Effects of clearcut logging and tree species composition on the diversity and community composition of epigeous fruit bodies formed by ectomycorrhizal fungi

D.M. Durall, S. Gamiet, S.W. Simard, L. Kudrna, and S.M. Sakakibara

Abstract: The objective of this study was to examine the effects of stand age and tree species composition on the abundance, diversity, and community composition of epigeous fruit bodies formed by ectomycorrhizal (ECM) fungi in the Interior Cedar Hemlock zone of British Columbia. Fruit bodies were collected and identified in May, June, August, September, and October of 1996, 1997, 1998, and 1999 from transects located in new (5 year old) plantations and mature (75–125 year old) wild forests composed of relatively pure *Betula papyrifera* Marsh. (paper birch), relatively pure *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (interior Douglas-fir), and mixtures of the two tree species. A total of 187 fungal taxa were collected during the study, of which 185 occurred in mature forests and only 17 occurred in the plantations. Thirty-four taxa were unique to mature predominantly birch forests, 35 were unique to mature predominantly Douglas-fir forests, 17 were unique to mixed mature forests, and 68 taxa were found in all three mature forest types. The abundance of fruit bodies in mature forests varied widely among sampling years and generally increased with annual precipitation. ECM species richness differed between stand ages but not among forest compositions in both plantations and mature forests. *Lactarius glyciosmus*, *Hygrophorus eburneus* var. *eburneus*, and *Cortinarius armillatus* were more abundant in mature birch than mature Douglas-fir forests. *Lactarius torminosus*, *Leccinum scabrum* var. *scabrum*, and *Rozites caperatus* were also found predominantly in mature birch and mixed forests, whereas *Gomphidius subroseus* was more abundant in Douglas-fir forests than in birch and mixed mature forests. *Russula brevipes* was also found predominantly in mature Douglas-fir and mixed forests. Our results indicate that clearcutting has a profound effect on abundance and composition of ECM fruit bodies, and that changes in forest tree species composition may lead to shifts in ECM fungal community composition.

Key words: fungal communities, *Pseudotsuga menziesii*, *Betula papyrifera*, internal transcribed spacer (ITS) DNA sequences, species richness, sporocarps.

Résumé : L'objectif du travail était d'examiner les effets de l'âge du peuplement et la composition des espèces arborescentes sur l'abondance, la diversité et la composition des frutifications épigées formées par les champignons ectomycorhiziens (ECM) dans la prûcheraie cèdreraie de l'intérieur de la Colombie Canadienne. Les auteurs ont récolté et identifié les fructifications en mai, juin, août, septembre et août 1996, 1997, 1998 et 1999, le long de transects localisés dans des plantations récentes (5 ans) et des forêts naturelles matures (75–125 ans) comportant des peuplements pures de *Betula payrifera* Marsh. (bouleau à papier) ou de *Pseudotsuga menziesii* var. *galuca* (Beissn.) Franco (sapin de Douglas de l'intérieur) ainsi que des mélange de ces deux espèces. Ils ont récolté un total de 187 taxons fongiques au cours de cette étude, dont 185 en forêts matures et seulement 17 en plantations. De ce total, 34 taxons s'avèrent exclusifs aux forêts matures dominées par le bouleau, 35 sont exclusifs aux forêts matures dominées par le sapin de Douglas, 17 aux forêts mixtes matures, alors que 68 ont été retrouvés dans les trois types de forêts matures. L'abondance des fructifications dans les forêts matures varie fortement selon les années d'échantillonnage et augmente généralement avec les précipitations annuelles. La richesse en espèces ECM diffère selon l'âge des peuplements, mais non pas selon la composition, en plantations aussi bien qu'en forêts naturelles. Les *Lactarius glyciosmus*, *Hygrophorus eburneus* et *Cortinarius armillatus* sont plus abondants dans les forêts matures de bouleaux que dans les forêts matures de douglas. Les *Lactarius torminosus, Leccinum scabrum* var. *scabrum* et *Rozites caperatus* prédominent également dans les forêts matures de bouleaux et mixtes, alors que le *Gomphidius subroseus* est plus abondant dans les forêts de douglas que dans les forêts de bouleaux ou mixtes.. Le *Russula brevipes* prédomine également dans les forêts de douglas ou mixtes. Les résultats indiquent que la coupe à blanc exerce des effets marqués sur la composition et l'abondance des fructifications des espèces de champignons ECM, et que les modifi-

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cations dans la composition des essences forestières peuvent conduire à un réarrangement de la composition des communautés fongiques ECM.

Mots clés : communautés fongiques, *Pseudotsuga menziesii*, *Betula payrifera*, séquences ADN ITS, richesse en espèces, sporocarpes.

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Introduction

Clearcutting is one of the primary methods by which ectomycorrhizal (ECM) forests are harvested in Canada, accounting for 89% of the one million hectares logged annually. Of this clearcut area, 41% is planted with one or a few commercially valuable tree species using seedling stock grown in nurseries, and the rest are left to regenerate naturally (Natural Resources Canada 2000). Clearcut logging affects the environment of ECM fungi and their plant hosts, while regenerating tree species composition affects ECM inoculum potential. Both forestry practices change ECM community composition and fruit body production compared with preharvest forest conditions (Pilz and Perry 1984; Deacon and Fleming 1992; Visser et al. 1998). According to Jones et al. (2003), clearcutting can cause a decline in ECM richness and fruit body production by reducing carbon sources for the fungi (Last et al. 1979), changing the age and species of the host plants (Clarkson and Mills 1994; Smith et al. 2002), disturbing the forest floor and density of fungal inoculum (Harvey et al. 1976), changing the soil microclimate and soil physical properties (Perry et al. 1989), and changing the soil food-web community structure (Forge and Simard 2000). It is important to understand the effects of clearcutting and regenerating tree species composition on different ECM fungi, because fungal species differ in their benefits to tree productivity (Wallander 2000; Baxter and Dighton 2001).

Fruit bodies of ECM fungi have typically been examined in studies investigating fungal species richness, diversity, and succession in forests around the world (Dahlberg et al. 1997; Durall et al. 1999; Smith et al. 2002). Fruit bodies play an important ecological role in above- and belowground food webs (Maser et al. 1978; Forge and Simard 2000), and can be used to confirm ECM fungal identifications from roots (Dahlberg et al. 1997). Studies have shown that ECM fungal species collected as epigeous macrofungi are not necessarily the dominant species forming ECM associations on roots (Gardes and Bruns 1996; Durall et al. 1999; Yamada and Katsuya 2001), possibly because many of the dominant ECM fungi form resupinate or sequestrate fruit bodies, and many rarely fruit (Dahlberg et al. 1997; Yamada and Katsuya 2001).

