The Effect of Disturbances on the Belowground System in the Black Spruce Boreal Forest:

Ectomycorrhizal Community, Nutrient Availability and Decomposition Rates

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Abstract

The Effect of Disturbances on the Belowground System in the Black Spruce Boreal Forest: Ectomycorrhizal Community, Nutrient Availability and Decomposition Rates

Disturbances are integral to the structure and functioning of the boreal forest. However their effects upon the underground components in this ecosystem are still largely unknown. In this thesis, I describe the ectomycorrhizal and understory plant communities in the black spruce boreal forest of the Abitibi region, Québec, and discuss the effects that both forest fires and logging have on the ectomycorrhizal community, nutrient supply rates and decomposition rates. The ectomycorrhizal community from black spruce, characterized by morphotyping and molecular techniques was dominated by *Cenococcum geophilum* and three *Piloderma* species. The plant community was made up of a mosaic of vegetation patches, which are described in this thesis, as either *Sphagnum* dominated plots, which associated with *Sphagnum, Gaultheria hispidula* and *Picea mariana*; or ericoid/lichen dominated plots, which associated with lichen and *Vaccinium angustifolium*. Statistical analysis revealed that the effect of the disturbances was largely insignificant to the ectomycorrhizal community, nutrient supply and decomposition rates, and most differences were between transects. However, both the understory plant community plot types and abundance of individual plant species were found to have significant correlations with the most abundant ectomycorrhizal species. This suggests that if we want to know how the ectomycorrhizal community will be affected by disturbances, we should look at changes in the plant community due to disturbances.

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Chapter 1: General Introduction

Disturbances create edges whose structure and composition will have an effect on belowground species diversity, soil conditions and decomposition (Hagerman et al. 1999a; Harper and MacDonald 2001; Kernaghan et al. 2003). Although the ectomycorrhizae of black spruce has been documented (Dahlberg 2001; Robertson et al. 2006) and nutrient supply and decomposition process are known, this study incorporates how different disturbances (fire and logging) within the same area affect the structure and function of these belowground components in the black spruce boreal forest ecosystem. Lack of existing knowledge in regards to underground components prevents the establishment of good industry practices (Lazaruk et al. 2005) and if ecosystem function is to be maintained over time, boreal forest management practices need to draw upon the available evidence in regards to ecosystem processes (Heaussler et al. 2002).

Ectomycorrhizae (EM) are a vital part of the underground system; they are plant root/fungus mutualisms in which the plant provides carbon to the fungus and the fungal partner provides key nutrients to the plant. Ectomycorrhizal fungi are obligate symbionts that form a fungal sheath over the fine root surface and form a Hartig net of fungal hyphae that grow between the cells of the root cortex. The latter is the site of nutrient and carbon exchange between fungus and plant (Smith and Read 1997). Estimates suggest there are 5000 species of EM fungi worldwide (Molina et al. 1992) and that 90% of land plants from 30 families participate in mycorrhizal associations. EM are primarily found in cool temperate and some tropical ecosystems (Hibbet et al. 2000). Most plants that form EM can have multiple fungal partners, although the *Russulaceae* and *Thelephoraceae* (eg. *Tomentella* sp.) and non-Thelephoroid resupinates are the most abundant taxa. Resupinate fungi are the crust fungi from families such as the *Corticiaceae* and form flat fruiting bodies that are fused to and face the substrate, usually decaying wood. EM are largely generalists, in that they can survive in a range of environmental conditions and often form associations with many different plant species. Most EM communities have high diversity and are patchily distributed at a fine scale (Horton and Bruns 2001).

While the importance of ectomycorrhizae for nutrient cycling and tree health has been well established (Smith and Read 1997), the ectomycorrhizal community in the boreal forest is still not well documented. A number of published studies exist that document EM communities in conifer dominated and mixed wood boreal systems. Bradbury et al. (1998), found that *Piloderma sp.*, *Cenococcum geophilum*, *Russula*-like and *Sullius* sp. were the most abundant groups of EM in a lodge-pole pine forest in Alberta. Dahlberg (2001) found that in 27 studies from the boreal forests of Sweden and Canada, *Cenococcum, Corticeaceae* and MRA/E strain EM all showed the greatest dominance. Jonsson et al. (1999) found that some of the most frequently occurring species were *Cenococcum geophilum, Suillus variegatus, Cortinarius* sp.*, and Phialocephala fortinii,* in a boreal Scots pine forest in Sweden. Lazaruk et al. (2005) examined 4431 root tips from mixed boreal woods in Northern Alberta and found 19 distinct morphotypes, the 7 most frequently occurring being: *Tomentella* spp., *Cortinarius* spp., *Amphinema byssoides, Lactarius* spp., E-strain, *Wilcoxina* spp., and *Hebeloma* spp.. Robertson et al. (2006) identified 27 morphotypes on 8858 root tips from a black spruce forest in British Columbia, with the most abundant being *Cenococcum, Lactarius, Amphinema,* and *Thelephoraceae* in wetlands and *Cenococcum,* *Corintarius, Russulaceae* and *Amphinema* in upland sites. Ectomycorrhizal communities have been shown to change along disturbance gradients (Visser 1995; Kranabetter and Wylie 1998), but little work has been done to compare these communities in both fire and logged areas at the same site. Additionally, nutrient cycles and decomposition in the boreal forest are affected by disturbances, including fires and logging (Bhatti et al. 2002). The burning of the soil organic layer and woody debris in forest fires, or removal during logging, greatly affect the availability of key limiting nutrients such as nitrogen. Disturbances normally initially increase the boreal forest's slow decomposition rates, through changes in soil nutrients, microbial activity, plant composition or changes in canopy cover. Burton defines the edge effect as “the influence exerted by a stand or forest cover polygon on the ecological processes and attributes of an adjacent stand or polygon,” and states that “they represent an interface between ecosystem ecology and landscape ecology” (Burton 2002). Edge effects usually consist of greater canopy openness, irradiance and wind conditions when compared to the intact forest and these result in a disturbance of ecosystem conditions and processes such as soil temperature and humidity, tree growth rates, understory plant composition, propagule dispersal and decomposition processes (Burton 2002, Chen et al. 1995). However, our knowledge of edge patterns in belowground systems is limited, and, given the important feedbacks between above and belowground systems, it is hoped that a study of the key soil dynamics will provide a more comprehensive understanding of edge effects as a whole.

An increased interest in sustainable forestry practices has led to more research into emulating natural disturbance. It is important to recognize both the important contribution and the confines of this approach (Bergeron et al. 2002). Natural variation in fire cycles creates unique structure and composition in the boreal forest and forestry practice tends to reduce this variability through even aged stand management.

Fire is one of the most important natural disturbances in the boreal forest, and follows a complex regime. Boreal forest fires are generally large and intense, although often different areas within the fire's range will experience different levels of impact, varying from severe to low. This shapes the forest at both landscape and regional levels (Bergeron et al. 2002).

Plants and animals living in the boreal forest have many adaptations to fire, since it is an integral part of the forest ecology. Ectomycorrhizae have been shown to have a pattern of succession after fire, especially where the fires are of high intensity (Dahlberg 2002; Visser 1995). Where fires are of lower intensity and size there was more continuity in the EM community, however, evenness was found to be lower (Jonsson et al. 1999).

In the case of logged sites, the regeneration of the EM community varies considerably between studies. Jones et al. (2003) found that generally, studies considering the effects of logging on EM show that species composition changes but not percent colonization. In cut blocks of different sizes, closeness to intact forest showed more of an effect than cut block size (Hagerman et al. 1999a). In mixed boreal forest, there was no increased colonization in gaps vs. cuts for birch EM, in selective cuts there was no effect on the birch EM community and the types of EM fungi colonizing the roots of birch seedlings from gaps did not differ from those in the intact forest (DeBellis et al. 2002). In a study in the boreal forest it was found that there were a reduced number of EM types in both fires and cuts when compared to the intact forest (Lazaruk et al. 2005).

Disturbances can cause changes in nutrient availability, whose characteristics can vary depending on the cause of the disturbance. Major causes of nutrient loss after a disturbance include biomass loss, leaching, combustion and erosion. When fire is the cause of nutrient loss, its intensity may also play an important role. High intensity fires may volitalize important nutrients such as N, S and P, while low intensity fires may actually cause nutrients to be released and increase the rate of regrowth (Bhatti et al. 2002).

In the case of logged sites, physical changes in the soil can cause nutrient loss through leaching (Ballard 2000). Additionally, it is common that all woody debris will be removed from a logged site, resulting in a large loss of carbon, one of the inputs for dead organic matter (DOM), typically much more than the carbon loss due to combustion in fire (Bhatti et al. 2002).

The understory plant community can greatly affect the below ground system, and mycorrhizal diversity has been shown to affect plant diversity (van der Heijden et al. 1998). This relationship is noticeable after a disturbance when the succession of plants may be reflected by a succession of ectomycorrhizae. It is also possible that certain pioneer plants may either inhibit or encourage the establishment of EM. Some understory plants of the family Ericaceae are thought to act as refuge species by forming EM and therefore a source of inoculum for colonization (Hagerman et al. 1999a; Dahlberg 2001). The importance of companion plants may affect the ability of EM to colonize neighbouring plants and the proportion of EM that develop (Massicotte et al. 1999).

EM have also been shown to have a mechanism which can control interactions in higher plants by changing rhizosphere chemistry (Zeng and Mallik 2006). The understory plants can help retain or rebuild the physical structure of the soil, which has an affect on nutrient pools, leaching and run off. They can also create nutrients by nitrogen fixation and add to DOM by dropping leaves, dead roots and woody material.

Increasingly, anthropogenic influences such as logging are putting pressure on the boreal forest, and are potentially affecting its long-term health. Natural disturbances, such as fire, are vital events in the boreal forest and shape it at the regional, landscape and site level. The Canadian government has specified that mitigating climate change through sustainable forest practices is a key focus in their climate change strategy (Natural Resources Canada, 2008), and the boreal biomes are an important part of Canadian forestry. The relationship between the aboveground and belowground systems means that a greater understanding of key underground components will make the links between ecosystem processes and function clearer (Dalhberg 2001), and provide us with more tools for successfully managing the boreal forest.

This study, therefore, examines natural and anthropogenic disturbances, specifically fires and logging, to compare their effects on belowground processes in the boreal black spruce forest of the Abitibi region. The study is designed to identify relationships between the ectomycorrhizal community, the type of understory plant cover, soil nutrient supply rates and rates of decomposition along 6 transects (3 in burned and 3 in logged sites) and to determine whether any effects of either of the disturbances occurs in relation to these factors, and, if so, how it is manifested.

It is hypothesized that 1) the ectomycorrhizal community will be more diverse and abundant away from the disturbance; 2) a difference in ectomycorrhizal diversity and abundance will be detected between cut sites and burn sites; 3) nutrient supply rates will be decreased in the disturbances and differences between disturbance types will be detected; 4) decomposition rates will be increased in the disturbances and differences between logged and burned sites will be detected; 5) plant cover type/plot type will affect nutrient supply rates, decomposition rates and abundances of specific ectomycorrhizal species.

In this thesis, Chapter 2 will describe the transects and characterize the ectomycorrhizal community and the understory plant community composition in the plots along these transects. Chapter 3 will discuss the influence of the two types of disturbances, forest fires and logging, on the ectomycorrhizal community, soil nutrient supply rates and decomposition rates. Chapter 4 will discuss the relationships between the understory vegetation and the disturbances and the effects of the plant community on nutrient supply rates, ectomycorrhizal abundance and decomposition rates. This chapter will focus on the important role of the vegetation in mediating the other underground components in the study site. The general conclusions will summarize the important findings of this study.

Chapter 2: The Ectomycorrhizal Community and the Understory Plant Community in the Boreal Black Spruce Forest of Abitibi Region, Québec.

Introduction

The boreal forest is the dominant forest of Canada, accounting for 77% of all forests and occupying 35% of the total Canadian land area, bordered by tundra and grassland to the north and mixed hardwood forests to the south. The climate of the boreal forest is characterised by long, extremely cold, dry winters and short, cool, moist summers, with low annual mean temperatures often below freezing, and a short frost free period between 50 and 100 days. Despite its severe climate and because of the large area it covers, the boreal forest accounts for a large amount of standing biomass (Statistics from Natural Resources Canada, 2008).

The boreal forest contains a large amount of water in its bogs, marshes, fens, rivers and lakes. A typical boreal bog is the muskeg, which forms when water collects in a depression with poor drainage over which a layer of *Sphagnum* moss forms. The *Sphagnum*'s high absorbency allows even more water to be retained, which greatly limits which other species can grow in the muskeg. Black spruce will typically grow on the edges of the muskeg and often spread by layering.

Coniferous trees typically dominate the canopy in the boreal forest of the Abitibi region, although zones of mixed and broadleaf trees and shrubs are also found. The understory vegetation is dominated by ericaceous plants, which thrive in acidic soils. Ferns and grasses can be found on the forest floor, especially in warmer mixed woods. Herbs, mosses and lichens commonly grow on the ground and other substrates close to the ground level.

The boreal forest has a distinct mosaic pattern of stands of trees differing in age and size. This is a result of both natural disturbances, such as forest fires, insect outbreaks, and windthrow and anthropogenic disturbances, primarily logging. The boreal forest is a forest ecosystem adapted to regular disturbances, and gaps with edges are a common characteristic of the canopy, which in turn will affect the understory community (Haeussler et al. 2002).

The boreal forest also has a wealth of fungal species; all with large underground networks of mycelium and some that fruit routinely, forming obvious sporocarps. Many of these fungal species form mycorrhizal associations with numerous plants in this biome. Deciduous and coniferous trees, shrubs, herbs, ericaceous plants and grasses all form various mycorrhizal relationships. The types of mycorrhizae formed depend on the plant and fungal species involved and the physical structure of the mutualism. All tree species in the boreal forest form mycorrhizae, and the families *Betulaceae, Pinaceae* and *Fagaceae* form obligate ectomycorrhizal (EM) relationships with many common fungal species. Studies of EM show that, in boreal forests, the *Corticiaceae, Cenococcum*, *Russulales*, and *Thelephoraceae* are the most common fungal partners (Dahlberg 2001). As with all classified groups of organisms, a few EM species are found frequently and abundantly and the large remainder are considered to be rare (Jonsson et al. 1999; Dahlberg 2001). In shaping EM communities, spatial variation is considered to be a more important factor than temporal variation and many species form clumped distributions (Gardes and Bruns 1996; Kranabetter and Wylie 1998). Even in forests dominated by a single tree species, the diversity of EM is high with 20 to 35 species normally identified in these circumstances (Bruns 1995). The regional diversity of EM is determined largely by the plant species present and other edaphic factors (Dahlberg 2001), and local diversity is shaped by resource partitioning, disturbance, competition and interactions with other organisms (Bruns 1995).

