The spatial influence of *Pseudotsuga menziesii* retention trees on ectomycorrhiza diversity

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Abstract: Living retention trees are being used in managed forests to promote a variety of values, including the maintenance of biological diversity. Federal forest plans for the northwestern USA include guidelines that require the retention of a minimum of 15% basal area in harvest units, with the goal of facilitating the development of late-seral stand structure, which is an important habitat element for old-growth forest-dependent species. However, effective levels and patterns of green-tree retention are unknown. We present results of a treatment consisting of 15% basal area, evenly dispersed retention (15%D). We quantified changes in the ectomycorrhiza (EM) community after the 15%D treatment, both near and away from retention trees. Pretreatment samples were obtained between 1 and 24 months before tree harvest. Post-treatment samples were collected within 14–25 months of harvest. In areas 8–25 m from retention trees, there was a 50% decline in the number of EM types per soil core from before to after treatment. Soil cores taken >5 m from retention trees exhibited a shift in EM community structure. EM-type richness was positively correlated with fine-root-tip density. We demonstrate the potential for retention trees to act as refugia for recolonization of newly established seedlings by ectomycorrhizal fungi.

Résumé : La rétention d'arbres vivants est utilisée dans les forêts aménagées pour promouvoir une variété de valeurs, incluant le maintien de la biodiversité. Les plans d'aménagement des forêts fédérales dans le nord-ouest des États-Unis contiennent des directives qui suggèrent de conserver au moins 15 % de la surface terrière dans les unités de récolte avec pour objectif de favoriser le développement de la structure du peuplement climacique, qui constitue un aspect important de l'habitat pour les espèces qui dépendent des forêts anciennes. Cependant, on connaît ni la proportion, ni la répartition des arbres à conserver qui permettraient d'atteindre cet objectif. Dans cet article, nous présentons les résultats d'un traitement où la rétention de 15 % de la surface terrière a été également dispersée (15 %D). Nous avons quantifié les changements dans la communauté d'ectomycorhizes après le traitement 15 %D, à proximité et loin des arbres conservés. Des échantillons ont été prélevés entre un et 24 mois avant la récolte et à l'intérieur de 14 à 25 mois après la récolte. Dans la zone située de huit à 25 m des arbres conservés, il y avait une diminution de 50 % du nombre de types d'ectomycorhizes par carotte de sol après le traitement. Les carottes de sol prélevées à plus de cinq mètres des arbres conservés montraient un changement dans la structure de la communauté d'ectomycorhizes. La richesse des types d'ectomycorhizes était pratiquement corrélée avec la densité d'apex de racines fines. Nos résultats démontrent que les arbres conservés peuvent servir de refuge.

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Introduction

Foresters and land managers today are expected to manage forests and ecosystems for a variety of values, including the maintenance or restoration of biological diversity. Management for uneven-aged stands is a silvicultural alternative to clear-cutting that retains biodiversity at the stand and landscape levels (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 (living) trees in the harvested units (Rose and Muir 1997).

Green-tree retention may enhance seedling nutrition and survival through maintenance of mycorrhizal inoculum on site. Several studies in northern temperate forests have examined the effects of silvicultural practices on the ectomycorrhizal fungus (EMF) community (see the review by Jones et al. 2003). Most studies have focused on the effects of disturbance on residual fungus inoculum and on the diversity of ectomycorrhiza (EM) types on seedlings planted in situ or in a greenhouse for use in experiments (Pilz and Perry 1984; Harvey et al. 1997). Some studies also examined EM diversity on seedlings planted near forest edges or aggregates of retained living trees (Kranabetter and Friesen 2002;

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Table 1. Descriptive characteristics of the three study blocks.

	Hamilton Buttes	Dog Prairie	Watson Falls
Elevation (m)	975–1280	1460–1710	945–1310
Slope (%)	40–53	34–62	4–7
Aspect	E-SE	SW	Flat
Precipitation (mm)[a]	1860	1683	1443
Stand age (years)	70–80	165	110–130
Forest zone[b]	*Tsuga heterophylla*	*Abies concolor*	*Tsuga heterophylla*
Overstory cover (%)[c]	72–82	68–78	51–70
Latitude and longitude	46.37°N, 121.59°W	43.20°N, 122.20°W	43.27°N, 122.34°W

Note: Where ranges are presented, minimum and maximum values represent treatment-unit means (modified from Halpern et al. 2005).

[a]Estimated mean annual precipitation, derived from DAYMET (Thornton et al. 1997), a set of 1 km GIS raster coverages that were generated from meteorological records (1980–1997) and digital elevation data.

[b]Defined by potential climax tree species (Franklin and Dyrness 1973).

[c]Estimated using a moosehorn densiometer.

Outerbridge and Trofymow 2004; Cline et al. 2005). A universal finding emerges from this work: the EMF community, as seen on root tips, changes significantly in disturbed sites compared with undisturbed nearby forests. These changes might be due as much to environmental and biotic factors as to loss of host trees (Jones et al. 2003).

Substantial research suggests that both the diversity and inoculation potential of EMF decline within 2 years of harvest (Parke et al. 1984; Harvey et al. 1997; Kranabetter et al. 1999). Because of the importance of mycorrhizal fungi in belowground food webs, alteration of the mycorrhizal community can affect early stages of plant succession (Gange and Brown 2002). Seen in this light, green-tree-retention harvesting may protect EMF diversity and maintain an ecological legacy from the preharvested stand that can be carried forward to the newly developing forest.

While the trophic resource for which EMF compete is carbon from individual root tips, the spatial resource for which they compete is the root tip itself (Smith and Read 1997). The community structure of EMF may vary with distance from the bole of host trees. Different species were observed to fruit at different distances from trees, and below ground, the EMF community varied similarly (Mason et al. 1987).

To provide habitat for the old-growth forest-dependent northern spotted owl, under the Northwest Forest Plan, a guideline was created that requires the retention of a minimum of 15% basal area in harvest units to facilitate the development of uneven-aged stands (USDA Forest Service and USDI Bureau of Land Management 1994*a*, 1994*b*). Although it is widely believed that retention harvests confer many ecological benefits on forest ecosystems, effective levels and retention patterns are unknown, and according to Franklin et al. (1999) there was little scientific basis for choosing this particular level (15% basal area) of retention for the Northwest Forest Plan.

