AN ABSTRACT OF THE THESIS OF

Christopher A. Stockdale for the degree of Master of Science in Forest Science, presented on November 29, 2000. Title: Green-tree Retention and Ectomycorrhiza Legacies: The Spatial Influences of Retention Trees on Mycorrhiza Community Structure and Diversity.

Abstract approved: Signature redacted for privacy.

Daniel L. Luoma

These studies are part of the Demonstration of Ecosystem Management Options (DEMO) study, a program researching the effects of different levels and patterns of green-tree retention on ecological, economic, and social phenomena. We restricted our studies to the 15% basal area, evenly dispersed retention treatment. Our objectives were, first, to quantify the change in ectomycorrhiza (EM) type richness after treatment. Second, to determine if changes in EM type richness depended on proximity to retention trees by quantifying EM type richness and root density at four distance classes from retention trees. Third, to determine the relationship between photosynthetic potential of retention trees (measured by cross-sectional sapwood area), root density, and EM type richness. Finally, to determine the effects of retention-tree productivity, root density, and distance from host tree on EM community structure. Three sites (blocks) of the DEMO study were used: Hamilton Buttes, Dog Prairie, and Watson Falls. Pretreatment samples were taken between one and three years before thinning. Post-treatment samples were collected within two years of the thinning. Ectomycorrhizae were sampled using 5.5 cm diameter by 15 cm deep soil cores and identified by morphotyping techniques. We found a significant reduction in EM type richness as a result of the thinning treatment. Within the dripline of retention trees, however, there was no significant decline in the number of EM types. In areas removed from trees, there was up to a 50% decline in the mean number of EM types per soil core. Samples within the dripline and at the edge of the dripline (host-tree samples) had no significant differences in EM type richness or community structure when compared to each other. When host-tree samples were compared to soil cores taken just outside the dripline and in open areas, significantly

lower EM type richness was detected, as was a shift in overall community structure. Ectomycorrhiza type richness was found to be significantly and positively correlated with fine-root tip density. Sapwood area of retention trees had no significant correlations with root density, EM type richness, or community structure. The community structure of EM, in terms of relative abundance, most closely followed the log-normal distribution. In the outside dripline soil cores, there were very few rare types observed, suggesting that the probability of an EM type being lost was linked with its pre-disturbance abundance and the loss of the host tree. *Cenococcum geophilum* was the most abundant EM type, accounting for 18.7% of EM tips, and occurring in nearly all samples. Retention trees serve as important refugia for EM. This biological legacy from the pre-disturbance stand may be important for recolonization of EM onto new seedlings. For those EM that are lost from these treatment units, early recolonization may occur from the spore bank or wind dispersal. Over time, hypogeous fruiting species and those adapted to conditions in a mature forest may re-colonize from neighboring forest stands, provided the distance to the edge of reserve areas is not too great for effective spore dispersal.

Green-tree Retention and Ectomycorrhiza Legacies:
The Spatial Influences of Retention Trees
on Mycorrhiza Community Structure and Diversity

By
Christopher A. Stockdale

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Christopher A. Stockdale, Author

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CHAPTER 1
INTRODUCTION

The Pacific Northwest coniferous forests are home to the highest diversity of tree species found in the west of the continent. The Cascade mountain range is within a belt containing the highest number of species within this zone, with approximately 80 species of coniferous and deciduous trees (Currie and Paquin, 1987). Intensive management of forest resources in this region dates back roughly a century. In this time, some of the forest has been converted to agricultural land, and many forests are characterized by even-aged stands dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) less than 100 years old (Franklin, 1988). The forest ecosystem is vital to hydrological processes which in turn regulate the climate in the region, and in turn influence the global climate. In addition to their importance in hydrological cycles, forests are vital to global carbon cycles. Forestry practices of the past century have changed the forests of the Pacific Northwest from a net carbon sink into a net carbon source (Harmon *et al.*, 1990). Although old-growth forests contain few endemic species that can not be found in mature successional forests, many managed forests are harvested before reaching an adequate state of maturity to allow for the existence of many of these species (Carey, 1998). The ecological implications include a potentially huge loss of biodiversity.

Ecological stability has been strongly linked to its diversity, be it biological or structural (Pimm, 1991). It is no longer adequate to set aside preserves for wilderness whilst harvesting the managed areas with impunity (Franklin, 1988; Franklin *et al.*, 1989). Human population growth and economic growth are

demanding an ever-increasing land base, encroaching into wilderness preserves bit by bit, and increasing the pressures placed on our managed lands. As such, there is great concern that we need to manage our forests in ways that maintain a diverse array of ecological elements and functions. The amount of biological diversity that has been lost through past practices is unknown, as a great deal of the existing diversity still has not been catalogued.

Conducting long-term, large-scale research on the effects of management practices on biological diversity is no easy task. Considerable resistance can be encountered in resource dependent communities when biologists propose these kinds of studies. Conflict between resource-extraction interests, recreational values, aesthetics, and concerns for ecological sustainability came to a head in the Pacific Northwest region of the United States in the 1980's, providing the impetus for research into timber harvesting that offered alternatives to clearcut logging. Environmental concerns of the general public and members of the scientific community, combined with the legal mandates carried by the Endangered Species Act led to the implementation of the Northwest Forest Plan (NWFP)(USDA, 1994; USDA and USDI, 1994). The need to provide habitat for the Northern Spotted Owl, an old-growth dependent species, was one factor leading to recommendations in the NWFP for retention of a minimum of 15% tree basal area (BA) in harvest units to facilitate the development of uneven-aged stands. This silvicultural prescription was considered to be an improvement over traditional methods of clearcutting for accelerating the development old-growth type structure in managed forests. Although it is widely believed that retention harvests confer many ecological benefits to Pacific Northwest forest ecosystems, the level and pattern of retention that are most effective is unknown, and according to Franklin *et al* (1999), there was little scientific basis for this particular prescription.

The studies undertaken in this thesis are a part of a larger study involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic and social phenomena: the Demonstration of Ecosystem Management Options (DEMO) study (Aubry *et al.*, 1999). One of the

treatments of the study replicates one of the components of the Northwest Forest Plan: 15% dispersed green-tree retention. This gives ecologists and managers the opportunity to test the effectiveness of this aspect of the plan, in addition to the many other hypotheses being tested within the context of the DEMO study (Aubry *et al.*, 1999). In one of the sociological experiments of the DEMO study, members of the public were shown pictures of the 15% BA dispersed retention treatment. There was no significant difference in their perception of this treatment and a full clearcut, both of which were negative. When people were then told that the trees were left to provide environmental benefits, there was a marked improvement in their rating of this treatment as compared to a total clearcut (Ribe, 1999). Given this response, we felt the need to provide more specific information regarding the impact of a 15% BA, evenly dispersed green-tree retention harvest on the diversity and community structure of ectomycorrhizal fungi (hereafter referred to as EMF).

Mycorrhizal fungi live in a symbiotic relationship with the roots of many plants. They supply the plant with inorganic nutrients in exchange for photosynthesized carbon. There is considerable variety in the form that mycorrhizae take, ranging from endomycorrhizae (vesicular-arbuscular) which penetrate the cell walls of the fine roots of the plant, to ectomycorrhizae which envelope the root in a structure called a mantle, with fungal tissue penetrating the surface of the root and surrounding the cells in the cortex of the root with a Hartig net, but not penetrating the cell walls (Allen, 1991). Several plant families form mycorrhizae that exhibit structures intermediate between the ecto- and endo- forms. These include the ericoid, arbutoid, and monotropoid forms (within the Ericaceae), and the orchidaceous (Orchidaceae) form. Other ectendo- types also exist. Within the Pinaceae, Fagaceae, and Betulaceae, ectomycorrhizae predominate. Ectomycorrhizae can confer a variety of benefits to the host plant (Brownlee *et al.*, 1983; Newman, 1988; Perry *et al.*, 1987; Read, 1991; Read *et al.*, 1985). Although testing the benefits of EMF in natural settings is difficult, laboratory and nursery studies show that most mycorrhizal plants have a growth advantage over those that are not mycorrhizal (Allen, 1991). Drought-stressed plants demonstrate the ability

to tolerate lower water potentials when they possess certain EMF partners (Parke *et al.*, 1993; Pederson and Sylvia, 1996). Other EMF types have been shown to give seedlings the ability to live in harsh environments where they would otherwise be unable to survive (Lee and Koo, 1983). EMF also mediate interactions between plants in several ways. They allow trees to compete for resources with herbs and grasses through acquisition of nutrients and detoxification of allelochemicals produced by these competitors (Perry and Choquette, 1987). EMF also have been shown to act as conduits for transfer of material and nutrients between trees intra- and interspecifically (Brownlee *et al.*, 1983; Read *et al.*, 1985).

It is suspected that each EMF's ecological role is quite specific and tree root systems are thus occupied by many different mycorrhizal fungi to broaden their tolerance of environmental conditions (Lee and Koo, 1983; Molina and Amaranthus, 1990; Pederson and Sylvia, 1996). Indeed, studies have shown that mycorrhizae demonstrate high beta diversity (Goodman and Trofymow, 1998; Luoma *et al.*, 1997), lending support to the idea that they may be adapted to very specific conditions (Bruns, 1995). When forests are logged, the amount and diversity of mycorrhizal fungi can be significantly reduced within two years (Parke *et al.*, 1984; Perry and Rose, 1983). Few studies have examined the effects of partial cutting (green-tree retention harvests) on the diversity of EMF.

There are inherent difficulties in researching community-level aspects of EMF ecology. Foremost among these is the problem of identification. By 1930, descriptions were being published with morphological and anatomical features of many EMF (Hacskaylo, 1983); however, the categories by which they were grouped were very broad. Since this time, descriptions have become more detailed and the groups within which particular types are categorized are better defined (Agerer, 1991, 1995). Even still, categories of EMF based on macroscopic and microscopic features (EM types) are broad, and rarely allow us to determine the species of the fungus involved, as classical species concepts in fungi are based on reproductive structures. There are, however, several ways by which EM types can be definitively identified (Agerer, 1995; Ingleby *et al.*, 1990; Trappe, 1967): (i)

physically linking them to their sporocarps, (ii) comparing them to previously identified specimens, or (iii) using characteristics established in sporocarp identification. Recently, there has been a shift to focusing on molecular identification by DNA analysis, and building sequence databases for comparisons (Bruns *et al.*, 1998; Gardes *et al.*, 1991; Eberhart and Luoma, 1997a, b).

Assignment of particular EM types to a fungal species may be accomplished by tracing mycelium from the roots of trees to the sporocarps of the fungi in order to determine their identity (Agerer *et al.*, 1996b). This type of work is very labour-intensive, and for extensive ecological studies may be impractical. This method is limited also by the temporal variability of the presence of sporocarps: many fungi fruit only seasonally, and some only every few years (Arnolds, 1981; Luoma, 1991). Many mycorrhizal fungi also lack conspicuous, readily identifiable, fruiting bodies.

Early morphological descriptions of EM tended to examine microscopic features in cross-section, and provided limited detail. Plan views of the mantle, however, which describe the organization of the mantle tissue are much more descriptive. Adding descriptions of associated hyphae and strands, in addition to the macroscopic features can provide a great deal of information (Agerer, 1995; Trappe, 1967; Zak, 1973). These sorts of descriptions have been used to study EMF populations on inoculated plants by several researchers (Haug and Oberwinkler, 1987; Ingleby *et al.*, 1990). EM types described in this fashion have been shown to vary less intrataxonomically than they do intertaxonomically (Agerer, 1986; Agerer *et al.*, 1996a).

Although it is rarely possible to assign a species to an EM type by its morphological description, these sorts of descriptions are useful when species richness is the primary response of interest. One study comparing morphological classification (by a biologist without taxonomic training) and taxonomic classification methods (by a taxonomic professional) in insects showed that although several individual species were divided into erroneous multiple species, this was offset by many species complexes being lumped together (Oliver and

Beattie, 1996). Although this type of information would not be accurate to use for producing species lists, it was shown that there was no significant difference between the diversity indices calculated from these two methods of identification. The advantage to using morphological classification is the ability to process larger numbers of samples, which has been one of the most significant obstacles to answering many questions regarding mycorrhizal ecology. In combination with molecular analysis, morphological classification can provide us with a wealth of information.

The objectives of our studies were:

1) To determine if EM type richness declined due to the thinning treatment and, if so, to quantify this loss (Chapter 2).

2) To determine if there was a differential loss in EM type richness dependent upon the proximity of retention trees in the treatment unit (Chapter 2).

3) To determine the relationship between the photosynthetic potential of retention trees and their subsequent root density and EM type richness (Chapter 3).

4) To determine the distance from the retention trees at which EM type richness and root density begin to noticeably decline (Chapter 3).

5) To determine the effects of retention-tree productivity, root density and distance from the tree on the community structure of EMF (Chapter 3).

CHAPTER 2
CHANGES IN ECTOMYCORRHIZAL DIVERSITY FOLLOWING HEAVY THINNING IN DOUGLAS –FIR FORESTS, AND THE BUFFERING CAPACITY OF RETENTION TREES

Christopher A. Stockdale, and Daniel L. Luoma

ABSTRACT

There has been substantial research to demonstrate that both the diversity and inoculation potential of ectomycorrhizal fungi (EMF) declines within two years of clearcut harvesting. Less is known regarding the impacts on EMF of variable retention harvests which preserve living mature trees in the harvest unit. This study is a part of the Demonstration of Ecosystem Management Options (DEMO) study, an interdisciplinary program involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic and social phenomena. This study is restricted to one of the treatments of the DEMO study, 15% basal area evenly dispersed retention. The primary objective of this study was to determine if EM type richness declined due to the thinning treatment and, if so, to quantify this loss. Secondly, we wanted to determine if there was a differential loss in EM type richness dependent upon the proximity of retention trees in the treatment unit. Three sites within the DEMO study were used and treated as blocks. Within each site, a control and treatment unit were used. Samples were taken between one and three years pretreatment, and within two years posttreatment. Six permanent sampling points were used in each unit to determine the loss of EM type richness. Additional sampling points were established post-treatment to determine the differential retention of EM types by proximity to retention trees. EMF were identified by morphotyping techniques widely used in the literature. In the treated units, a total of 61 EM types were found prior to thinning, and this number was

reduced to 47 EM types after treatment, representing a net 23% loss in richness. There was a decline from 9.67 EM types per soil core pretreatment, to 6.55 EM types per soil core after treatment. Within the dripline of retention trees, however, there was no significant loss of EM types, but in areas sampled farthest from trees, there was a 50% decline in EM types per soil core. This study shows that retention trees can act as islands of refugia for EMF. These islands of biological legacy from the pre-disturbance stand may serve as multiple staging grounds for recolonization of EMF onto new seedlings being established. For those fungi that are lost from these treatment units, recolonization of some hypogeous and late-stage fungi (those that only associate with roots in mature forests) may occur from neighbouring forest stands, provided the distance to the center of the harvested area is not too great.