As there is relatively little information available on the ectomycorrhizal communities of the boreal black spruce forests of eastern North America, this chapter describes the ectomycorrhizal fungal community of the roots of black spruce as determined by morphological and molecular techniques. The plant community found within our two distinct plot types is also described, as all data were extracted from these plots and subsequent chapters discuss the important role of the plant community on the underground components of this forest system.

Existing studies, largely from Canada and Sweden, show that the EM fungal symbions in boreal forests are normally diverse and commonly composed of *Piloderma sp., Cenococcum geophilum, Russula*-like, *Suillus* spp., *Corticeaceae*, MRA/E strain *Phialocephala fortinii, Tomentella* spp., *Lactarius* spp*., Wilcoxina spp., Hebeloma* spp., *Amphinema* and members of the *Thelephoraceae*. It is expected that this study will yield some of the species commonly occurring in other boreal forest systems but that unique aspects of this assemblage will be also be found, given the different geographical location, local climate conditions and plant species composition.

Materials and Methods

Site description. The sites for this study were located in Hébécourt Township (79ºW, 48ºN) in the boreal forest of Abitibi region of north western Québec. The coniferous forest is dominated by Black Spruce (*Picea mariana*) (Miller) (BSP) with Tamarack

(*Larix laricina*) (Du Roi) (Koch) and Balsam fir (*Abies balsamea*) L. (Miller) also present. The understory vegetation is composed largely of *Sphagnum*, lichens and ericaceous plants such as Leather leaf (*Cassandra calyculata* (L.) D. Don.), Labrador tea (*Ledum groenlandicum* Retzius) and Blueberry (*Vaccinium* sp.). The climate of the boreal forest is characterised by long, extremely cold, dry winters and short, cool, moist summers. The weather station closest to the site is in La Sarre, Hébécourt Township, with an annual mean temperature of 0.6 ºC, and a low total annual precipitation of 822.7mm, which occurs largely during the summer. There are about 64 frost-free days per annum (Dansereau and Bergeron 1993, from Environment Canada 1982). The black spruce bog is characterized as having acidic soils, a long cold season and poor drainage. The dominant tree species and general tree cover at the site indicates peaty Gleysols and organic soils (Fibrisols) typical of this area of the Boreal forest (Clayton et al. 1977). A more detailed description of the site can be found in Harper et al. (2004).

Transects were created in sites where either logging or forest fires had occurred (see Sampling design below). The fire transects were between 6 to 7 years since the disturbance and the logged sites were between 5 to 6 years since the disturbance. Harvesting was carried out by “careful logging”, meaning all harvested trees were larger than 9 cm diameter at breast height (DBH) and advanced regenerating soils were protected by using machinery in parallel trails that cover no more than 30% of the area harvested (Harvey and Brais 2000; Harper et al. 2004). Burned areas are normally partially or completely salvage cut where possible, however the transects used in this study were not salvage cut (Harper et al. 2004).

Sampling Design. Six transects across disturbance edges were created (Harper et al. 2004), three at natural burn sites (F1, F2, F3) and three at logged sites (C1, C2, C3). The specific locations of the transects are: F1 and F2 (78ºW, 49ºN), F3 (79ºW, 49ºN), C4, C5 and C6 are all located at (79ºW, 49ºN). Transects from Harper et al. (2004) correspond to this study as follows; fire transect A is F1, B is F2, and H is F3; and cut transect 1 is C1, 4 is C2 and 3 is C3. The transects started 10 m inside the disturbance and extend 200 meters into the intact forest from the edge of the disturbance. Twenty 1 m^2 plots were created along each transect at ten locations, -10m, -5m, 0m, 5m, 10m, 15m, 25m, 50m, 100m, and 200m.

At each location on the transects, two plots were created within 5m of and perpendicular to the transect line, for a total of 120 plots across all six transects. Including all six transects, the total number of plots was 120. The plot types were chosen deliberately at each location along the transect for dominance of either *Sphagnum* or ericoid/lichen vegetation types, to determine whether differences in vegetation had an effect on the other variables in this study. This means that the dominant vegetation in plots will vary considerably over the entire number of plots along all 6 transects.

Percent Cover of Understory Plant Community. Percent plant cover was recorded to characterize the understory plant community within the plots. A digital photograph was taken of each plot to record the plant species and their percent cover in the plot using a Nikon Coolpix 5700 digital camera. Percent cover of a plant species was estimated, based on the approximate area it covered in the plot.

Soil Sampling and Morphological Analysis of Ectomycorrhizae (EM). Soil samples were taken from each plot to characterize the EM community on black spruce roots. Soil samples were collected in September 2003 by taking soil cores measuring 5cm in diameter and between 10-20 cm deep. A sample was collected from each of the 120 plots. Soil samples were stored in resealable plastic bags and transported in coolers before being permanently stored in a walk-in fridge at 2-4° C for no longer than 9 months. Soil samples for plots that did not yield any viable roots for morphotyping were re-sampled in the fall of 2004. Twenty four new soil cores were taken, with more than 80% of those being in the disturbances or at the edge.

Fine spruce roots were separated from the soil using sieves of 38-850 micron mesh openings from Combustion Engineering Canada Inc., St. Catherines, Ontario. In samples from *Sphagnum* plots, fine roots were separated with tweezers. Root sections were cut into small pieces (~ 2cm) and placed on INTEGRID gridded Petri dishes (Beckton Dickson Labware, Lincoln Park, NJ). Numbered squares were randomly selected for root tips until 100 colonized tips were located from each soil core, and these 100 tips were then morphotyped. This was repeated for each of the 120 soil samples and the 24 new samples the following year. Some of the soil samples did not contain live roots or enough live roots for 100 tips, and therefore morphotyping was either partially complete or was not possible in these soil cores. To determine whether a root tip was colonized, a Wild Heerbrugg M5 dissecting microscope (128-800 X magnification) was used.

EM were then placed into morphotype groups depending on gross morphological characteristics such as colour, tip shape, branching pattern and presence or absence of hyphae, (Agerer 1987-1998; Ingleby et al. 1990; Goodman et al. 1996) using a Wild Heerbrugg M5 dissecting microscope. Stains were used to help group EM into types if considered necessary. Stains used were: Melzer's solution (to stain the ornamentations of *Lactarius* and *Russula*), Sulphovanillin (to stain cystidia of certain *Russula* spp. grey/purple and some *Cortinarius* spp. bright pink) and KOH 15 % (Agerer 1987-1998). Morphotype groups were further categorized by examining mantle peels or squashed tips using bright field microscopy with a Nikon Optiphot compound microscope at 200, 400 and 1000 X magnification. Morphotypes were described using characteristics such as mantle pattern, hyphae and other characteristics (Agerer 1987-1998; Ingleby et al. 1990; Goodman et al. 1996). Photographs were taken of the gross morphological and cellular characteristics of each morphotype with a Nikon Optiphot compound microscope camera.

Where quantity allowed, sub samples of each morphotype from each soil sample were placed in 1.5 ml ependorf tubes on ice and lyophilised in a Speed Vac Plus, SC 110, Savant. These samples were stored and used for molecular analysis.

EM Diversity, Abundance and Frequency of Occurrence. EM diversity was measured in each transect using the Simpson's Diversity Index (Simpson 1949) to determine whether any differences between disturbance types existed. A simple T-test assuming equal variances (Microsoft Excel) was performed to determine whether any differences existed between cuts and burns in regards to morphotype diversity. Abundance (percent colonization) and frequency of occurrence of each morphotype was calculated as a total over all the 6 six transects as a measure of overall abundance and also for both disturbance types.

Molecular Analysis of Ectomycorrhizae (EM). Molecular analysis was performed to further clarify the EM community by determining the species of EM present in this forest and for the purposes discussed above in the Morphological Analysis section. The 8 most abundant morphotypes were chosen for molecular analysis as this would account for 91% of percent of all colonized root tips. Additionally the more rare morphotypes would have few stored root tips with which to perform molecular analysis.

DNA was extracted from each of the 8 most abundant EM morphotypes using a Dneasy^{R} Plant Mini Kit from Qiagen^{R} (DNeasy^{R} Plant Mini Kit handbook, 2001.). The mycorrhizal root tip was ground with liquid nitrogen with a mortar and pestle. The ground tissue was immediately transferred to a supplied tube with supplied buffer and Rnase solution then added and mixed in a vortex mixer at 8000 rpm. The mixture was then incubated for at 1hr at 65 °C and mixed 2-3 times during incubation. Then 130 µl of supplied buffer were added to the lysate, mixed and incubated on ice for 5 minutes. The lysate was then added to a supplied spin column (QIAshredder) with a 2 ml collection tube and centrifuged for 2 m at 13, 000 rpm. The flow-through was transferred to a new tube without disturbing the debris pellet that had formed. Then 1.5 volumes of the supplied buffer were added to the lysate and mixed with a pipette in the fume hood. Six hundred and fifty µl of the lysate solution were then added to a supplied Dneasy mini spin column with a 2 ml collection tube and centrifuged for 1 minute at 8000rpm and the flow-through discarded along with the collection tube. The last step was repeated with any remaining sample not used from the 1.5 volumes addition. The Dneasy column was placed in a new 2 ml collection tube and 500 µl of supplied buffer added to the column and centrifuged for 1 minute at 8000rpm. The flow-through was discarded and the collection tube was kept. Another 500 µl of supplied buffer were added to the column and centrifuged for 2 minutes at 13000 rpm to dry the membrane. The column was then transferred to a new 2ml collection tube and 100 µl of preheated (65 °C) supplied buffer was pipetted onto the membrane, incubated for 5 minutes at room temperature and centrifuged again for 1 minute at 8000rpm. The previous elution step was repeated. The DNA eluate was stored in the -80 freezer for PCR, cloning and sequencing.

The ITS region of ribosomal DNA was amplified using the Polymerase Chain Reaction (PCR) method with the fungal specific primer ITS1-F (5'CTTGGTCATTTAGAGGAAGTAA 3') (Gardes and Bruns 1993) and the universal primer ITS4 (5'TCCTCCGCTTATTGATATGC 3') (White et al. 1990). Stored DNA was re-suspended in micropure/autoclaved water in different dilutions (1:5, 1:10, 1:20. 1:100 and 1:1000); normally the 1:100 gave the best results. The PCR mixture was made up of 25.5 µl water, 1 µl dNTP's, 5 µl CB Buffer, 4µl of MgCl, 0.5 µl of Taq DNA polymerase and 2.5 µl of two primers, ITS 4 and ITS 1F. Five µl of template were added to make a 50 µl reaction solution. Fischer pipettes were used under sterile conditions for the procedure. The PCR was completed with thermal parameters similar to those cited in Gardes and Bruns (1993) (De Bellis et al. 2006).

Extracted DNA was run on a 2% agarose gel with ethidium bromide to determine if DNA was present and the size (number of base pairs) of the product. Fermentas GeneRuler^{TM} 100bp DNA Ladder Plus was used in the PCR product gels to determine the size of the fragment. PCR product was stored at –20°C for purification and cloning.

A QIAquick^{R} PCR Purification Kit (using the microcentrifuge method) from Qiagen^{R} was also used to purify PCR product for cloning (QIAquick^{R} Spin Handbook, 2002-2006). In some cases a gel extraction (PCR product was run on a gel and cut out and re-suspended) was used prior to purification to isolate a fragment of DNA of a specific size.

Purified PCR product was then cloned for RFLP analysis and sequencing. DNA was cloned into a vector using the pGEM-T Easy Kit^{R} from Promega^{TM}. The solutions and methods from the pGEM^{R}-T Easy Vector Systems Kit (handbook at www.Promega.com) were used for the cloning procedure. Successfully cloned colonies were then picked and 2ml of liquid LB media were inoculated. The solution was incubated overnight at 37° C at 250 RPM. One µl of the culture broth was added to 50 µl of reaction mixture for PCR procedure. PCR was performed using the same equipment and program as above. The product was run on a 2% agarose gel with ethidium bromide and the Fermentas GeneRuler^{TM} 100bp DNA Ladder Plus to show the size of the product. Ten clones from each morphotype were chosen randomly to perform a restriction fragment length polymorphism (RFLP) analysis.

RFLP and Sequencing. RFLP analysis shows genotypic variation between clones within a morphotype. The PCR product from 10 successful clones of each morphotype was added in a reaction mixture in order to run RFLP gels. Nine point five µl purified/autoclaved water, 1.5 µl buffer, 0.2 µl BSA and 0.5 µl restriction enzymes; Nde, Hinf, or Taq (Promega Inc., Madison WI) were mixed with 10 µl PCR product (ratio could increase for larger gels) and gels were run on a 1% agarose with ethidium bromide and the Fermentas GeneRuler^{TM} 100bp DNA Ladder Plus to show restriction length polymorphisms in each morphotype selected. Only the 8 most abundant morphotypes were chosen for RFLP analysis. *Cenococcum geophilum* was not used for RFLP analysis due to difficulties with the extraction process, even after pooling samples. Sclerotia (a compact mass of mycelium) of *C. geophilum* were used to represent this morphotype for the purposes of RFLP and sequencing. The morphotypes used were Yellow *Piloderma*-like, Striated, Green, *Russula*-like, White wefts, Yellow wefts, Sclerotia of *C. geophilum* and Orange Fan. Genome Québec, Montréal, Canada then sequenced each unique RFLP type from each morphotype**.** To identify the fungal species producing the RFLP types, sequences obtained from the clones were aligned using nucleotide-nucleotide BLAST (blastn) in Genbank to establish similar EM fungal sequences.

Results

Plant Community Characterization. Within the plots, the tree canopy was almost solely *Picea mariana* (Miller) (BSP) (Black spruce), with *Abies balsamea* L. (Miller) (Balsam fir) occurring a few times only and no *Larix laricina* (Du Roi) Koch. (Tamarack). No broadleaf trees or large shrubs were recorded in our plots although *Alnus sp.* (Alder) was common in some of the disturbed areas and *Populus balsamifera* L. (Balsam poplar) was found on nearby roadsides. Ericaceous plants, which thrive in acidic soils, dominate the understory vegetation. The most common shrubs and herbs in our plots were *Vaccinium angustifolium* Ait. (Blueberry), *Cassandra calyculata* (L.) D. Don.) (Leather leaf), *Gaultheria hispidula* L. (T & G), (Snowberry), and *Ledum groenlandicum* Retzius, (Labrador Tea). Other herbs and shrubs were also present in the plots but occurred rarely and at less than 5% cover. These included *Cornus canadensis* L. (Bunchberry), *Equisetum sylvaticum* L. (Horsetail), *Rubus chamaemorus* L. (Cloudberry), *Petasites* *palmatus* (Aiton) Gray (Palmate Sweet Colt), Sedges and mosses other than *Sphagnum*. *Kalmia angustifolia* L. (Sheep laurel) and *Epilobium angustifolium* L. (Fireweed) were found commonly in the disturbed areas, but not recorded in our plots.

