicts exist over whether fertilization ameliorates site nutrient deficiencies or acts to temporarily enhance tree growth. Bengston (1978) contended that fertilizers play an important role in forest site productivity in areas where a single nutrient is known to be limiting. An example of a highly

successful application of nitrogen fertilizer has been in the Pacific Northwest (R.F.N.R.P., 1982). Miller (1981) has argued that only trees benefit from fertilizers, not the site. If a measureable, permanent improvement is desired, consideration must be made of the amount of nutrient applied in relation to the soil capital and stand age.

The intensive management practice utilizing Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco.) as the sole tree for revegetation in much of the deforested lands of western Oregon and Washington has put a demand on the available N-limited soil capital (Gessel et al. 1965). Nitrogen fertilization used in an effort to amend soil nutrition and increase productivity, has yielded varying results. Above-ground responses of Douglas-fir to fertilization have been reported for a variety of different forest components. A few studies have concentrated on 1. assessing response by determining levels of foliar nutrition during both active and dormant periods (Waring and Youngberg, 1972), 2. comparing foliage production in thinned and fertilized Douglas-fir stands over a period of 5-7 years (Brix, 1981), and 3. studying the effect of fertilization on the whole forest community and the resultant dynamics of nutrient cycling (Heilman, 1961)

Research has been conducted in an effort to derive production and component biomass values for fertilized versus unfertilized forest stands. An important factor that has been neglected until very recently is the effect of heightened nutrient status on the below-ground ecosystem. Many of the net production values have remained incomplete due to the lack of root data. Fine roots and mycorrhizae are of primary importance to the system due to involvement in plant nutrient and water uptake (Hermann, 1977). Fine root and mycorrhizal biomass of second-growth, lowland Douglas-fir stands are very dynamic (Keyes and Grier, 1981) and may have the capacity to change in response to nutrient amendment (Vogt et al. 1986).

It is necessary to draw upon past research in order to substantiate the aforementioned assumption. An important factor missing from most forest stand studies is the evaluation of both above- and below-ground components. With biomass determinations prior to and preceeding fertilization, one has the potential to document a shift in resource allocation patterns.

Research is needed which examines assimilation patterns in response to changes in nutrient availability in deficient forest stands. Ideally, assimilation patterns are determined from research conducted over an

extended period of time, detailing production and turnover values. However, this study will examine changes in resource partitioning through biomass determinations over a short time interval.

Two hypotheses were examined in this study relating to nitrogen control of carbon allocation on a short-term basis. The first hypothesis stated that nitrogen amendment will result in changes in fine root and mycorrhizal biomass and root tip morphology within four months after urea fertilization. The second hypothesis stated that vertical distribution of rooting within the profile will shift after fertilization. The specific objectives of this study were to determine 1. fine root and mycorrhizal biomass following heightened levels of available nitrogen, 2. changes in root tip density and variation of infection following fertilization, 3. shifts in vertical rooting distribution within the soil profile, and 4. changes in above-ground biomass increment as a response to fertilization.

Chapter 2

LITERATURE REVIEW

A. Forest stand response to fertilization

A.1. Below-ground response to nitrogen fertilization

Researchers recognize that differences in root biomass exist among sites and between different aged stands (Keyes, 1979; Vogt et al. 1983a), yet information on the effect of nitrogen fertilization on fine root and mycorrhizal biomass is scanty. Field research in this only began in the middle 1970's and little information is available at this time. Two early studies, one examining the effect of fertilization and irrigation on root numbers in a 42 year-old red pine (Pinus resinosa Ait.) plantation in New York state (Farrell and Leaf, 1974), and the other examining the effect of fertilization on the biomass of fine roots in a 90-year-old Beech-Birch-Maple stand (Fagus grandifolia Ehrh., Betula sp., and Acer sp.) in New

Hampshire (Safford, 1974), were conducted. Another study examined the effect of fertilization on root growth and mycorrhizal numbers in two 11-year-old Loblolly pine (Pinus taeda L.) plantations in North Carolina (Menge et al. 1977). More recently the nitrogen fertilization effect on numbers, biomass, and seasonal variation of fine roots and mycorrhizae in 35-year-old Sitka spruce (Picea sitchensis (Bong.) Carr.) plantation in Scotland was examined (Alexander and Fairley, 1983).

The four studies mentioned above had different goals and methodologies. Information on whether plant growth on the sites was nutrient limited and why the particular fertilization regimes were chosen was not given. In many cases, fertilizer results were minimized or neglected. A common denominator acknowledged in all four study areas was that canopy closure had occurred and the trees were fully occupying the sites. Despite methodological discrepancies, the root biomass results were tangible stand estimates and comparisons of the values is useful.

The study of root numbers on the red pine plantation consisted of counting root tips within each sample (Farrell and Leaf, 1974). The upper 0-15 cm of soil was found to have 10 times more root tips than the 15-30 cm depth. Root numbers reached their minima in the fertilization and fertilization/irrigation treatments

(28.0 and 3.15 root tips cm^{-1} surface soil, respectively), representing half as many root tips as compared to the control or irrigated plots. The authors spoke primarily of an irrigation effect. The response to lowered root numbers in fertilizer treatments was briefly described as due to increased senescence and decomposition of roots. The researchers failed to address the question of a fertilization effect. The decrease in root tip numbers was perhaps a response by the trees to "divest" themselves of a portion of their root system "investment" in response to an increasing nutrient pool. Lacking in this study were comparisons of above-ground biomass production needed to further document stand level response to fertilization and/or irrigation.

Deciduous forests sampled after fertilization yielded contrasting results. Estimates of dry weights of fine roots (< 3 mm diameter) collected during the summer revealed that total fine root biomass from the fertilized treatment exceeded the control by a factor of 2 (2711 g m^{-2} and 1246 g m^{-2} , respectively, Safford, 1974). This increase in root biomass was distributed throughout the entire soil profile, excluding the C horizon. Safford (1974) attributed the increase in fine root biomass following fertilization to improved site fertility. Before and after tree harvest, the estimated 27 t ha^{-1}

root biomass would release additional organic matter and mineral nutrients into the mineral soil. It was inferred that the greater soil occupancy following fertilization gave a competitive edge for nutrient and water. The pattern of extensive shoot growth for deciduous trees in the spring, and continuous rainfall may have allowed for root volume expansion during the summer months, even in light of heightened nutrient availability. Due to phenological differences of root and shoot extension it was difficult to compare these results with evergreen conifers. Similar to the previous work, had the author conducted simultaneous above-ground sampling, a better understanding of total fertilizer response may have been obtained.

Work in a loblolly pine plantation examined mycorrhizae numbers in relation to tree growth (Menge et al. 1977). The researchers found that over the 2 year study period nitrogen fertilization resulted in 14-29% fewer mycorrhizal tips than in the unfertilized plots. The significant difference in mycorrhizal tips between paired plots lasted only for the first year following fertilization. Also a negative correlation between mycorrhizal tip numbers and tree height growth was seen (Menge et al. 1977).

Menge et al.'s (1977) study suggested that although

there have been many reports of a reduction in mycorrhizae following fertilization, the effect of moderate applications of N and P was relatively short-lived. The researchers speculated that mycorrhizal fungi present on nutrient deficient sites would be adversely affected by nitrogen fertilization (Menge et al. 1977), thus explaining the apparent overall decline. But their findings revealed a few fungal types which significantly increased, potentially representing seral competitors.

Menge et al. (1977) compared above- and below-ground processes following fertilization. The negative correlations between both mycorrhizal numbers and tree height, and mycorrhizal numbers and diameter growth supported assumed changes in assimilate partitioning following fertilization. Unfortunately, the findings were compared to work with seedlings, thus the significance for forest stands with closed canopies was not discussed.

A recent work reported detailed seasonal variation of both biomass and numbers of fine roots and mycorrhizae in the humus layer of a Sitka spruce stand (Alexander and Fairley, 1983). During the summer and fall following fertilization, root biomass and root tip numbers were elevated above the controls. The second year after nutrient amendment, root activity decreased. By the study's end (26 months after fertilization), root biomass

in the fertilized plots had risen again and was higher than the controls (1100 kg ha^{-1} and 970 kg ha^{-1} , respectively).

Alexander and Fairley (1983) proposed that in the months following fertilization the roots remained an effective sink for photosynthate by virtue of their increased capacity to supply N. Due to a readjustment of assimilate partitioning, it required one year before roots were shed. The authors speculated that increased net assimilation may have allowed for an overall increase in stand growth which would possibly explain the increased fine root biomass after two years (Alexander and Fairley, 1983). Continued research on the site determined that growth was not nutrient limited, thus possibly explaining the shifts in root biomass production (Alexander, personal communication, 1984). Unfortunately, no data were published concerning the above-ground component, thus overall growth response was not known.

The study by Alexander and Fairley (1983) also dealt with root production over the two year period. A decrease in production of mycorrhizae, fine roots (1-5 mm), and finest roots (<1 mm) was seen following fertilization (15%, 31%, and 22% decrease, respectively). While mycorrhizae accounted for only 10% of the biomass, they made up 50% of the turnover; thus remaining the most

dynamic component of the system. Turnover time of the fine root system was found to decrease from 26 weeks in unfertilized plots to 16 weeks in treated plots (Alexander and Fairley, 1983). They suggested that reduced turnover time may have allowed reallocation of nutrients obtained through fertilization to tissues elsewhere in the tree. The results, while scanty, lend themselves very well to comparisons with other root work conducted in soil organic layers. This work suggested that a lag period of fertilizer response may occur, stressing the need for comparable short-term growth studies to understand plant adaptations to nutrient amendments (Alexander and Fairley, 1983).

Changes in root biomass due to fertilization may not be similar in the organic versus mineral horizons. The organic horizons, usually contain the greatest amount of available nutrients and frequently hold the greatest number of root tips (Farrell and Leaf, 1974). Perhaps the mycorrhizal species in this nutrient rich layer which have adapted to greater levels of nutrients (Menge et al. 1977), would not be adversely affected by added nutrients. These fungal species might be able to continue to transfer the increased available nutrients to the tree. This could explain Alexander and Fairley's (1983) findings of heightened root biomass in the humus for 6 months

following fertilization. If the above-ground component responded positively to increased nutrients, more assimilates could be allocated to the root system. As fertilizer leachs down through the soil profile, mycorrhizal fungi in deeper horizons may not be adapted to heightened nutrient availability. Also, the tree will no longer invest as highly in the below-ground component in order to obtain nutrients. Depending on the effective residence time of the fertilizer, the below-ground biomass may either return to its original pretreatment status (Miller, 1981), or increase beyond the control (Alexander and Fairley, 1983).

A.2. Above-ground response to nitrogen fertilization

In the past, researchers have studied changes in allometric relations with fertilization in an attempt to better understand its' effects. At present, results and subsequent hypotheses vary considerably. Stand age, and current productivity levels are among the many site specific variables which affect fertilizer growth response. General theories propose increased response to fertilization in lower site quality stands than in higher site quality stands (Gessel et al, 1965).

In order to clarify how stands react to nitrogen fertilization, growth response over time has been investigated. From the outset, researchers have encountered problems as it is often difficult to assess initial growth response to nitrogen fertilization. It has been suggested that species with preformed leaf primordia would exhibit increased numbers of leaves in response to an increased nutrient supply several months to a year after application (Linder and Rook, 1984). Work with Corsican pine (Pinus nigra var. maritima (Ait.) Melv.) showed that within the first year of fertilizer application, litterfall weight was reduced (Miller and Miller, 1976). While no stemwood or height effect was seen, current foliage was larger and needle retention was increased. Another study documented leader elongation within the first growing season following fertilization (Brix, 1981). Increased net photosynthetic efficiency was reported for current shoots (Miller and Tarrant, 1983), while no significant effect was shown in older shoots (Brix, 1971).

As current foliage production increases, the trees ability to benefit from increased overall production is dependent on light and other limiting site factors. With unencumbered growth, Brix (1983) suggested a linear relationship between production and foliage quantity.

With time fertilizer response becomes easier to measure. After 1-2 years, response in DBH became evident for moderate to high levels of fertilization (Barclay and Brix, 1985). Brix (1971) attributed the second year diameter response to the long availability period of urea fertilizer. In addition to an increased diameter increment, yearly needle production response of Douglas-fir to fertilization peaked within 2-3 years (Brix, 1981). Within 4-5 years height growth increases became apparent (Brix, 1981a). Studies have documented response up to 18 years following fertilization (Binkley and Reid, 1985). General findings include increased stemwood production and leaf area (Binkley and Reid, 1985), decreased litterfall (Miller and Fight, 1979), and possible changes in growth patterns (Brix, 1983).

A potential change in allometric relations of Douglas-fir within the first two years following fertilization is pointed out in two studies. Brix (1983) documented a greater percentage allocation of dry matter production to branches and foliage and less to stemwood. Archibald (1983) determined that fertilizer effect was the most noticeable in regressions of total current foliage and total current twigs against DBH. Both variables were significantly different between control and treatment trees. It was suggested that the greater current leaf

biomass production on the fertilized plots may have been caused by increased photosynthetic efficiency (Brix, 1983). Archibald (1983) suggested that the duration of this response depended on: 1.) the relationship of the stands' foliage deficiency to its ability to attain maximum foliage production and 2.) site nitrogen availability (Brix, 1983; Grier et al. 1984).

B. Root and mycorrhizal response to fertilization

The nutrient status of soils has long been implicated as a determinant of fine root and ectomycorrhizal biomass. Most of the research which produced this assertion has been conducted on greenhouse grown seedlings. The scope of studies dealing with the effect of fertilization on seedlings has ranged widely. A few of these studies include: 1.) nutrient effects on different aged plants; 2.) assessing the effects on plant response of different forms of fertilizers; 3.) assessments of nutrient uptake interactions after fertilization; and 4.) estimating relationships between nutrient content of the root and the percent of mycorrhizal infection. The nutrient most frequently studied in relation to ectomycorrhizae is nitrogen, due to its growth-limiting status in many ecosystems.

Seedling study results bear few similarities to responses of forest trees to fertilization. With information solely from greenhouse studies, a forest ecologist would have difficulty predicting the reaction of below-ground biomass of a site to fertilization. Environmental factors, site quality, age, stand density, and species composition determine the level of function of an ecosystem. Greenhouse and pot culture studies have provided ecologists with a basic understanding with which attempts at quantification of forest response to such site preparation practices as fertilization have been made.

Generalizations of the effect of fertilizers on below-ground biomass have been predominantly based on greenhouse studies. The general trend states that nitrogen fertilization usually depresses mycorrhizal development (Richards and Wilson, 1963; Richards, 1965; Bengston and Holstener-Jorgensen, 1976). The symbiotic association of trees with mycorrhizal fungi is considered to be an adaptative characteristic response to nutrient stress (Fogel, 1983), thus the alleviation of a nutrient deficiency through fertilization would presumably suppress mycorrhizal development (Johnson, 1979). Few studies in forest stands have attempted to quantify this assertion.

C. Generalized rooting distribution

Investigations of root systems have been conducted since the turn of the century. The bulk of the research has examined the rooting structure of various plants. Seedlings experiments have constituted a majority of the research. Work with mature trees, an extremely labor and time intensive task, has produced detailed maps and descriptions of rooting patterns in relation to tree crown distributions, or based on the vertical extension into the soil profile (Lyr and Hoffman, 1967; Meyer and Göttsche, 1971). While discrepancies in sampling techniques and resultant findings exist, data documenting biomass (weight per unit area) and net productivity (dry matter production over time) in many ecosystems are becoming increasingly available.

Root biomass information is a necessary key to understanding the structure and function of ecosystems. Yet, biomass determinations are only static estimates of living material. The ability to understand how root biomass differs with age of a species or between site qualities leads to information concerning ecosystem function. Santantonio et al. (1977) determined that the previously established correlation between root biomass and stem diameter for 10-50cm diameter trees extended to

large (94-135cm DBH) old-growth Douglas-fir in western Oregon. Yet, they warned of the site specific nature of these findings. Keyes and Grier (1981) determined that peak fine root biomass was considerably higher on a "low" productivity 40-year-old Douglas-fir stand (8.3 t ha^{-1}) than on the "high" productivity site (2.7 t ha^{-1}). Large seasonal fluctuations of fine root biomass on the "low" productivity site, and virtually no fluctuation on the higher site were noted. While these findings compared well with data in the literature, sampling discrepancies made direct comparisons somewhat difficult.

Research by Keyes and Grier (1981) was able to address the question of assimilate partitioning in stands of different site classes. It was suggested that differences in productivity values between the high and low sites may be lessened if root production was included. Keyes (1979) postulated that the generally accepted method of above-ground component estimation was a poor representation of total net production. Differences in carbon allocation in response to site productivity potential were determined. On the high site, only 26% of the total dry matter produced by the tree was used for root production while on the low productivity site, 60% of the annually produced dry matter went into fine root development (Keyes and Grier, 1981). These findings led to a hypothesis that

species plasticity may allow for a shifts in assimilate allocation on sites where nutrients or water were limiting.

Recently, the phrase "cost and benefit" has been associated with fine root work. Fine roots and mycorrhizae produce a major portion of the organic matter entering the decomposition cycle (Fogel, 1983; Vogt and Grier, 1983; Vogt et al. 1983a, 1983b). Despite the fact that root biomass estimates detail a single period of production, the large input of both fine roots and mycorrhizae to the decomposition process makes it important to determine mycorrhizal biomass (Fogel, 1983). Annual turnover rates for fine roots in Douglas-fir stands are reported to be between 30-86% (Fogel and Hunt, 1979). This represents a considerable "cost" to trees, yet it has been determined that roots return 4 to 5 times more material to the forest floor than leaf or branch litter (Fogel, 1983). The high rate of fine root turnover has been described as an "adaptive strategy" or necessary expenditure for trees in stressful environments.

Vogt et al. (1983a) examined both live and dead root biomass in the forest floor of different site quality stands of Douglas-fir and determined that before canopy closure the higher site quality stand had higher root biomass. During and after full occupancy, the lower

productivity site had significantly higher root biomass than the former site. The lower productivity site also had greater fine root necromass. This contributed to the forest floor and soil organic matter and presumably enhanced nutrient cycling (Vogt et al. 1983a). These findings strongly supported those of Keyes (1979).

Persson (1983) examined the variation of fine root death and replacement for 2 Scots pine (Pinus sylvestris) stands of different ages in Sweden. While the young stand had more dead fine roots than the mature stand, its overall level of fluctuation of fine root biomass was lower. Persson (1983) attributed the results to the continually expanding root systems of the young stand working to occupy new volumes of soil. He suggested that yearly fluctuations of fine roots may be more helpful in differentiating systems than biomass comparisons between sites.

Seasonal changes in fine root and mycorrhizal root biomass in both young and mature Pacific silver fir Abies amabilis (Dougl.) Forbe) stands supported the thesis of Persson (1983). Both young and mature stands had the lowest level of mycorrhizal root biomass in the summer and the highest in the fall (Vogt et al. 1980). In both stands, mycorrhizal roots made up the greatest proportion of fine root weight during the season with substantial

snow cover. The old stand had significantly higher mycorrhizal root biomass in comparison to the young stand. Yet, in the young stand (which had not reached full site occupancy) the increase in fine root biomass during peak root growth was a result of increased mycorrhizal growth. This study suggested that the mycorrhizal root increase may have been in response to increased available nutrients or to higher levels of photosynthate translocation to the root systems during the winter months (Vogt et al. 1980).

Chapter 3

METHODS

A.1. Study site

This study was conducted in a second-growth Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco.) stand in Mason County, 4.8 km north of Matlock, Washington, on land owned by the Washington State Department of Natural Resources (Fig. 1). The stand was located in T 21 N, R 6 W, at an elevation of 137 m. The ground was essentially flat with no measurable slope or aspect.

The climate of the area is characteristic of the Puget Sound region, with mild, wet winters and warm, dry summers. The frost-free growing season is 120-140 days at this site which is located only 65 km east of the Pacific Ocean. Mean annual temperature is ± 10 C and mean annual precipitation is 182.9 cm, 90% of which falls as rain between October and June. Moist, east-drifting air masses add small but frequent amounts of moisture as condensation

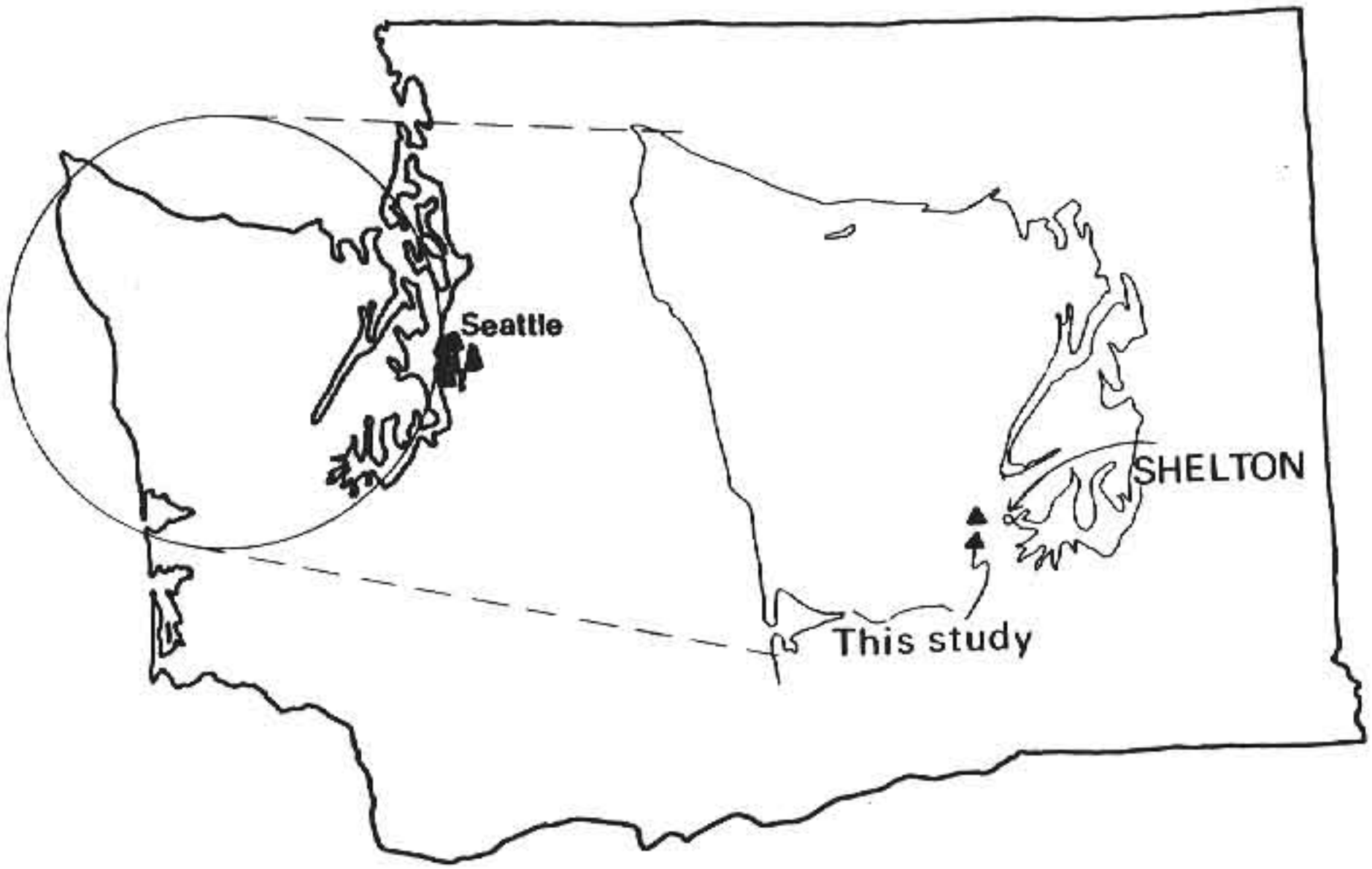


Figure 1. Map of Washington state detailing the Olympic peninsula and showing study site.

and fog-drip (Gessel et al. 1965).

