Mycorrhiza (2007) 17:461–467
DOI 10.1007/s00572-007-0132-7

SHORT COMMUNICATION

Ectomycorrhizal colonization of naturally regenerating *Pinus sylvestris* L. seedlings growing in different micro-habitats in boreal forest

Michał Iwański · Maria Rudawska

Received: 08 January 2007 / Accepted: 18 April 2007 / Published online: 15 May 2007

Abstract We investigated the species richness and composition of ectomycorrhizal (EM) fungi colonizing *Pinus sylvestris* L. seedlings naturally regenerating in boreal forest, in three different microhabitats: on forest ground, on decaying stumps, and within moss layer on erratic boulders. We tested the hypothesis that habitat differences would affect the composition of the EM community of regenerating pine seedlings. In total, 16 EM species were detected, from which none occurred on seedlings growing in all three microhabitats. *Piloderma croceum* and *Cenococcum geophilum* were common for seedlings growing in forest ground and on boulders, while *Tricholoma aestuans* and *Suillus luteus* were shared between seedlings growing on forest ground and decaying stumps. EM species richness and composition were strikingly different between seedlings regenerating in different microhabitats. Results are discussed as a function of dispersal and niche differentiation of EM fungi.

Keywords *Pinus sylvestris* · Natural regeneration · Micro-habitats · Ectomycorrhizal community · Niche differentiation

Introduction

Ectomycorrhizal (EM) fungal communities are typically species rich. About 700 species of macrofungi are EM in the Fennoscandia region (Dahlberg 2002), with up to few dozen in a single stand of boreal forest (Dahlberg et al. 1997; Jonsson et al. 1999a). However, mechanisms that maintain diversity and composition of EM communities are still poorly understood (Bruns 1995; Ekschmitt and Griffiths 1998). The major processes that are thought to drive EM community dynamics include interactions between disturbance and EM colonization potential, fungal competition, and resource partitioning (Bruns 1995; Allen et al. 2003).

EM fungal assemblages on young seedling roots varies greatly between those growing in potted soil, nursery, or disturbed conditions, and those naturally regenerating under the canopy of mature trees (Jones et al. 2003; Fleming 1983; Horton et al. 1998; Menkis et al. 2005; Jonsson et al. 1999b). EM species that rapidly respond to soil disturbance seem to colonize seedlings via resistant propagules (Taylor and Bruns 1999), whereas under forest conditions, colonization occurs mainly via vegetative expansion of established EM mycelia, resulting in a similar set of EM fungi present on seedlings and surrounding trees (Jonsson et al. 1999b). Although this pattern seems to be general, some evidence suggests that spore establishment is important in mature forests, at least for certain EM species (e.g., *Amanita francheti*, *Russula cremicolor*, *Lactarius xanthogallus*; Redecker et al. 2001). In contrast, genets of *Suillus* species that spread effectively via the mycelial system in mature forests (Dahlberg and Stenlid 1994; Dahlberg 1997) are also abundant under nursery conditions (Iwański et al. 2006) and after disturbance (Visser 1995). Differences in dispersal strategies of EM fungi and uneven distribution of different types of EM inoculum in forest microhabitats may potentially influence spatial structure of EM community (Jones et al. 2003).

Other factors, such as variation in resource uptake ability of different EM species and differential responses to abiotic

M. Iwański · M. Rudawska (✉)
Institute of Dendrology, Polish Academy of Sciences,
5 Parkowa St.,
62-035 Kórnik, Poland
e-mail: mariarud@man.poznan.pl

factors, also contribute to EM community distribution (Erland and Taylor 2002). Circumstantial evidence suggests that resource partitioning and consequently niche differentiation exists in EM communities, both on spatial (Goodman and Trofymow 1998; Tedersoo et al. 2003; Rosling et al. 2003) and temporal scales (Visser 1995; Palfner et al. 2005, Smith et al. 2002) leading to nonrandom distribution of EM taxa in heterogeneous environment.