The two distinct plot types at our sites showed dominance of either *Sphagnum* moss or lichen/ericoid plants, as expected. Within the *Sphagnum* plots, the moss tended to show a consistent dominance in regards to percent cover, often sharing the space with one or more ericaceous plants, of which *Ledum groenlandicum* was the most commonly occurring. Lichen/ericoid plots tended to be more even and share dominance with two or three plants, often *Sphagnum*, *L. groenlandicum* and lichens were the most commonly occurring. The *Sphagnum* plots tended to be much wetter, often with large amounts of standing water below and the lichen/ericoid plots tended to be on drier ground.

EM Community Characterization from Morphotyping. From the 120 soil cores taken, 111 contained live root tips from which morphotyping could be carried out. This included the 24 replacement soil cores taken to account for the lack of live roots from the initial samples. There were 7 cores from the burn transects that contained no live roots, all of them from the disturbance, with the exception of one core. There were 2 samples from the cut transects that contained no live roots, both from the disturbance in transect C3. From each of 111 soil cores containing live roots, 100 root tips were examined and 19 different morphotypes were identified. In total 10981 root tips were morphotyped, as some soil cores did not yield 100 live root tips.

Two distinct morphotypes dominated most of the samples, *Cenococcum*-like and Striated, accounting respectively for 42.8% and 24% of total tips examined. Six other morphotypes were found in relatively low abundance: Yellow *Piloderma*-like, *Russula*-like, Orange fan, Green, White wefts and Yellow wefts. The *Russula*-like morphotype was found frequently in soil cores (39.2%), but not in great abundance (4.1%). The remaining types occurred in very low abundance. The C*enococcum*-like, Striated and Yellow *Piloderma*-like morphotype frequencies of occurrence were 85%, 60% and 24.2% respectively. Table 1 contains complete details on EM morphotype abundances.

EM Morphotype Diversity. Diversity Indices showed similar trends between all transects (Table 2). No significant difference in morphotype diversity existed between logged and burned transects (t-test; p=0.12) in regards to morphotype diversity.

EM Community Characterization from Molecular Analysis. All successful extractions were considered for cloning and RFLP analysis and this represents 8 distinct morphotypes. PCR-RFLP results were used to evaluate intraspecific variation or genotypic variation within a morphotype. Table 3 shows the number of different genotypes in each morphotype, which varies from 4 types for the Sclerotia of *Cenococcum*-like and Yellow wefts to just 1 type for the Green morphotype, as well as the number of base pairs in the fragments.

Sequencing of the 8 morphotypes (23 genotypes; Table 4) confirms the presence of two dominant species/genera, *Cenococcum geophilum* from the *Cenococcum*-like morphotype and *Piloderma* (*Piloderma* sp. 1, *Piloderma* sp. 2, *Piloderma* sp. 3) from both the Striated and the Yellow *Piloderma*-like morphotype. The *Russula*-like morphotype, which occurred frequently in samples, although its abundance was moderate to low, was not successfully sequenced. Other species of low abundance identified through sequencing were *Hygrophorus roseobrunneus*, *Cortinarius cinnamomeus* and *Cortinarius* sp..

Table 1: Abundance of ectomycorrhizal morphotypes and percent colonization of root tips by each morphotype. The total number of root tips was 10981. The total number of root tips from burned transects was 5192 and from cut transects was 5789.

EM Morphotype	Abundance	Percent Colonization (Total)	Percent Colonization in all Plots in Burned Transects	Percent Colonization in all Plots in Cut Transects
Cenoccocum-like	4700	42.8	40	45.3
Striated	2641	24	27	21.4
Yellow *Piloderma*-like	778	7.1	9.7	4.7
Russula-like (FRB)	453	4.1	2.7	5.5
Orange Fan	422	3.8	3.5	4.2
Green	377	3.4	3.5	3.4
White Wefts	355	3.2	2.7	3.7
Yellow Wefts	260	2.4	2.2	2.5
White Verrucose	200	1.8	2.9	0.8
Small Cigar	153	1.4	1.5	1.3
Big Brown	114	1	0.8	1.3
Brown Clamp	90	0.8	0.5	1.1
Clear Bulb	90	0.8	0.2	1.4
White Clamp	89	0.8	0.4	1.2
Striated Clamp	82	0.75	0	1.1
Big Orange	72	0.7	0.7	1.3
Cort	40	0.4	0.8	0
White *Piloderma*-like	38	0.35	0.7	0
Cystidia	28	0.3	0.1	0.4

Table 2: Ectomycorrhizal diversity (Simpson’s diversity index) in burned and logged transects

Disturbance Type	Transect	Simpson’s Diversity Index
Burns	F1	0.4571
	F2	0.5191
	F3	0.4715
Cuts	C1	0.5317
	C2	0.5347
	C3	0.5046

Table 3: RFLP patterns in each cloned ectomycorrhizal morphotype and the base pair length of each pattern

Morphotype	Number of RFLP Patterns And Corresponding Clone	Bp Length of Template Respectively
Yellow *Piloderma*-like	3 (b, d, e)	700, 700, 700
Sclerotia (*Cenococcum*)	4 (a, d, f, h)	1031, 600, 650, 1031
Green	1 (d)	650
Striated	2 (d, j)	650, 650
White wefts	3 (c, d, g)	650, 650, 600
Yellow wefts	4 (a, b, d, e)	600, 700, 600, 700
Russula-like (FRB)	3 (d, h, g)	700, 700, 700
Orange fan	3 (a, b, d)	700, 600, 600

Table 4: Species or genus from sequencing of ectomycorrhizal morphotypes. The letter with species corresponds to morphotypes specific RFLP pattern (refer to RFLP table).

Morphotype	Genus or Species result from Sequencing	Name given to ectomycorrhizal fungi identified by sequencing or morphotyping
Yellow *Piloderma*-like	B *Piloderma* sp.	B *Piloderma* sp. 1
	D *Lecythophora* (fungal endophyte)[1]	
	E Contaminated (*Agaricus bisporus*)[2]	
Sclerotia of *Cenococcum*-like	A *Cenococcum geophilum* /Uncultured *Cenococcum*	A, H *Cenococcum geophilum* F Uncultured (ecto or ericoid) mycorrhizal fungus
	D *Penicillum* (mold)[1] /Uncultured fungus[5]	
	F *Piloderma* sp.2[3] /Uncultured ectomycorrhizae (Atheliaceae) / Uncultured fungus / Uncultured mycorrhizal fungus[6]	
	H *Cenococcum geophilum*	
Green	D *Hygrophorus roseobrunneus*	D *Hygrophorus roseobrunneus*
Striated	D Uncultured *Piloderma*	D *Piloderma* sp. 2
	J Uncultured *Piloderma*	J *Piloderma* sp. 3
White wefts	C *Aphanocladium album* (rust), *Verticillum* sp .(plant pathogen)[1]	D *Cortinarius sp.*
	D *Cortinarius paragaudis*, *Cortinarius sp.*, *Cortinarius cacaocolor*	
	G *Clonostachys rosea or Glocladium roseum* (microfungi, endophyte)[1]	
Yellow wefts	A *Hygrophorus roseobrunneus*	A *Hygrophorus roseobrunneus*
	B, E *Cortinarius cinnamomeus*	B, E *Cortinarius cinnamomeus*
	C Uncultured basidiomycete (from floor dust)[1]	
Russula-like	D, H, G Contaminated (*Agaricus bisporus*)[2]	*Russula*-like
Orange fan	A, B Contaminated (*Agaricus bisporus*)[2]	D Pezizomycotina / Leotiomycete
	D Uncultured Pezizomycotina/ Leotiomycete [4]	

[1] Not ectomycorrhizal; [1a] Some fungi in this family form ericoid mycorrhizae (Hymenoscyphus)

[2] Test runs of PCR used *Agaricus bisporus* and contamination may have occurred in these cases

[3] *Piloderma* and *Cenococcum* genera are easily distinguished morphologically. It is therefore probable that this sequence was obtained from the accidental presence of *Piloderma* hyphae in the sample

[4] Some fungi in this subphylum/family form mycorrhizae (Hymenoscyphus)

[5] Fungus is from ericaceous plant roots

[6] Uncultured fungi from Hemlock and also *Vaccinium myrtillus* roots

Discussion

Understory Plant Community. The plots in this study were deliberately chosen to represent two different understory vegetation types, *Sphagnum* and ericoid/lichen dominated. The understory composition is in fact a continuum of all the species present, which are found where conditions favour their establishment and growth, creating a mosaic pattern throughout the understory.

An important mechanism that shapes the understory plant community composition is widely regarded to be overstory canopy structure (Legaré et al. 2001; Macdonald and Fenniak 2007; van Oijen 2005). The overstory has a direct effect by altering light, moisture, nutrient and pH as well as indirect effects through competing for resources (Macdonald and Fenniak 2007). Moisture is most likely playing a part in the plant species composition in our sites due to the large differences in the amounts of standing water between the *Sphagnum* dominated plots and the ericoid/lichen plots.

In general the species richness within our plots is low, with only 14 species occurring in total, compared to the 64 species found in the western conifer dominated forests (Macdonald and Fenniak 2007). Harper et al. (2004) found 8 commonly occurring shrubs, 9 herbs, as well as mosses and lichens in the same sites, however their study included much larger areas sampled as well as a greater number of transects. The deliberate sampling of small plots for different vegetation types will not give a full picture of the plant species composition in this community. In our plots only 8 species of plants occurred with any notable frequency and abundance. Some plants that were obvious inhabitants of the disturbed areas, such as *Kalmia* and *Alnus*, were not found in our plots. This is most likely due to the fact that we sampled only 10 m from the forest edge into the disturbances while plants such as *Kalmia* thrive in the open areas of disturbance, most notably in logged sites (Inderjit and Mallik 1996).

A number of the plots in the disturbed areas in this study did have large areas of bare ground, and this was more evident in the ericoid/lichen plots, even when bare ground occurs within the intact forest. This is largely due to the lack of abundant *Sphagnum* cover in drier plots.

The Ectomycorrhizal (EM) community. EM species richness has been found to range from 7 to over 200 species in a single study and most communities are diverse even when dominated by a single plant species (Visser 1995; Dahlberg et al. 1997; Hagerman et al. 1999a; Jonsson et al. 1999). As with all organisms, the normal pattern in EM communities is that of a few dominant species and many rare ones (Horton and Bruns 2001; Dahlberg 2001), a pattern seen in the results from this study.

The areas inside the disturbance at our sites contained considerably fewer live spruce trees or seedlings from which to sample, as regeneration was not advanced (Harper et al. 2004). This made obtaining live colonized roots difficult near the forest edge. In total, even after resampling in plots that did not yield live roots initially, 11 plots did not contain live roots with which to characterize the EM community. These plots were almost exclusively in the disturbances and 7 out of 9 were in the burned areas.

The overall diversity of EM from this system was relatively low and no differences in diversity were detected between cut and burned transects (t-test, p=0.12). A study in the boreal forest in northern Alberta found that from 2083 root tips of *Picea glauca*, 16 different morphotypes were described (Lazaruk et al. 2005). Robertson et al.

(2006) found that in *Picea mariana* in British Columbia 33 morphotypes were described from 8858 root tips, with 65 genotypes from RFLP analysis. This is compared to the 10981 root tips characterized by morphotyping in this study, which yielded 19 morphotypes in total and 23 genotypes from 8 of those morphotypes.

Sampling techniques can have a large effect on the diversity results from within a study. In general, as the number of samples increases the number of morphotypes increases, suggesting that an adequate number of samples to include all morphotypes may be quite high in most ecosystems (Horton and Bruns 2001). In this study a large number of soil samples were taken, many of which would have been redundant as each transect goes 200m from the edge into the intact forest. It is therefore probable that a good representation of the number of morphotypes was acquired. A community level study requires a lot of time spent on morphotyping, and as a result some of the DNA may have degraded over time (Horton and Bruns 2001). This may account for the difficulty with the extraction procedure in general and the failure to extract any *Cenococcum geophilum* from root tips (only sclerotial DNA was extracted successfully). Root tips of the same morphotypes from different samples were combined to improve the chance of extracting DNA, which may account for more than one banding pattern from the RFLP analysis and more than one species from the sequencing. Some morphotypes have similar and difficult to distinguish characteristics that make combined root tip samples prone to this sort of result (Dahlberg et al. 1997).

Some results suggest the structure of the ectomycorrhizal community described in this study is unique. *C. geophilum* is common in many forest types, however, it is not usually as dominant as was found in this study. The presence of *Piloderma* spp. as the second most abundant EM is interesting in that *Piloderma* is often considered to be an indicator of old growth forests (Dahlberg et al. 1997). Some commonly occurring EM in other studies, such as *Russula,* were not found in abundance and not detected by sequencing. Other species found by sequencing that occur rarely are *Hygrophorus roseobrunneus* and *Cortinarius cinnamomeus.*

C. geophilum and some Pilodermas are associated with old growth forests (Bradbury et al. 1998; Dahlberg et al. 1997; Goodman and Trofymow 1998) and conditions after stand-replacing fires are not considered good for some *Piloderma* species (Dahlberg 2002). The ubiquitous nature of *C. geophilum* is well established from papers and reviews (see general introduction) and is often among the most abundant EM in many boreal forest ecosystems. In this study *C. geophilum* accounts for 42.8% of total abundance and occurs in 101 out of the 120 soil samples taken. This suggests that *C. geophilum* has an unusually high dominance in this particular site and perhaps this type of boreal forest. *C. geophilum* possesses a strong dark mantle with melanized hyphae and morphological identification is typically simple (Goodman et al. 1996). *C. geophilum* can be identified even after the mantle has dessicated; it is therefore possible that this morphotype can be identified more often than is accurately representative of live root tips (Valentine et al. 2004; De Bellis et al. 2006).