The soils in the area of the study site are Xerochrepts of the Grove Series. The soil specific to the site has developed from continental glacial outwash, modified more recently by inclusions of basaltic rock and mixed material from the Olympic Mountain glaciers (Soil Survey Staff, 1960).

The Grove cobbly sandy loam is located on level outwash plains. It is described as containing an organic horizon (O horizon), approximately 3 cm deep composed of needles, roots, and moss. The lower part of the O horizon is moderately decomposed and very dark greyish brown. The surface soil (A horizon) is up to 7 cm thick and consists of a gravelly sandy loam with a 73% gravel content. The weak, granular structure supports abundant fine roots and hyphae. The underlying B horizon extends between 56-69cm deep, and is a gravelly sandy loam. Despite the 68% gravel content this weak structured horizon supports abundant fine and coarse roots. The Bw horizon, extending between 56-68 cm, differs from the above by virtue of its lack of structure due to an increase in sand. Coarse and fine root occurrences are limited. The bedrock horizon is of sandy texture and contains no roots. This soil is classified as low fertility and is a site index III for Douglas-fir growth (King, 1966).

The stand, naturally established after clear-cutting and burning, is a second-growth 45-55 year-old Douglas-fir with an average height of 30 m. It has an average of 1025 live Douglas-fir trees per hectare ranging from 10-55 cm diamter measure at DBH (1.37 m above the ground). Average basal area is 44 m^2 ha^{-1}. While Douglas-fir is the sole overstory species, the putative climax species, western hemlock (Tsuga heterophylla (Raf.) Sarg.) is sparingly present in the understory. Tree suppression and competitive mortality are evident in this closed canopy stand.

Understory vegetation composition is typical for seral forest stands on low sites within the Tsuga heterophylla zone (Franklin & Dyrness, 1973). The dominant shrub at the site is salal (Gaultheria shallon (Pursh)) which ranges between 45-67% cover (Appendix I). All other shrub cover was less than 10%. Herb cover is dominated by twinflower (Linnaea borealis L.). The remaining herbs occurred infrequently. Moss, (species unidentified) accounts for 58-78% ground cover on the plots (Appendix I).

A.2. Site selection

The stand satisfied a number of criteria specified for this study including: species composition of > 90% Douglas-fir in the overstory canopy; tree age between 30-55 years; elevation < 200 m, little or no slope; site class low III or IV; and with nitrogen as an important growth limiting variable. The research plots for this study are near the Regional Forest Nutrition Research Project (R.F.N.R.P.) installation # 55. This R.F.N.R.P installation was established in 1972 and the plots have been fertilized three times with either 224 kg urea N ha^{-1} or 448 kg urea N ha^{-1}. Fertilization has shown a 18% increase in net primary production above the control plots (Appendix II). This result lent assurance of a nitrogen limited site.

A.3. Plot Establishment and Fertilization

Six circular plots (0.04 ha) were located within this stand in as homogeneously stocked areas as possible. Three of the six plots were randomly chosen to receive fertilization and the remaining 3 were used as controls. In an attempt to markedly improve the nitrogen availability in the soil system, 224 kg N ha^{-1} as Union

Oil Co. forestry grade urea prill (46-0-0) was broadcast on the treatment plots twice prior to bud burst in spring 1984 (March 20 and April 18). Buffer strips 8 m wide, the approximate diameter of two tree canopies, increased the size of the treatment plots. Sampling was conducted within the original plot boundaries. The treatment plots were squared off and sectioned into equidistant strips to facilitate even fertilizer spread. Urea was applied during rainstorms to leach the fertilizer into the soil and thus minimize the volatilization losses reported by Crane (1972).

B.1. Root cores

Two sample dates for root coring were chosen based on previous study of phenology of root extension in similar stands. Keyes and Grier (1981) observed that low site Douglas-fir stands in western Washington had a bimodal biomass production of roots. While biomass fluctuations are specific to site and climatic variations, October through April appears to represent a period of low root growth, or a period of root maintenance. Peaks in root biomass production have been observed during June and September. Based on these observations, March and June, were chosen as sampling periods for this study in an

attempt to measure root biomass at a time in which the greatest contrast between control and treatment would occur. The first sample period (March 15, 1984) occurred prior to fertilizer treatment of the plots and the second sampling period occurred four months after fertilizer treatment of plots (June 10, 1984).

Four soil cores were randomly collected from each plot at each sampling time. Azimuths and distances from plot center were drawn from a random numbers table. If problems collecting a core were encountered, the sample was abandoned and another random sampling position was chosen.

The coring device consisted of a one meter long steel tube with an inside diameter of 3.81 cm and a sharp, bevelled tip. Polyvinyl chloride (PVC) tubes of 3.18 cm in diameter were placed within the steel tube. The coring device was driven through the forest floor into the mineral soil to a depth of 50-70 cm with a sledge hammer. The depth corresponded to the bottom of the B horizon. The PVC tube containing the core was removed from the steel corer, the ends were capped, and the intact soil sample was returned to the lab. Prior to sorting, the cores were stored in a 3° C cold room.

B.2 Root biomass and tip number determination

Soil was carefully removed from the PVC tubes to maintain the integrity of the profile. The O, A, and B horizons were separated and stored in polyethylene bags at 3° C. Any C horizon material was discarded as it was not under examination for the study. Each sample period required 6 months for complete sorting, therefore, samples were subject to some amount of respiration weight loss. This value was not obtained.

Prior to sorting, a sample was submerged in distilled water and refrigerated for one hour to facilitate washing the sample. The sample was then washed through a 900 u m sieve. Past work has shown no live root loss through this size sieve (Vogt et al. 1980). The washed sample was then transferred to a water-filled petri dish. All live root material was removed with watchmaker forceps under 5X magnification.

Only live roots were examined for this fertilizer response study. Live roots were distinguished on the basis of appearance and ease of disintegration. Active roots were firm and resilient, an intact stele was visible, and a range of mycorrhizal fungi was evident. In contrast, dead roots were easily fragmented, the stele was often fractured, and a dull, muddy brown color was

often exhibited (Santantonio, 1982). Final determination of live or dead was made with the use of a dissecting microscope (10X).

No strict convention exists from past studies for root size categorization. For this study roots were separated by diameter, species, and infected versus uninfected categories. The size categories were : <1 mm mycorrhizal infected Douglas-fir; 1-2 mm mycorrhizal infected Douglas-fir; <1 mm uninfected Douglas-fir; 1-2 mm uninfected Douglas-fir; 2-5 mm uninfected Douglas-fir; and <5 mm angiosperm. Distinguishing between conifer and angiosperm roots presented no problem. Gross morphology and color aided distinction. Conifer roots were strongly to weakly branched, exhibited a range of colors, and were translucent when young and thickly suberized when older. Angiosperm roots (primarily Gaultheria shallon) were very angular, and were translucent to rust brown.

Active Douglas-fir root tips were classfied into six categories based on mantle color. The six categories differed macroscopically and counts of tips in each category were conducted with the use of a dissecting microscope. The groups were: 1."nocolor" - fine unsuberized root growing past a pre-existing mycorrhizal mantle - rust-yellow, translucent, long, thin, sparcely branched root (Plate 1); 2. black - short roots, curly,

Plate 1. "Nocolor" mycorrhizal root tip characterized by a fine unsuberized root growing past a pre-existing mycorrhizal mantle (30x).

black hyphae growing perpendicular to the jet, black, swollen tip (Plate 2); 3. brown - short roots, highly branched, dark brown-red sheath with no hyphae (Plate 3); 4. white - short roots, light brown-rust sheath, thick mat of grey-white hyphae (Plate 4) ; 5. green - short roots, branched, smooth, shiny green sheath with no hyphae; 6. yellow - short root, light brown-rust sheath, hyphae bright yellow extending from the tip.

Root tips were considered mycorrhizal if they were macroscopically ensheathed by a mantle of hyphae. Mycorrhizal root tip biomass was calculated from counts of mycorrhizal root tips multiplied by a mean dry weight of an average root tip (0.034 mg . root tip $^{-1}$).

Sorted roots were dried in a forced-air oven at 70°C for 24 hours then weighed. Ash-free weights to the nearest 0.1 mg were determined for each category by weight loss on ignition. Subsamples from all categories were ashed in a Lindberg muffle furnace at 450°C for 24 hours or until a consistant weight was achieved. All values are reported as ash-free weights.

Fine root biomass being presented here consists of all roots <5 mm in diameter. Fine roots and mycorrhizae were sorted by hand from soil cores.

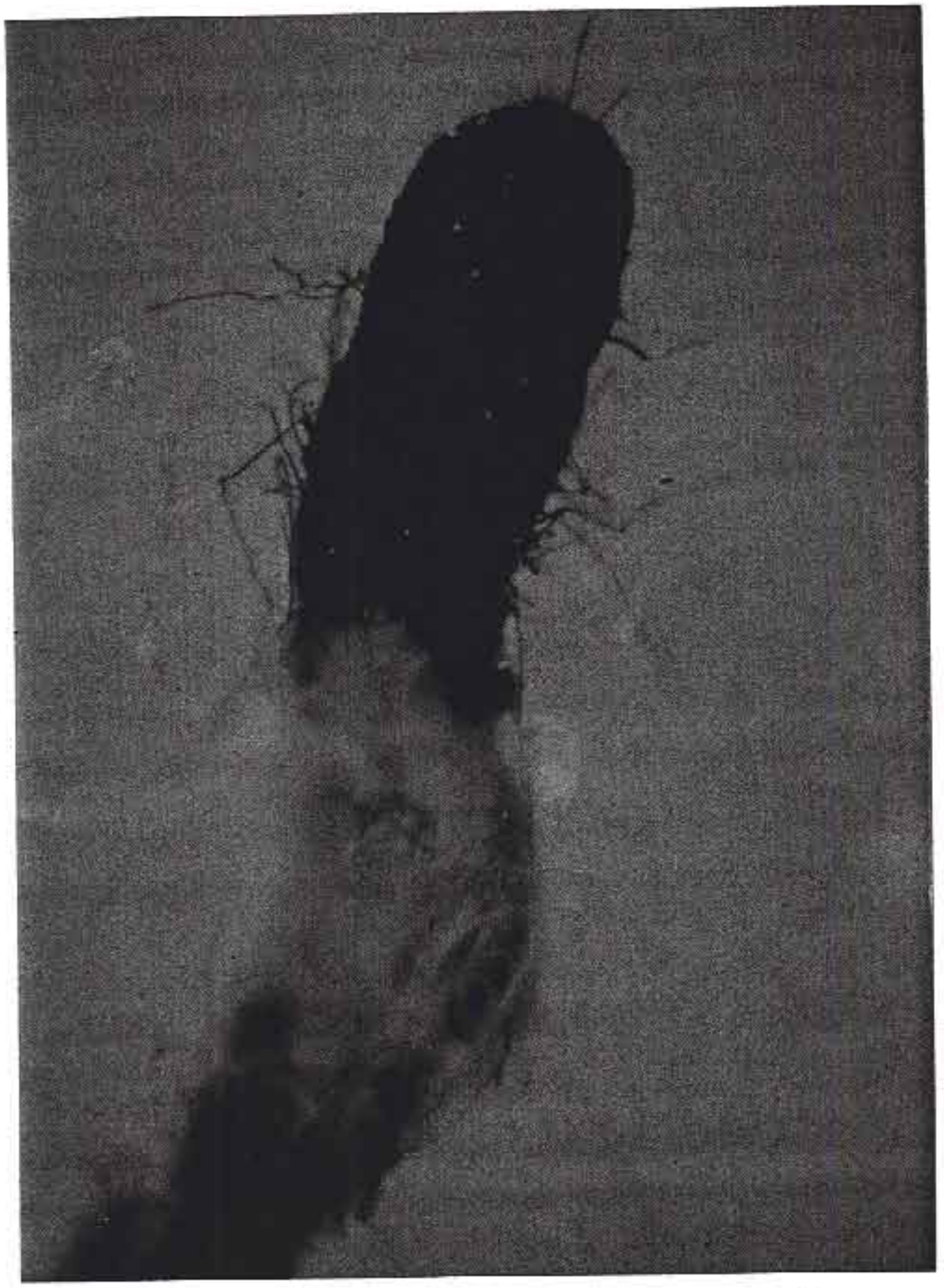


Plate 2. Black mycorrhizal root tip characterized by curly black hyphae growing perpendicular to the jet black tip (30 x).

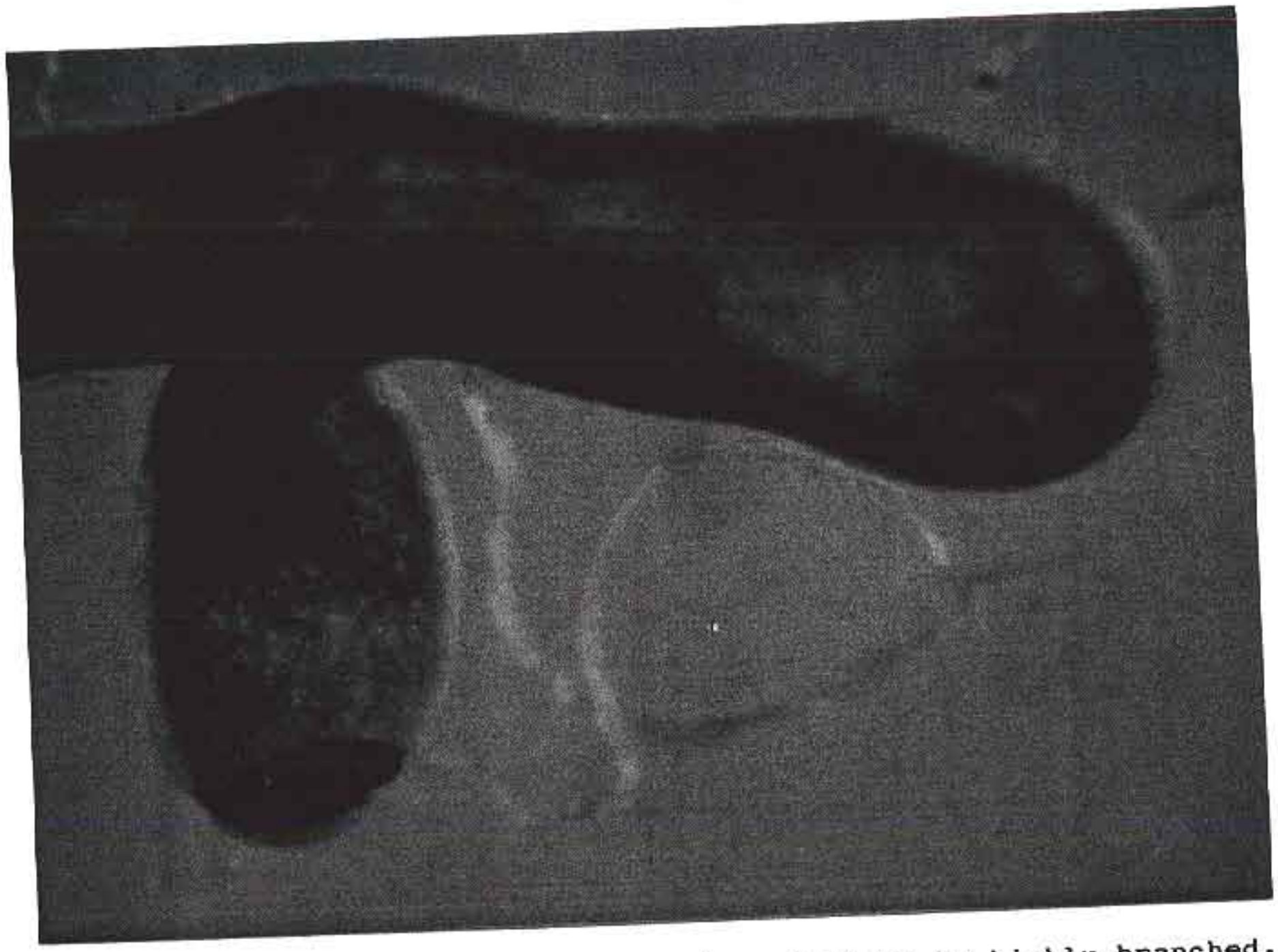


Plate 3. Brown mycorrhizal root tip characterized by highly branched, dark brown-red sheath with no hyphae (30x).

Plate 4. White mycorrhizal root tip characterized by a light brown-rust sheath covered with a thick mat of grey-white hyphae (30 x).

B.3. Root biomass and root tip statistical methods

Fine root biomass (March and June) and root tip numbers were subjected to Randomized Block ANOVAS to assess a block effect among the plots (Zar, 1984). Every variable within each data set was subjected to both Kolmogorov-Smirnov Normality tests and Bartlett's Homogeneity of Variance tests. Based on the results, parametric one-way ANOVAS were employed to test for differences between treatment and control. The three soil horizons were analyzed separately and lumped together to arrive at soil profile totals and means. Because of the way data were collected, comparisons between horizons could not be statistically tested. Standard computer statistical packages (SPSS and Minitab) were used to analyze the data.

B.4. Biomass increment determinations

All trees were remeasured at DBH in March 1985, one year following fertilization. Approximately 7-50% of the trees in each plot were smaller by at least 0.1 cm from the previous year's measurement. Shrinkage could have been due to winter dessication (Lassoie, 1979), or sampling error. Due to this discrepancy, these values

were disregarded. A mortality check was conducted on all tagged trees. Mortality biomass was estimated by regression for stemwood, stembark, and branch weight on stem dbh of 1984.

Biomass increment for live trees was calculated as the difference between 1984 and 1985 biomass. Plot trees ranged from 10-55 cm in dbh. For calculation, diameters were segregated into 10 diameter classes. Thirty percent of the trees in each dbh class, for both treatment and control plots, were randomly chosen and 2 increment cores were extracted at breast height from each tree. Cores were returned to the lab in plastic straws and maintained at initial moisture content until processing. Cores were mounted on wooden stages, and annual growth rings were measured to the nearest 0.01 mm using a microscope with a micrometer designed for growth ring measurement (Bannister Mfg. Co., Montana). The annual radial growth was averaged for each tree. The current increment was multiplied by the bark growth adjustment for Douglas-fir (1.1, Grier, personal communication, 1984), doubled, and multiplied by 100. Annual growth increment was thus determined.

Aboveground biomass was calculated from existing regressions for fertilized and non-fertilized Douglas-fir for both 1984 and 1985 diameters (Archibald, 1983). Annual biomass increment was obtained by subtracting 1984 from

1985 biomass. Average annual biomass increment between 1981 and 1985 was calculated to provide a longer term comparison for the 1985 growing season.

Shrub and herb cover was visually estimated within each 0.04 ha plot in June 1985 during peak biomass production. Shrub and herb biomass ($g\ m^{-2}$) were also determined then for treatment and control plots by destructive sampling of two 1 m subplots per plot. Procedures were as follows: all undergrowth was clipped to ground level within a vertical projection of the subplot boundaries. Shrubs were separated into Gaultheria shallon and "other" shrubs. Due to its dominance on the site, G. shallon, an evergreen shrub was further separated into 5 categories: 1. new leaves; 2. new twigs; 3. old leaves; 4. old twigs; 5. dead leaves and twigs (Appendix III). Distinguishing new from old growth was not a problem as current year's growth was green and succulent. Shrub and herb material was oven-dried at 70° C for 24 hours, or until a constant weight was obtained, and weighed to the nearest 0.01 g.

C.1. Soil sampling

Bulk density of A and B horizons (mass of dry soil volume^{-1}) was determined for four pits using the

excavation method outlined by Gessel and Cole (1958). Samples were returned to the lab, oven-dried, weighed to the nearest 0.01 g, sieved and reweighed to determine gravel content. An average bulk density was determined for the forest floor and A horizons from values obtained from the four sampling locations.

Gravimetric moisture content (Gardner, 1965) was determined bimonthly for 1 year. Forest floor samples and samples of the A horizon sieved to <2 mm were dried in a forced-air oven at 70° C and 105° C, respectively, for 48 hours or until a constant weight was obtained. Moisture was expressed on a dry weight basis ((wet wt. of soil - dry wt. of soil / dry wt. of soil) X 100).

Available soil nitrogen (NH_4^+- and NO_3^--) was measured bimonthly for 1 year following fertilization on both fertilized and control plots. Procedures were as follows: two to three grams of forest floor and 10 g of the <2 mm fraction of the A horizon were placed individually into 100 ml of 2N KCL with 0.1N phenylmercuric acetate solution (Bremner, 1965). All samples were hand shaken for 1 minute in the field and were returned to the lab and stored at 3° C until processing. Samples were vacuum filtered through Whatman #1 filterpapers. Ammonium and nitrate concentrations in extracts were determined with a Technicon Autoanalyzer II.

Nitrogen ion concentrations were corrected for soil moisture dilution of KCL solution used for extraction. Results were expressed on a dry soil mass basis.

C.2. Available nitrogen statistical analyses

Ammonium values were highly statistically normal across all dates and horizons as determined by the Kolmogorov-Smirnov Normality test. Student's t-distribution tests were run for each horizon at each date. The nitrate concentrations were generally below detection limits of the analytical procedure, thus no statistical analyses were conducted.

Chapter 4

RESULTS

A. Below-ground biomass

A.1. Prefertilization

This low productivity site had an overall live fine root biomass (<5mm) of 3.6 t ha^{-1} prior to fertilization in March, 1984. Comparisons of individual root categories between all plots showed very few differences (Table 1). In the organic horizon, the 1-2mm mycorrhizal size category varied among plots ($P < 0.10$). The <1mm mycorrhizal category in the A horizon also varied among the six plots ($P < 0.10$). Further testing with Tukey's Multiple comparison test was unable to distinquish between any distinct populations for either of the above two root categories. This may have been due to the lower statistical power of the Multiple Comparison test (Zar, 1984). These tests indicated that relatively little between-plot variation occurred in fine root and

Table 1. Pre-fertilization fine root and mycorrhizal biomass per unit area separated by soil horizon - March, 1984 (t ha^{-1})(ash-free weight).[a]

HORIZON	<1mm MYCORR[b]	1-2mm MYCORR	<1mm UNINFECT	1-2mm UNINFECT	2-5mm UNINFECT	<1-5mm ANGIO	PROFILE TOTAL
O	0.49 ± 0.07[c]	0.13 ± 0.03 *	0.02 ± 0.01	0.06 ± 0.03	0	0.09 ± 0.05	0.79 ± 0.08
A	0.48 ± 0.06 *	0.23 ± 0.05	0.01 ± 0.00	0.03 ± 0.02	0.15 ± 0.06	0.05 ± 0.03	0.94 ± 0.13
B	0.62 ± 0.07	0.56 ± 0.09	0.03 ± 0.01	0.12 ± 0.04	0.47 ± 0.16	0.20 ± 0.11	1.91 ± 0.27
TOTAL ROOTS	1.49 ± 0.04	0.92 ± 0.04	0.06 ± 0.00	0.21 ± 0.02	0.61 ± 0.06	0.36 ± 0.04	3.64 ± 0.12

a values followed by * are significantly different ($P < 0.10$) between all plots.

b fine root and mycorrhizal size categories:
- < 1 mm mycorrhizal Douglas-fir
- 1-2 mm mycorrhizal Douglas-fir
- < 1 mm uninfected Douglas-fir
- 1-2 mm uninfected Douglas-fir
- 2-5 mm uninfected Douglas-fir.

c values presented as mean ± one standard error (n=24).

mycorrhizal biomass.

Comparison of rooting patterns between control and treatment plots prior to fertilization showed few statistical significant differences (Table 2). In the organic horizon, the 1-2mm uninfected conifer category within the treatment group was 93% greater than the control ($P < 0.10$). The < 1mm uninfected conifer category varied between the two groups in the A horizon ($P < 0.10$). No differences were determined between soil profile totals for any root size or infection category. This finding reemphasizes the similarity of rooting homogeneity of the treatment and control plots.

Root size category distribution within the soil profile is shown in Figure 2. The <1mm mycorrhizal roots were the most highly distributed. This size category accounted for 41% of all root mass in the soil profile. Two other size categories, 1-2mm mycorrhizal and <5mm uninfected roots comprised another 25% of root mass in the rooting zone. Finally, angiosperm roots (<5mm) made up the remaining 10% of the below-ground biomass. No differences in rooting distribution existed between the two treatment groups prior to fertilization (Fig. 2).