The objectives of the present study were (1) to compare EM fungal assemblages of naturally regenerated Scots pine seedlings, growing in three different microhabitats: within the moss layer on erratic boulders (EB), on decaying tree stumps (DS), and on forest ground (FG) and (2) to quantify the extent of spatial variability of EM community because of microhabitat differences in a single boreal Scots pine stand.

Materials and methods

Sampling of naturally regenerating seedlings was carried out in a 100×100 m plot, approximately 25 km northwest from Rovaniemi, northern Finland (66°49′N, 25°19′E) in mid-September 2006. The study site is a mature multiaged (dominant trees approximately 70 years old) and multilayered *Pinus sylvestris* forest developed on typical podzolic soils of sandy till texture and thin humus layer (2.5 cm± 1.3) over a 5–15 cm thick E horizon. Accompanying species are *Picea abies* and *Betula pubescens*, while ground vegetation is dominated by *Vaccinium myrtillus* and *V. vitis-idaea*, with a patchily distributed ground cover of mosses (*Hylocomium splendens*, *Pleurozium schreberi*). Large, sandstone erratic boulders with a thick moss layer (8.4 cm±5.7) are scattered on the site. The mean annual rainfall is 535 mm, and mean annual temperature is +0.2°C.

Naturally regenerating pine seedlings (1–3 years old) were carefully collected with surrounding soil from three microhabitats: (1) FG, (2) EB, and (3) DS. To get the root system as intact as possible, each sampled seedling was extricated with a cylinder (approximately 15 cm diameter, 15 cm depth) of adjacent substrate and packed in labeled plastic bags. As physical and chemical properties of rotting wood may differ between tree species and stages of decay, DS seedlings were sampled only from pine stumps in advanced stages of decay. The root system of EB seedlings had no physical contact with surrounding soil. In total, 30 seedlings were sampled, ten from each examined microhabitat. One seedling per single erratic boulder and tree stump was sampled; seedlings regenerating on the forest floor were collected near the sampled stumps and boulders at a 5–8 m distance from the nearest tree. Samples were stored at −10°C until further analysis and were processed within 2 weeks after collection.

Root systems of seedlings were extracted from the soil on a sieve under tap water and cut into 5-cm fragments. All fine roots from each seedling were counted and examined for mycorrhizal colonization under a dissecting microscope at a 10–60× magnification. Mycorrhizas were classified into morphotypes based on morphological characters (ramification system, color, shape, texture, and thickness of the mantle, presence and organization of the emanating hyphae, rhizomorphs, and other elements) according to Agerer (1987–1998), Ingleby et al. 1990, and morphological descriptions of EM species developed in our laboratory (not published). The number of mycorrhizas of each morphotype was recorded separately for each seedling. In the case of coralloid mycorrhizas, each root tip was counted, while tubercules were counted as five root tips (mean number of tips per tubercule=4.8; n=20). Two samples, each consisting of a single mycorrhizal tip per morphotype, per seedling were placed in Eppendorf tubes and kept at −20°C for DNA extraction. We made no attempt to relate morphotypes between seedlings until molecular analysis was complete; thus, each morphotype sample was treated separately in a subsequent molecular typing and pooled for abundance calculations only after the molecular analysis indicated that morphotypes are identical.

DNA was extracted according to the protocol of Lanfranco et al. 1998, and the internal transcribed spacer (ITS) region of rDNA was amplified using polymerase chain reaction (PCR) (comprising 2.5 U of *Taq* DNA polymerase, 1.5 mM $MgCl_2$, 200 μM each deoxyribonucleotide triphosphate, and 0.5 μM of primer pairs ITS1 and ITS4 per reaction) for sequence analysis. PCR products were purified with a MinElute PCR Purification Kit (Quiagen, Canada) according to the manufacturer's instructions and sequenced with ITS1 and ITS4 primers, using a Beckman Coulter DTCS Quick Start Kit and CEQ 20000XL automatic sequencer.