Piloderma is typically associated with aggregated formation, so that it appears abundant but does not occur frequently (Dahlberg et al. 1997). The Pilodermas from our study occurred abundantly, especially *Piloderma* sp. 2 and *Piloderma* sp. 3 (Striated morphotype), which colonized 24% of root tips, and it was also uncharacteristically found frequently in 73 out of 120 soil cores. The *Piloderma* sp. 1 (Yellow *Piloderma-*

like morphotype) was found less abundantly, colonizing 7.1% of root tips, and in 29 out of 120 soil cores, still relatively frequent. It was common for both *C. geophilum* and Pilodermas to show a clumped distribution.

That *Piloderma* spp. are often associated with old growth coniferous forest, and the presence of woody debris (Smith et al. 2000) helps explain their abundance in our soil samples. There is evidence that suggests some EM fungi, including Pilodermas, can take up organic N through the use of proteolytic enzymes (Cairney and Burke 1994; Cairney and Burke 1998; Dahlberg 1997) and Pilodermas are associated with woody substrates and can live as a saprophyte (living off dead organic matter) as well as mutualistically (Erland et al. 1990; Hagerman et al. 1999b). Dahlberg et al. (1997) and De Bellis et al. (2006) suggest that the ability of Pilodermas to extract limiting nutrients in old growth forest systems could help explain their abundance.

In summary, our results show the understory plant community is composed of ericaceous shrubs, a few common herbs, sphagnum moss and lichens and is a continuous mosaic of dry ericoid/lichen and wetter *Sphagnum* dominated patches. The ectomycorrhizal community is composed of a few dominant and a number of more rare species, typical of EM assemblages. There were no significant differences detected in abundances of EM between cut and burned transects (t-test, see Results). The EM community appears to be unique in that it has an unusually high dominance of *C. geophilum,* although this may be due to overestimation. A number of *Piloderma* species are also abundant as well as occurring frequently in soil samples. *Russula,* an EM genus typically common in many forest types, was detected by morphotyping, however not abundantly, and it was not detected by sequencing.

Chapter 3: How Disturbances (Forest Fire and Logging) Affect the Ectomycorrhizal Community, Nutrient Supply Rates and Decomposition Rates in the Black Spruce Boreal Forest of Abitibi Region, Québec.

Introduction

The boreal forest consists of a mosaic of stands of trees differing in age and size, resulting from both anthropogenic, primarily logging, and natural disturbances, such as forest fires, insect outbreaks, and windthrow. In Canada there are about 9000 forest fires recorded annually, which burn on average 2.1 million hectares of forest, primarily boreal. Most of the fires are small and burn only a few hectares, but a few of them are large, burning 100,000 hectares or more, with approximately 35% of the fires being less than 50 ha and 30% being greater than 1000 ha (Statistics from Natural Resources Canada, 2008; Payette et al. 1989). Fire frequencies and size in the boreal forest vary with latitude, decreasing in more northerly regions, resulting in an almost 100 fold reduction in the fire rotation period from 9320 years in the northern shrub tundra to 100 years in the northern boreal forest (Payette et al. 1989).

The boreal forest is increasingly affected by logging (Harper et al. 2004). The Canadian forestry industry is the country's largest natural resource based industry and makes Canada the world’s largest exporter of forest products. In recent years about 1 million hectares of Canadian forest has been harvested annually, of the harvested area, 53% was naturally regenerated, 45% replanted and 2% directly seeded. Sustainable forest management practices are now an important part of the forestry industry and government planning, and 138 million hectares of forest are certified sustainably managed by international certification (Natural Resources Canada, 2008). The other main disturbance that is common in the boreal forest is insect outbreaks, which in 2007 affected 10.6 million hectares of forest.

The frequency, intensity and type of disturbances in the boreal forest will affect the humus layer, both physically and chemically and, consequently, the rates of decomposition. The effects of disturbances have been found to be detectable in the soil's chemical composition and rates of decomposition for up to two decades and these effects differ depending on the type of disturbance (Thiffault et al. 2008). Logging will have a negative impact on an area’s biomass, reducing long-term inputs to dead organic matter (DOM) and consequently reducing soil nutrient levels (Pietikainen and Fritze 1995). Soil compaction due to logging can negatively affect nutrient exchange, decomposition, understory recovery and seedling establishment. Wildfire can bind up organic nutrients and make them less available to plants, but allows a long-term exchangeable Ca and Mg pool to exist, while clearcuts do not (Thiffault et al. 2008). Fires can also cause forests to experience nutrient loss through volatilization and humus loss through burning, however, inputs from ash and the increased soil pH that can result in higher N mineralization can cause nutrient flushes (Prescott et al. 2000b). Loss of the humus layer may negatively affect the microbial community and therefore decomposition after fires, however conditions associated with increased microbial and invertebrate populations, such as increased debris and soil temperatures, may increase decomposition (Prescott et al. 2000b; Ballard 2000). The effects of clearcutting on decomposition are unclear as results differ depending on climate and region. However, in cooler climates, such as the boreal forest, accelerated decomposition in clearcuts may result due to the increase in temperature without the drying effect of warmer climates during the growing season (Prescott et al. 2000a).

A fire's effect on the EM community depends primarily on the intensity of the fire; high intensity fires may result in a succession of EM after the fire, while low intensity fires tend to shift the EM community composition rather than diversity (Visser 1995; Dahlberg 2002). Logging has also been found to change species composition rather than cause a loss of root colonization (Jones et al. 2003), however Hagerman et al. (1999a) found that EM diversity and richness were higher near the forest than in cut blocks. Lazaruk et al. (2005) found that logging significantly decreased EM diversity and richness and this increased with the intensity of the disturbance.

In this chapter, I will examine the data on the ectomycorrhizal community, nutrient supply rates and decomposition rates in three burned transects and three logged transects in order to test the following hypotheses: that 1) a difference in the EM community composition and abundance of specific species/morphotypes will be detected away from the disturbance; 2) a difference in the EM community composition and abundance of specific species/morphotypes will be detected between the two disturbance types depending on the varying sensitivity of the fungi to the disturbance type; and, 3) nutrient availabilities will be lower in the disturbances and edge areas of the transects and these losses will vary between disturbance type due to the different effects of fires and logging on soil conditions and plant cover; and that 4) decomposition rates will be greater in the disturbances and edge areas of the transects and these losses will vary between disturbance type due to the different effects of fires and logging on soil conditions and plant cover.

Materials and Methods

Study site. The study sites and the sample plots are described in Chapter 2.

Soil pH. The pH of each soil core was measured by mixing distilled water into soil from the cores and taking 3 readings from a hand-held pH meter. The average of the 3 readings was taken as the pH of the core. The pH was calculated as an average over 3 distinct areas of each transect, the disturbance, the edge and the intact forest.

Ectomycorrhizal (EM) Abundances. EM abundances were calculated as described in Chapter 2, Methods and Results.

Decomposition Rates. Decomposition rates were measured using 10 cm x 10 cm litterbags made from 1 mm mesh fibreglass mosquito netting filled with pre-weighed dry poplar litter. To determine the average moisture content of dry leaf litter, the average of 10 pre-weighed leaf litterbags contents was determined by drying contents overnight in a warm drying oven at 35 ^{o}C, which was then reweighed the next morning. One of these bags was placed in each of the plots (as described in Chapter 2) in July 2003 and affixed to the surface using wire pegs. The litterbags were retrieved in July 2004 and the poplar litter was dried overnight in a warm drying oven at 35 ^{o}C and reweighed to give a measure of leaf litter decomposition rate. Popsicle sticks were also placed into the ground in each plot as a measure of wood decomposition. The popsicle sticks were placed and retrieved on the same dates as the litter bags and weighed, dried and reweighed in the same manner as above.

Nutrient Supply Rates. Nutrient Supply Rates were measured in all of the plots using Plant Root Simulator^{TM} from Western Ag. Innovations, Saskatoon, Sask. The probes act as an ion sink and measure both the ions adsorbed from the labile pool and ions replenishing the labile pool from less available pools. Four cation and four anion probes were placed in each plot and the data pooled for supply rates. The probes were placed in the plots in early July 2003 and retrieved in late September that same year, making a total burial time of approximately 3 months. The measurements for nutrient supply rate were given as ug ion / 10 cm^2 membrane surface area / 3 months.

Statistical Analyses. Effects of Disturbances on the Ectomycorrhizal Community, Nutrient Supply and Decomposition Rates:

Indicator Species Analysis. An ISA was performed using the percent cover of plant species and abundance of EM using Version 5 of PC-ORD^{TM} to determine whether abundances of EM were associated with 1) distance along transects, and 2) plots in cut or burned transects.

O*rdinations.* Bray Curtis (BC), Principle Coordinate Analysis (PCA) and NonMetric Multidimensional Scaling (NMDS) (McCune and Grace 2002) were performed to test the hypotheses that 1) there will be a difference between disturbance types, and 2) there will be a gradient in EM abundances, decomposition rates and nutrient supply rates along the transect. Version 5 of PC-ORD^{TM} from MjM Software was used to perform all ordinations. Three different ordinations using mycorrhizal abundances and plant species percent cover as variables were performed to see if the results corroborated one another.

The Bray Curtis and NMDS ordinations used Sorenson's distance measure and variance endpoint selection for determining axes. The data were ordinated based on abundances of EM and plant species cover. Correlation coefficients (Pearson r and Kendal tau) show relationships between Bray Curtis axes/NMDS axes created in the ordination and the input variables. The PCA ordination used Euclidean distance measure and the Variance-covariance cross products matrix to determine the axes. Unlike the other ordinations, this is an indirect ordination. Correlation coefficients Pearson r and Kendal tau show relationships between the PCA axes created in the ordination and the input variables. With all 3 types of ordination performed, relationships between the ordination axes created (with mycorrhizal abundances and plant species percent cover) and the remaining variables (nutrients supply rates, decomposition rates and pH) were calculated.

A Bray Curtis ordination of the nutrient supply rates, decomposition rates and pH was also performed. The data were ordinated based on the input variables mentioned and then relationships between the ordination axis scores and the abundances of EM and plant species percent cover were explored. Correlation coefficients (Pearson r and Kendal tau) show relationships between Bray Curtis axes created in the ordination and physical variables.

All data for all ordinations were scaled by the maximum value to make all variables range from 0 to 1. Biplots show the ordination space created and the relationship to variables that were most correlated with the axes scores. Biplots were also created for each ordination to see if any variables had significant relationships with plots in the cut and burned transects as well as *Sphagnum* and ericoid/lichen plots and any relationship with distance along the transects.

Results

Soil pH. The pH values showed a consistent pattern in transects F1, F2, F3, C1 and C2 of highest at the edge, moderate in the disturbance and lowest in the intact forest. In transect C3 the highest pH value was in the forest, moderate was in the edge area and the lowest was in the disturbance. The range of pH within a transect, considering all transects, was 3.64-4 at its lowest and 3.92-4.03 at its highest. No significant trends were found for pH in the ordinations (Table 5).

Ordinations. The ordinations (NMDS, PCA and Bray Curtis) of ectomycorrhizal abundances and plant species percent cover show the following results for the axis. For the NMDS ordination the coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space, R squared, is 0.432 for Axis 1 and 0.312 for Axis 2, with a cumulative R squared for both axes of 0.744. Bray Curtis ordination Axis 1 extracted 20.91% of the original distance matrix and Axis 2 extracted 15.41% of the original distance matrix with a Cumulative result of 36.32%. For the PCA ordination, the first 2 axes have the highest Eigen values (24.579 and 11.653 respectively) and therefore explain the largest amount of variance (% variance is 24.623 and 11.679 respectively), the third axis was therefore not included. The sign of the Bray Curtis correlations is reversed when compared with the other ordinations, however the groups of variables that correlate with each other are consistent.

With all 3 types of ordination, relationships between the created ordination axes (using mycorrhizal abundances and plant species percent cover) and the remaining variables (nutrients supply rates, decomposition rates and pH) were calculated and the results show that the relationships are weak (result not included).

The Bray Curtis ordination of nutrient supply rates, decomposition rates and pH show the following results for the axes. Axis 1 extracted 18.54% of the original distance matrix, Axis 2, 24.99% and Axis 3 11.21%, with a cumulative result of 54.74%.

With the Bray Curtis ordination of the nutrient supply rates, decomposition rates and pH, the relationship between the ordination axis scores and the abundances of EM and plant species percent cover were explored and results show only weak relationships between the sets of variables (results not included).

Plots created to compare the Bray Curtis axes from the first set of ordinations (EM abundance and plant cover) to the axes from the second Bray Curtis ordination (nutrient supply rates, decomposition and pH) show no linear relationships between these sets of variables (results not included).

Effect of the Disturbances on the Ectomycorrhizal Community. No significant trends were found in regards to the abundances of EM and distance along the transects (ISA and ordination results not included).

There were, however, some trends with regard to EM abundance and specific transects. Some EM were associated with either plots within burned transects or cut transects. *Cenococcum geophilum* (p=0.0242), Clear bulbous (p=0.0728) and *Russula*-like (p=0.0122) were significantly correlated with plots in transects containing burned areas and no specific EM were associated with plots within logged transects (ISA, Table 1).

Piloderma sp. 1, White verrucose and Cort along with *L. groenlandicum* and *V. angustifolium* show a trend towards more abundance in the transects containing burned plots, and *Cenococcum geophilum*, Big orange, Brown Clamp and Clear Bulbous along with lichen, *P. mariana* and *Sphagnum* show a trend towards more abundance in transects containing cut plots (Fig. 1a; variables significantly associated with axis 2; Table 2, 3 & 4). The ordination biplots show no strong trend with regard to EM abundance and distance along the transects (Fig 1b).

Effects of the Disturbances on Decomposition Rates and Nutrient Supply Rates. Percent decomposition for litter bags ranged from 9.1% to 43.6%, with most values between 10% and 25%. Wood decomposition values ranged between 1.8 % and 86.3 %, with most values between 2 % and 40%. No relationship with distance along the transects was detected within the ordinations, with either litter or wood decomposition (all ordinations, results not shown). A group of plots in burned transects show higher rates of wood decomposition along with higher values for certain nutrients (Total N, NH_4^+, Cu and Zn) (Fig 3a and 4a). These plots are largely in transects F1 & F2 which are separate from the other transects (Fig 3b and 4b).

No relationship was found between nutrient supply rates and distance along the transects in the ordinations (results of all ordinations, results not shown). The availability of most nutrients (most strongly B, Mg and Ca as well as Pb, K Fe, Mn, Al) are negatively correlated with the availability of Nitrogen (as Total N and NH_4^+). Cu and Zn are the only exceptions and correlate more closely with Nitrogen (Fig 2a, 3a and 4a). Higher Nitrogen levels are found in a group of plots in burned transects, most notably F1 and F2. Some of these plots will share higher levels of wood decomposition, Cu and Zn. Higher levels of B, Mg and Ca are found in a group of logged plots, most notably C1 and C2 (Fig. 2b, 3b and 4b). Decomposition is only significantly positively correlated with Zn and negatively with K (Fig. 3a and 4a; and Table 5).

