

Effects of Fire on Ectomycorrhizal Fungi in Fennoscandian Boreal Forests

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Fire, the primary natural disturbance factor in Fennoscandian boreal forests, is considered to have exerted major selection pressure on most boreal forest organisms. However, recent studies show that few ectomycorrhizal (EM) fungi appear to have evolved post-fire adaptations, no succession of EM fungi following fire is apparent after low intensity fires, and only two EM fungal taxa exclusively fruit at post-fire conditions. In this paper I review the present knowledge of effects of forest fire on EM fungal communities in Fennoscandian boreal forests, put into perspective by a comparison from other parts of the world. Characteristically, these boreal forests consist of less than a handful of tree species, e.g. Scots pine and Norway spruce, while the below ground communities of EM fungi is impressively species rich with presently more than 700 known taxa. Commonly, forest fires in Fennoscandia have been of low intensity, with a considerable portion of the trees surviving and the organic humus layer partly escaping combustion. Hence, EM fungi appear to largely have evolved under conditions characterised by a more or less continuous presence of their hosts. In fact, the composition of EM fungi within a forest appear be more variable due to spatial variation than due to wildfire. However, in areas with high intensity burns and high tree mortality, most EM fungi may locally be killed. Thus, the legacy of EM fungi following wildfire depends on the survival of trees, which determine the potential for mycorrhizal growth, and the combustion and heating of the organic soil, which directly correlate to mortality of mycorrhizas. The questions if and to what degree fires may be of significance for yet unidentified spatiotemporal dynamics of EM fungal populations and communities are discussed. Recent experiments indicate a few EM fungi are favoured by high intensity burn conditions whereas others disappear. The consequences of wildfires in temperate conifer forests differ considerably from those in boreal forests. Wildfires in temperate conifer forests are typically high intensity stand-replacing fires that cause a total combustion of organic layers. Subsequently, pre-fire EM fungal communities are largely eradicated and a succession of post-fire EM fungi is initiated.

Keywords ectomycorrhizal fungi, fire, boreal forests, community, population

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1 Introduction

Boreal forests constitute the largest terrestrial biome, covering 11% of the earth's terrestrial surface and forming a continuous northern circumpolar vegetation zone (Bonan and Shugart 1989). Environmental factors that determine the vegetation patterns are largely similar throughout the region. Coniferous trees prevail at all sites, typically with single or few tree species of *Picea*, *Pinus*, *Larix* and *Abies*. Boreal forests of Fennoscandia (e.g. in Sweden, Norway and Finland) are relatively homogeneous. Two conifers dominate, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), with minor contributions of birch (*Betula* spp), aspen (*Populus tremula*), alder (*Alnus* spp), and goat willow (*Salix caprea*) (Ahti et al. 1968, Essen et al. 1992). Before active fire suppression started at the end of 1900 century, recurring fire was a common feature in the boreal forests of Fennoscandia (Zackrisson 1977). Forest fire is considered to be one of the major disturbance factors in this ecosystem and most forest organisms are presumed to have evolved under a strong selection pressure from wildfires (Essen et al. 1992, Johnson 1992, Goldammer and Furyaev 1996, Engelman 1999).

Forest fires have since long been the focal point of interest for boreal forest ecologists. However, due to earlier methodological difficulties to monitor belowground ectomycorrhizal (EM) fungal communities, knowledge of fire effects on EM fungi is yet scarce. Furthermore, most such studies have examined effects of prescribed burning after clear-cutting (i.e. Mikola et al. 1964, Harvey et al. 1980a and 1980b, Pilz and Perry 1984, Stendell et al. 1999, Dahlberg et al. 2001, Mah et al. 2001). The common feature of these studies is a reduction in diversity and abundance of EM fungi caused by cutting rather than by fire. However, recently effects of natural wildfires have been studied (Visser 1995, Jonsson et al. 1999a, Baar et al. 1999, Grogan et al. 2000). Fennoscandian studies indicate that fire effects on the EM fungal community are low, probably because most fires are of low intensity and a considerable portion of the trees survives. (Mikola et al. 1964, Jonsson et al. 1999a, Dahlberg et al. 2001). In contrast, fires strongly affect EM fungal com-

munities in temperate forests where fires commonly are of high intensity and result in stand replacement, e.g. in Mediterranean and in temperate North America (Danielson 1984, Visser 1995, Torres and Honrubia 1997, Horton et al. 1998, Baar et al. 1999, Grogan et al. 2000)

2 Fungal Species Richness in Fennoscandian Boreal Forest

Boreal forests characteristically have a low number of plant species, but a high number of fungal species. A recently compiled database of all known Swedish macrofungi and their ecology, contains 4200 taxa, of which at least 2100 species are recorded from boreal forests (Hallengbäck and Aronsson 1998). The species richness of macrofungi in Finnish and Norwegian boreal forests is largely considered to be the same (Esteri Ohenoja, Oulu and Tor Erik Brandrud, Oslo, personal communication). The majority of these 2100 macrofungi are saprotrophic; about 700 are soil- and litter dwelling, about 700 are wood inhabiting saprotrophs and slightly more than 700 species are EM fungi (Table 1, Hallengbäck and Aronsson 1998, Dahlberg et al. 2000). The total number of fungal taxa in this ecosystem is considerably greater as about 65% of fungal taxa in Sweden are microfungi, i.e. either lacking known sexual structures or having sporocarps smaller than 1 mm (Gärdenfors 2000).

