Effects of partial cutting on the ectomycorrhizae of *Picea glauca* forests in northwestern Alberta

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Abstract: This study assessed the impact of various harvesting practices (including those designed to emulate natural disturbances) on ectomycorrhizae (ECM) associated with white spruce (*Picea glauca* (Moench) Voss) in northwestern Alberta, Canada. Treatments included clearcuts, partial cuts (dispersed green-tree retention with 20%, 50%, and 75% residual live trees, and aggregated green-tree retention), unharvested control sites, and a burned stand. The percentage of active white spruce root tips and ECM richness and diversity, as observed in soil cores collected throughout the study site, all decreased with increasing disturbance intensity. Effects were particularly pronounced in clearcuts, machine corridors used for access by harvesting equipment in the dispersed green-tree retention stands, and in burned areas. Reductions in ECM biodiversity could be attributed to the sensitivity of late-stage ectomycorrhizae (e.g., *Cortinarius* spp., *Lactarius* spp., and *Russula* spp.) to soil disturbances and changes in microclimate associated with harvesting or burning. Areas of dispersed and aggregated green-tree retention were not dramatically different than unharvested forest in terms of root tip density and ECM richness, diversity, and composition. Harvesting practices that retain a percentage of residual live trees, either dispersed throughout the cutting unit or in aggregated patches, could be an effective means of maintaining ectomycorrhizal biodiversity at the stand level.

Résumé : Cette étude évalue l'impact de diverses pratiques de récolte (incluant celles qui sont conçues dans le but d'imiter les perturbations naturelles) sur les ectomycorhizes (ECM) associées à l'épinette blanche (*Picea glauca* (Moench) Voss) dans le nord-ouest de l'Alberta, au Canada. Les traitements incluaient la coupe à blanc, la coupe partielle (dispersée avec réserves constituées de 20, 50 et 75 % de tiges résiduelles ou avec des réserves regroupen îlots), des sites témoins non récoltés et un peuplement brûlé. Le pourcentage d'apex racinaires actifs d'épinette blanche, ainsi que la richesse et la diversité des ECM, tels qu'ils ont été observés dans les carottes de sol prélevées partout dans la zone d'étude, diminuaient tous avec l'augmentation de l'intensité des perturbations. Les effets étaient particulièrement marqués dans les coupes à blanc, les corridors d'accès utilisés par les équipements de récolte dans les peuplements où étaient conservées des tiges résiduelles dispersées et dans les zones brûlées. La baisse dans la diversité des ECM pouvait être attribuée à la sensibilité des ectomycorhizes de fin de succession (p. ex. *Cortinarius* spp., *Lactarius* spp. et *Russula* spp.) aux perturbations du sol et aux variations du microclimat associées à la récolte ou au feu. Les zones avec rétention de tiges résiduelles, dispersées ou en îlots, n'étaient pas dramatiquement différentes de la forêt non récoltée en termes de densité des apex racinaires, de richesse, diversité et composition des ECM. Les pratiques de récolte qui conservent un certain pourcentage de tiges résiduelles, soit dispersées un peu partout dans l'unité de coupe, soit regroupées en îlots, pourraient constituer un moyen efficace de maintenir la biodiversité ectomycorhizienne à l'échelle du peuplement.

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Introduction

In recent decades forestry companies have shown increased interest in ecologically sustainable management practices in an attempt to conserve forest biodiversity. By conserving forest biodiversity it is argued that the ecological processes that the organisms govern will also remain intact, and thus,

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the integrity of the forest will not be compromised (Galindo-Leal and Bunnell 1995). The natural disturbance paradigm of forest management (landscape management and silvicultural practices that aim to emulate natural disturbances such as fire) is an example of one approach towards sustainable practices (Bergeron et al. 1999).

In northwestern Alberta, wildfire has historically been responsible for shaping the forest landscape. As opposed to traditional forestry practices, which uniformly remove the majority of trees in a harvesting area, forest landscapes created by wildfire tend to be a heterogeneous mosaic of burned and unburned patches (Eberhart and Woodard 1987; Johnson 1992). Thus, even within stand-replacing wildfires, patches of live trees will remain. These unburned patches, or fire residuals, are believed to be important ecosystem structures that can act as refugia and serve as a source of colonization for weakly dispersing species (Rowe and Scotter 1973).

Colonization of plant roots by ectomycorrhizal (ECM) fungi improves plant water and nutrient uptake (Duddridge

et al. 1980; Smith and Read 1997), as well as resistance to disease (Duchesne et al. 1988; Morin et al. 1999) and tolerance to temperature fluctuations (Marx et al. 1970). At the same time, ECM fungi depend on carbon fixed by the host plant and receive from 10% to 20% of the plant's net primary productivity (Smith and Read 1997; Vogt et al. 1982). This high level of dependency makes ECM fungi vulnerable to factors that disturb their associated plant symbionts. For example, both traditional forest harvesting practices such as clear-cutting (Bradbury et al. 1998; Byrd et al. 1999; Durall et al. 1999; Hagerman et al. 1999a, 1999b; Harvey et al. 1980a) and stand-replacing wildfires (Stendell et al. 1999; Visser 1995) have been shown to decrease the biodiversity of ectomycorrhizae.

Given the ecological importance of ECM fungi and the high degree of physiological variation among ECM fungal species (Cairney 1999; Newton 1992; Zak and Visser 1996), it seems that maintaining ECM diversity would be important for preserving critical ecosystem processes. Although the impacts of some alternative harvesting practices on ECM communities have been investigated in northwestern British Columbia, Canada (Durall et al. 1999; Kranabetter and Wylie 1998), the pattern of natural disturbance in these forests (small gap formations caused by single-tree mortality) contrasts significantly with the natural disturbance processes inherent to much of the boreal forest. Moreover, our current knowledge of forest ecosystem structure and function (especially with regard to belowground components) is still inadequate for forest managers to formulate sound practices and policies for natural disturbance management (Maini 1998).

The objectives of this study were to assess the effectiveness of forestry practices designed to emulate natural disturbance in maintaining *Picea glauca* (Moench) Voss ECM communities. Two complementary studies were undertaken: (1) assessment of composition and diversity of ECM morphotypes associated with different levels of dispersed green-tree retention and with burning; and (2) assessment of changes in ECM morphotype diversity across the edges of two patch sizes of aggregated green-tree retention left within clearcuts.

Materials and methods

Study site

This research is one of numerous studies undertaken at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site (Work et al. 2004), which is located in the Boreal Mixedwood ecoregion (Strong and Leggat 1992) of northwestern Alberta, Canada (56°44′N, 118°20′W). The dominant tree species are white spruce (*Picea glauca*) (ranging from 114 to 131 years old), trembling aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.). Black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and paper birch (*Betula papyrifera* Marsh.) are also found scattered throughout the site. The understory is dominated by *Alnus* spp., *Calamagrostis canadensis*, *Cornus canadensis*, *Epilobium angustifolium*, *Ribes triste*, *Rosa acicularis*, *Rubus pubescens*, *Shepherdia canadensis*, and *Viburnum edule* (Fenniak 2001). Forests in this region receive an average precipitation of 464 mm·year^{-1} (nearly two thirds during the summer months) and have an average

summer temperature of 12.8 °C (Strong and Leggat 1992). The parent material was glaciolacustrine, and soil types varied from imperfectly drained Luvisols (Dark Gray Luvisol, Orthic Gray Luvisol) to a well-drained Orthic Luvic Gleysol. The organic layer pH ranged from 4.41 to 4.74 (for further details see Kishchuk 2004).