Our study of ectomycorrhizae is a part of an integrated research program that examines the effects of various levels and patterns of green-tree retention on a variety of ecological and social values: the Demonstration of Ecosystem Management Options (DEMO) experiment (Aubry et al. 1999). The experimental design, with five treatments and a control, was replicated at six sites, two in Oregon and four in Washington. Treatments included 75% basal area retention with group selection, 40% basal area aggregated and dispersed retention, and 15% basal area aggregated and dispersed retention. DEMO harvests began in the spring of 1997 and were completed in 1998. For additional details on the overall experiment see Aubry et al. (1999) and Halpern et al. (2005).

The 15% basal area dispersed green-tree retention DEMO treatment allows examination of one silvicultural component of the Northwest Forest Plan. Given concerns regarding the loss of EMF diversity and inoculum potential in clearcuts, we perceived a need to document the effects of 15% basal area, evenly dispersed (hereinafter referred to as 15%D) green-tree-retention harvest on EMF diversity at the spatial scale of individual trees. We hypothesized that there would be an overall decline in EMF diversity within the harvested stands, and that the retention trees would serve as refugia, maintaining a higher level of EMF diversity near them than would be found in treeless areas between them. Furthermore, based on the pipe model theory (Shinozaki et al. 1964) we hypothesized that greater photosynthetic potential (measured by cross-sectional sapwood area) in a tree correlates with denser roots, and supports higher levels of EMF diversity, owing to an increased number of fine roots available for colonization. Our objectives were to quantify changes in EM-type richness after the 15%D treatment, both near and away from retention trees; determine relationships among cross-sectional sapwood area of retention trees, root density, and EM-type richness; and test for effects of retention-tree photosynthetic potential, root density, and distance from the tree on EMF community structure.

Materials and methods

Description of study sites

Three DEMO study sites (blocks) were used: Hamilton Buttes (Gifford-Pinchot National Forest, Washington), Dog Prairie, and Watson Falls (Umpqua National Forest, Oregon). Block and stand characteristics are presented in Tables 1 and 2. Hamilton Buttes had no previous history of timber harvesting, Dog Prairie was previously thinned in 1986, and Watson Falls was salvage-logged between 1970 and 1978. All blocks were strongly dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Tsuga*, *Abies*, and *Pinus* species were also present. For more complete site descriptions see Aubry et al. (1999) and Halpern et al. (2005). Fifteen percent of dominant- and codominant-tree

Table 2. Forest-structure characteristics of each experimental unit.

Block	Retention treatment[a]	No. of trees/ha	Basal area (m^2/ha)	Quadratic mean DBH (cm)	Stand-density index
Hamilton Buttes	100%	1119	58.2	25.7	1143
	15%D, pre	757	55.7	30.6	1021
	15%D, post	176	12.0	29.5	224
Dog Prairie	100%	295	89.6	62.2	1241
	15%D, pre	385	79.7	51.3	1191
	15%D, post	85	20.1	54.8	293
Watson Falls	100%	310	43.7	42.3	704
	15%D, pre	382	51.6	41.5	840
	15%D, post	87	8.4	35.1	147

[a]The 15%D treatment consisted of 15% basal area, evenly dispersed retention; "pre" denotes pretreatment and "post" denotes post-treatment.

basal area was retained in an evenly dispersed pattern in the treated stands. The treatment was applied in summer 1997 at Hamilton Buttes and summer 1998 at Dog Prairie and Watson Falls. Hamilton Buttes and Dog Prairie were yarded by helicopter and slash was left ungathered on site. Watson Falls was ground-yarded, with slash piled and burned. A control treatment unit was included in each block. All units were approximately 13 ha (slope-corrected) in size.

Field methods

Pretreatment sampling of EM was done in spring 1995 at Watson Falls, spring 1997 at Hamilton Buttes, and spring 1998 at Dog Prairie. Six 5.5 cm diameter by 15 cm deep soil cores (0.36 L) were extracted from both the 15%D and control experimental units at each site. For each soil core, the O_1 layer (fresh litter) was removed, leaving the rest of the L layer atop the 15 cm deep core. The F and H layers were little developed, totaling less than 1 cm in depth. One soil core was taken from each end of three strip plots that had been established to assess EM mushroom production (Fig. 1). These locations will hereinafter be referred to as permanent sampling points. The mushroom strip plots were systematically placed to provide distributed samples within each experimental unit (for details see Luoma et al. 2004). Six post-treatment soil cores were taken from the permanent sampling points (at a distance of 5–10 cm from the pretreatment soil-core holes) in both the control and 15%D treatment units. These were taken in June 1999 (Hamilton Buttes) and October 1999 (Dog Prairie and Watson Falls).

To address objectives related to individual trees, further post-treatment sampling involved subdividing the 15%D treatment unit at each site into nine equal-sized subplots (Fig. 1). In each subplot, three Douglas-fir trees were randomly selected and increment-bored once at breast height on the uphill side of the tree. A proxy measurement of photosynthetic productivity was obtained by calculating the cross-sectional sapwood area of each tree selected, using the methods of Waring et al. (1982).

It was found that trees at Hamilton Buttes had a lower mean sapwood area than trees at the other two sites. To permit better cross-site comparisons, trees at Hamilton Buttes with a sapwood area smaller than 400 cm^2 were excluded from the study, and trees at the other two sites with a sapwood area above 1400 cm^2 were excluded. At each site, the remaining range of sapwood areas was then divided into nine equal segments, and one tree was chosen from within each sapwood-area-range segment so that a single tree represented each subplot within each site. The nine selected trees at each site were then increment-bored a second time (120° around the tree from the first borehole). Sapwood area for each selected tree was then obtained as the mean of the two measurements calculated from the increment bores. These

Fig. 1. Schematic diagram of the sampling design for soil-core extraction within Demonstration of Ecosystem Management Options (DEMO) experimental units. Permanent points were sampled in the control and the treatment consisting of 15% basal area, evenly dispersed retention (15%D); open-area cores and host-tree cores were taken from the 15%D treatment only.