2.1 Mycorrhizal Fungi in Boreal Forest

With few exceptions, all plants in boreal forests form mycorrhizal associations and rely upon them for their fitness and acquisition of nutrients. Grasses, ferns and most herbs form arbuscular mycorrhiza (AM), the most ancient and widespread mycorrhizal form of fungi lacking reproductive structures. The actual number of AM-forming fungal taxa in boreal Fennoscandia is not known, but low, as not more than 150 taxa are recognised worldwide. Forest fire effects on AM fungi have not been studied in Scandinavia, but likely resemble the decrease or total loss reported from grassland ecosystems in the United

Table 1. The number of macromycetes in Swedish boreal forests divided into wood- and soil-inhabiting saprotrophs and ectomycorrhizal fungi. The number of fire-dependent and red-listed fire dependent taxa within each group is shown. (Source: Hallingbäck and Aronsson 1998, Gärdenfors 2000).

	Wood saprophytes	Soil and litter saprophytes	Ectomycorrhizal fungi	Total no. of fungi
No. of macrofungal species in boreal forests	700	500	700	ca. 2100
No. of fire dependent fungi	2	38 ¹	0	40
Additional fungi mainly occurring at post fire conditions	0	3	2	5
No. of red listed fungi associated with fire ²	6	2	2	10

¹ of which six taxa fruit of wood pieces on the ground.

² all favoured but not exclusively associated by post-fire conditions. In total 200 of the 609 fungi red listed in Sweden, occur in boreal forests.

States (e.g. Wicklow-Howard 1989, Amaranthus and Trappe 1993). Ericaceous plants, that characteristically monopolise and constitute the field vegetation layer in boreal forests, form ericoid mycorrhiza. Worldwide, about 10 fungal taxa, predominantly ascomycetes, are known to form this association, which colonise the hair-roots. Because rhizomes and hair-roots of ericaceous plants are more superficially located in the organic layer of the forest floor than are roots of trees (cf. Persson 1983), fire will have a more detrimental effect on communities of ericoid fungi than on those of EM fungi. However, the survival of ericoid fungi is probably considerable, as rhizomes of ericaceous plants commonly survive after fires of low severity or spatially varying severity (Uggla 1958, Schimmel and Granström 1996).

The boreal forest trees, both conifers and broad-leaved, form ectomycorrhiza (EM) and the majority of these trees' root tips (>95%) are colonised by symbiotic EM fungi (Melin 1927, Smith and Read 1997). The root tips and the fungi form composite organs termed mycorrhizas, the sites of nutrient and carbon transfer between the two symbionts (Smith and Read 1997). The approximately 700 species of EM macrofungi recorded in Swedish boreal forests constitute 10–15% of all worldwide known EM fungi (Dahlberg et al. 2000, Molina et al. 1992). The most species rich genera are *Cortinarius* with slightly more than 200 taxa, *Russula* with about 80 taxa and *Lacatrius* with about 60 taxa.

2.1.1 EM Fungal Communities

Sporocarp surveys of Fennoscandian boreal forest stands reveal more than 100 fruiting EM fungal species as present (Dahlberg 1991, Ohe-noja 1993). The great majority of the EM fungal biomass and fungal activity, however, is located in the forest floor as mycorrhizas and from the extending mycelia (Mikola el at. 1966, Smith and Read 1997). Studies of composition and dynamics of EM fungal communities have been severely hampered by the typically invisible growth of forest fungi (Dahlberg 2001, Horton and Bruns 2001). However, the last decade's progress in identification of mycobionts on single mycorrhizas has repeatedly demonstrated that fungi that do not form obvious fruiting structures, form the major mycorrhizal abundance (Gardes and Bruns 1996, Horton and Bruns 2001).

Boreal EM fungal communities are impressively diverse, have high species richness, and fruiting species typically constitute less than 30% of the community of mycorrhizas (Dahlberg et al. 1997, Jonsson et al. 1999a, Jonsson et al. 2000, cf. Horton and Bruns 2001). Typically, a few EM fungal taxa account for the greatest proportion of the mycorrhizal biomass while the contribution of most taxa is small (Horton and Bruns 2001). Apparently, resource allocation to production of sporocarps versus mycorrhizas and mycelial growth varies among species (Gardes and Bruns 1996). Certain species that abundantly form mycorrhizas are poorly or non-represented

in the aboveground fruiting record and commonly fruiting species may conversely have only a limited representation in below-ground mycorrhizal networks. Some EM fungal taxa may be abundant both as sporocarps and mycorrhizas, e.g. species of *Suillus* (Gardes and Bruns 1996). Other EM fungal taxa, e.g. corticoid or tomentelloid fungi, may either produce small amounts of inconspicuous sporocarps or completely lack sporocarps, despite being abundant as mycorrhizas (Erland and Taylor 1999, Kojlag et al. 2001, Dahlberg et al. 2001).

The mechanisms that create this impressive diversity are yet poorly understood. Two main hypotheses are; 1) those based on niche differentiation between coexisting EM fungal species, and, paradoxically, 2) those based on similarities in competitive ability, i.e. non-equilibrium models. An example of the former is the intermediate disturbance hypothesis stating that a disturbance leads to a predictable sequence of species replacing each other. An intermediate range of disturbance would allow a range of species traits, early to late successional species, to coexist and lead to high species richness. The latter assumes stochastic elements which enhance coexistence: so called lottery models, state that due to poor dispersal ability, low local abundance and chance events, species may be absent in a neighbourhood and their abundance recruitment may thus be limited. The best competitor that happens to colonise a particular local site may well be inferior on a larger scale. Potentially, this can lead to unlimited species richness.