The study site was harvested during the winter of 1998–1999 in a randomized block design. Our work focused on unharvested controls, clearcuts, and three levels of dispersed green-tree retention (DGTR; 20%, 50%, and 75% residual live trees). Three replicate stands for each treatment were positioned throughout the EMEND site. The DGTR stands were strip harvested, resulting in a striped pattern where 20 m wide residual strips (containing the retained live trees) alternated with 5 m wide machine corridors. In the 75% retention level trees were only removed along the machine corridor. All of the harvesting treatments were applied to areas of approximately 10 ha. Originally, a series of controlled burns was planned for the experiment as well; however, only one conifer-dominated burned stand was available at the time of this study. It was burned in July 1999 with ignition by an aerial drip torch. In the stand the fire had a medium rate of spread and burned relatively hot but patchily (EMEND 2004). Residual trees were also left in the partially harvested and clearcut stands in the form of two elliptical patches (approximately 0.25 and 0.75 ha; aggregated green-tree retention). These ellipses were designed to emulate "fire skips", which are common features inherent to wildfire-dominated forest landscapes.

Field sampling

Sampling locations

For the assessment of dispersed green-tree retention and burning we had a total of 150 sample locations, with five sample location in each of three replicate stands for each of 10 treatments: (1) clearcut, (2) unharvested control, (3) 20% DGTR, partially cut residual strip, (4) 20% DGTR, machine corridor, (5) 50% DGTR, partially cut residual strip, (6) 50% DGTR, machine corridor, (7) 75% DGTR, residual strip, (8) 75% DGTR, machine corridor, (9) unburnt control, and (10) burned stand. Replicate stands of each treatment were grouped in blocks (except the burned stand and unburnt control). For the unharvested control and clearcut stands samples were taken from five random locations (at least 20 m apart) in each of the three replicate stands. For each of three replicate stands for the DGTR treatment, we took samples from five random locations along machine corridors and five random locations within the residual strips.

Although there was only one burned stand, it was highly heterogeneous (burnt to mineral soil in some areas with other areas unburnt (EMEND 2004)). We therefore divided the stand into three burned blocks and three unburnt control blocks, which were subsequently considered to be independent replicates of the burn and unburnt control treatments. Again, we took five samples from each of the three replicates of these two treatments, samples were taken 6 m apart along a single 30-m transect that was at least 30 m from a burnt–unburnt edge. Portions of the stand characterized as burned were void of an organic soil horizon and standing live trees. Unburned portions of the stand were untouched by fire and, thus, were visually similar to the unharvested con-

trol stands. In subsequent statistical analysis, stands were considered independent replicates of each treatment, while samples were treated as subsamples.

For the evaluation of aggregated green-tree retention we utilized a further 96 sampling locations, which were established in association with a total of six residual ellipses (0.25- and 0.75-ha ellipses in each of the three clearcut stands). At each ellipse we took a total of 16 samples from four transects situated perpendicular to the edge and at right angles to one another. Samples were taken along each transect at the center of the ellipse, at the edge of the ellipse, and at 10 and 20 m from the edge into the clearcut. The four samples from the centre of the ellipse were taken approximately 1 m apart. In subsequent statistical analysis the individual ellipses were considered independent replicates, and the two ellipse sizes were treated as the main effect and the sampling position as a subplot factor in a split-plot ANOVA (see below).

Fine root tip density

The density of white spruce fine roots was determined by obtaining a soil core (2 cm diameter by 15 cm deep) in June 2000 (two growing seasons post disturbance) from each of the 135 sampling locations in the clearcut, unharvested control, dispersed green-tree retention, and burned stands (but not the unburnt control or ellipses). For the control and partially cut sites the cores only included the organic layer. For the clearcuts and, to some extent, the machine corridors in the partially cut stands, the organic and mineral horizons were somewhat mixed, and the organic layer was compacted such that some mineral soil was often included in the cores. In the burned sites consumption of the LFH by the fire was such that cores typically included a substantial portion of mineral soil.

The soil cores were placed in a plastic Ziplock® bag and stored at 4 °C for up to 3 months until processing was completed. Processing involved placing the soil cores in two nested soil sieves (32 and 115 mesh per inch) and isolating the root tips by gently rinsing off the adhering soil and organic debris. The fine roots from both sieves were subsequently characterized as inactive or active, using a stereomicroscope, based on morphological criteria outlined by Harvey et al. (1976). Inactive root tips were characterized by a wrinkled texture and a dark apex. In contrast, the majority of active root tips were smooth and turgid and had a pale or creamy white apex. Ectomycorrhizae formed by *Cenococcum geophilum* and *Tomentella* spp., however, were exceptions. The mantles formed by these species are hard and darkly pigmented; thus, root tips associated with these fungi are uniformly smooth and dark. For this reason root tips associated with these two morphotypes were carefully examined during the characterization process. Only white spruce fine root tips were examined. White spruce roots can be readily distinguished from those of poplar, pine, and ECM shrubs but roots of black spruce or balsam fir could be mistaken for white spruce (Kernaghan 2003). Since pine, fir, and black spruce were all very infrequent in the areas we sampled, we are confident that the vast majority of the roots we examined were white spruce. All root tips lacking a distinguishable apex were disregarded.

Ectomycorrhizal community

The white spruce ECM community at each of the 246 sampling locations was characterized by obtaining a soil core (3.5 cm diameter by 15 cm deep). The clearcut, dispersed green-tree retention, unharvested control, burn, and unburnt control treatments (5 samples × 10 treatments × 3 replicates) were sampled in August 2000 (end of second postdisturbance growing season), while the samples from the aggregated green-tree retention (4 samples × 4 transects per ellipse × 2 sizes of ellipse × 3 replicates) were obtained in May 2001 (start of third postdisturbance growing season). The soil cores were stored in PVC pipe (to maintain the integrity of the core during transport) for up to 4 months at 4 °C prior to processing. The isolation of the fine roots was as described above. Once isolated, all active root tips were further classified as ectomycorrhizal or nonectomycorrhizal. ECM root tips were examined with both stereo (Zeiss Stemi 2000-C, 7–40×) and compound (Leitz Labrolux K, 500–1000×) microscopes and subsequently grouped based on their morphological and anatomical characteristics according to the protocol outlined by Goodman et al. (1996). Morphological features included shape, color, and texture of the ECM system and emanating elements (hyphae and mycelial strands). Some examples of anatomical features include mantle patterning; the size, color, ornamentation, and contents of hyphal cells; the type and frequency of septa; and reactions to specific chemical compounds (e.g., KOH, sulphovanillin). Active root tips lacking distinguishable mantle features were designated "undetermined" according to Kranabetter and Wylie (1998). This included root tips with an immature or poorly developed mantle.