Table 1. Results of Indicator Species Analysis to see if either ectomycorrhizal abundances or plant species percent cover were associated with 1(burned) or 2 (cut) plots. The bold variables were significantly associated with burned plots and the * symbol with cut plots (alpha = 0.10). The *p* value is equal to the proportion of randomised trials with indicator values equal to or exceeding the observed indicator value (*p*= 1 + number of runs >= observed) / (1+ number of randomised runs). Alpha is equal to 0.10. The Maxgroup is equal to the group identifier for group with the maximum observed IV (Indicator Value).

Species	Observed Indicator Max Value	IV from randomized groups (IV)	Mean	Standard Deviation	p value
C. geophilum	2	52.1	45.8	2.66	**0.0242**
Piloderma sp. 1	1	18.4	15.9	3.15	0.1978
Piloderma sp. 2/ *Piloderma* sp. 3	1	30.1	34.2	3.37	0.9792
Striated Clamp	2	3.8	3.4	1.46	0.4851
H. roseobrunneus	2	8.7	9.7	2.59	0.5665
H. roseobrunneus/ C. cinnamomeus	2	18.5	19.7	3.48	0.5459
White clamp	2	9.0	6.8	2.19	0.1756
Cortinarius sp.	2	18.3	16.8	3.50	0.2895
White verrucose	1	3.8	5.4	2.03	0.7620
Orange fan	2	9.6	10.4	2.81	0.5301
Small cigar	2	5.8	7.3	2.34	0.6899
Clear bulbous	2	8.9	5.4	1.98	**0.0720**
Russula-like	2	35.3	24.2	3.79	**0.0122**
Cort	1	5.0	3.1	1.25	0.2366
Brown clamp	2	3.6	3.4	1.49	0.4991
Cystidia	2	2.5	2.9	1.21	0.4915
Big brown	2	6.6	7.3	2.28	0.5399
Big orange	2	5.1	5.7	2.00	0.5421
White pilo	1	1.7	1.7	0.02	1.0000
Sphagnum	2	50.9	46.8	2.76	**0.0894**
Lichen	2	39.6	34.2	3.95	**0.0994**
L. groenlandicum	1	64.1	52.8	2.54	0.0002 *
V. angustifolium	1	56.2	36.7	3.99	0.0006 *
G. hispidula	1	29.0	28.7	4.26	0.3995
C. calyculata	2	22.1	24.1	3.99	0.6203
P. mariana	2	46.8	28.0	3.82	**0.0008**

Table 2: Bray Curtis ordination of ectomycorrhizal abundance and plant species percent cover, axes 1 and 2. Results in bold are significant correlations.

Bray Curtis				Bray Curtis			
Axis 1:	r	r-sq	Tau	**Axis 2:**	r	r-sq	tau
Lichen	**0.678**	**0.46**	**0.568**	***L.groenlandicum***	**0.652**	**0.426**	**0.49**
***Piloderma* sp. 1**	**0.398**	**0.158**	**0.249**	*Piloderma*. sp. 1	0.196	0.038	0.145
V.angustifolium	0.289	0.084	0.293	*V.angustifolium*	0.177	0.031	0.161
Russula-like	0.288	0.083	0.082	White verrucose	0.157	0.025	0.044
Small cigar	0.199	0.04	0.152	Cort	0.127	0.016	0.104
Cort	0.135	0.018	0.075	*H.roseobrunneus*	0.087	0.008	0.027
Cystidia	0.109	0.012	0.096	White pilo	0.074	0.006	0.079
White pilo	0.107	0.011	0.094	*Cortinarius* sp.	0.042	0.002	-0.031
Straited clamp	0.096	0.009	0.126	*Piloderma* sp. 2/ sp.3	0.001	0	-0.005
White verrucose	0.081	0.007	0.101	*C.calyculata*	-0.037	0.001	-0.192
H.roseobrunneus	0.073	0.005	0.093	Hygrophorus roseobrunneus/ Cortinarius cinnamomeus	-0.043	0.002	-0.03
Clear bulbous	0.072	0.005	-0.032	Big brown	-0.048	0.002	-0.01
Cortinaruis sp.	0.052	0.003	-0.042	White clamp	-0.051	0.003	-0.03
C.calyculata	0.035	0.001	0.009	Striated clamp	-0.056	0.003	-0.036
C.geophilum	0.03	0.001	0.045	Orange fan	-0.062	0.004	-0.162
White clamp	-0.016	0	0.058	*Russula*-like	-0.065	0.004	-0.187
Big brown	-0.026	0.001	0.017	Small cigar	-0.074	0.005	-0.07
Orange fan	-0.046	0.002	-0.122	*G.hispidula*	-0.081	0.007	-0.044
Hygrophorus roseobrunneus/ Cortinarius cinnamomeus	-0.086	0.007	-0.056	Cystidia	-0.098	0.01	-0.087
Brown clamp	-0.099	0.01	-0.063	Clear bulbous	-0.126	0.016	-0.123
Big orange	-0.104	0.011	-0.058	Brown clamp	-0.135	0.018	-0.157
L.groenlandicum	-0.117	0.014	-0.095	*Sphagnum spp.*	-0.151	0.023	-0.141
G.hispidula	-0.18	0.032	-0.283	Big orange	-0.156	0.024	-0.174
P.mariana	-0.184	0.034	-0.121	*P.mariana*	-0.178	0.032	-0.165
***Piloderma* sp.2/sp.3**	**-0.643**	**0.413**	**-0.562**	***Lichen***	**-0.371**	**0.138**	**-0.128**
Sphagnum spp.	**-0.848**	**0.719**	**-0.61**	***C.geophilum***	**-0.644**	**0.415**	**-0.48**

Table 3: NMDS ordination of ectomycorrhizal abundances and plant species percent cover, axes 1 and 2. Results in bold are significant correlations.

	NMDS				NMDS		
Axis 1:	r	r-sq	tau	**Axis 2:**	r	r-sq	tau
Lichen	**-0.616**	**0.379**	**-0.552**	***C.geophilum***	**-0.664**	**0.441**	**-0.558**
V.angustifolium	**-0.356**	**0.127**	**-0.293**	*Sphagnum spp.*	-0.28	0.078	-0.206
Small cigar	-0.289	0.084	-0.129	Big orange	-0.275	0.076	-0.2
C.geophilum	-0.276	0.076	-0.209	*G. hispidula*	-0.264	0.07	-0.112
Piloderma sp. 1	-0.215	0.046	-0.149	Brown clamp	-0.241	0.058	-0.187
Cystidia	-0.199	0.04	-0.169	Cystidia	-0.22	0.048	-0.194
White pilo	-0.172	0.03	-0.123	Clear bulbous	-0.176	0.031	-0.139
Cortinarius sp.	-0.118	0.014	-0.029	*Hygrophorus roseobrunneus/ Cortinarius cinnamomeus*	-0.157	0.025	-0.041
C.calyculata	-0.091	0.008	-0.003	*P.mariana*	-0.135	0.018	-0.116
Russula-like	-0.082	0.007	-0.012	*C.calyculata*	-0.075	0.006	-0.039
Clear bulbous	-0.079	0.006	0.004	White clamp	-0.072	0.005	-0.064
Cort	-0.078	0.006	-0.073	Lichen	-0.066	0.004	0.033
White verrucose	-0.015	0	-0.047	Small cigar	-0.049	0.002	-0.061
Striated clamp	-0.014	0	-0.063	Striated clamp	-0.043	0.002	0.008
Orange fan	0.007	0	0.092	*Piloderma* sp. 2/ sp.3	-0.04	0.002	0.018
L.groenlandicum	0.09	0.008	0.07	Big brown	0.005	0	0.024
White clamp	0.098	0.01	-0.005	White pilo	0.068	0.005	0.088
H.roseobrunneus	0.101	0.01	0.037	*Cortinarius sp.*	0.085	0.007	-0.037
Hygrophorus roseobrunneus/ Cortinarius cinnamomeus	0.102	0.01	0.048	*V.angustifolium*	0.093	0.009	0.059
Big orange	0.111	0.012	0.071	Orange fan	0.119	0.014	-0.003
Brown clamp	0.118	0.014	0.112	*Piloderma.* sp. 1	0.232	0.054	0.137
Big brown	0.139	0.019	0.055	White verrucose	0.274	0.075	0.088
G.hispidula	0.209	0.044	0.334	*L.groenlandicum*	0.279	0.078	0.267
P.mariana	0.218	0.048	0.082	*Russula*-like	0.282	0.079	0.018
***Piloderma* sp. 2/sp.3**	**0.589**	**0.347**	**0.452**	Cort	0.333	0.111	0.089
Sphagnum spp.	**0.88**	**0.775**	**0.664**	*H.roseobrunneus*	0.438	0.192	0.172

Table 4: PCA ordination of ectomycorrhizal abundances and plant species percent cover, axes 1 and 2. Results in bold are significant correlations.

PCA				PCA			
Axis 1:	r	r-sq	tau	**Axis 2:**	r	r-sq	tau
Lichen	**-0.629**	**0.396**	**-0.558**	*L.groenlandicum*	-0.368	0.135	-0.262
V.angustifolium	**-0.299**	**0.09**	**-0.27**	*Piloderma* sp. 2/ sp.3	-0.257	0.066	-0.141
C.geophilum	-0.251	0.063	-0.2	*Piloderma* sp. 1	-0.24	0.058	-0.129
Small cigar	-0.229	0.052	-0.148	*H.roseobrunneus*	-0.232	0.054	-0.126
Cystidia	-0.177	0.031	-0.146	Cort	-0.17	0.029	-0.057
Piloderma sp. 1	-0.172	0.03	-0.136	White verrucose	-0.132	0.017	-0.037
Russula-like	-0.12	0.014	-0.03	*Hygrophorus roseobrunneus/ Cortinarius cinnamomeus*	-0.109	0.012	-0.053
Clear bulbous	-0.101	0.01	-0.005	*Russula*-like	-0.095	0.009	0.058
White pilo	-0.1	0.01	-0.09	*Cortinarius sp.*	-0.091	0.008	0.048
Cortinarius sp.	-0.094	0.009	-0.019	Orange fan	-0.059	0.003	0.011
Cort	-0.091	0.008	-0.052	White pilo	-0.036	0.001	-0.034
C.calyculata	-0.068	0.005	-0.016	*V.angustifolium*	-0.034	0.001	-0.04
Striated clamp	-0.065	0.004	-0.102	Big brown	-0.002	0	-0.032
White verrucose	-0.061	0.004	-0.078	Striated clamp	0.006	0	-0.002
White clamp	0.013	0	-0.032	White clamp	0.013	0	0.054
Orange fan	0.018	0	0.098	Small cigar	0.016	0	0.015
H.roseobrunneus	0.02	0	-0.025	*C.calyculata*	0.043	0.002	0.076
Big brown	0.064	0.004	0.008	Lichen	0.05	0.002	-0.033
L.groenlandicum	0.069	0.005	0.094	Clear bulbous	0.104	0.011	0.106
Brown clamp	0.074	0.005	0.058	*P.mariana*	0.144	0.021	0.132
Big orange	0.088	0.008	0.049	Big orange	0.155	0.024	0.113
Hygrophorus roseobrunneus/ Cortinarius cinnamomeus	0.11	0.012	0.058	Cystidia	0.156	0.024	0.15
P.mariana	0.167	0.028	0.055	Brown clamp	0.167	0.028	0.164
G.hispidula	0.183	0.033	0.283	*G.hispidula*	0.213	0.045	0.12
***Piloderma* sp.2/sp.3**	**0.679**	**0.461**	**0.563**	*Sphagnum spp.*	0.233	0.054	0.175
Sphagnum spp.	**0.946**	**0.895**	**0.712**	*C.geophilum*	0.901	0.811	0.737

Table 5: Bray Curtis ordination using the variables; decomposition rates, nutrient supply rates and pH. Below are the correlations of input variables with the Bray Curtis Axes. Results in bold are significant correlations.

Axis:		1			2			3	
	R	r-sq	tau	r	r-sq	Tau	r	r-sq	tau
Litter decomp.	-0.071	0.005	-0.066	-0.117	0.014	-0.131	-0.023	0.001	-0.037
Wood decomp	0.273	0.075	0.141	0.086	0.007	0.017	**0.506**	**0.256**	**0.248**
TotN	0.087	0.007	0.021	**0.504**	**0.254**	**0.439**	0.37	0.137	0.339
NO_3^-	0.085	0.007	-0.001	0.086	0.007	0.237	0.123	0.015	0.222
NH_4^+	0.052	0.003	0.012	**0.601**	**0.362**	**0.482**	0.394	0.156	0.328
Ca	0.43	0.185	0.377	**-0.824**	**0.678**	**-0.536**	-0.211	0.045	-0.193
Mg	**0.52**	**0.27**	**0.432**	**-0.717**	**0.514**	**-0.406**	-0.251	0.063	-0.172
K	0.364	0.132	0.207	0.273	0.074	0.169	**-0.422**	**0.178**	**-0.317**
P	0.278	0.078	0.229	0.022	0	0.093	0.032	0.001	0.007
Fe	**0.409**	**0.167**	**0.449**	0.072	0.005	0.219	0.041	0.002	0.205
Mn	0.406	0.165	0.233	-0.039	0.002	0.067	0.069	0.005	0.002
Cu	0.455	0.207	0.35	0.386	0.149	0.301	0.345	0.119	0.269
Zn	**0.507**	**0.257**	**0.382**	0.363	0.132	0.28	**0.463**	**0.214**	**0.307**
B	0.38	0.144	0.294	**-0.635**	**0.404**	**-0.49**	-0.032	0.001	-0.022
S	0.395	0.156	0.41	-0.138	0.019	-0.026	0.016	0	0.038
Pb	**0.521**	**0.271**	**0.415**	0.295	0.087	0.211	-0.355	0.126	-0.265
Al	**0.343**	**0.117**	**0.433**	-0.149	0.022	-0.413	-0.173	0.03	-0.096
pH	-0.083	0.007	0.001	-0.142	0.02	-0.154	0.312	0.098	0.104

Figs. 1a and 1b: The biplots are from the Bray Curtis ordination of ectomycorrhizal abundances and plant species percent cover. Along axis 2, the burned plots had higher values than the cut plots (Fig. 1a).

The ordination correlations and biplots show no strong trend in regards to EM abundance and plant species and distance along the transects (Fig 1b).