2.1.2 EM Fungal Populations

Spatiotemporal patterns and demographic processes of fungal populations are not well known, as efficient monitoring of fungal genotypes is precluded by their growth within opaque substrates. Mycelial growth ensures the persistence and local spread of established genotypes while sexual spores secure both short and long distance dispersal and the rise of new genotypes. EM fungi do not form asexual spores, conidia, important for many saprotrophic and pathogenic fungi (Hutchison 1989).

Potentially, mycelia may have unlimited growth

and age. It is merely the resource a mycelium occupies that establishes the limit of space and age of a fungal individual. Fungi that occupy discrete resource units such as wood require regular dispersal for their long-term survival. However, soil-dwelling fungi such as EM fungi, exploiting more or less indefinite resources have the capacity for extensive mycelial growth and long survival without sexual reproduction and dispersal of spores. Hypothetically, the longevity of an individual EM fungal mycelium could be as long as their host trees are continuously present. However, the relative fitness of an individual EM fungal mycelium is strongly influenced by changes in its local environment as well as by competition with other EM fungi.

Circumstantial evidence suggests that the ability of established mycelia and mycorrhizas to colonise new short roots is probably much higher than that of spores to successfully establish in forest conditions, i.e. clonal traits have a higher fitness than sexual traits in normal forest conditions (cf. Deacon and Fleming 1992). The few EM fungi that have been studied in boreal forests, (*Suillus bovinus*, *S. variegatus* and *Hydnellum ferrugineum*) reveal that genotypes may be both large (>300 m²) and old (>150 years). Studies demonstrated the ability of these fungi to spread by mycelial growth in soil in excess of 30 m (Hintikka and Näykki 1967, Dahlberg and Stenlid 1995, Dahlberg 1997). Large genets indicate old mycelial structures that have grown from a point source over decades (Dahlberg and Stenlid 1995). The potential annual mycelial extension is probably a few decimetres in forest conditions (cf Fioro-Donno and Martin 2001). It has been demonstrated that naturally regenerated seedlings are colonised by the same set of EM fungi that are present on the surrounding trees, and probably largely from mycelia (Jonsson et al. 1999b).

Recent investigations of EM fungi from disturbed temperate forests with *Hebeloma cylindrosporum* and from undisturbed forest settings with *Laccaria* spp *Amanita frenchati*, *Russula cremoricolor*, and *Lactarius xanthogalus* demonstrate numerous small sized and short-lived genotypes (Gryta et al. 1997, 2000, Gherbi et al. 1999, Redecker et al. 2001, Fioro-Donno and Martin 2001). These results suggest, that spore establishment may be more important, at least

for certain species in undisturbed forests, than mycelial spread. In saprotrophic and pathogenic fungi, population structures have been examined for a large number of species. Genotypes of different species are found to range in size from millimetres to kilometres with considerable heterogeneity in the size range for a single species (Anderson and Kohn 1998).

3 Frequency and Behaviour of Fennoscandian Forest Fires

Fennoscandian wildfires in boreal forests are commonly of low intensity, large Scots pines usually survive and a significant portion of the organic layer is left intact below the uppermost charcoal layer (Schimmel and Granström 1997). The occurrence of high temperatures within and beneath the mor-humus layer during a fire is coupled to the depth of burn, and directly influences the survival of biological structures in the ground (Schimmel and Granström 1996). Detrimental temperatures normally extend less than a 2–3 cm into the mineral soil (Schimmel and Granström 1996). Among and within different fires, the variation in depth of burn can range from most of the organic soil left intact, to combustion of almost all organic material (J. Schimmel, personal communication), affecting the local composition of EM fungi and influencing their spatial patchiness.

Spatiotemporal variations at both the regional and local scale are important to consider when evaluating biological effects of fires (cf Engelmark 1999). Historically, forest landscapes consisted of forests with different historic fire frequency and varying probability of ignition.

Hörnberg et al. (1998) suggested three post-fire patterns in different Scots pine–Norway spruce forest types; a) frequently disturbed dry-mesic forests where fires occurred every 50–100 years (Zackrisson 1977, Engelmark 1984), b) non-frequently disturbed swamp forests, with an average interval between fires of over 400 years, and c) nonpyrogenic, mainly mesic, forests. The latter Scots pine forest type is known close to the Fennoscandian mountain range (Zackrisson et al. 1995).

At the local scale, the effects of fire on living organisms vary both between fire events and between different sections of the same fire, largely owing to differences in fire behaviour (Van Wagner 1983). The energy output in the spreading front of a forest fire, together with properties of the tree species involved, determine the level of tree mortality caused by the fire (Van Wagner 1983). Fires in Scandinavian boreal forests have commonly been of low intensity (Östlund et al. 1997). A substantial number of trees usually survived through several fire events (Zackrisson 1977, Engelmark 1984, Niklasson 1998). Still, high intensity fires can also occur and tree survival may vary considerably within the same fire. Burn intensity is influenced by fuel loading, wind speed, and the moisture content of fine fuel particles (Schimmel and Granström 1996). Irrespective of the fire intensity, fires in boreal forests typically combust part of the organic soil layer. The degree of consumption of the organic soil layers, i.e. the depth of burn, depends primarily on the depth of the dry soil layer which in turn is determined by the length of time without rain before the fire (Schimmel and Granström 1997).

