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Forest management and maintenance of ectomycorrhizae: A case study of green tree retention in south-coastal British Columbia

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Abstract

Assessment of ectomycorrhizal (EM) colonization was carried out in a variable green tree retention experimental block near Powell River, British Columbia. We hypothesized that increasing retention level enhances colonization of EM fungi onto seedlings in harvested areas. We also investigated the role of isolated trees in EM maintenance. Transects were established in treatments where 0% (a clearcut), 5%, 10%, and 30% of trees were retained. Douglas-fir seedlings (*Pseudotsuga menziesii*) were planted at 5, 15, 25 and 45 m from the remaining forest edge and excavated 18 months later for analysis of EM colonization. Within the forest, soil cores and sporocarp surveys provided information on EM species potentially available for colonization of seedlings. We observed a total of 85 EM morphotypes. The edge effects—declines with distance from the forest, observed in the 0% retention treatment—were diminished in the higher-retention treatments. EM richness and root colonization increased insignificantly with increasing tree retention when the influence of ubiquitous early-stage EM fungi and inherent microsite differences were accounted for. EM diversity next to isolated trees was greater than at 10 m from the trees, but lower than at 5 m from the forest edge. We discuss the implications of these relationships and the role of isolated trees in the context of these exploratory findings. While these results suggest certain trends, they are for a single installation and their applicability to forests elsewhere in the region needs further study.

KEYWORDS: *Douglas-fir seedlings, ectomycorrhizal ecology, edge effects, mature second-growth forests, single green tree retention, variable retention silviculture.*

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Introduction

The majority of forests on the south coast of the British Columbia (BC) mainland and Vancouver Island are young to mature second-growth plantations, the result of many years of timber harvesting. The survival, health, and bio-diversity of these new forests will depend on many things, including management of the many complex biotic factors that constitute a forest. Many important biotic factors are still insufficiently studied, misunderstood, or even overlooked (Trofymow et al. 2003; Kremsater et al. 2003; Winder and Shamoun 2006). Ectomycorrhizal (EM) fungi, being microscopic, underground, and poorly known taxonomically, are an example. Although the important role of EM fungi in tree physiology has been documented and known for years (Smith and Read 2008), much research on EM fungi has focused on their role in seedling establishment and growth (Trofymow and van den Driessche 1991). Less is known about their importance in forest condition in the long term. Should EM fungi be significantly depleted (as in many parts of Europe (Arnolds 1991), and forest decline occur, future financial losses to BC's forestry-based economy could be significant. Ectomycorrhizae are major contributors to nutrient dynamics and carbon cycling in forest ecosystems (Read and Perez-Moreno 2003). Furthermore, EM fungi produce many commercially important mushroom species and the sustainability of their production will depend on forest harvest practices (Pilz and Molina 2002). Ectomycorrhizae and their fruiting bodies are also an essential component of forest ecosystems, as a source of food for animals, of carbon for achlorophyllous plants (e.g., *Allotropa* sp. and the endangered phantom orchid, *Cephalanthera austiniae*), and thus may play a role in maintaining diversity of other species in the forest (Ingham and Molina 1991; Molina et al. 2001).

Research on the biological foundation of forest sustainability is urgently needed for the forest industry. EM fungal species are an important component of biodiversity, and should be a major consideration when assessing the effects of variable retention (VR) forestry (Kohm and Franklin 1997). In coastal British Columbia, the use of clearcutting began decreasing in 1995, first as a result of recommendations of the Clayoquot Scientific Panel, and then in 1998 when MacMillan Bloedel Ltd. announced the introduction of variable retention silvicultural systems. These systems were subsequently implemented by Weyerhaeuser Coastal BC Group after their purchase of MacMillan Bloedel in 1999 (Dunsworth and Beese 2000), and their use continues on most tenures of Western Forest Products Ltd. (eventual successor after sale of Weyerhaeuser in 2003) (B. Beese, Western Forest Products, pers. comm., April, 2007).

In this study, we extend our research to examine how different levels of dispersed green tree retention affect ectomycorrhizal colonization by measuring the effect of various treatments at an experimental variable retention block.

In our previous work in several forest sites located in southern Vancouver Island (formerly Weyerhaeuser's Shawnigan and Nanaimo River Operations), we found clear evidence of edge effects in VR sites (Outerbridge et al. 2001; Outerbridge and Trofymow 2004). We observed significantly lower abundance and diversity of EM fungi with increased distance from retained forest patches. In this study, we extend our research to examine how different levels of dispersed green tree retention affect colonization by measuring the effect of various treatments at an experimental variable retention block established as part of Weyerhaeuser's Adaptive Management Program (Beese et al. 2003; Bunnell and Dunsworth 2004). More detailed review of VR practices and research in BC can be found in Bunnell and Dunsworth (2004) and Outerbridge and Trofymow (2004).

A few studies show that live trees within natural forest disturbances or clearcuts could shelter populations of ectomycorrhizal fungi (albeit at lower levels than pre-disturbance), thus potentially serving as EM refugia (Kranabetter 1999; Egli et al. 2002; Cline et al. 2005; Luoma et al. 2006). This research contributes more information needed to understand the effects of VR harvesting on ectomycorrhizae by exploring two questions:

1. Which level of retention is best suited to maintain Douglas-fir EM fungi on a site?
2. Could single-tree retention provide useful mycorrhizal refugia to increase the mycorrhizal inoculation potential of harvested sites?

Materials and methods

Site description and plot establishment

In April 2004, 12 study transects (three per treatment) were established near Powell River, BC on a site referred to as the Stillwater Variable Retention Experimental Comparisons Block (VRECB). The region is characterized by warm, dry summers and mild, wet winters. The study site is located in the Dry Maritime Coastal Western Hemlock subzone (CWHdm; 90% mesic) at an elevation of 170–260 m. The forest—composed of 54% Douglas-fir (*Pseudotsuga menziesii*), 27% western hemlock (*Tsuga heterophylla*), 15% western redcedar (*Thuja plicata*), and 4% red alder (*Alnus rubrus*)—was hand-felled in winter of 2001/2002 and replanted in the spring with 85% Douglas-fir and 15% western redcedar. Pre-harvest stand composition, post-harvest vegetation along transects, and other site characteristics are presented in Table 1.

The VRECB had four green tree retention treatments. Each treatment was based on the basal area of retained trees (m^2/ha), and had young mature (66–78-year-old) Douglas-fir-dominated forest edge next to a specific level of tree retention: 0% (clearcut), 5% (dispersed single trees), 10% (dispersed paired trees), and 30% (group dispersed, small groups). Locations for transects were chosen arbitrarily from the limited number of spots available to us within each treatment area, given the constraints inherent in setting up transects for EM sampling (e.g., presence of road, large boulders, small pond). Full replication of transects to control for slope/aspect, soil moisture, pre-harvest stand condition, and dominant vegetation was not possible due to pre-existing layout of treatments, but the results of this exploratory study are later discussed with this limitation and our relatively small sample sizes in mind.

From the forest edge, each transect extended 15 m inside the forest and 45 m into the harvested

TABLE 1. Characteristics of the Stillwater variable retention experimental block treatment areas used in the study of green tree retention effects on ectomycorrhizae.