Distribution of total biomass values across horizons is shown in Figure 3. Within the O horizon, 79% of all root mass was composed of <2mm diameter mycorrhizal roots.

Table 2. Pre-fertilization fine root and mycorrhizal biomass per unit area separated by soil horizon - March, 1984 (t ha^{-1})(ash-free weight).[a]

ROOT CLASS	O HORIZON cont[b]	fert[c]	A HORIZON cont	fert	B HORIZON cont	fert	PROFILE TOTAL cont	fert
<1mm mycorrhizal[d]	0.49 ± 0.09[e]	0.50 ± 0.12	0.50 ± 0.07	0.48 ± 0.09	0.85 ± 0.10	0.39 ± 0.10	1.84 ± 0.14	1.44 ± 0.18
1-2mm mycorrhizal	0.18 ± 0.06	0.07 ± 0.02	0.16 ± 0.05	0.29 ± 0.08	0.62 ± 0.13	0.61 ± 0.13	0.68 ± 0.16	0.98 ± 0.18
<1 mm uninfected	0.01 ± 0.00	0.02 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.06 ± 0.02 *	0.01 ± 0.01	0.07 ± 0.02	0.04 ± 0.02
1-2mm uninfected	0.01 ± 0.01 *	0.11 ± 0.05	0.03 ± 0.02	0.03 ± 0.03	0.17 ± 0.07	0.07 ± 0.07	0.22 ± 0.07	0.21 ± 0.07
2-5mm uninfected	0	0	0.13 ± 0.06	0.17 ± 0.09	0.42 ± 0.10	0.51 ± 0.07	0.55 ± 0.30	0.68 ± 0.21
<1-5mm angiosperm	0.04 ± 0.02	0.14 ± 0.10	0.01 ± 0.01	0.09 ± 0.06	0.31 ± 0.12	0.10 ± 0.04	0.37 ± 0.23	0.33 ± 0.11
TOTAL ROOTS	0.73 ± 0.12	0.85 ± 0.11	0.85 ± 0.15	1.04 ± 0.23	2.03 ± 0.19	1.79 ± 0.15	3.61 ± 0.58	3.68 ± 0.44

a values followed by * are significantly different ($P < 0.10$) between treatment and control plots.
b pre-fertilization control plot.
c pre-fertilization fertilizer plot.
d categories representing Douglas-fir roots.
e values presented as mean ± one standard error (n=12).

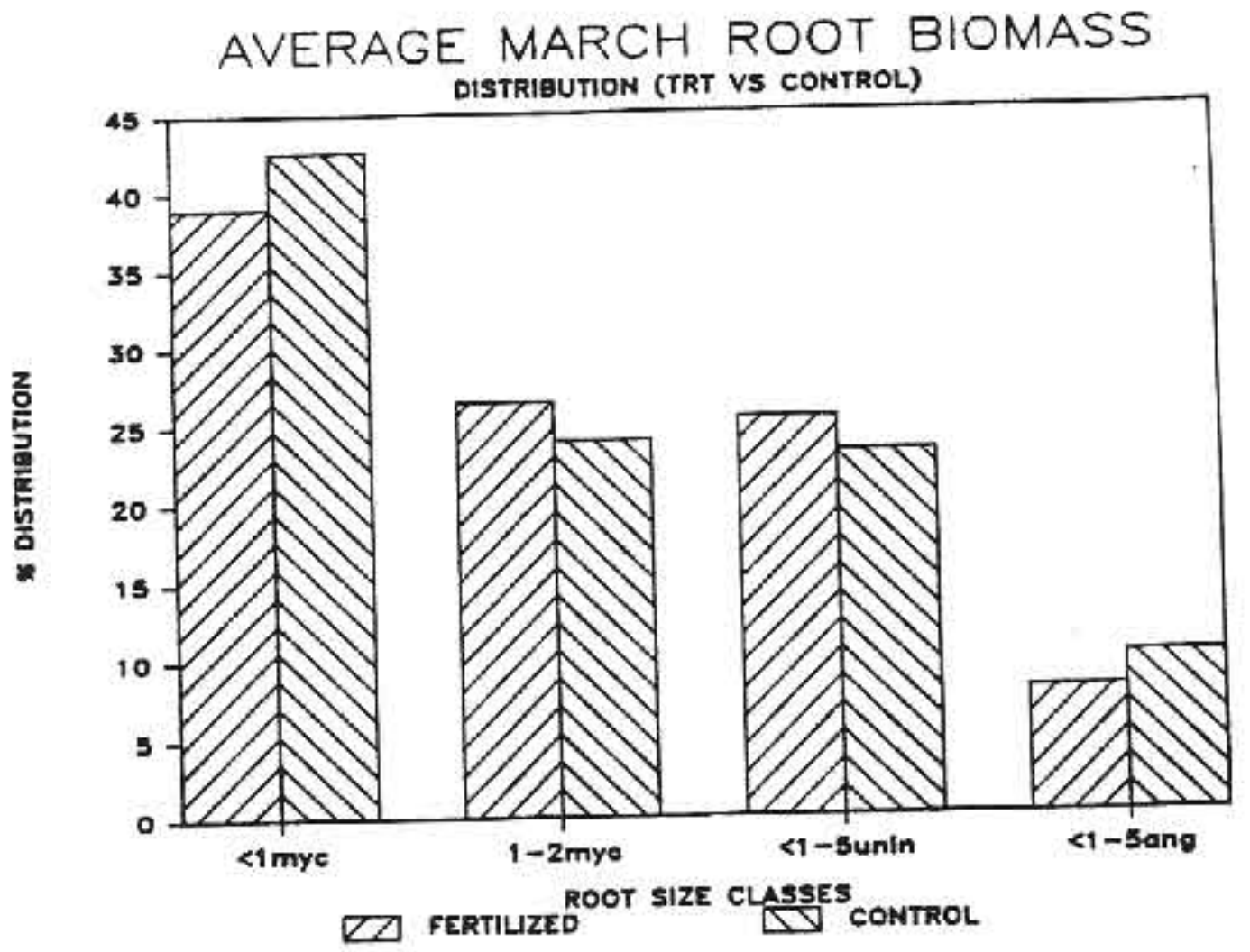


Figure 2. Pre-fertilization fine root and mycorrhizal biomass distribution separated by size and infection categories within the entire soil profile in the fertilized and control plots.

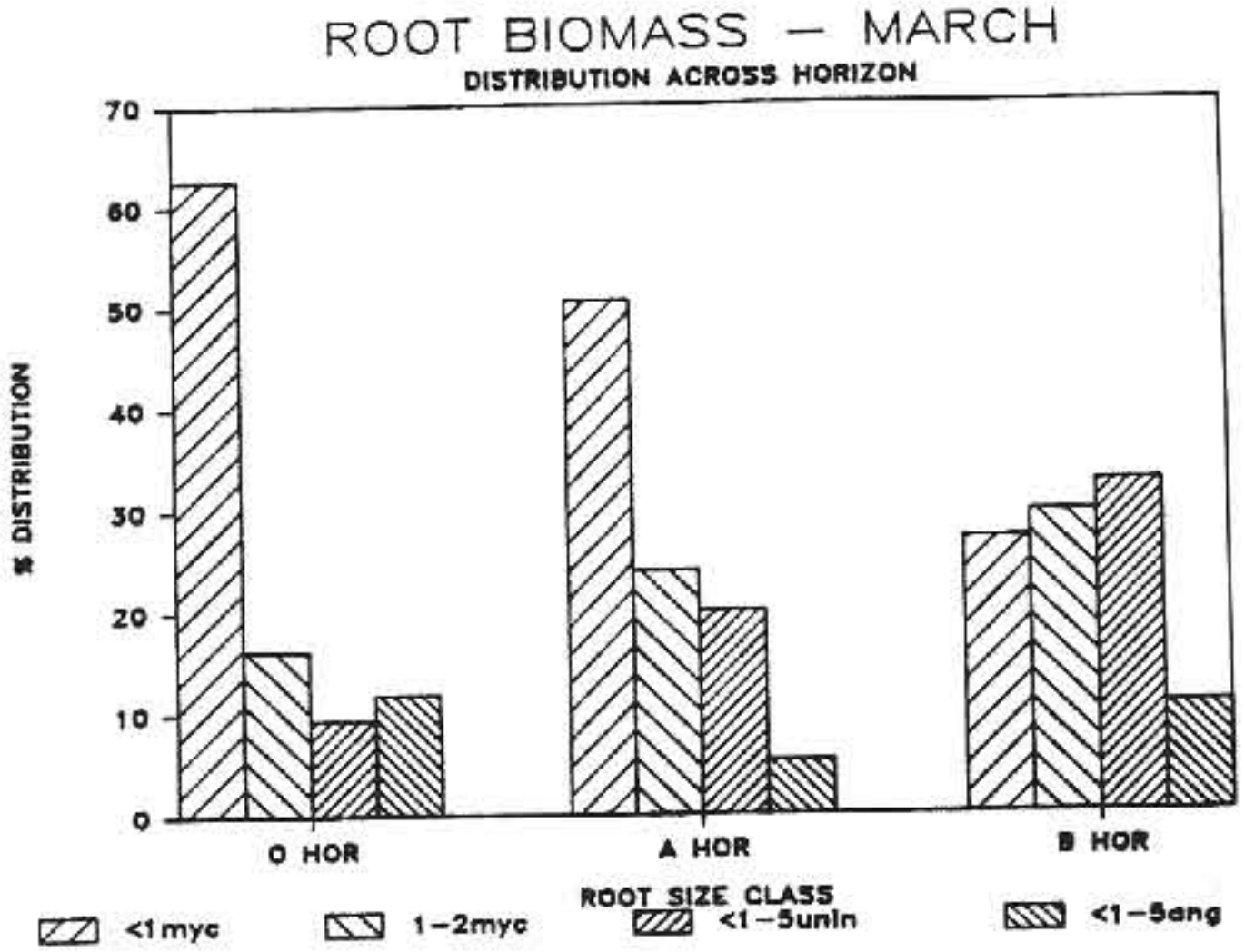


Figure 3. Pre-fertilization fine root and mycorrhizal biomass distribution separated by size and infection categories as it occurred within individual soil horizons.

This size category also comprised 75% of all root mass in the A horizon. Within the B horizon, the mass of <2mm mycorrhizal roots was 57% of the total, with uninfected conifer roots accounting for 33% of the total. Angiosperm roots constituted between 5-12% of root mass depending upon horizon (Fig. 3).

Vertical distribution of root categories in the soil profile are shown in Figure 4. During this period of low root-growth activity, the majority of rooting was found in the B horizon. Biomass of mycorrhizal roots in this horizon was 1.08 t ha^{-1} (or 45% of total) while uninfected conifer and angiosperm roots represented 0.62 t ha^{-1} (70%) and 0.20 t ha^{-1} (59%). While this represented absolute rooting values, root density which accounts for the thickness of soil horizons showed different patterns.

Root density values are presented in Table 3. The organic horizon of both treatment and control plots contained the greatest average root density (0.263 g root biomass $\cdot$ 100 cm^{-3}), with the < 1mm mycorrhizal roots comprising 37% of that total. Similarly, angiosperm roots were dominant in the O horizon (0.030 g root biomass $\cdot$ 100 cm^{-3}). Within the A horizon, the larger infected (1-2 mm) and the largest uninfected (2-5 mm) roots predominated. Rooting densities of all root categories decreased dramatically with increasing depth of the B

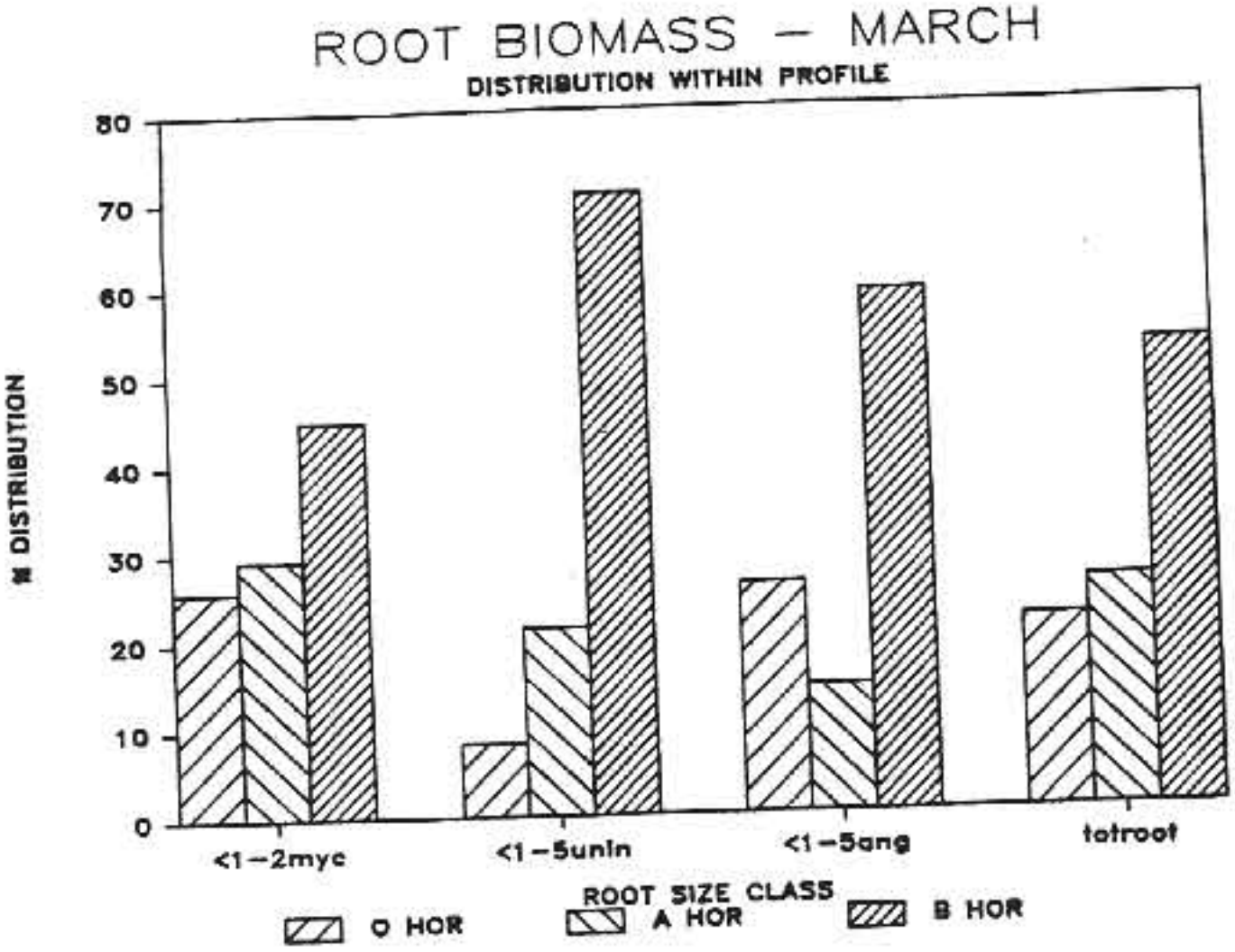


Figure 4. Individual pre-fertilization fine root and mycorrhizal biomass categories as they are distributed among the soil horizons.

Table 3. Pre-fertilization fine root and mycorrhizal density separated by horizon - March, 1984 (g 100 cm^{-3})(ash-free weight).[a]

ROOT CLASS	O HORIZON cont[b]	fert[c]	A HORIZON cont	fert	B HORIZON cont	fert
<1mm mycorrhizal[d]	0.16 ± 0.03[f]	0.17 ± 0.04	0.07 ± 0.01	0.07 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
1-2mm mycorrhizal	0.06 ± 0.02	0.02 ± 0.01	0.02 ± 0.01	0.04 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
<1mm uninfected	(T)[e]	0.01 ± 0.00	(T)	(T)	(T)	(T)
1-2mm uninfected	(T)	0.04 ± 0.02	(T)	(T)	(T)	(T)
2-5mm uninfected	0	0	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.00	0.01 ± 0.00
<1-5mm angiosperm	0.01 ± 0.01	0.05 ± 0.03	(T)	0.01 ± 0.01	(T)	(T)
TOTAL ROOTS	0.24 ± 0.04	0.28 ± 0.04	0.12 ± 0.02	0.15 ± 0.03	0.03 ± 0.00	0.03 ± 0.01

a equation used to derive values: ((g/10,000cm^{2})x(1/horizon depth))/100.
b pre-fertilization control plots.
c pre-fertilization fertilizer plots.
d categories represent Douglas-fir roots.
e (T) indicates trace amount.
f values presented as mean ± one standard error (n=12).

horizon. Density values present a distinctly different picture of soil occupancy than absolute biomass values.

A.2. Post-fertilization

Results of the statistical tests between pre- and post-fertilization root biomass showed a marked response to treatment (Table 4 & 5). Within the total soil profile of the control group, most root biomass categories had a higher biomass in June than March (Table 4). The A horizon showed the greatest degree of change, with angiosperm and total root biomass significantly greater in June than March ($P < 0.01$). Both mycorrhizal size categories also increased in June within the A horizon ($P < 0.10$). Uninfected conifer root biomass was generally higher for all horizons during the March sample period (Table 4).

Fertilized plots showed generally lower root biomass values in June than in March (Table 5). For the entire soil profile, the <1mm mycorrhizal root category was significantly less in June (0.377 t ha^{-1}, $P < 0.10$) than in March. A marked decrease of uninfected roots was seen in June in the fertilized plots. Due to the low biomass values for the uninfected group on the control plots, it is difficult to determine if this is a fertilizer

Table 4. Fine root and mycorrhizal biomass per unit area on the control plots separated by soil horizon (t ha^{-1})(ash-free weight).[a]

ROOT CLASS	O HORIZON JUNE[b]		MARCH[c]		A HORIZON JUNE		MARCH		B HORIZON JUNE		MARCH		PROFILE TOTAL JUNE		MARCH	
<1mm mycorrhizal[d]	1.26	± 0.19[e]	0.55	± 0.05	0.08	± 0.15	0.58	± 0.07	0.42	± 0.15	0.08	± 0.10	1.48	± 0.20	1.04	± 0.15
1-2mm mycorrhizal	1.01	± 0.02 *	0.10	± 0.06	0.01	± 0.13 * *	0.15	± 0.08	0.72	± 0.20	0.52	± 0.13	1.34	± 0.20	0.88	± 0.14
<1mm uninfected	0.02	± 0.02	0.01	± 0.00	0		0.01	± 0.00	0.01	± 0.01 * *	0.06	± 0.02	0.01	± 0.02	0.07	± 0.02
1-2mm uninfected	0		0.01	± 0.01	0		0.02	± 0.02	0	* *	0.17	± 0.07	0	* *	0.22	± 0.07
>2mm uninfected	0		0		0.04	± 0.03	0.10	± 0.08	0		0.02	± 0.10	0.04	± 0.21	0.06	± 0.30
>1mm angiosperm	0.01	± 0.04	0.01	± 0.02	0.08	± 0.08 * * *	0.01	± 0.01	0.12	± 0.08	0.01	± 0.12	0.01	± 0.32	0.02	± 0.23
TOTAL ROOTS	0.14	± 0.27	0.72	± 0.12	1.98	± 0.34 * * *	0.88	± 0.18	1.81	± 0.38	2.13	± 0.19	4.21	± 0.05	2.61	± 0.58

a values followed by * are significantly different ($P < 0.10$) between sample periods
values followed by * * are significantly different ($P < 0.05$) between sample periods
values followed by * * * are significantly different ($P < 0.01$) between sample periods.
b post-fertilization period - June, 1984.
c pre-fertilization period - March, 1984.
d categories represent Douglas-fir roots.
e values presented as mean ± one standard error (n=12).

Table 5. Fine root and mycorrhizal biomass per unit area on fertilized plots separated by soil horizon (t ha^{-1})(ash-free weight).[a]

ROOT CLASS	O HORIZON JUNE[b]		MARCH[c]	A HORIZON JUNE		MARCH	
<1mm mycorrhizal[d]	0.25 ± 0.10[e]		0.50 ± 0.12	0.43 ± 0.11		0.45 ± 0.09	
1-2mm mycorrhizal	0.16 ± 0.06		0.07 ± 0.02	0.32 ± 0.09		0.29 ± 0.08	
<1mm uninfected	0.01 ± 0.00		0.02 ± 0.01	0.02 ± 0.01		0.01 ± 0.00	
1-2mm uninfected	0	*	0.11 ± 0.05	0		0.03 ± 0.03	
2-5mm uninfected	0.07 ± 0.07		0	0.34 ± 0.24		0.17 ± 0.09	
<1-5mm angiosperm	0.04 ± 0.01		0.14 ± 0.10	0.11 ± 0.05		0.09 ± 0.06	
TOTAL ROOTS	0.52 ± 0.18		0.85 ± 0.11	1.21 ± 0.37		1.04 ± 0.23	

a values followed by * are significantly different ($P < 0.10$) between sample periods
values followed by * * are significantly different ($P < 0.05$) between sample periods
values followed by * * * are significantly different ($P < 0.01$) between sample periods.
b post-fertilization period - June, 1984.
c pre-fertilization period - March, 1984.
d categories represent Douglas-fir roots.
e values presented as mean ± one standard error (n=12)

Table 5. continued.

ROOT CLASS	B HORIZON JUNE		MARCH		PROFILE TOTAL JUNE		MARCH	
<1mm mycorrhizal	0.31 ± 0.10		0.39 ± 0.10		0.99 ± 0.16	*	1.44 ± 0.16	
1-2mm mycorrhizal	0.38 ± 0.09		0.61 ± 0.13		0.86 ± 0.14		0.98 ± 0.16	
<1mm uninfected	0.01 ± 0.01		0.01 ± 0.01		0.04 ± 0.02		0.04 ± 0.02	
1-2mm uninfected	0	*	0.07 ± 0.07		0	* * *	0.21 ± 0.07	
2-5mm uninfected	0.10 ± 0.10	*	0.51 ± 0.07		0.51 ± 0.28		0.68 ± 0.21	
1-5mm angiosperm	0.22 ± 0.10		0.10 ± 0.04		0.36 ± 0.14		0.33 ± 0.11	
TOTAL ROOTS	1.02 ± 0.23	* *	1.79 ± 0.15		2.76 ± 0.48		3.68 ± 0.44	

response.