INTRODUCTION

Tree seedling growth and survival, and thus regeneration of the forest, ultimately depend upon ecosystem health. Plant-plant interactions and soil structure are two factors affecting the health of the seedlings: these factors depend on processes in the rhizosphere, which is the region of the soil profile immediately within the influence of roots (Perry *et al.*, 1987). In the Pacific Northwest, mycorrhizal fungi are symbiotic partners with the roots of most plants in the Pinaceae, Fagaceae and Betulaceae families. These families represent the majority of trees found in the region. The fungus translocates inorganic nutrients, principally nitrogen and phosphorous to the plant, and receives photosynthetically manufactured carbon compounds from the plant in return. Ectomycorrhizae (unlike other mycorrhizal types) envelope plant fine roots with fungal tissue, and penetrate between the cortex root cells, but not into the cell walls. Testing for the effects of ectomycorrhizal fungi (hereafter referred to as EMF) in natural settings is difficult, but in laboratory and nursery studies, most mycorrhizal plants have been shown to

be at a growth advantage over those that are not mycorrhizal (Allen, 1991). Drought-stressed plants demonstrate the ability to tolerate lower water potentials when they possess certain EMF partners (Parke *et al.*, 1983; Pederson and Sylvia, 1996). Other EMF types have been shown to give seedlings the ability to live in harsh environments where they would otherwise be unable to survive (Lee and Koo, 1983).

EMF also may play a role in mediating competitive interactions between different plants, and sometimes, plants that compete for aboveground resources prove to be allies when viewed in terms of their mycorrhizal associations (Perry *et al.*, 1987). EMF also mediate interactions between plants in several ways. They allow trees to compete for resources with herbs and grasses through acquisition of nutrients and detoxification of allelochemicals produced by these competitors (Perry and Choquette, 1987). EMF also have been shown to act as conduits for transfer of material and nutrients between trees intra- and interspecifically (Brownlee *et al.*, 1983; Read *et al.*, 1985, Simard *et al.*, 1997).

EMF exert a significant influence over ecosystem processes. Griffiths *et al.* (1991) found all seedlings of Douglas-fir in a 65-70 year old stand associated with the EMF species *Gautieria monticola* and *Hysterangium setchellii*. Concentrations of dissolved organic carbon (DOC), oxalate, phosphorus, sulfate, hydrogen ions, aluminum, iron, copper, magnesium, and zinc were significantly higher in the mats formed by these two EMF species than in soil not possessing these EMF mats (Griffiths *et al.*, 1994). *H. setchellii* has been shown to concentrate nutrients in hyphal tissue that are important to the growth and productivity of Douglas-fir forests (Entry *et al.*, 1992). Although experimental evidence suggests that these mats may survive up to two years following harvest of the host trees (Griffiths *et al.*, 1996), there is substantial research to suggest that both the diversity and inoculation potential of EMF declines within two years of harvest (Harvey *et al.*, 1980; Harvey *et al.*, 1997; Kranabetter and Wylie, 1998; Mahmood *et al.*, 1999; Parke *et al.*, 1984; Parsons *et al.*, 1994; Perry and Rose, 1983).

Clearcutting has been the predominant harvesting method used for forestry in most coniferous ecosystems, especially on the west side of the Cascade mountains of Oregon and Washington states. This practice results in the creation of even age stands, which decreases diversity at the landscape, stand and micro scales. When the scale at which clearcutting is done does not exceed the historical disturbance regime of the ecosystem in question, this may not be problematic, but in the Pacific Northwest, forest ecosystems may now have lowered resistance and resilience to disturbance (Franklin, 1988; Franklin *et al.*, 1989; Pimm, 1994; Schulze and Gertsberger, 1994; Schulze and Mooney, 1994). Currently, a paradigm shift is taking place within many circles of forest management. The focus is turning to the ecosystem as the management unit as opposed to the individual stand (top-down versus bottom-up). This shift is predominantly due to the increasing numbers of forest ecologists concerned with conservation biology. Opposing ideals on how best to preserve and restore biological diversity are represented by the coarse filter and the fine filter approaches. Coarse filter conservation operates under the belief that forest and landscape level structural characteristics dictate underlying layers of biological diversity, ecosystem function, nutrient cycling, and hydrological processes (Franklin *et al.*, 1989). The coarse filter approach stands in contrast to fine-filter conservation, or bottom-up management. This philosophy of conservation requires the development of plans for each species of concern, many of whose autecological requirements are unknown. This can lead to mutually exclusive management plans. Human managers then have to choose favourite species, excluding others, which can result in an extremely biased landscape. The top-down, coarse-filter approach allows the manager to be more objective, or at least, to not have to choose between species. Where there are species of concern, however, one can modify a top-down plan to include room for it.

One of several silvicultural alternatives to clearcutting for the purposes of maximizing diversity at the biological and landscape scales is uneven aged management (Franklin, 1988). This method is used to regenerate spatially heterogeneous stands with mixed ages, species, and size classes of trees, and

requires the retention of green-trees (living trees) in the harvested units (Acker *et al.*, 1998; Rose and Muir, 1997; Schulte and Buongirno, 1998). This form of management is often touted as an example of forest management serving as a coarse filter for biodiversity conservation.

This study is a part of a larger effort involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic, and social phenomena: the Demonstration of Ecosystem Management Options (DEMO) study (Aubry *et al.*, 1999).

An experimental design with five treatments and a control was replicated at six sites, two in Oregon and four in Washington. The treatments in the DEMO study are 75% Basal Area (BA) retention with group selection, 40% BA aggregated and dispersed retention, and 15% aggregated and dispersed retention. DEMO harvests began in the spring of 1997, and were completed in 1998. For full details on the goals, the experiment, time plan, cooperation, and justification for the study, see *Northwest Science*, 73, Special Issue (1999).

In one of the sociological experiments of the DEMO study, members of the public were shown pictures of the 15% BA dispersed retention treatment. There was no significant difference in their perception of this treatment and a full clearcut, both of which were negative. When people were then told that the trees were left to provide environmental benefits, there was a marked improvement in their rating of this treatment as compared to a clearcut (Ribe, 1999). Given concerns regarding the loss of EMF diversity and inoculum potential in clearcuts, we felt the need to document the effects of the 15% BA, evenly dispersed (hereafter referred to as 15% BA-D) green-tree retention harvest on EM type diversity.

We hypothesized that there would be an overall decline in EMF diversity within the thinned stands, and that the retention trees would serve as refugia, maintaining a higher level of EMF diversity than would be found in the areas most removed from trees. Our objectives were:

1)   To determine if EMF diversity declined due to the thinning treatment and, if so, to quantify this loss.

2) To determine if there was a differential loss in EMF diversity dependent upon the proximity of retention trees in the treatment unit.

METHODS AND MATERIALS

FIELD METHODS

Three sites (blocks) within the DEMO study were used: Hamilton Buttes (Gifford-Pinchot National Forest, Randle Ranger District, Washington), Dog Prairie, and Watson Falls (both in the Umpqua National Forest, Diamond Lake Ranger District, Oregon). For full site descriptions see Aubry *et al* (1999). Fifteen percent of dominant and codominant tree basal area (BA) was retained in an evenly dispersed pattern in the treated stands. The thinning treatment was applied in the summer of 1997 at Hamilton Buttes, and in the summer of 1998 at Dog Prairie and Watson Falls. Both Hamilton Buttes and Dog Prairie were logged by helicopter and slash was left ungathered on-site, whereas Watson Falls was logged using heavy ground equipment, with the slash piled and burned. A control stand which received no treatment was included in each block. All units were about 13 slope-corrected hectares in size.

Pre-treatment sampling was done in the spring of 1995 at Watson Falls, in the spring of 1997 at Hamilton Buttes, and in the spring of 1998 at Dog Prairie. After removal of the litter layer of the soil profile, six 5.5 cm diameter by 15 cm deep soil cores (356.5 cc) were extracted from both the 15% BA-D and control units at each site. One soil core was taken from each end of three systematically placed 50-meter long transects (hereafter referred to as permanent sampling points). Figure 2.1, below, illustrates the sampling scheme described here. Six post-

treatment soil cores were taken from the permanent sampling points (immediately adjacent to the pretreatment soil core holes) in both the control and treatment units. These were taken in June 1999 at Hamilton Buttes, and in October 1999 at both Dog Prairie and Watson Falls. The sampling scheme described above for the permanent sampling points is additionally described in (Cazares *et al.*, 1999a).

Additional post-treatment soil cores were extracted from the thinned stands. The 15% BA-D treatment unit at each site was divided into 9 equally sized subplots. Within each subplot, the three most-isolated Douglas-fir trees were selected. These trees were selected to represent a broad range of tree vigour and levels of photosynthetic productivity. There is a strong allometric relationship between leaf area and the cross-sectional sapwood area in trees (Waring *et al.*, 1982). Photosynthetic productivity was measured by increment boring trees at breast height and calculating the cross-sectional sapwood area of each tree selected. The trees at Hamilton Buttes contained smaller sapwood areas (mean = 529 cm^2, range = 210-955 cm^2) than at the other two sites (Dog Prairie, mean = 1099 cm^2, range = 583–2022 cm^2, Watson Falls, mean = 1000 cm^2, range = 615–1878 cm^2). To permit better cross-site comparisons, trees at Hamilton Buttes with sapwood areas smaller than 400 cm^2 were excluded from the study, and those above 1400 cm^2 at the other two sites were excluded. At each site, the range in sapwood area was divided into 9 equal segments, and one tree (hereafter referred to as host trees) was chosen from within each sapwood-range segment so that there was a single tree from each subplot within each site. The nine selected host trees at each site were then increment-bored a second time (120 degrees around the tree from the first bore hole). Sapwood area for each host tree was then determined as the mean of the two measurements taken from the increment-bores. At each host tree, a transect was either established across slope, or east-west at Watson Falls (0% slope), and a single 5.5 cm diameter x 15 cm deep soil core (356.5 cc) was taken at 0.5 times the distance from the edge of the dripline to the center of the bole of the tree. These soil cores are hereafter referred to as 0.5 dripline cores. A further 9 soil cores were taken at each site: one core from within each subplot. From the host-tree

in each subplot, a random compass bearing was followed and a soil core was taken at the point farthest from any tree. These soil cores are hereafter referred to as "open area" cores. The mean distance from these "open area" cores to the nearest tree was 12.8m.

Six each of the 9 soil cores at the 0.5 dripline distance and from open areas were randomly selected (using a random number table) for inclusion in this study. In summary, there were a total of 6 permanent sampling points (sampled pre- and post-treatment) in each unit for both the control and thinned stands. In the thinned stands only, there were 12 additional sample points: 6 post-treatment soil cores taken halfway between the bole and edge of the dripline of retention trees, and 6 soil cores taken from open areas in the thinned stands.
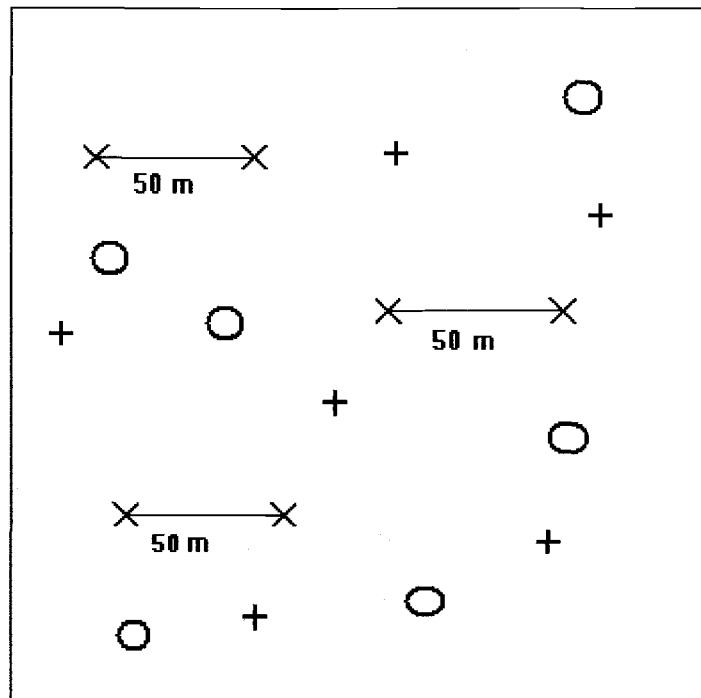
FIGURE 2.1: Schematic diagram depicting the sampling scheme for soil core extraction within a 13 ha unit of the DEMO study. (**x** = 6 permanent sampling points, sampled pre- and post-treatment, in control and treated units. **O** = 6 "host tree" samples, treated units, post-treatment only. **+** = 6 "open area" soil cores, treated units, post-treatment only)

LAB METHODS

Soil cores were refrigerated in the field and stored at –20 degrees Celsius immediately after returning from the field. Soil cores were thawed and examined within 48 hours. Soil cores were washed with an elutriator and screened with a 1mm sieve to remove soil particles and retain the fine roots. The contents of the sieve were examined under a stereomicroscope at 15-30X magnification in a water-filled flat tray divided into 36 subcompartments. The presence of each mycorrhizal

type found in each subcompartment was noted, providing an index of relative abundance for each type that ranged from 1-36 (Eberhart *et al.*, 1996). Each mycorrhizal type encountered was classified by morphological characteristics similar to those described in Goodman *et al.* (1996) and Ingleby *et al.* (1990). Morphological characteristics included colour, texture, presence/absence of rhizomorphs and emanating hyphae, presence/absence of clamp connections in emanating hyphae and rhizomorphs, and mantle pattern. Morphotype identities were determined by comparison to the database maintained by Eberhart *et al.* (1996). EM type identities represent morphotypes, not taxonomic species, with the exception of those that we could compare to published descriptions (Eberhart and Luoma, 1996; Eberhart and Luoma, 1997a, b; Goodman, 1996; Harniman and Durrall, 1996a, b).