Level of retention	Slope / Aspect	Soil moisture[a]	Pre-harvest stand composition[b]	Dominant vegetation along the transects	Ectomycorrhizal mushroom genera (total number of species)[c]
0% (clearcut)	Flat / na[d]	normal to moist	Fd 53, Hw 18, Cw 24, Os 5	*Gaultheria shallon*, *Vaccinium parvifolium*, Douglas-fir, western redcedar	*Cortinarius, Russula, Inocybe (15)*
5%	Flat / na	normal to somewhat dry	Fd 42, Hw 38, Cw 10, Os 10	*Gaultheria shallon*, Douglas-fir, western hemlock	*Cortinarius, Craterellus, Hygrophorus, Laccaria, Russula, Tricholoma (21)*
10%	12% / NE, sloping down from uncut forest edge	normal	Fd 24, Hw 27, Cw 35, Os 14	*Gaultheria shallon*, *Vaccinium parvifolium*, Douglas-fir, western hemlock	*Cortinarius, Laccaria, Russula (20)*
30%	10% / W, sloping downwards to uncut forest edge	moist to wet	Fd 26, Hw 25, Cw 41, Os 8	*Gaultheria shallon*, *Vaccinium parvifolium*, *Rubus ursinus*, *Sambucus racemosa*, *Rubus spectabilis*, Douglas-fir, western hemlock	*Armillaria* (pathogenic), *Lactarius, Russula (15)*

[a] based on visual observation during spring and fall

[b] rough estimate based on a 2001 vegetation cover study (Jeff Sandford, Western Forest Products, pers. comm., April 2008); Fd = Douglas-fir, Hw = western hemlock, Cw = western redcedar, Os = other species; numbers represent percentage

[c] based on sporocarp surveys spring and fall inside the forest at –15 m from edge

[d] na = not applicable

area, with sampling stations established at: –15 m, 5 m, 15 m, 25 m, and 45 m (Figure 1). With the exception of the –15m station, each station was planted with two 1+0 Fd seedlings (*Pseudotsuga menziesii*) that acted as "trap seedlings" for monitoring EM colonization, according to methods of Outerbridge et al. (2001) and Outerbridge and Trofymow (2004). A single retained tree was chosen in the vicinity of the 45-m station and used as one end of a "mini-transect" (10 m), which was oriented so that it remained at least 10 m away from neighbouring trees. Along each mini-transect, two seedlings were planted within 1 m of the tree at point "0" and two seedlings were planted 10 m from the tree (Figure 1). The distance of 10 m was chosen partly because our previous research showed considerable drop-off in EM counts between 5 m and 15 m from the edge of forest patches (Outerbridge and Trofymow 2004) and partly because of spatial constraints in the field. In the 0% retention, wooden posts were used instead of single trees.

Field sampling and measurements

Seedlings planted at each station were the primary sampling unit for this study. All seedlings were allowed to grow for two growing seasons prior to excavation in November 2005. Distances and bearings from each station to the nearest retained host tree (if present within 10-m radius) were measured at planting time. The presence of all woody vegetation, including planted seedlings, was recorded within a 1-m radius of each station. At the time of transect installation, three soil cores were also taken from each transect at the –15-m stations, at the base of the nearest mature Douglas-tree (within 1 m radius, at least 0.65 m apart). There were 36 soil cores in total, each 5 cm x 15 cm, taken from the forest floor surface after removing coarser debris, thus each containing varying amounts of organic and mineral soil. No attempt was made to separate the horizons for the analyses due to time constraints and because the main purpose of the soil core sampling was to familiarize ourselves with the EM morphotypes present in the area and to provide data to examine for potential pre-existing microsite differences among the treatment areas.

Laboratory processing

A random sample of 20 seedlings was taken from a Douglas-fir planting stock to check their initial mycorrhizal status, and no obvious mycorrhizae were found (no attempts were made to look for Hartig nets on short roots). After the field sampling, all soil cores and seedlings were stored at 2°C. Soil cores were processed as described in the methods of Goodman (1995) and tree seedlings were processed using a commonly used technique, recently applied by

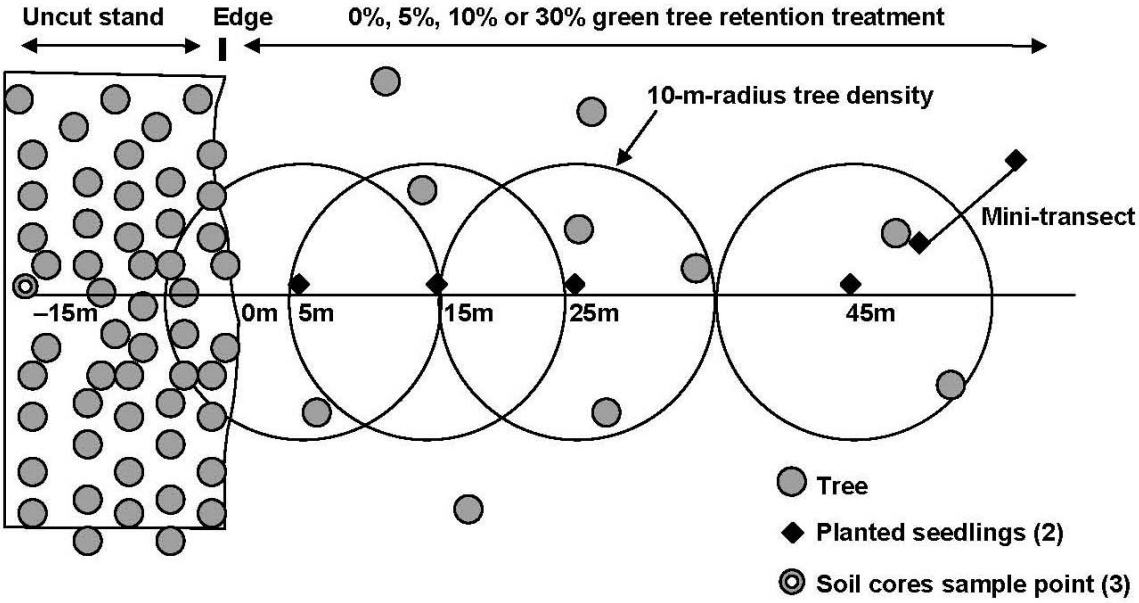

FIGURE 1. Sampling design for measuring diversity of ectomycorrhizal fungi on a single transect from forest edges at the Stillwater variable retention experimental comparison block subject to four levels of green tree retention (0%, 5%, 10%, and 30%). Three transects were sampled for each retention treatment.

Kranabetter and Friesen (2002). Seedling plugs and soil cores were washed individually using sieves to remove soil and debris. The roots were then cut to a length of 3–5 cm and placed in distilled water in a grid-lined plastic tray. *Thuja* roots and herbaceous or shrub material were removed. The root pieces of each sample (the entire sample for each soil core or each seedling) were thoroughly mixed and spread throughout the tray. For each soil core, all root pieces were examined for the presence of ectomycorrhizae. For the seedlings, the grid lines were followed under a stereo microscope and a sub-sample of the first 300 root tips was examined for all the mycorrhizae on the closest root segment to an intersection. The following categories were quantified for each sample (seedling or soil core):

- dead roots (if decaying or dried up);
- non-mycorrhizal roots (including short roots without changed root system morphology, if no mantle was present);
- mycorrhizal roots; and
- individual ectomycorrhizal morphotypes.