In North America, fungal fruit bodies have been studied in coniferous forests primarily in the northwest (Gamiet and Berch 1992; Durall et al. 1999; Smith et al. 2002), whereas similar studies in deciduous hardwood forests have occurred mainly in the east (Bills et al. 1986; Villeneuve et al. 1989; Nantel and Neumann 1992). Bills et al. (1986) found that ECM fruit body diversity was greater in mixed hardwood plots than in single-species coniferous forests, and very few fruit bodies were common to both forest types (Bills et al. 1986). Villeneuve et al. (1989) found similar results for fruit bodies formed by saprotrophic fungi, but there were no differences between the different forest types with respect to fruit bodies formed by ectomycorrhizal fungal species. Of North American deciduous hardwood forests, predominantly *Alnus* (Brunner et al. 1992) and *Populus* forests (Cripps and Miller 1993) have been examined, whereas *Betula* forests have remained unstudied. In Europe, however, birch plantations or forests have been studied (Mason et al. 1984; Watling 1984). In contrast with pure conifer or pure deciduous hardwood forests, ECM fruit bodies have rarely been studied in forests containing a mixture of both coniferous and deciduous tree species (Kranabetter and Kroeger 2001).

The primary objective of this study was to examine the effects of stand age and tree species composition on the richness, diversity, and taxa composition of epigeous fruit bodies formed by ECM fungi in relatively pure birch (*Betula papyrifera* Marsh.), relatively pure interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and mixtures of two dominant tree species in the Interior Cedar Hemlock (ICH) biogeoclimatic zone of British Columbia. Our study represents an advancement over many previous studies by including permanent plots, replication among stand types, and sampling over sufficient years to adequately characterize annual variation (Watling 1995; Roberts et al. 2004; Trudell and Edmonds 2004). We also verified morphologically identified species using molecular techniques, including DNA sequencing (Dahlberg 2001; Horton and Bruns 2001; Kennedy et al. 2003), and compared the morphological and molecular identity of our fruit bodies with those of ECM root tips on seedlings growing in the same clearcut plantations, which were sampled prior to this study (Jones et al. 1997; Simard et al. 1997; Sakakibara et al. 2002). In addition, our fruit body patterns were compared with seasonal and annual variation in precipitation. We hypothesize, based on fruit bodies, that: (*i*) ECM fungal species richness and diversity decrease following clearcutting; (*ii*) ECM fungal species richness and diversity are higher in mixed than in relatively pure forests; and (*iii*) ECM fungal species composition is affected by stand age and tree species composition.

Materials and methods

Study areas

The study was conducted in three geographically distinct areas in the ICH zone in the Southern Interior Forest Region of British Columbia, Canada. Two of the areas, Adams Lake and Malakwa, were located in the Thompson Moist Warm ICH (ICHmw3) variant, and the Hidden Lake area was located in the Shuswap Moist Warm ICH (ICHmw2) variant (Lloyd et al. 1990). The climate in the study area is continental with warm, moist summers and moderately cold, snowy winters. Mean annual temperature during the growing

season typically ranges from 14 °C to 16 °C, and mean minimum temperature in January ranges from –7 °C to –12 °C. Annual precipitation averages 520–670 mm, of which 220–290 mm normally falls as rain during the growing season (Lloyd et al. 1990). The soil great group at Adams Lake and Malakwa was Humo-Ferric Podzol, and that at Hidden Lake was Dystric Brunisol (Soil Classification Working Group 1998). Soils on all sites were deep, well drained, of loamy sand to sandy loam texture, and derived from glacial moraine parent material.

Two age classes of forest were studied: (1) 5–9 year old clearcut plantations and (2) 75–125 year old wildfire-origin mature forest. Three clearcut plantations were used, one in each of the three study areas. They were part of an addition series experiment established in 1992 that is examining tree species composition, density and proportional effects on forest productivity (Simard 1996; Jones et al. 1997; Sakakibara et al. 2002). The clearcut sites had been harvested in 1978 (Hidden Lake), 1987 (Adams Lake), and 1988 (Malakwa). The sites were prepared within 2 years of harvesting, and planted to Douglas-fir or interior spruce (*Picea engelmannii* Parry ×*glauca* [Moench] Voss) within 1 year of site preparation. Stumps were removed from all sites in 1991–1992 to reduce *Armillaria ostoyae* (Romagn.) Herink inoculum loads, which involved careful extraction and windrowing of stumps using a D-6 cat, removal of all tree seedlings, and minimal displacement of mineral soil and forest floor. The sites were immediately replanted to paper birch and Douglas-fir in the addition series treatment structure that included the three species composition treatments used in this study: pure Douglas-fir, pure paper birch, and a 50:50 mixture of paper birch and Douglas-fir, all planted at a density of 1600 stems/ha. These treatments had been randomly allocated to 40 m × 40 m treatment plots, and were replicated once on each of the three clearcut sites. The clearcut sites were of mesic moisture regime and medium nutrient regime, and before clearcutting had been dominated by 90–140 year-old wildfire-origin forests of Douglas-fir, paper birch, western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). The clearcut sites were similar in slope (0%–5%), elevation (650–750 m), and aspect (north to northeast) (Table 1).

For the mature age class, the closest stands to the clearcut sites with the appropriate tree species composition were selected for sampling. The predominantly pure stands contained at least 50% basal area of the focal species (Douglas-fir or paper birch), and the mixed stands had at least 10% of basal area in each of the two focal species (Table 1). The selected stands occurred on circum-mesic site series and typically had an understory dominated by falsebox (*Paxistema myrsinites* (Pursh) Raf.), prince's pine (*Chimaphila umbellata* Pursh), twinflower (*Linnea borealis* L.), red stem feather moss (*Pleurozium schreberi* (Brid.) Mitt.), and step moss (*Hylocomnium splendens* (Hedw.) B.S.G.). Site index values for Douglas-fir and paper birch fell within the medium site class (Thrower et al. 1994). Elevations of the mature stands ranged from 650 to 850 m, and slope gradients ranged from 0 to 30%. All mature stands had naturally regenerated after stand-destroying wildfire (Table 1).

Experimental design, treatments, and sampling procedures

The study included two forest age classes and three tree species compositions in a 2 × 3 factorial treatment structure with threefold replication applied in a randomized block design, where blocks were represented by geographic area. The two age classes were represented by (*i*) 5–9 year old clearcut plantations, and (*ii*) 75–100 year old mature forests. The three tree species compositions were (*i*) relatively pure paper birch, (*ii*) relatively pure Douglas-fir, and (*iii*) mixed paper birch and Douglas-fir. Each stand constituted an experimental unit.

All stands were sampled for epigeous fruit bodies five times a year (mid-May, mid-June, mid-August, mid-September, and mid-October) for 4 years in a row (1996, 1997, 1998, and 1999). Each measurement period spanned 2 weeks to include all stands. Sampling occurred over a 4-year period because fruit body production and composition are known to vary annually with changing weather patterns (Worley and Hacskaylo 1959; Eveling et al. 1990; Trudell and Edmonds 2004). All sampling was conducted by the authors.