DATA ANALYSIS

To determine the change in EM type richness due to the thinning treatment at each of the 12 permanent sampling points (6 each in the control and 15% BA-D treatment) at each block, the pre-treatment and post-treatment number of EM types found in each soil core were used. The number of EM types in each post-treatment permanent sample was subtracted from its pre-treatment condition, yielding a variable indicating the change in the number of EM types from the pre-treatment sampling period to the post-treatment sampling period (n=36, 18 each in treatment and control groups). An ANOVA model was run with the DEMO site entered as a blocking factor (n=3), and a treatment variable with two levels (thinning or control) entered as a fixed-effects factor, and a term for site by treatment interaction was included. The change in the number of EM types due to the thinning treatment was reported from the estimated marginal means, calculated from the final statistical model.

To determine the influence of retention trees on the EM type richness maintained in the thinned stand, only the treated units at each site were used. An ANOVA model was run with the DEMO site (n=3) entered as a blocking factor, and a three-level "condition" variable. The three levels for the condition were "pre-treatment" (six pre-treatment cores from the permanent sampling points at each site), "post-treatment with host tree" (using the six 0.5 dripline cores as described in field methods), and "post-treatment, open-area" (using the six open-area cores as described in field methods). A term for interaction between site and condition was entered in the model. Three-way comparisons for differences in EM type richness by condition were run using Tukey's test for post-hoc comparisons. Means for the number of EM types per soil core by condition were reported using the estimated marginal means from the final ANOVA model. Statistical tests described above were run using the General Linear Model module, General Factorial procedure in SPSS v7.0 software (SPSS, 1996).

EM-type-accumulation curves were constructed using the Species-Area Curve Module of PC-ORD v4.28 (McCune and Mefford, 1999), which performs 500 randomizations of the sample units. These were done separately for pre-treatment and post-treatment conditions in the treated units, and only using the six permanent sampling points in each unit. Estimates of the expected number of EM types for each grouping were provided by the first-order (Heltshe and Forrester, 1983; Palmer, 1990) and second-order (Burnham and Overton, 1979; Palmer, 1991) jackknife estimates.

RESULTS

The thinning treatment had a significant effect on the change in EM type richness in the treated stands ($F_{(1,32)} = 4.59$, $p = 0.04$), with a mean loss of 3.11 EM types per soil core after treatment (Table 2.1) with no significant influence due site ($F_{(2,32)} = 1.67$, $p = 0.20$). The interaction term between site and treatment was

insignificant and removed from the final model. In the treated units, a total of 61 EM types were found prior to thinning, and this number was reduced to 47 EM types after treatment, a net 23% loss in richness (Table 2.2). Figure 2.2 shows the EM-type accumulation curve.

TABLE 2.1: Loss of EMF diversity due to thinning. Number of EMF types per core reported as the mean and (standard error), calculated from estimated marginal means from final statistical model). * - significant difference, $\alpha = .05$

	Mean number of EM types per soil core		
	Pre-treatment	Post-treatment	Change in diversity
TOTAL (n=36)	9.31 (.59)	-------------	
Control (n=18)	8.94 (.99)	8.56 (1.18)	-0.39 (.90)
Thinned (n=18)	9.67 (.67)	6.56 (0.72) *	-3.11 (.90)*

TABLE 2.2: EM type richness sampled in treatment units, pre- and post-treatment with estimates of total richness. Estimates are taken from the 1st and 2nd-order jackknife estimates.

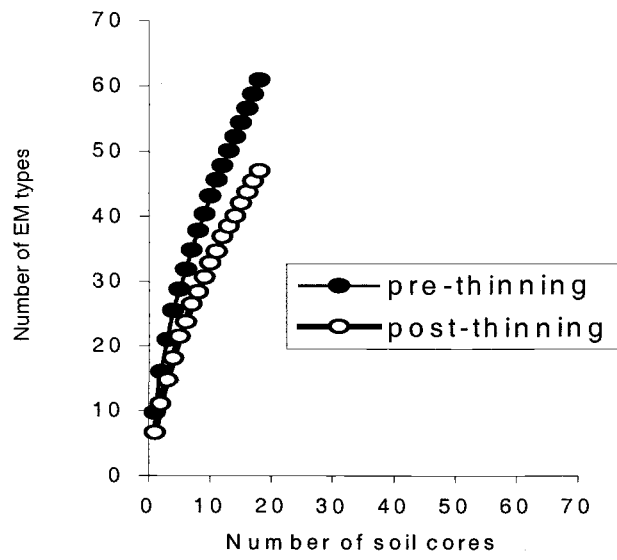|	Mean number of EM types per soil core				
	Total population (n=18)	Estimated number	Hamilton Buttes (n=6)	Dog Prairie (n=6)	Watson Falls (n=6)
Pre-treatment	61	97-127	22	35	30
Post-treatment	47	74-96	23	25	20

FIGURE 2.2: EM type accumulation curves for 15% BA-D
treatment stands only, from three DEMO sites.

There were significant differences in the number of EM types found in soil cores in the treated stands, depending upon whether they were taken from the pre-treatment stand, near a post-treatment retention tree or in open areas ($F_{(2,49)} = 25.24$, $p < 0.0005$). The site by condition interaction term was insignificant and dropped from the final model. The mean number of EM types per soil core by sampling location and time are shown in Table 2.3. These means are the estimated marginal means, reported from the final ANOVA model, which takes into account the differences in EM type richness due to the block factor. This results in the standard error being the same for each treatment condition. Three-way Tukey's comparisons of the mean number of EM types found by sampling time or location show no significant loss of mean EM type richness per soil core post-treatment when samples are taken within the dripline of a retention tree, but open area soil cores have significantly fewer EM types than either pre-treatment cores or post-treatment, host tree cores.

TABLE 2.3: Estimated mean number of EM types (standard error) by treatment condition. Estimates account for block differences, reported from ANOVA model. Means that do not share the same superscript are significantly different at p<0.0001. Open area cores were an average of 12.8m from the nearest tree.

Condition	Number EMF types per soil core
Pre-treatment	9.67 (.55)[a]
Post-treatment, Host tree	8.67 (.55)[a]
Post-treatment, Open area	4.50 (.55)[b]

DISCUSSION

Although the time between the application of treatment and post-treatment sampling varied by site, it is clear that more than a year after harvest, there were substantially reduced numbers of live EM root tips. We detected a 32% decline in EM type diversity per soil core after application of the thinning treatment at the permanent sampling points. This is similar to the findings of Hagerman *et al* (1999), who detected an approximate 33% decline in EM type richness per soil core between points 40 m inside the forest and those 2 m into an adjacent clearcut, two years post-harvest. This also parallels the findings of Kranabetter (1999) who detected a 38% decline in EM morphotype diversity, six years post-harvest, on seedlings growing within the rooting zone of birch trees in a retention harvest and seedlings growing outside the rooting zone. The similarity of results among these studies provides evidence that diverse methods of sampling yield comparable interpretations as the effects of tree harvesting on EMF community structure.

Although the mean loss of EM type richness at our permanent sampling points is nearly identical to the findings of these other studies, additional sampling revealed that the losses are greater in areas more removed from retention trees. There was more than a 50% reduction in EM type richness observed between pre-treatment samples and post-treatment open-area soil cores. Harvey *et al* (1980) found that soil cores extracted in a 2 year old clearcut, 1.5m from the edge of an adjacent Douglas-fir/larch forest in Montana, had both significantly lower root density and EMF diversity than those extracted at the forest edge itself. At a distance of only 7.6m into the clearcut, they found that the root density and EMF diversity were effectively zero. We found considerable numbers of EM root tips in the open-area cores (mean distance to the nearest tree = 12.8m) suggesting that the threshold distance-from-trees limit was not reached in this study. Measurements of root density were not an objective of this study, but discussion of the relationship between root density and EMF diversity is presented in Chapter 3 (this volume).

There was no significant loss of mean EM type richness within the dripline of retention trees, and EMF richness did not drop to zero: the retention trees have been shown to be pivotal in maintaining EMF diversity on these sites. From a management perspective, the size of the treatment unit over which a thinning treatment of 85% BA is implemented may be critical. There was significant loss of EMF diversity due to this treatment, but recovery can come from the retention trees and the surrounding landscape.

Epigeous EMF (above-ground fruiting species, *i.e.* mushrooms) can effectively utilize wind to disperse their spores and could readily disperse to the treatment area, but spores of hypogeous fungi (below-ground fruiting species, *i.e.* truffles) require different means for dispersal. Wind-blown topsoil can transport some spores from hypogeous fungi, but evidence suggests this mechanism is insufficient to maintain the mycorrhizal inoculation potential of a disturbed area (Malajczuk *et al.*, 1987). Instead, many hypogeous fungi require mammal mycophagists (fungus eaters) to disperse their spores. Truffles and truffle-like fungi are the primary food source for species of mammals such as the northern flying squirrel (*Glaucomys sabrinus*), and the California red-backed vole (*Clethrionomys californicus*), which in turn are the primary prey of the Northern Spotted Owl (*Strix occidentalis*). These animals dig up fungal sporocarps, consume them and disperse the spores in their feces (Cazares *et al.*, 1999a; Fogel and Trappe, 1978; Griffiths *et al.*, 1996; Luoma, 1991; Maser *et al.*, 1978). These animals, however, rarely enter large clearcuts (C. Maguire, unpublished data), and dispersal of these fungi is subsequently limited in heavily cut areas. Even for those fungi that utilize wind dispersal, there are suggestions that some fungi may be unable to colonize seedlings in the absence of mature trees to support these fungi (Deacon *et al.*, 1983; Fleming, 1983, 1985; Mason *et al.*, 1983). Other fungi may not be present in clear-cut units until the stand has developed adequate structural characteristics to ameliorate microclimate conditions.

CONCLUSIONS

A survey of the literature reveals two major methods for sampling EM morphological-type richness by soil cores. The one we used in this study uses a fixed-volume sampling scheme, where a soil core is used and all the root tips are examined in it. This method has additionally been used by Goodman and Trofymow (1998), Harvey *et al.* (1976), Ferrier and Alexander (1985), Parsons *et al* (1994), Jonsson *et al* (1999), and Visser (1994). The other method widely used involves counting a fixed number of ectomycorrhizal root tips in the soil cores, to reflect equal sampling effort of mycorrhizal root tips. In the second method, the volume of soil examined varies between samples. This method has been used by Hagerman *et al.* (1999), Kranabetter and Wylie (1998), Kranabetter (1999) and Kranabetter *et al.*, (1999), Mahmood *et al* (1999), and Gehring *et al* (1998). Both methods, however, yield useful and comparable results.

This study has shown that retention trees act as important refugia for EMF. Similar results were reported by Kranabetter (1999), who found that birch seedlings growing within the dripline of retention trees in a variable retention harvest had significantly higher EM type richness than seedlings growing outside of the rooting system of the retention trees. These islands of biological legacy from the pre-disturbance stand serve as multiple recolonization staging grounds for EMF. For those fungi that are lost from these treatment units and forests managed in a similar fashion, recolonization of some hypogeous and late-stage fungi (those that only associate with roots in mature forests) can occur from neighbouring forest stands, provided the distance to the center of the harvested area is not too great.

ACKNOWLEDGEMENTS

CHAPTER 3
SPATIAL AND PRODUCTIVITY RELATIONSHIPS OF ECTOMYCORRHIZAL FUNGI TO INDIVIDUAL TREES IN THINNED DOUGLAS-FIR STANDS.

Christopher A. Stockdale, and Daniel L. Luoma

ABSTRACT

This study is a part of the Demonstration of Ecosystem Management Options (DEMO) study, an interdisciplinary program involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic and social phenomena. This study is restricted to one of the treatments of the DEMO study, 15% basal area evenly dispersed retention. Three sites within the DEMO study were used and treated as blocks. Within each treatment unit, ectomycorrhizal fungal (EMF) diversity was significantly reduced. There is a 50% loss of EM types per soil core in the areas most removed from retention trees, but no significant difference in EM type richness between soil cores taken from within the dripline of retention trees and the pretreatment condition of the stand. The objectives of this study were to determine the distance from the retention trees at which EM type richness and root density begin to noticeably decline, to determine the relationship between the photosynthetic potential of retention trees (as measured by cross-sectional sapwood area), their root density and subsequent EM type richness, and to determine the effects of retention-tree productivity, root density and distance from the tree on the community structure of EMF. One to two years posttreatment, nine trees were selected in each unit and 5.5 cm diameter by 15 cm deep soil cores were taken halfway from the bole of the tree to the edge of its dripline, at the edge of the dripline, and at half the distance again beyond the edge of the dripline. Nine additional soil cores were taken in "open areas" as far from retention trees as possible. Soil cores taken within the dripline

and at the edge of the dripline (inside dripline cores) had no significant differences in EM type richness or community structure when compared to each other. There was a 35% reduction in EM types per soil core from the inside dripline cores to the soil cores taken just outside the dripline and open area cores (outside dripline cores). Among outside dripline cores there was no significant differences in either EM type richness or community structure. EM type richness was significantly and positively correlated with fine-root tip density in the soil. The sapwood area of retention trees had no significant correlations with either root density, EM type richness or community structure. The EMF community structure closely followed the log-normal distribution seen in complex, mature communities. In the outside dripline soil cores, there were very few rare or infrequent types observed, which suggests that the probability of an EM type being lost is linked with its pre-disturbance relative abundance, and less to do with adaptation to specific microsite differences. *Cenococcum geophilum* was the most abundant EM type observed, accounting for 18.7% of the total community, and occurring in nearly every sample, which has been observed in many other studies.