BioEdit version 7.0.0 (Hall 1999) software was employed for sequence editing. Consensus sequences were queried in sequence databases at the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov) and UNITE (http://unite.ut.ee) using the nucleotide–nucleotide basic local alignment search tool algorithm. Sequences were considered as identified at the species level when more than 97% identity with reference sequences (if available, derived from sporocarps) was obtained. Otherwise, sequences were aligned with closest matches and their associates and submitted to neighbor-joining analysis (BioEdit 7.0.0) for taxonomic interpretation at the genus or family level.

Calculations of EM abundances are based on the assumption that all mycorrhizas of an individual morphotype on a single seedling consists of a single EM species. The relative abundance of EM species were calculated separately for each seedling as a proportion of the number

of EM root tips of a given species to total number of ectomycorrhizas present on seedling and then averaged over all seedlings from a given microhabitat.

Estimates of true species richness (bootstrap, first-order, and second-order jackknife) were calculated with the EstimateS program version 7.51 (Colwell 2005), as were indices of similarity (Sorenssen and Morista–Horn indices) of EM fungal assemblages from different microhabitats. To compare mean species richness between microhabitats, we used analysis of variance followed by the Tukey's test. To investigate the effect of different microhabitats on EM community composition, detrended correspondence analysis (DCA) was performed using Canoco program version 4.51. Species abundance was square-root transformed before the analysis.

Results and discussion

We identified 16 EM fungal species on the naturally regenerating seedlings, with none occurring on seedlings in all three microhabitats (Table 1). Two species were shared between FG and EB seedlings (*Piloderma croceum*, *Cenococcum geophilum*), while two others were shared between FG and DS (*Tricholoma aestuans*, *Suillus luteus*). The number of observed EM species on seedlings growing in FG, DS, and EB microhabitats was 10, 6, and 4, respectively. The mean species richness per single seedling was 4.2±0.63, 4.4±0.7, and 2.6±0.69 for FG, DS, and EB microhabitats, respectively, and was significantly lower for EB seedlings ($p>0.001$, Tukey's test). Shared species accounted for 40.8% of the mycorrhizas on FG seedlings, 37.5% on DS seedlings, and 58.8% of those on EB.

Seedlings growing in different microhabitats were distinguished by DCA according to EM fungal species abundances (Fig. 1). *Piloderma* spp. occurred mainly on EB seedlings, colonizing more than 95% of the fine roots; *Phialophora finlandia*, *Dermocybe* spp., *Lactarius glyciosmus*, and *Leccinum vulpinum* were limited to roots of FG seedlings, while *Suillus variegatus*, *Lactarius rufus*, and tomentelloid species were found exclusively on DS seedlings.

Table 1 Molecular identification, relative abundance (percent roots colonized), mean, and observed and estimated total species richness of ectomycorrhizal (EM) taxa colonizing seedlings in different microhabitats

Species	Closest match	Identity (%)	Relative abundance (percent roots colonized)		
			FG seedlings	DS seedlings	EB seedlings
Phialophora finlandia	*Phialophora finlandia* AF486119	96	26.3		
Tricholoma aestuans	*Tricholoma aestuans* DQ494699	97	25.6	17.6	
Lactarius glyciosmus	*Lactarius glyciosmus* DQ097872	99	14.5		
Piloderma croceum	*Piloderma croceum* AJ438982	98	12.2		53.4
Suillus luteus	*Suillus luteus* DQ440568	97	5.4	19.9	
Leccinum vulpinum	*Leccinum vulpinum* AF454580	98	4.3		
Dermocybe sp.3	*Dermocybe* spp.	–	4.2		
Cenococcum geophillum	*Cenococcum geophillum* AM084698	98	3		5.4
Dermocybe crocea	*Dermocybe crocea* DCU56038	99	2.8		
Dermocybe semisanguinea	*Dermocybe semisanguinea* DQ481909	99	1.7		
Suillus variegates	*Suillus variegatus* AJ272419	99		39.5	
Pseudotomentella nigra	*Pseudotomentella nigra* AF274770	98		9	
Tomentelloid-2	*Tomentella* spp.	–		7.2	
Lactarius rufus	*Lactarius rufus* DQ097868	99		6.8	
Piloderma byssinum	*Piloderma byssinum* DQ365681	98			28.6
cf. *Piloderma reticulatum*	cf. *Piloderma reticulatum* AF481387	99			12.6
Mean no species per seedling			4.2±0.63	4.4±0.7	2.6±0.69*
Observed species richness			10	6	4
Mean estimated species richness[a]					
Bootstrap			10.84	6.26	4.11
Jackknife 1			11.8	6.84	4.56
Jackknife 2			12.68	7.25	5.44
Sorenssen index			1	0.25	0.285
Morista–Horn index			1	0.264	0.23