When possible, 50 ECM root tips per core were morphotyped; however, because of the limited number of active root tips observed in some of the cores this was not always possible. In this instance, all of the active root tips encountered in the soil core were characterized. The distinct groups, or "morphotypes", were then identified to the genus level by comparing them with published ectomycorrhizal descriptions (Agerer 1987–1998; Ingelby et al. 1990; Goodman et al. 1996; Kernaghan 2001; see Lazaruk 2002 for further details). No attempt was made to identify the morphotypes past the genus level (but some genera had only one known species) because of the morphological similarities among species within genera. In recent years there has been increasing use of molecular techniques for studies of mycorrhizal richness and community composition, often as a supplement to morphotyping (Sakakibara et al. 2002). Such an approach would have allowed us to confirm the identity of taxa and, perhaps, to identify species within genera. Thus, molecular analysis would have likely resulted in higher mycorrhizal richness. For example, Smith et al. (2004) detected a total of 140 mycorrhizal "restriction fragment length polymorphism (RFLP) species" (17 identified genera) in a study of prescribed burning in ponderosa pine (*Pinus ponderosa*) forest (compared with our 19 morphotypes). However, a recent comparison of morphotyping versus molecular analysis of mycorrhizae (Sakakibara et al. 2002) has shown that a single RFLP pattern strongly predominates for many morphotypes, including several found in our study (*Cenococcum*, E-strain, *Mycelium radicis atrovirens* (MRA), *Thelephora*); indeed, *Lactarius* and *Russula* morphotypes each showed only a sin-

gle RFLP pattern. Two morphotypes found in our study showed more than one common RFLP patterns (*Amphina*: two; *Piloderma*: five) (Sakakibara et al. 2002). Overall, for our purpose of detecting treatment effects on the ECM community, morphotyping was deemed sufficient.

Data analysis

Prior to analysis, all data were tested for normality and homoscedasticity with a Kolmogorov–Smirnov test. All ANOVAs were performed using SPSS version 10.0 (SPSS Inc. 1999).

Fine root tip density

The percentage of active fine root tips was calculated, for each soil core, as a proportion based on the total number of white spruce fine root tips observed. An analysis of variance (ANOVA) was used to test the treatment effects on the total number of fine root tips and the percentage of active fine root tips (the main effects were treatment (fixed), block (random), and treatment × block (random)). The stands (grouped by blocks) were considered the true replicates of treatment type, while the soil cores collected within the various treatments were treated as subsamples. The percentage data were log transformed prior to the analysis to meet the assumption of normality.

Ectomycorrhizal community

For the clearcut, dispersed green-tree retention, unharvested control, burn, and unburnt control treatments, the relative abundance of each morphotype was calculated as a proportion based on the total number of active root tips characterized. The frequency of occurrence for each morphotype was calculated according to the percentage of soil cores and stands in which each particular morphotype was observed. ECM richness was determined for each stand within treatment based on the total number of morphotypes observed in the five soil cores collected. Lastly, ECM diversity was calculated at the stand level (according to the average relative abundance of morphotypes from the five soil cores sampled per stand for each treatment) with the Shannon–Wiener diversity index (Shannon and Weaver 1949). Active fine root tips classified as nonmycorrhizal or undetermined (see Kranabetter and Wylie 1998) were excluded from the calculation of both morphotype richness and diversity.

For the residual ellipse treatments we calculated the following values for each position for each replicate ellipse: relative abundance of each morphotype (calculated as a proportion of the total number of ECM root tips characterized in each soil core) and ECM richness and diversity (per four soil cores). We also calculated frequency of occurrence of each morphotype per position based on the number of soil cores in which the morphotype was observed. Again, root tips characterized as undetermined were not included in the morphotype richness and diversity calculations.

An ANOVA was used to test for differences in ECM richness and diversity among the 10 treatments, with the following main effects: treatment (fixed), block (random). Treatment × block could not be included in the model because richness and diversity were calculated at the stand (within-block) level. The stands were considered the true replicates of treatment type. Significant ANOVA results ($p < 0.05$) were fol-

Table 1. Results of the ANOVA model testing for treatment effects on the percentage of active fine root tips and ectomycorrhizal richness and diversity, and the split-plot ANOVA model testing for effects of patch (ellipse) size (main plot) and sampling position (subplot) on ectomycorrhizae richness and diversity associated with the aggregated green-tree retention patches located within clearcuts.

Source	df	F	p >F
ANOVA[*]			
Percentage of active root tips[†]			
Treatment	8	13.630	<0.001
Block	2	0.813	0.461
Treatment × block	16	1.659	0.066
Error	109		
Richness			
Treatment	9	8.309	<0.001
Block	2	0.245	0.785
Error	18		
Diversity			
Treatment	9	9.614	<0.001
Block	2	1.357	0.283
Error	18		
Split-plot ANOVA[‡]			
Richness			
Block	2	1.00	0.500
Ellipse size	1	0.04	0.868
Ellipse size × block	2	0.42	0.666
Position	3	19.90	<0.001
Ellipse size × position	3	0.86	0.491
Error	12		
Diversity			
Block	2	14.33	0.065
Ellipse size	1	3.10	0.220
Ellipse size × block	2	0.08	0.928
Position	3	17.97	<0.001
Ellipse size × position	3	0.58	0.665
Error	12		

[*]Treatments were as follows: clearcut, dispersed green-tree retention (20%, 50%, and 75% retention including both residual strips and machine corridors), unharvested control, and burn.

[†]Tests performed using log-transformed data.

[‡]Sampling positions were as follows: within the patch, at the edge, and 10 and 20 m into the clearcut.

lowed by Tukey–Kramer honestly significant difference test to further distinguish differences among treatments. Following initial analysis by correspondence analysis, a detrended correspondence analysis (DCA) was chosen to examine the treatment effects on the ECM community. Only common morphotypes, those observed in more than 5% of the soil cores, were included in the analysis, which was performed using CANOCO version 4.0 (ter Braak and Šmilauer 1998).

The effect of increasing distance from the edge and residual ellipse size on the ECM community was tested with an ANOVA using a split-plot design with ellipse size as the main plot factor and sampling position as the subplot factor. The test was performed using the ECM richness and diversity values for each position at each replicate ellipse. Significant ANOVA results ($p < 0.05$) were followed by a Tukey–Kramer honestly significant difference test to further distin-

Fig. 1. The mean percentage of active white spruce fine root tips in soil cores collected from burn (burn), clearcut (CC), dispersed green-tree retention cut (with 20%, 50%, and 75% residual live trees and sampled in both machine corridors (m) and residual strips (r)), and unharvested control stands (con) in conifer-dominated boreal forest two growing seasons after harvesting. Treatment means with different letters are significantly different (Tukey–Kramer honestly significant difference test, $p \leq 0.05$, after ANOVA with $p < 0.001$)). Analyses were performed with log-transformed data. Error bars represent 1 SE (based on the 15 soil cores per treatment).
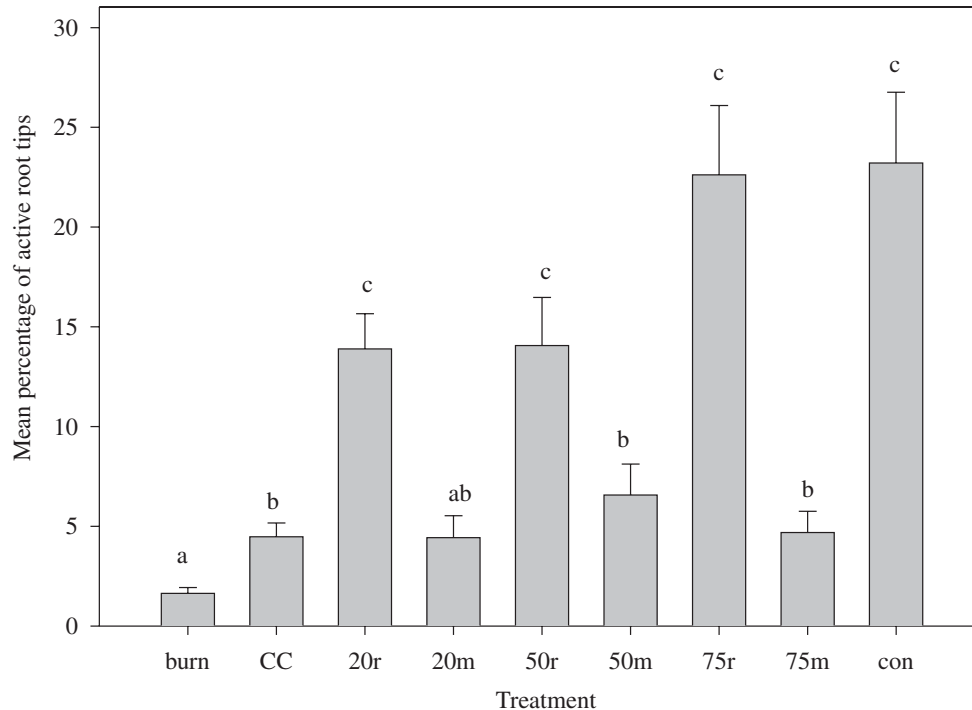
guish differences among sampling positions. Further analysis was required to determine if differences in the ECM richness between the clearcut and residual ellipse sampling positions were due to genuine positional effects on the community or were simply due to the lower number of active root tips encountered in clearcut soil cores (see Table 3). To examine this we plotted morphotype richness against number of root tips. An average richness (for a given number of root tips) was calculated based on data from 10 repeats of random selections of 1 to 20 root tips from either residual ellipse or clearcut soil cores.