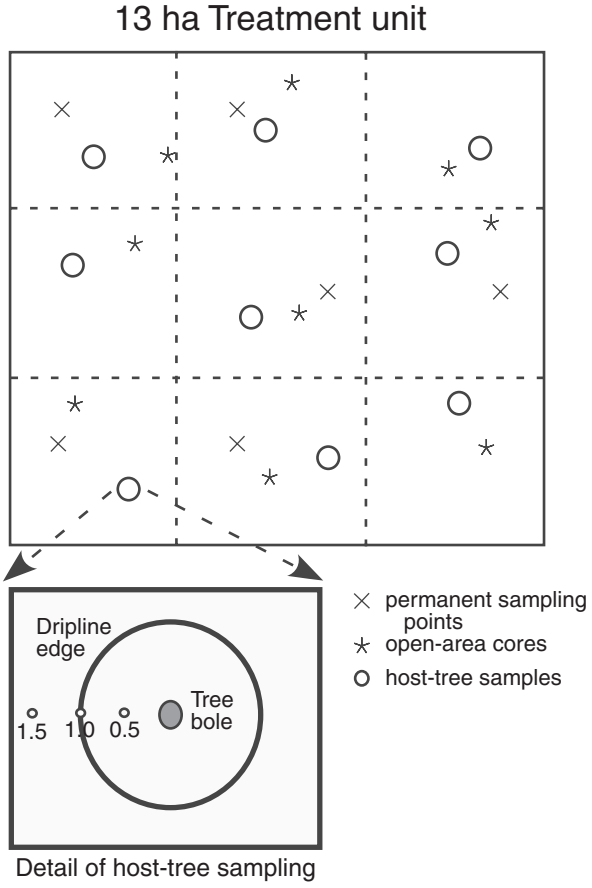


Table 3. Characteristics of host trees in the 15%D treatment, by block.

Block	Sapwood area (cm^2)[a]	Crown radius (m)	Open-area distance (m)[b]
Hamilton Buttes	651 (61)	2.8 (0.3)	9.8 (0.7)
Dog Prairie	966 (83)	3.4 (0.3)	12.1 (0.6)
Watson Falls	965 (95)	3.5 (0.4)	16.6 (1.2)

Note: Values are given as the mean with the standard error in parentheses.
[a]Cross-sectional sapwood area 1.35 m above mean ground level.
[b]Mean distance from open-area soil cores to the nearest tree.

trees are termed "host" trees for the EMF aspects of this study (Table 3).

We used crown width as a surrogate for root spread (Smith 1964). A transect, centered on each host tree, was established either across the slope or, in the case of Watson Falls, east–west (0% slope), and soil cores were taken at 0.5, 1.0, and 1.5 times the distance from the host-tree crown edge (dripline) to the center of the bole of the tree. Mean crown radius at each site is presented in Table 3. These soil cores are hereinafter referred to as 0.5 dripline, 1.0 dripline, and 1.5 dripline cores (Fig. 1). A further nine 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 an "open-area" soil core was taken in the opening that was the largest and farthest removed from any retention trees (Fig. 1). The distance of the open-area soil core from the nearest tree ranged from 8.3 to 14.7 m at Hamilton Buttes, from 10.2 to 15.0 m at Dog Prairie, and from 12.1 to 25.0 m at Watson Falls (also see Table 3).

In summary, there was a total of six permanent sampling points (sampled before and after treatment) for both the control and 15%D treatments at each site. In addition, for the 15%D treatment, there were 3 sites × 9 subplots per site × 1 tree per subplot × 3 soil cores per tree + 1 open-area soil core per subplot, for a total of 108 soil cores (27 independent samples with 4 subsamples each).

Laboratory methods

Soil cores were refrigerated in the field and stored at –20 °C immediately after return from the field. When soil cores were thawed they were examined within 48 h. Previous comparisons between refrigerated and frozen soil cores showed no effect on EM-type morphology when the cores were processed within this time frame (J. Eberhart, unpublished data). Soil cores were washed with an elutriator and screened with a 1 mm mesh sieve to remove soil particles and retain the fine roots. The contents of the sieve were spread evenly, with enough water to cover them, in the bottom of a 38 cm × 17 cm × 2 cm tray that was divided into 36 compartments by an inserted Plexiglas® partition. Roots were first examined with a stereomicroscope at 15–30× magnification and subsequently at 400–1000× magnification, with a compound microscope as necessary to confirm morphotype identity. All EM types found in each compartment were recorded, providing an index of abundance for each type that ranged from 1 to 36 (Eberhart et al. 1996). The abundance index was calculated as the percentage of the total number of compartments (soil-core subsamples) occupied by that type in each core (Table 4). Each EM type encountered was classified according to morphological characteristics similar to those described in Ingleby et al. (1990) and Goodman et al. (1996). Morphological characteristics included colour, texture, presence/absence of rhizomorphs and emanating hyphae, presence/absence of clamp connections, and mantle pattern. Morphotype identities were determined by comparison with the database maintained by Eberhart et al. (1996). EM types did not represent taxonomic species, with the exception of those that we could match to published descriptions (e.g., Eberhart and Luoma 1996; Goodman 1996; Harniman and Durall 1996*a*, 1996*b*; Eberhart and Luoma 1997, 2000) or identify using molecular techniques. Some of the commonest types (Table 4) were identified molecularly by use of restriction fragment length polymorphism (RFLP) or sequence matching of the ITS region of nuclear rDNA (Gardes and Bruns 1993; Horton and Bruns 2001). Reference material for RFLP matching consisted of sporocarps collected at the sites. Voucher collections are maintained in the laboratory of the senior author and were deposited with the Oregon State University herbarium (OSC).

For each soil core from the permanent sampling points, two EM root tips of each morphotype group were each placed in separate 1.5 mL Eppendorf tubes with 300 µL CTAB and stored at 5 °C until the DNA could be extracted. DNA was extracted using the cetyltrimethylammonium bromide (CTAB) extraction method without the β-mercaptoethanol (Gardes and Bruns 1993). Extracts that did not amplify using this method were cleaned using the GENE Clean III kit from Q-Biogene. Extracted DNA samples were stored in 50 µL Tris–EDTA buffer (1 mmol/L Tris–HCl, 0.1 mol/L EDTA) at –20 °F (–29 °C) until they were used in a polymerase chain reaction. For sequencing, DNA samples were sent to the Central Services Laboratory at Oregon State University and sequenced using an ABI 3100 capillary sequence machine. DNA sequences were edited using Sequence Editor and entered into the National Center for Biotechnology Information BLAST program to search for matches in the GenBank database. Sequence dissimilarities >2% were considered different species (Horton and Bruns 2001). EM types from the individual-tree soil cores were identified molecularly as necessary to integrate the morphotypes into the existing EM morphotype database developed from the permanent sampling point soil cores.