No attempts were made to look for Hartig nets on short roots without mantle unless root system morphology was changed (e.g., with dichotomous branching). The EM types were then sorted and counted using gross anatomical features. Some observations of cellular structures were made using a compound Nikon Eclipse 80i microscope, with Differential Interference Contrast attachment, under 400 X magnification and 1000 X oil immersion. Morphological types (or "species") were labelled according to colour or a set of distinguishing morphological features (e.g., "Wcott" for a white, cottony EM type). Some morphological types were later identified to fungal genus and/or species using methods and descriptions of Goodman et al. (1996–2000), Agerer (1987–2002, 1996–2002), and Ingleby et al. (1990), and by searching the online Database of Descriptions of Ectomycorrhizae (DDE) (Goodman et al. 2000; now replaced by the Ectomycorrhiza Descriptions Database [EDD] on the website of the BC Ectomycorrhizal Research Network [BCERN 2008]). The sample roots and the remaining plug roots were then placed in a glass Petri dish, oven-dried at 75°C for 48 hours, and weighed. Samples of root tips with representative morphotypes were placed in sterile water and frozen at –82°C for future reference and DNA analysis. Sporocarps of ectomycorrhizal fungi and plant species were identified based on taxonomic literature and field guides.

Statistical analysis

Data were analyzed separately for the soil cores, the main transects, and the mini-transects, using the same approach. The statistics on nine soil cores were obtained by combining the data from the three replicate transects per treatment. "Treatment" refers to a level of green tree retention (LOR). Richness was defined as number of EM morphotypes found in a sample of 300 root tips from a seedling or soil core. The mean number of root tips per soil core was 308.5 (SD 88.7). The total number of root tips examined was 11 106. The sub-sample of 300 tips was taken from a randomization of all root tips, bearing in mind the differences in vertical distribution of EM fungi. We maintained this sampling intensity consistently for each seedling. Average richness was defined as the mean richness of seedlings at a station or treatment. Total richness was the total number of EM types observed at a station or treatment. Percent root colonization was measured for each seedling or soil core sample (i.e., number of root tips colonized by one or more EM fungi divided by the total number of root tips examined). Mean values and standard deviations of percent colonization and richness were calculated for each distance from forest edge (n = 24 seedlings) and each retention treatment (n = 24). Regression, one-way, and two-way Analysis of Variance (ANOVA) with replication, and mean comparisons tests were performed using SAS, (Version 8.0, Cary, NC, USA; SAS Institute 2007). Means separation was performed using Tukey's multiple comparison test. We used $\alpha = 0.05$ to identify statistical significance. For the section of the results dealing with distance to the nearest tree (DNT) within 10-m radius from each station (Figure 1), all the calculations were based on an average of two seedlings per station.

Results

Ectomycorrhizal morphotypes and their frequency of colonization

Eighty-five ectomycorrhizal morphotypes were observed among all the seedlings and soil cores sampled in the study (Table 2). The numbers of morphotypes in soil cores, seedlings from main transects, and seedlings from mini-transects were 31,

55, and 42, respectively. Collectively, the seedling survey yielded 65 distinct EM morphotypes. The average EM richness on seedlings was 4.69 overall. The majority of the types have not been identified to species or genus, hence the necessity for morphotype codes and the accompanying brief descriptions (Table 2). The most frequent EM types were *Rhizopogon* cf. *vinicolor, Cenococcum geophilum*, and *Piloderma fallax*. Other identified taxa included: *Amphinema byssoides, Lactarius rubrilacteus*, "*Pseudotsugaerhiza baculifera*," and *Truncocolumella citrina*. Seventy-four percent of fungi had relative abundance lower than 1%. On average, ectomycorrhizae colonized 63% of the examined live root tips per seedling.

Inherent site differences: Soil core data and uncut forest

Examination of soil cores for presence and abundance of ectomycorrhizae inside the uncut forest revealed inherent differences across the VRECB in species composition as well as the percent live root colonization (Table 3). The forest adjacent to 0% retention area tended to have the lowest percentage of EM colonization despite the highest number of live root tips per soil core; however, a one-way ANOVA showed the differences in percent colonization among the uncut areas was only significant at P = 0.123. The uncut forest adjacent to 30% retention had overall low numbers of roots in each category in comparison with the uncut forest adjacent to the 5% and 10% retention (possibly reflecting differences in environmental factors as discussed below; see also Table 1). One-way ANOVA showed average and total richness were significantly lower (P = 0.0118) in the uncut forest adjacent to 30% retention compared to in uncut forest adjacent to the other retention treatments (Table 3). *Cenococcum geophilum* was the only consistently occurring morphotype, occurring in almost all samples and constituting 35.88% of colonized root tips amongst all soil cores. It was followed by *Rhizopogon* cf. *vinicolor* and *Piloderma falax*, found in over half the samples, though, again, not in uncut forest adjacent to the 30% retention. The possible inherent differences in EM richness across the VRECB, as indicated by the soil core results (Table 3) and the sporocarp surveys, vegetation surveys, and pre-harvest forest cover (Table 1), suggested the need for additional analyses of the seedling richness data—this was done on a percentage basis by normalizing the seedling richness data at the 15-, 25-, and 45-m stations against EM richness at the 5-m station data in the same transect. We elected to normalize against the seedling data from 5-m stations (the closest possible to the uncut forest edge) since uncut forest data were soil core samples from mature forest, and therefore not directly comparable to other stations' seedling data. Further evidence that there were inherent microsite differences among treatments was the variation in the EM richness at the 5-m stations where the mean (standard error) in the 0%, 5%, 10%, and 30% retention levels were 8.67 (SD = 0.42), 6.5 (SD = 0.43), 6.67 (SD = 0.95), and 5.0 (SD = 1.46), respectively.

Effects of retention levels on richness and EM root colonization

The four retention treatments differed significantly in the richness and frequency of EM colonization on the roots of the planted seedlings. Two-way ANOVA on non-normalized data showed level of retention to be a significant source of variance for overall richness (P = 0.0114, Table 4a). This was due to the fact that mean richness in 30% retention (3.75 ± 0.42 SE) was significantly lower than at 0% retention (5.08 ± 0.48 SE) (Table 5). Results of one-way ANOVA, testing for the effects of retention on richness at each transect station, were all insignificant (Table 4b). EM richness did not increase with level of retention as either the mean or total number of morphotypes (Table 5), except when data were normalized against richness at 5-m stations (Figure 2). One-way ANOVA performed on normalized data showed a significant result for the effect of retention treatments on richness (P = 0.02).

Two-way ANOVA showed level of retention to be a significant source of variance for overall percent root colonization (P = 0.0237 Table 4a). Mean percent colonization increased consistently with the level of retention and highest in 30% retention (67.5% ± 4.7 SE) and the lowest in 0% retention (55.0% ± 3.9 SE) (Table 5). Results of one-way ANOVA, testing for the effects of retention on percent root colonization at each transect station, were insignificant with one exception at 15 m (Table 4b).

Based on Tukey's multiple comparison tests, the 0% retention treatment differed from the 30% retention with respect to both percent colonization and richness. Viewed by distance, the percent colonization and richness data fell into two groups, with 5-m stations being distinct from the other stations (Table 5).

TABLE 2. Relative abundance (percentage of all colonized root tips) of EM morphotypes in the main transects, "mini-transects," and soil cores.