FG Forest ground, *DS* decaying stumps, *EB* erratic boulders

*Indicates significant difference with Tukey's test, $p>0.001$

[a] All estimates of species richness (bootstrap, first-order jackknife, and second-order jackknife) based on 100 iterations without replacement

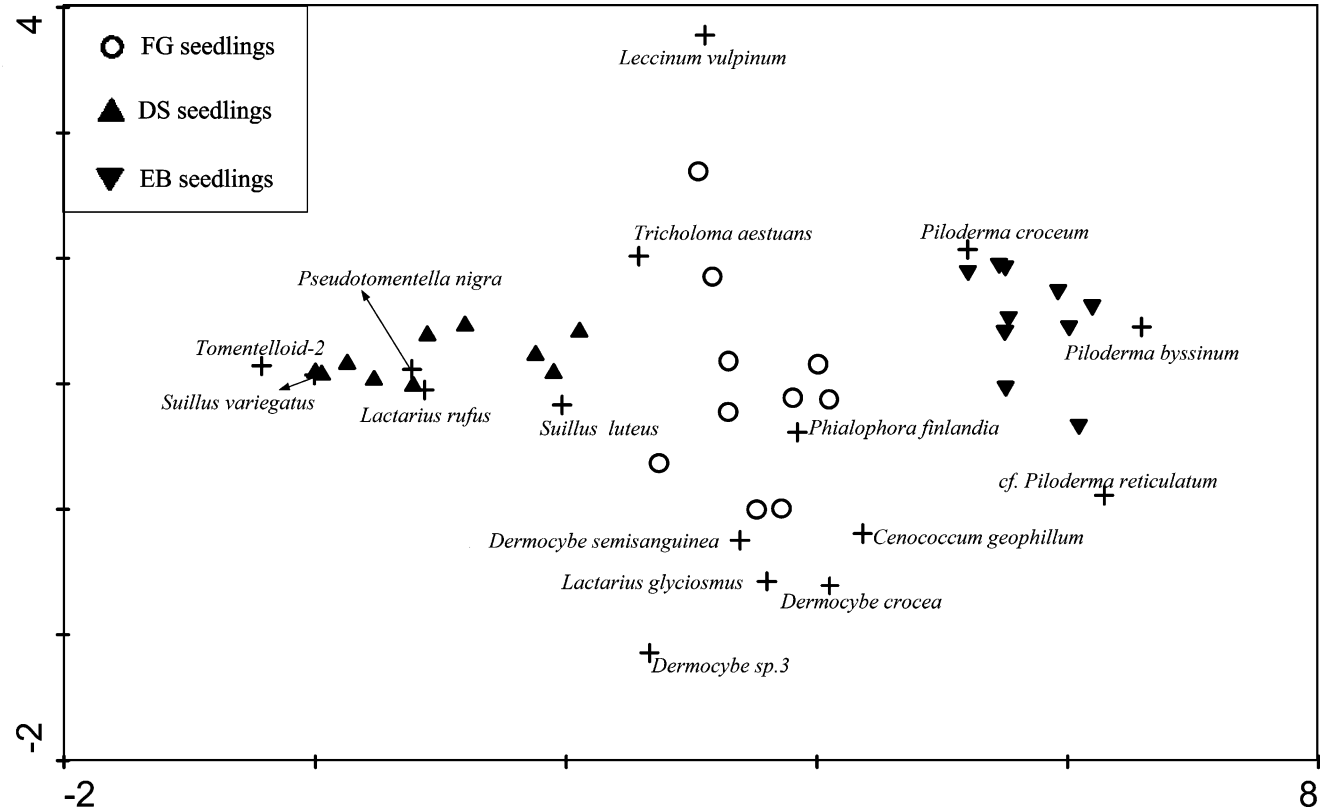

Fig. 1 Detrended correspondence analysis (DCA) based on reciprocal averaging of EM species abundances (*plus sign*) and seedling samples. Seedlings growing in different microhabitats are marked with different labels, as shown in a legend (*FG* forest ground, *DS* decaying stumps, *EB* erratic boulders). Eigen values of first and second DCA axes are 0.89 and 0.38, respectively

Morphotype Tomentelloid-2 could not be identified to species level, but in neighbor-joining analyses, it was consistently placed among tomentelloid species. Because of the similarity of the ITS sequences, discrimination between *Dermocybe crocea* and *D. aurantiobasis*, likewise between *L. rufus* and *L. decipens*, was impossible, preventing precise identification of the queried sequences from two morphotypes. We decided to assign these morphotypes as *D. crocea* and *L. rufus*, respectively. Sequences of morphotype 'Piceirhiza bicolorata' (n=9) matched with members of the *Hymenoscyphus ericaceae* aggregate (*P. finlandia, Hymenoscyphus* spp.) but also with a number of sequences derived from uncultured EM and ericoid root tips. Phylogenetic relationships and species separation within this group are not clear (Vrålstad et al. 2000, 2002), and intraspecific variation of the ITS sequence might occur (Menkis et al. 2004); therefore, we suggest that all sequences of the 'Piceirhiza bicolorata' morphotype in this study are eligible for assignment to *P. finlandia*.

As in this study, *Piloderma* spp. are typically found in the organic layer of the forest floor (Visser 1995; Goodman and Trofymow 1998) and in coarse woody debris (CWD; Smith et al. 2000; Tedersoo et al. 2003). However, Rosling et al. 2003 found mycorrhizas of *Piloderma* spp. also deeper in a podzol profile. Bending and Read 1996 showed that *P. croceum* produced extracellular proteases