INTRODUCTION

Conflict between timber harvest interests, recreational values, aesthetics and concerns for ecological sustainability came to a head in the Pacific Northwest region of the United States in the 1980's, and provided the impetus for research into timber harvesting that offered alternatives to clearcut logging. Environmental concerns of the general public and members of the scientific community, combined with the mandates under the Endangered Species Act, 1973, led to the implementation of the Northwest Forest Plan (NWFP)(USDA Forest Service, 1994; USDA Forest Service and USDI Bureau of Land Management, 1994). The need to provide habitat for the Northern Spotted Owl, an old-growth dependent species, was a major factor leading to recommendations in the NWFP for retention of a

minimum of 15% basal area (BA) in harvest units to facilitate the development of uneven-aged stands. This silvicultural prescription was an improvement over traditional methods of clearcutting for accelerating the development old-growth type structure in managed forests. Although it is widely believed that retention harvests confer many ecological benefits to Pacific Northwest forest ecosystems, the level and pattern of retention that are most effective is unknown, and according to Franklin *et al* (1999), there was little scientific basis for choosing this particular level (15%) of retention.

This study is a part of a larger study involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic and social phenomena: the Demonstration of Ecosystem Management Options (DEMO) study. One treatment represents one component of the Northwest Forest Plan: 15% dispersed green-tree retention. The DEMO study gives ecologists and managers the opportunity to test the effectiveness of this aspect of the plan, in addition to the many other hypotheses being tested within the context of the DEMO study (Aubry *et al.*, 1999). In one of the sociological experiments of the DEMO study, members of the public were shown pictures of the 15% BA dispersed retention treatment. There was no significant difference in their perception of this treatment and a full clearcut, both of which were negative. When people were then told that the trees were left to provide environmental benefits, there was a marked improvement in their rating of this treatment as compared to a total clearcut (Ribe, 1999). Given concerns regarding the loss of EMF diversity and inoculum potential in clearcuts, we felt the need to document the effects of the 15% BA, evenly dispersed (hereafter referred to as 15% BA-D) green-tree retention harvest on EMF diversity.

EMF confer a variety of benefits to their host plants. In their natural setting, most mycorrhizal plants possess a growth advantage over those that are not mycorrhizal (Allen, 1991). Drought-stressed plants demonstrate the ability to tolerate lower water potentials when they possess certain mycorrhizal partners (Pederson and Sylvia, 1996). Other mycorrhizal types have been shown to give

seedlings the ability to live in harsh environments where they would otherwise be unable to survive (Lee and Koo, 1983). Mycorrhizae also may play a role in mediating competitive interactions between different plants, and sometimes, plants that appear to be competitors prove to be allies when viewed in terms of their mycorrhizal associations (Perry *et al.*, 1987). The symbiotic nature of the mycorrhizal relationship demonstrates the importance of these fungi in nutrient cycles within the forest ecosystem. Host plants photosynthesize and provide the sugars they produce to their fungal partners in exchange for inorganic nutrients, principally nitrogen and phosphorus (Chang and Li, 1998; Entry *et al.*, 1992; Griffiths *et al.*, 1994; Griffiths *et al.*, 1996; Read *et al.*, 1985). Not only do mycorrhizae extend the volume of potentially exploitable soil for the host plant, they increase nutrient uptake rates in plants (Read *et al.*, 1985). Decomposition processes within the litter and organic horizons of soils have been shown to be strongly influenced by mycorrhizal fungi which increases the pool of nutrients available for the plants (Entry *et al.*, 1991a; Entry *et al.*, 1991b, 1992; Griffiths *et al.*, 1994; Griffiths *et al.*, 1991).

It is thought that each EMF's ecological role may be specific and tree root-systems are occupied by a diversity of EMF to broaden their tolerance of environmental conditions (Lee and Koo, 1983; Molina and Amaranthus, 1990; Pederson and Sylvia, 1996). Indeed, studies have shown that EMF demonstrate extremely high beta diversity (Goodman and Trofymow, 1998; Luoma *et al.*, 1997), and may be adapted to very specific conditions (Bruns, 1995). When forests are clearcut, the diversity and inoculum potential of EMF is greatly reduced within a period of less than two years (Parke *et al.*, 1984; Perry and Rose, 1983).

Many fungi can disperse via large numbers of spores. Epigeous ectomycorrhizal fungi can effectively utilize wind to disperse their spores, but the spores of hypogeous fungi require different means for dispersal. Most hypogeous fungi require mammal mycophagists (fungus-eaters) to disperse their spores (Malajczuk *et al.*, 1987; Cazares *et al.*, 1999a; Fogel and Trappe, 1978; Griffiths *et al.*, 1996; Luoma, 1991; Maser *et al.*, 1978). Truffles and truffle-like fungi are the

primary food source for species of mammals such as the northern flying squirrel (*Glaucomys sabrinus*), and the California red-backed vole (*Clethrionomys californicus*), which in turn are the primary prey of the Northern Spotted Owl (*Strix occidentalis*). These animals dig up fungal sporocarps, consume them and disperse the spores in their feces (Cazares *et al.*, 1999a; Griffiths *et al.*, 1996; Luoma, 1991). These animals, however, rarely enter large clearcuts (C. Maguire, unpublished data), and dispersal of these fungi is subsequently limited in heavily cut areas. Even for those fungi that utilize wind dispersal, there are suggestions that some may be unable to colonize seedlings in the absence of mature trees, and will not be present in clear-cut units until the trees are of an adequate maturity to support these fungi (Deacon *et al.*, 1983; Fleming, 1983, 1985; Mason *et al.*, 1983). Whether this is a result of tree age alone, or the concurrent development of stand structural characteristics which ameliorate the microclimate is unknown.

Some EMF species may be able to lay dormant in the soil for a long period of time through the formation of sclerotia and other bodies. For species not capable of dormancy, in the absence of green-trees or other suitable hosts, colonization of dispersal-limited, and "late-stage" fungi that are lost as a result of the retention harvest will only occur from the adjacent forest edge. The presence of green-trees in the harvest unit should provide multiple sources for the spread of EMF, in addition to colonization from the edge of the adjacent stand, and should effect a more rapid and thorough colonization of EMF in the harvest unit. Retention trees in the harvest unit preserve a significant legacy of the pre-treatment EMF community. Chapter 2 (this volume, above) compared pre-treatment and post-treatment EMF diversity in the 15% BA-D treatment of the DEMO study, where we found a 32% reduction in EM type richness per soil core across the treatment unit as a whole, and a 27% decline in total EM type richness. Within the treatment unit, however, soil cores taken within the dripline of retention trees post-treatment had no loss of diversity. The loss of diversity occurred primarily in the areas where trees had been removed.

Mason *et al.* (1987) showed differences in EMF community structure relative to the distance from the bole of the host tree. Different species were observed to fruit at spatially explicit distances from the bole of the tree, and the below-ground view appeared to be the same (Fleming, 1983; Fleming *et al.*, 1984; Mason *et al.*, 1983). Below-ground views can be obtained by soil cores taken at various distances from the host tree, or by using "trap seedlings", where seedlings are planted at various distances from the tree, allowed to grow for a period of time, and then harvested and the root systems examined. Deacon and Fleming (1992) surmised that the observed differences in mycorrhizal establishment with regard to position and distance from the host tree were reflective of the temporal order in which colonization had occurred. They speculated that earlier colonists occupied positions further from the tree, advancing with the roots as they developed.

The trophic resource for which EMF compete is carbon from the host plant (Deacon and Fleming, 1992), whereas the spatial resource they compete for is the root tip itself. McArthur and Wilson (1967) showed that species diversity, across a wide range of taxonomic groups, directly correlated to the habitat area available to them. If EMF follow a similar pattern, then EMF diversity should be higher in areas with greater root density.

What factors regulate the rooting density of plants? Root production is one of three primary pools of photosynthetically manufactured carbon allocation. The other two primary pools are wood and leaf production (Taiz and Zeiger, 1998). These three pools interact in a highly complex fashion. Roots are required to acquire nutrients (often through mycorrhizal associates) to produce leaves, which in turn are required to produce the sugars that construct the whole plant and create the root system itself. Among a cohort of trees, genetic differences, microsite conditions and nutrient availability all influence the relative success of one tree over another. Trees in a stand with higher leaf area tend to grow taller and in utilize more site resources than less productive trees (Waring and Running, 1998). Leaf area is the primary indicator of plant productivity, but is very difficult to measure with accuracy. There is, however, a strong allometric relationship between the

sapwood area and leaf area of a tree (Waring *et al.*, 1982). Sapwood area of *Pseudotsuga menziesii* (Mirb.) Franco (the only tree examined in this study) can be easily obtained by increment boring trees. This can be used as a proxy variable for the productivity of individual trees.

We hypothesized that higher carbon fixation in an individual tree would result in denser root production, and support a more diverse population of EMF due to increased number of fine roots available for colonization. We wanted to determine the relationship between trees of varying productivity and vigour and the density of roots and diversity of EMF it could support. This was partly due to concerns that silvicultural prescriptions for green-tree retention might lead foresters to leave the lowest quality trees on site to serve as green-trees, in effect, high-grading the stand (Schulte and Buongirno, 1998). The EM type richness of soil cores taken within the dripline of retention trees does not differ significantly from the pre-treatment condition of the forest, as compared to the loss of EM type richness of soil cores taken from open-areas (Chapter 2 this volume). Due to the fact that there is a significant difference in EMF diversity with regards to distance from the retention trees in the post-treatment stand, we wanted to determine where the this loss of diversity became significant with regards to distance from the retention trees.

The objectives of this study were:

1) To determine the relationship between the photosynthetic potential of retention trees and their subsequent root density and EM type richness.

2) To determine the distance from the retention trees at which EM type richness and root density begin to noticeably decline.

3) To determine the effects of retention-tree productivity, root density and distance from the tree on the community structure of EMF.

METHODS AND MATERIALS

FIELD METHODS

Three sites within the Demonstration of Ecosystem Management Options (DEMO) study were used: Hamilton Buttes (Gifford-Pinchot National Forest, Randle Ranger District, Washington), Dog Prairie and Watson Falls (Umpqua National Forest, Diamond Lake Ranger District, Oregon). For full site descriptions see Aubry et al (Aubry et al., 1999). Only one of the five treatments applied in the DEMO study was used for this study: 15% BA-D. This thinning treatment was applied in the summer of 1997 at Hamilton Buttes, and in the fall of 1998 at Dog Prairie and Watson Falls. Both Hamilton Buttes and Dog Prairie were logged by helicopter and slash was left ungathered on-site, whereas Watson Falls was logged using heavy ground equipment, with the slash piled and burned.

Sampling for this study was done in May, 1999 at Hamilton Buttes and in October, 1999 at Dog Prairie and Watson Falls. The 13-hectare, slope-corrected treatment unit at each site was subdivided into 9 equally sized subplots. Within each subplot, three Douglas-fir trees (*Pseudotsuga menziesii* (Mirb.) Franco) were randomly selected and increment-bored once at breast height on the uphill side of the tree. Sapwood area was calculated from these increment borings.

The trees at Hamilton Buttes contained smaller sapwood areas (mean = 529 cm^2, range = 210-955 cm^2) than at the other two sites (Dog Prairie, mean = 1099 cm^2, range = 583–2022 cm^2, Watson Falls, mean = 1000 cm^2, range = 615–1878 cm^2). To permit better cross-site comparisons, trees at Hamilton Buttes with sapwood areas smaller than 400 cm^2 were excluded from the study, and those above 1400 cm^2 at the other two sites were excluded. At each site, the range in sapwood area was divided into 9 equal segments, and one tree (hereafter referred to as host trees) was chosen from within each sapwood-range segment so that there was a

single tree from each subplot within each site. The nine selected host trees at each site were then increment-bored a second time (120 degrees around the tree from the first bore hole). Sapwood area for each host tree was then determined as the mean of the two measurements taken from the increment-bores.

At each tree, a transect was either established across the slope, or East-West in the case of Watson Falls (0% slope), and three 5.5 cm radius x 15 cm deep soil cores (356.5 cc) were taken at 0.5, 1.0, and 1.5 times the distance from the dripline to the center of the bole of the tree. Figure 3.1 illustrates the sampling design. These soil cores are hereafter referred to as 0.5 dripline, 1.0 dripline, and 1.5 dripline cores. All trees within 3 crown-widths upslope from the host tree (1 crown width is equal to 2 times the dripline distance), and 2 crown-widths downslope were increment bored twice to calculate sapwood area for neighbouring trees. At Watson Falls, which is flat, all trees within a 3 crown-width radius were increment bored.