		EM root tips colonized by morphotype (%)		
EM morphotype	**Brief description or fungal species**	**Main transects**	**Mini-transects**	**Soil cores**
Ambys	*Amphinema byssoides*	2.70	2.14	
BeigMetLng	Beige, metallic, long tips	0.81		
BicWBrLng	Bicolorous, white brown, long tips	0.20	2.16	
BlkBr	Blackish brown	1.58	0.08	
BlkBrLthr	Blackish brown, leathery	2.64	2.18	
BlkBrPub	Blackish brown, leathery, pubescent	0.72		
BlkPkMoz	Black–pink mosaic	0.07	0.15	
Blksndp	Black, sandpaper-like	1.24	0.42	
Blkwarty	Black, warty, "*Piceirrhiza nigra*"?		0.58	0.16
BluBr	Blue-brown	0.22		
BluRhiz-L	Bluish, *Rhizopogon*-like	0.58	0.15	
BrmetpYtip	Brown, metallic, pale yellow apex			0.90
BrilCrO	Brilliant cream–orange			0.05
BrVerCor	Brown, verrucose, coralloid		0.28	
Canth	*Cantharellus formosus*-like	0.93	0.98	
CarotOr	Carrot orange	1.90		
Cenoc.	*Cenococcum geophilum*	13.50	13.54	35.88
ChBrSndp	Chocolate brown sandpaper-like	0.36		
Copper-like	Copper, metallic, smooth, white emanating hyphae			3.19
DkAsh	Dark ashy grey			0.50
DkOrSmMP	Dark orange, smooth, monopodial pinnate	0.19	0.92	
DtYevLgth	Dirty yellow, even-length tips			0.14
GinSlen	Resembling slender ginger roots	3.06	4.41	
GldRhWtoRY	White to reddish–yellow, golden rhizomorphs	0.12		
Hebel-L	White, patchy, *Hebeloma*-like	0.81		
Hister-L	White, fanning, *Histerangium*-like	0.44		
HonVelv	Honey-colored, velvety	4.77		
Humaria	*Humaria*-like		0.11	
IrFpYoB	Irregular, fanning, pale yellow over brown			0.36
Laccaria sp. ?	Similar to *Laccaria proxima*	0.77	0.27	
Laccaria sp.? #2	Smooth, cream-coloured, some tinged blue at apex	0.99	0.33	
Lactarub	*Lactarius rubrilacteus*	0.50	0.28	1.63
Lglyc-L	*Lactarius glyciosmus*-like	0.91		
LtBrFzLngCor	Light brown, fuzzy, long tips, coralloid	2.90		
NtmegIvor	Ivory-colored with brown specs (like nutmeg seed)	0.62	0.33	
OLBrLgdkhy	Olive brown, long dark hyphae	1.11	3.96	
OldSnow	Dirty white, reflective, aging yellowish	0.04		
OlYshSpiny	Olive yellow, tomentose			6.04
OR group	Orange, pale to dark, medium-thick, smooth to fibrous	2.82	3.42	0.93
OrCon	Orange, smooth, constricted			0.75
OrtoBrShgCor	Orange to brown, shaggy, coralloid	0.15		
OtoBrCntPit	Orange to brown, contorted, pitted	0.21		
Pbaculi	*"Pseudotsugaerrhiza baculifera"*	1.96	1.57	5.50
PchWSc	Peach-coloured, white, scaly		1.13	
Pilo	*Piloderma falax*	1.78	0.62	8.89

TABLE 2 (*concluded*). Relative abundance (percentage of all colonized root tips) of EM morphotypes in the main transects, "mini-transects," and soil cores.

		EM root tips colonized by morphotype (%)		
EM morphotype	**Brief description or fungal species**	**Main transects**	**Mini-transects**	**Soil cores**
PinkFan	Pink, fanning			0.70
PkIvorCot	Pinkish ivory, cottony		0.81	
PlumShgLng	Plum-coloured, shaggy, long tips		0.09	
POrComat	Pale orange, comatose	0.18		
POrSpecW	Pale orange, speckled white	0.85		
PtchSilPk	Patchy silvery pink	0.66	8.11	
pYfzArb	Pale yellow, fuzzy, arbuscular	0.28		
RBcontCott	Reddish brown, contorted, cottony			3.91
Rhizop	*Rhizopogon* cf. *vinicolor*	34.10	38.80	7.76
SilBrWPtch	Silvery brown with white patches	0.14		
SilvstO	Silver, staining orange			0.75
Tgilva-L	*Tricharina gilva* (or *Wilcoxina*)-like	0.81		
Thelephora	*Thelephora*-like		1.06	
ThickRus	Thick mantle, pale yellow, *Russula* sp.?	0.14	1.22	
ThkOr	Thick mantle, orange			0.07
ThkWhCy	Thick mantle, white, long cystidia			0.20
TkOrCor	Thick mantle, orange, coralloid	0.23		
TkpaleO	Thick mantle, pale orange			2.62
TkpSalCor	Thick mantle, pale salmon-coloured, coralloid	0.77	0.60	
Toment-like	*Tomentella*-like			3.62
TortThrO	Tortuous, thin, reddish orange			1.11
Trfelt	Transluscent white, felty	0.60	0.05	7.29
Trthin	Transluscent thin			1.88
Trunc	*Truncocolumella citrina*	2.40	2.79	1.38
TrWPyrCor	Transluscent white, pyramidal to coralloid	2.05		
Tuber-L	Tuber-like	0.59	0.33	
WaxSilW	Waxy, silvery white	0.53	0.09	
WaxWtoG	Waxy, white to grey	1.30	1.70	
Wcott	White, cottony	0.28	0.49	0.36
Wfanvtkr	White, fanning, very thick rhizomorphs			0.34
WHphob	White, mantle very hydrophobic	0.20	0.10	0.93
Whptchwov	White, patchy, woven	0.55	1.53	
WPkLngCorapxPrp	White to pink, long, coralloid, apex purplish	0.13		
Wporcine	White to beige, fuzzy to minutely scaly	0.27		
WptchShr	White, patchy, short rhizomorphs			2.10
Wshortrh	White, short rhizomorphs		0.09	
WtoMetBlapxPrp	White to metallic blue, apex purplish		1.00	
WtoSalLng	White to salmon-coloured, long tips		0.90	
WYBsm	White to yellow to brown, smooth	1.30	0.20	
Ybmetcot	Yellowish brown, metallic, cottony emanating hyphae			0.07
Total number of morphotypes		55	42	31

TABLE 3. Abundance at each retention treatment, total abundance, and relative abundance (percentage of all colonized root tips) of most abundant EM morphotypes (> 1 % relative abundance) in soil cores from adjacent uncut forest –15 m from the edge of retention treatments, followed by total number of morphotype and live root tips (in all nine cores) and average richness and percent colonization per soil core. The soil cores were pooled from 36 (3 cores/treatment).

		Root tips colonized by a morphotype in all 9 soil cores					
		Adjacent retention treatment					Relative abundance
Rank	EM fungus	0%	5%	10%	30%	Total	(%)
1	Cenoc	480	478	589	39	1586	35.88
2	Pilo	69	122	202	0	393	8.89
3	Rhizop	99	80	162	2	343	7.76
4	Trfelt	11	13	10	288	322	7.29
5	OlYshSpiny	10	0	0	257	267	6.04
6	Pbaculi	138	73	30	2	243	5.5
7	RBcontCott	84	78	11	0	173	3.91
8	Toment-like	0	0	6	154	160	3.62
9	Copper-like	0	141	0	0	141	3.19
10	TkpaleO	27	9	42	38	116	2.62
11	WptchShr	87	0	6	0	93	2.1
12	Trthin	0	35	48	0	83	1.88
13	LactOr	36	12	16	8	72	1.63
14	Trunc	21	19	18	3	61	1.38
15	TortThrO	0	0	0	49	49	1.11
Total number of morphotypes		18	15	21	13	31	
Total number of live root tips		2161	1682	1860	1513	7216	
Average (SE) number of morphotypes per soil core		5.6 (0.9)	5.1 (0.5)	6.0 (0.6)	2.9 (0.6)	4.9 (0.4)	
Average (SE) % root colonization per soil core		52 (7.5)	67 (4.8)	68 (3.0)	58 (5.7)	61 (2.9)	

Distance effects on richness and EM root colonization

Distance from the forest edge was a significant source of variation for overall richness ($P < 0.0001$), however interaction of distance and level of retention was not significant ($P = 0.1656$, Table 4a). One-way ANOVA for each retention treatment showed the edge effect was strongly significant for richness in 0% retention and 5% retention, but had no effect at higher retention treatments (Table 4c). Across all retention levels, regression analyses testing for the effect of distance from the edge on richness produced weak but significant results: number of morphotypes = $6.203x - 0.0674$ (Distance [m]), $r^2 = 0.2416$, $P < 0.0001$.