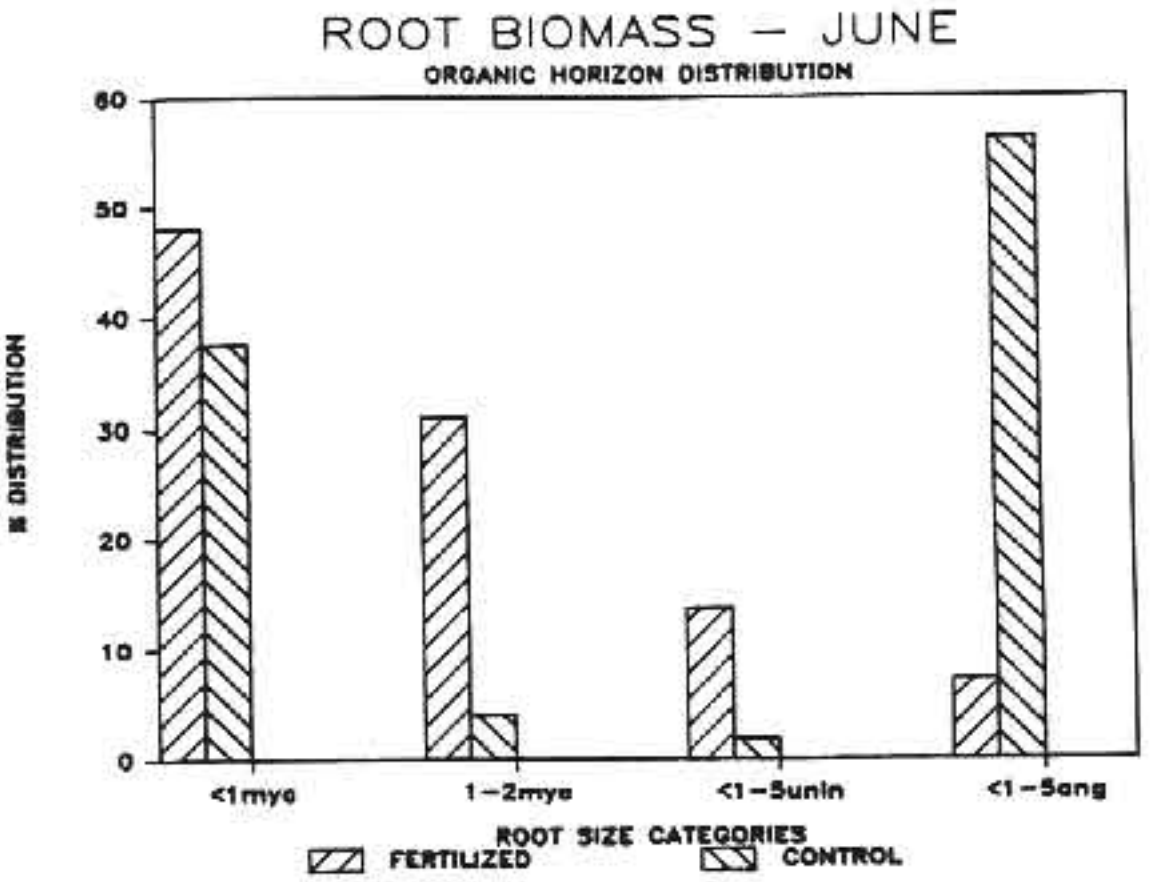
Live root biomass of fertilized and control plots are shown in Table 6. Total biomass for the treated plots (2.8 t ha^{-1}) was significantly different from that of the control plots (4.2 t ha^{-1}, $P < 0.10$). Moreover, the biomass of < 1 mm mycorrhizal roots in the soil profile of fertilized plots differed significantly from that of the control plots ($P < 0.05$). Significant differences between treatment and control were also found for the A horizon for this category ($P < 0.05$). In both cases, fertilized plots had 50-59% less live root biomass in the <1mm mycorrhizal category than the control plots. Two other root categories, the 1-2mm mycorrhizal root (in the organic horizon), and angiosperm roots (for the entire profile) were significantly different between the treatment and control plots ($P < 0.10$).

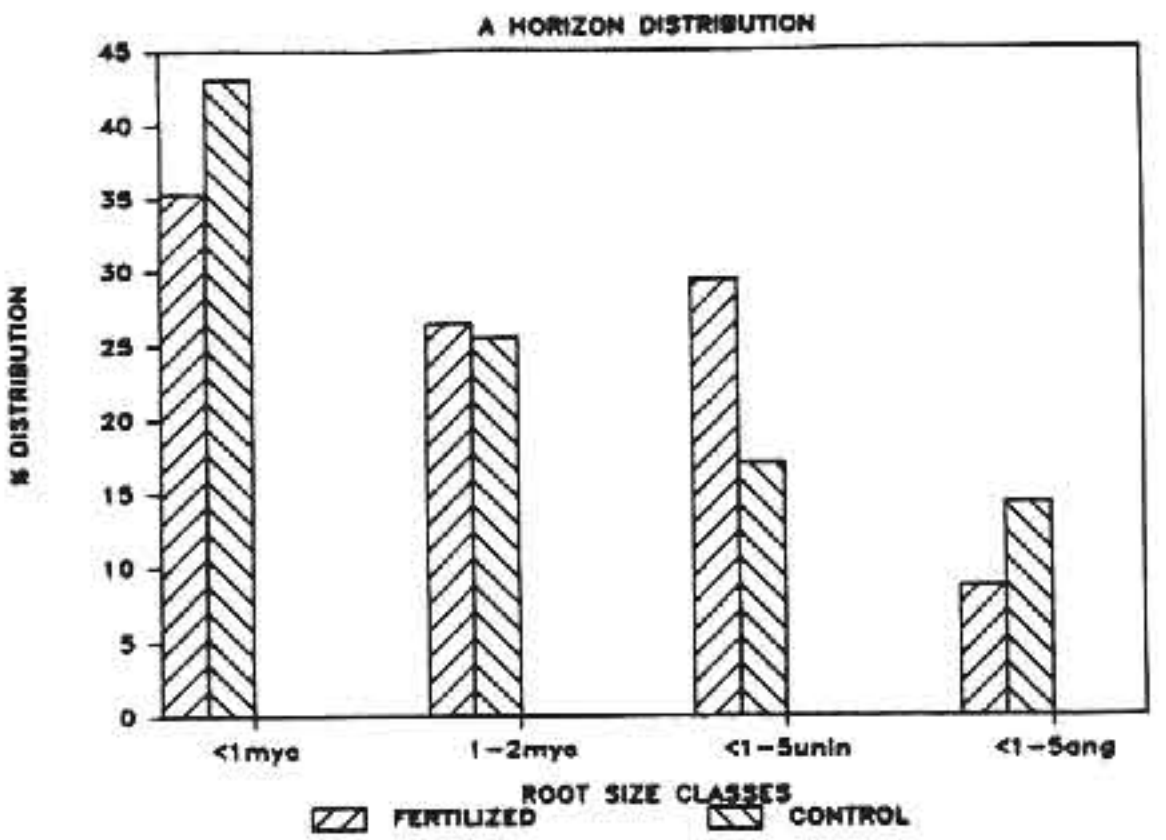
Comparisons of the various root size categories as they are distributed across genetic soil horizons are shown in Figures 5-8. Infected and uninfected conifer roots in the organic horizon were 37% and 12% greater in the fertilized than in the control plots, while angiosperm roots decreased by 49% in response to fertilization (Fig. 5). Infected and angiosperm roots in the A horizon decreased by 7% and 6% in the fertilizer plots (Fig. 6), respectively, while uninfected root biomass increased by

Table 6. Post-fertilization fine root and mycorrhizal biomass per unit area separated by soil horizon - June, 1984 (t ha^{-1})(ash-free weight).[a]

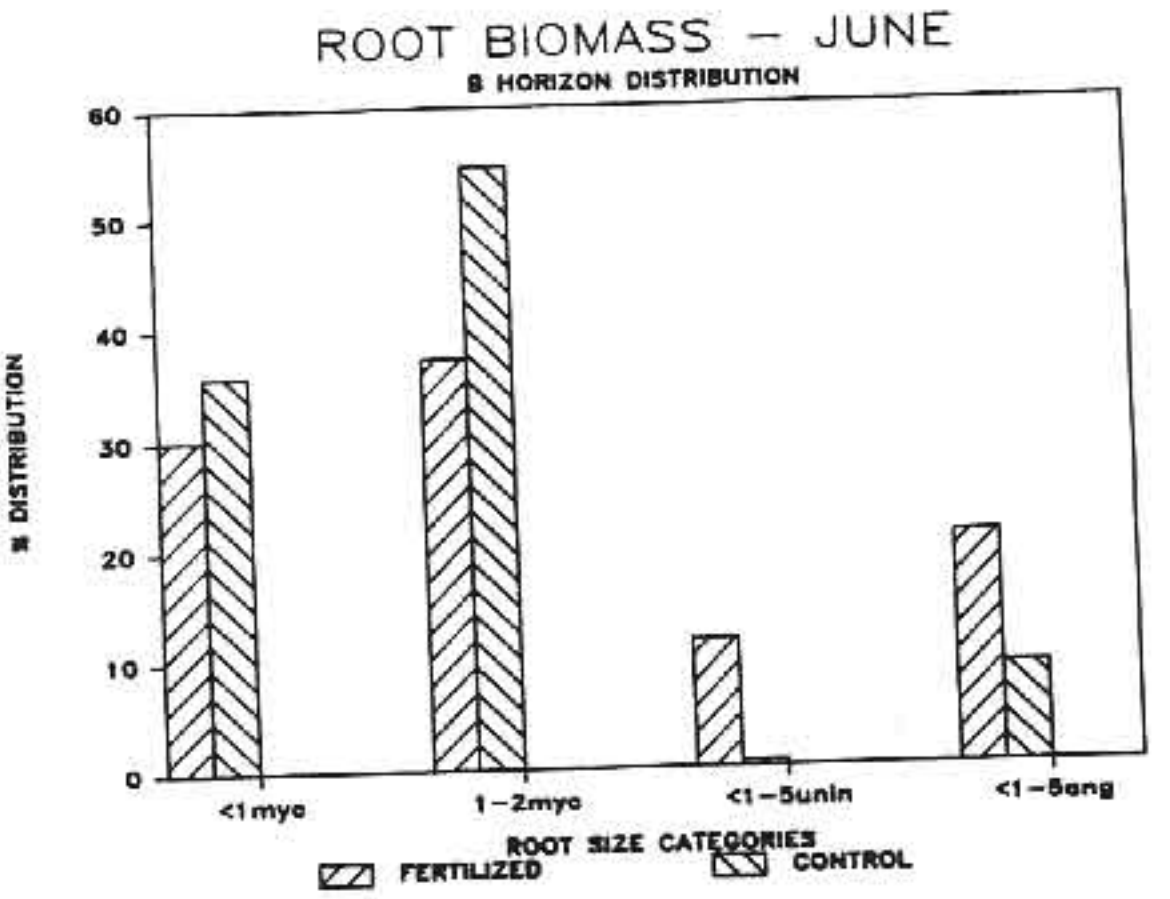
ROOT CLASS	O HORIZON cont[b]	O HORIZON fert[c]	A HORIZON cont	A HORIZON fert	B HORIZON cont	B HORIZON fert	PROFILE TOTAL cont	PROFILE TOTAL fert
<1mm mycorrhizal[d]	0.36 ± 0.10[e]	0.26 ± 0.10	0.86 ± 0.15 *	0.49 ± 0.11	0.47 ± 0.15	0.31 ± 0.10	1.60 ± 0.25 *	0.99 ± 0.18
1-2mm mycorrhizal	0.04 ± 0.02 *	0.16 ± 0.06	0.81 ± 0.13	0.32 ± 0.09	0.72 ± 0.20	0.38 ± 0.09	1.26 ± 0.28	0.86 ± 0.14
<1mm uninfected	0.02 ± 0.02	0.01 ± 0.00	0	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.04 ± 0.02
1-2mm uninfected	0	0	0	0	0	0	0	0
2-6mm uninfected	0	0.07 ± 0.07	0.34 ± 0.23	0.34 ± 0.24	0	0.10 ± 0.10	0.34 ± 0.23	0.51 ± 0.28
>6mm angiosperm	0.53 ± 0.30	0.04 ± 0.01	0.28 ± 0.06	0.11 ± 0.08	0.12 ± 0.03	0.22 ± 0.10	0.93 ± 0.32 *	0.36 ± 0.14
TOTAL ROOTS	0.94 ± 0.37	0.52 ± 0.18	1.96 ± 0.34	1.21 ± 0.37	1.31 ± 0.38	1.02 ± 0.23	4.24 ± 0.55 *	2.76 ± 0.40

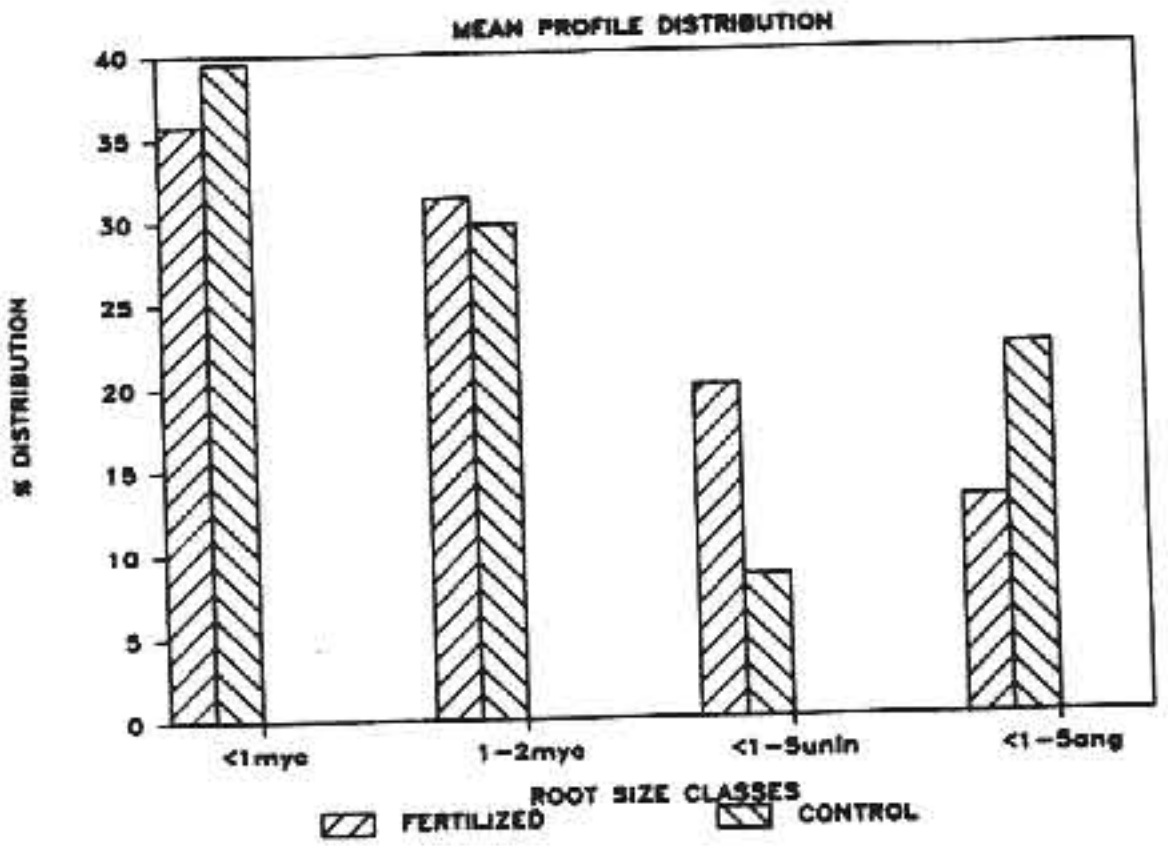
a values followed by * are significantly different ($P < 0.10$) between treatment and control plots.
b post-fertilization control plots.
c post-fertilization fertilizer plots.
d categories represent Douglas-fir roots.
e values presented as mean ± one standard error (n=12).





Figures 5a & 6b. Post-fertilization fine root and mycorrhizal biomass distribution separated by size and infection categories as it occurred in the organic and A horizons of the fertilized and control plots.



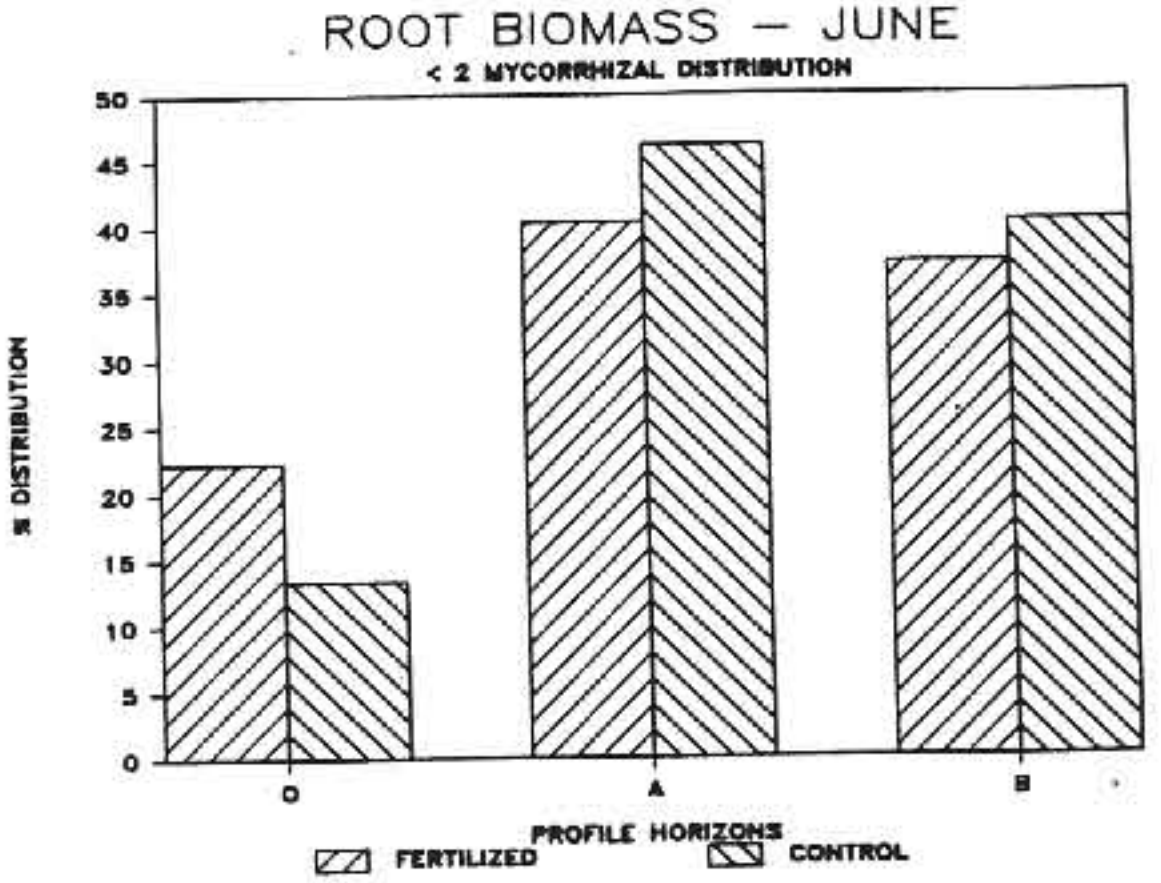


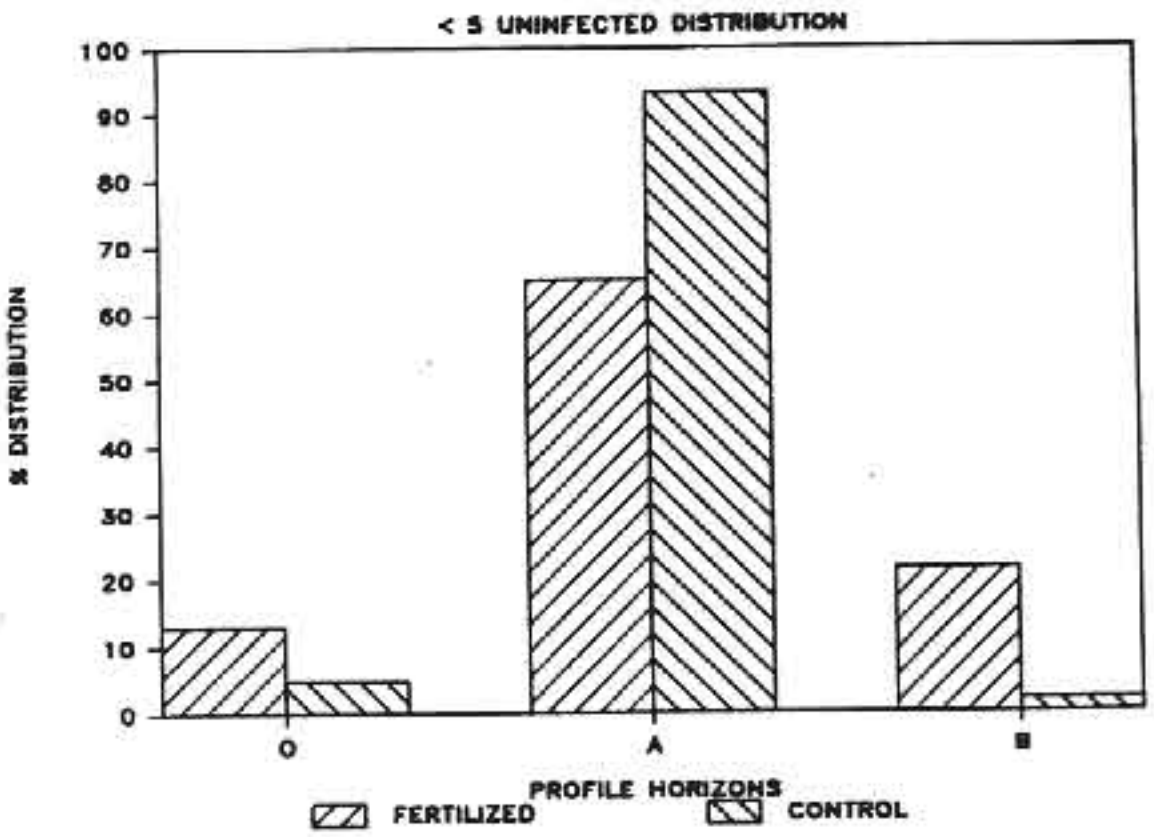
Figures 7a & 8b. Post-fertilization fine root and mycorrhizal biomass distribution separated by size and infection categories as it occurred in the B horizon and total profile of the fertilized and control plots.

12%. In the B horizon of treated plots both uninfected and angiosperm roots were 11% greater than control plot biomass while infected conifer roots decreased by 23% (Fig. 7). The total soil profile showed slight decreases in both the infected and angiosperm root category with fertilization while uninfected roots increased by 11% (Fig. 7).

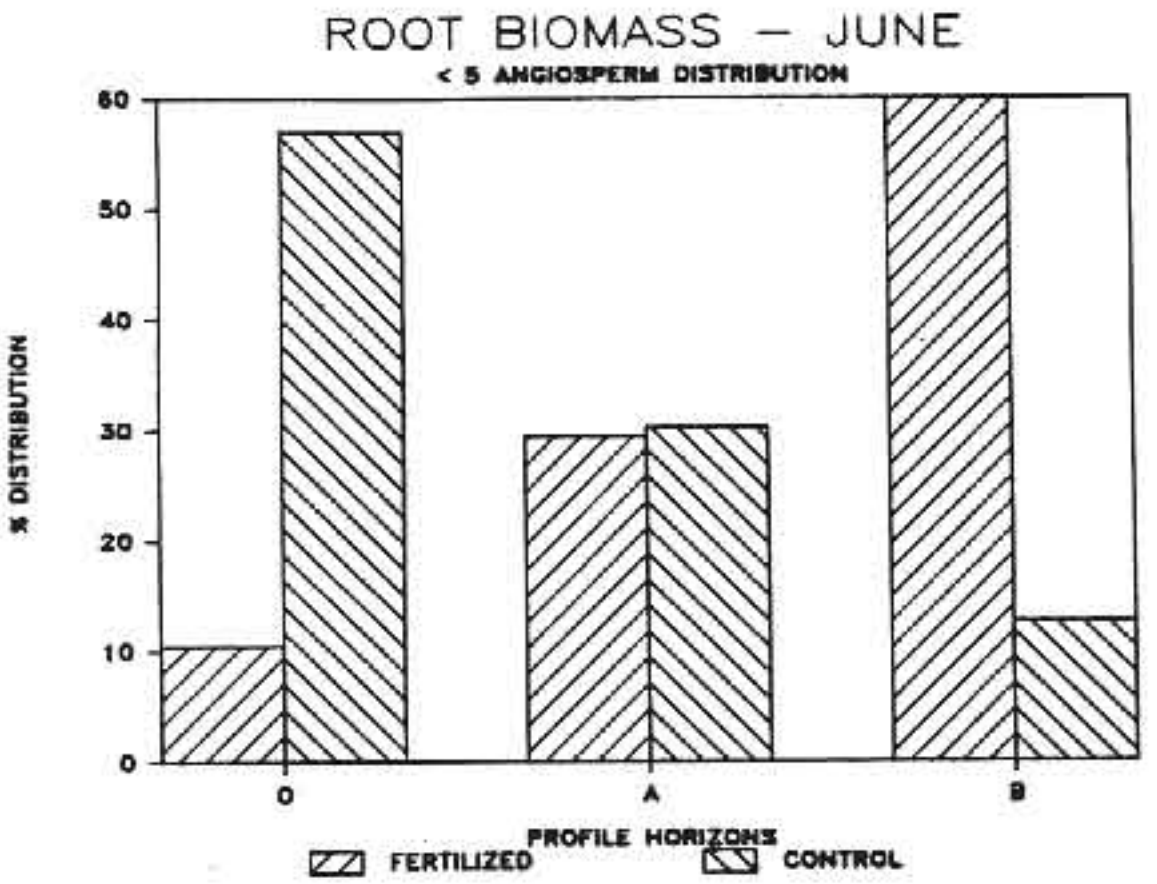
Distribution of individual root categories within the total soil profile is shown in Figures 9-12. Both the infected and uninfected conifer root categories in the fertilized and control plots predominated in the A horizon (Figs. 9-10). Angiosperm roots in the fertilized plots were most strongly dominant in the B horizon, while they dominated the organic horizon in the control plots (Fig. 11). Total root distribution closely mimicked the infected root category distribution, with predominance in the A horizon in both treated and control plots (Fig. 12).