4 Fire Dependent Organisms in Boreal Forest

Slightly more than 80 species in Swedish boreal forests are considered fire-dependent, i.e. dependent upon fire and the immediate post-fire conditions to complete their life cycles and secure their long-term survival. This set of species includes more than 38 for insects, 40 for macrofungi (i.e. taxa fruiting exclusively at immediate post-fire conditions), fewer than five for vascular plants, a few lichens, but no mosses (Engelmark 1999, Gärdenfors 2000, Johannesson and Dahlberg 2001). The major impact of forest fire on organisms in boreal forests is attributed to the conditions created by fire and the subsequent interactions of organisms with those environmental conditions. Accordingly, an estimated several hundred boreal organisms (pyrophilic or post-fire adapted) are favoured by forest fire rather than being strictly fire-dependent. It is apparent that

the spatial and temporal heterogeneity created by fire among and within forests at the landscape level, combined with varying biological legacy, will affect the presence and abundance of the succeeding forest organisms. Fire-dependent macrofungi in Sweden are predominantly saprotrophs; 32 occur on soil or litter and two occur on wood. Five additional taxa fruit almost exclusively at post-fire conditions, of these three are saprotrophs, one is the EM basidiomycete *Hebeloma antracophilum* and one is the putative EM ascomycete fungus *Geopyxis carbonaria* (Vrålstad et al. 1998). *Hebeloma antracophilum* has a more southern distribution and just reaches the boreal zone, whereas *G. carbonaria* is common throughout the boreal zone (Hallingbäck and Aronsson 1998). Ten of the 296 red-listed macrofungi present in the boreal parts of Sweden are associated with post-fire conditions (Table 1). None is strictly associated with burnings.

5 Impacts of Fire on Fungi

Forest fires cause radical changes in the community of fruiting saprotrophic fungi (Moser 1949, Petersen 1970 and 1971, Holm 1995, Rahko 1997). The destructive nature of fire immediately effects wood inhabiting fungi by decreasing species richness and altering species composition (Penttilä and Kotiranta 1996). Several studies report a succession of ground-dwelling post-fire fungi, in particular the early successional and abundant fruiting of discomycetes within the order Pezizales (Moser 1949, Petersen 1970 and 1971, Holm 1995, Rahko 1997). EM fungi are affected by factors influencing the photosynthesis of the trees. For example, changes in stand biomass, successional age, or disturbances such as forest fire will quantitatively effect the abundance of ectomycorrhizas and the production of sporocarps. Such quantitative and qualitative fire effects on EM fungi are summarised and discussed below.

5.1 Effects on Sporocarp Production of EM Fungi

Severe fires in coniferous forests with high tree mortality cause a drastic or total disappearance of fruiting of EM fungi (Petersen 1971, Holm 1995). When fire intensity is low, only the upper portion of humus is consumed, trees survive, and the number, biomass and species composition of fruiting EM fungi remains largely unchanged (Rahko 1997, Jonsson et al. 1999a, Dahlberg et al. 2001).

In a 1–50-year-old chronosequence of four burned stands paired with adjacent old forests in Northern Sweden, differences in the occurrence of fruiting species were attributed more to natural spatial variation than to fire (Jonsson et al. 1999a, personal observations). In one of the stands, a low intensity underburn occurred beneath the mature forest canopy in an old-growth forest with low tree mortality. In this stand, the number of fruiting EM fungal taxa the following two years was 26, compared to 41 in the nearby old stand (Linder et al. 1999, Jonsson et al. 1999a). This difference in fruiting may be due to spatial variation as well as to: a) reduced allocation of photosynthate to the forest soil resulting from fire damaged trees, b) reduced abundance of mycorrhizas, but not necessarily extermination of EM fungal taxa, and c) hampered fruiting due to altered environmental conditions in the organic layer, i.e. presence of charcoal and absence of bottom and field vegetation. In another comparison between underburned and nonburned forests, sporocarp production was strongly affected, yet species richness of fruiting EM taxa was similar and minor differences in composition could not be attributed to the fire (Dahlberg et al. 2001). Recurrent fire reduces the organic layer and field observations suggest a thin humus layer as a prerequisite for fruiting of certain *Cortinarius* taxa (Phlegmacium) (Tor Erik Branderud, personal communication). Sporocarp studies after fires in boreal Canada suggest low survival of EM fungi (Danielson 1984, Visser 1995), while a study after low-intensity fire in Virginia, USA, showed fruiting of most EM fungi was unaffected (Palmer et al. 1994).

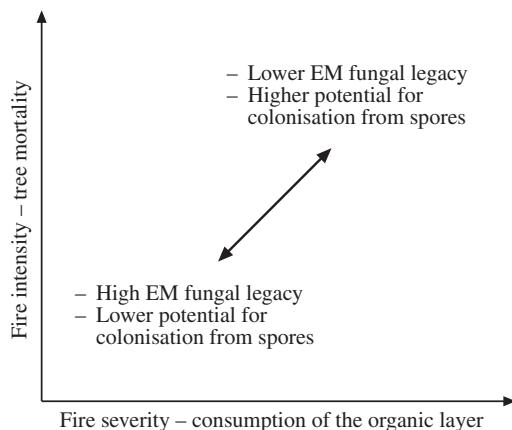


Fig. 1. Schematic relationships between fire intensity, fire severity and survival of the mycorrhizal community.