As described above, to account for the inherent microsite differences in EM richness, the richness data were normalized at 5 m, and ANOVA repeated. Normalized richness data, showed a sharp and persistent decline in the number of morphotypes at 15 m from the edge of the 0% retention, less of a decline in the 5% and 10% retention, and no change with distance at 30% retention (Figure 2). The rise in richness at 15 m in the 30% retention treatment coincided with the greater number of "nearest trees" at that distance. Two-way ANOVA analysis performed on normalized richness data produced a significant main effect of distance ($P = 0.0100$) and retention treatment ($P = 0.0404$); however, the interaction was not significant ($P = 0.8642$).

TABLE 4. Effects of level of retention treatment and distance from the forest edge on EM root colonization (%) and richness (number of morphotypes) on experimentally planted seedlings: (a) overall, (b) for each distance, and (c) for each retention treatment.

Source of Variance	% Root colonization P-value	Number of morphotypes P-value
(a) Overall: Two-way ANOVA testing for effect of level of retention treatment and distance (n = 96 seedlings)		
Level of retention (LOR)	0.0237*	0.0114*
Distance from forest edge	< 0.0001*	< 0.0001*
LOR x distance	0.0019*	0.1656
(b) Distance: One-way ANOVA testing for effect of level of retention for each distance from forest edge (n = 24 seedlings per distance)		
5 m	0.0573	0.0759
15 m	0.0103*	0.0865
25 m	0.0704	0.2308
45 m	0.0864	0.8974
(c) Retention: One-way ANOVA testing for effect of distance for each level of retention treatment (n = 24 per retention level)		
0% retention	0.0002*	0.0001*
5% retention	0.1694	0.0025*
10% retention	0.0370*	0.0508
30% retention	0.0007*	0.3765

* Statistically significant at $\alpha = 0.05$

Distance from the forest edge was a significant source of variation for percent root colonization ($P < 0.0001$). The edge effect was strongly significant for percent root colonization in 0% retention, but less consistent in the other treatments (Table 4c). The interaction of distance from the forest edge and retention level was also significant for overall percent root colonization ($P = 0.0019$) (Table 4a, Figure 3). Regression analyses testing for the effect of distance from the edge on percent colonization produced weak but significant results: percent colonization = 75.46x – 0.569 (Distance [m]), $r^2 = 0.17708$, $P < 0.0001$. Figure 3 shows a non-linear decline in percent colonization vs. distance in the VR plots. It also shows high variability as well as an unexpected rise in percent colonization in the 0% retention treatment area at 45 m. The rise was caused by increased presence of *Cenococcum* and *Rhizopogon* at that location (Figure 4), and was eliminated when percent colonization data were plotted without these two species (Figure 5). Two-way ANOVA, with *Cenococcum* and *Rhizopogon* removed, produced significant results for distance effect ($P < 0.0001$) and for interaction of retention level with distance ($P = 0.03$).

Effects of single tree retention and distance to the nearest host tree

In the mini-transects at the 45-m station, seedlings in the 0% retention had a total EM richness of 15 morphotypes, compared to 20 morphotypes at 5% retention, or 20 and 19 morphotypes in 10% and 30%

TABLE 5. Mean EM root colonization (%) and mean and total richness (number of morphotypes) for seedlings in each level of retention treatment and distance from forest edge. Means sharing the same letter are not statistically different from each other.

Location	Mean % root colonization	Mean number of morphotypes	Total number of morphotypes
Level of retention			
0%	54.98*a*	5.08*a*	28
5%	61.42*ab*	4.88*ab*	21
10%	66.79*ab*	5.04*ab*	29
30%	67.47*b*	3.75*b*	29
Distance (m)			
5	79.23*a*	6.71*a*	44
15	60.73*b*	4.42*b*	29
25	57.33*b*	4.00*b*	26
45	53.37*b*	3.63*b*	16
All	62.66	4.69	55

retention treatments, respectively. For the 5%, 10%, and 30% retention treatments, mean richness was significantly higher at the base of a single retained host tree (Douglas-fir), than 10 m away from it (Table 6). Results of regression analysis of distance to the nearest host tree on richness were significant: number of morphotypes = 6.86x – 0.221 (Distance [m]), $r^2 = 0.3552$, $P < 0.0001$.

Mean percent colonization was significantly higher at the base of a single retained host tree (Douglas-fir), than 10 m away from it (Table 6). Results of regression analyses of distance to the nearest host tree on percent colonization were significant (% colonization = 85.18x – 2.28 (Distance [m]), $r^2 = 0.4179$, $P < 0.001$).

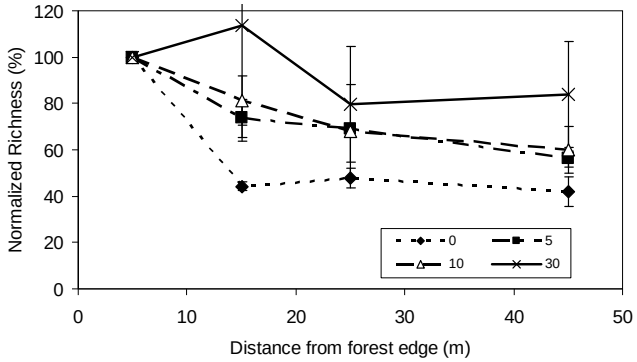

FIGURE 2. Changes in normalized EM richness (number of morphotypes) on planted seedlings at increasing distance from forest edge under four levels of green tree retention (0%, 5%, 10%, and 30%). Data normalized using values 5 m from forest edge. Bars show the standard error.

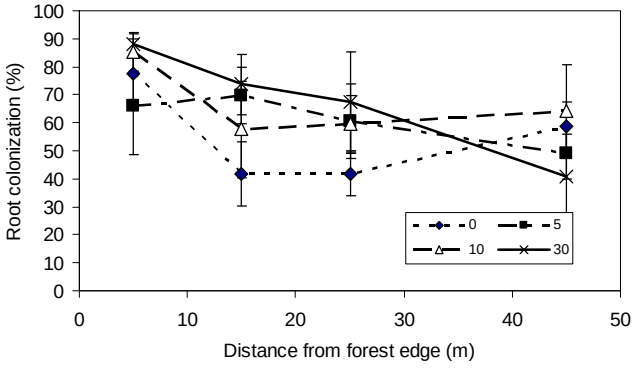

FIGURE 3. EM root colonization (%) on planted seedling at increasing distance from forest edge under four levels of green tree retention (0%, 5%, 10%, and 30%). Bars show the standard error.