A 200 m transect, comprising 20 contiguous 10 m × 10 m square plots, was established in each stand. Transects were generally linear in the 2–3 ha mature stands. In the plantations, each transect was run in three parallel lines to accommodate the smaller stand size (0.16 ha). At each sampling period in each stand, the number of sample plots in which each epigeous ECM species occurred was recorded. Each fruit body was described and identified to the lowest rank possible, usually to genus, in the field or at the end of the field day without the use of a compound microscope. At least one sample fruit body of each species was collected in every stand at each sampling period for more detailed examination and herbarium deposit.

Specimen identification and processing

At the end of each day, a fresh subsample (<0.1 g) was taken from each identified fruit body for DNA analysis. The remainder of the collection was dried in a portable dehydrator for 48 h until constant dried mass was achieved. Further identification of collections, typically to species level, was accomplished in the laboratory using predominantly North American literature (e.g., Smith and Thiers 1964; Miller 1971; Smith et al. 1979; Thiers 1975; 1982, 1985*a*, 1985*b*, 1997; Moser 1983; Largent 1985; Tylutki 1987; Methven 1997; Redhead 1997; Shanks 1997; Moser and Ammirati 2000; Peintner et al. 2002) Voucher specimens of each identified species that occurred in more than 1% of the plots were placed in the Pacific Forestry Centre Fungal Herbarium (DAVFP). The DNA subsamples were stored in a refrigerator overnight, and DNA was extracted the following day.

DNA isolation, polymerase chain reaction amplification, and restriction enzyme digest

Total genomic DNA from morphologically identifiable fruit bodies was extracted and isolated from fresh fruit body tissue using the procedures of Baldwin and Egger (1996) and Egger (1995). Following DNA isolation, the internal transcribed spacer (ITS) region of the fungal nuclear rDNA was specifically amplified by the primers ITS 1f (Gardes

Table 1. Site and stand characteristics of the study sites.

Site name[a]	Age class[b]	Tree species composition[c]	Latitude, longitude	Elevation (m)	Aspect, slope	BEC unit, site series[d]	Stand age (years)	Site index (m)	Basal area (m^2/ha)	Species composition (% of basal area)[c,e]
Adams	CP	Pure Fd pure Ep mixed Fd/Ep	51°28′00″N, 119°27′00″W	700	East, 0%–5%	ICHmw3, 01	5	Fd 23, Ep 22	n/a[f]	100% Fd 100% Ep 50% Fd, 50% Ep
Malakwa	CP	Pure Fd pure Ep mixed Fd/Ep	50°58′30″N, 118°43′00″W	750	North, 0%–5%	ICHmw3, 01	5	Fd 26, Ep 23	n/a[f]	100% Fd 100% Ep 50% Fd, 50% Ep
Hidden	CP	Pure Fd pure Ep mixed Fd/Ep	50°34′N, 118°50′W	650	East, 0%–10%	ICHmw2, 01	5	Not known	n/a[f]	100% Fd 100% Ep 50% Fd, 50% Ep
Flat (A)	MF	Pure Fd	51°27′40″N, 119°26′30″W	650	East, 0%–1%	ICHmw3, 01	77	Fd 23, Ep 22	37.9	Fd 60, Hw 16, Cw 16 (Ep, Pw, Sx)
White (A)	MF	Pure Ep	51°27′00″N, 119°26′00″W	750	East, 5%–15%	ICHmw3, 01	75	Fd 28, Ep 20	36.5	Ep 64, Cw 12, At 12, Hw 7, (Fd, Pw)
Back (A)	MF	Mixed Fd/Ep	51°28′00″N, 119°27′00″W	700	East, 0%–5%	ICHmw3, 01	78	Fd 26, Ep 23	37.5	Fd 66, Ep 23, Pw 6, (Cw, Ba, Sx)
River (M)	MF	Pure Fd	50°58′40″N, 118°43′30″W	750	North, 0%–5%	ICHmw3, 01	125	Fd 25	66.0	Fd 50, Hw 30, Cw 11, Pw 7, (Ep)
Slope (M)	MF	Pure Ep	50°57′30″N, 118°44′00″W	800	North, 30%	ICHmw3, 04	81	Fd 25, Ep 21	38.0	Ep 59, Cw 22 (Fd, Hw, Sx, Pw)
Bear (M)	MF	Mixed Fd/Ep	50°58′30″N, 118°43′00″W	750	North, 0%–5%	ICHmw3, 01	104	Fd 25, Ep 24	60.5	Fd 20, Ep 10, Cw 69, (Hw)
Road (H)	MF	Pure Fd	50°25′00″N, 118°55′00″W	650	East, 5%–10%	ICHmw2, 01	91	Fd 24	70.9	Fd 78, Cw 15, Lw 6, (Hw)
Okay (H)	MF	Pure Ep	50°27′20″N, 118°49′30″W	700	East, 5%–30%	ICHmw2, 04	88	Fd 21, Ep 14	28.1	Ep 54, Cw 44, (Se, Hw, Pw)
Grade (H)	MF	Mixed Fd/Ep	50°27′00″N, 118°48′10″W	700	East, 5%–20%	ICHmw2, 01	97	Fd 16, Ep 14	34.4	Fd 47, Ep 39, (Hw, Pw, Cw)

[a]For mature forests, letters in brackets represent: A, Adams area; M, Malakwa area; H, Hidden area.

[b]CP is clearcut plantation (5 years old), MF is mature forest (75–100 years old).

[c]Species codes are as follows: Fd, Douglas-fir (*Pseudotsuga menziessii* (Mirb.) Franco); Ep, paper birch (*Betula papyrifera* Marsh.); Cw, western redcedar (*Thuja plicata* D. Don.); Lw, western larch (*Larix occidentalis*); Hw, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.); Pw, western white pine (*Pinus monticola* Dougl.); Sx, hybrid spruce (*Picea engelmannii* var. *glauca*); Ba, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt. Designation of pure is relative. The predominantly pure stands contained at least 50% basal area of the focal species (Douglas-fir or paper birch), and the mixed stands had at least 10% of basal area in each of the two focal species.

[d]BEC variant, biogeoclimatic ecosystem classification variant (Lloyd et al. 1990).

[e]Species that represent <5% of stand basal area are listed in brackets.