Figure 1a

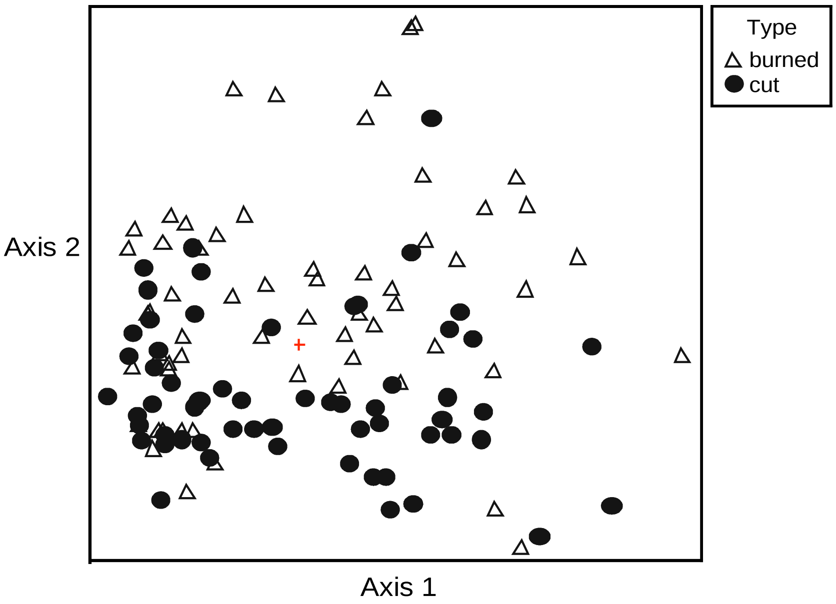
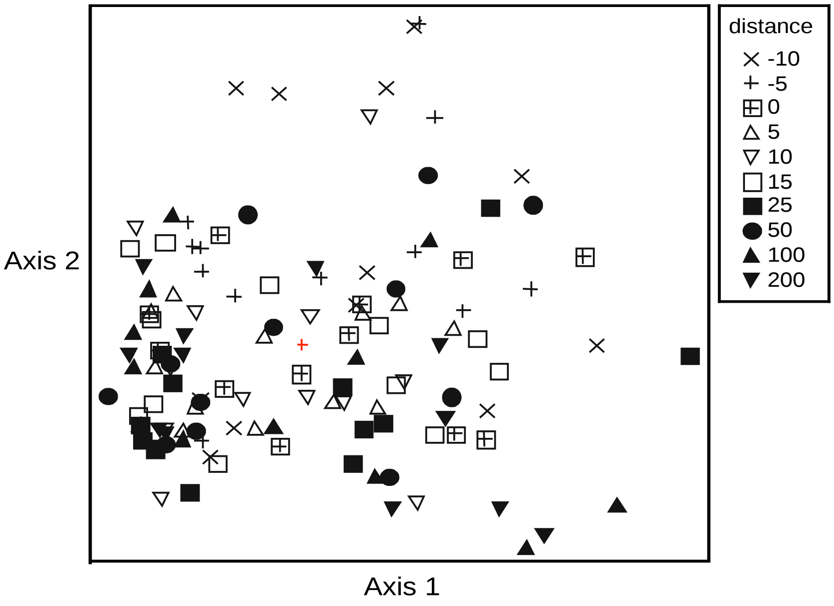


Figure 1b



Figs. 2a and 2b: The biplots are from the Bray Curtis ordination of nutrient supply rates and decomposition rates along axes 1 and 2 and show some separation of cut and burned plots in regards to nutrient supply rates (Fig. 1a). Fig. 2b shows the separation of nutrient supply rates in regards to transects.

Figure 2a

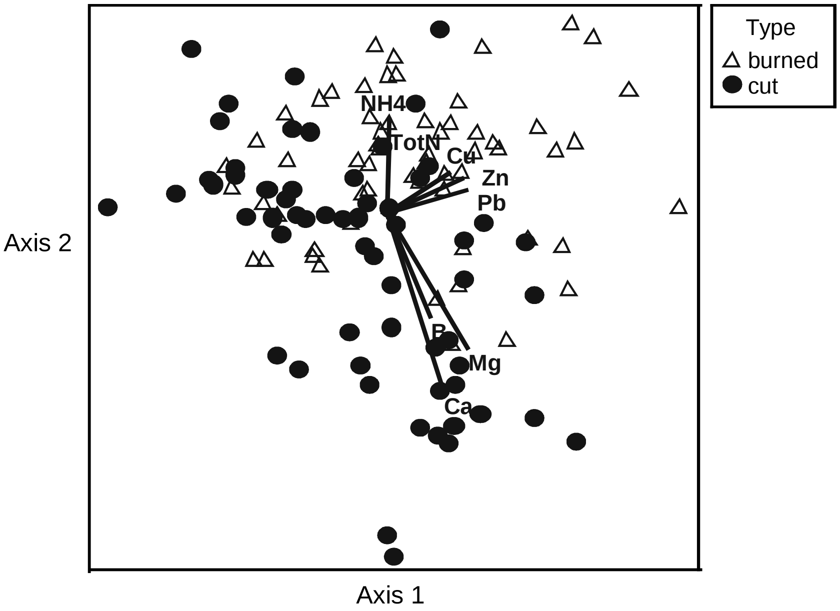
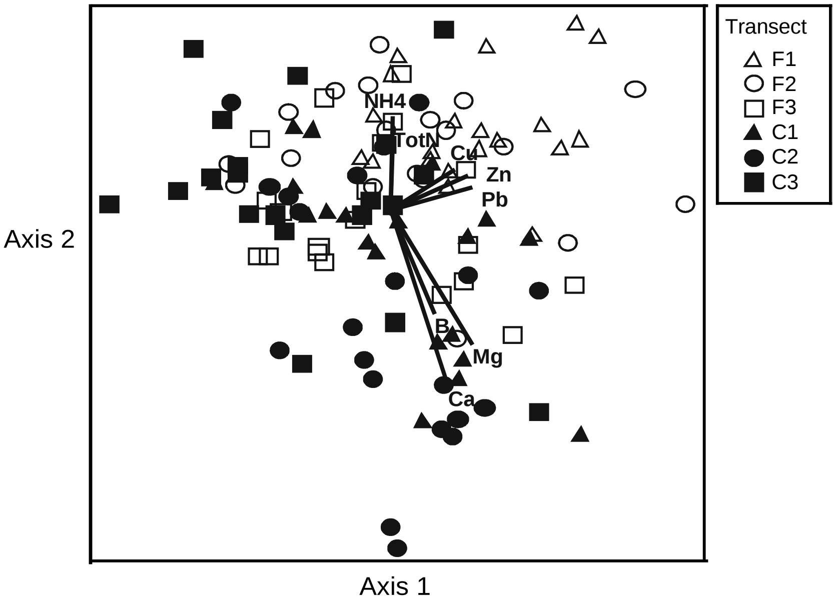


Figure 2b



Figs. 3a and 3b: The biplots shows similar relationships as Fig. 2a and b, but along axis 1 and 3 of the Bray Curtis ordination of nutrient supply and decomposition rates. Fig. 3a shows a separation of cut and burned plots in regards to nutrient supply rates. Fig. 3b shows these are mainly from transects F1 and F2, which are separate from the other transects.

Figure 3a

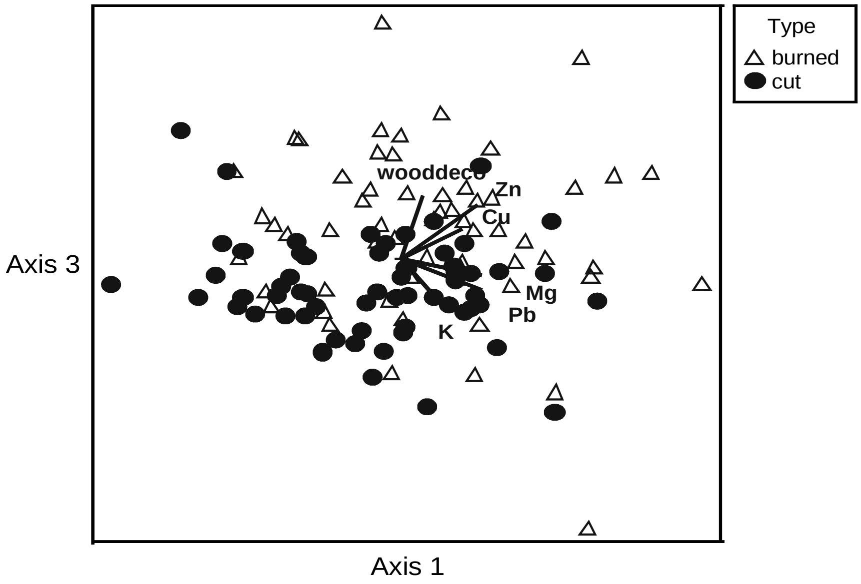
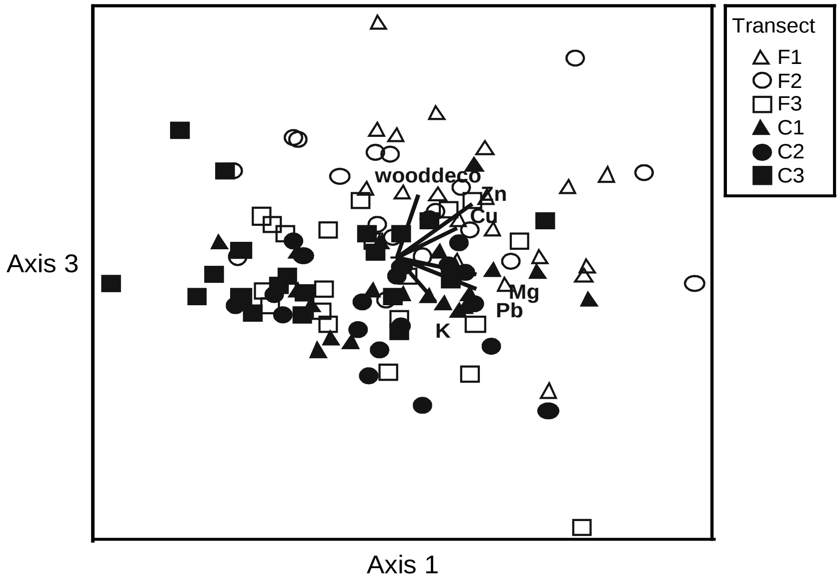


Figure 3b



Figs. 4a and b: The biplots show similar relationships as Fig 2a and b, but along axis 2 and 3 of the Bray Curtis ordination of nutrient supply and decomposition rates.
Fig 4a shows some separation of cut and burned plots in regards to nutrient supply rates and wood decomposition. Fig 4b shows that the plots in the burned transects are largely from F1 & F2 are in the upper right quadrant, while the plots in the logged transects are largely from C1 and C2.

Figure 4a

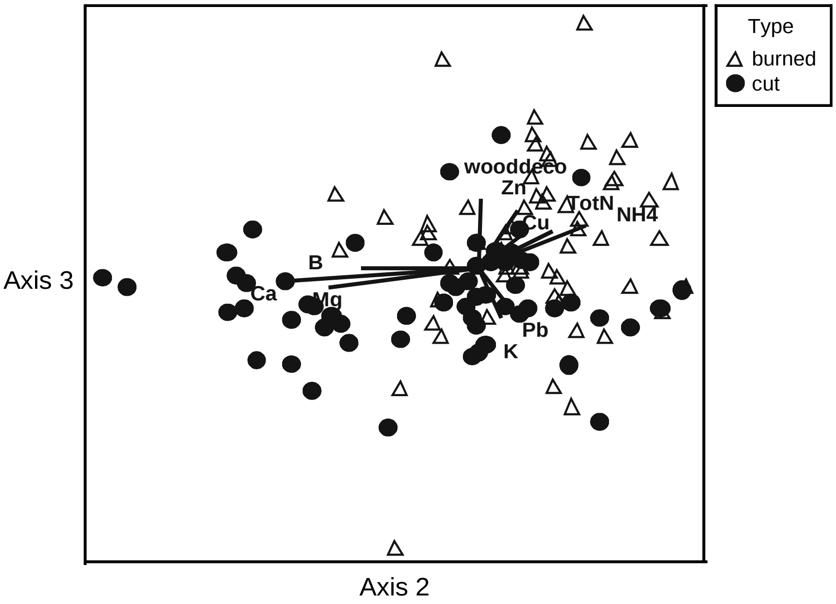
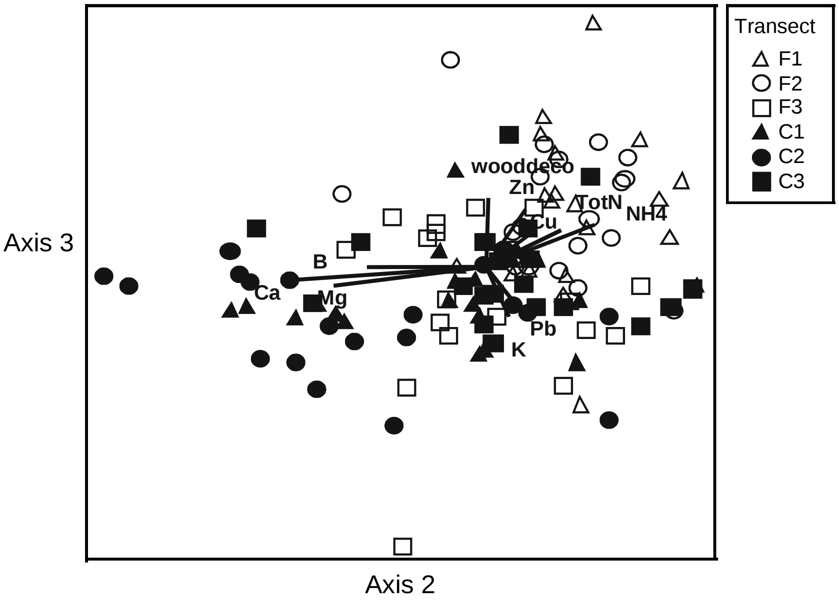


Figure 4b



Discussion

Effect of the Disturbances on the Ectomycorrhizal (EM) Community. The abundance of the various EM taxa showed no trends with regards to distance along the transects, suggesting that the disturbances had little effect. However, some of the EM associated with either transects with burned plots or transects with cut plots. This suggests that localized conditions within transects is of greater importance in determining abundances of individual EM taxa than the effects of disturbances in general or the type of disturbance.