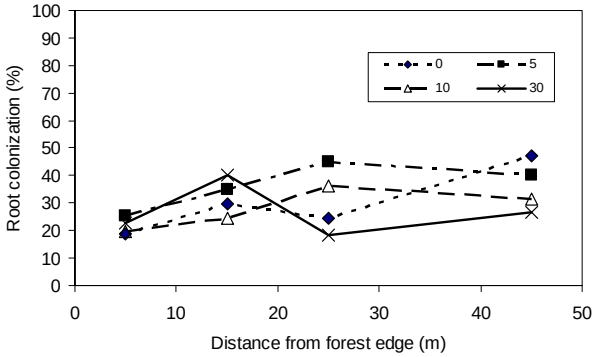

FIGURE 4. EM root colonization (%) by *Rhizopogon* sp. and *Cenococcum* sp. combined, on planted seedling at increasing distance from forest edge under four levels of green tree retention (0%, 5%, 10%, and 30%).

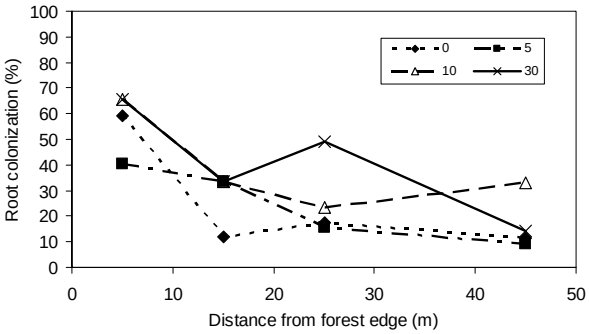

FIGURE 5. EM root colonization (%), excluding *Rhizopogon* sp. and *Cenococcum* sp., on planted seedlings at increasing distance from forest edge under four levels of green tree retention (0%, 5%, 10%, and 30%).

Discussion

Considerable differences exist among sites and operations with regards to VR practices. While in some locations, either individual or dispersed or group green tree retention is applied, in others the focus is on varying the percentage retention of the original stand (Franklin et al. 1997). This study examined treatment areas in a single experimental block containing increasing levels of green tree retention, including widely scattered single trees, which allowed us to assess the impact of these practices on EM morphotype diversity on young Douglas-fir seedlings. Several differences and trends emerged with respect to EM composition, frequency, and richness versus the various levels of tree retention, distance from the forest edge, or the nearest host tree. Single tree retention has the most habitat altering potential, second only to clearcuts for which effects are already well documented elsewhere.

TABLE 6. a) Mean values and b) results of ANOVA testing for the effect of proximity of single host tree and retention treatment (5%, 10%, 30%) on planted seedling EM root colonization (%) and richness (number of morphotypes).

a) Mean % root colonization and richness at base and 10 m from host tree

Location	% Colonization	Richness
Next to host tree	82.32	5.78
10 m from host tree	50.58	3.44

b) Two-way ANOVA analyses testing for the effect of host tree proximity and retention level

	% Colonization P-value	Richness P-value
Level of retention (LOR)	0.5909	0.4691
Proximity to host	< 0.0001*	0.0013*
LOR x Host	0.8267	0.938

* Statistically significant at $\alpha = 0.05$

EM morphotypes

Research on ecology of ectomycorrhizae in the Pacific North-west has been slowly growing but is still generally characterized by the very limited knowledge about their identity (Goodman et al. 1996–2000). Researchers often employ various codes or descriptive names for the EM fungi in order to monitor their occurrence and to calculate species richness (Jones et al. 1997; Wurzburger and Bledsoe 2001; Menkins 2005). Following this morphotyping method (Agerer 1991), we were able to obtain an estimate of the different EM types present and their frequency in the four VR treatment areas, despite the taxonomical difficulties. Despite increasing interest in using molecular tools to study ectomycorrhizal ecology and community structure, it seems that the results of such investigations frequently only confirm what we already knew from morphological approaches (see, for example, Horton and Bruns 2001). Difficulties with finding a universal community profiling technique for various soils and circumstances and other technological limitations also continue to surface (Anderson and Cairney 2004). It is for these reasons, and the fact that we were not overly concerned about missing closely related species, that we decided to use a traditional morphological approach. Notwithstanding, some EM types from this work have been analyzed using PCR methods and are described online (BCERN 2008). We found a total of 85 different morphotypes in the study area, a fairly high number in comparison with other EM studies on Vancouver Island (Goodman 1995; Outerbridge and Trofymow 2004) and elsewhere in British Columbia (Goodman 1995; Roth and Berch 1992; Kranabetter and Friesen 2002). This might indicate that, although we used only three soil cores or two seedlings per station, our overall sampling intensity (including microscopy work) was adequate for this type of study. From an ecological point of view, the high EM diversity could be explained by the fact that the research block was fairly diverse in general, supporting a variety of sporocarps and vegetation. *Cenococcum geophilum* and *Rhizopogon* cf. *vinicolor* were most widely distributed. They occurred on almost every seedling and in the majority of soil cores. The genus *Cenococcum* is a ubiquitous member of the EM community throughout the world (Trappe 1964; Douhan and Rizzo 2005; Jany et al. 2002). While the presence of ubiquitous or cosmopolitan EM species on a site seems beneficial (perhaps ensuring a certain degree of resilience to disturbance), it is equally important to maintain high EM species richness, which is linked to physiological and functional diversity (Allen and Allen 1992; Ho and Trappe 1980). It was beyond the scope of this paper to focus on the status of various species within the taxonomically difficult genus *Rhizopogon*, especially since we did not observe any fruiting bodies. From an examination of peridia, rhizomorph, and mantle morphology, and an analysis of DNA from two collections (Ka Hyeon Kang, Korea Forest Research Institute, pers. comm., August 2007), we believe that, in majority of cases, we were dealing with *Rhizopogon vinicolor* (Zak 1971; Goodman 1996). However, there was some phenotypic variability among the samples

and, based on molecular work to date (Kretzer et al. 2003), it is quite possible that other species, especially *R. vesiculosus*, could be present.

Other common ectomycorrhizae identified to species were *Truncocolumella citrina*, *Piloderma falax*, and a tentatively named ectomycorrhiza "*Pseudotsugaerrhiza baculifera*," probably formed by a *Piloderma* fungal species (Muller and Agerer 1996). These five morphotypes were also very common in our survey of ectomycorrhizae in a VR setting on Vancouver Island (Outerbridge and Trofymow 2004), and are frequently encountered in other studies (Berch and Roth 1993; Jones et al. 1997; Goodman and Trofymow 1998a, 1998b; Byrd et al. 2000; Jones et al. 2002). Our "Blkwarty" appears very similar if not identical to "*Piceirrhiza nigra*" described by Berg and Gronbach (1988). This could mean an extension of host specificity for this morphotype, from *Picea abies* to *Pseudotsuga menziesii*, as well as a possible identification to family (Thelephoraceae), based on preliminary DNA analysis (Ka Hyeon Kang, Korea Forest Research Institute, pers. comm.. August 2007. The majority of morphotypes were infrequent and/or very localized. While only 10 out of 85 morphotypes occurred in all four treatment areas (BlkBrLthr, BluBr, Canth, Cenoc, GinSlen, ORgroup, Pbaculi, Rhiz, Trunc, BicWBLng), 35 morphotypes (41%) were found only at a single site, a slightly lower rate compared to our previous work (46%; Outerbridge and Trofymow 2004). The highly skewed frequency patterns and patchy distribution of ectomycorrhizal fungi that we observed have been previously mentioned in literature (Agerer and Gottlein 2003; Koide et al. 2005).