Results

Dispersed green-tree retention and fire

White spruce fine root tip density

Nearly 107 000 white spruce fine root tips were characterized as inactive or active throughout the clearcut, dispersed green-tree retention (DGTR), unharvested control, and burn treatments. The percentage of active fine root tips differed significantly among the treatments ($p <0.001$) and appeared to be correlated with the level of disturbance (Table 1, Fig. 1). Similar, but less dramatic, trends were seen for the total number of active fine root tips (not shown). In areas with a high level of disturbance, such as the burned and clearcut stands and the machine corridors within the DGTR stands, there was a significantly lower percentage of active fine root tips than in the control stands. For the machine corridors there were no significant differences among the different retention levels, and the percentage of active fine root tips was

just as low as in the clearcut stands. The lowest percentage of active root tips was found in the burn treatment. Within the residual strips of the DGTR stands, the percentage of active fine root tips increased from the 20% to the 50% and 75% retention levels, and in each case it was significantly greater than in the machine corridors with the same retention level. The percentage of active root tips did not differ between the residual strips and the unharvested control stands.

Ectomycorrhizal community

A total of 4431 white spruce fine root tips were classified as active, and of these tips, an overwhelming majority was also characterized as ectomycorrhizal (99.4%). Throughout the clearcut, DGTR, unharvested control, and burn treatments a total of 19 distinct morphotypes were described (Table 2). The most common morphotype was *Tomentella* spp. followed by *Cortinarius* spp., *Amphinema byssoides*, *Lactarius* spp., E-strain (*Wilcoxina* spp.), MRA, and *Hebeloma* spp., respectively. These seven morphotypes formed the majority of the ectomycorrhizae (nearly 72% of the root tips), while none of the remaining 12 morphotypes were observed on more than 5% of the root tips. The most ubiquitous morphotype was *Tomentella* spp., which was observed in nearly 57% of the soil cores and was the only morphotype found in every stand. Only nine root tips were classified as undetermined.

ECM richness and diversity (Table 1, Fig. 2) differed significantly among the treatments according to the level of disturbance. The values were significantly greater in the control stands than in the burned and clearcut stands. Within the residual strips of the DGTR stands, richness and diversity in-

Table 2. The total number of active root tips colonized by a given ectomycorrhizae morphotype, relative abundance (precentage of root tips), and frequency of occurrence (percentage of soil cores or stands in which the morphotype occurred) based on sampling of 10 treatments throughout the EMEND research site (n = 150) two growing seasons after harvesting.

Morphotype	No. of tips	Abundance (%)*	Frequency (%)† Cores	Stands
Tomentella spp.	822	18.6	56.7	100.0
Cortinarius spp.	820	18.5	25.3	56.7
Amphinema byssoides	508	11.5	26.7	70.0
Lactarius spp.	368	8.3	13.3	40.0
E-strain	233	5.3	13.3	46.7
Mycelium radicis atrovirens	224	5.1	24.7	66.7
Hebeloma spp.	221	5.0	14.0	53.3
Cenococcum geophilum	199	4.5	28.0	76.7
Piloderma spp.	170	3.8	10.7	33.3
Russula spp.	163	3.7	7.3	36.7
cf. *Tricholoma*	156	3.5	8.7	26.7
Tuber spp.	118	2.7	4.0	20.0
Unknown A	87	2.0	4.0	20.0
Basidiomycete 1	81	1.8	2.0	10.0
Thelephora spp.	67	1.5	5.3	23.3
Unknown D	58	1.3	1.3	6.7
Unknown B	50	1.1	0.7	3.3
Dermocybe spp.	31	0.7	2.7	13.3
Nonmycorrhizal	29	0.7	4.0	20.0
cf. *Paxillus involutus*	17	0.4	0.7	3.3
Undetermined	9	0.2	1.3	6.7
Total no. of tips	4431			

Note: Treatments were as follows: clearcut; 20%, 50%, and 75% dispersed green-tree retention (including both residual strips and machine corridors); unharvested control; burn; and unburnt control.

*Relative abundance for each morphotype was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled) × 100.

†Frequency of occurrence for each morphotype was calculated as follows: (number of soil cores or sites in which morphotype was observed) / (total number of soil cores or sites) × 100.

creased slightly from the 20% to the 50% and 75% retention levels. For the machine corridors of the DGTR, stands with 50% retention had greater richness and diversity than stands with 20% or 75% retention. Overall, ECM richness and diversity tended to be greater in the residual strips than in the machine corridors for each of the levels of retention; however, this difference was not statistically significant. Furthermore, the residual strips had richness and diversity values similar to those of the control stands. The burn treatment resulted in the lowest values for both ECM richness and diversity.

The results from the ordination provided insight into the treatment effects on the ECM community (Fig. 3). The clustering of the stands along the first ordination axis (λ = 0.4787) implies a correlation with disturbance intensity. The site scores for the DGTR stands were intermediate between the heavily disturbed burned stands and clearcut stands, which were positioned on the left of the first DCA axis, and the undisturbed control stands, which were positioned on the right end of first DCA axis. Morphotypes such as MRA and

Tomentella spp. were associated with the burned and clearcut stands, while morphotypes such as *Amphinema byssoides*, *Cortinarius* spp., E-strain, *Piloderma* spp., and *Lactarius* spp. were associated with the control stands. Furthermore, *Cenococcum geophilum*, *Hebeloma* spp., *Russula* spp., and *Thelephora terrestris* were positioned among the DGTR stands.

Aggregated green-tree retention (ellipses)

Ectomycorrhizal community

A total of 2083 active white spruce root tips were characterized and 16 different morphotypes were described from the samples taken in association with the aggregated green-tree retention patches (ellipses) (Table 3). The most common morphotype was *Cortinarius* spp. followed by *Amphinema byssoides*, *Tomentella* spp., *Cenococcum geophilum*, E-strain (*Wilcoxina* spp.), MRA, *Lactarius* spp., and *Piloderma* spp., respectively. These eight morphotypes formed the majority of the ectomycorrhizae (nearly 85%), while the other eight morphotypes were observed in less than 5% of the soil cores. Only 15 root tips were classified as undetermined.