[f]Basal area not applicable in clearcut plantations. In all treatments in clearcut plantations, density totaled 1600 stems/ha.

and Bruns 1993) and NLB4 (Kendall and Rygiewicz 2005). Polymerase chain reaction (PCR) reactions typically included 1 μL template DNA, 18.6 μL sterile milicue water, 0.2 mmol/L deoxyribonucleotides (dNTPs) (Applied Biosystems, Foster City, California), 2.5 μL 10× PCR buffer, 1.5 mmol/L $MgCl_2$, 0.48 mmol/L each primer, 1.6 mg/mL bovine serum albumin (BSA), and 0.25 U/μL AmpliTaq Gold (Applied Biosystems). Samples were amplified using a PTC-200 thermal cycler (MJ Research Inc., Waltham, Massachusetts). A 10 min hot start was followed by PCR cycling as follows: 34 cycles of denaturation at 94 °C for 45 s, annealing at 54 °C for 45 s, ramping 72 °C for 1 min, and extension at 72 °C for 10 min, and then the temperature was held at 4 °C. The PCR products were visualized on 1.5% agarose gels using a Gel Logic 440 (Kodak Instruments, Rochester, New York). The PCR product was cleaned using the QIAquick PCR purification kit (Qiagen Inc., Valencia, California) and quantified using a Nanodrop ND-1000 spectrophotometer (Nanodrop Technologies, Wilmington, Delaware),

Prior to sequencing, the large ITS fragment produced above was reamplified in a nested PCR reaction using the primers ITS 1 and ITS 4 (White et al. 1990). The amplified product was sequenced using a 3700 DNA capillary sequencer (Applied Biosystems) at the University of British Columbia Nucleic Acid and Protein Services Unit (NAPS). Sequenced samples were aligned (when possible) using Sequencher 4.2 software (Gene Codes Corp., Ann Arbor, Michigan). Basic local alignment search tool (BLAST) results were generated, and the closest taxonomic matches in the National Center for Biotechnology Information (NCBI) GenBank database are presented in Table 4. Taxa listed include those that were morphologically identifiable at the time of collection and that produced reliable sequences for successful blasting. Submissions to GenBank were made for all taxa that were sequenced and blasted.

Data analysis

Percent frequency of epigeous fruit bodies formed by ectomycorrhizal fungi was calculated for each sampling year by tallying the number of plots with at least one fruit body present and dividing the sum by 300 (i.e., 20 plots × 3 treatments × 5 months). These values were averaged over the three replicate stands. Mean percent frequency was graphically compared with precipitation accumulated during the sampling period (May to the end of October) for each year. The precipitation data, obtained from Environment Canada, was based on measurements from Salmon Arm, British Columbia, which was located midway between the three different sites.

The number of fungal taxa was tallied for each of the five monthly collections in each year to provide a picture of seasonal pattern in taxa richness, and how this pattern varied from year to year. For the two stand age classes, cumulative richness of fungal taxa over the 5 month growing season was calculated for each tree species composition treatment in each sampling year. Percent frequency of occurrence of an individual fungal taxon in each treatment over the duration of the study was calculated by tallying the number of plots that had a given taxon present and dividing the sum by 400 (i.e., 20 plots × 5 months × 4 years). Mean percent frequency of occurrence was determined as the average of the three replicate stands. Frequency of occurrence of individual taxa was used to determine the diversity of the fungal community in each experimental unit according to the Shannon and Weaver (1949) diversity index:

$$[1] \qquad H = -\left(\sum_{i=1}(n_i/N)\log(n_i/N)\right)$$

where n is the frequency of individual taxa and N is the sum of frequency of all taxa. The Sorenson similarity coefficient was used to determine differences in the fungal community between the different tree species compositions (Sorenson 1948). This was calculated as:

$$[2] \qquad S_s = 2a/2a + b + c$$

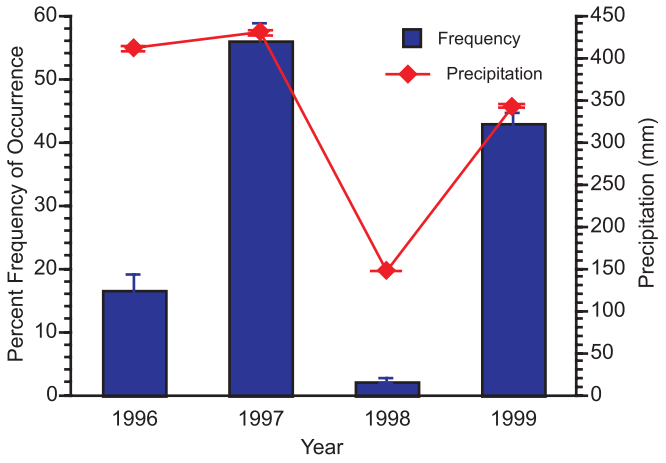
Where a is the number of taxa in sample A and sample B; b is the number of taxa in sample B but not in sample A, and c is the number of taxa in sample A but not in sample B.

For each year, richness and diversity were compared among stand ages and tree species compositions using a mixed model two-way analysis of variance (ANOVA). Repeated measures analysis was not used in this study because of the small number of measurement years relative to treatments (Meredith and Stehman 1991). For the mature age class only, one-way ANOVA was used to compare the frequency of sample plots in which each dominant ECM taxon (≥2% frequency of occurrence, see Table S1[2] for a list of dominant taxa) occurred at any time over the study period. One-way ANOVA was also used to compare similarity indices among tree species composition treatments for the mature age class only. Significant ANOVA results ($P \leq 0.05$) were followed by a Tukey–Kramer's test (Sokal and Rohlf 1981) to distinguish differences among treatments for these variables. The distribution of residuals, tests for normality, and tests for equality of variance showed that transformations were not necessary for taxa richness, diversity, or frequency of occurrence data to meet the assumptions of the models. The fungal taxa data required transformation using the arcsin of the square root.

In addition to ANOVA for comparing diversity indices and abundance of individual taxa, a χ^2 test was used to test for tree species composition effects in the mature forests on the distributions of fungal taxa with >1% frequency of occurrence. Detrended correspondence analysis (DCA) was used to examine treatment effects on the ECM community in mature forests only (Hill 1979). Only dominant taxa (>1% frequency of occurrence) were included in the DCA, which was performed using CANOCO version 4.0 (ter Braak and Šmilauer 1998). All other statistical analyses were performed with SAS for Windows (version 7.0, SAS Institute Inc., Cary, North Carolina; for taxa richness, diversity, and distribution data), and JMP (version 3.0, SAS Insti-

[2] Supplementary data for this article are available on the journal Web site (http://canjbot.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5063. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 1. Comparison of precipitation (based on Salmon Arm, British Columbia, measurements between May and October) and abundance of epigeous fruit bodies of ECM fungal species (based on percent frequency of occurrence) collected from the entire study. Percent frequency of occurrence is based on 300 plots (i.e., 20 plots × 3 treatments × 5 months). Values of percent frequency of occurrence are means ± SE (n = 3). One-way ANOVA indicated a significant difference in percent frequency of occurrence between years at $P \leq 0.05$, $F = 131.65$.



tute Inc.; for percent frequency of occurrence and individual fungal taxa data).