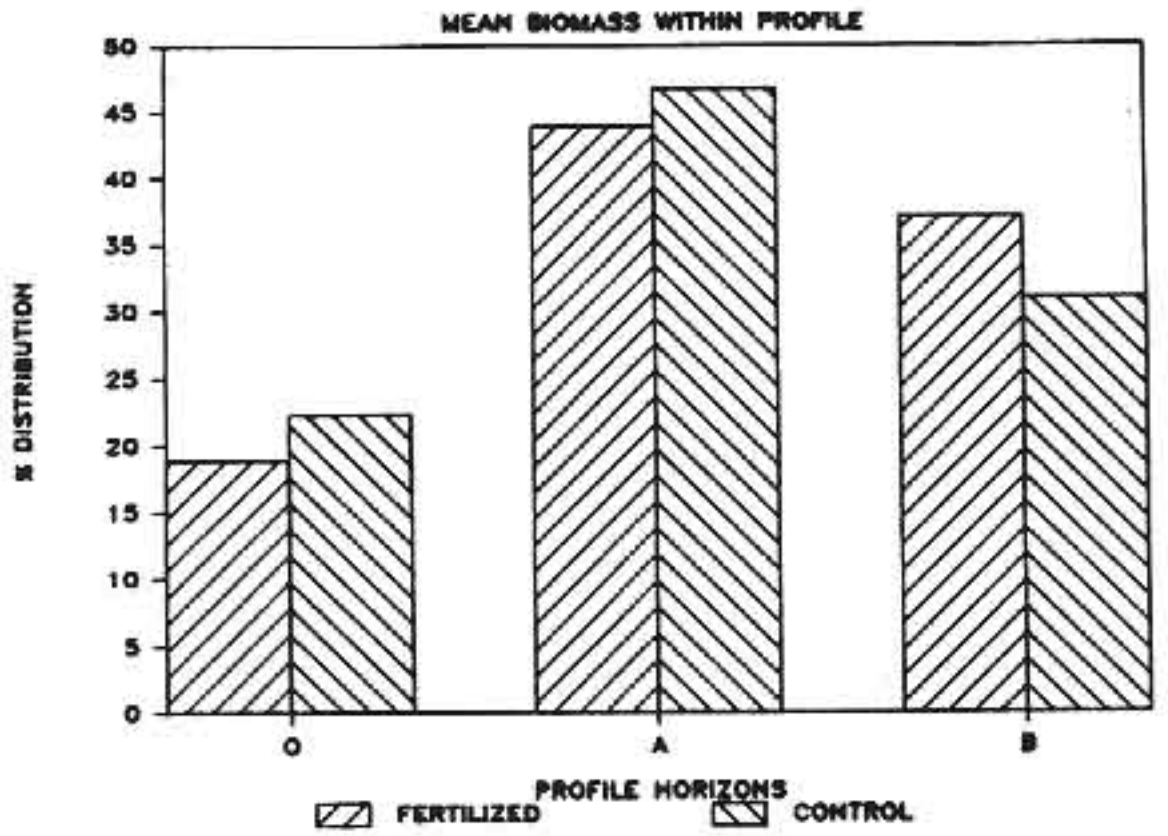
Rooting density decreased across the entire soil profile following fertilization (Table 7). Similar to pre-fertilization density, the organic horizon was the most densely occupied with 0.175 g roots $\cdot$ 100cm^{-3} in the treated plots versus 0.315 g total roots $\cdot$ 100cm^{-3} in the control plots. Total root density in the A horizon of the treated group, equaled that of the treated organic horizon, while the A horizon of the control group had





Figures 9a & 10b. Post-fertilization distribution of the < 2 mm mycorrhizal and < 5 mm uninfected categories within individual soil horizons of the fertilized and control plots.





Figures 11a & 12b. Post-fertilization distribution of the < 5 mm angiosperm and total root categories within individual soil horizons of the fertilized and control plots.

Table 7. Post-fertilization fine root and mycorrhizal density separated by horizon - June, 1984 (g 100 cm^{-3})(ash-free weight).[a]

ROOT CLASS	O HORIZON cont[b]	O HORIZON fert[c]	A HORIZON cont	A HORIZON fert	B HORIZON cont	B HORIZON fert
<1mm mycorrhizal[d]	0.12 ± 0.03[f]	0.08 ± 0.03	0.12 ± 0.02	0.06 ± 0.02	0.01 ± 0.00	0.01 ± 0.00
1-2mm mycorrhizal	0.01 ± 0.01	0.05 ± 0.02	0.07 ± 0.02	0.05 ± 0.03	0.01 ± 0.00	0.01 ± 0.00
<1mm uninfected	0.01 ± 0.01	(T)[e]	0	(T)	(T)	(T)
1-2mm uninfected	0	0	0	0	0	(T)
2-5mm uninfected	0	0.02 ± 0.02	0.05 ± 0.03	0.05 ± 0.03	0	(T)
<1-5mm angiosperm	0.18 ± 0.10	0.01 ± 0.00	0.04 ± 0.01	0.02 ± 0.01	(T)	(T)
TOTAL ROOTS	0.32 ± 0.12	0.17 ± 0.06	0.28 ± 0.05	0.17 ± 0.05	0.02 ± 0.01	0.02 ± 0.00

a equation used to derive values: ((g/10,000 cm^2)x(1/horizon depth))/100.
b post-fertilization control plots.
c post-fertilization fertilizer plots.
d categories represent Douglas-fir roots.
e (T) indicates trace amount.
f values presented as mean ± one standard error (n=12).

0.282 g roots $\cdot 100cm^{-3}$, 10% less density than the organic horizon. The greater depth of the B horizon lead to negligible root occupancy with; 0.017 g total roots $\cdot 100cm^{-3}$ in the fertilized group and 0.021 g total roots $\cdot 100cm^{-3}$ in the control group.

B.1. Conifer root tips

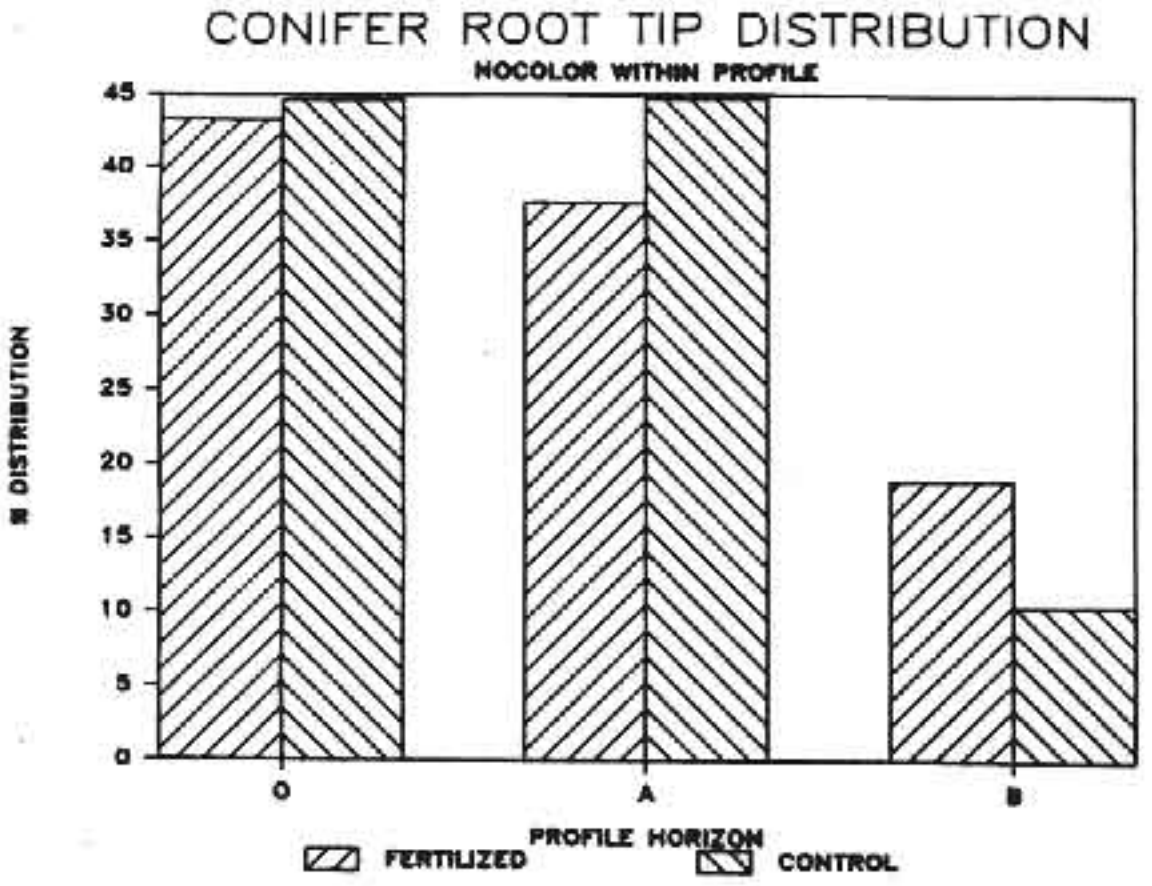
Root tip number per square meter for the June sample period is shown in Table 8. Total root tips in the entire soil zone in the fertilized plots were significantly less than the control values ($P < 0.10$). Two color groups, "nocolor" and white mycorrhizal, were significantly greater in the treatment plots than in the control for the entire soil rooting zone ($P < 0.05$). Similarly, within the A horizon, "nocolor" and total tips were significantly greater in the treatment plots ($P < 0.10$).

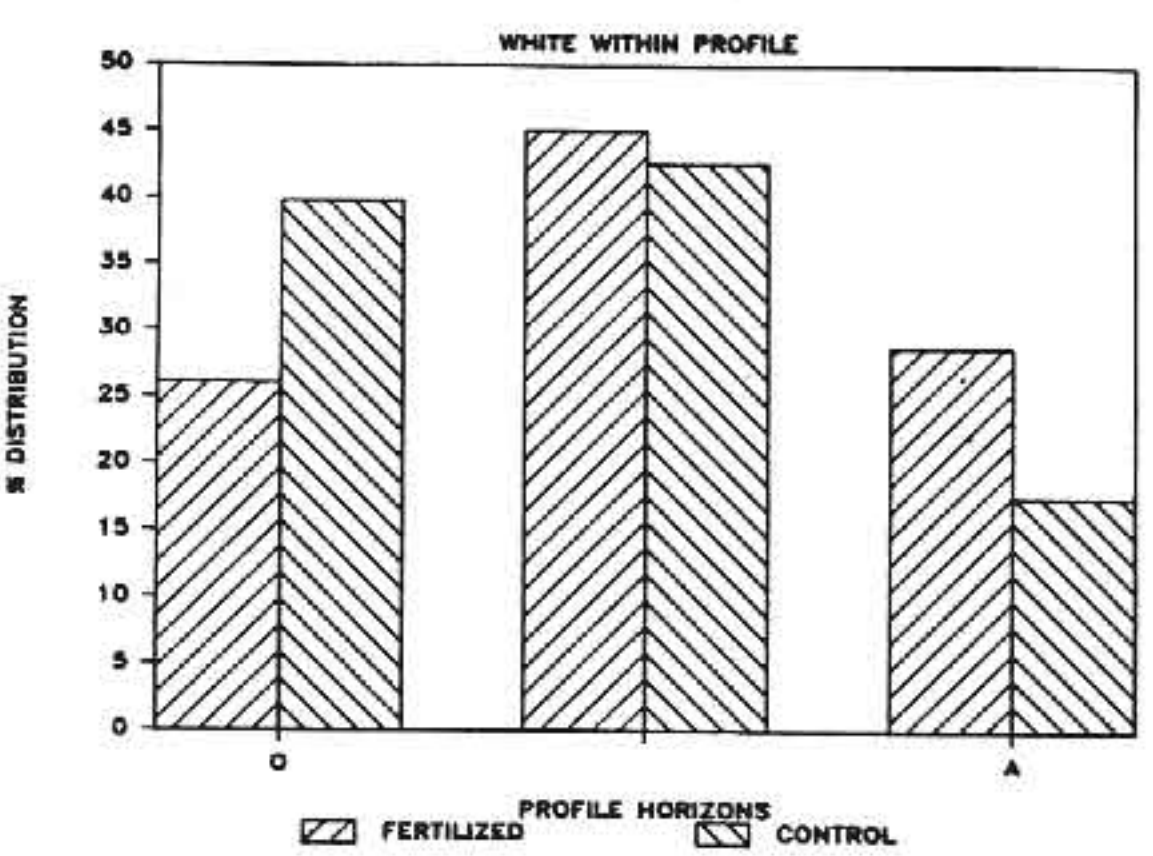
Root tip distribution within the soil profile is shown in Figures 13-18. Within the control plots, the majority of all root tip color types were found in the A horizon (Figs. 13-18). Predominant tip distribution in the fertilized plots was more evenly scattered among the three horizons. Generally, a trend of decreased percent root tip distribution within the O and A horizons followed fertilization. Conversely, rooting tended to increase in

Table 8. Douglas-fir root tip color type distribution per unit area separated by horizon - June, 1984 (tips m^{-2} (in thousands)).[a]

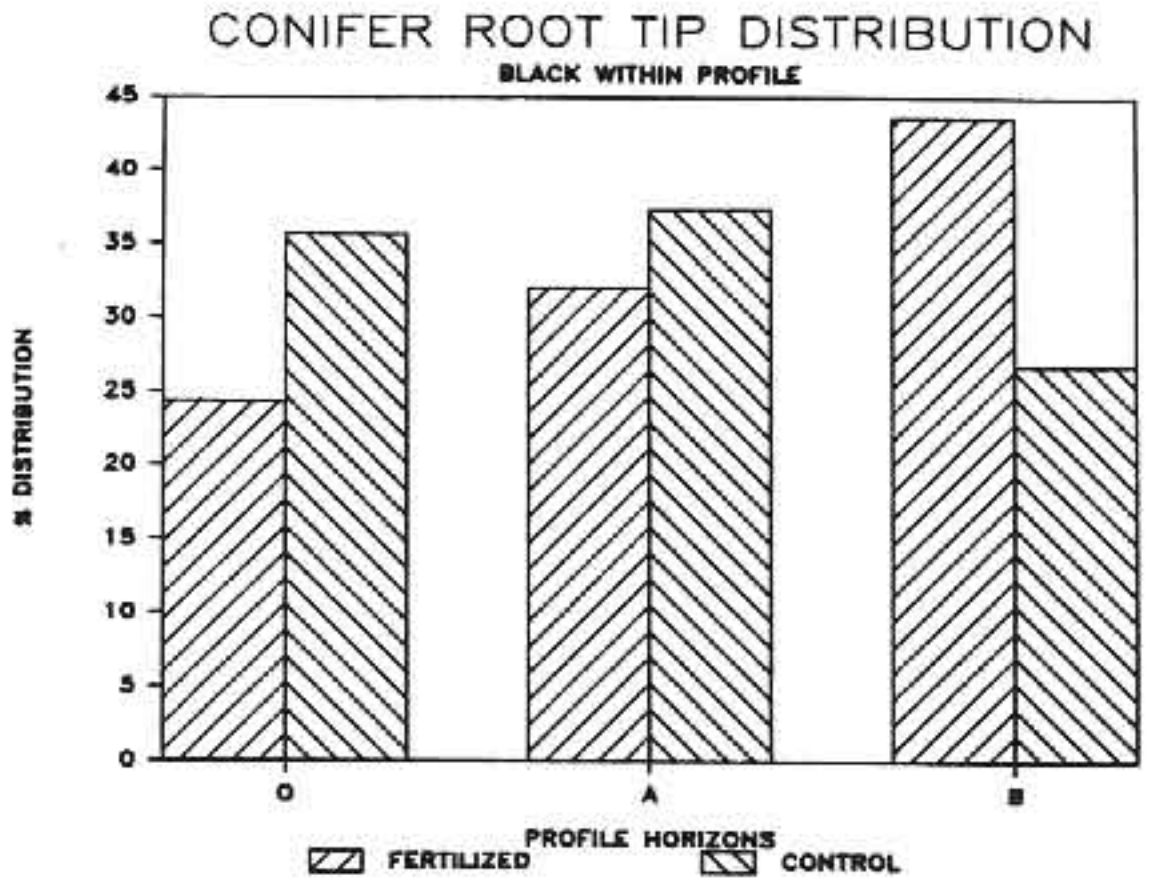
COLOR TYPE	O HORIZON cont[b]		fert[c]		A HORIZON cont		fert		B HORIZON cont		fert		PROFILE TOTAL cont		fert	
nocolor	26.3	± 9.4[d]	11.4	± 5.6	28.4	± 9.6	9.9	± 3.6	6.7	± 4.2	6.0	± 2.0	68.4	± 4.9 *	26.4	± 2.4
white	27.9	± 14.7	5.2	± 2.7	29.8	± 12.9	9.0	± 4.7	12.3	± 4.8	5.7	± 1.7	78.0	± 6.6 * *	19.9	± 2.6
black	11.0	± 3.8	7.8	± 4.6	11.6	± 3.3	10.3	± 3.9	8.3	± 3.5	13.9	± 8.1	30.9	± 2.9	32.1	± 3.2
brown	72.1	± 21.2	76.0	± 25.8	172.2	± 31.7	113.6	± 34.7	79.8	± 16.5	49.0	± 24.0	324.0	± 15.7	269.3	± 16.5
green	4.0	± 3.9	3.4	± 2.6	9.5	± 8.0	1.2	± 4.9	2.1	± 0.8	3.7	± 2.4	15.6	± 3.8	8.3	± 1.2
TOTAL TIP	143.5	± 40.8	103.7	± 31.8	261.6	± 41.4 *	144.1	± 41.4	109.4	± 26.5	98.2	± 33.0	804.8	± 23.1 *	346.8	± 20.4

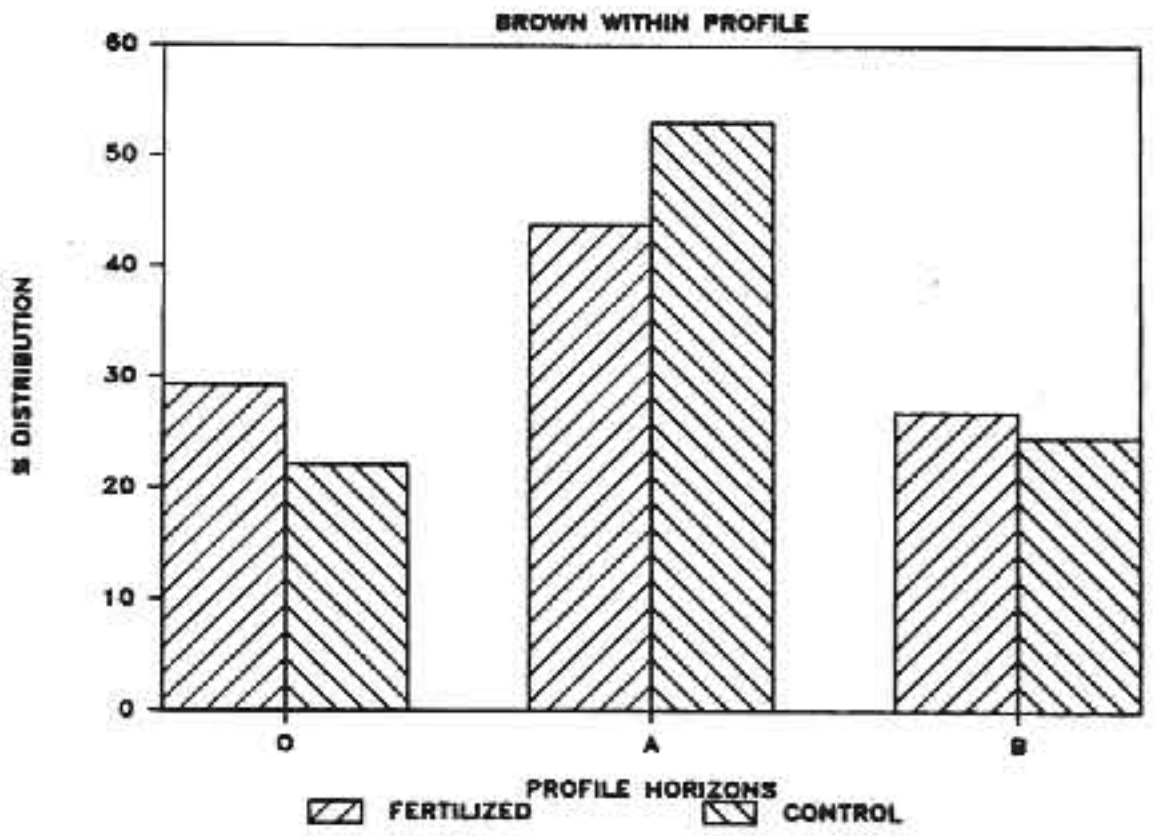
a values followed by * are significantly different ($P < 0.10$) between treatment and control plots
values followed by * * are significantly different ($P < 0.05$) between treatment and control plots.
b post-fertilization control plots.
c post-fertilization fertilizer plots.
d values presented as mean ± one standard error (n=12).