Root density was determined as the number of living fine-root tips in a standardized subsample of the soil core. In every sixth compartment of the tray, i.e., 6 of the 36 compartments, all living fine-root tips were counted. Fine-root tips were counted as living if the cortex was clearly turgid along some portion of its length. Roots of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were excluded from analysis at Hamilton Buttes, where this species was encountered as a minor understory component of the stand. No attempt was made to exclude roots of *Abies* or *Pinus* occurring in the samples, as these genera were rarely present near the selected *P. menziesii.*

Data analysis

EM-type richness

To test for significant changes in local (i.e., sampling point) EM-type richness associated with the 15%D treat-

Table 4. Mean constancy and abundance of the 10 commonest EM types found in the 15%D treatment in the Demonstration of Ecosystem Management Options (DEMO) study, stratified by inside- and outside-dripline soil cores.

Morphotype	ID method[c]	Constancy (%)[a]		Abundance (%)[b]	
		Inside dripline (n = 54)	Outside dripline (n = 54)	Inside dripline (n = 54)	Outside dripline (n = 54)
Cenococcum geophilum	PD	100	93	58	46
Lactarius rubrilacteus	PD, RFLP	69	41	28	12
Rhizopogon villosulus[d] (group)	PD, RFLP, sequence	46	31	7	6
Russula spp., primarily *R. xerampalina*	Sequence	37	31	18	17
Genea harknessii	Sequence	26	30	10	11
Truncocolumella citrina	PD, RFLP	28	19	6	6
Piloderma sp.	Sequence	35	11	13	4
Phialophora finlandia	Sequence	22	17	5	8
Unidentified "2C"		24	13	10	8
Amphinema byssoides-like	PD	20	17	4	5

[a]Percentage of soil cores with the type present.
[b]Mean percentage of subsamples within soil cores with the type present.
[c]PD, published description; RFLP, restriction fragment length polymorphism.
[d]Includes *Rhizopogon vesiculosus* and *Rhizopogon vinicolor.*

ment, each of the 12 permanent sampling points (6 each in the control and 15%D treatment) in each block were used. In addition, to tie any such changes spatially to retention trees, data from inside-dripline and open-area soil cores were used. For the control plots, an ANOVA model was run with the DEMO site entered as a blocking factor (n = 3) and a treatment variable with two levels (before or after) entered as a fixed-effects factor. For the 15%D treatment, 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 "pretreatment" (six pretreatment cores from the permanent sampling points at each site), "post-treatment with host tree" (to provide a balanced analysis, we used six randomly chosen 0.5 dripline cores from each site), and "post-treatment, open-area" (six randomly chosen open-area cores from each site). A term for the interaction between site and condition was entered in the model. When an overall difference was found, 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 are reported using the estimated marginal means from the final ANOVA model. The statistical tests described above were run using the General Linear Model module, General Factorial procedure in SPSS® software (SPSS Inc. Advanced Statistics version 7.0, SPSS Inc., Chicago,1996). In the case of the 15%D treatment, post-treatment analysis of the permanent sampling point soil cores was not included because the permanent sampling points were not stratified with regard to relative dripline location and thus would not have served to address the objectives of this study.

EM-type-accumulation curves were constructed using the Species–Area Curve Module of PC-ORD version 4.28 (McCune and Mefford 1999), which performs 500 randomizations of the sampling units. These were done separately for pre-treatment and post-treatment conditions in the treated units, and using only the six permanent sampling points in each unit. Estimates of the expected number of EM types for each grouping were provided by first-order and second-order jackknife estimates (Palmer 1990, 1991) using PC-ORD version 4.28.

Relationships among photosynthetic potential, root density, and EM-type richness

To determine the effects of tree photosynthetic potential on under-crown root density, a multiple regression model was constructed. Root density (the dependent variable) was log-transformed for normality. The independent variables in the model were host-tree sapwood area and a blocking factor for site. For this test, only inside-dripline soil cores (1.0 and 0.5 dripline distance classes) were used, as they were considered to be directly under the influence of the host tree. Since initial results showed that the two distance classes did not differ, the pooled data were used such that for each host tree, two root-density samples were obtained.

To determine the effects of photosynthetic potential on EM-type richness, another multiple-regression model was constructed. This model was constructed identically to that used to test for the relationship between photosynthetic potential 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.

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 factor subplot nested within the blocking factor (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 × root density interaction term. All the above statistical tests were run using the General Linear Model module General Factorial procedure with command-line syntax modifications for nesting block

Table 5. Number of ectomycorrhizal (EM) types per soil core, comparing the 100% and 15%D retention treatments, before and after treatment, and by dripline position.

	100% treatment	15%D treatment
Before treatment		
Permanent sampling points (n = 36)	8.9 (1.0)a	9.7 (0.7)a
After treatment		
Permanent sampling points (n = 36)	8.6 (1.2)a	na
Inside dripline (n = 18)	na	8.7 (0.6)a
Open area (n = 18)	na	4.5 (0.6)b

Note: Values are given as the mean with the standard error in parentheses. Values that are not followed by the same letter are significantly different at $p \leq 0.0001$ (na, not applicable, in the case of the 15%D treatment because the permanent sampling points were not stratified with regard to relative dripline location).

factors in SPSS® software (SPSS Inc. Advanced Statistics version 7.0, SPSS Inc., Chicago, 1996).

Analysis of community structure

EM-type-accumulation curves were constructed using the Species–Area Curve Module of PC-ORD version 4.28 (McCune and Mefford 1999), which performs 500 randomizations of the sample units. These were constructed for the pretreatment and post-treatment samples by site, and for post-treatment samples 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).