5.2 Effects on Mycorrhizal Abundance

Fire causes a significant loss of EM biomass in the upper litter and organic soil horizons. The mycorrhizal abundance in the organic layer is generally strongly reduced (Jonsson et al. 1999a). However, Mikola et al. (1964) reported that EM fungi protected by the soil-layer from the detrimental penetration of heat, survive and may thus link the EM fungal community between fire affected forest generations. The mortality of mycorrhizas correlates with severity of the burn and tree survival (Fig. 1, Dahlberg et al. 2001). However, irrespective of fire severity, live mycorrhizas were present in the mineral layer (Dahlberg et al. 2001). A vertical stratification of different EM fungal taxa has been briefly described, but is not yet well studied, e.g. that some taxa are more prolific in the organic layer and some taxa are more prolific in the mineral soil (Visser 1995, Stendell et al. 1999, Taylor and Bruns 1999, Dahlberg et al. 2001). In dry forests, mycorrhizas are located deeper in the mineral soil than in mesic forests. Mycorrhizas are probably present as deep as tree roots are, i.e. several meters (Kalela 1949). Whereas mycorrhizal biomass was reduced eight-fold in the litter- and organic layer in a prescribed burning of a ponderosa pine forest in USA, it was not significantly

reduced in the mineral layer (Stendell et al. 1999). Even after a stand replacing wildfire on the Californian coast, USA, the five most abundant EM fungal pioneers colonising the emerging coniferous seedlings appeared to have survived the fire primarily as resistant propagules (spores, sclerotia or mycorrhizal root tips) in the mineral soil rather than as re-colonising spores (Baar et al. 1999).

5.3 Effects on Composition of EM Fungal Species

General successional patterns of EM fungal communities in relation to successions of fire history are not apparent in Fennoscandian boreal forests. Certain EM fungal species occur exclusively in conditions associated with old forests, others are predominant after specific disturbance events, but most EM fungal taxa appear at almost any forest successional age (cf. Hallingbäck and Aronsson 1998, Gärdenfors 2000, Dahlberg 2001). Spatial variation in species composition seems to be more prominent than the effects of fire, supporting the hypothesis of significant survival of EM fungi in boreal forests disturbed by wildfire (Mikola et al. 1964, Jonsson et al. 1999a). The natural shift in composition of trees during forest successions will, however, affect the EM fungal community as some EM fungi differ in the preference and specificity for host trees (Molina et al. 1992, Dahlberg et al. 2000). Soil composition and litter quality subsequently influence the properties of the organic layer and may also affect EM fungi (cf Wardle et al. 1998). For example, after a forest fire no immediate effects on the frequency or distribution of EM fungal taxa were detected, despite reduction in mycorrhizal abundance (Dahlberg et al. 2001). These findings are likely due to high spatial variation, as only a few taxa were widespread and the majority were recorded only once (Dahlberg et al. 2001).

Island size is frequently a major determinant of the species composition of biological communities. A study of fifty islands of varying size in an archipelago in the northern Swedish boreal forest zone, in which larger islands naturally burn more frequently than smaller ones through wildfire arising from lightning strike, revealed a significant relationship between island area and

plant species composition (Wardle et al. 1997). We have conducted an analysis of the EM fungal communities on these islands, and our preliminary results demonstrate high species richness, high heterogeneity within and among islands, but no apparent taxa or set of EM fungal taxa occurring exclusively in early or late forest succession (Anders Dahlberg, personal observations).

Wildfire produces a charcoal layer, which in forests in northern Sweden may range from 1000–2000 kg ha⁻¹ (Zackrisson et al. 1996). These amounts of charcoal appear to be sufficient to have an important ecological effect through adsorption (Zackrisson et al. 1996, Pietikainen et al. 2000). For example, charcoal efficiently adsorbs phenolic compounds produced by the late successional dwarf shrub *Empetrum hermaphroditum*. Phytotoxic effects, produced by this shrub, negatively influences the composition of boreal forest plants and may also affect EM fungal composition (Wardle et al. 1998). More subtle indirect effects from ash leaching have also been suggested to affect mycorrhizal fungi via pH and nutritional shifts (Stendell et al. 1999), but a controlled study in United States suggested composition and distribution EM fungal inocula to be the primary determinants of EM community structure (Grogan et al. 2000).

In contrast, Danielson (1984) and Visser (1995) showed wildfire in jack pine (*Pinus banksiana*) stands in Canada to have large impacts on EM fungal communities by both reducing the mycorrhizal abundance and changing species composition. The high intensity, stand-replacing fires in these studies strongly altered the ground vegetation and humus conditions. The foliage of jack pine is highly combustible, and in dense forests intense crown fires often result in tree mortality (Engelmark 1999).

5.4 Effects on Fungal Population Dynamics

Presently, we know little about necessary conditions for colonisation by EM fungi or of the frequency of new colonisation in secondary forest conditions and even less to what extent fire alters these processes in boreal forests. It has been suggested that fungal genotypes of *S. variegatus* have the potential to survive fires and to persist

between forest generations, although a severe fire with high tree mortality may be fatal to most genets (Dahlberg 1997). It has also been speculated that certain post-fire conditions, particularly following deep-burning fires that result in high tree mortality as well as mortality of much of the existing EM community, may provide recruitment for colonisation of new genets (Dahlberg et al. 2001). However, a recent study fails to support that post-fire conditions affect the establishment or spatial population structure of *S. variegatus* (Dahlberg, personal observations). Furthermore, a recent experiment demonstrates both mycorrhizal abundance and fruiting of *Lactarius mammosum* to be strongly enhanced after severe burns. Such conditions are clearly disadvantageous for *Piloderma reticulatum*, the EM fungus dominating mycorrhizas in Swedish Scots pine forests (Anders Dahlberg, personal observations).