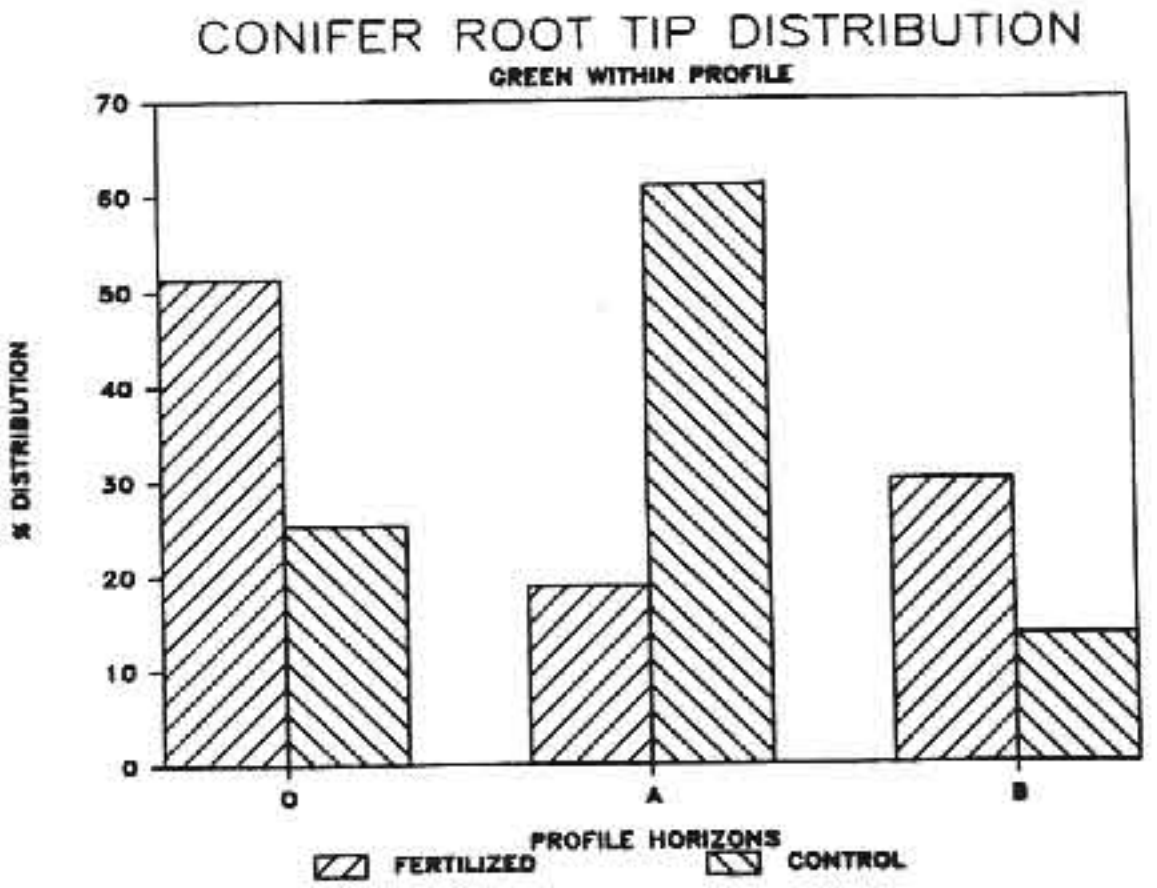


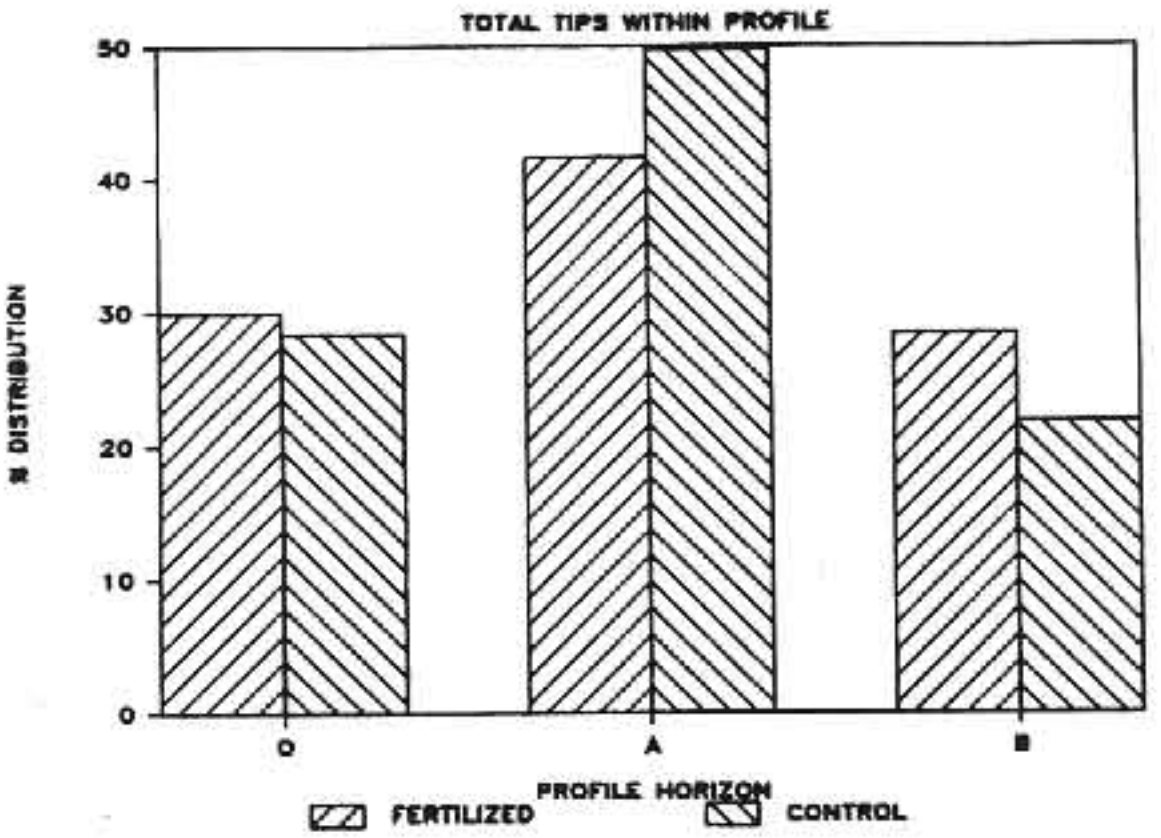
Figures 13a & 14b. Post-fertilization distribution of the "nocolor" and white mycorrhizal conifer root tip color types within individual soil horizons of the fertilized and control plots.





Figures 15a & 16b. Post-fertilization distribution of the black and brown mycorrhizal conifer root tip color types within individual soil horizons of the fertilized and control plots.





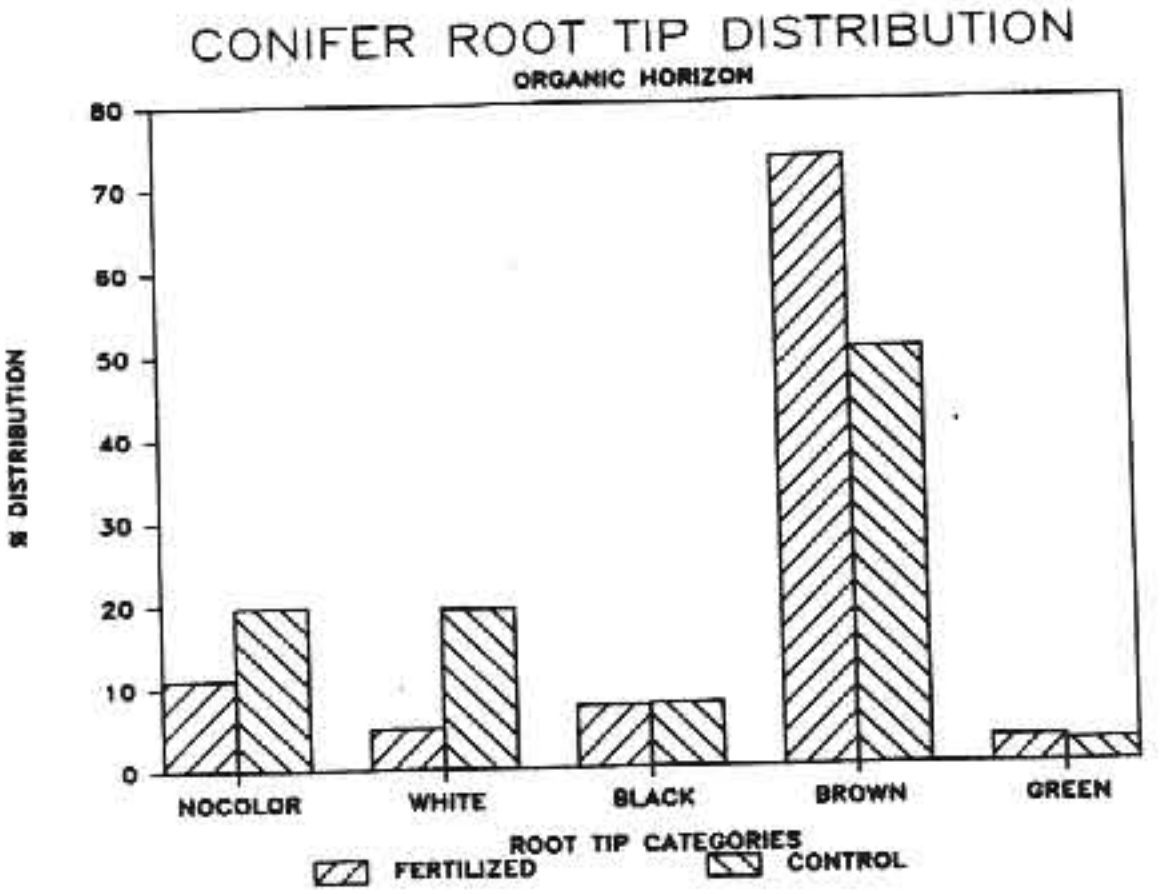
Figures 17a & 18b. Post-fertilization distribution of the green mycorrhizal and total conifer root tip color types within individual soil horizons of the fertilized and control plots.

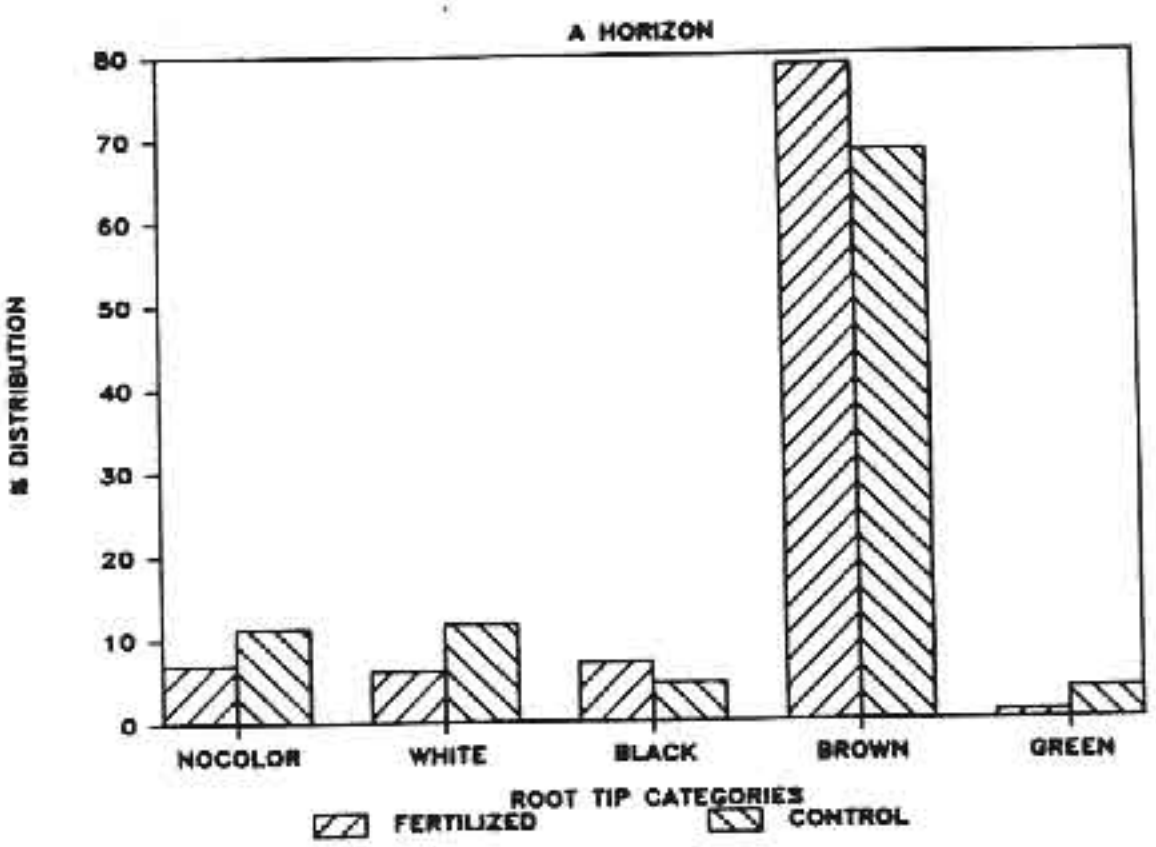
the B horizon with fertilizer treatment (Figs. 13-18).

Distribution of color types across horizons is presented in Figures 19-22. Within all horizons of the control plots, the brown color type strongly prevailed (50-72%). It was followed by both "nocolor" and white types, ranging from 6-20% in all horizons. The fertilized plots displayed trends similar to the control plots with the brown type occurring on 71% to 79% of the root tips in all horizons (Figs. 19-22). The remaining tips consisted of the "nocolor", white and black types.

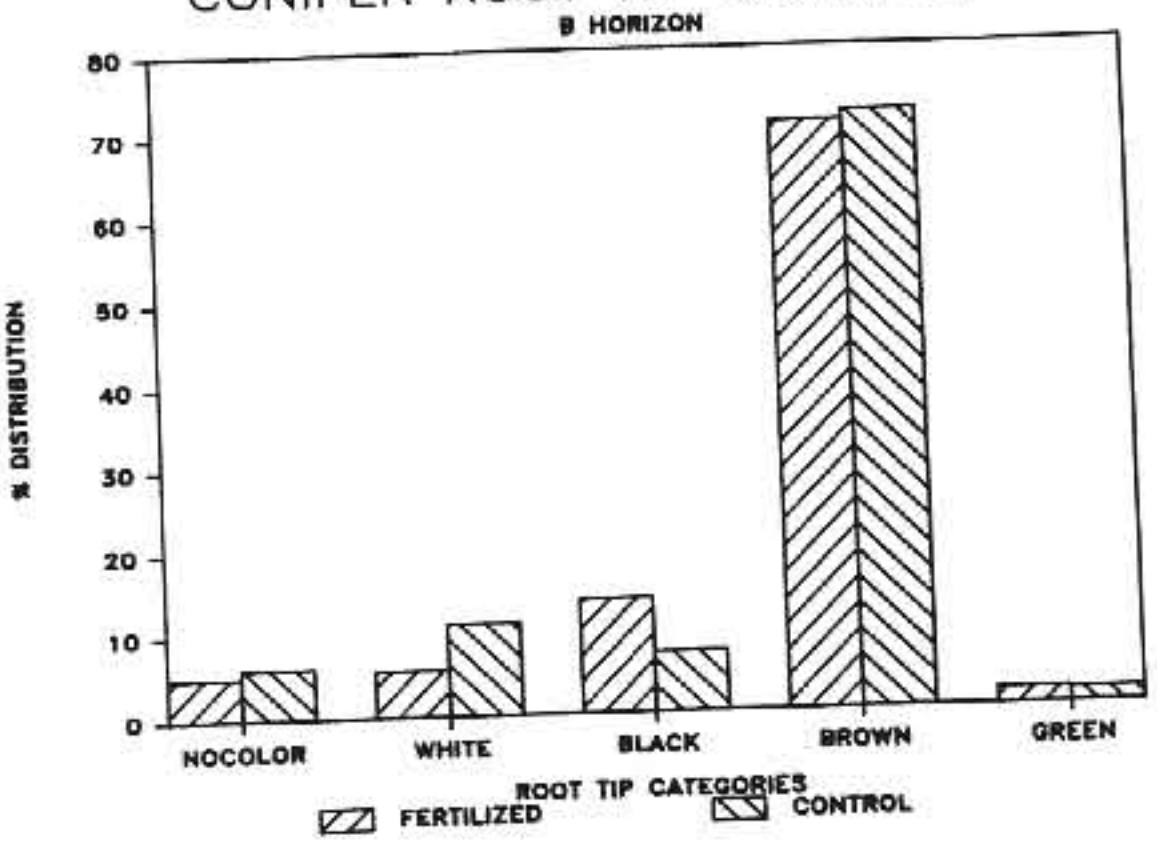
Root tip density (number of tips $\cdot$ 100 cm^{-3}) followed trends similar to root weight density (Table 9). The organic horizon in both treatment groups had the greatest density of tips, and tip density decreased with increasing depth. Diminished numbers of tips per $100cm^{-3}$ were evident among all color types in every horizon following fertilization. Similar to percent root tip distribution, the brown color type dominated all horizons (Table 9).

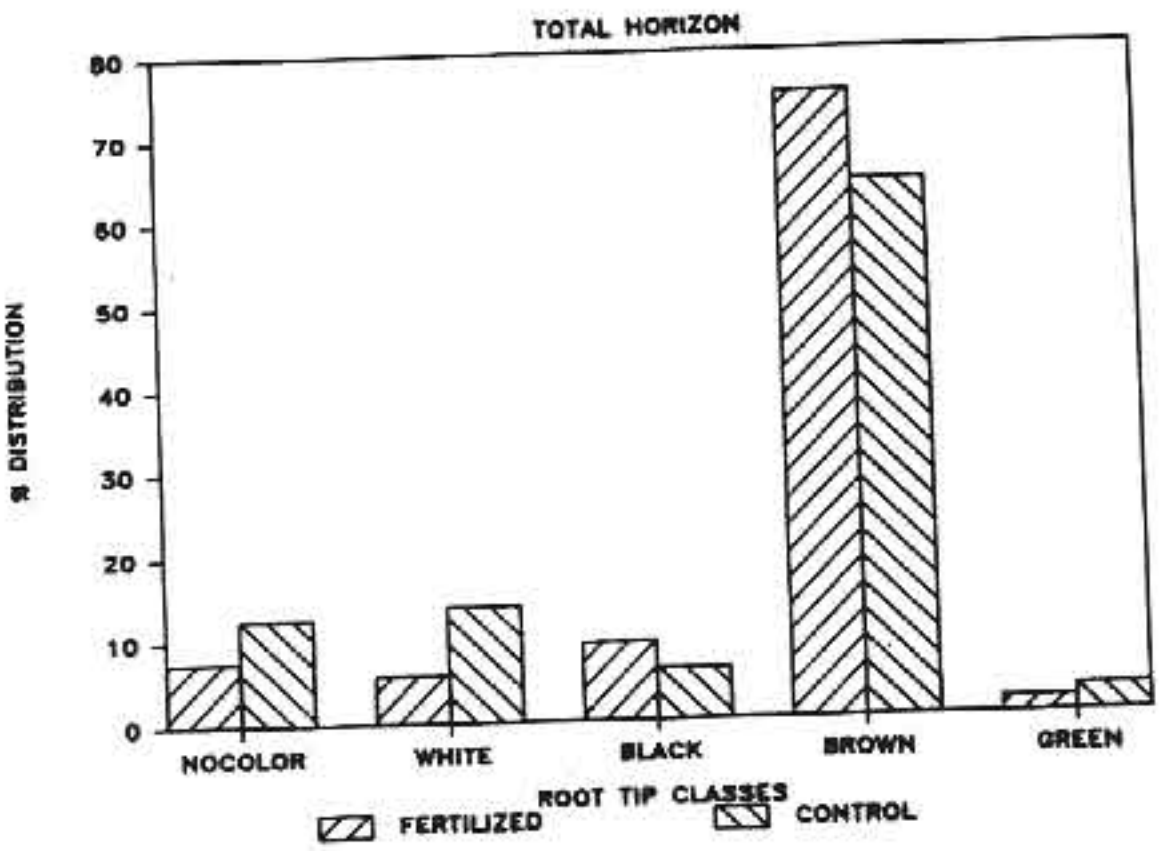
The fertilized plots contained smaller tip biomass per meter squared than control plots. (Table 10). Tip weight in the organic horizon accounted for 75% of infected root biomass. The value of 108% for the untreated organic horizon can not be explained, yet it falls within the bounds of the error term. For both A and





Figures 19a & 20b. Post-fertilization conifer root tip color type distribution as it occurred in the organic and A horizons of the fertilized and control plots.





Figures 21a & 22b. Post-fertilization conifer root tip color type distribution as it occurred in the B horizon and total profile of the fertilized and control plots.

Table 9. Douglas-fir root tip color type density separated by soil horizon - June, 1984 (tips 100 cm $^{-3}$).[a]

COLOR TYPE	O HORIZON cont[b]	O HORIZON fert[c]	A HORIZON cont	A HORIZON fert	B HORIZON cont	B HORIZON fert
nocolor	94.4 ± 31.3[d]	38.0 ± 18.7	40.6 ± 13.7	14.2 ± 5.1	1.1 ± 0.7	0.8 ± 0.4
white	93.0 ± 48.9	17.2 ± 9.0	42.6 ± 18.4	12.8 ± 9.6	2.0 ± 0.7	0.9 ± 0.3
black	36.8 ± 12.7	26.0 ± 15.3	16.5 ± 4.7	14.7 ± 5.6	1.3 ± 0.6	2.2 ± 1.3
brown	240.3 ± 70.7	253.2 ± 86.0	246.0 ± 42.3	162.3 ± 49.6	12.9 ± 3.0	11.2 ± 3.9
green	13.2 ± 13.0	11.1 ± 8.7	13.5 ± 11.4	1.8 ± 7.0	0.3 ± 0.1	0.3 ± 0.4
TOTAL TIP	478.3 ± 136.0	345.6 ± 105.0	359.4 ± 59.2	205.9 ± 59.2	17.9 ± 4.3	15.8 ± 5.4

a equation used to derive values: ((tips/10,000 cm ^{2})x(1/horizon depth))/100.
b post-fertilization control plots.
c post-fertilization fertilizer plots.
d values presented as mean ± one standard error (n=12).

Table 10. Douglas-fir root tip color type biomass per unit area separated by soil horizon - June, 1984 (g m^{-2})(ash-free weight).[a]

COLOR TYPE	O HORIZON cont[b]	fert[c]	A HORIZON cont	fert	B HORIZON cont	fert	PROFILE TOTAL cont	fert
nocolor	9.65 ± 3.20[d]	3.87 ± 1.90	9.65 ± 3.26	3.33 ± 1.22	2.28 ± 1.43	1.07 ± 0.86	21.58 ± 1.67	8.95 ± 0.82
white	9.47 ± 5.80	1.75 ± 0.92	10.17 ± 4.39	3.87 ± 2.28	4.21 ± 1.63	1.93 ± 0.66	23.77 ± 2.24	6.75 ± 0.85
black	3.77 ± 1.29	2.63 ± 1.86	3.96 ± 1.12	3.81 ± 1.33	2.81 ± 1.19	4.74 ± 2.75	10.43 ± 0.68	10.88 ± 1.09
brown	24.86 ± 7.21	25.79 ± 8.77	68.81 ± 10.70	36.60 ± 11.80	27.11 ± 6.29	23.68 ± 8.16	110.18 ± 5.34	88.16 ± 5.61
green	1.32 ± 1.33	1.14 ± 0.88	3.26 ± 2.72	0.44 ± 1.67	0.70 ± 0.27	0.79 ± 0.81	5.26 ± 1.02	2.19 ± 0.41
TOTAL TIP	48.77 ± 13.87	35.26 ± 10.71	85.83 ± 14.88	49.83 ± 14.08	37.46 ± 9.01	33.42 ± 11.49	171.84 ± 7.85	117.63 ± 6.94

a post-fertilization control plots.
b post-fertilization fertilizer plots.
c values presented as mean ± one standard error (n=12).