To determine differences in EMF community structure, five multiresponse permutation procedure tests were done, four blocked (MRBP) and one unblocked (MRPP), using PC-ORD version 4.28 and employing the Euclidean distance measure (McCune and Mefford 1999). In the MRBP and MRPP tests we used the A statistic as a measure of effect size. The A statistic is dependent on within-group homogeneity and has a maximum value of 1. A values < 0 indicate that homogeneity within groups is less than that expected by chance alone. An A value of 0 indicates that within-group variation equals that expected by chance alone. An A value > 0 indicates that homogeneity within groups is greater than that expected by chance alone, hence group differences may be significant (McCune and Grace 2002). Owing to the high level of β diversity among soil cores, group differences in the MRBP and MRPP tests were considered significant at $\alpha \leq 0.01$ (Mielke 1991). For all tests on group differences, the sample dissimilarity space was determined using an abundance matrix of 108 soil cores × 115 EM morphotypes.

Test 1 (MRBP) examined differences in the EMF community according to distance from the host tree, using subplot as the blocking factor. The test was run using four soil-core distances (0.5, 1.0, and 1.5 dripline cores and open-area cores) as a single variable with four classes. Test 2 (MRBP) compared the EMF community between the inside-dripline and outside-dripline soil core location classes. Test 3 (MRBP) determined the effect of host-tree photosynthetic potential on the EMF community. Host-tree photosynthetic potential, measured as sapwood area, 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. Test 4 (MRBP) determined the effect of root density on the EMF community. Root density was recoded into a categorical variable with three levels: low, medium, and high. Variable partitioning was done as for test 3. Test 5 (MRPP) examined differences in EMF community structure across blocks with site as the categorical variable.

Rank-abundance curves for the inside- and outside-dripline samples were constructed using Biodiversity Pro® software (McAleece et al. 1995). The resultant curves were visually compared with various species-abundance models presented by Magurran (1988) to infer the species-distribution models observed in the study.

Results

EM-type richness

In total, 115 EM types were recorded from 108 soil cores obtained from the 15%D treatment samples as part of the post-treatment retention-tree-centered study. Eighty-eight percent of these EM types were observed in the inside-dripline soil cores, while only 60% were observed in the outside-dripline cores. Non-EM root tips were virtually absent (<0.05%).

Three-way Tukey's comparisons of the mean number of EM types per soil core showed that open-area cores had fewer EM types than either pretreatment cores or post-treatment, host-tree cores ($F_{[2,49]} = 25.24$, $p < 0.0005$) (Table 5). Also, there was no difference in mean EM-type richness between control pre- and post-treatment and host-tree cores. The means reported in Table 5 are the estimated marginal means from the final ANOVA model, which takes into account the differences in EM-type richness due to the block (site) factor. Post-treatment 15%D permanent sampling plot cores are not included in the analysis because they are not part of the retention-tree-centered study (i.e., they were not located with respect to a "host-tree" dripline distance class).

Distance from the host tree had a highly significant effect on mean EM-type richness per soil core ($F_{[3,78]} = 24.75$, $p < 0.0005$; Fig. 2), while the tree-nested-within-site effect was not significant ($p > 0.1$). The 95% confidence intervals for EM-type richness overlapped between the open-area and 1.5 dripline classes, and between the 1.0 and 0.5 dripline classes (Fig. 2). This allowed them to be pooled into "outside-dripline" and "inside-dripline" soil-core classes, respectively. Outside-dripline soil cores average 32% fewer total EM types than inside-dripline soil cores (Table 6). Hamilton Buttes had the highest total EM-type richness of the three sites (using first-order and second-order jackknife estimates)

Table 6. Total observed numbers and estimated ranges of EM types, by dripline position, found in the 15%D treatment across three sites of the DEMO experiment.

	Inside dripline		Outside dripline	
Site	Observed no.	Estimated range	Observed no.	Estimated range
Hamilton Buttes	64 (n = 18)	105–134	36 (n = 18)	61–79
Dog Prairie	46 (n = 18)	65–72	30 (n = 18)	45–54
Watson Falls	44 (n = 18)	65–80	22 (n = 18)	31–35
Total	101 (n = 54)	136–145	69 (n = 54)	103–129

Note: Estimated ranges of total EM types represent results obtained from the first- and second-order jackknife estimators, respectively, using PC-ORD version 4.28.

Fig. 2. Estimated marginal mean numbers of ectomycorrhiza (EM) types per soil core by distance class within the 15%D treatment (with 95% confidence limits). Estimates account for the influence of site.

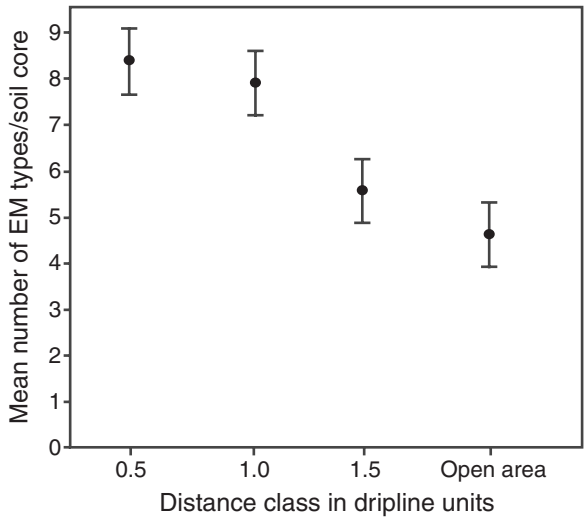


Fig. 3. EM-type-accumulation curves for inside- and outside-dripline groups (n = 54) based on 500 randomizations of the soil-core data.