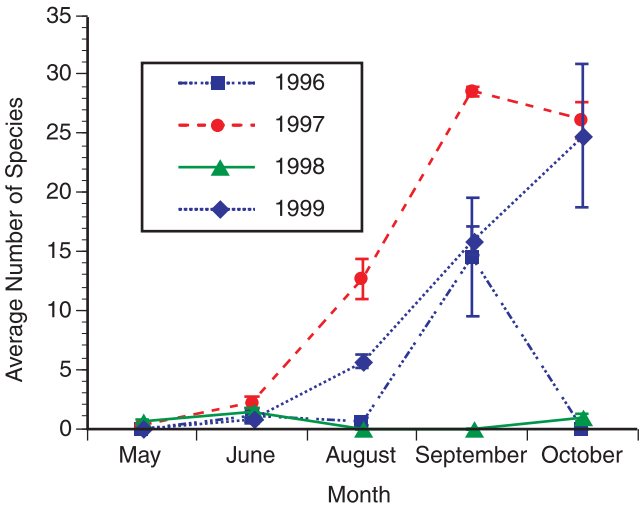
Results

The abundance of fruit bodies, expressed as percent frequency of occurrence within a given year, varied widely among sampling years. Abundance generally increased with annual precipitation, except during the wet year of 1996 when fruit body occurrence was relatively low (Fig. 1). Extremely low precipitation in 1998 coincided with very few fruit body observations (Figs. 1, 2).

A total of 187 taxa were collected over the course of the study. We found 185 taxa in mature forests and only 17 in clearcut plantations. Two species, *Thelephora terrestris* and *Inocybe albidodiscus*, were the only species found solely in the clearcut plantations. Thirty-nine taxa were found in the predominantly birch forests, but not in the Douglas-fir forests. Forty-six were found in the Douglas-fir forests, but not in the birch forests. Seventy-nine taxa were found in both the birch and Douglas-fir treatments, and 68 taxa (not tallied in Table 2) were found in all three tree composition treatments. Seventeen were found in mixed forests comprising predominantly birch and Douglas-fir, but were not in birch or Douglas-fir forests (Table 2). All dominant fungal taxa (>2% frequency of occurrence) were found in all three tree species compositions in the mature age class (Table S1[2]). In plantations, three taxa were unique to birch, four were unique to Douglas-fir, and four were unique to the mixture. Six taxa were common to both the birch and Douglas-fir treatments (Table 2). Clearcut plantations did not have any taxa with ≥2% frequency of occurrence (Table S1[2]).

Of the dominant taxa, we found three taxa that were more abundant in paper birch than Douglas-fir mature forests; these were *Lactarius glyciosmus* (P = 0.0270; F = 7.00), *Hygrophorus eburneus* var. *eburneus* (P = 0.0976; F = 3.52), and *Cortinarius armillatus* (P = 0.1638; F = 2.48). *Lactarius torminosus* (P = 0.4422; F = 0.94), *Leccinum scabrum* var. *scabrum* (P = 0.2673; F = 1.6569), and *Rozites caperatus* (P = 0.5531; F = 0.66) also occurred predominantly in birch and mixed forests, although their abundance did not differ signficantly from Douglas-fir forests. *Gomphidius subroseus* (P = 0.0248; F = 7.29) was significantly more abundant in Douglas-fir than in paper birch and mixed mature forests. *Russula brevipes* (P = 0.4787; F = 0.84) was found predominantly in Douglas-fir forests, although its abundance did not differ significantly from birch and mixture mature forests (Table S1[2]). The χ^2 test showed that the distributions of the dominant taxa, based on their frequency of occurrence, differed among the tree species compositions (χ^2 = 112.66, P = 0.0040).

Fig. 2. Effect of month and sampling year on species richness of epigeous fruit bodies. Values of species richness are means ± SE (n = 3).



Richness of fruit body taxa was 2–8 times greater in the mature forests than plantations (P < 0.0001; F = 62.40), but did not differ between tree species compositions (P = 0.8784; F = 0.13) (Fig. 3). Diversity followed the same pattern, with a mean Shannon–Weaver diversity index of 0.041 and 1.063 in plantations and mature forests, respectively (P < 0.0001; F = 52.57), and no difference between tree species compositions (P = 0.7566; F = 0.28). The similarity index did not differ between tree species compositions (P = 0.5564; F = 0.65) (Table 3).

The results from the ordination agreed with our ANOVA results and provided further insights into tree species composition effects on the ECM community of mature forests (Fig. 4). The clustering of stands along both the first (λ = 0.209) and second ordination axis (λ = 0.115) implies a trend associated with birch abundance. The site scores for the mixed stands were intermediate between the birch stands along both axes. Birch stands were clustered on the left side of the first DCA axis and top side of the second axis, while Douglas-fir stands were positioned on the right side of the first DCA axis and bottom of the second axis. Two of the three mixed stands were positioned centrally within the

Table 2. Number of fungal taxa associated with specific treatments.

Stand type	Birch[a]	Douglas-fir[b]	Mixture[c]	Birch and Douglas-fir[d]	Total richness[e]
Plantation	3	4	4	6	17
Mature forest	39	46	17	79	181[f]

[a]Found in predominantly birch transects but not in predominantly Douglas-fir transects.

[b]Found in predominantly Douglas-fir transects but not in predominantly birch transects.

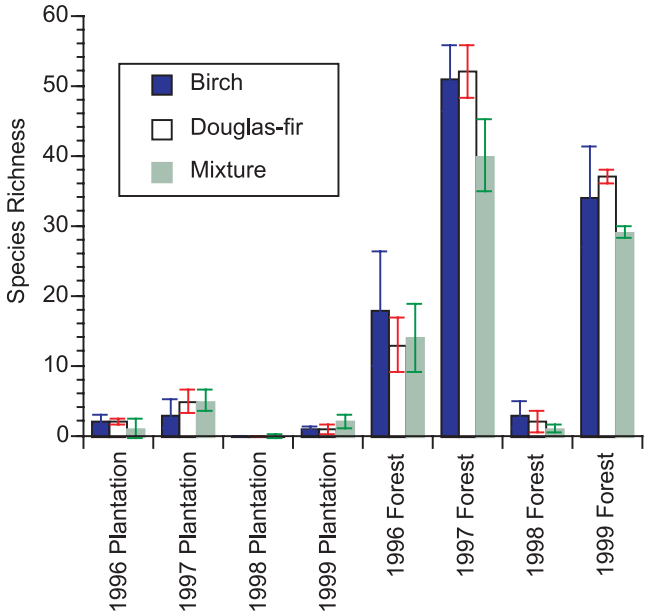
[c]Found in a mixture of predominantly Douglas-fir and birch but not in predominantly birch transects nor in predominantly Douglas-fir transects.

[d]Found in both predominantly birch and predominantly Douglas-fir transects.

[e]Total richness is based on all fruit bodies collected from all 9 replicates.

[f]There were 189 taxa collected in the whole study. Two taxa were unique to the plantations and six taxa were associated with treatment combinations not shown in the table.