constitutively and was able to degrade protein, but this ability was inhibited when a protein–tannin complex was used instead of pure protein (bovine serum albumin). The affinity of *Piloderma* to organic substrates is related also to its resupinate fruiting habitat on decomposing organic residues. *Piloderma* spp., found on seedlings growing within the moss layer on EB, formed mats with densely distributed mycorrhizas and rhizomorphs, closely adhering to the boulder surface beneath the organic material. This might suggest the *Piloderma* spp. potential of mineral weathering. Indeed, similar distribution pattern of *Piloderma* (among other species) was found on granite in the E horizon in boreal forests in Sweden and Finland (Van Breemen et al. 2000), and it was attributed to 'rock-eating' abilities of EM fungi. EM hyphae extending from mycorrhizas formed envelopes around mineral grains and entered the pores and fissures in strongly weathered granite and feldspar. The mechanisms involved in fungal weathering remain largely unknown, but the role of low molecular weight (LMW) organic acids exuded by fungi seems to be important. Similarly, LMW organic acids produced by *Hysterangium* and *Gautieria* were responsible for accelerated mineral weathering by these mat-forming fungi (Griffiths and Caldwell 1992).

Tomentelloid species are common EM symbionts in boreal and temperate forests (Köljalg et al. 2000). This group of closely related genera (*Tomentella*, *Pseudotomentella*, and *Tomentellopsis*) is known to form resupinate sporocarps on decaying wood debris. Hence, the presence of two tomentelloid species (*Pseudotomentella nigra* and Tomentelloid-2) on DS seedlings might be a function of their high inoculum potential in decaying wood material. In other studies, tomentelloid fungi were also found mostly in the forest floor and CWD (Visser 1995; Taylor and Bruns 1999; Tedersoo et al. 2003). It has been suggested that the preference of tomentelloid fungi for decaying plant materials might be related to their capability of utilizing organic sources of nutrients and decomposition of decayed conifer stumps and logs (Köljalg et al. 2000).