Spore germination of certain saprophytic and pathogenic post-fire fungi is stimulated by heat (El-Abyad and Webster 1968, Jalaluddin 1967). This response is not known from EM fungi, but addition of charcoal has been demonstrated to improve germination by removing inhibitory compounds for some EM fungi (i.e. Fries and Sun 1992). However, spores from the post-fire discomycete *G. carbonaria* germinate without any external stimuli. The life cycle of *G. carbonaria* has been suggested to include a biotrophic association, possibly EM with Norway spruce, and where sexual reproduction and dispersal occur only at immediate post-fire conditions (Vrålstad et al. 1998). Similarly, the wood inhabiting ascomycete *Daldinia loculata* exclusively fruits in post-fire conditions on dead trees, but latent mycelia are apparently present in living birches between fire events (Johannesson et al. 2001).

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References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales botanici Fennici* 5: 169–211.
- Ammananthus, M.P. & Trappe, J.M. 1993. Effects of erosion on ecto- and VA-mycorrhizal inoculum potential of soil following forest fire in Southwest Oregon. *Plant and Soil* 150: 41–49.
- Anderson, J.B. & Kohn, L.B. 1998. Genotyping, gene genealogies and genomics bring fungal population genetics above ground. *Trends in Ecology and Evolution* 13: 444–449.
- Baar, J., Horton, T.R., Kretzer, A.M. & Bruns, T.D. 1999. Mycorrhizal colonisation of *Pinus muricata* from resistant propagules after a standreplacing wildfire. *New Phytologist* 143: 409–418.
- Bonan, G.B. & Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* 20: 1–28.
- Dahlberg, A. 2001. Structures and dynamics of ectomycorrhizal fungal communities. *New Phytologist* 150: 555–562.
- , 1997. Spatial structures of *Suillus variegatus* genets in old Swedish Scots pine forest. *Mycological Research* 101: 47–54.
- , 1991. Ectomycorrhiza in coniferous forest: structure and dynamics of populations and communities. PhD-thesis, Swedish University of Agricultural Science, Uppsala, Sweden.
- , Schimmel, J., Taylor, A. & Johannesson, H. 2001. The legacy of ectomycorrhizal fungal communities as mycorrhizas in boreal, following cutting and prescribed burning at different intensities. *Biological Conservation* 100: 151–161.
- , Croneborg, H. & Hallingbäck, H. 2000. Sveriges ektomykorrhizasvampar, översikt av arter, förekomst och ekologi. *Svensk Botanisk Tidskrift* 5: 267–285.
- , Jonsson, L. & Nylund J-E. 1997. Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old Norway spruce forest in south Sweden. *Canadian Journal of Botany* 8: 1323–1335.
- & Stenlid, J. 1995. Spatiotemporal patterns in ectomycorrhizal populations. *Canadian Journal of Botany* 73: 1222–1230.
- Danielson, R. M. 1984. Ectomycorrhizal associations in jack pine stands in northeastern Alberta. *Canadian Journal of Botany* 62: 932–939.
- Deacon, J.W. & Fleming, L.V. 1992. Interactions of ectomycorrhizal fungi. In: Allen, M. (ed.). *Mycorrhizal functioning – an integrative plant-fungal process*. Chapman & Hall, London. p. 249–300.
- El-Abyad, M.S.H. & Webster, J. 1968. Studies on pyrophilous discomycetes. I. Comparative physiological studies. *Transaction of the British Mycological Society* 51: 353–367.
- Engelmark, O. 1999. Boreal forest disturbances. In: Walker, L.R. (ed.). *Ecosystems of the world* 16 – Ecosystems of disturbed grounds. Elsevier, Amsterdam. p. 161–186.
- 1984. Forest fires in Muddus National Park (northern Sweden) during the past 600 years. *Canadian Journal of Botany* 62: 839–898.
- Erland, S. & Taylor, A.F.S. 1999. Resupinate ectomycorrhizal fungal genera. In: Cairney, J.W.G. & Chambers, S.M. (eds.). *Ectomycorrhizal fungi: key genera in profile*. Springer Verlag, Heidelberg. p. 347–363.
- Essen, P-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletin* 46: 16–47.
- Fiore-Donno, A-M. & Martin, F. 2001. Populations of ectomycorrhizal *Laccaria amethystina* and *Xerocomus* spp. show contrasting colonization patterns in a mixed forest. *New Phytologist* 152: 533–542.
- Fries, N. & Sun, Y-P. 1992. The mating system of *Suillus bovinus*. *Mycological Research* 96: 237–238.
- Gärdenfors, U. (ed.). 2000. The 2000 red list of Swedish species. The Swedish Threatened Species Unit, Uppsala.
- Gardes, M. & Bruns, T.D. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* 74: 1572–1583.
- Gherbi, H., Delaruelle, C., Selosse, M-A. & Martin, F. 1999. High genetic diversity in a population of the ectomycorrhizal basidiomycete *Laccaria amethystina* in a 150-year-old beech forest. *Molecular Ecology* 8: 2003–2013.
- Goldammer, J. G. & Furyaev, J.G. (eds). 1996. *Fire in ecosystems of boreal Eurasia*. Dordrecht London, Kluwer. *Forestry Sciences* 48.