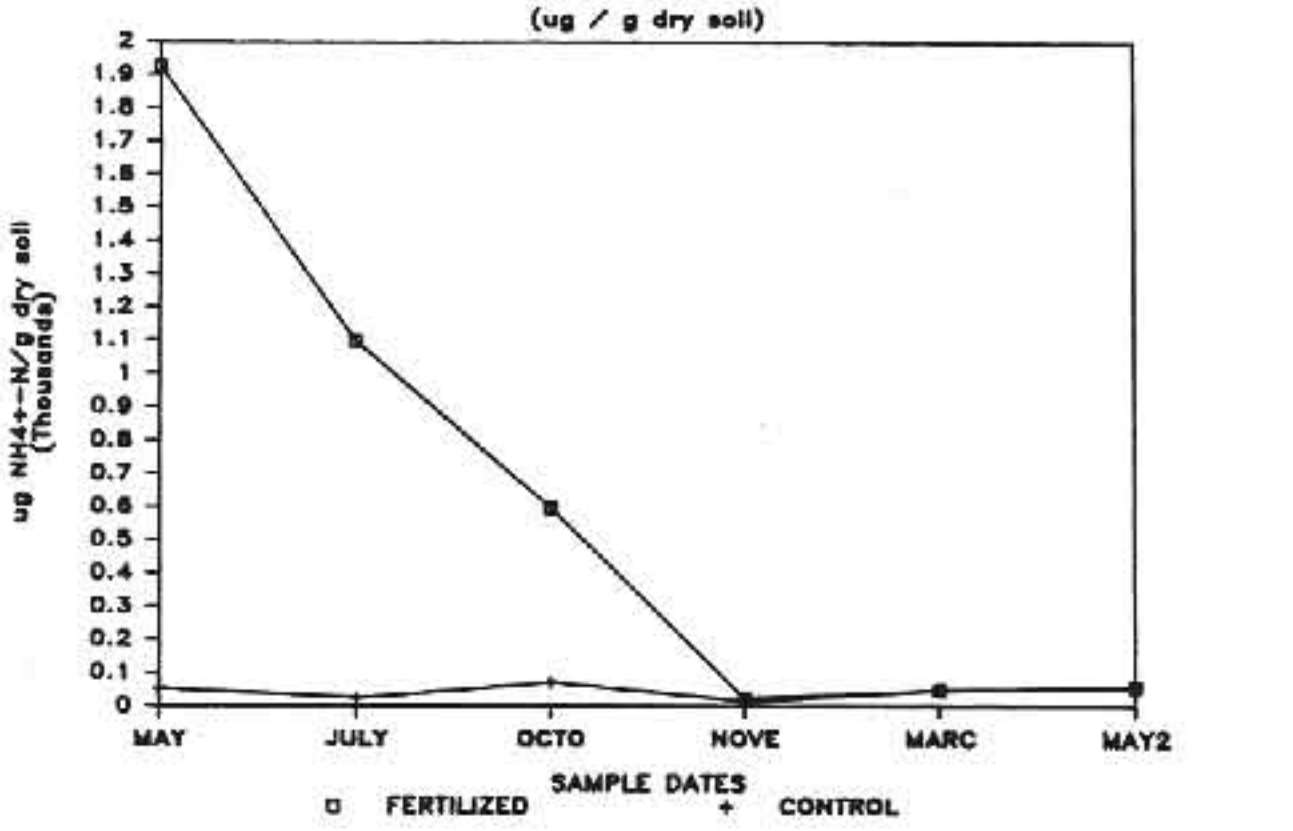
B horizons in fertilized plots, the percent tip biomass of total mycorrhizal biomass was 57% and 42%, respectively. These values were greater than those of the untreated plots, despite the fact that total root tips accounted for greater biomass in the untreated plots.

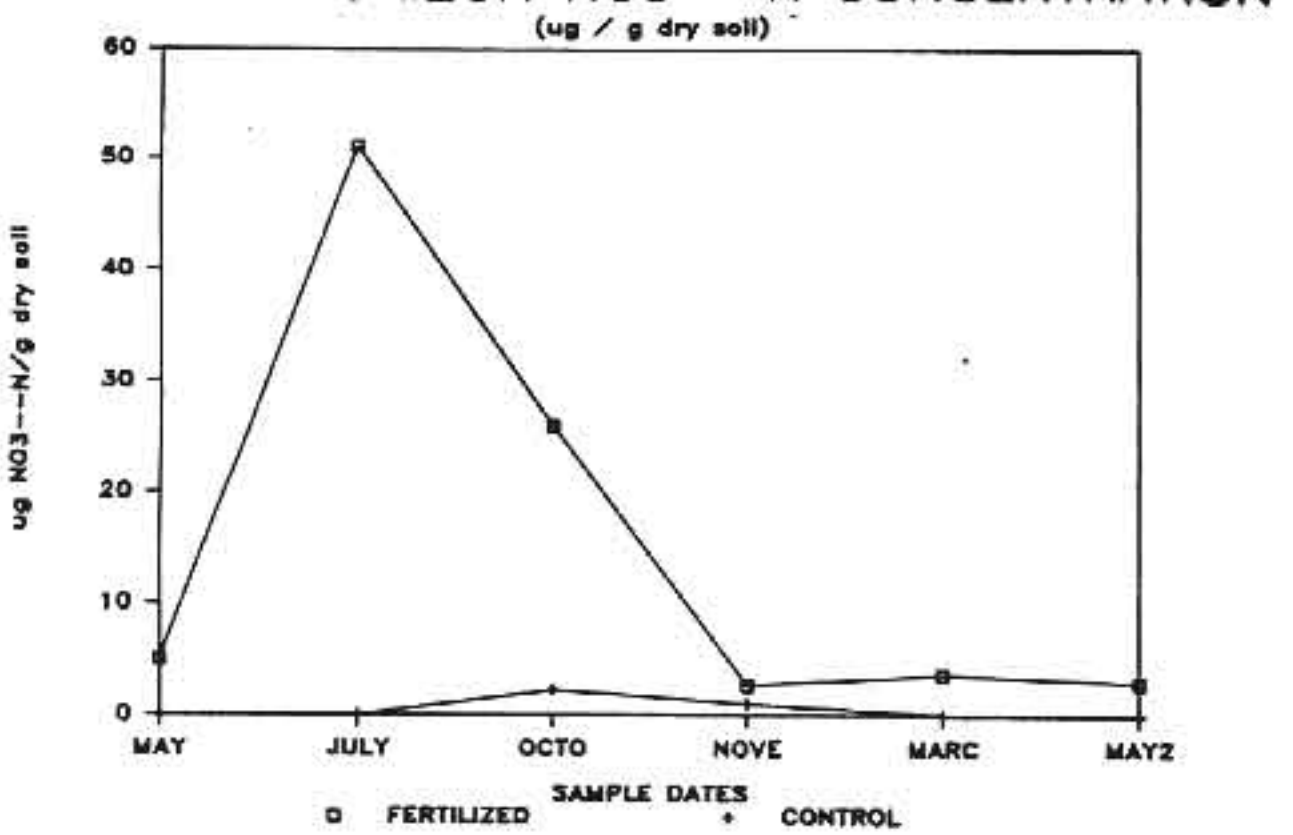
C. Available soil nitrogen

C.1. Forest floor Ammonium and Nitrate concentrations

Seasonal ammonium concentration changes in the litter layer comparing treatment and control plots are shown in Figure 23. The first (2 months after fertilization) and second (4 months after fertilization) samples of the litter layer collected after fertilization showed 98% more $NH_4^+ - N$ in treatment plots than in control plots (Fig. 23, $P < 0.05$). Eight months following fertilization, NH_4^+ concentration in the litter layer of treatment plots was still significantly greater than the control plots ($P < 0.10$). Thereafter, differences in $NH_4^+ - N$ values were not statistically significant.

Nitrate concentrations were not subject to statistical tests since most values were below the detection limits of the analytical procedure. Trends of $NO_3^- - N$ within the fertilized litter layer showed slightly





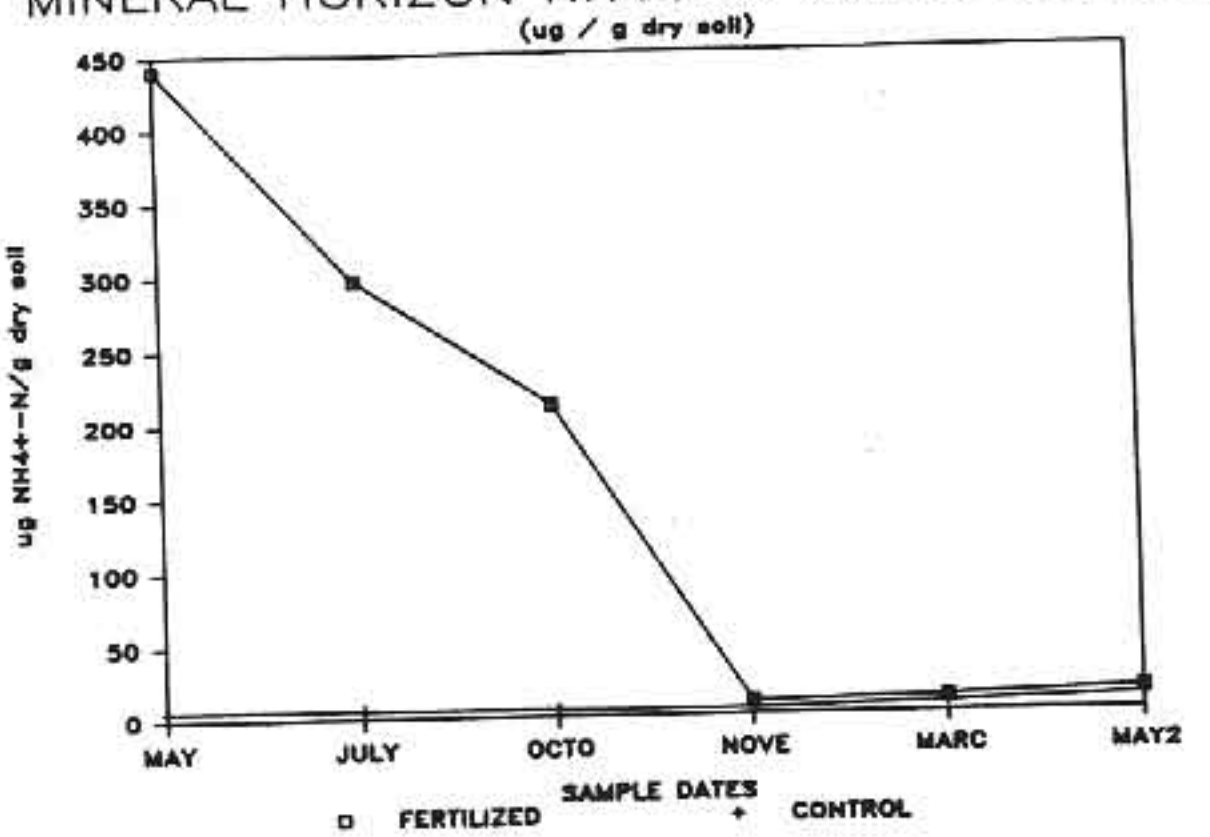
Figures 23a & 24b. Seasonal changes in organic horizon ammonium and nitrate concentration in the fertilized and control plots.

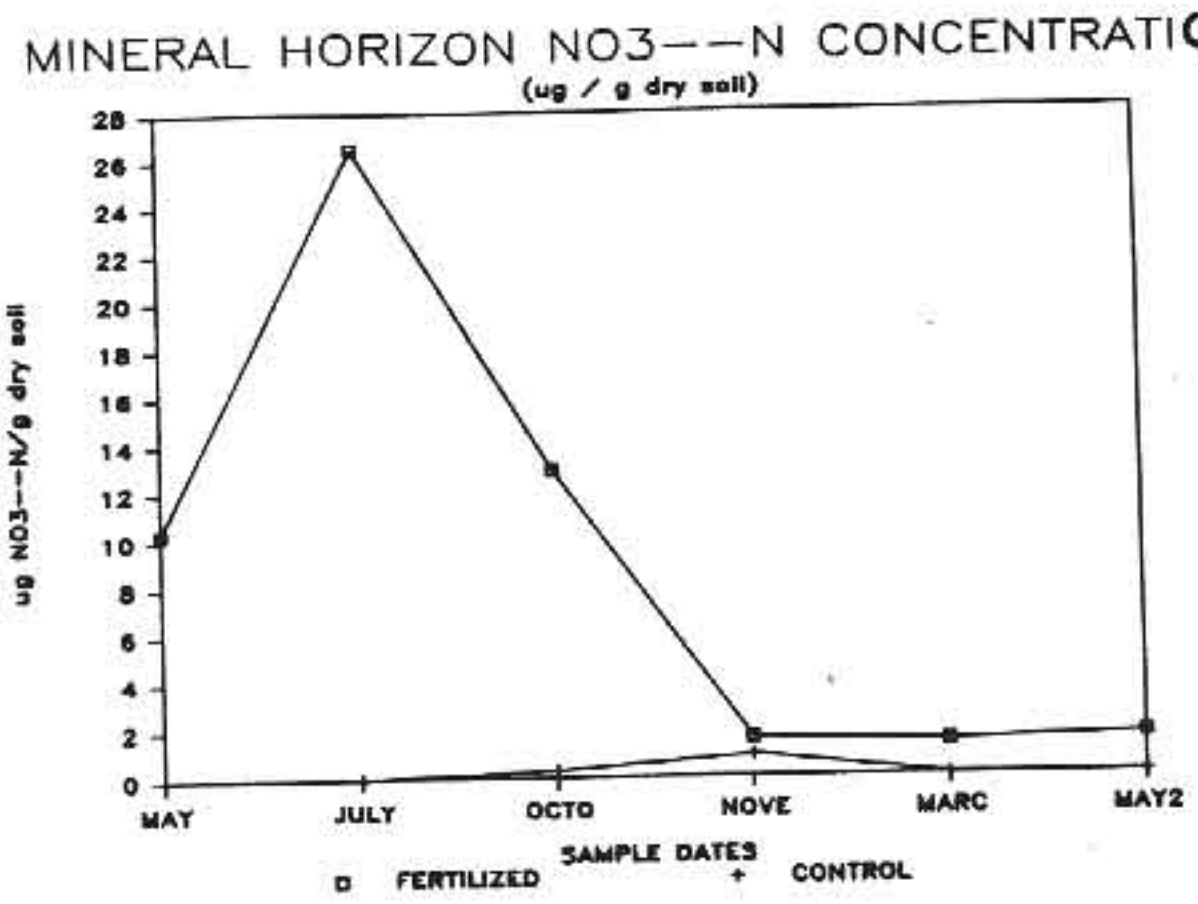
higher values until the November sample period, 9 months following treatment (Fig. 24).

C.2. Mineral soil Ammonium and Nitrate concentrations

Seasonal changes of ammonium concentrations in the mineral soil of treatment versus control plots are shown in Figure 25. Levels of $NH_4^+ - N$ in the mineral soil of treated plots remained 98% higher than controls for eight months following fertilization (Fig. 25, $P < 0.05$). Similar to the organic horizon differences in $NH_4^+ - N$ concentration between treatment and control became less pronounced after 8 months, however the differences were still significant ($P < 0.05$). More than one year following fertilization, soil of the treatment plots had 33% more available $NH_4^+ - N$ than that of the control plots ($P < 0.01$).

Nitrate concentrations in the mineral soil were similar to those in the organic horizons (Fig. 26). Soil of the treatment plots had a slightly higher $NO_3^- - N$ concentration than the soil of the control plots until November, but diverged during the March and May sampling (Fig. 26).





Figures 25a & 26b. Seasonal changes in mineral soil ammonium and nitrate concentration in the fertilized and control plots.

C.3. Ammonium concentration among horizons

Organic horizon $NH_4^+ - N$ concentration in the fertilized plots remained 22-37% greater than mineral soil throughout the entire sample period ($P < .05$) Similarly, $NH_4^+ - N$ concentration in the organic horizon of the control plots was 9-29% greater than mineral soil between May 1984 and May 1985 (Table 11).

C.4. Soil moisture content

Soil moisture changes in the organic and A horizon closely reflected precipitation patterns between the months of May 1984 and May 1985. During this period statistical tests did not yield differences in moisture content between treated and control plots for either the O or A horizons. Yet, water content in the organic horizon remained between 190% and 370% higher than in the mineral soil. Much of this was due to differences in bulk density between forest floor and mineral soil. Despite these differences between horizons, plant available water was ample and was assumed not to be a growth limiting factor in this study.

Table 11. Ammonium concentration in organic (O) and mineral (A) horizons by sample period (u g NH_4^+ — N · g dry soil $^{-2}$).[a]

SAMPLE DATE	CONTROL PLOTS		FERTILIZED PLOTS	
1984	O horizon	A horizon	O horizon	A horizon
MAY	53.3 ± 5.9[b] * * *	6.0 ± 0.7	1925.9 ± 470.0 * *	440.1 ± 158.3
JULY	23.7 ± 1.4 * * *	5.5 ± 0.5	1099.2 ± 348.9 * *	296.0 ± 90.5
OCTOBER	71.9 ± 43.8	4.3 ± 0.7	599.2 ± 271.5	212.0 ± 67.2
NOVEMBER	14.1 ± 4.0 * *	4.1 ± 0.3	23.2 ± 6.2 * *	8.6 ± 1.3
MARCH	50.9 ± 12.6 * * *	6.9 ± 0.7	49.7 ± 7.2 * * *	10.8 ± 1.6
1985				
MAY	60.3 ± 6.5 * * *	9.9 ± 1.1	59.1 ± 3.2 * * *	14.8 ± 0.7

a values followed by * are significantly different ($P < 0.10$) between O and A horizons
values followed by * * are significantly different ($P < 0.05$) between O and A horizons
values followed by * * * are significantly different ($P < 0.01$) between O and A horizons.

b values presented as mean ± one standard error (n=12).

D. Above-ground biomass

Prior to fertilization, the control plots averaged 602.8 t ha^{-1} above-ground living biomass, while biomass of treatment plots averaged 501.6 t ha^{-1} (Table 12). In both groups of plots, the factors contributing most greatly to this estimate were stemwood, stembark, live branch, and total foliage biomass. The control plot contained 18% more stembark and total foliage biomass than the treatment group. This discrepancy may be due to stocking and tree diameter differences between the two plots.

Despite the fact that treatment plots contained 20% less total aboveground biomass than the control, the proportionate distribution of that biomass among components was approximately equal (Table 12). Stembark and total foliage, the greatest contributors to the total living biomass estimate, varied only 1-2% between treatment plots. New foliage and new twig component biomass contributed very little to overall total biomass and were similar for both treatment plots.

Above-ground living biomass, determined one year following fertilization, exhibited interesting trends. Total biomass for the control plots was estimated at 641.0 t t ha^{-1}, while treatment plots was estimated at 510.5 t

Table 12. Above-ground biomass on stand basis of control and treatment plots prior to fertilization - March, 1984.[a]

COMPONENT	CONTROL ($t\ ha^{-1}$)	% of total[a]	FERTILIZED ($t\ ha^{-1}$)	% of total[a]
STEM WOOD	381.0	63	318.9	64
STEM BARK	67.6	11	55.4	11
LIVE BRANCH	85.5	14	70.7	14
DEAD BRANCH	40.8		35.1	
TOTAL FOLIAGE	68.7	11	56.5	11
NEW FOLIAGE	10.9	2	9.3	2
NEW TWIGS	3.1	0.5	2.6	0.5
TOTAL LIVING	602.8		501.6	

a values presented as a percent of total living biomass.

ha^{-1} (Table 13). Similar to the pre-fertilization difference, the ratio between control and treatment remained fairly constant. The major differences in above-ground living biomass between treatment and control plots occurred in the proportionate contributions of the components.

The major difference between treatment and control plots was exhibited by the new foliage and new twig components (Table 13). In the fertilized group, new foliage represented 3% of the total aboveground living biomass versus 1% in the untreated group. This amounted to 30% more new foliage biomass than the control plots (16.7 t ha^{-1} and 11.6 t ha^{-1}, respectively). Similarly, new twigs in the fertilized plots had 41% more component biomass than in control plots (5.5 t ha^{-1} and 3.2 t ha^{-1}, respectively). Despite these dramatic differences, the increased new foliage and new twig biomass did not appreciably increase total biomass.

Absolute biomass values from both plots prior to and following fertilization may clarify the lack of potential differences due to fertilizer response. Total aboveground biomass increased only by 2% in the treatment plots. Conversely, biomass in the control plots increased by 5% in one year. The control plots contained larger diameter trees averaging 32.7 cm DBH while the treatment plots

Table 13. Above-ground biomass on stand basis of control and treatment plots following fertilization - March, 1985.[a]

COMPONENT	CONTROL ($t\ ha^{-1}$)	% of total[a]	FERTILIZED ($t\ ha^{-1}$)	% of total[a]
STEM WOOD	404.8	63	324.5	64
STEM BARK	72.0	11	56.5	11
LIVE BRANCH	91.0	14	72.0	14
DEAD BRANCH	43.2		35.7	
TOTAL FOLIAGE	73.2	11	57.6	11
NEW FOLIAGE	11.6	2	16.7	3
NEW TWIGS	3.2	0.5	5.5	1
TOTAL LIVING	641.0		510.5	

a values presented as a percent of total living biomass.

trees averaged 27.5 cm DBH. The greater size and number of dominant trees in the control plots had greater competitive potential for native resources. A difference of 5cm, used in established regression equations to estimate component biomass, will cause substantial variation in total biomass.

The estimate of aboveground biomass increment shows the importance of new foliage and new twig biomass following fertilization (Table 14). New foliage biomass increment in treated plots (7.4 t ha^{-1}) was 97% greater than in control plots (0.2 t ha^{-1}). Also, the new twig component had 98% more biomass increment in the fertilized plots (2.8 t ha^{-1}) than in the control plots (0.1 t ha^{-1}). These differences were reflected in the decreased biomass increment of all other components of the fertilized group.

Table 14. Above-ground biomass increment on stand basis of control and treatment plots (t ha^{-1})(T_o (1985)- T_1 (1984)).[a]

COMPONENT	CONTROL (t ha^{-1})	% of total[a]	FERTILIZED (t ha^{-1})	% of total
STEM WOOD	7.7 ± 1.4[b]	60	5.6 ± 1.3	29
STEM BARK	1.5 ± 0.3	12	1.1 ± 0.2	6
LIVE BRANCH	1.8 ± 0.3	14	1.3 ± 0.3	7
DEAD BRANCH	0.7 ± 0.1		0.5 ± 0.1	
TOTAL FOLIAGE	1.5 ± 0.3	12	1.1 ± 0.2	6
NEW FOLIAGE	0.2 ± 0.0	2	7.4 ± 1.3	38
NEW TWIGS	0.1 ± 0.0	1	2.8 ± 0.5	15
TOTAL LIVING	12.8 ± 2.6		19.3 ± 3.9	

a values presented as percent of living biomass.
b values presented as mean ± one standard error (n=71).

CHAPTER 5

DISCUSSION

Nitrogen fertilization studies have been conducted in Douglas-fir stands of varying ages (Archibald, 1983; Brix, 1971; Shumway and Atkinson, 1978). Despite all of the available information on above-ground growth response, little attention has been paid to below-ground fertilizer response of fine roots and mycorrhizae. In an effort to completely characterize the response of a system, it is important to estimate below-ground biomass production. With information from both above- and below-ground components, the topic of carbon allocation can be addressed. In this study, root biomass of a second-growth Douglas-fir stand was examined in relation to nutrient availability. Nitrogen fertilizer in the form of urea prills was added to the treatment plots. Prior to and four months following fertilization, root biomass samples were collected. The overall objective of this study was

to document short-term shifts in both above- and below-ground biomass in response to nitrogen amendment.

5.2 BELOWGROUND BIOMASS

5.2.1 Pre-fertilization biomass

Due to inherent ecological and structural differences between stands, as well as a lack of established sampling convention, one must proceed cautiously when directly comparing biomass information. Investigations of Douglas-fir fine root and mycorrhizal biomass have yielded a range of values. An old-growth Douglas-fir stand in the Oregon Cascades was estimated to have a small root (< 10mm) biomass of 11.3 t ha^{-1}. (Santantonio et al. 1977). The samples for this study were collected in late summer. While no climatic information was given, Waring and Franklin (1979) have documented extensive mid-summer droughts for that area. This may have resulted in lower biomass values. Fogel and Hunt (1983) determined fine root (< 5mm) biomass of a 35-50-year-old Douglas-fir stand in the Coast Range of Oregon to range from 3.2 t ha^{-1} and 6.7 t ha^{-1}. They interpreted the lower value to have been due to the severe summer drought during the first sampling season (Fogel and Hunt, 1983).

Comparisons of fine root (< 2mm) biomass between different aged low site quality Douglas-fir stands of the Washington Cascades have yielded values ranging from 0.23 t ha^{-1} to 4.19 t ha^{-1} for 11- and 163-year-old stands, respectively (Vogt et al. 1983). The increases in below-ground biomass in the low productivity stands were most dramatic at canopy closure. A study of the interactions of site and climatic factors on low site quality, second-growth Douglas-fir fine root (< 2mm) biomass yielded an average value of 5.9 t ha^{-1} (Keyes and Grier, 1981). Based on the findings of Keyes and Grier (1981), pre-fertilization root sampling for this study was conducted during a period of root maintenance. The stand was found to have 3.6 t ha^{-1} fine root and mycorrhizal biomass. This value was less than the 4.7 t ha^{-1} found in the 67-year-old , low site Douglas-fir stand by Vogt et al. (1983), yet it falls within the established range for this species. Roots infected by mycorrhizal fungi were dominant in every horizon. They accounted for 75-79% of roots in the A and organic horizons but were slightly less important in the B horizon. Studies have documented increased occurrences of infected, short roots in stands of low nutrient status (Bowen, 1984; Head, 1973; Lyr and Hoffman, 1967). Thus mycorrhizae distribution within the profile compares well with the established levels.