The relative abundance of individual morphotypes varied among sampling positions (Table 3). *Lactarius* spp., *Piloderma* spp., *Tuber* spp., and "cf. *Tricholoma*" were only found within and at the edge of the residual ellipses. While no morphotypes were exclusive to the clearcut sampling positions, the relative abundance of *A. byssoides*, E-strain, and *Tomentella* spp. was greater in soil cores collected from the clearcut than in soil cores collected from the center and at the edge of the residual ellipses. *Cenococcum geophilum* and *Tomentella* spp. were the only morphotypes observed at all sampling positions; *Amphinema byssoides* was absent from only the 10 m sampling position of the 0.75-ha ellipse. In addition, the average number of root tips observed, and thus characterized, in the soil cores was much lower in the clearcut sampling positions.

The richness of ECM morphotypes also differed among sampling positions (Fig. 4a). ECM richness and diversity were nearly four times greater in the center and at the edge of the residual ellipse than in the clearcut (Fig. 4). No relationship was observed between the size of the residual ellipse and ECM richness or diversity (Table 1, Fig. 4).

The relationship between morphotype richness and number of root tips examined differed between the clearcut and the residual ellipse soil cores (Fig. 5). In the clearcut soil cores the maximum number of morphotypes was encountered after approximately 14 root tips, while in the residual ellipse soil cores the number of morphotypes encountered continued to increase even after 20 root tips. This suggests that the ECM biodiversity in the clearcut soil cores would not have been higher even if more root tips had been encountered, and thus the clearcut ECM community is different for reasons other than just a limitation in host availability.

Discussion

Dispersed green-tree retention

Clear-cut harvesting and fire were associated with dramatic reductions in abundance and diversity of ECM and changes in community composition. Effects of dispersed green-tree retention (DGTR) were heterogeneous, however,

Fig. 2. Richness (*a*) and diversity (*b*) of ectomycorrhizal morphotypes (averaged over three replicate stands per treatment based on five soil cores (subsamples) per replicate stand) observed in burn (burn), unburnt control (bcon), clearcut (CC), dispersed green-tree retention cut (with 20%, 50%, and 75% retained live residual and sampled in both machine corridors (m) and residual strips (r)), and unharvested control stands (con) two growing seasons after harvesting. Treatment means with different letters are significantly different (Tukey–Kramer honestly significant difference test, $p \leq 0.05$). Error bars represent 1 SE (based on the three replicate stands per treatment).
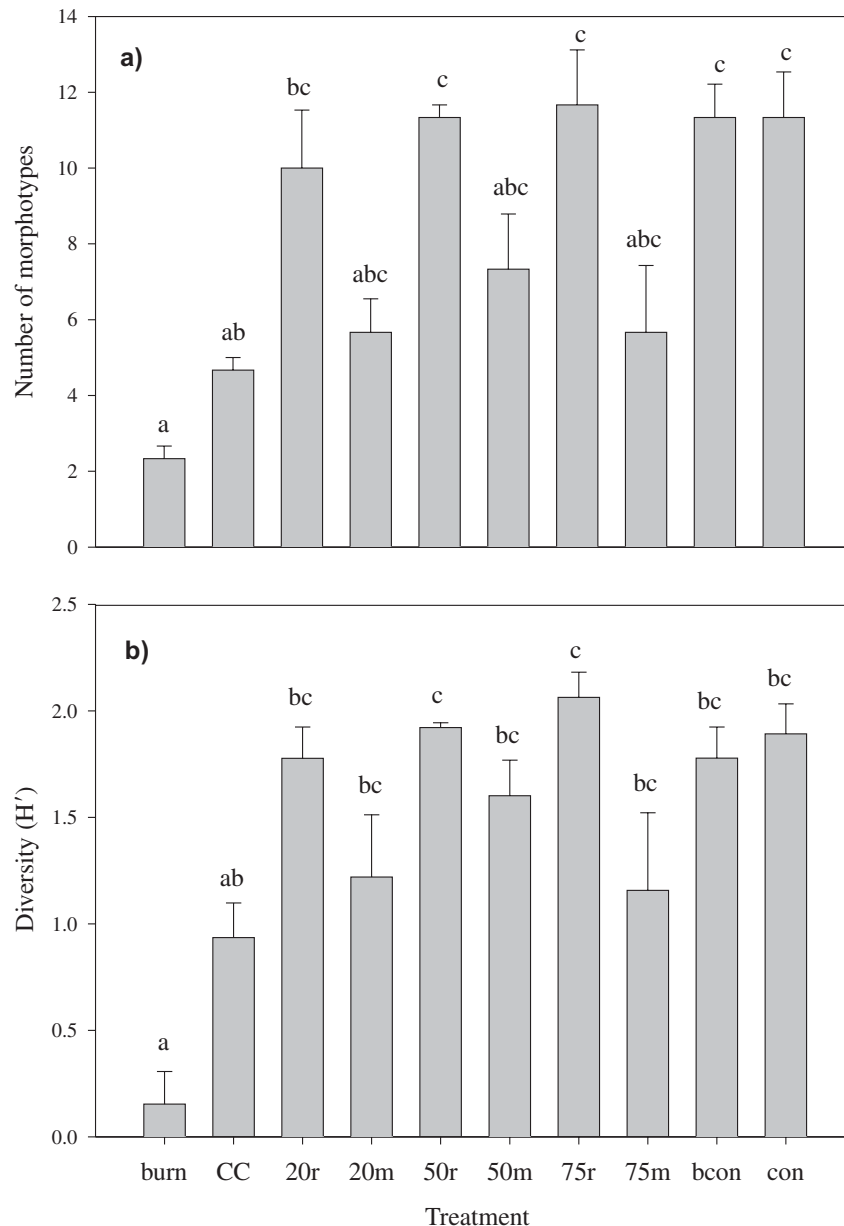

such that the machine corridors were similar to clearcuts, while the residual strips were similar to unharvested forest.

Clear-cut harvesting significantly reduced the overall density of active fine root tips. Previous studies have also reported a substantial reduction (to 4%, Hagerman et al. 1999*a*) or complete elimination (Harvey et al. 1980*a*; Parsons et al. 1994) of active root tips 2 years after clear-cutting. Not surprisingly, the burn treatment resulted in the lowest percentage of active root tips. Since white spruce has a shallow rooting system, the majority of the root tips were likely consumed along with the organic horizon.