A further 9 soil cores were taken at each site: one core from within each subplot. From the host-tree in each subplot, a random compass bearing was followed and a soil core was taken in the largest opening, farthest removed from any retention trees. These soil cores are hereafter referred to as "open area" cores. The "open area" cores were a mean distance of 12.8m from the nearest tree. This totals 3 sites * 9 subplots per site * 1 tree per subplot * 3 cores per tree + 1 open area core per subplot = 108 cores (27 independent samples with 4 subsamples each).
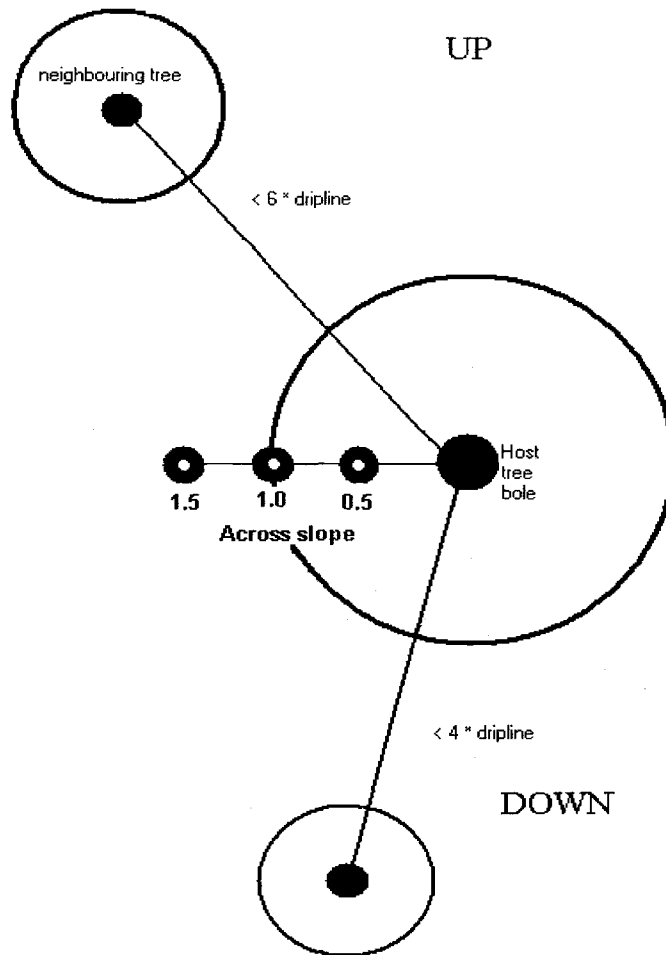
FIGURE 3.1: Sampling scheme layout for tree-centered soil core extraction and distance limits for increment boring neighbouring trees within the 15% BA-D treatment at three DEMO blocks. Units expressed are multiples of the distance from the center of the bole of the host tree to the edge of its dripline.

LAB METHODS

Soil cores were refrigerated in the field, and stored at −20 degrees Celsius immediately after returning from the field. Soil cores were thawed and examined within 48 hours. Soil cores were washed with an elutriator and screened with a 1mm sieve to remove soil particles and retain the fine roots. The contents of the sieve were examined under a stereomicroscope at 15-30X magnification in a water-filled flat tray divided into 36 subcompartments. The presence of each mycorrhizal type found in each subcompartment was noted, providing an index of relative abundance for each type from 1-36 (Eberhart *et al.*, 1996). Each mycorrhizal type encountered was classified by morphological characteristics similar to those described in Goodman *et al.* (1996) and Ingleby *et al.* (1990). Morphological characteristics included colour, texture, presence/absence of rhizomorphs and emanating hyphae, presence/absence of clamp connections in emanating hyphae and rhizomorphs, and mantle pattern. Morphotype identities were determined by comparison to the database maintained by Eberhart *et al.* (1996). EM type identities represent morphotypes, not taxonomic species, with the exception of those that we could compare to published descriptions (Eberhart and Luoma, 1996; Eberhart and Luoma, 1997a, b; Goodman, 1996; Harniman and Durrall, 1996a, b).

Root density was counted as the number of living fine-root tips in a standardized subsample of the soil core. In every sixth subcompartment of the tray, all living fine-root tips were counted, totaling 6 of the 36 subcompartments. Fine-root tips were counted as living if the cortex was clearly turgid along some portion of its length. Roots of *Tsuga heterophylla* (Raf.) Sarg. were excluded from analysis. *T. heterophylla* was encountered only at Hamilton Buttes, and was a minor component of the stand. Fine roots of *T. heterophylla* were not common, rarely accounting for more than a trace amount of any given sample's total number roots. No attempt was made to exclude roots of *Abies* or *Pinus* species occurring in the samples. These trees were rare in the stands (Halpern *et al.*, 1999).

DATA ANALYSIS

Relationships between productivity, root density and EMF diversity

To determine the effects of tree productivity on root density a multiple regression model was constructed. Root density (the dependent variable) was log-transformed for normality. Independent variables in the model were host tree productivity as measured by sapwood area and a blocking factor for site. For this test, inside dripline soil cores (1.0 and 0.5 dripline distance classes) were pooled. Only these soil cores were used, because they were considered to be directly under the influence of the host tree. To test for any additional influence of neighbouring trees, total productivity (the sum of the host tree's sapwood area and that of all measured neighbouring trees) was entered in the model in place of host tree productivity.

To determine the effects of tree productivity on EM type richness another multiple regression model was constructed. This model was constructed identically to that used to test for the relationship between tree productivity and root density. For this test, inside dripline soil cores (1.0 and 0.5 dripline distance classes) were pooled. EM type richness was the dependent variable, and required no transformations. To test for any additional influence of neighbouring trees, total productivity (the sum of the host tree's sapwood area and that of all measured neighbouring trees) was entered in the model in place of host tree productivity.

Two separate nested-ANOVA models (Montgomery, 1997) were used to test the effect of distance from host tree on root density and EM type richness using all soil cores (n=108). These models were run with the blocking factor of subplot nested within the blocking factor for site, and distance entered as a fixed-effects

class variable. Means and standard errors for root density and EM type richness by distance class and site are reported from the output of these models.

The correlation between EM type richness (dependent variable) and root density (independent variable, covariate) was tested with a nested-ANCOVA design, with subplot nested within site as above and a site-by-root-density interaction term. All above statistical tests were run using the General Linear Model module, General Factorial procedure with command-line syntax modifications for nesting block factors in SPSS v7.0 software (SPSS, 1996).

Analysis of community structure

EMF type accumulation curves were constructed using the Species-Area Curve Module of PC-ORD v4.28 (McCune and Mefford, 1999), which performs 500 randomizations of the sample units. These were done for the total population sample, for the sample populations at each site, and for the total population sample divided into an 'inside dripline' class (a combination of the 0.5 dripline and 1.0 dripline distance classes) and an 'outside dripline' class (a combination of the 1.5 dripline and open area cores). Estimates of the expected number of EMF morphotypes for each grouping were provided by the first-order (Heltshe and Forrester, 1983; Palmer, 1990) and second-order (Burnham and Overton, 1979; Palmer, 1991) jackknife estimates.

Five blocked multi-randomization permutation procedure (MRBP) tests to determine differences in EMF community structure by were done using PC-ORD v4.28 software (McCune and Mefford, 1999). The Euclidean distance measure was used for all of these tests, as it is the only distance measure available in PC-ORD (McCune, 2000).

1)   To test for differences in community structure by distance from the host tree, an MRBP tests was used with subplot serving as the blocking factor. The test was run using four soil core distances

(0.5, 1.0, 1.5 dripline cores and open area cores) as a single variable with four classes.

2)   To compare the inside dripline and outside dripline groupings, an MRBP test was run using two soil core distance classes.

3)   To determine the influence of subplot on the community structure of EMF, an MRBP test was done, using site as the blocking factor.

4)   To determine the effect of host tree productivity on EMF community structure, an MRBP test was used. Host tree productivity was recoded into a categorical variable with three levels: low, medium and high. The range for each variable at each site was partitioned so that an equal number of samples fell into each category (n=12 at each site), which is a prerequisite for the MRBP test.

5)   To determine the effect of root density in EMF community structure, an MRBP test was used. Root density was recoded into a categorical variable with three levels: low, medium, and high. The prerequisites for the MRBP test were fulfilled as described for #4 above.

Additionally, to test for EMF community structure differences across blocks, a multi-randomization permutation procedure (MRPP test, not blocked) was performed with site as the categorical variable. Due to the high level of beta-diversity among soil cores, group differences among both the MRBP and MRPP tests were only considered to be significant at $\alpha = .01$ (Mielke, 1984). For all tests on group differences above, the full samples-in-species-space matrix (108 samples x 115 morphotypes) was used.

Ordination was performed on the entire sample population by use of non-metric multidimensional scaling (NMS) (Beals, 1984) of samples-in-species-space. Morphotypes occurring in only a single sample (singletons) were excluded to minimize the coefficient of variation and reduce skewness in the data. An

ordination solution was not found to be significant for any level of dimensionality, therefore Beals smoothing was applied, with singletons removed, to extract the dominant gradients in community structure (McCune, 1994). NMS ordination was then run on the resultant matrix of 108 samples x 78 morphotypes with the Euclidean distance measure, three dimensions, 200 iterations, and a step-length of 0.20.

Rank-abundance curves (Shaw *et al.*, 1983) for the inside and outside dripline samples were constructed using Biodiversity Pro software (McAleece *et al.*, 1995). The resultant curves were visually compared to the different species-abundance models in Magurran (1988) to infer the species distribution models observed in the study.

RESULTS

MORPHOTYPE RICHNESS AND ROOT DENSITY

The sapwood area of the host tree had no significant effect on either EM type richness or on root density ($F_{(1,23)}$= .97, p = .34, and $F_{(1,23)}$= 1.90, p = .18, respectively). Sapwood area of the total productivity measure (host tree plus neighbouring trees) also had no significant effect on either EMF type richness or root density ($F_{(1,23)}$= .33, p = .57, and $F_{(1,23)}$= 1.47, p = .24, respectively).

Distance from the host tree had a highly significant effect on mean EM type richness per soil core ($F_{(3,78)}$= 24.75, p < .0005, Figure 3.2), with no significant effects (p > .10) for either the tree-nested-within-site effect or block (site) effect alone. The 95% confidence intervals for EM type richness overlap between the open area and 1.5 dripline class, and between the 1.0 and 0.5 dripline class, but not between each other. Therefore the respective classes were pooled into "outside

dripline" and "inside dripline" soil cores. Outside dripline soil cores average 35% fewer EM types than inside dripline soil cores.

Root density significantly declined at the edge of the dripline ($F_{(3,78)}$= 2.61, p = .057, Figure 3.3). A significant block effect on root density was found ($F_{(2,24)}$= 4.38, p = .024). The Hamilton Buttes block had considerably higher root density than the other sites.
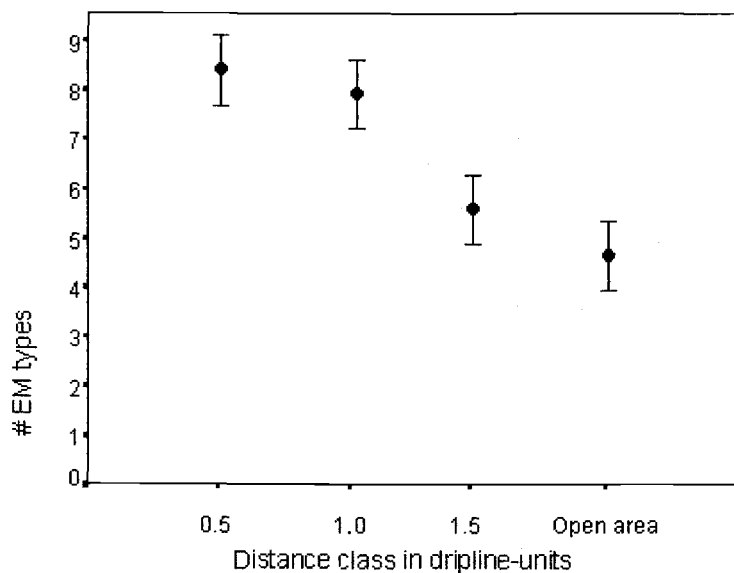

FIGURE 3.2: Estimated marginal mean number of EM types per soil core by distance class at three DEMO sites. Error bars denote 95% confidence interval. Estimates account for influence due to site. "Open area" cores were a mean distance of 12.8m from the nearest tree.
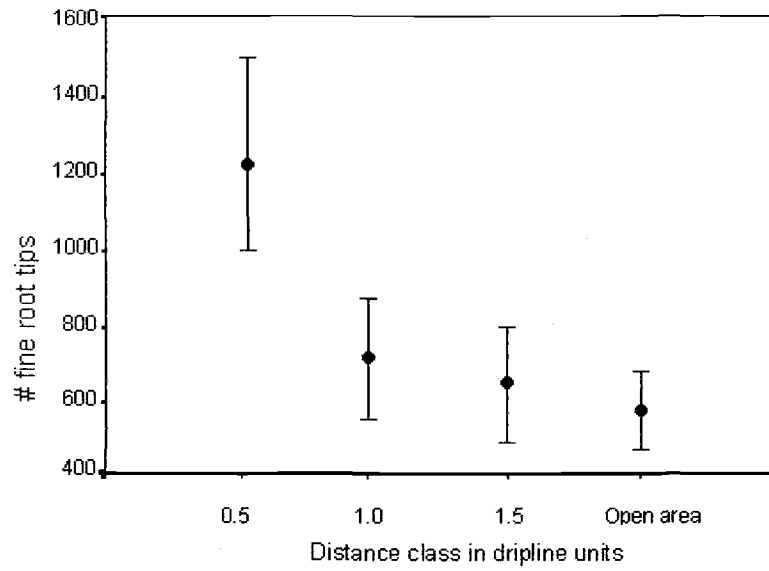
FIGURE 3.3: Estimated marginal mean number of fine-root tips per soil core by distance class at three DEMO sites. Error bars denote 95% confidence interval. Means account for influence due to site. "Open area" cores were a mean distance of 12.8m from the nearest tree.

There was a strong correlation between the log EM type richness (dependent variable, transformed for homogeneity of variance) and log root density ($F_{(1,78)}$ = 39.36, p < .0001, Figure 3.4A) with no influence due to the tree-within-site effect ($F_{(24,78)}$ = 0.57, p = 0.94). There was a significant block effect ($F_{(2,80)}$ = 3.14, p = 0.049), and a significant block-by-log-root-density interaction ($F_{(2,78)}$ = 3.36, p = 0.04). The block and block-by-root-density interactions show that the relationship between root density and EM type richness varies by site. Hamilton Buttes and Dog Prairie both have strong positive relationships between root density and EM type richness (Figures 3.4B and 3.4C), whereas EMF diversity has no apparent relationship with root density at Watson Falls (Figure 3.4D).