Distribution within the profile on an area basis showed the greatest root mass to be in the B horizon. This is in contrast with results of many other studies (Deans, 1979; Grier et al. 1982; McClaugherty et al. 1982; Squire et al. 1978; Vogt et al. 1981), which indicate that root mass decreases with increasing soil depth. During the winter sample period, elevated precipitation levels and low soil and ambiant temperatures, may have caused either higher mortality or lower regrowth rates of roots in the upper horizons of a soil profile (McClaugherty et al. 1982). Yet with depth, root mortality rates may be more constant (Keyes and Grier, 1981; Bowen, 1984). As root necromass was not determined, it is not possible to test this assumption.

Comparisons of area based root occupancy between horizons can lead to erroneous conclusions. The greater thickness of the B horizon offered a considerably greater volume for root growth. Root density may allow for a more realistic representation of the exploitation of the soil layers (Kimmins and Hawkes, 1978). It was evident, when viewed on a volume basis, that root occupancy within the B horizon did not constitute major space utilization. Thus, density measures corresponded with previously observed patterns of decreasing root density with increased horizon depth. In order to compete for available nutrients with

soil microorganisms, trees may have to invest larger energy allotments to roots in the organically enriched O and A horizons.

The high density of < 1mm mycorrhizal and 1-5mm angiosperm roots in the organic horizon posed an interesting situation. While understory roots were 18% less abundant than conifer fine roots, they may compete with conifer roots for available nutrients. The high occupancy of conifer short roots in the organic horizon may have acted to enhance water and mineral uptake for the tree. Althought maintenance of fine roots and mycorrhizae is an "expense" for the tree, the expenditure may prove to be a competitive advantage over underatory angiosperms (Janos, 1985).

The dominance by larger conifer roots in the A horizon (with slower turnover rates, Vogt et al. 1982), may have been a means of decreasing the energy investment in the potentially less competitive soil zone. McClaugherty et al. (1982) determined the greatest live fine root biomass (< 3mm) to occur in the mineral soil between 0-15 cm in a red pine plantation.

5.2.2 Post-fertilization root biomass

According to Keyes and Grier (1981), seasonality was associated with the live fine root and mycorrhizal biomass on the low productivity site. In this present study, total roots in the A horizon of the control plots were significantly greater in June than in March. Peak fine root biomass of Douglas-fir growing in western Washington has been shown to occur in June/July (Keyes, 1979), thus significantly higher values in June were expected. Infected conifer and angiosperm roots constituted the majority of the June increase. A trend was seen with a shift in root biomass from the B horizon in March, into the A horizon in June. A similar shift was documented in a Pacific silver-fir stand during the summer growing season (Vogt et al. 1982). This may have been in response to the naturally occurring peaks of available nutrients and increasing soil temperatures (McClaugherty et al. 1982; Persson, 1981; Theodorou and Bowen, 1971; Vogt, 1985, personal communication).

Within the treatment plots, root biomass values did not vary between the two sample periods. In June, the most active component, mycorrhizal roots, (Linder and Rook, 1984) remained at virtually the same level as in March suggesting that the nitrogen amendment had affected

this below-ground component. Comparisons of root biomass between treatment and control plots during the second sample period lent further support to the hypothesis of a nitrogen fertilization effect on fine root and mycorrhizal biomass.

Root growth response to fertilization can occur in a variety of ways. A significant difference between fertilized and control plots of total root biomass within the entire rooting zone was seen in this study. This finding was supported by Alexander's (1985) assertion that patterns of fine root and mycorrhizae distribution were imposed by substrate variation of either moisture or nutrient availability. Water and nutrients are supplied to the tree by the roots and mycorrhizae. Thus, limitation of one or more of the above components may determine how root distribution patterns would occurr (Alexander, 1985).

Strong contributors to the overall differences of root biomass between treatment and control plots were the < 1mm mycorrhizal conifer roots. Mycorrhizae have been shown to be a carbon drain on the tree (Melin, 1953), and researchers have asserted that when the association becomes superfluous, as in an excess of available nutrients, ectomycorrhizal occurrence decreases (Bowen, 1984). It has also been conjectured that an imposed

stress such as over-fertilization may impose mycorrhizal senescence (Fogel, 1980). Whatever the cause, the decrease in both biomass and density values of the < 1mm mycorrhzal size category was evident in all three horizons within only four months of fertilization. This finding exemplifies the dynamic nature of the mycorrhizal component.

In contrast to infected roots, all sizes of uninfected conifer roots in the fertilized plots increased slightly over those of control plots. It is not possible to speculate on the cause of the elevated levels. This component accounted for less than 20% of total root biomass for either treatment plots. This may have been indicative of the minor role played by uninfected roots in this low productivity site in competition for soil water and nutrients. The low nutrient status of the site may have favored the infection by mycorrhizal fungi over long-root growth and nutrient absorption by root hairs (Alexander, 1985).

Understory plants can compete with tree crops for available nutrients and water. In this study, angiosperm roots decreased significantly with fertilization, dropping from 22% of total root biomass in the control plots to only 13% of total root biomass in the treated plots. Also, a dramatic shift in the root occupancy was observed.

Greatest density shifted from the O horizon in the control plots to the B horizon in the treated plots. Understory angiosperms, once thought to be shallow rooting plants, appear to be negatively effected by nutrient amendment as indicated by the dramatic decrease in their root biomass in the O and A horizons of the treated plots. No significant increases of above-ground understory biomass was seem with fertilization. Based on these findings, it appears that the angiosperms were not a strong competitive presence, and that they were not able to benefit from the fertilization.

5.2.3 Conifer root tips

The observed decreases in root biomass with fertilization imply shifts in energy expenditure from below- to above-ground biomass production. Yet, biomass values alone did not give information on how nutrient amendments might have decreased carbon costs or affected nutrient uptake. Root tip counts are sensitive indicators of soil properties for forest trees, and directly address the question of absorption capacity of root systems (Farrell and Leaf, 1974; Kimmins and Hawkes, 1978). Comparisons of infected versus uninfected conifer root tips can indicate root growth as a response to

fertilization (Ericsson and Persson, 1980).

Within the control plots, on an area basis, all root tip categories were dominant in the A horizon and were 57% more abundant than in the B horizon. This agreed with the dogma of the greatest root tip occupancy in the top 15cm of a soil profile (Farrell and Leaf, 1974). With fertilization, root tips per square meter significantly decreased in the A horizon, and dominance of different color types became scattered among the 3 horizons. It is not possible to explain this phenomenon, particularly when Meyer and Göttsche (1971) suggested that root tips in the profile became more evenly distributed with enhanced site conditions.

It has been stated that there is a low probability of altering types of mycorrhizae in forest plantations (Mikola, 1973). In this study, two categories of mycorrhizal fungi decreased significantly with fertilization. This suggests that fertilization may be used to modify mycorrhizal species. Other studies documented decreased root tip numbers with fertilizer treatments (Alexander and Fairley, 1983; Farrell and Leaf, 1974; Menge et al. 1977; Gill and Lavender, 1983). Two tip categories, "nocolor" and white mycorrhizal type decreased with fertilization. These types may have been well suited to the nitrogen limiting status of the site.

Some aspect of nutrient amendment may have adversely affected these types, causing their reduction. A hypothesis for the decrease of root tips proposed that rapid senescence and subsequent decomposition of roots may be promoted with fertilization (Farrell and Leaf, 1974). It is stated that mycorrhizal infection can enhance the longevity of fine roots (Harley, 1959), thus, this decrease may be attributable to an increase in root tip mortality.

The results of the "nocolor" category can be compared to the findings of Ericsson and Persson (1980). They documented that only 3% of the total root tip numbers were uninfected by mycorrhizal fungi for both treatment and control groups. Thus, on this nutrient limited site, mycorrhizal roots predominated (Ericsson and Persson, 1980). The present study with Douglas-fir found "nocolor" (a form of uninfected tip) accounted for 12% of all tips in the entire profile in the control plots which decreaseed to 7% after fertilization. If, after fertilization, the tree had reduced carbon allocation to the mycorrhizal component due to the infected fine roots being a greater carbon sink, then an increase in the "nocolor" should have occurred. Because "nocolor" tips were those that grew past the ruptured mantle of the mycorrhizal fungus that used to infect the root tip, it is

not known whether they would become reinfected or would continue to grow as a conifer long-root in the light of heightened nutrient status. Based on the abundance and prevalence of mycorrhizal-forming fungi in the soil of this site, it is predicted that reinfection would occur with the return of available nitrogen levels to that of the control plots.

Within all horizons, the significant decrease of the "nocolor" and white mycorrhizal types with fertilization was accompanied by an increase in dominance (% occurrence) of the brown mycorrhizal type. Different mycorrhizae are thought to benefit trees differently in their uptake of water and nutrients (F. T. Last, 1985, personal communication; Bowen and Theodorou, 1967). I did not attempt to identify to species the separate mycorrhizal categories or determine their costs and benefits. Similarly, successional changes over time were not studied. Nevertheless, it was inferred that the brown mycorrhizal type, which was ubiquitous in all plots, may have been better able to adapt to the heightened nutrient status, and may have been more competitive than the other fungi. Perhaps the brown type was able to take up available forms of nitrogen at a low cost to the tree. In this way, its association would continue to be advantageous for tree growth (Alexander and Fairley,

1983). The understanding of why mycorrhizae either increase or decrease with fertilization is still in the nascent stages (Gill and Lavender, 1983; Menge et al. 1977), thus the effect on stand level function can only be speculated.

Root tip biomass was determined through the use of a mean tip dry weight estimate (Hunt and Fogel, 1985; Vogt et al. 1983). The tip biomass values were similar to those of the < 1mm mycorrhizal category in that they were dominant in the A horizon of both treatment and control plots. The proportion of tip biomass to total mycorrhizal biomass within the entire rooting zone was approximately equal for both treatment and control plots. Yet, in each horizon, root tips were strongly affected by fertilization. This is supported by the dramatic decrease of the proportion of tip biomass to total mycorrhizal biomass in the organic horizon of the treatment plots. Fungal types in the O horizon, characterized by low nutrient availability, may be adversely effected by a large influx of available nitrogen. This may explain the drop in tips per gram of mycorrhizal root biomass.

Comparisons of root tip density values and tip numbers on an area basis presented two different patterns. Despite overall decreases in both indices with fertilization, tip density remained dominant in the

organic horizon of the treatment plots. This dominance in the organic horizon may have indicated continued exploitation of the substrate in competition with the soil microflora (Alexander and Fairley, 1983). It is known that microbial activity is high in this horizon (Alexander, 1977), and that nitrogen can be readily immobilized in the A horizon for both treatment and control plots. These findings indicated the importance of standardization of root tip measures for ecosystem level research.

The abundance of root tip density in the organic horizon of both treatment and control plots agreed with the findings of the mycorrhizal (< 1mm) weight per volume determinations. Evidently, after four months of increased nutrient status, the trees continued to invest in mycorrhizae in the litter layer, albeit not as much as in the control group. It is not known whether time will show further deterioration of the mycorrhizal association. Gill and Lavender (1983) suggested that the relative proportions of mycorrhizal types associated with urea fertilized western hemlock persisted longer than the reduction in total mycorrhizal tips. Despite these findings, the bearing of western hemlock fertilizer response on that of Douglas-fir may not be direct.

5.3 Nitrogen availability following fertilization

Urea prill in a forest soil has the potential to be transformed, taken up by the biological occupants of the soil or lost from the system. It is difficult to predict how a nitrogen amendment will be affected by any of the above three processes. Many biotic and abiotic factors determine the route and fate of a nitrogen amendment (Heilman, 1974; Crane, 1972; Johnson, 1979). And in a forest stand, the intended recipients, the trees, may be at a disadvantage for immediate utilization of nitrogen supplied in the form of urea (Johnson et al. 1980). On the other hand, it has been proposed that established forests will take up available nutrients in excess of immediate requirements (Miller, 1984).

Nitrogen was supplied at a rate of 448 kg N ha^{-1} in this study in an attempt to assure that after the distribution among the many competing fractions, there would be an appreciable amount left for plant uptake. This nitrogen amendment had the potential to increase the amount of nutrient diffusing to the root through an increase in the concentration gradient (Barber, 1974). While no mineralization, immobilization, or leaching studies were conducted following fertilization, available ammonium and nitrate increased after fertilization.

Ammonium concentrations in both the litter layer and mineral soil of the treated plots remained elevated above the controls for 8-12 months following fertilization. This effect lasted much longer than the five months reported by Johnson et al. (1980). A possible cause has been put forth by Bledsoe and Rygiewicz (1985) that the acidic nature of northwestern forest soils acts to reduce mineralization rates. This nutrient deficient site may have had inadequate soil microfloral populations to successfully compete for the large input of inorganic nitrogen (Dangerfield & Brix, 1979), thus allowing for a prolonged increased ammonium concentration.

Ammonium concentrations in the organic layer of the fertilizer plots returned abruptly to control levels at the time of autumn litterfall. At this time an upsurgance of microflora may have occurred in response to increased carbon. This increased carbon might be expected to immobilize nitrogen through microbial uptake (Alexander, 1977). Also, nitrogen could have become bound to decay resistant biomass (Johnson, 1979). Immobilization by microbes or adsorption on soil exchange sites could have been the cause of decreases in ammonium levels in the treated mineral soil. One explanation for the autumn decrease in the litter layer may be its tremendous number of exchange sites and a greater physical discontinuity

which acts to slow the transfer of nutrients (Bowen, 1984; Miller, 1984).

In both treatment and control plots available ammonium levels began to rise in March and continued into May. This is probably due to warming soil causing increased activity of microbial populations or increased decomposition activity (Alexander, 1977; Nadelhoffer et al. in press). Edmonds (1979) documented increased needle decomposition during the spring in a number of Douglas-fir stands with subsequent increases in nitrogen. The past years litterfall, replete with nutrients, could have liberated nitrogen at this time. This slight increase of available nitrogen is confirmed by Miller et al. (1979). Whatever the cause, the trends observed in this study were clearly evident and statistically significant. It has been suggested that nutrient stressed, closed-canopy systems will strongly retain nutrients from fertilizer amendments within tree biomass (Miller and Miller, 1976; Miller, 1984)

Available nitrogen (NH_4^+ - N) differed significantly between horizons of both the treatment and control plots. Dangerfield and Brix (1979) suggested that most of the ammonium produced by ureolysis is immobilized in the humus layers. Differences were more pronounced in the control plots possibly due to less variation among replicate

samples. During the month of October, despite the fact that the organic horizon ammonium concentration was 35% and 6% greater that the A horizon in the fertilized and control plots, respectively, no statistically significant difference was found. It is known that mineralization is closely linked to both temperature and soil water content and can become retarded in cold, wet soils (Alexander, 1977; Tisdale et al. 1985). It appears as though the onset of winter rains and low temperature inhibited ureolysis during the month of October.

The results of the nitrate concentrations agreed with findings in the literature. Due to an initally small population size of nitrifying bacteria at the time of urea fertilization, low levels of NO_3^- - N formation have been encountered in forest soils (Crane, 1972; Heilman, 1974; Johnson et al. 1980; Nadelhoffer et al. in press). Trends of the NO_3^- - N concentrations in this study showed slightly increased levels in the fertilized plots in July and downward movement in October and November. In the control plots, NO_3^-—N levels began to increase in October and peaked in November. Alexander (1977) suggested that nitrate formation was most rapid in spring and autumn in temperate zone. Either NO_3^- - N was not produced in the spring (Dangerfield and Brix, 1979) or, as it is very susceptible to leaching, any indication of its formation

in the spring may have been outweighed by high rainfall causing increased movement through the soil profile or low nitrification in this system.

Presumably, available $NH_4^+ - N$ levels in the fertilized plots were quite high during the month of June, and probably were high immediately following fertilization. The enhancement of available nitrogen might be compared to an upgrading of the site index of the stand (Bengston, 1978). Or it can be likened to a change in the stand's successional status with an accumulation of nutrients in the litter layer (Gosz, 1984). Vogt et al. (1983) found considerably less conifer fine root and mycorrhizal biomass in the high site quality II Douglas-fir stand than in the lower productivity stands of similar ages. With increased stand age, the below-ground component was seen to decrease. Persson (1983) also documented a slower exploitation of the rooting space by mature stands than of younger stands. A substantial decrease in fine roots and mycorrhizae have been documented in the present study perhaps implying an acceleration of succession of the below-ground component to that of an older stand.

5.4. Above-ground response

Fertilizer growth response has been documented for low site quality Douglas-fir stands in the Pacific Northwest (Grier et al. 1984; Brix, 1983; Gessel et al. 1965; Shumway and Atkinson, 1978). In order to estimate above-ground fertilizer response without destructive analysis, one must use existing regression equations. Such equations allow for the determination of linear relationships of dry matter component biomass against DBH or the quadratic mean diameter (Husch et al. 1972). This study employed regressions calculated from data collected in a 23-year-old, site quality III Douglas-fir stand in western Washington. Archibald (1983) derived regression equations from fertilized and non-fertilized trees two years following treatment, and determined that fertilization had an effect of increasing basal area increment.

This study's above-ground biomass estimates, based on DBH, showed increased new foliage and new twig biomass with fertilization. This response has also been reported from other studies examining initial responses to fertilization (Brix, 1981a; Brix, 1983; Miller and Miller, 1976). In contrast to the increases in the new twig and foliage biomass, the major contributors to total above-

ground biomass increment decreased considerably. Thus a reapportionment of resources has already begun on this site. If such a response could be documented in just over one year after treatment, it seems reasonable to assume that increased growth would continue given that no other limiting factors prevailed. Similarly, if increased above-ground growth continued, fertilizer response could eventually be determined by direct measurement.

As this study only examined the short-term response to fertilization, one must infer the long-term pattern of growth. The magnitude of a urea fertilization response would be determined by the initial nutrient deficiency of the stand, light limitations and other site factors (Brix, 1983). It is known that this site has exhibited significant growth responses to a continuous fertilization regime (Appendix II). If light were not limiting, and the initial response of increased new foliage biomass increment and weight of older foliage continued up to maximum foliage production, the photosynthetic capacity and efficiency of the stand could be increased (Archibald, 1983; Brix, 1971; Linder and Rook, 1984). Another important longer-term effect of fertilization is enhanced competitive mortality (Shumway and Atkinson, 1978). The combination of the above two responses could lead to larger trees with accelerated above-ground biomass production.

Chapter 6

CONCLUSION

Significant decreases in mycorrhizal root and fine root biomass were observed only four months after nitrogen fertilization application to a 50-year-old Douglas-fir stand. The 35% decrease in total root biomass measured with fertilization occurred mainly with the < 1 mm mycorrhizal root and the < 5 mm angiosperm root categories. These two root categories showed decreases in both biomass and density values, suggesting decreasing occupancy of the environment by roots due to nitrogen fertilization. The decrease in biomass in the mycorrhizal category in response to fertilization may have been due to increased senescence (Fogel, 1980), or to a shift in energy expenditure by the tree once this very costly association was no longer needed (Bowen, 1984). The response of the angiosperm category to fertilization may have been due to its inability to compete with overstory roots for the additional nutrients (Janos, 1985), or to a

toxicity effect of urea prill application. Perhaps these results have some bearing on the ability of nutrient amendment to change the successional status of the site (Persson, 1983).

A significant decrease in conifer root tip biomass and density also occurred in response to short-term nitrogen fertilization. The greatest change in biomass and density was observed in the A horizon which also showed the highest proportional increase in availability of mineral nitrogen. It has been speculated that fertilization causes increased root tip mortality and subsequent root decomposition (Farrell and Leaf, 1974), which would account for the decreases observed in the A horizon since the forest floor was shallow in these sites. Fertilization also resulted in changes in the frequency of infection of root tips by specific mycorrhizal fungi and those classified as "nocolor" (root tip grown past the fungal infection zone). A decrease in the number of "nocolor" root tips measured after fertilization contributed substantially to the overall decline in root tip biomass and density. Since this category represents the potential for additional mycorrhizal fungal infection of root tips, a decrease in the number of sites for infection may occur leading to a decrease in mycorrhizal symbiosis. These findings raise questions of how nutrient

amendments alter root tip morphology and the eventual infection of roots by mycorrhizal fungi over the long-term. In addition, the relationships between nutrient amendments and carbon allocation to roots and shoots needs to be investigated in a long-term study.

Fertilization also appeared to influence root distribution patterns within the soil profile. For instance, the zone of greatest root activity (measured as root biomass) shifted from from the B horizon in March to the A horizon in June in the control plots. In contrast, in the fertilized plots no vertical shift in root biomass dominance was observed four months after fertilization. It has been suggested that patterns of root distribution are related to changing soil temperature and nutrient availability (McClaugherty et al. 1982). Results from this study suggest that nitrogen additions may decrease seasonal shifts in the dominant zones of root activity in the soil horizons. This probably reflects the fact that nitrogen availability is more evenly distributed in a fertilized site and roots are not responding to seasonal changes in nitrogen availability by horizon.

Nitrogen fertilization increased new foliage and new twig biomass increment for Douglas-fir. These increases may reflect a reapportionment of carbon resources from the below-ground to the above-ground component following

fertilization. This study has interesting implications for long-term tree response to fertilization. If repeated fertilizer additions resulted in increased above-ground but decreased below-ground growth, then the improved photosynthetic capacity would be used to produce larger trees with accelerated above-ground biomass production at the expense of the below-ground component.

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Appendix I - Vegetation cover presented as a percent of total cover separated into life forms as determined in July, 1985 ((T) < 1 %).

PLANT SPECIES	% COVER	
	CONTROL	FERTILIZED
SHRUBS		
Gaultheria shallon Gray	67	45
Symphoricarpos albus (L.) Blake	3	1
Rosa gymnocarpa Nutt.	3	8
Rhamnus purshiana Esch.	1	1
Rubus ursinus Cham. & Schlecht.	4	1
Lonicera ciliosa (Pursh) Dc.	(T)	(T)
Vaccinium parvifolium Smith	(T)	1
Holodiscus discolor (Pursh.) Maxim.	0	1
Amelanchier alnifolia Nutt.	(T)	1
Symphoricarpos mollis Nutt.	0	(T)
TREE SEEDLINGS		
Tsuga heterophylla (Raf.) Sarg.	(T)	(T)
HERBS		
Linnaea borealis L.	6	23
Trientalis latifolia Fisch. Ex Hook.	(T)	(T)
Listera cordata (L.) R. Er.	(T)	(T)
Cornus canadensis L.	(T)	(T)
Campanula scouleri Hook. Ex. A. Dc.	(T)	(T)
Pyrola sp.	(T)	(T)
Galium sp.	(T)	(T)
Trillium ovatum Pursh.	(T)	(T)
Erythronium sp.	(T)	(T)
Polystichum munitum (Kaulf.) Presl.	(T)	(T)
Pteridium aquilinum (L.)	2	2
GRASS	0	(T)
MOSS	58	78

Appendix II - Net primary productivity of above-ground components and site description of installation # 55. Data compiled from Regional Forest Nutrition Research Project.

PARAMETERS		VALUES
Site index		94
Original stocking		640 - 1330
Precipitation		110"
Biomass increment (t/ha)	control	7.2
	fertilized	6.8
Mortality (t/ha)	control	2.2
	fertilized	5.3
NPP (t/ha/yr)	control	11.9
	fertilized	14.6

Appendix III - Understory biomass determined in July, 1985.

VEGETATION TYPE	BIOMASS (t/ha) control	fertilized
Herbs	0.07	0.11
Shrubs		
New leaves	0.24	0.17
New twigs	0.24	0.13
Old leaves	0.11	0.03
Old twigs	0.92	0.59
Dead leaves & twigs	0.13	0.04
Other	0.12	(T)
Total	1.76	0.96