Fig. 3. Species richness of epigeous fruit bodies compared between sampling years, age classes, and tree species compositions. Values of species richness are means ± SE (n = 3).



birch stands on the first axis, and the third one within the Douglas-fir stands, likely because it contained a higher proportion of Douglas-fir (see the site, Back, Table 1). The leftmost Douglas-fir stand along the first axis had the lowest Douglas-fir composition (50% versus 60%–78% Douglas-fir, see the site, River, Table 1). We found that *Russula brevipes* and *Gomphidius subroseus* were more strongly associated with Douglas-fir stands, while *Lactarius glyciosmus*, *Hygrophorus eburneus* var. *eburneus*, and *Cortinarius armillatus* were more strongly associated with paper birch and mixed stands. *Lactarius torminosus, Rozites caperatus*, and *Leccinum scabrum* were also positioned among the birch and mixed stands.

DNA was extracted from 71 taxa (includes those taxa that were morphologically identifiable at the time of collection); 60 of these produced quality sequences and are listed in Table 4 with their GenBank accession number. Thirty-four of the quality sequenced taxa had a BLAST match of 90% or greater with species in the GenBank database. The GenBank accession numbers of the closest match for these taxa are given in Table 4. Sequences of all 60 taxa were submitted to GenBank and were assigned unique accession numbers (Table 4).

Table 3. Similarity indices of the whole fungal community from mature forests.

Sites	B vs. DF	B vs. M	DF vs. M
Adams	0.889	0.862	0.885
Hidden	0.711	0.800	0.755
Malakwa	0.569	0.824	0.711
Average[a]	0.723	0.829	0.784

Note: Comparisons are between the different pairings of the three tree species composition treatments (birch versus Douglas-fir, birch versus mixture, Douglas-fir versus mixture). B, birch; DF, Douglas-fir; M, mixture.

[a]One-way analysis of variance indicated no significant difference at $P = 0.5564$, $F = 0.65$.

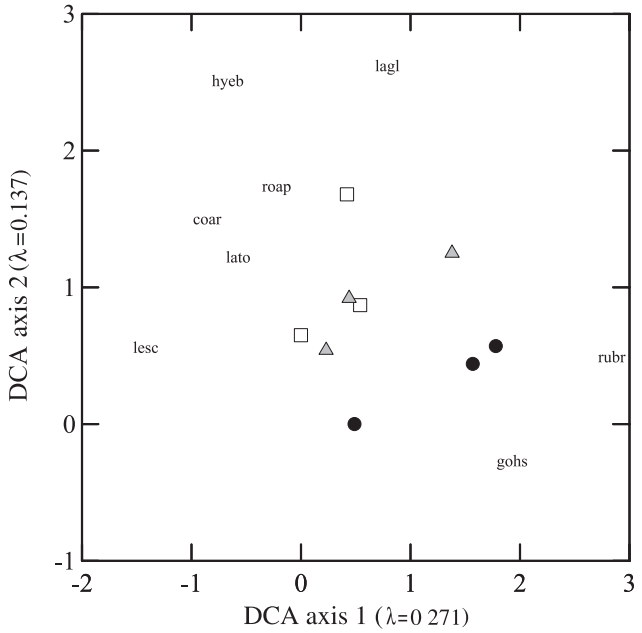
Discussion

Factors influencing fruiting and species diversity

The total abundance of fruit bodies collected over a given year varied widely among sampling years, and generally increased with growing season precipitation. In 1996, however, high precipitation corresponded with low total fungal abundance, largely because of a drought in August and an early frost in October. These factors limited fruit body production in August and October of 1996. Available moisture and temperature have been shown to influence fruit body production of both saprotrophic and ECM fungi (Worley and Hacskaylo 1959; Eveling et al. 1990; O'Dell et al. 1999; Trudell and Edmonds 2004), and likely were the strongest determinants of annual and seasonal patterns observed in our study. Seasonal patterns of below-ground C allocation, as well as photoperiod, could also partly account for the monthly and yearly variation in production and diversity (Godbout and Fortin 1992; Lamhamedi et al. 1994).

Curtailment of below-ground C allocation to ECM roots following clearcut logging also reduces fruit body abundance (Jones et al. 2003). This, along with a relatively low ECM diversity and the possibility that small trees do not provide enough carbon to enable some ECM species to fruit, are likely the main factors causing lower fruit body occurrence, diversity, and abundance in our clearcut plantations as compared with our mature forests. Although clearcutting will curtail fruiting of most ECM fungi for at least 5 years, as seen here and in other studies (Durall et al. 1999; Krana-

Fig. 4. Results of detrended correspondence analysis (DCA) based on the relative abundance of ectomycorrhizal fruit bodies (>0.5% frequency of occurrence) encountered in the sampling of birch, Douglas-fir, and mixed mature forest types. See text for details on tree species composition of each forest type. Fruit bodies shown are those showing strong forest composition affinities. Abbreviations are as follows: hyeb, *Hygrophorus eburneus* var. *eburneus*; lagl, *Lactarius glyciosmus*; roap, *Rozites caperatus*; lato, *Lactarius torminosus*; coar, *Cortinarius armillatus*; lesc, *Leccinum scabrum* var. *scabrum*; gohs, *Gomphidius subroseus*; and rubr, *Russula brevipes*. Symbols are as follows: ●, Douglas-fir forest; □, birch forest; △, mixed forest.



better et al. 2005), retention of green trees can help buffer reductions in production and diversity (Kranabetter and Kroeger 2001; Luoma et al. 2004). Luoma et al. (2004), for example, found that reductions in epigeous ECM fruit bodies were minimized with 75% green tree retention compared with 100%, 40%, or 15% retention. Thinning also maintains ECM fruit body production in conifer forests (Kropp and Albee 1996).

We did not find ECM diversity significantly lower in our predominantly pure than in our mixed stands, contrasting with the results of Bills et al. (1986) and Ferris et al. (2000). This may be due to the greater influence of nearby tree species in our predominantly pure stands, where interspecific roots sometimes occurred 15–20 m away from our transects (see Table 1). Single species stands are rare in the ICH zone, with most stands comprisingtwo to eight tree species (Simard et al. 2004). Nevertheless, our results are similar to those of Villeneuve et al. (1989), who showed that the diversity of epigeous ECM fruit bodies did not differ between predominantly coniferous forests and predominantly mixed hardwood forests. As with our study, their relatively pure conifer and hardwood forests contained more than one tree species. In contrast with ECM fungi, Villeneuve et al. (1989) found that saprotrophic fruit bodies were more species diverse in mixed hardwood than in coniferous forests.