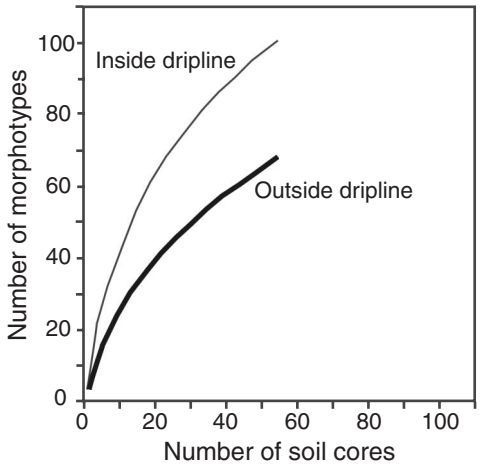
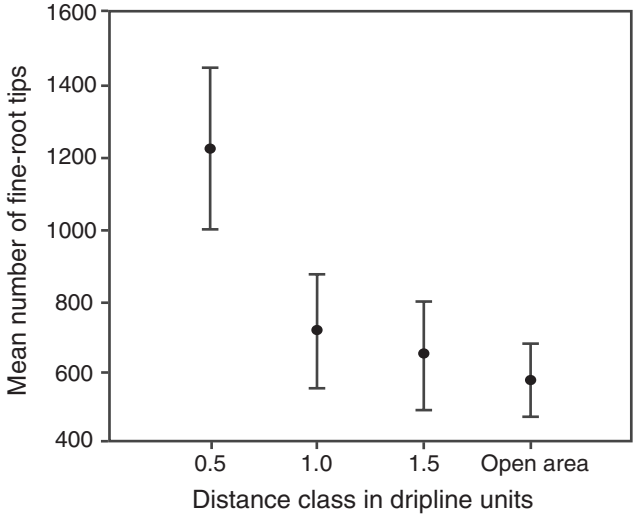


Fig. 4. Estimated marginal mean numbers of fine-root tips per soil core by distance class within the 15%D treatment (with 95% confidence limits). Estimates account for the influence of site.



but trends in EM-type accumulation by relative dripline position class were similar across blocks (Table 6 and Fig. 3).

EM-type richness and root density

The sapwood area of the host tree had no detectable effect on either EM-type richness or root density ($F_{[1,23]}$ = 0.97, p = 0.3, and $F_{[1,23]}$ = 1.9, p = 0.2, respectively). Root density declined at the edge of the dripline ($F_{[3,78]}$ = 2.6, p = 0.06; Fig. 4). The Hamilton Buttes block had higher root density than the other blocks ($F_{[2,24]}$ = 4.38, p = 0.02).

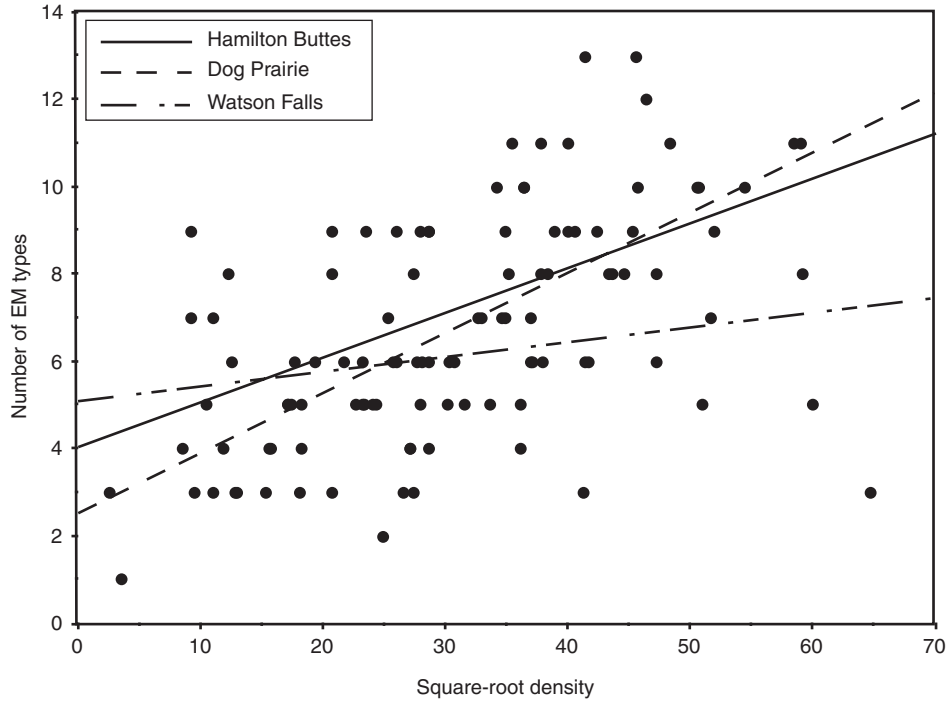
There was a strong positive correlation between EM-type richness and square-root root density (p < 0.0001), with no effect due to tree-within-site variance (p = 0.9). However, the relationship between root density and EM-type richness varied by site (p = 0.04). Hamilton Buttes and Dog Prairie both showed strong a positive correlation between root density and EM-type richness, whereas the weak positive correlation at Watson Falls was not significant (Fig. 5).

EM constancy and abundance

Cenococcum geophilum Fr. was the most commonly observed EMF, both in terms of the proportion of soil cores in which it was present (constancy) and in its frequency within soil cores (abundance). *Lactarius rubrilacteus* Hesler and Smith was the second most common EMF observed with respect to constancy and abundance. There was slight variation among the rankings of the other dominant morphotypes between the tree dripline classes (Table 6).

Visual inspection of the rank-abundance curves, by constancy and abundance (Fig. 6), suggests a log-normal distribution (Magurran 1988). One morphotype is dominant in all

Fig. 5. Regression relationships between square-root root density (number of EM root tips in a soil-core subsample) and EM-type richness (number of types in a soil core). The correlation was significant at Hamilton Buttes ($Y = 1.482 + 0.164 \times X$; $R^2 = 0.49$, $p < 0.0001$) and Dog Prairie ($Y = 2.521 + 0.141 \times X$; $R^2 = 0.51$, $p < 0.0001$) but not at Watson Falls ($Y = 5.084 + 0.033 \times X$; $R^2 = 0.04$, $p = 0.23$).



cases (*C. geophilum*), with five to seven subdominant types. This is followed by a lengthy tail of a relatively even distribution of types, with a smaller number of very rare types, roughly equivalent to the number of dominant types. The outside-dripline cores exhibit a shorter tail than the inside-dripline cores. The dominant EM type within individual soil cores varied, but it was usually one of the high-constancy morphotypes.