The EM morphotype diversity presented here should not be viewed without consideration given the limitations inherent in this type of work. The sampling intensity was in all probability too low to obtain a complete view of the EM community on the site (Taylor 2002). Trap seedlings, although frequently used in EM research, will likely not attract those species which prefer to colonize older or mature trees (Twieg et al. 2007). One should consider the data as yet another continuation point in filling the enormous gap in our knowledge on EM fungal communities in British Columbia.

The EM morphotype diversity presented here should not be viewed without consideration given the limitations inherent in this type of work.

Effects of increased green tree retention on richness, percent colonization, and overall diversity

Overall, the percent colonization of the seedling roots was comparable to that seen in other studies with Douglas-fir seedlings (Outerbridge and Trofymow 2004; Parke et al. 1984; Jones et al. 1997). The percent colonization of the soil core roots from the uncut forest were somewhat lower, possibly a reflection of different seasons of collection (cores in April, seedlings in November). The treatment areas had different pre-harvest levels of *Pseudotsuga menziesii* cover, with potentially different root density, which (combined with the small number of soil cores examined) may explain the "anomalous" results from the soil cores taken at –15-m stations of the 30% retention treatment. Nonetheless, even with the inherent differences among the four retention treatment areas, treatment effects were evident with distance along the transect. Level of retention was a significant source of variance for both percent colonization and EM richness overall. Average percent colonization increased consistently with the increase in the retention level of the host trees, while overall richness was highest in 0% retention (due to high number of morphotypes at 5-m stations, mirroring the high richness in the –15-m soil cores) and lowest at 30% retention (due to lowest number of morphotypes at 5-m stations, mirroring the low richness in the –15-m soils cores), possibly caused by wet microsite conditions (Outerbridge 2002). If seedling fine-root growth was similar among treatments and stations, we then interpret the differences in percent colonization among treatments and stations as an indication of the amount of EM inoculum in the soil surrounding the seedling. Analyses of 15-, 25-, and 45-m station richness data, normalized using data from the 5-m station in each transect, showed that normalized richness increased with increasing retention level. Data from the 5-m station seedlings rather than data from the –15-m cores were used for normalization as the former represent a sample from the population of EM fungi colonizing new seedling roots, while the latter roots represent a different population (i.e., EM fungi colonized on roots of older trees in the closed stand).

For effective maintenance and re-establishment of EM fungal populations, survival requirements of other organisms with which they form relationships have to be considered… It is the preservation of biological diversity, and not the increased abundance of a few species, which is the concern in this study.

The effect of retention level on percent colonization was more definitive following removal of *Rhizopogon* and *Cenococcum* morphotypes. We felt justified in removing these two morphotypes for some of the analyses based on their ubiquity and seemingly lower sensitivity to forest disturbance (if not thriving on it)—despite this biological rationale for the adjustment of the sample, the removal was primarily aimed at better revealing significance in the results. Given the above interpretation of the percent-colonization variable, examination of percent colonization by all other EM species gives a clearer indication of their prevalence in the soil around the seedling (though biological significance in the symbiotic community cannot be inferred on the basis of these adjusted data). *Cenococcum geophilum* may well be the most common ectomycorrhizal fungus in the world. It uses many hosts, including understorey shrubs and even herbaceous plants (Trappe 1964). *Rhizopogon* has several strategies for successful colonization and survival, such as enclosure of root tips in protective tubercles, production of truffle-like fruiting bodies dispersed by animals feeding upon them, formation of abundant, highly differentiated rhizomorphs, and—in contrast to late stage EM fungi—successful colonization of new substrates via spores (Bruns 1995; Goodman 1996; Colgan III and Claridge 2002; Peterson et al. 2004).

The edge effect (declining percent root colonization and richness with distance from edge) documented in our previous work (Outerbridge and Trofymow 2004) was still observed in the 0% retention treatment, especially with respect to the sharp drop in richness within 15 m of the edge. The most significant VR treatment effect was a strong relationship between the level of retention and percent colonization at the 15-m distance from the forest edge. Interestingly, most "nearest trees" were located around the 15-m stations (i.e., the distance to the nearest tree was lowest at 15 m from the edge of the forest). Overall, the increasing retention treatments appeared to have positive effects on both percent colonization and normalized richness, thus diminishing the edge effects. However, the influences are not strong and are confounded by inherent microsite variability within the experimental block. This suggests that higher retention levels should be tested to confirm the trend. Also, for effective maintenance and re-establishment of EM fungal populations, survival requirements of other organisms with which they form relationships have to be considered. In the context of forest ecosystems, it is well documented that organisms such as mammals, birds, amphibians, and arachnids, as well as fungi, are adversely affected by logging and indirect effects of timber harvesting—in some cases, the damage to their populations was found directly proportional to the intensity of their habitat alteration (Wilcove et al. 1998; Kranabetter and Wylie 1998; Luoma et al. 2004; Yezerinac and Moola 2006; Kremsater et al. 2007). It is the preservation of biological diversity, and not the increased abundance of a few species, which is the concern in this study.

Some might argue that fungi, as part of the microbiota, are ubiquitous and resilient, and should be able to survive various environmental alterations. But it is essential to remember that ectomycorrhizae are a special group of fungi, not randomly or evenly distributed within a plant community (Allen and Allen 1992; Ettema and Wardle 2002). Their dispersion patterns are related in part to environmental gradients, like those of other soil organisms (Carroll and Wicklow 1992; Johnson 1976; Boerner 1986; Boerner et al. 1996, Outerbridge 2002), but most of all to the presence of their symbiotic host, the "green tree." Evidence exists from related studies that removal of trees has a detrimental effect on survival and growth of ectomycorrhizae associated with them. Most of these studies focus on other silvicultural practices such as thinning, clearcutting, forest fertilization, or forest gaps (Kropp and Albee 1996; Hagerman et al. 1999a and b; Durall et al. 1999; Kranabetter et al. 1999; Massicotte et al. 1999; Kranabetter and Friesen 2002; Outerbridge 2002; Jones et al. 2003; Toljander et al. 2006). This study examines relationship between the level of EM fungal diversity and green tree "gradient" by the use of sites subject to different levels of variable retention. Our findings, although lacking in evidence for a strong

response to such a gradient, are in general agreement with those of Luoma et al. (2004) who studied response of ectomycorrhizal fungus sporocarp production to varying levels and patterns of green tree retention—the researchers found that 40% green tree retention treatments maintained higher levels of EM sporocarp biomass and diversity of fruiting species than 15% retention treatments.

The role of single trees as EM refugia

Our preceding conclusions are supported and extended by our analyses of the effect of distance to the nearest host tree and also by our analyses of the effect of a 10-m distance from an isolated tree. Not surprisingly, the number of morphotypes increased where a live host was present. We cannot be certain of the exact nature of the relationship (in terms of absolute diversity values) as we have to consider the limitations of this type of monitoring (the "trap seedlings") and also the limitations of using morphotyping alone. In other words, some of the diversity found on the trap seedlings might be independent of the proximal single trees, but rather due to residual inoculum in the soil or on other vegetation. However, this should not have affected our results in comparative terms, and the hypothesis that retained single trees play a positive role in providing refugia and a source of inoculum for some ectomycorrhizal fungi was supported. Significantly, more EM types were found at the base of a host than 10 m away from it. As well, analyses of the effects of the nearest tree showed a significant overall relationship for both EM colonization and richness.