Taxa abundance and host specificity

A total of 187 taxa were observed over the course of our study. As with other macrofungal studies (O'Dell et al. 1999; Smith et al. 2002), this is probably an underestimate of species number because some genera consist of numerous morphologically unidentifiable species (e.g., the *Cortinarius* subgenera *Telamonia, Myxacium, Phlegmacium,* and *Leprocybe*; and *Russula* genera). Our result falls within the range of 70–241 epigeous fruit body taxa reported from other multi-year ECM studies in western North America. Roberts et al. (2004), observing different microhabitats, found approximately 241 taxa over 5 years; Luoma et al. (2004), in a study designed to follow the effects of green tree retention, found 150 taxa over 8 years; Smith et al. (2002), comparing different stand ages, found approximately 215 taxa over 4 years; Kranabetter and Kroeger (2001) found approximately 70 taxa in a 3 year period studying the effect of partial cutting; Durall et. al. (1999), studying the effect of forest gap size on fruiting of ECM fungi, found 89 taxa in a 2 year period; and O'Dell et al. (1999) found 150 taxa over 2 years when studying ECM fruit body occurrence along a moisture gradient. Given the variation in forest types and objectives of these studies, it is surprising that there is so little variation in total number of taxa identified.

In our mature forests, when comparing forests of predominantly birch with those of predominantly Douglas-fir, 39 taxa were unique to the birch stands and 46 to the Douglas-fir stands. Seventeen taxa were unique to the mixed forests. Most of these 17 taxa were relatively rare (<2% frequency of occurrence), thus they are likely to occur just through chance rather than being species that fruit only in a mixed forest. We found 68 taxa were common to all three tree species compositions. These results contrast with Bills et al. (1986), who found that few taxa (8 out of 54) were common to both mixed hardwood and pure spruce forests. Of 54 fungal species encountered over 3 years, Bills et al. (1986) found 19 in pure spruce plots, 27 in pure hardwood plots, and only 8 in both forest types. Our value of 68 is likely an overestimate because of the presence of neighboring trees other than Douglas-fir and birch (e.g., larch and western white pine). Nevertheless, this value is similar to results from studies examining ECM root tips of birch and Douglas-fir, where there was a moderate to high incidence of shared morphotypes (Jones et al. 1997; Simard et al. 1997; Hagerman et al. 2001; Kernaghan et al. 2003). Other studies examining ECM root tips have shown varied results, ranging from very few ECM fungal species shared between different tree species (Douglas et al. 2005) to a substantial number (Horton and Bruns 1998; Horton et al. 1999; Kennedy et al. 2003).

Fungal community composition

Lactarius glyciosmus, *H. eburneus* var. *eburneus*, and *C. armillatus* were some of the most dominant species found in this study (>2% frequency of occurrence) and were more abundant in birch than in Douglas-fir forests. *Hygrophorus eburneus* var. *eburneus* is known to associate with either conifer or hardwood roots (Largent 1985; Molina et al. 1992), but in our study, it favoured paper birch. *Cortinarius armillatus* and *C. pholideus* are thought to associate exclusively with birch, *Cortinarius trivialis* with poplar and birch,

Table 4. GenBank accession data for a portion of the samples collected during the study (taxa listed include those that were morphologically identifiable at the time of collection and produced reliable sequences for successful blasting).

Taxa	OUC No.	GenBank accession No. of closest match	GenBank accession No. of submitted sequence	Base pair ratio of closest match	Blast %	Reference
Boletus mirabilis	97630	AF335451	DQ367893	972/975	99	Berbee et al. (unpublished data)
Chroogomphus rutilus	97213	AF205639	DQ367894	659/716	92	Miller and Aime (2002)
Clavariadelphus borealis	99108		DQ097871			
Cortinarius alboviolaceus	97234		DQ097877			
Cortinarius armillatus	99061	AF037223	DQ367895	448/471	95	Karen et al. (1997)
Cortinarius callisteus	99190		DQ097876			
Cortinarius collinitus = *C. trivialis*	99366	AY083185	DQ367896	641/659	97	Peintner et al. (2001)
Cortinarius croceus	99298		DQ097881			
Cortinarius crystallinus	99252		DQ097879			
Cortinarius glaucopus	99392		DQ097885			
Cortinarius hemitrichus	99106		DQ097870			
Cortinarius junghuhnii	99166		DQ097874			
Cortinarius laniger	97072	AF325592	DQ367897	342/377	90	Peintner et al. (unpublished data)
Cortinarius limonius	97063		DQ093853			
Cortinarius paragaudis group.	97241		DQ097866			
Cortinarius salor	99394		DQ097886			
Cortinarius sanguineus	99387	U56057	DQ367898	567/589	96	Liu et al. (1997)
Cortinarius semisanguineus	97474	AF430260	DQ367899	698/723	96	Haug (2002)
Cortinarius spilomeus group	97199		DQ093855			
Cortinarius traganus	99393	AF335446	DQ367900	738/740	99	Berbee et al. (unpublished data)
Cortinarius vibratilis	99295		DQ097880			
Gomphidius subroseus	99229		DQ099900			
Hydnellum peckii	97055	AY569030	DQ367901	710/727	97	Westmoreland and Volk (unpublished data)
Hydnum repandum L.	99198	AJ889949	DQ367902	596/630	94	Kjoller (unpublished data)
Hydnum umbilicatum	99371	AJ534973	DQ367903	356/378	94	Grebenc et al. (unpublished data)
Hygrophorus albicastaneus	99143		DQ097873			
Hygrophorus bakerensis	99237		DQ097878			
Hygrophorus eburneus var. *eburneus*	99263	AY463485	DQ367904	566/599	94	Larsson and Jacobsson (unpublished data)
Hygrophorus speciosus	99357		DQ097884			
Inocybe geophylla var. *geophylla*	97144		DQ093854			
Inocybe lanuginosa var. *lanuginosa*	99161	AY038319	DQ367905	289/294	99	Matheny et al. (2002)
Laccaria bicolor	97014	AY254878	DQ367906	620/625	99	Smit et al. (2003)
Lactarius affinis	97619		DQ097869			
Lactarius alnicola	97059		DQ099898			
Lactarius glyciosmus	99130		DQ097872			
Lactarius kauffmanii	99182		DQ097875			
Lactarius pallescens	97047		DQ093852.			
Lactarius rubrilacteus	99303		DQ097882			

Table 4 (*concluded*).