FIGURE 3.4A: Relationship between root tip density and number of EMF morphotypes per soil core. Includes simple-regression line-of-best-fit and 95% CI bands (r^2 = 0.32, p<0.001). Data from three sites within the DEMO study, 15% BA-D treatment.

FIGURE 3.4B: Relationship between root tip density and number of EMF morphotypes per soil core. Includes simple-regression line-of-best-fit and 95% CI bands ($r^2 = 0.50$, p<0.001). Data from Hamilton Buttes (DEMO study, 15% BA-D treatment).

FIGURE 3.4C: Relationship between root tip density and number of EMF morphotypes per soil core. Includes simple-regression line-of-best-fit and 95% CI bands ($r^2 = 0.54$, p<.001). Data from Dog Prairie (DEMO study, 15% BA-D treatment).
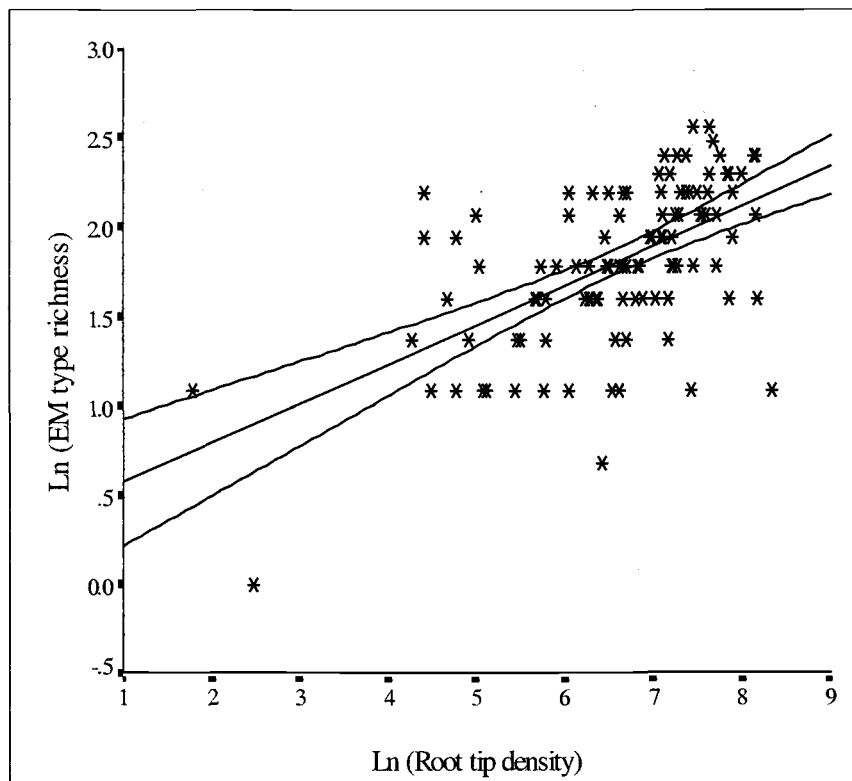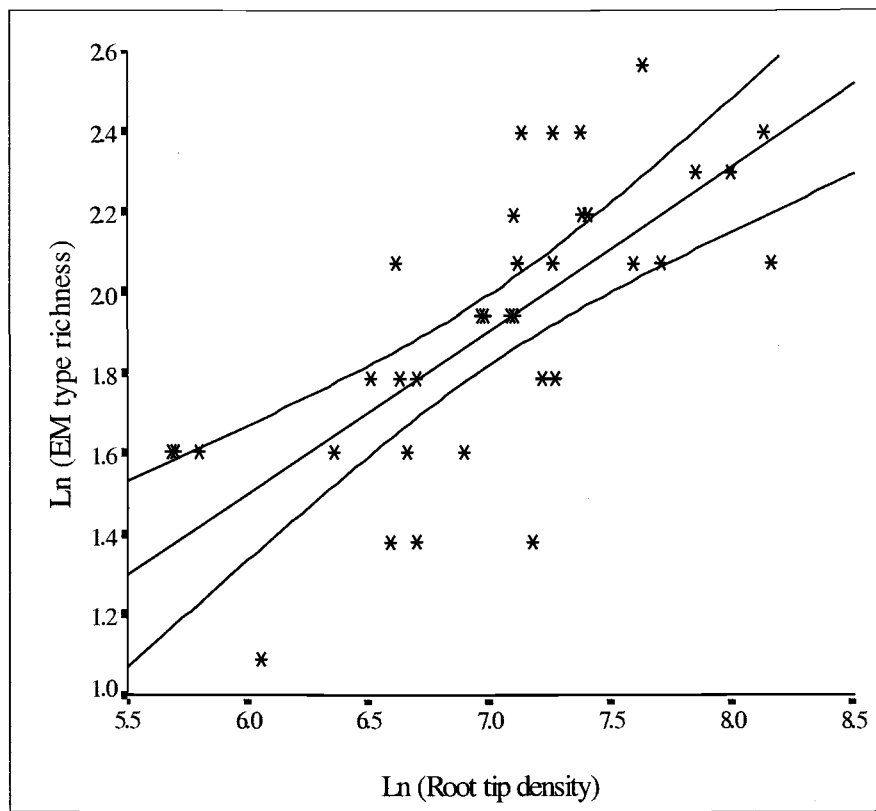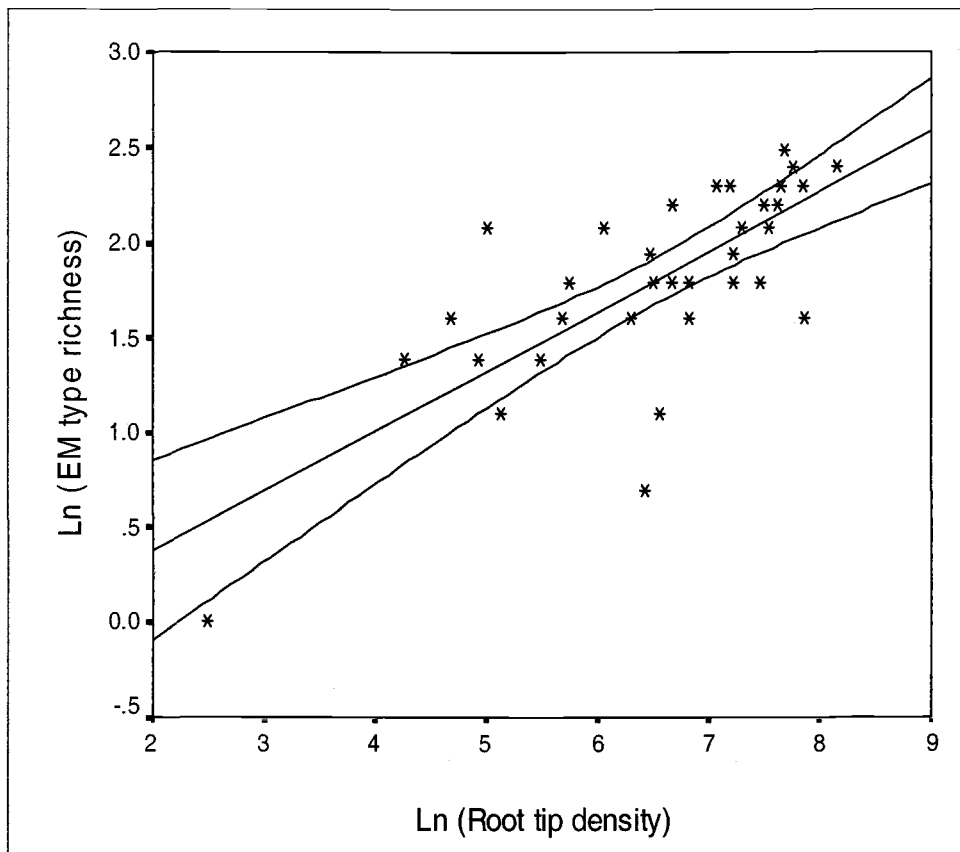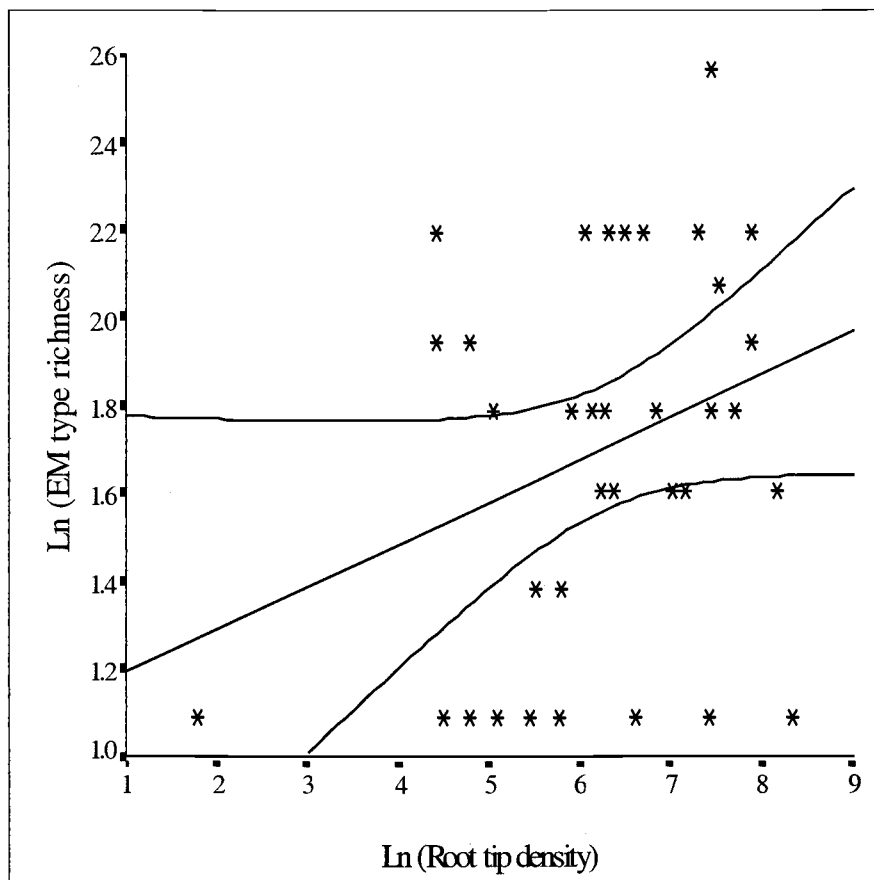
FIGURE 3.4D: Relationship between root tip density and number of
EMF morphotypes per soil core. Includes simple-regression line-of-
best-fit and 95% CI bands ($r^2 = 0.09$, p=0.08). Data from Watson
Falls (DEMO study, 15% BA-D treatment).

Hamilton Buttes had the highest total EM type richness of the three sites (Table 3.1). It also had the highest number of EM types by inside and outside dripline classes. Species-area curves for the total population, each site, and inside and outside dripline communities reveal an incomplete sampling of the total EMF community (Figures 3.5 and 3.6).

TABLE 3.1: Number of EMF types found by site and total area sampled. Range in estimated #EMF types from first-order to second-order jackknife estimates.

| | Number Of EMF Types | | | | | |
| | Total Study | | Inside Dripline | | Outside Dripline | |
SITE	Found	Estimated	Found	Estimated	Found	Estimated
Hamilton Buttes n = 36	77	116-134	64 n = 18	105-134	37 n = 18	61-79
Dog Prairie n = 36	50	67-76	47 n = 18	65-72	31 n = 18	45-54
Watson Falls n = 36	47	67-81	44 n = 18	65-80	22 n = 18	31-35
TOTAL n = 108	115	152-166	101 n = 54	136-145	69 n = 54	103-129

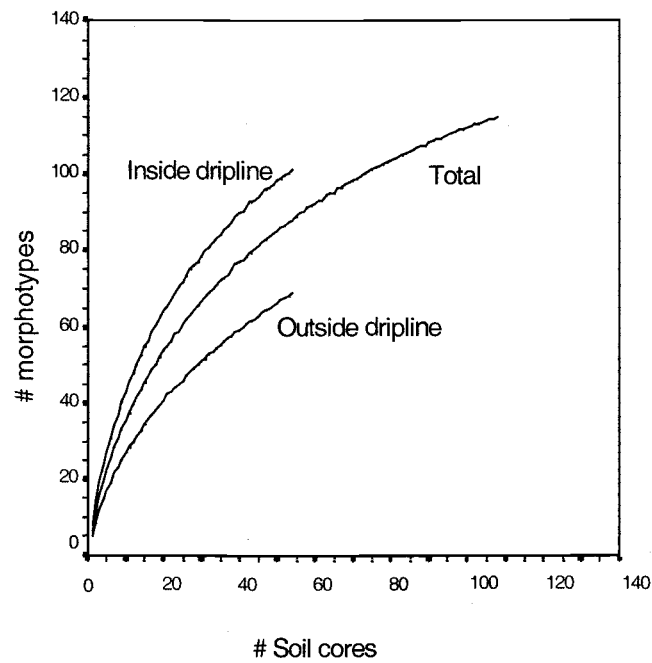FIGURE 3.5: EM type accumulation curve for total sample
population (n = 108) and by inside- and outside- dripline subgroups.
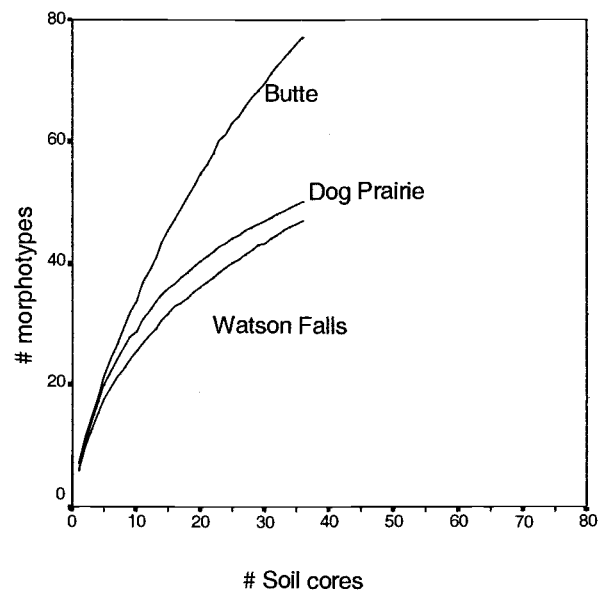n = 54, 500 randomizations of sample points.