The fire edges were more gradual and wider with more structural change due to partial burning into the forest and more snags. Logged edges were more abrupt and regeneration was more affected by edge influence on the disturbance side of the edge for cut edges, however DEI extended further for fire edges. Overall, fewer understory species were affected by edge influence on forest side of the fire edges, with the exception of shrubs, which had greater DEIs at fire edges (Harper et al. 2004). Although these edge characteristics were found to be very different between burned and logged transects, this is not reflected in a difference in the abundances of EM species in disturbed areas.

Logging has been shown to affect the EM community, but studies show a range of results. DeBellis et al. (2002) found that in selective cuts, where gap size was small and there was quick regeneration of seedlings, logging did not have a negative impact on the EM community. It was suggested that quick regeneration of hosts and limited soil disturbance would facilitate EM recovery. Kranabetter and Wylie (1998) found that EM species richness and evenness decreased significantly from the forest into naturally regenerating gaps, despite quick regeneration and lack of soil disturbance. The cause may have been lower diversity and lack of innoculum, which shifted EM competitive balances in the disturbed areas (Kranabetter and Wylie 1998). Bradbury et al. (1998) found that although the general trend of increased diversity with increased stand age was reported, no obvious succession of fungal species was observed in a range of different stand ages.

The recovery of spruce was slow in the disturbances in this study and a greater degree of soil disturbance, such as burned organic layer and machinery damage, was most likely playing a role in the slow recovery of these sites (Harper et al. 2004). Greene et al. (2005) found that mineral soil exposure was less near fire edges than in the disturbances, creating less ideal sites for spruce seedbeds, which could in part explain the lack of regeneration of host trees at fire edges. Despite the effects of the disturbances on host recovery and soil conditions, other factors appear to be more influential in determining the EM community. It has been suggested that the lack of specificity in mycorrhizal associations, particularly in spruce forests, presents certain advantages, which contribute to the resilience of forests when they are prone to a cycle of disturbances. In these circumstances different genotypes or species may thrive under different conditions (Taylor et al. 2000). In addition, different genotypes or species would possess a range of abilities, such as with nutrient assimilation (Perez-Moreno and Read 2000).

Studies also show varied results with regard to the effects of forest fires on the EM community. Jonsson et al. (1999) found that the only difference in disturbed areas was that the evenness of the EM community was reduced when compared to the intact forest. Fire intensity is thought to play an important role in determining the extent of the effect on EM communities (Visser 1995; Jonsson et al. 1999) since the extent of the damage to host trees, the soil organic layer and ground vegetation would all be significant factors affecting the EM community. The lack of live roots in some soil cores from the disturbed areas, even after repeated sampling, should also be taken into consideration when assessing the pattern of EM distribution at our sites (see EM discussion in Ch. 1 for details).

It is unlikely that EM distribution is governed primarily by temporal factors such as stand age (Bradbury et al. 1998) and even when fungal succession was noted after disturbances, it has been viewed as an indirect effect of altered soil conditions. Izzo et al. (2005) found that the EM community across a year was more similar within a plot than between plots, showing that species were more constant at large spatial scales, but varied across years at small spatial scales. This demonstrates the dynamic and resilient nature of the EM community even without large-scale disturbances (Izzo et al. 2005). Studies in general agree that fungal distribution is more dependent on spatial variation than disturbances, especially those of low impact, such as low intensity fires (Dahlberg 2002; Jonsson et al. 1999). Local transect climate and soil conditions may be more influential in regards to EM distribution and this may be a contributing factor to the association of some EM with particular transects. If disturbances are not showing large direct effects on EM fungal communities, other factors such as the plant community, pH, nutrients, inoculation potential and edaphic factors are all considered to be major influences (Dahlberg 2002; Dahlberg et al. 2001), and these factors will in part be regulated by disturbance dynamics in the boreal forest.

The Effect of Disturbances on Decomposition Rates. Disturbance by forest fires have an effect on decomposition in boreal forests, by altering the soil microbes and fauna as well as the physical environment such as soil temperature and moisture (Bhatti et al. 2002; Ballard 2000; Chen et al. 1995; Prescott et al. 2000b). Higher rates of wood decomposition were associated with a group of plots within burned transects (Fig 4a), notably F1 and F2 (Fig. 4b). At our sites, the canopy structure was negatively affected at the forest edges (Harper et al. 2004), however burned edges were less abrupt than cut edges due to partial burning into the forest. Consequently, the edge effect for understory plants was measured further into the forest for burns, up to 40m (Harper et al. 2004). Conditions created by loss of canopy cover, such as increased irradiance and soil temperatures may have had a small positive affect on decomposition rates in the disturbance and edges in the burned transects. This affect may have been more pronounced in the burns due to the less abrupt nature of the edge, partial burns into the forest and a further reaching edge effect on the understory.

Local microclimate may be a confounding factor when attempting to detect differences in decomposition rates between transects in our study as soil and air temperatures may be dependent on local site conditions. It was found that edge orientation played an important role in determining local microclimate conditions at different sites (Chen et al. 1995). The edges at our sites had a wide range of orientations in both the cut and burn transects (Harper et al. 2004).

Results regarding decomposition rates in clearcuts have been varied (Prescott et al. 2000a; Chen et al. 1995), some studies showing increases and others, similar rates to within intact forests. Yin and Perry (1989) found that decomposition in clearcuts varied with regional climate conditions, and cutting only stimulated decomposition rates in colder climates due to increased temperatures associated with the clearcuts. Prescott et al. (2000a) found that decomposition rates for different substrates were the same in cold and warm climactic conditions and were also similar in clearcuts and in the forest, with the exception of pine needles that tended to decompose more slowly in the clearcuts. The fact that decomposition was not effected in logged areas of the transects in this study indicates that the conditions arising from changes in the canopy and soil conditions had a negligible effect and that large spatial variation in decomposition rates may be masking the effects of the disturbances.

Effect of the Disturbances on Nutrient Supply Rates. Nitrogen in the forms of NH_4^+ and Total N was found to be more abundant in a group of plots found within the burned transects, notably F1 and F2 as well as a few found in the cut transects, however, a larger group of plots in the cut transects are low in N and NH_4^+ and higher in B, Mg and Ca, notably C1 and C2 (Fig. 2a & 3b). Fires tend to release N as N_2 to the atmosphere through volatilization. N is also lost due to leaching and wind-blown ash. N loss is often offset by increased N fixation, due to higher microbial activity associated with post disturbance conditions as well as increased pH, soil temperatures and mineralization that occurs with increased decomposition (Ballard 2000; Bhatti et al. 2002: Wan et al. 2001). This N flush is used quickly by the initial regrowth of plants, which then replenish the soil N with their litter, but at a slower rate. The disturbances studied would have passed this period of highly fluctuating N levels. As with EM and decomposition rates, conditions within transects may have been more significant to nutrient supply rates, than those created by the disturbances.

The fire edges were uneven and partial burning into the forest from the edge was common (Harper et al. 2004). This structure may make detecting effects from the fires on nutrients along the edges difficult, as the edge measurements may not reflect actual edge at any given point. The edge effect in burns was much greater for understory plants, up to 40m into the forest (Harper et al. 2004). This may have had an effect on litter inputs and consequently nutrient supplies at the burn edges, however the structure of the edges themselves may have made detecting any effects of this difficult. Transects F1 and F2 were also located close together in a small burn. The character of this small fire and the consequent effects would be most likely be different from those in transect F3, which was located in a larger fire at a different site. The small burn transects would also be more likely to share similar localized conditions, such as drainage and stand age.

In logged sites, the loss of C from removal of tree biomass and through lack of leaf litter and woody debris inputs would have a significant effect on N levels (Bhatti et al. 2002; Ballard 2000). Soil compaction and loss of some organic layer may also have had an initial effect on N levels, as soil texture and pore size can effect C inputs and N mineralization (Côté et al. 2000). Palvianinen et al. (2005) found a decrease in N, P, K and Ca uptake by understory plants was detected in logged sites in Finnish boreal forest. Loss of cations such as Mg^+ and Ca^+ is correlated with the compaction of soil after disturbances, which is common in logged sites where machinery is used (Ballard 2000). Thiffault et al. (2008) found Ca and Mg in higher levels in soils disturbed by fires than in soils disturbed by logging. This is due to their high volatilization temperature, addition from ash with cations and its association with charred materials with high exchange capacities. A group of plots in the logged transects had higher supply rates of Ca, Mg and B and lower supply rates of Total N and NH_4^+, but none of these trends showed any relationship with the logged portions of the transects. Ca and Mg have a high retention in the soil exchange system and this may account for the high levels in some of our logged sites (Thiffault et al. 2008). The soil may have recovered from compaction, since the logging at these transects occurred 5 to 6 years before sampling and, as with the EM and decomposition rates, variation in nutrient levels within the transects appears to be more significant than the effects of the disturbances. Differences between transects may be partially explained by location. Transect C1 and C2 are located beside each other and may share more similar site conditions than C3. Within site variation of nutrients can be a confounding factor when attempting to detect what determines significant differences in nutrient levels. Laiho et al. (2004) found that, with a number of nutrients (Zn, Mn, Mg, Ca, K, Fe and P) within peat sites, differences between samplings would have to be considerable to overcome the uncertainty of site variation.

Conclusions. There is no evidence for the disturbances having had a significant effect on EM abundance, nutrient supply rates or decomposition rates, either as differences between disturbance types or as gradients along the transects. The only differences appear to be between transects. The EM community appears to be defined more readily by local and micro site conditions and perhaps, like other organisms in this forest system, is adapted to disturbances. Wood decomposition shows only a slight increase for a small number of plots in fire transects F1 and F2, but shows no association with the burned portions of the transects. Some nutrients also show correlations with either plots in cut (Ca, Mg and B) or burned transects (N) and again there are no significant effects of the disturbances. Differences between transect types may be associated with the structure of the fire edges, which are less abrupt, with many snags and partial burns into the forest and the fairly extensive edge effect in regards to understory plants (Harper et al. 2004). Local site conditions, such as stand characteristics, drainage, edge orientations and physical soil properties appear to have more of an effect on EM abundances, nutrient supply and decomposition rates than direct effects of the disturbances.

Chapter 4: Relationships between the Understory Plant Community and the Ectomycorrhizal Community, Nutrient Supply Rates and Decomposition Rates in the Boreal Black Spruce Forest of Abitibi Region, Québec.

Introduction

Plants in the boreal forests of Québec have adapted to major disturbances, such as forest fires. A number of strategies help plants to re-establish after a fire, including the production of long-lived fire dependent seeds, ericoid plants which act as reservoirs of mycorrhizal fungi and underground structures such as roots or rhizomes which are able to survive fires (Dahlberg 2002; Bradbury et al. 1998). Plant species life-history strategies are also important, for example, after a disturbance ruderal species may thrive initially until later stage plants can re-establish when local site conditions have changed (Haeussler et al. 2002; Chen et al. 1995). The influence of the fire regime on understory composition is well documented, including the lowering of cover by shrubs, altered composition due to a higher incidence of pioneer species and a reduction in plant cover, richness and diversity as species recover over time (De Grandpré et al. 1993; Harper et al. 2004). Harvesting has been shown to affect understory plant richness and B diversity (a measurement of species turnover) at larger scales (MacDonald and Fenniak 2007). In general the understory composition is affected by edaphic conditions and overstory composition (MacDonald and Fenniak 2007; Legaré et al. 2001).

Low diversity is typical of the black spruce forest in the Abitibi region of Québec, with ericaceous plants, *Sphagnum* and lichens dominating. Typically, ericaceous plants can tolerate the acid soils and the low availability of key nutrients (N and P). The litter type and volume produced by coniferous trees creates acidic conditions. Higher litter mass in coniferous forests in general may also inhibit the germination of understory plants, thus affecting understory biomass (Barbier et al. 2007). It is interesting to note that while mosses can typically survive in thick conifer litter cover, as they grow over litter with no contact with soil, they often are shaded and killed by large deciduous leaf-litter due to their slow growth rates and low height (Barbier et al. 2007). Our understanding of how both the overstory and understory respond together to site conditions and disturbance is not comprehensive and they may not respond in a parallel fashion (Barbier et al. 2007).

Disturbances such as fire and harvesting drastically reduce the overstory and, therefore, reduce the amount of litterfall, and moisture availability, and increase available light and near-surface temperatures. Since understory plants can respond to slight changes in soil conditions such as pH (Barbier et al. 2007; Haeussler 2002) overstory composition and biomass are important factors for the understory community. Different species of plants have different distances from tree trunks that are considered to be ideal for germination and growth. This, in part, creates the spatial heterogeneity of the understory. Loss of whole trees would therefore change the patterns of growth in the understory community (Barbier et al. 2007; Chen et al. 1995).

Plant composition is an important determining factor of fungal distribution within an ecosystem and patchy spatial distributions are typically found in EM communities (Dahlberg 2001). Links between mycorrhizal function and plant successions have been suggested; Massicotte et al. (1999) found that maintaining host diversity played an important role in mycorrhizal diversity and suggested a strong likelihood of the importance of fungal linkages between host trees; Janos (1980) found in tropical systems that this effect of plant composition on fungal communities will in turn influence which plants succeed and appear next in the succession. Net Carbon transfer by hyphal linkages has been shown to occur between different tree species (Simard et al. 1997) and if the direction of this transfer is primarily from early to late succession plants, Dahlberg (2001) suggests that mycorrhizae may be playing an important role in mediating the development of plant communities. Different fungal species in the EM relationship show some versatility in their ability to use nutrients (Perez-Moreno and Read 2000). This variability may play an important role in maintaining fungal diversity in a plant community. This varied and reciprocal interaction between the plant community as a whole and mycorrhizae is well documented and has a broad scope of possible implications.

Palviainen et al. (2005) found that the decrease in ground vegetation due to logging was accompanied by a decrease in the nutrient pools for up to 2 years after the disturbance. When the understory began to re-establish after the 2 year period, this was mirrored by a recovery of the nutrient pool. It was suggested that the understory was playing a vital role in controlling nutrient leaching long before the overstory was re-established.

Decomposition in the boreal forest is typically a slow process, largely due to the climatic conditions. Important factors influencing decomposition rates in the boreal forest are temperature, precipitation, substrate quality and soil drainage conditions (Bhatti et al. 2002). The characteristic topsoil of the boreal forest is an organic humus layer where decomposition takes place. It is composed of the remaining fragmented products of decomposition, such as the partly decomposed forest floor material, and it is chemically stabilized (Prescott et al. 2000b). In regions where temperatures are cold and excess moisture creates anoxic soil conditions, humus may accumulate and only decompose slowly, which can have a negative effect on seed germination and seedling growth (Prescott et al. 2000a).