Multiresponse permutation procedures detected significant differences in EM-type community structure among sites (A statistic = 0.045, $p \leq 0.001$) by inside- or outside-dripline class (A statistic = 0.029, $p \leq 0.001$) (e.g., Tables 4 and 6, Figs. 3 and 6) and by subplot (A statistic = 0.068, $p \leq 0.001$). Differences among the original four dripline-position classes were less strong, likely as a result of homogeneities of the inside- or outside-dripline soil cores, as noted above (A statistic = 0.046, $p = 0.042$) (e.g., Figs. 2 and 4). There was no significant difference due to the sapwood area of the host tree (A statistic = 0.017, $p = 0.262$) or root density (A statistic = 0.030, $p = 0.109$) after differences due to site were accounted for. For tests revealing significant group differences, it must be cautioned that within-group homogeneity was low.

Discussion

EM-type richness

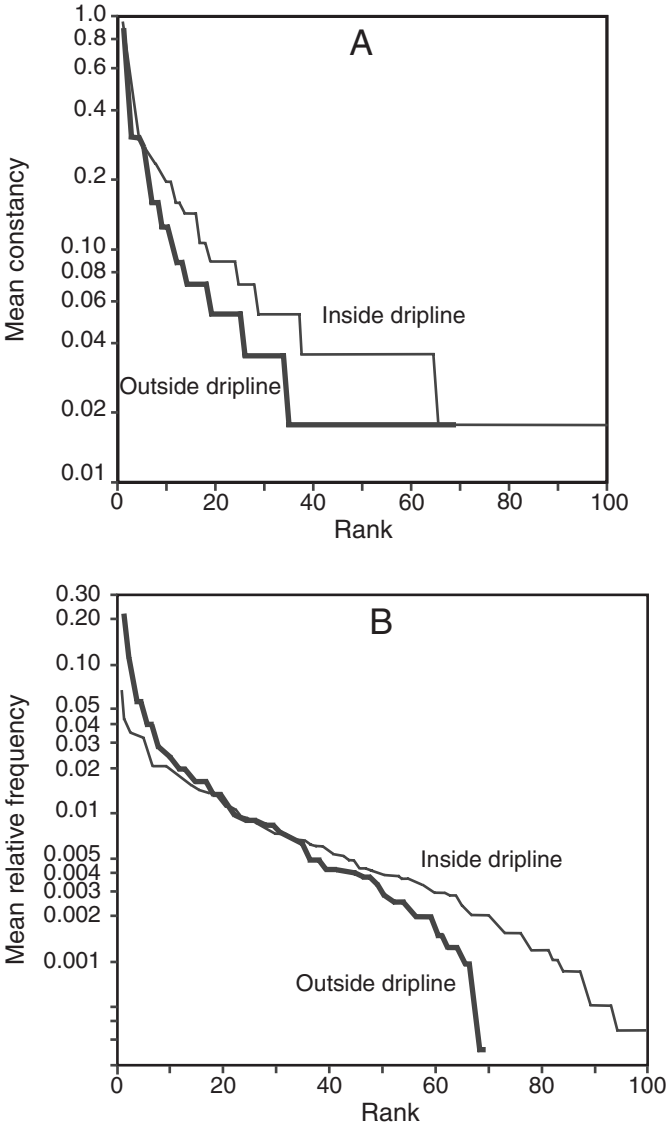
At the outside-dripline sampling points, we detected a 32% decline in total EM-type richness and 54% fewer EM types per soil core after the 15%D treatment. These results are similar to those of Hagerman et al. (1999), who detected an approximately 36% decline in EM-type richness per soil core between points 40 m inside the forest and those >2 m into an adjacent clearcut, 2 years after harvest. That difference increased to about 72% fewer EM types per soil core 3 years after harvest. In a retention harvest, Kranabetter (1999) detected 38% fewer EM morphotypes, 6 years after harvest, on birch seedlings growing outside the rooting zone of refuge trees than on seedlings growing within the rooting zone of birch trees. Cline et al. (2005) recorded 21% fewer EMF taxa on seedlings planted >16 m from retention trees than on seedlings planted <6 m from retention trees 4–8 years after harvest.

The similarity of results among studies that looked at different aspects of EM response to disturbance (residual EM from green-tree retention versus EM observed on "bait" seedlings) provides a generalized model of the effects of tree harvest on EMF community structure. Our sampling also revealed that the losses of EMF diversity are greatest in areas farthest removed from retention trees, where more than 50% of the pretreatment EM types were absent from post-treatment open-area soil cores.

Influence of sapwood area on fine-root density and EM-type richness

Although we detected no relationship between photosynthetic potential and root density in samples from any of the three host-tree dripline-distance classes, several studies have shown that root density can be related to aboveground 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-

Fig. 6. Rank curves for EM types, showing 101 morphotypes from inside-dripline soil cores and 69 from outside-dripline cores (n = 54). (A) Rank-constancy curve for inside- and outside-dripline populations. Constancy is the proportion (percentage) of soil cores containing a given EM type. (B) Rank-abundance curve for inside- and outside-dripline populations. Abundance is the mean percentage of subsamples within soil cores with the type present. See Materials and methods for more details.



root system at the expense of aboveground growth. These findings were supported by Vogt et al. (1983), who found that aboveground productivity of stands was inversely correlated with root biomass. Since the relationship between total root biomass and productivity has been established (Vogt et al. 1987), our results may reflect a relationship between sapwood area and total root-tip number rather than root density under individual trees.

Influence of distance from retention tree on root density and EMF diversity

The structural root system of Douglas-fir is concentrated within the dripline of the tree (McMinn 1963; Kuiper and Coutts 1992), and Bruns (1995) has discussed several processes affecting EMF diversity that could be influenced by root density. 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 EM tips per unit volume of soil declined sharply at a distance of 1.5 m into a clearcut and declined to zero 7.6 m into the clearcut. That study was conducted in Douglas-fir–larch forests in Montana, which generally have smaller diameter trees than forests in the western Cascade Range.

Our results (decline of EM 4–5 m from the tree bole) agree with the results of Parsons et al. (1994), who found that the number of "active" EM tips declined significantly within 3–6 m from the boles of trees (*Pinus contorta* Dougl. ex Loud.) in experimentally designed canopy gaps. They do not provide crown size, but the dripline radius of *P. contorta* could be expected to be in the 2–3 m range (Burns and Honkala 1990; Herman et al. 1996). In a study of edge effects on Douglas-fir seedlings planted in a clearcut, Outerbridge and Trofymow (2004) found that EM colonization and EM-type richness often declined at distances >5 m from the intact stand edge. However, direct comparisons with our study are difficult to make because those authors contrasted distance-from-edge classes (5, 15, 25, and 45 m) that would have been virtually always in our "outside crown" distance class. Kranabetter (1999) found that birch seedlings within the dripline of retention trees in a variable-retention harvest had significantly higher EM-type richness than seedlings outside the rooting system of the retention trees.