FIGURE 3.6: EM type accumulation curve for each study site.
n = 36, 500 randomizations of sample points.

COMMUNITY STRUCTURE

Cenococcum geophilum Fr. was the most abundant EMF observed in this study, both in terms of relative frequency within soil cores (abundance), and in the proportion of soil cores in which it was present (constancy). *Lactarius rubrilacteus* Hesler and Smith, was the second most common EMF observed in constancy and abundance. For each species, this applied to both the full sample (n = 108) and for the inside and outside dripline cores (n = 54 each). Table 3.2 presents these results and the 10 most common morphotypes observed in this study. The most common EM types, stratified by inside or outside dripline groupings, were no different than those for the total study. There were slight differences in the rankings for each morphotype within each subgroup, and even lesser differences in relation to site (not shown). Table 3.3 shows the most abundant EM types prior to the application of the thinning treatment. This is not directly comparable to the post-treatment condition, as the samples were taken in different places than the post-treatment samples.

Visual inspection of the rank-abundance curves, by constancy (Figure 3.7A) and abundance (Figure 3.7B) suggests that they all most-closely follow the log-normal distribution (Magurran, 1988). One morphotype is dominant in all cases (*C. geophilum*), with 5-7 subdominant types. This is followed by a lengthy tail of a relative even distribution of types, with a smaller number of very rare types, roughly equivalent to the number of dominant types. The outside dripline cores lack the long tail of successively rarer types. The dominant EM type within individual soil cores varied, but it was usually one of the morphotypes that was most common across the whole study.

TABLE 3.2: Overall constancy, and constancy stratified by inside- and outside- dripline position for the ten most common EM types found in the 15% BA-D treatment of three blocks in the DEMO study.

Morphotype	Constancy[1]		
	Total	Inside	Outside
	n = 108	n = 54	n = 54
Cenococcum geophilum	96.3	100	92.6
Lactarius rubrilacteus	54.6	68.5	40.1
Rhizopogon vinicolor	40.0	44.4	31.5
11C (russuloid)	30.6	29.7	40.1
8G (thelephoroid)	27.8	25.9	29.6
Truncocolumella citrina	23.1	27.8	18.5
8B (??*Hysterangium spp.* Or Cortinoid.??)	23.1	35.1	11.1
12E	19.4	22.2	16.7
Amphinema byssoides-like	18.5	20.4	16.7
2C (??*Gautieria spp.* ??)	18.5	24.1	12.9

[1] Percent of soil cores with the type present

TABLE 3.3: Overall constancy for the ten most common EM types found pretreatment in the 15% BA-D treatment of three blocks in the DEMO study.

Morphotype	Constancy[1]
	Total
	n = 36
Cenococcum geophilum	94
Lactarius rubrilacteus	67
Suillus lakeii	50
10A (*Rhizopogon* villosuli-group)	47
8B (??*Hysterangium spp.* Or Cortinoid??)	44
Rhizopogon vinicolor	44
12B (Cortinoid)	44
9B/10D (*Russula xerampalina/ R. spp.*)	36
12E	31
2C (*Gautieria spp.??*)	28

[1] Percent of soil cores with the type present

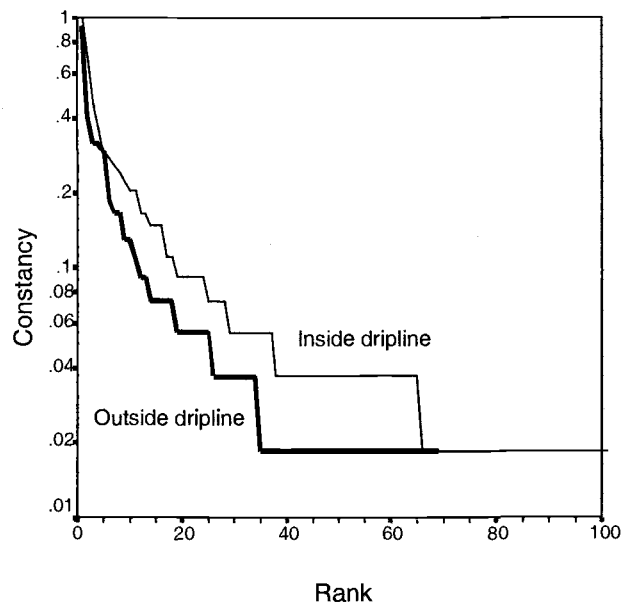FIGURE 3.7A: Rank-constancy curve for inside and outside dripline populations. (n = 54 each, 101 morphotypes for inside dripline, 69 for outside dripline. Constancy = proportion of samples containing a given EM type.)
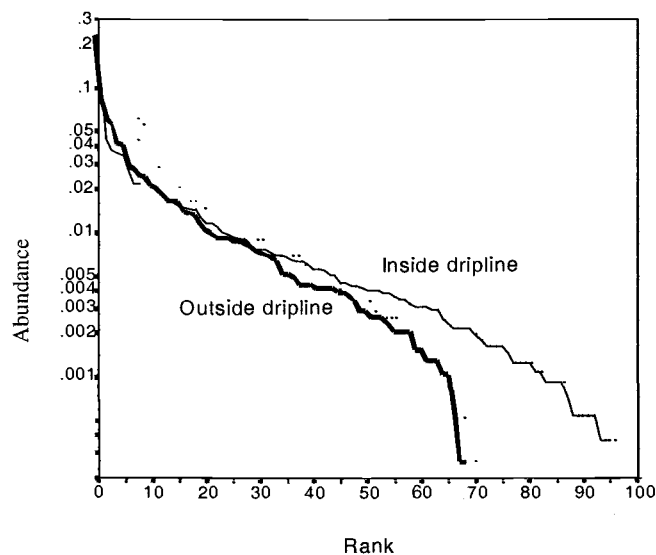
FIGURE 3.7B: Rank-abundance curve for inside and outside dripline populations. (n = 54 each, 101 morphotypes for inside dripline, 69 for outside dripline. Abundance = mean relative frequency of each morphotype)

There were significant differences in community structure among sites, by dripline position class, and by subplot (Table 3.4). There was a suggestive influence by dripline position. There was no significant difference due to the sapwood area of the host tree or root density, after accounting for differences due to the site influence. The A-statistic in the MRBP and MRPP tests ranges from –1 to +1. A value of zero indicates that the within-group variation equals what would be expected by chance alone, a value of +1 indicates absolute within-group agreement, and a value of –1 indicates that the variation within groups exceeds that expected by chance alone. For those tests revealing significant group differences, it must be cautioned that the agreement within groups is still highly variable.

An ordination of sample points coded by site reveals a distinct composition for each site (Figure 3.8). Watson Falls and Dog Prairie more similar to each other than either is to Hamilton Buttes (Figure 3.8). The abundance of three

morphotypes, exhibited high correlations with the first axis of the NMS ordination (accounting for 31.6% of total community variation): *Truncocolumella citrina* (r^2 = 0.494), *Lactarius rubrilacteus* (r^2 = 0.573), and *Rhizopogon vinicolor* (r^2 = 0.635). Samples from Hamilton Buttes site tended to have higher scores on NMS Axis 1, while samples from the Dog Prairie site had higher scores on Axis 2.

TABLE 3.4: Tests for group differences by dripline position, inside- or outside dripline position, sapwood area, root density (MRBP tests) and site, and subplot (MRPP tests).

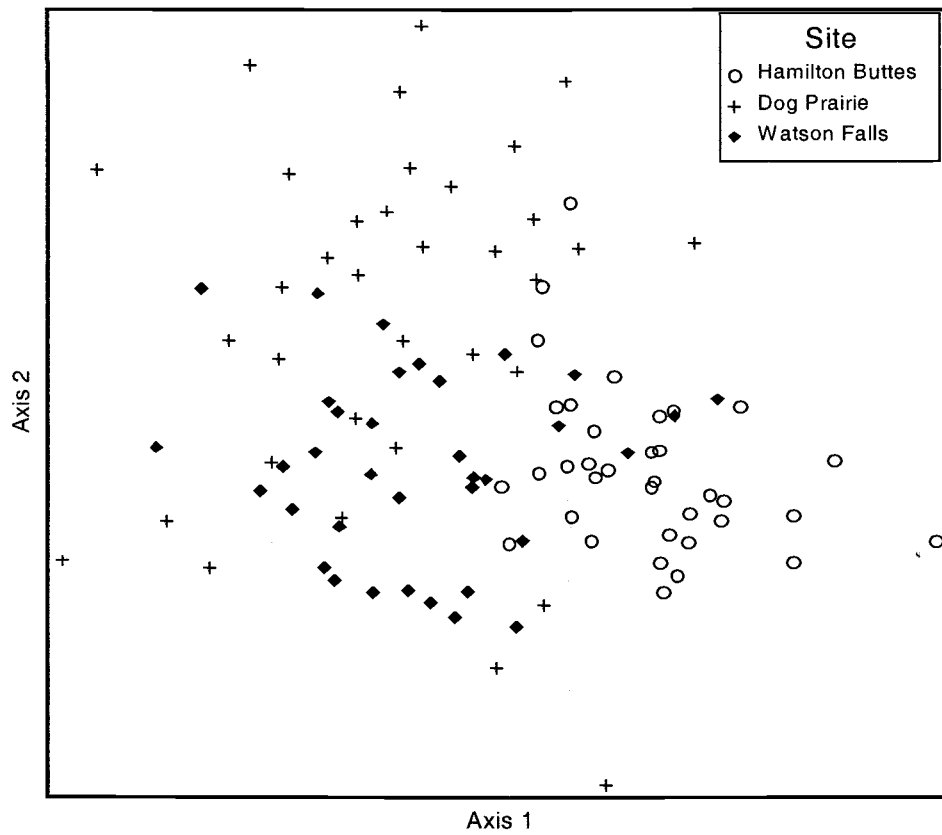| Group distinction	A-statistic	p-value
Dripline	.046	.042
Inside vs. outside dripline	.029	<.001
Sapwood area	.017	.262
Root density	.030	.109
Site	.045	<.001
Subplot	.068	<.001

FIGURE 3.8: First two axes of NMS ordination of samples in species-space. Axis 1 $r^2 = 0.32$, Axis 2 $r^2 = 0.27$. For three blocks of the 15%BA-D treatment in the DEMO study.

DISCUSSION

SAPWOOD-AREA INFLUENCE ON FINE ROOT DENSITY AND EM TYPE RICHNESS

We detected no relationship between tree productivity and root density, but several studies have shown that root density is related to above-ground productivity. Ares and Peinemann (1992) found that higher root density was associated with low site productivity, and individual tree height-growth in conifer plantations in Argentina. They suggested that trees maintain a large fine root system at the expense of above-ground growth. These findings were supported by Vogt *et al.* (1983, 1987), who found that above-ground productivity of stands was inversely correlated to root biomass. A variety of biological mechanisms may be responsible for our failure to reject the null hypothesis that the sapwood area of retention trees had no effect on root density or EMF morphotype diversity per soil core. The trees available in this study were relatively homogeneous: trees retained in our study sites were dominant or codominant trees in the pre-thinned stand (Aubry *et al.*, 1999), thus there were no suppressed trees available for inclusion in our study. This was problematic, as the range of tree sapwood area in retention trees was much lower than it would have been in an unmanaged forest. Suppressed trees would have greatly expanded the lower end of the host-tree sapwood area scale, giving us greater resolution to test our hypothesis of the relationship between tree productivity, root density and EM type richness.

Curtis (1987) found that the largest, most productive trees in a stand increased their dominance in the stand after thinning was applied. That study examined a wide range of levels of thinning, and the results were consistent across treatments. Trees released by thinning allocate a lower proportion of total photosynthate below-ground, increasing wood production instead (Waring and

Running, 1998). The most productive trees in the pre-thinned stand will allocate proportionally less carbon below ground than those that were less productive. In Chapter 2 (this volume) we demonstrated that there was no significant difference in mean EM type richness between soil cores taken from the pre-treatment and soil cores taken within the dripline of retention trees post-treatment. It is possible that the inside dripline EMF richness reflected a legacy from the pre-treatment condition of the forest. The sapwood area measured post-treatment instead reflected the individual tree's response to thinning, and may not represent the pre-treatment productivity of a given tree.

Another rationale that may relate to our inability to reject the null hypothesis invokes the observation that more productive trees frequently have greater lateral spread of their crowns, and thus their root system, too (Eis, 1987; Kuiper and Coutts, 1992; McMinn, 1963). Although increased total EM type richness may well be a property of productive trees, it might not be reflected in equal small-volume samples. This study utilized a sampling scheme where each tree was sampled equally. A two-tiered sampling scheme may have been more appropriate: firstly, using a fixed volume sample to determine root density, and secondly sampling an equal proportion of each trees' root system to determine EM type richness.

DISTANCE-FROM-RETENTION-TREE INFLUENCE ON ROOT DENSITY AND EMF DIVERSITY

Studies have shown that the structural root system of Douglas-fir trees is primarily restricted within the dripline of the tree (Eis, 1987; Kuiper and Coutts, 1992; McMinn, 1963). This study has shown that fine roots are concentrated in the same area, confirming the results of Parsons *et al.* (1994), who found that the number of living fine roots significantly declined within 5-6 m from the boles of trees in experimentally formed canopy gaps. Wilczynski and Pickett (1993) report

similar results, however, reduced numbers of living roots can still be found well-removed from the dripline area of trees. Ferrier and Alexander (1985) found that living fine roots persisted for at least 9 months after excision from their parent tree. Although sampling in this study was from 15-21 months post-harvest, many of the roots found in the outside dripline soil cores may have been remnant from the root systems of harvested trees. In these soil cores, a large number of dead roots were observed, but not quantified. Parsons *et al* (1994) suggest that intraspecific root grafting may be responsible for keeping fine roots alive in the soil in areas well removed from retention trees. Such root grafting could explain the maintenance of low levels of root density and EM type richness away from green trees in this study.