Management implications

Are single trees merely useful or are they sufficient to maintain EM diversity on a site? From these and previous results (Outerbridge and Trofymow 2004; Cline et al. 2005), it appears that isolated trees do maintain a certain proportion of the ectomycorrhizal fungal species characteristic of mature forests. However, we also suggest that the role of single green trees in providing viable long-term support for survival and growth of ectomycorrhizal fungi is uncertain and tenuous. Limitations will differ from situation to situation. One of several important factors to consider is the high rate of windfall along forest edges, in small patches of timber, or for individually standing trees, as documented in

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literature (Beese et al. 2003; Busby et al. 2006) and observed in all the VR sites we studied to date.

Host specificity is another factor. Many EM fungi are host-specific and, therefore, are not evenly distributed in the soil. Though still the subject of speculation and ongoing research, EM distribution appears to change with time, either in direct synchrony with the aging host (Dighton and Mason 1985) or, as some researchers argue, with changes in soil characteristics brought about by the aging or otherwise altered forest (Keizer and Arnolds 1994). It should be noted, however, that Goodman and Trofymow (1998a), using soil core and morphotyping methods, did not find significant differences between old-growth and mature second-growth forests in richness and abundance of ectomycorrhizae. Previously, we showed a significant drop in EM abundance and EM morphotype diversity at 25–45 m away from the forest edge into a clearcut (Outerbridge and Trofymow 2004). Cline et al. (2005) found that seedlings planted within 6 m of residual Douglas-fir trees had higher EM species richness and diversity compared to those planted more than 16 m from host trees. Despite ample sporocarp production, most EM fungi are more adapted to dispersing via vegetative mycelia in contrast to the predominance of dispersion by spores in other fungi (Taylor and Bruns 1999; Agerer 2001). They also have different rates of mycelial spread and different abilities to withstand temporary loss of host and environmental pressures (Carroll and Wicklow 1992). All of the above suggests that root-to-root contact is of utmost importance for many EM species, so the distance of a single standing tree from the forest edge will be crucial as well (Egli et al. 2002; Taylor and Bruns 1999). Some tree species are known to form ectomycorrhizae with as many as 2000 EM fungi

throughout their distribution, while a minority of others form none (Trappe 1977). In this context, it could be instructive to consider several scenarios:

- a single 80-year-old Douglas fir, 10 m from the forest edge, in loamy soil in a protected area;
- an 80-year-old hemlock 55 m distant from the same forest edge;
- a spruce emerging from a boggy area; and
- a withered 200-year-old pine or arbutus tree at the edge of a barren, rocky seashore.

These trees would all play a different role as ectomycorrhizal refugia. Some may promote the maintenance of an EM community, while others may be kept alive by their EM symbionts. At the other end of the spectrum, western redcedar might play an inhibitory role (Kranabetter and Kroeger 2001), possibly due to its antifungal compounds. Many understorey trees, shrubs, and herbs, which proliferate in cut-over areas, can compete with conifer trees and seedlings for space and resources, although important facilitative effects are also taking place (Allen and Allen 1992; Simard and Vyse 2006). Single live large trees are of value for some animal species at this and other VRECB sites monitored by Weyerhaeuser (B. Beese, Western Forest Products, pers. comm., March, 2006) and for some fungi (Kranabetter 1999). Generally speaking, however, it would seem logical that single retained trees are of limited use as habitat for those animals and plants whose survival depends on the presence of contiguous forest. Large mammals are not the only living things that require forest soils and unbroken canopy (Lutz and Chandler 1946). Since EM fungi live in tightly woven relationships with many of other organisms (including mammals), the integrity of their habitat influences, in turn, the integrity of the ectomycorrhizal networks, an integral element of all forest ecosystems (Fogel and Trappe 1978; Ingham and Molina 1991; Ettema and Wardle 2002; Hogberg and Hogberg 2002; Read and Perez-Moreno 2003). It is well known that mycorrhizal diversity is lower in grasslands than in forest soils (Carroll and Wicklow 1992), and that mushrooms (providing spore dispersal) are found primarily in forests. Relying on single green tree retention treatment alone to provide fungal refugia would most likely result in impoverished EM diversity on a site over time. In considering level of tree retention as a silvicultural practice of choice, with the purpose of maximizing EM fungal maintenance and dispersal in mind, one needs to analyze the problem from a biological as well as operational point of view. How likely is it that any pre-conceived harvesting strategy will take into account the complexity of the EM fungal ecology, and how likely is it that a complex harvesting strategy would be judiciously followed in the field? If unavoidable, we recommend that single tree retention be used in combination with group retention, in clearcuts of small sizes (under 5 ha), and where prompt forest replanting (within two years) can take place.

Conclusions and recommendations

This exploratory study has shown that the level of ectomycorrhizal diversity in an experimental variable retention block was related to the level of green tree retention. Examination of EM root colonization and morphotype richness on Douglas-fir trap seedlings supported the hypothesis that increased level of tree retention translates into increased levels of EM diversity. The strong edge effect was still present in 0% retention, but diminished in other retention treatments. The number of "unique" EM species was also lowest in the 0% retention and highest in the 30% retention treatment. The latter could be due to the lowest inoculation potential for aggressive fungi or the more unique environment of the 30% retention area. We also found significant differences in the EM community on the seedlings compared to the EM community on the adult trees.

Based on the limited sampling used here, we tentatively conclude that retention of dispersed single trees create temporary refugia and source of inoculum for a fraction of ectomycorrhizal morphotypes present in the pre-harvest area. More intensive sampling of pre-harvest areas might confirm if these were trends or true effects. Until long-term effectiveness of dispersed single tree retention is known, we recommend that forest managers consider using the highest level of green tree retention possible. Depending on the original stand density, this might represent retention levels of 30% or more. This preliminary conclusion is based on our research to date, other studies on effects of tree removal on biodiversity, and the current knowledge of the relationships among ectomycorrhizal fungi and other organisms in forest ecosystems. Ideally, an attempt should be made to maintain the uninterrupted root-to-root contact in

Until long-term effectiveness of dispersed single tree retention is known, we recommend that forest managers consider using the highest level of green tree retention possible. Depending on the original stand density, this might represent retention levels of 30% or more.

order to promote ectomycorrhizal fungal spread. This is especially important for the numerous smooth or short-range exploration types. Will variable retention be sound, both economically and ecologically? Given that EM fungi can be as vital to establishment of trees as the presence of trees is to EM fungal communities, future studies on this topic are clearly needed to answer this question and to establish realistic objectives for maintenance of mycorrhizal populations in managed forests of this region.

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Test Your Knowledge . . .

Forest management and maintenance of ectomycorrhizae: A case study of green tree retention in south-coastal British Columbia

How well can you recall some of the main messages in the preceding Research Report?
Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. Ectomycorrhizal fungi play an important role in the forest ecosystems because:
   - A) They are major contributors to the ecosystem nutrient dynamics and tree nutrition
   - B) Fruiting bodies of some species are commercially important
   - C) They are a food source for some animal species
   - D) All of the above

2. Variable retention forestry has the potential to enhance maintenance of ectomycorrhizal fungal diversity on a site through:
   - A) Leaving trees to shade the ground to prevent mushrooms from drying out
   - B) Leaving trees that are still in connection to the fungi, serving as refugia for those species
   - C) Leaving trees that can serve as source of EM fungi from which seedling can be recolonized
   - D) A, B, and C
   - E) A and B
   - F) B and C

3. The level of tree retention used to maintain ectomycorrhizal fungal diversity on a site:
   - A) Is not known
   - B) Can increase EM fungal diversity and improve their ability to disperse
   - C) Will vary for different EM fungal species and needs more research

Answers

1. D 2. F 3. B and C