The persistence of a small proportion of root tips in clearcuts and burned areas may be attributed to (1) the use of car-bon reserves present in excised roots (Ferrier and Alexander 1985); (2) a supply of the root tips with carbon, via hyphal linkages, by ectomycorrhizae associated with refuge plants (Kranabetter 1999; Hagerman et al. 2001); and (3) physical protection against desiccation provided by the fungal mantle itself (Smith and Read 1997), enabling certain root tips to persist, at least temporarily, without a host. This may have been the case for *Cenococcum geophilum* and *Tomentella* spp., which form thick, hard mantles. In fact, the majority of active root tips encountered in the burn and clearcut soil cores in this study were morphologically similar to these ectomycorrhizae. This may also explain the increased abundance of both *Cenococcum* (Byrd et al. 1999; Hagerman et

Fig. 3. Results of detrended correspondence analysis (DCA) based on the relative abundance of ectomycorrhizal (ECM) morphotypes encountered in the sampling of unharvested, clearcut, dispersed green-tree retention, and burn treatments in conifer-dominated boreal forest. See text for details of treatments. Each point represents the location in ordination space of a stand for a given treatment. Morphotype abbreviations indicate the location of the morphotype in ordination space. Points close to one another were more similar in terms of the composition of the ECM community and were characterized by higher abundance of the morphotypes placed close to them. Abbreviations are as follows: A, unknown A; amph, *Amphinema byssoides*; ceno, *Cenococcum geophilum*; cort, *Cortinarius* spp.; estr, E-strain; hebe, *Hebeloma* spp.; lact, *Lactarius* spp.; MRA, *Mycelium radicis atrovirens*; pilo, *Piloderma* spp.; russ, *Russula* spp.; thel, *Thelephora terrestris*; toma, *Tomentella* spp.; tric, cf. *Tricholoma*; tube, *Tuber* spp. Symbols are as follows: ■, control and unburnt control; ▲, residual strips; △, machine corridors; ○, clearcut; □, burn.
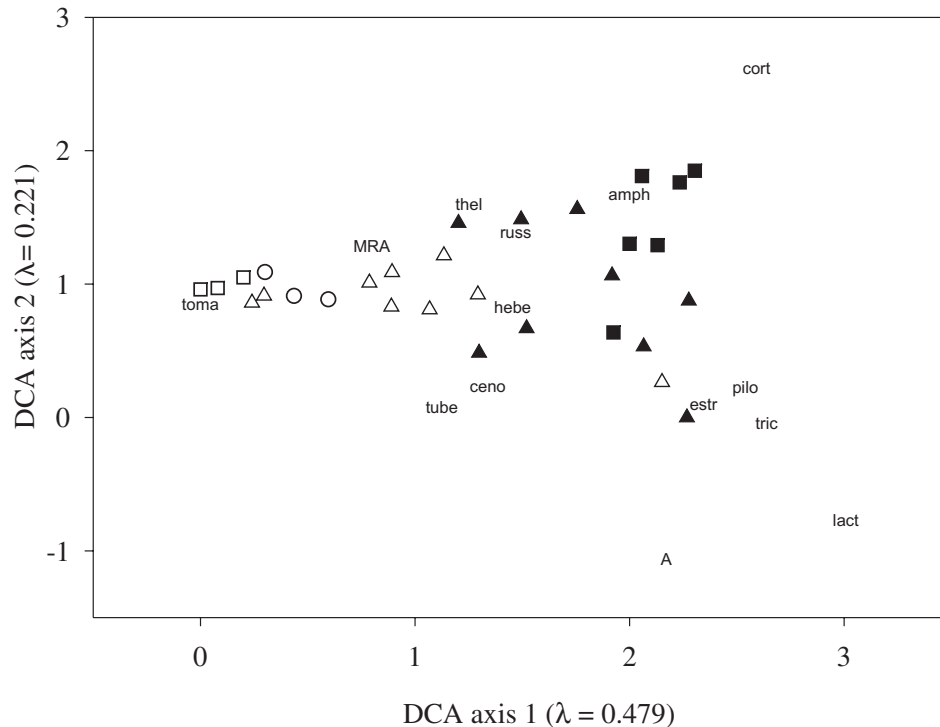
al. 1999*a*; Schoenberger and Perry 1982) and *Tomentella* (Bradbury et al. 1998; Purdy et al. 2002) morphotypes in disturbed sites.

Fine root tip density was also drastically reduced in the machine corridors of the DGTR stands, although they were only 5 m wide and thus well within the rooting zone of adjacent trees. Others have also found reductions in active root tip density within 2–6 m of a forest edge (Parsons et al. 1994; Hagerman 1997). Thus some factor, such as soil compaction or microclimatic effects, other than an absence of host tree roots must thus be involved in the reduced root tip density in the machine corridors. Compaction caused by harvesting equipment can increase the bulk density of soil, in turn reducing the hydraulic conductance and infiltration rate (Startsev and McNabb 2001; Williamson and Neilson 2000). Thus, compaction caused by machine traffic could physically imped root growth and also restrict it indirectly by anoxia (Startsev and McNabb 2001).

Other than in the machine corridors there was little effect of DGTR harvesting on density of active fine root tips. In the residual strips the percentage of active fine root tips was lower (but not significant) in the 20% and 50% retention levels than in the 75% retention level (where trees were only removed in the machine corridors) or the control stands. Not surprisingly, the latter two treatments had similar percentages of active fine roots. In a previous study Harvey et al.

(1980*b*) found no effect of partial cutting (~50% retention) on active root tip density in a Douglas-fir – larch forest stand.

The burn treatment had the most substantial impact on ECM biodiversity. Stand-replacing wildfires differ from harvesting in that in addition to the removal of trees, the organic layer of soil is often consumed (Johnson 1992). Since most (up to 95%) of ectomycorrhizae are found in the organic layer (Goodman and Trofymow 1998; Harvey et al. 1976), a dramatic reduction in diversity, followed by slow recovery, is expected. Young, fire-origin jack pine stands (6 years old) had significantly lower ECM abundance and diversity than did stands 41 to 122 years post fire (Visser 1995). Prescribed fire has also been shown to dramatically reduce ECM biomass of a ponderosa pine stand (Stendell et al. 1999) and mycorrhizal richness of a ponderosa pine forest (following fall underburning, Smith et al. 2004).

Of the harvesting treatments, clear-cutting had the greatest effect on ECM biodiversity. Significant reductions in ECM biodiversity have been previously reported in clearcuts for lodgepole pine (Bradbury et al. 1998; Byrd et al. 1999), Douglas-fir – larch (Harvey et al. 1980*a*), subalpine fir – Engelmann spruce (Hagerman et al. 1999*a*), and interior cedar–hemlock forests (Durall et al. 1999). The DGTR harvesting also lowered ECM richness and diversity. However, as for active root tip density, this was primarily due to ef-

Table 3. The total number of root tips sampled, overall relative abundance (percentage of root tips), frequency of occurrence (percentage of soil cores), and the average relative abundance for ectomycorrhizae morphotypes at the different sampling positions associated with the aggregated green-tree retention patches (n = 96 soil cores) at the start of the third postharvest growing season.

| Morphotype | No. of tips | Overall relative abundance (%)* | Frequency (%)† | Relative abundance (%)‡ | | | | | | | |
| | | | | 0.25 ha | | | | 0.75 ha | | | |
				Center	Edge	10 m	20 m	Center	Edge	10 m	20 m
Cortinarius spp.	376	18.1	21.9	13.3	15.1	16.7	—	33.8	12.5	—	3.0
Amphinema byssoides	275	13.2	26.0	10.8	7.1	28.6	6.0	10.4	19.0	—	30.3
Cenococcum geophilum	256	12.3	31.3	15.1	13.9	50.0	16.7	14.4	1.9	9.1	5.4
Tomentella spp.	269	12.9	25.0	6.0	12.6	4.8	22.7	12.8	12.6	90.9	5.4
E-strain	177	8.5	11.5	4.7	5.6	—	—	4.9	13.9	—	21.5
Mycelium radicis atrovirens	166	8.0	11.5	14.9	6.5	—	21.4	6.7	—	—	—
Lactarius spp.	127	6.1	6.3	9.0	—	—	—	5.2	14.1	—	—
Russula spp.	126	6.1	12.5	7.4	26.2	—	—	3.2	2.4	—	1.1
Piloderma spp.	113	5.4	5.2	7.9	1.8	—	—	8.5	10.0	—	—
cf. *Tricholoma*	64	3.1	5.2	2.3	4.5	—	—	—	4.6	—	—
Unknown A	40	1.9	1.0	6.3	—	—	—	—	—	—	—
Tuber spp.	35	1.7	4.2	—	6.7	—	—	0.2	1.6	—	—
Thelephora terrestris	15	0.7	2.1	—	—	—	—	—	2.4	—	—
Undetermined	15	0.7	2.1								
Hebeloma spp.	12	0.6	1.0	—	—	—	—	—	4.0	—	—
Unknown B	13	0.6	1.0	2.4	—	—	—	—	—	—	—
Basidiomycete 1	4	0.2	1.0	—	—	—	—	—	1.1	—	—
Total no. of tips	2083			552	409	50	59	496	432	43	42

Note: Sampling positions were as follows: in the center, at the edge, and at 10 and 20 m from the edge of 0.25- and 0.75-ha residual ellipses.