- Grogan, P., Baar, J. & Bruns T.D. 2000. Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. *Journal of Ecology* 88: 1–13.
- Gryta, H., Debaud, J.-C., Effosse, A., Gay, G. & Marmeisse, R. 1997. Fine spatial structure of populations of the ectomycorrhizal fungus *Hebeloma cylindrosporum* in costal sand dune forest ecosystems. *Molecular Ecology* 6: 353–364.
- , Debaud, J.-C., & Marmeisse, R. 2000. Population dynamics of the symbiotic mushroom *Hebeloma cylindrosporum*: mycelia persistence and inbreeding. *Heredity* 84: 294–302.
- Hallingbäck, T. & Aronsson, G. (eds.). 1998. Macrofungi and myxomycetes of Sweden and their ecology. The Swedish Threatened Species Unit, Uppsala, 2nd revised and extended printing. The database is available at www.dha.slu.se.
- Harvey, A.E., Jurgensen, M.F. & Larsen, M.J. 1980a. Clearcut harvesting and ectomycorrhizae: survival of activity on residual roots and influence on a bordering forest stand in western Montana. *Canadian Journal of Forest Research* 10: 300–303.
- , Larsen, M.J. & Jurgensen, M.F. 1980b. Partial cut harvesting and ectomycorrhizae: early effects of fire in Douglas-fir-larch forests of western Montana. *Journal of Forest research* 10: 436–440.
- Hintikka, V. & Näykki, O. 1967. Notes on the effects of the fungus *Hydnellum ferrugineum* (Fr.) Karst. on forest soil and vegetation. *Communicationes Instituti Forestales Fenniae* 62. 23 p.
- Holm, C. 1995. Succession and spatial distribution of post-fire fungi in a southern boreal coniferous forest in Norway. M.Sc. thesis. University of Oslo, Norway.
- Hörnberg, G., Zackrisson, O., Segerström, U., Svensson, B.W., Ohlson, M. & Bradshaw, R.H.W. 1998. Boreal swamp forests – biodiversity “hotspots” in an impoverished forest landscape. *Bioscience* 48: 795–802.
- Horton, T.R. & Bruns, T.D. 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. *Molecular Ecology* 10: 1855–1871.
- , Cazares, E. & Bruns, T.D. 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.
- Hutchison, L.J. 1989. Absence of conidia as a morphological character in ectomycorrhizal fungi. *Myco-*logia 81: 587–594.
- Jalaluddin, M. 1967. Studies on *Rhizina undulata*. I. Mycelial growth and ascospore germination. *Transactions of the British Mycological Society* 50: 449–459.
- Johannesson, H. & Dahlberg, A. 2001. Färsk brandfält ett måste för brandskikttdyan och över 80 andra arter. *Fakta Skog* 2.
- , Vasiliauskas, R., Dahlberg, A., Penttila, R. & Stenlid, J. 2001. Genetic differentiation in Eurasian populations of the post-fire ascomycete *Daldinia loculata*. *Molecular Ecology* 10: 1665–1677.
- Johnson, E. 1992. Fire and vegetation dynamics. Cambridge University Press, Cambridge.
- Jonsson, L., Dahlberg, A., Nilsson, M-C., Zackrisson, O. & Kårén, O. 1999a. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests and composition following wildfire. *Molecular Ecology* 8: 205–217.
- , Dahlberg, A., Nilsson, M-C., Kårén, O., & Zackrisson, O., 1999b. Continuity of ectomycorrhizal fungi in self-regenerating boreal forests of *Pinus sylvestris*: comparative analysis of diversity of mycobionts of seedlings and old trees. *New Phytologist* 142: 151–162.
- , Dahlberg, A. & Brandrud, T-E. 2000. Spatio-temporal distribution of an ectomycorrhizal community in an oligotrophic Swedish *Picea abies* forest subjected to experimental nitrogen addition: above- and below-ground views. *Forest Ecology and Management* 132: 143–156.
- Kalela, E.K. 1949. Männikön ja kuusikon juurisuhdistusta I. (Summary in English: On the horizontal roots in pine and spruce stands I.) *Acta Forestalia Fennica* 57.
- Kölgalg, U., Dahlberg, A., Taylor, A., Larsson, E., Halberg, N., Stenlid, J., Larsson, K.-H., Fransson, P., Kårén, O. & Jonsson, L. 2001. Diversity and abundance of tomentelloid fungi in Swedish boreal forests. *Molecular Ecology* 9: 1985–1996.
- Linder, P., Jonsson, P. & Niklasson, M. 1999. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. *Silva Fennica* 32: 339–349.
- Mah, K., Tackaberry, L.E., Egger, K.B. & Massicotte, H.B. 2001. The impacts of broadcast burning after clear-cutting on the diversity of ectomycorrhizal fungi associated with hybrid spruce seedlings in central British Columbia. *Canadian Journal of Forest Research* 31: 224–235.