In the present study, we found two *Lactarius* species, *L. glyciosmus* colonizing FG seedlings and *L. rufus* on DS seedlings. Some evidence suggests that *Lactarius* spp. might also possess the ability to take up the nutrients from organic sources. Two *Lactarius* spp. were able to clear the precipitate of a protein–tannin complex (Bending and Read 1996) and was attributed to a high production of extracellular phenoloxidases by *Lactarius* and *Russula* (Agerer 2001). The belowground abundance of Russulaceae tends to increase with forest age (Visser 1995; Palfner et al. 2005; Iwański, unpublished) and thus may be related to forest litter accumulation. However, Lilleskov et al. 2002 observed a strong relationship between the abundance of *L. theiogallus* mycorrhizas and net N mineralization over an atmospheric N deposition gradient (r^2=0.98, p=0.01) and termed this species 'nitrophilic.' This indicates that ecophysiological traits might be species specific, and caution must be taken when drawing conclusions at a higher taxonomical level.

Dermocybe spp. frequently occur in coniferous forests (Hintikka 1988; Termorschuizen 1991; Smith et al. 2002; Kranabetter and Friesen 2002; Kranabetter et al. 2005). Rosling et al. 2003 demonstrated that mycorrhizas of *Dermocybe* spp. occur generally in the E horizon. This is consistent with our findings that *Dermocybe* prefers mineral substrates and was absent on seedlings growing on organic materials (DS and EB).

Although this study employed a limited sampling effort, results suggest that microhabitats should be considered as an important source of variation of EM community composition, at least for the examined Scots pine stand. The results of this study show that the colonization pattern of EM fungi depends, to a large extent, on the microhabitats in which seedlings regenerate. Most of the identified EM species showed differential preference to microhabitats; however, because of the small sample size, it is not clear whether this pattern would apply to other pine stands. This study was carried out in a single Scots pine forest; thus, results are relevant only to this particular stand and cannot be extrapolated to pine forests in general. Therefore, any generalizations concerning the affinity of individual EM species to microhabitats require further investigations.

Differences in EM species composition of seedlings growing in these microhabitats might be attributed either to dispersal strategies and competitiveness of EM taxa, or to their variation in enzymatic nutrient mobilization and niche differentiation, or both factors together. The highest EM species richness found on FG seedlings is possibly the result of their integration into common mycelial networks of the EM community of surrounding mature trees (Jonsson et al. 1999b). The occurrence of species classified as 'medium- and long-distance exploration types' (Agerer 2001) such as *Tricholoma*, *Leccinum*, and *Dermocybe* can be explained in terms of facilitated colonization through mycelium extending from mycorrhizas of mature trees. On the other hand, the dominance of suilloid fungi on DS seedlings, together with their low abundance on FG seedlings, indicates superior dispersal ability but poor vegetative competitiveness of these fungi. Not surprisingly, seedlings regenerating on boulders had the lowest species richness, as their root systems were physically isolated from EM mycelial networks of forest soil and only a small suite of well-adapted species were able to colonize this habitat.

Generally, two distinct concepts can be recognized as explanatory models of the processes maintaining species richness within a trophic level. The first concept emphasizes the stochastic spatiotemporal dynamics of disturbance and colonization events, and the second highlights deterministic niche partitioning and resource differentiation (Ekschmitt and Griffiths 1998). Although based on contrasting hypotheses, both models predict that a species-poor community is likely to perform its ecological functions less efficiently than a species-rich community because of the environmental fluctuations and functional redundancy of the latter. As shown in this study, patchiness of the natural forest facilitates the establishment of unique EM assemblages and their nonrandom distribution in microhabitats. Obviously, both spatiotemporal population dynamics and niche partitioning play a role in EM communities, and it is reasonable to consider both processes as equally significant. Although little is known about the autecology and life-time strategies of EM taxa, it is a challenge to test to what extent these processes contribute to EM community dynamics and to merge the criteria from these two models into a single testable hypothesis.