*Relative abundance for each morphotype was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled) × 100.

†Frequency of occurrence for each morphotype was calculated as follows: (number of soil cores in which morphotype was observed) / (total number of soil cores) × 100.

‡Relative abundance for each morphotype at a given position was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled at that position) × 100.

fects in the machine corridor and not in the residual strips of the DGTR stands. Indeed, richness and diversity were only marginally greater in the machine corridors than in clearcuts. As described above, this may be attributed to soil compaction and (or) microclimatic effects. Soil compaction has been previously found to be related to reduced ECM morphotype richness on outplanted seedlings (Page-Dumroese et al. 1998) and to negate any positive effects of ECM inoculation of seedlings prior to outplanting (Teste et al. 2004).

The residual strips of the DGTR stands had richness and diversity similar to those of control stands. Similarly, previous studies failed to observe a relationship between basal area retained in thinned forest stands and sporocarp production (Kranabetter and Kroger 2001; Waters et al. 1994). Waters et al. (1994) did observe, however, an association between thinning and the relative frequency of the most common genera of ECM fungi.

Differences in ECM community composition among treatments mirror those observed for diversity and were similar to those of previous studies on harvested (Hagerman et al. 1999*a*; Bradbury et al. 1998; Byrd et al. 1999) and wildfire sites (Visser 1995). Previous studies have classified ectomycorrhizae as "early stage", "late stage", or "multistage" on the basis of their association with different ages or successional stages of forest (Last et al. 1987; Deacon and Fleming 1992; Visser 1995), and we have used these classifications in the interpretation of treatment effects on the composition of the

ECM community. While none of the common morphotypes were exclusive to the disturbed sites, the relative abundance of multistage ectomycorrhizae (e.g., *Hebeloma* spp., *Thelephora terrestris*, *Cenococcum geophilum* as per Visser 1995) was greater on harvested, burned, and machine corridors sites. Furthermore, fungi that have been characteristically associated with older forest (e.g., *Cortinarius* spp., *Piloderma fallax*, *Lactarius* spp., cf. *Tricholoma*; late-stage ectomycorrhizae as per Deacon and Fleming 1992; Visser 1995) were associated with the undisturbed sites (Fig. 3). Thus, the reduction in ECM richness and diversity in the disturbed sites was, in large part, due to the exclusion of late-stage ectomycorrhizae. As such, the ECM community observed in both the clearcut and burned stands was strikingly similar. The position of *Tomentella* spp. among the disturbed stands in the ordination diagram suggests that they may be characterized as early-stage ectomycorrhizal fungi; however, it was the only morphotype observed in every stand at the EMEND site, suggesting that it may have been the only broad generalist. The presence of *Amphinema byssoides* and *Cenococcum geophilum* in every treatment supports their characterization as multistage fungi (Visser 1995), which may be capable of colonizing root tips irrespective of the successional status of the site.

E-strain (*Wilcoxina* spp.) possesses early-stage characteristics (Deacon et al. 1983; Mason et al. 1983) and has been found on seedlings grown in clearcuts (Bradbury 1998;

Fig. 4. The mean ectomycorrhizal morphotype richness (*a*) and diversity (*b*) (per four soil cores) based on samples collected from the center, at the edge, and 10 and 20 m into the clearcut from two different sizes of residual ellipse in the aggregated green-tree retention harvesting. Samples were taken at the start of the third growing season post harvest. Treatment means with different letters are significantly different ($p < 0.05$; Tukey–Kramer honestly significant difference test). Error bars represent 1 SE (based on the three ellipses per position). * denotes SE = 0.
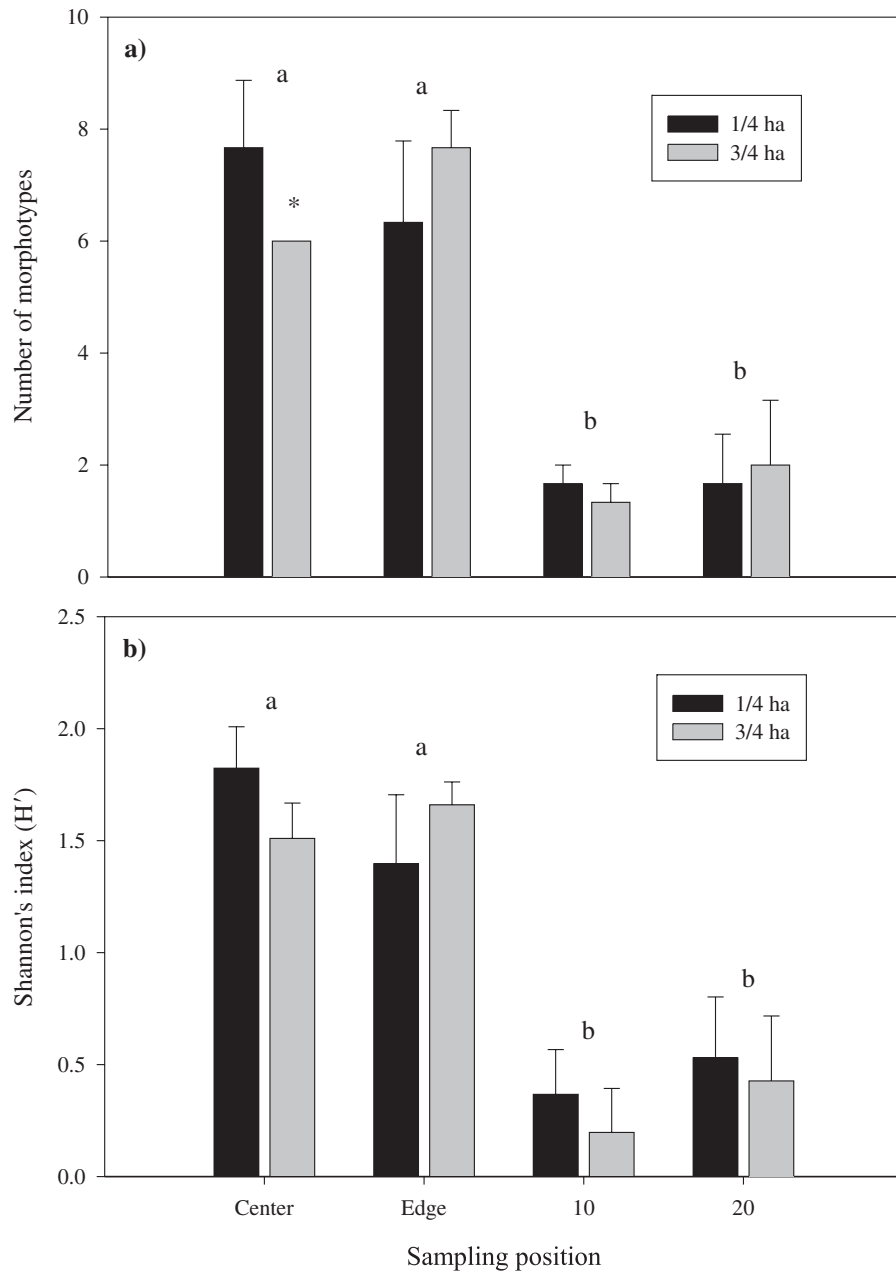
Hagerman et al. 1999*b*), but we observed E-strain in only 20 soil cores, only three of which were from disturbed (e.g., machine corridors) habitats. Hagerman et al. (1999*a*) noted that E-strain was rarely observed in soil cores collected from subalpine clearcuts in British Columbia, despite its presence on seedlings collected from the same sampling locations (Hagerman et al. 1999*b*). This discrepancy may be due to the fact that the root tips of planted seedlings represent a new, uncolonized resource for ruderal ECM fungi present in the soil, whereas mycorrhizae on the root tips of overstory trees (as found in soil cores) are formed in intimate contact with the fungi already colonizing the previous cohort of fine