EM type richness per unit area declines with distance from the retention trees in accordance with the decline in root density. Since the trophic resource for which EMF compete is carbon from the individual root tip, this decline can be examined within the context of McArthur and Wilson's (1967) Island Theory of Biogeography: species richness responds to the habitat area available to them. Harvey *et al* (1980) examined the effect of distance from a forest edge into a clearcut on EMF diversity and root density. Two years after harvest they found that the mean number of ectomycorrhiza tips per unit volume soil declined sharply 1.5m into the clearcut, and declined to zero at a distance of 7.6m into the clearcut. That study was conducted in Douglas-fir/larch forests in Montana. Those forests generally have smaller diameter trees than forests in the western Cascades. Therefore it is likely that the 1.5m distance at which they detected a significant effect is similar, relative to the spatial spread of the root system and dripline of the trees, to the distance at which effects were found in this study. Barg and Edmonds (1999) detected a 22% decline in microbial biomass (including mycorrhizal fungi), within 2-5 years of harvest, between sampling points within 1m of retention trees in a Douglas-fir forest and 6m distant from retention trees: roughly the same distance over which this study distinguished between inside and outside dripline soil cores.

Bruns (1995) acknowledged the importance of elucidating the relationship between mycorrhizal diversity and root density in the soil. Although the design of this study did not allow us to make any statements regarding causation, it is clear that there is a strong, positive correlation between EM type richness and root density in the soil. This relationship has profound implications, because high root density is associated with both low individual tree growth and site productivity (Vogt *et al.*, 1987; Fraser and Gardener, 1967; Keyes and Grier, 1981; Meyer, 1967; Reynolds, 1975; Sika, 1969). Vogt *et al* (1987) suggest that trees on low productivity sites have high root density to facilitate greater nutrient uptake. Therefore, in poor environments, it may be vital to preserve existing EMF diversity to preserve forest productivity. Both highly productive managed and unmanaged forests, however, may well have inherently low EMF diversity due to readily available nutrient pools. This may be explained by the findings of Castellano and Molina (1989), who demonstrated that plants are less likely to engage in mycorrhizal partnerships when nutrients are in abundance.

Although light is frequently considered the space-limiting resource for new-plant colonization, the importance of the creation of below-ground gaps in the rooting matrix of the soil cannot be ignored. The spatial extent and magnitude of the root gap may be critical. There likely are trade-offs between the creation of complete root gaps which allow space for colonization, but the loss of EMF inoculum potential (Harvey *et al.*, 1980), and partial root gaps (Parsons *et al.*, 1994; Wilczynski and Pickett, 1993) which can retain up to 65% of EM type richness *in situ*.

COMMUNITY STRUCTURE OF EMF IN THINNED STANDS

Like many other studies of EMF diversity and community structure in temperate coniferous forests, the most common EM type found was *Cenococcum geophilum* Fr.. By our measure of relative abundance, *C. geophilum* accounted for

18.7% of the total EMF community in the 15% BA-D treatment, and was found in nearly every sample (Table 3.2). This measure of the relative abundance of *C. geophilum* is close to the 20% of EMF root-tips in clear-cuts, found two years post harvest found by Hagerman *et al.* (1999). Kranabetter and Wylie (1998) found that *C. geophilum* accounted for 18.9% of EM root-tips in their study on naturally regenerated hemlock seedlings in harvested forest gaps. Goodman and Trofymow (1998) found *C. geophilum* to account for 24% of EM root-tips in their study, and it was most common in the surface layers of the soil. Although *C. geophilum* is clearly one of the most abundant EM types in coniferous ecosystems, it is more resistant to decay than most other EM types due to its highly melanized mantle structure. Its high relative abundance is, then, partially due to a slower turnover rate.

The other most frequent known EM types encountered were *Lactarius rubrilacteus* Hesler & Smith, *Rhizopogon vinicolor*, *Truncolumella citrina* Zeller, and *Amphinema byssoides*. *R. vinicolor*, and *T. citrina* both produce hypogeous sporocarps. This prescription for green-tree retention (15% BA-D on Unit 5 of the DEMO study) clearly preserves viable populations of these fungal species in the system. In contrast to *C. geophilum*, *R. vinicolor*'s relative abundance is underestimated. It forms clusters (tuberculate mycorrhizae) of more than 100 root-tips within a single tubercle. In our scheme of measuring relative abundance, each tubercle usually only receive a score of 1 (out of 36). We do not know the identities of the other most-common EMF types found, and some of the morphotypes may represent multiple taxonomic entities. Although this may call into question the accuracy of the measures we obtained for EMF type richness per soil core, it is a systematic bias that should make cross sample comparisons valid. Egger *et al.* (1999) showed that many EM morphotypes (especially those with a thick mantle) produce a single, repeatable genetic pattern when using RFLP analysis, whereas some EM morphotypes (primarily those with poorly developed mantles) did produce multiple genetic patterns. In another system, a study comparing morphological classification (by a biologist without taxonomic training) and

taxonomic classification methods (by a taxonomic professional) in insects showed that although several individual species were divided into erroneous multiple species, this was offset by many species complexes being lumped together (Oliver and Beattie, 1996). Although this type of information would not be accurate to use for producing species lists, it was shown that there was no significant difference between the diversity indices calculated from these two methods of identification.

The rank-abundance curves in this study show the same log-normal distribution as many other studies of EMF communities in disturbed temperate coniferous forest habitats (Gehring *et al.*, 1998; Horton and Bruns, 1998; Jonsson *et al.*, 1999; Kranabetter *et al.*, 1999; Mahmood *et al.*, 1999). Visser (1994) found that the communities they sampled best approximated the broken-stick model of species abundance. According to a review by Sugihara (1980), the log-normal distribution is one of the most common observed in community ecology, and is strongly associated with complex, mature communities. Unlike the broken-stick model, which is theoretically restricted to ecological communities structured along a single resource gradient, the log-normal distribution implies that there are many different gradients acting simultaneously to structure the community, which is in agreement with the general principles of niche theory. This suggests that EMF communities are not simply full of redundant species, but that species are responding differentially to various habitat factors. One factor that may shape community structure of EMF is moisture. As mentioned in the results, Hamilton Buttes were sampled within a few weeks of snowmelt. Therefore, soil moisture was considerably higher than at Watson Falls and Dog Prairie, which were sampled in the late summer after a prolonged hot dry period. The sampling points from Hamilton Buttes all have high NMS scores on the first axis (Figure 3.8). The abundances of *T. citrina,* and *R. vinicolor* both have strong positive correlations with this axis of ordination, and *T. citrina* has been observed to fruit less in drier habitats (Luoma, 1991).

The complex nature of the community structure of EMF in this study is further illustrated by the fact that differences increased as the distance between

sampling points grew, but there was greater within-group similarity again at the stand level. It appears as though there are stand level phenomena significantly affecting EMF community structure, in addition to individual tree influences. These findings are supported by Kranabetter and Wylie (1998) who found community similarity decreased with increasing distance between sampling points within the stands they sampled, but with greater similarity within stands than across stands.

That there is a loss of EM type richness due to timber harvesting is undisputed, but which particular EM types are being lost? Chapter 2 (this volume) demonstrated that there was no significant difference in mean sample EM type richness between the pre-treatment forest condition and that found at the base of the retention trees. We also saw a minor shift in which EMF types were most common inside and outside the dripline of retention trees. The rank-abundance curves (Figure 3.7b) for the inside versus outside dripline cores shows that the distribution of types is similar up to the rapidly declining tail, representing rare types not found outside the dripline. Although some of the losses may be due to microclimate changes attributable to the thinning, this lack of rare types suggests that the probability of a type being lost from the harvest unit is tightly connected to low abundance pre-treatment, and the loss of the host tree, and less to do with microclimatic shifts due to thinning. If this is true, EMF communities seem to fall closer to the individualistic type of community structure originally theorized by Gleason (1926) than the organismic model proposed by Clements (1916). Gleason's model of community structure states that the community is a collection of species that have come to be present due to random events in the history of the community, as opposed to Clements view which states that the community is a more tightly coevolved unit. The loss of EM types seems to be concentrated on those that are more rare. It seems that the community structure (over the time frame we were able to examine it) is not driven by species differential responses to the disturbance, but more directly to the probability that some types are lost by nature of being attached to roots of trees that are killed.

CONCLUSIONS

No relationship was detected between the photosynthetic potential of retention trees and their root density and EM type richness. We did detect higher variability in community structure, reduced root density, and subsequently lower EM type richness immediately outside the dripline of retention trees, as compared to inside the dripline. However, as long as the spacing of trees in green-tree retention harvests is not so wide to create major root gaps (absence of all roots), these types of harvests may prove to be an effective way of preserving EMF diversity and retaining legacy material from the parent stand. This may be critical if the objectives of management decisions are to preserve biological diversity and to facilitate the conversion of even-aged stands into more old-growth-like structures. Even in cases where the mycorrhizal fungi may be able to recolonize, the importance of maintaining ecological processes in the soil cannot be understated.

There is considerable difficulty in analyzing the structure of ecological communities that demonstrate such high beta-diversity as EMF communities. No study of EMF community structure has sampled intensively enough to capture all EM morphotypes or species in any given area. EM type accumulation curves generated in this study showed an incomplete sampling of the EMF community. The labour-intensive nature of sampling these cryptic communities precludes enough sampling to obtain a reasonable approximation of community structure in all but the simplest of communities. Using the second-order jackknife estimate, our sampling scheme detected 70% of the EM types predicted to exist within the study areas. But, the jackknife estimates of the total number of morphotypes present by inside- versus outside-dripline position, in each block, and for the whole study may underestimate the real level of diversity present. The jackknife estimator variables are sensitive to extremely heterogeneous communities, and can never be greater than two times the number of species observed (Palmer, 1995).

The species-accumulation curves for each site (Figure 3.6) appears as though it would flatten at roughly 55-60 samples for Watson Falls and Dog Prairie.

For a more nearly complete survey of EM morphotypes over this spatial scale, further sampling would be necessary, with even greater sampling effort necessary at Hamilton Buttes. This study spanned considerable geographic distance: from the Umpqua River watershed of southern Oregon to Mount Adams in the central Washington Cascades. Due to the similarity of the dominant and codominant EM types at all three sites in this study, it may not be necessary to capture all morphotypes at any given site, but only to ensure capture of adequate numbers of dominant types for the purposes of testing the hypotheses laid out for this study. This is analogous to sampling plant communities and focusing on trees and shrubs in order to determine what the major patterns of community structure are. This is a level of detail in EMF communities that so far continues to elude us. The use of an increased number of smaller samples may well provide us with the level of replication required for conducting robust community statistical analysis. It is also vital to measure as many environmental variables suspected to be important in the regulation of EMF communities as possible.

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CHAPTER 4
CONCLUSION

These studies were part of the Demonstration of Ecosystem Management Options (DEMO) study, an interdisciplinary program involving research into the effects of various levels and patterns of green-tree retention on a variety of ecological, economic and social phenomena. We restricted our analysis to a single treatment of the DEMO study (15% BA-D). Three sites within the DEMO study were used and treated as blocks. We found a significant reduction in EMF type richness as a result of the thinning treatment. Within the dripline of retention trees, however, there was no significant decline in the mean number of EM types, but in areas as far removed from trees as possible, there was up to a 50% decline in the richness of EM types per soil core. The soil cores taken within the dripline and at the edge of the dripline had no significant differences in EM type richness or community structure when compared to each other. When compared to soil cores taken just outside the dripline and in open areas, a significant loss of EM type richness was detected, as was a shift in overall community structure. EM type richness was found to be significantly, and positively, correlated with fine-root tip density in the soil. The sapwood area of retention trees, however, had no significant correlations with either root density, EM type richness or community structure.

The structure of the EMF community studied here closely followed the log-normal distribution. This distribution is most often seen in complex, mature communities. In the outside dripline soil cores, there were very few rare or infrequent types observed, which suggests that the probability of an EM type being lost is linked with its pre-disturbance abundance, and the loss of its tree host. It probably has less to do with adaptation to specific microsite differences. *Cenococcum geophilum* was the most abundant EMF type observed, accounting for 18.7% of the total EM root tips examined. This type occurred in nearly every sample, and its dominance has been observed in many other studies.

This study showed that retention trees can serve as important refugia for EMF. These biological legacies from the pre-disturbance stand may serve as multiple staging-grounds for recolonization of EMF onto new seedlings. For those fungi that are lost from these treatment units, some hypogeous fruiting species, and those fungi adapted to mature forest structural elements (ie. moisture, temperature and nutrient regimes) recolonization may occur from neighbouring forest stands, provided the distance to the center of the harvested area is not so great as to limit spore dispersal.

Silvicultural methods that are designed to maintain higher levels of biodiversity in a stand are a new phenomenon in forestry. The existence of a goal such as this within an industry that has been concerned, primarily, with providing humans with wood products for consumption, is testament to the changing paradigms in forestry. This study showed that retention of green-trees can be an effective method to preserve EMF. This preservation should facilitate more rapid formation of mycelial networks of dispersal-limited fungi and those limited by poorly understood establishment requirements. By maintaining these elements in the harvest unit, diversity of EMF is maintained at higher levels than in clearcuts. As a result of this, recovery of biodiversity and maintenance of biological productivity in forests should be enhanced. Preservation of a wide diversity of EMF should increase the resilience of damaged ecosystems and maintain resilience where it might otherwise be threatened.

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