Acknowledgments The fieldwork was carried out during the Cost E38 conference in Finland, Rovaniemi, on September 2006. We wish to thank the conference organizers Tarja Lehto and Helja-Sisko Heelmisari for field guidance. Sequence analysis was performed at the Laboratory of Molecular Biology of Adam Mickiewicz University. We also would like to thank two anonymous reviewers for helpful

comments on this manuscript. This study was financed by the Polish Ministry of Sciences and Higher Education (Grant KBN-1002/P06/2005/29 to authors).

References

Agerer R (1987–1998) Colour atlas of ectomycorrhizae. Einhorn, Schwäbisch Gmünd, Germany

Agerer R (2001) Exploration types of ectomycorrhizae. Mycorrhiza 11:107–114

Allen MF, Swenson W, Querejeta JI, Egerton-Warburton LM, Treseder KK (2003) Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. Annu Rev Phytopathol 41:271–303

Bending GD, Read DJ (1996) Nitrogen mobilization from protein–polyphenol complex by ericoid and ectomycorrhizal fungi. Soil Biol Biochem 28:1603–1612

Bruns TD (1995) Thoughts on the processes that maintain local species diversity of ectomycorrhizal fungi. Plant Soil 170:63–73

Colwell RK (2005) EstimateS: statistical estimation of species richness and shared species from samples, version 7.5. www.purl.oclc.org/estimates

Dahlberg A (1997) Spatial structures of *Suillus variegatus* genets in old Swedish Scots pine forest. Mycol Res 101:47–54

Dahlberg A (2002) Effects of fire on ectomycorrhizal fungi in Fennoscandian boreal forests. Silva Fenn 36(1):69–80

Dahlberg A, Stenlid J (1994) Size, distribution and biomass of genets in populations of *Suillus bovinus* (L. :FR) Roussel revealed by somatic incompatibility. New Phytol 128:225–234

Dahlberg A, Jonsson L, Nylund J-E (1997) Species diversity and distribution of biomass above and belowground among ectomycorrhizal fungi in an old Norway spruce forest in south Sweden. Can J Bot 8:1323–1335

Ekschmitt K, Griffiths BS (1998) Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. Appl Soil Ecol 10:201–215

Erland S, Taylor AFS (2002) Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic factors. In: van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Springer, Berlin, pp 163–195

Fleming LV (1983) Succession of mycorrhizal fungi on birch: infection of seedlings planted around mature trees. Plant Soil 71:263–267

Goodman DM, Trofymow JA (1998) Distribution of ectomycorrhizas in micro-habitats in mature and old-growth stands of Douglas-fir on Southeastern Vancouver Island. Soil Biol Biochem 30:2127–2138

Griffiths RP, Caldwell BA (1992) Mycorrhizal mat communities in forest soils. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB, Wallingford, p 98–105

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

Hintikka V (1988) On the macromycete flora in oligotrophic pine forests of different ages in South Finland. Acta Bot Fenn 136:89–94

Horton TR, Cázares E, Bruns TD (1998) Ectomycorrhizal, vesicular–arbuscular and dark septate fungal colonization of bishop pine (*Pinus muricata*) seedlings in the first 5 months of growth after wildfire. Mycorrhiza 8:11–18

Ingleby K, Mason PA, Last F, Fleming LV (1990) Identification of ectomycorrhizas. HMSO, London

Iwański M, Rudawska M, Leski T (2006) Mycorrhizal associations of nursery grown Scots pine (*Pinus sylvestris* L.) seedlings in Poland. Ann For Sci 63:715–723

Jones MD, Durall DM, Cairney JWG (2003) Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. New Phytol 157:399–422

Jonsson L, Dahlberg A, Nilsson M-C, Zackrisson O, Kårén O (1999a) Ectomycorrhizal fungal communities in late-succesional Swedish boreal forests and composition following wildfire. Mol Ecol 8:205–217