roots. Use of a seedling bioassay, rather than soil cores, might have revealed higher abundances of early-stage ECM fungi, particularly in disturbed sites.

Aggregated green-tree retention

Our results suggest that aggregated green-tree retention in small patches can maintain ECM biodiversity within clearcuts but its role in facilitating recolonization of the surrounding harvested area is less certain. Both ECM richness and diversity were significantly greater in and at the edge of the residual ellipse than in the surrounding clearcut. Hagerman et al. (1999*a*) reported a significant reduction in morphotype rich-

Fig. 5. The relationship between the number of randomly selected root tips examined and the total number ectomycorrhizal morphotypes observed in soil cores collected from residual ellipses and clearcut sampling positions associated with the aggregated green-tree retention harvesting. The lines are based on the average of 10 randomized samples.
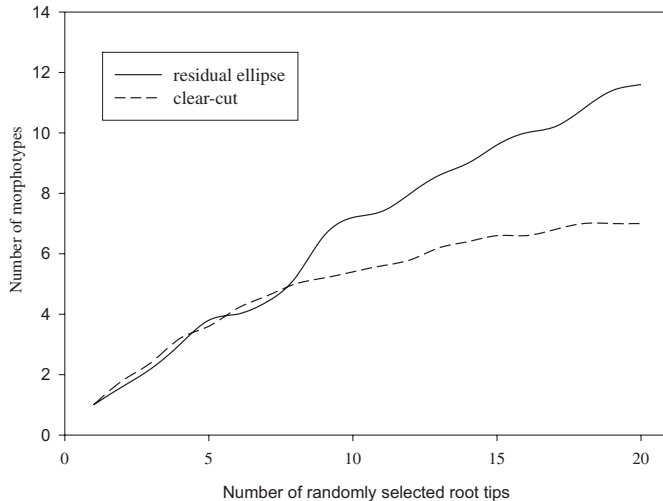
ness and diversity in soil cores 16 m from the edge of intact forest. Kranabetter (1999) examined the effect of refuge trees on ECM communities and found that within clearcuts, seedlings growing within 5 m of a single mature birch tree were associated with significantly more morphotypes than seedlings collected 25–50 m from mature birch trees. This suggests that even single trees left within clearcuts may be capable of providing refuge for ECM communities. A study by Simard et al. (1997) illustrates the influence of connection to roots of mature trees on mycorrhizal richness and composition on seedlings. Trenching (removal of contact with roots of mature trees) reduced mycorrhizal (morphotype) richness on Douglas-fir seedlings by about 50% and also changed the composition (Simard et al. 1997).

While, to our knowledge, no other study has investigated the ability of retention patches to act as a refuge for ectomycorrhizae, Durall et al. (1999) and Kranabetter and Wylie (1998) have examined the effects of different sized stand openings on the ECM communities of seedlings in northwestern British Columbia. In effect, this represents the inverse situation of our residual ellipses. Both studies reported a decrease in the number of ECM morphotypes with increasing distance from the forest edge. Thus, ECM communities appear to be strongly correlated with, or dependent upon, connections to intact forest. The change in community composition between the forest and clearcut sampling positions in our study provides further evidence for this.

Lactarius spp., *Piloderma* spp., *Russula* spp., cf. *Tricholoma*, and the three undetermined morphotypes ("unknown A", "unknown B", and "basidiomycete 1") were more abundant in soil cores collected from the center and at the edge of the residual ellipse than in the clearcut. Ectomycorrhizae formed by species of *Lactarius*, *Piloderma*, and *Russula* possess late-stage characteristics (Last et al. 1987; Newton 1992; Deacon and Fleming 1992; Visser 1995). *Lactarius* and *Russula* ECM produce extracellular phenoloxidases (Agerer 2000)

and have an affinity for leaf litter. *Piloderma* is a resupinate basidiomycete that fruits on decomposing plant litter and decaying wood (Goodman and Trofymow 1998) and may be an indicator of old-growth forests (Smith et al. 2000). It is not surprising therefore that these fungi were observed in association with the residual ellipses. Ectomycorrhizae with multistage characteristics, such as *Hebeloma* and *Thelephora* (Visser 1995), were only observed at the edge of the residual ellipses.

Despite their early-stage characteristics, MRA and E-strain (Deacon et al. 1983; Mason et al. 1983) were only slightly more abundant in the clearcut sampling positions. As these fungi are capable of colonizing root tips via spores, excised root tips, and hyphal fragments, it is unlikely that inoculum sources were limiting in the clearcut. However, it is possible that these species are unable to compete effectively with persisting preharvest ECM species. A lack of root tips for colonization also could have influenced the ECM community in clearcuts, since samples were collected at 10 and 20 m from the edge of the residual ellipse, and there were few white spruce seedlings in the clearcuts (L. Lazaruk, personal observation). Thus, as mentioned above, a seedling bioassay might have resulted in higher abundance of the early-stage ECM. As mentioned above, however, it is clear that direct connection to roots of mature trees is important for mycorrhizal richness and composition of seedlings. Also, Fig. 5 clearly shows that lack of available root tips cannot explain the reduced ECM richness of the clearcuts, as compared with the residual ellipses.

The relationship between morphotype richness and number of root tips clearly indicates that the low ECM richness in the clearcuts was not due only to a lack of available root tips. In this study, the ECM community in the clearcuts likely consisted largely of root tips that had persisted in the soil since harvesting. Ferrier and Alexander (1985) noted that excised ECM root tips were capable of remaining metabolically active for up to 9 months after being disconnected from their host, and Hagerman et al. (1999a) suggested that some root tips can survive up to three growing seasons in a clearcut in the absence of a host.

Conclusions

The results of this study suggest that partial cutting, either in the form of dispersed or aggregated green-tree retention (GTR) can be an effective means of maintaining ECM biodiversity. At the stand level, the dispersed GTR appeared to emulate the heterogeneity inherent to burned stands. However, both burning and clear-cutting significantly decreased ECM richness and diversity, suggesting that emulating natural disturbance is not synonymous with maintaining biodiversity, at least in the short term. Future research is required to determine the ability of the ectomycorrhizae associated with aggregated GTR patches to recolonize the surrounding clearcut and, in turn, their role in reforestation. While this study was capable of addressing the immediate impacts of these harvesting practices on ECM communities, further research is required to assess the long-term impacts.

Acknowledgements

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