Ferrier and Alexander (1985) found that living fine roots persisted for at least 9 months after excision from their parent tree. Parsons et al. (1994) suggested that intraspecific root grafting may be responsible for keeping fine roots alive in soil well removed from retention trees. Such root grafting is also likely to have contributed to the observed root densities and EM-type richness away from green trees in our study.

Generally, EM-type richness per unit area declines with distance from retention trees in accordance with the decline in root density. We found a strong positive correlation between EM-type richness and root density in two out of three partially harvested stands. However, our analysis suggested that density declined faster than EM-type richness in relation to distance. This may be due to the use of different tree-harvesting techniques on the experimental blocks. The ground-yarding used during tree harvest at Watson Falls caused soil disturbance and compaction, with a resulting reduction in root density at the 1× dripline distance, thereby changing the richness–distance relationship. The other two blocks were helicopter-logged, thereby minimizing soil disturbance and maintaining the richness–density relationship (Fig. 5).

EMF community structure

Similar to findings from other studies of EMF diversity in temperate coniferous forests, *C. geophilum* was the most common EM type we found, being present in nearly every sample from the 15%D treatment (Table 4). Hagerman et al.

(1999) found that *C. geophilum* accounted for 20% of EMF root tips in clearcuts 2 years after harvest. Kranabetter and Wylie (1998) found that *C. geophilum* accounted for 19% of EM root tips on naturally regenerated western hemlock seedlings in harvested forest gaps. Goodman and Trofymow (1998) found that *C. geophilum* accounted for 24% of EM root tips on Douglas-fir in undisturbed old-growth and mature forests on Vancouver Island, and was most common in soil surface layers.

In contrast to *C. geophilum*, *Rhizopogon vinicolor*'s abundance is likely underestimated because it forms clusters (tuberculate mycorrhizae) of several to more than 100 root tips within a single tubercle. In our scheme of measuring abundance, each tubercle is classified as a single observation. Identities of other common EM types remained unknown and some morphotypes may represent multiple species, although many EM morphotypes (especially those with a thick mantle) produce a single repeatable genetic pattern when RFLP analysis is used (Mah et al. 2001). However, in the DEMO study, such similar EM types often represented species within the same genus (Kolaczkowski 2005). Sakakibara et al. (2002) concluded that combining morphotyping with molecular methods was an efficient way to assess EMF diversity.

Our rank-abundance curves are similar to the approximate log-normal distributions seen in other studies of EMF communities in temperate coniferous forest habitats (Horton and Bruns 1998; Kranabetter et al. 1999; Taylor and Finley 2003; Cline et al. 2005). In particular, comparison of our rank-abundance curves (Fig. 6) with those in Goodman and Trofymow (1998) shows that our inside-dripline cores have the long tail exhibited by their data from soil cores obtained in natural Douglas-fir old-growth and second-growth stands. In contrast, our outside-dripline cores exhibit a truncation in the distribution of the rare EM types. Sugihara (1980) considered the log-normal distribution to be one of the most common observed in community ecology, and to be strongly associated with complex, mature communities. The log-normal distribution implies that many different gradients act simultaneously to structure the community (Sugihara 1980).

The structural complexity suggests that EMF communities are not simply full of redundant species, but that species are responding differentially to various habitat factors. Ashkannejhad and Horton (2006) also reached the conclusion that EMF species are not broadly functionally redundant, based on findings that suilloid fungi were the dominant colonizers of *P. contorta* seedlings established in sand dunes, which lacked networks of mycelia, and that spores of *Rhizopogon* spp. were more resistant to desiccation than those of *Suillus* spp.

There is considerable difficulty in analyzing the community structure of soil organisms, owing to their cryptic habit and high levels of β diversity. The findings presented here reinforce our view that EMF community structure, as revealed by current techniques, provides only an index to the structural complexity in any given area (Luoma et al. 1996; see also Lilleskov et al. 2004). However, these limited views are nonetheless effective for the detection of treatment and spatiotemporal effects (Taylor and Finley 2003; Luoma et al. 2004; Cline et al. 2005; Izzo et al. 2005).

Conclusions and management implications

Silvicultural methods that are designed to maintain biodiversity are relatively new in forestry. Through green-tree retention, EMF diversity is maintained at higher levels than in clearcuts, and we expect that retained trees will provide some legacy of EMF during the development of the next stand. Maintenance of EMF diversity is important for ecosystem health and resilience (Amaranthus et al. 1990, 1996; Perry et al. 1990; Amaranthus 1997), and Bruns (1995) noted that high levels of EMF diversity may contribute to ecosystem efficiency (i.e., through resource partitioning). For instance, retention of a diversity of EMF in common mycelial networks may facilitate seedling uptake of N and P differentially under varying conditions (Nara 2006). Further use and development of this type of knowledge are essential when management objectives include facilitating the conversion of even-aged stands into structures that are more old-growth-like.

Luoma et al. (2004) found that the 15%D treatment significantly reduced EMF sporocarp production during the first 3 years following cutting and that the reduction was generally greater than expected relative to the proportion of basal area removed. We have shown that retention of green trees was effective in retaining a legacy of EMF on roots even though sporocarp production was minimal. Our retention trees were spaced about 20–35 m apart, depending on the block (Table 3), and mortality from windthrow was about 4% during the first 3 years following harvest (C. Halpren, unpublished data). Generally, wind damage has not limited successful implementation of green-tree-retention silviculture (Moore et al. 2003), and a combination of aggregated and dispersed retention may further mitigate this concern.

This study spanned a considerable geographic range — from the Umpqua River watershed of southern Oregon to the vicinity of Mount Adams in the central Washington Cascade Range. The similarity of dominant- and codominant-EM-type responses that we observed across study sites leads us to conclude that our results are broadly applicable in *Pseudotsuga*-dominated forests of the region.

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