Jonsson L, Dahlberg A, Nilsson M-C, Kårén O, Zackrisson O (1999b) Continuity of ectomycorrhizal fungi in self-regenerating *Pinus sylvestris* forests studied by comparing mycobiont diversity on seedlings and mature trees. New Phytol 142:151–162

Köljalg U, Dahlberg A, Taylor AFS, Larsson E, Hallenberg E, Stenlid J, Larsson K-H, Fransson PM, Kårén O, Jonsson L (2000) Diversity and abundance of resupinate thelephoroid fungi as ectomycorrhizal symbionts in Swedish boreal forests. Mol Ecol 9:1985–1996

Kranabetter JM, Friesen J (2002) Ectomycorrhizal community structure on western hemlock (*Tsuga heterophylla*) seedlings transplanted from forests into openings. Can J Bot 80:861–868

Kranabetter JM, Friesen J, Gamiet S, Kroeger P (2005) Ectomycorrhizal mushroom distribution by stand age in western hemlock—lodgepole pine forests of northwestern British Columbia. Can J For Res 35:1527–1539

Lanfranco L, Perotto S, Longato S, Mello A, Cometti V, Bonfante P (1998) Molecular approaches to investigate biodiversity in mycorrhizal fungi. In: Varma A (ed) Mycorrhiza manual. Springer, Berlin, pp 353–372

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM (2002) Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83:104–115

Menkis A, Allmer J, Vasiliauskas R, Lygis V, Stenlid J, Finlay R (2004) Ecology and molecular characterization of dark septate fungi from roots, living stems, coarse and fine woody debris. Mycol Res 108:965–973

Menkis A, Vasiliauskas R, Taylor AFS, Stenlid J, Finlay R (2005) Fungal communities in mycorrhizal roots of conifer seedlings in forest nurseries under different cultivation systems, assessed by morphotyping, direct sequencing and mycelial isolation. Mycorrhiza 16:33–41

Palfner G, Cassanova-Katny MA, Read DJ (2005) The mycorrhizal community in a forest chronosequence of Sitka spruce [*Picea sitchensis* (Bong.) Carr.] in Northern England. Mycorrhiza 15:571–579

Redecker D, Szaro TM, Bowman RJ, Bruns TD (2001) Small genets of *Lactarius xanthogallus, Russula cremicolor* and *Amanita francheti* in late stage ectomycorrhizal successions. Mol Ecol 10:1025–1034

Rosling A, Landeweert R, Lindahl BD, Larsson K-H, Kuyper TW, Taylor AFS, Finlay RD (2003) Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. New Phytol 159:775–783

Smith JE, Molina R, Huso MMP, Larsen MJ (2000) Occurrence of *Piloderma fallax* in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, USA. Can J Bot 78:995–1001

Smith JE, Molina R, Huso MMP, Luoma DL, McKay D, Castellano MA, Lebel T, Valachovic Y (2002) Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A. Can J Bot 80:186–204

Taylor DL, Bruns TD (1999) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagules communities. Mol Ecol 8:1837–1850

Tedersoo L, Köljalg U, Hallenberg N, Larsson K-H (2003) Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytol 159:153–165

Termorschuizen AJ (1991) Succession of mycorrhizal fungi in stands of *Pinus sylvestris* in the Netherlands. J Veg Sci 2:555–564

Van Breemen N, Finlay R, Lundström U, Jongmans AG, Giesler R, Olsson M (2000) Mycorrhizal weathering: A true case of mineral plant nutrition? Biogeochemistry 49:53–67

Visser S (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol 129:389–401

Vrålstad T, Fossheim T, Schumacher T (2000) *Piceirhiza bicolorata*—the ectomycorrhizal expression of the *Hymenoscyphus ericae* aggregate? New Phytol 145:549–563

Vrålstad T, Schumacher T, Taylor AFS (2002) Mycorrhizal synthesis between fungal strains of the *Hymenoscyphus ericae* aggregate and potential ectomycorrhizal and ericoid hosts. New Phytol 153:143–152