Taxa	OUC No.	GenBank accession No. of closest match	GenBank accession No. of submitted sequence	Base pair ratio of closest match	Blast %	Reference
Lactarius rufus	97250		DQ097868			
Lactarius theiogalus	97103	AF349716	DQ367907	615/622	98	Bidartondo and Bruns (2001)
Lactarius torminosus	97057	AY336959	DQ367908	681/686	99	Nuytinck et al. (2004)
Paxillus involutus	99185	AY230243	DQ367909	667/680	98	Preston et al. (unpublished data)
Phellodon niger	97590		DQ099899			
Ramaria stricta	97191	AF442097	DQ367910	169/172	98	Daniels et al. (unpublished data)
Rozites caperatus	99187	AF325614	DQ367911	651/659	98	Peintner et al. (2001)
Russula brevipes	97423	AF349714	DQ367912	467/468	99	Bidartondo and Bruns (2001)
Russula decolorans	99188	AY194601	DQ367913	697/748	93	Fransson (unpublished data)
Russula fragilis var. *fragilis*	97490	AF335443	DQ367914	372/405	91	Berbee et al. (unpublished data)
Russula nigricans	99137	AY228357	DQ367915	684/730	93	Gendron et al. (unpublished data).
Russula xerampelina var. *xerampelina*	97303	AY228344	DQ367916	423/449	94	Fischer et al. (unpublished data)
Suillus lakei	97024	L54086	DQ367917	635/641	99	Kretzer et al. (1996)
Suillus luteus	97128	AJ272416	DQ367918	636/696	91	Manian et al. (unpublished data)
Tricholoma aurantium	99349	AF377233	DQ367919	594/596	99	Bidartondo and Bruns (2002)
Tricholoma focale	99147	AF462638	DQ367920	731/733	99	Horton (unpublished data)
Tricholoma intermedium	99244		DQ097867			
Tricholoma pardinum	99350	AF377228	DQ367921	682/687	99	Bidartondo and Bruns (2002)
Tricholoma saponaceum var. *saponaceum*	99343	AF349695	DQ370440	616/620	99	Bidartondo and Bruns (2001)
Tricholoma venenatum group	99352	AF377230	DQ367922	623/632	98	Bidartondo and Bruns (2002)

and *L. glyciosmus* with only alder and birch. In contrast with literature predictions, we found these species also fruiting in our Douglas-fir forests, most likely because birch occasionally occurred 20 m from the pure Douglas-fir transect. The presence of larch within 30 m of some transects also likely explains why the obligate larch associates, *Suillus grevillei* and *Hygrophorus speciosus* (Molina et al. 1992), were sometimes found in the birch and Douglas-fir forests. In addition, *Cantharellus subalbidus* and *Suillus lakei,* reputed to be strict Douglas-fir associates (Molina et al. 1992), were collected in birch forests, likely because of the presence of Douglas-fir trees within 30 m of the transect.

Other dominant fungal species found predominantly in the birch and mixed forests include *Lactarius torminosus*, *Leccinum scabrum var. scabrum*, and *Rozites caperatus*. The first two of these taxa are known to associate preferably or exclusively with birch, whereas *R. caperatus* is known to associate with both conifers and hardwoods (Molina et al. 1992). Dominant fungal species found predominantly in Douglas-fir and mixed forests included *Gomphidius subroseus* and *Russula brevipes*. Although *G. subroseus* grows exclusively with conifers (Miller 1971; Thiers 1985*b*; Miller and Aime 2002), *R. brevipes* has previously been associated with both hardwoods and conifers (Thiers 1997; Bergemann and Miller 2002). *Craterellus tubaeformis*, a mycorrhizal species that is predominantly associated with mature to old-growth western hemlock and to a lesser extent with Douglas-fir stands (Trappe 2004) in the Pacific North West of North America, was found on our much younger mature mixed and conifer stands.

As illustrated by the ordination diagram, the ECM fruit body community of mature mixed stands was intermediate between that of birch and Douglas-fir, but with stronger affinities to the birch community (Fig. 4). The larger number of dominant taxa that were associated with birch than Douglas-fir stands likely weighted the ECM community of mixed stands toward birch, even though all mixed stands were made up of a larger basal area of Douglas-fir than birch. Paper birch has been shown in other studies to have keystone qualities on soil ecology in ICH ecosystems (Simard et al. 2004). For example, including paper birch in Douglas-fir forests has resulted in higher nutrient capital (Wang et al. 1996), greater total tree biomass production (Sachs 1995), tendency toward a moder humus form (Klinka et al. 2000), larger populations of *Armillaria ostoyae*-antagonistic fluorescent pseudomonads (DeLong et al. 2002), and reduced Douglas-fir mortality caused by *Armillaria ostoyae* root disease (Baleshta et al. 2005). Paper birch thus has an important influence on forest soils and productivity, and also appears to exert a strong influence on ECM community composition of mixed forests, as suggested by our ordination diagram.

Relationship to ectomycorrhizal fungi on root tips

As with many ECM macrofungal studies, the epigeous ECM fruit bodies we found in plantations were not representative of the ECM community found earlier on seedling roots on the same sites (Jones et al. 1997). Of the six most common morphotypes found in soil bioassays by Jones et al. (1997), we observed epigeous fruit bodies of only *Thelephora* sp. Inconsistencies between above- and below-ground studies is common, particularly in relatively young stands (Gardes and Bruns 1996; Dahlberg et al. 1997; Karen and Nylund 1997; Durall et al. 1999; Jonsson et al. 1999; Yamada and Katsuya 2001). As with Jones et al. (1997), many of the dominant ECM fungi found on roots form resupinate or sequestrate fruit bodies. In addition, many ECM fungi never (e.g., *Cenococcum*) or rarely fruit (Dahlberg et al. 1997; Yamada and Katsuya 2001). One study that sampled intensively for resupinate, sequestrate, and epigeous fruit bodies found a good correspondence between ECM fungal species forming fruit bodies with those associated with roots (M.E. Smith, G.W. Douhan, and D.M. Rizzo, unpublished data). Sampling fruit bodies over an extensive period of time (e.g., 10–15 years) would also help reduce the difference found between above- and below-ground studies. Inconsistencies will still persist, however, because many fungi exhibit irregular annual fruiting patterns, and sometimes do not fruit for over 15 years (Watling 1995; Straatsma et al. 2001; Straatsma and Krisai-Greilhuber 2003). Addition of DNA sequences to databases, such as GenBank, will make it easier in the future to link ECM fungi in their anamorphic state to their teleomorph. Thus, this will reduce the number of unknowns in ECM tip and soil data sets. Our addition of 60 ectomycorrhizal species to the GenBank database (Table 4) will be useful in future ecological studies where researchers are interested in the identification and distribution of ectomycorrhial fungi growing in the soil or on root tips.

Summary and management implications

We found that clearcutting profoundly reduced abundance of ECM fruit bodies and shifted composition toward ruderal-like species. We expect the community to recover in tandem with forest development, but other studies suggest this recovery may be hastened with refuge plant and green tree retention during clearcut harvesting. We also found that a small group of ECM fruit bodies had strong affinities for particular tree species compositions, but that there was considerable variability and overlap among ECM communities. While managed changes in forest composition will likely reduce the frequency of these specialized fungi, the ECM community appears to be well buffered against small shifts in native tree species composition. Our results suggest, however, that including a strong component of paper birch in forest stands will protect the greatest number of specialized species. Finally, annual variation in precipitation strongly affected fruiting of ECM fungi, with a dramatic reduction during the driest year in all forest types and stand ages. Based on climate change predictions for warming and drying in southern interior British Columbia (Hamann and Wang 2005), we expect there will be substantial declines in fruit body frequency and diversity in these interior forests over the next century.

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