- Melin, E. 1927. Studier över barrträdsplantans utveckling i råhumus. Meddelande från Statens Skogs-forsoksanstalt 23: 433–486.
- Mikola, P., Hahl, J. & Torniaisen, E. 1966. Vertical distribution of mycorrhizae in pine forests with spruce undergrowth. *Annales botanici Fennici* 3: 406–409.
- , Laiho, O., Erikäinen, J. & Kuvaja, K. 1964. The effect of slash burning on the commencement of mycorrhizal association. *Acta Forestalia Fennica* 77: 3–13.
- Molina, R., Massicotte, H. & Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbioses: Community-ecological consequences and practical implications. In: Routledge, A.M.F. (ed.). Mycorrhizal functioning, An integrative plant-fungal process. Chapman & Hall, Inc. New York. p. 357–423.
- Moser, M. 1949. Untersuchungen über den Einfluss von Waldbränden auf die Pilzvegetation. I. *Sydowia* 3: 336–383.
- Niklasson, M. 1998. Dendroecological studies in forest and fire history. PhD-thesis. Acta Universitas Agriculturae Sueciae, Silvestria 52, Swedish University of Agricultural Sciences, Umeå, Sweden.
- Ohenoja, E. 1993. Effects of weather conditions on the larger fungi in different forest sites in northern Finland 1976–1988. PhD thesis. Scientiae Rerum Naturalium 243. University of Oulu. Finland.
- Östlund, L., Zachrisson, O. & Axelsson, A.L. 1997. The history and transformation of a Scandinavian boreal forest landscape since 19th century. *Canadian Journal of Forest Research*. 27: 1198–1206.
- Palmer, J.G., Miller Jr, O.K. & Gruhn, C. 1994. Fruiting of ectomycorrhizal basidiomycetes on unburned and prescribed burned hard-pine/hardwood plots after drought-breaking rainfalls on the Allegheny Mountains of southwestern Virginia. *Mycorrhiza* 4: 93–104.
- Penttilä, R. & Kotoranta, H. 1996. Short-term effects of prescribed burning on wood-rotting fungi. *Silvia Fennica* 30: 399–419.
- Perry, D.A., Molina, R. & Amaranthus, M.P. 1987. Mycorrhizae, mycorrhizospheres and reforestation: current knowledge and research needs. *Canadian Journal of Forest Research* 17: 929–940.
- Persson, H. 1983. The distribution and productivity of fine roots in boreal forests. *Plant and Soil* 71: 87–101.
- Petersen, P.M. 1970. Danish fireplace fungi, an ecological investigation of fungi on burns. *Dansk Botanisk Arkiv* 27: 6–97.
- 1971. The macromycetes in a burnt forest area in Denmark. *Botanisk Tidskrift* 66: 228–248.
- Pietikainen, J., Kiikka, O. & Fritze, H. 2000. Charcoal as a habitat for microbes and its effect on the microbial community of the underlying humus. *Oikos* 89: 231–242.
- Pilz, D.P. & Perry, D.A. 1984. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. *Journal of Forest Research* 14: 94–100.
- Rahko, T. 1997. Macrofungal succession after wildfire and after clear cutting and prescribed burning in eastern Finland 1994–1996. M. Sc. thesis. Department of Biology, University of Oulu, Finland.
- Redecker, D., Szaro, T.M., Bowman, R.J. & Bruns, T.D. 2001. Small genets of *Lactarius xantogalactus*, *Russula cremoricolor* and *Amanita franchetii* in late stage ectomycorrhizal successions. *Molecular Ecology* 10: 1025–1034.
- Schimmel, J. & Granström, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77: 1436–1450.
- & Granström, A. 1997. Fuel succession and fire behaviour in the Swedish boreal forest. *Canadian Journal of Forest Research* 27: 1207–1216.
- Smith, S.E. & Read, D.J. 1997. Mycorrhizal symbiosis, 2nd edition. Academic Press, London.
- Stendell, E.R., Horton, T.R. & Bruns, T.D. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. *Mycological Research* 103: 1353–1359.
- Taylor, D.L. & Bruns, T.D. 1999. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. *Molecular Ecology* 8: 1837–1850.
- Torres, P. & Honrubia, M. 1997. Changes and effects of natural fire on ectomycorrhizal inoculum potential of soil in a *Pinus halepensis* forest. *Forest Ecology and Management* 96: 189–196.
- Uggla, E. 1958. Skogsbrandfält i Muddus nationalpark. *Acta Phytogeografica Suecia* 41: 1–116.
- Van Wagner, C.E. 1983. Fire behavior in northern conifer forests and shrublands. In: Wein, R.W. & MacLean, D.A. (eds.). The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York. p. 65–80.

- Visser, S. 1995. Ectomycorrhizal succession in jack pine stands following wildfire. *New Phytologist* 129: 389–401.
- Vrålstad, T., Holst-Jensen, A. & Schumacher, T. 1998. The post-fire discomycete *Geopyxis carbonaria* (Ascomycota) is a biotrophic root associate with Norway spruce (*Picea abies*) in nature. *Molecular Ecology* 7: 609–616.
- Wardle, D.A., Nilsson, M-C., Gallet, C. & Zackrisson, O. 1998 An ecosystem-level perspective of allelopathy. *Biological Reviews of the Cambridge Philosophical Society* 73: 355–319.
- Wicklow-Howard, M. 1989. The occurrence of vesicular-arbuscular mycorrhizae in burned areas of the Snake River Birds of Prey area, Idaho. *Mycotaxon* 34: 253–257.
- , Zackrisson, O., Hörnberg, G. & Gallet, C. 1997. The influence of island area on ecosystem properties. *Science* 277: 1296–1299.
- Zackrisson, O. 1977. Influence of forest fires on the northern Swedish boreal forests. *Oikos* 29: 33–32.
- , Nilsson, M-C. & Wardle, D.A. 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos* 77: 10–19.
- , Nilsson, M-C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in non-pyrogenic boreal Scots pine stands. *Journal of Ecology* 83: 469–483.

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