In this Chapter I will discuss 1) the relationships between the understory plant plot types and specific plant species cover on the ectomycorrhizal community, nutrient supply rates and decomposition rates. It is hypothesized that the patterns in the understory plant community, created directly or indirectly by disturbances will correlate with 1) abundances of specific ectomycorrhizae and 2) increased or decreased nutrient supply rates, depending on the nutrient and 3) variations in decomposition rates which will depend on plot type and the dominant plants (by percent cover) in the plot. Therefore shifts in the belowground components of this ecosystem can be viewed as a response to the changing understory plant community, which is shaped by natural and human disturbances.

Materials and Methods

The Understory Plant Community. Data were collected from plots in 6 transects that started in disturbances (3 burns and 3 cuts) and continued into the intact forest, as described in Chapter 2. The plots were chosen to represent two extreme types of vegetation: ericoid/lichen and *Sphagnum*.

Characterization of the Ectomycorrhizal (EM) Community. The EM community from the created plots was characterized as described in Chapter 2.

Decomposition Rates and Nutrient Supply Rates. Decomposition and nutrient supply rates were determined as described in Chapter 3.

Statistical Analyses

Indicator Species Analysis (ISA). An ISA was performed as described in Chapter 3 to determine 1) whether any of the plant species were associated either with *Sphagnum* or ericoid/lichen plots, and 2) whether any relationships between the percent cover of specific plant species and EM abundances exist.

Ordinations. Bray Curtis, PCA and NMDS ordinations of EM abundances and plant species percent cover and a Bray Curtis ordination of nutrient supply rates, decomposition rates and pH were performed as described in Chapter 3 to determine whether any relationships exist between plant species percent cover and 1) ectomycorrhizal abundances, and 2) decomposition rates, and 3) nutrient supply rates.

Classification Tree. A Classification Tree was used to test the hypothesis that the different plot types will have different EM abundances, decomposition rates and nutrient supply rates. This analysis helps to determine which set of variables (the abundance of morphotypes, nutrient supply rates, decomposition rates and plant species percent cover) best describes whether a plot is cut-*Sphagnum*, fire-*Sphagnum*, cut-ericoid/lichen, fire-ericoid/lichen. A Classification Tree was performed using Version 6 of CART Pro.$_{\text{TM}}$ from Salford Systems, California Statistical Software Inc. The Gini algorithm was used, 10 fold cross validation (data split into 10 groups and best model that fit or predicted for all 10 groups was selected) and the most efficient tree was selected as the tree with the fewest nodes within 1 standard error of the tree with the fewest nodes (in this case they were the same).

The classification tree is a nonparametric analysis that finds threshold values of the variables that best divide the data set into predefined groups. It can identify the most important of these variables by progressively splitting samples into more homogeneous groupings. Continuous and categorical data can be used without assumptions. A full tree and a most efficient tree were created.

Results

The Understory Plant Community Composition in Sphagnum and ericoid/lichen plots. These two plot types represent the two extremes of the plant community in the transects. The *Sphagnum* plots, as expected, had more *Sphagnum,* but also more *G. hispidula* and *P. mariana,* while the ericoid/lichen plots had more lichen and *V. angustifolium* (ISA, Table 1). lichens and *V. angustifolium* are significantly correlated with each other in the two of the ordinations first axes (Tables 3 & 4, Ch.3). The same plant species that are associated in the ISA, group together in the ordinations axes and are therefore correlated with each other (Tables 2, 3 & 4, Ch.3).

The Understory Plant Community and the Ectomycorrhizal Community. Piloderma sp. 2/*Piloderma* sp. 3 are significantly more abundant in *Sphagnum* plots and significantly positively correlated with plant species associated with these plots, *Sphagnum, G. hispidula* and *P. mariana* (ISA, Table 1). *Piloderma* sp. 2 /*Piloderma* sp. 3 are significantly associated with *Sphagnum* in all three ordinations (Tables 2, 3 & 4, Ch.3; biplot, Fig. 1). The same general associations between the EM and plant species found in the ISA, also are found in the ordinations (Tables 2, 3 & 4, Ch.3; biplot, Fig. 1).

The *Piloderma* sp. 1 is more abundant in ericoid/lichen plots and significantly positively correlated with species found in these plots, that is lichens and *V. angustifolium* (ISA, Table 1). *Piloderma* sp. 1 is significantly associated with lichen in the first axis of the Bray Curtis ordination (Table 2, Ch. 3). The same general associations of the EM and plant species found in the ISA, are also seen in the ordinations (Table 2, Ch.3; biplot, Fig 2*)*.

Cenococcum geophilum is not strongly associated with either plot type (ISA Table 1; biplot, Fig. 3). *C. geophilum* is only significantly positively associated with the abundance of lichen in the second axis of the Bray Curtis ordination (Table 2, Ch.3) but is closely associated with lichen and *V. angustifolium* in the first axes of the other ordinations (Tables 3 and 4, Ch.3).

The rare morphotype Small cigar is more abundant in ericoid/lichen plots and associated with plant species correlated with these plots, that is, lichen and *V.angustifolium* (ISA Table 1; ordinations, Table 2, Ch.3).

The Understory Plant Community and Decomposition Rates and Nutrient Supply Rates.

In general, the majority of nutrient supply rates do not show strong associations with different plot types (ordination, Table 5, Ch.3). The exceptions are Pb and K, which are positively correlated with a group of ericoid/lichen plots (biplots, Fig. 1a and Fig. 1b).

Zn is positively associated with *Sphagnum* plots from the burned transects. The most efficient classification tree shows that of *Sphagnum* plots with more than 65% cover *Sphagnum*, those with Zn concentration greater than 4.8 were all from transects containing burned areas (see Classification tree, Results).

Some nutrient supply rates are associated with specific transects, Ca, Mg and B with C2 and C3; and Zn, Cu, total N and NH_4^+ with F1 and F2, but not with plot types within these transects (biplot, Fig. 1b).

A group of *Sphagnum* plots have increased rates of wood decomposition (biplot, Fig. 1a) Theses plots tend to be found in transects F1 and F2 (biplot, Fig. 1b). These plots also show increased Zn and lower levels of K.

Table 1: Results of Indicator Species Analysis to see if ectomycorrhizal abundances or plant species percent cover were associated with 1(ericoid/lichen) or 2 (*Sphagnum*) plots. The bold variables were significantly associated with *Sphagnum* and the *symbol with ericoid/lichen plots (alpha = 0.10). The *p* value is equal to the proportion of randomised trials with indicator values equal to or exceeding the observed indicator value (*p*= 1 + number of runs >= observed) / (1+ number of randomised runs). The alpha is equal to 0.10. The Maxgroup is equal to the group identifier for group with the maximum observed IV (Indicator Value).

Species	Observed Indicator Max Value	IV from randomized groups (IV)	Mean	Standard Deviation	p value
C. geophilum	1	42.5	45.8	2.62	0.9984
Piloderma sp. 1	1	23.2	16.0	3.22	0.0348 *
Piloderma sp. 2/ *Piloderma* sp. 3	2	60.6	34.1	3.30	**0.0002**
Striated Clamp	1	3.0	3.4	1.50	0.6177
H. roseobrunneus	2	7.5	9.8	2.60	0.8034
H. roseobrunneus/ C. cinnamomeus	2	16.7	19.8	3.60	0.7864
White clamp	1	4.9	6.8	2.23	0.8028
Cortinarius sp.	1	17.6	16.8	3.56	0.3423
White verrucose	1	4.5	5.4	2.03	0.5907
Orange fan	2	9.5	10.4	2.81	0.5285
Small cigar	1	12.1	7.4	2.36	0.0446 *
Clear bulbous	1	6.1	5.4	1.97	0.3125
Russula-like	1	19.9	24.2	3.76	0.9502
Cort	1	3.2	3.2	1.25	0.5085
Brown clamp	2	3.9	3.4	1.48	0.3673
Cystidia	1	5.0	2.9	1.22	0.2438
Big brown	2	6.5	7.3	2.26	0.5685
Big orange	2	6.1	5.7	1.97	0.3451
White pilo	1	1.7	1.7	0.02	1.0000
Sphagnum	2	85.9	4.7	2.71	**0.0002**
Lichen	1	92.2	34.1	3.92	0.0002 *
L. groenlandicum	2	54.5	52.8	2.60	0.2256
V. angustifolium	1	57.8	36.6	3.97	0.0002 *
G. hispidula	2	53.4	28.6	4.16	**0.0002**
C. calyculata	1	21.5	24.2	4.03	0.6965
P. mariana	2	33.8	28.1	3.85	**0.0882**

Figure 1a and b: Biplots are from the Bray Curtis ordination of nutrient supply and decomposition rates. Fig. 1a shows the relationship between nutrient supply, decomposition rates and plot type. Fig. 1b shows the relationship between nutrient supply rates, decomposition and individual transects.

Figure 1a

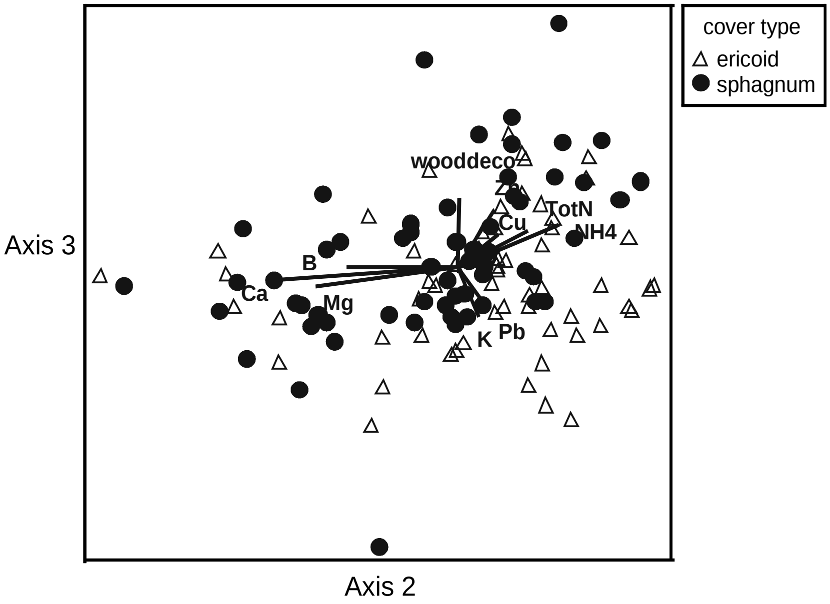
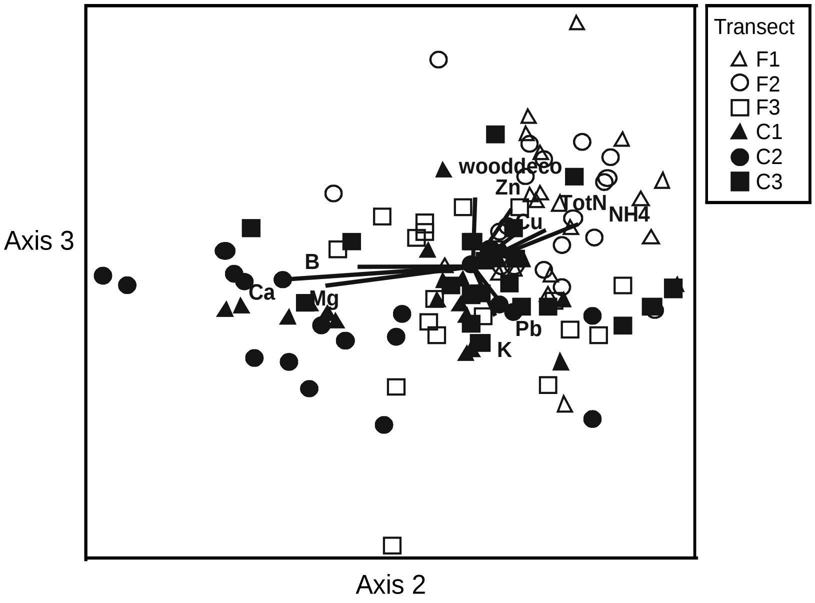


Figure 1b



Discussion

Relationships Between the Understory Plant Community and the EM Community. The most abundant and frequent EM species found in this study, *C. geophilum, Piloderma sp. 1 and Piloderma sp. 2/Piloderma sp. 3* show the most significant association with specific plot types and the percent cover of specific plant species. The results show, that, not only are the most abundant morphotypes showing important relationships with the plant community, but that some of the more rare types also show similar, but weaker trends. The specific EM/plant associations found, and the fact that the understory vegetation is affected by the disturbances (Harper et al. 2004), suggests that if we want to explore how the ectomycorrhizal community will be affected by disturbances, we can look at how the understory vegetation responds to the disturbances. What kinds of mechanisms could be at work in the plant community and the mycorrhizosphere that would establish these preferential relationships?

Shrub density, litter patch size and quality have been shown to be associated with EM distribution. Conn and Dighton (2000) showed that the density of ericaceous stems positively affected the litter patch size in upland pine/oak forests. Smaller patches contained a higher percentage by weight of needles and large patches a higher percentage by weight of oak leaves. This suggests that if a disturbance had an effect on ericaceous shrubs, this may in turn affect the type and amount of litter that collects in a given patch. Conn and Dighton (2000) found that EM diversity was higher in larger litter patches and that different morphotypes were found in different litter types. The physical environment could be changed by removal, damage or burning of shrubs or by naturally occurring difference in the environment due to the patchy understory plant composition. This could alter the chemical environment through changes in litter accumulation and in turn affect EM diversity and community composition. The association of different ectomycorrhizae with different plot types in our study may be in part the result a similar type of mechanism determining a highly spatially variable EM community that still shows some microsite preferences in part determined by the plant species and their percent cover.

EM communities are often very diverse even in stands dominated by a single tree species (Bruns 1995), however, links between overstory tree diversity and EM diversity have been made (DeBellis et al. 2006; Kernaghan et al. 2003). In the boreal forest at our sites, the canopy is almost solely dominated by *P. mariana*, (*A. balsamea* and *L. laricina* were uncommon) and the EM characterized were only from Spruce roots. Kernaghan et al. (2003) showed a correlation between overstory diversity and EM diversity in mixed boreal stands of different types, and no correlations were found between other factors measured, such as understory diversity and soil chemistry. DeBellis et al. (2006) found that the distribution of EM was influenced by the relative proportion of overstory host trees. Given that the overstory at our site is dominated by one tree species and therefore EM host preference or relative proportion of overstory trees would not be playing a role in EM diversity or composition at the local site level, the understory plant community composition may play a more vital role in indirectly determining local EM composition through litter characteristics, soil chemical and physical characteristics and nutrient cycling. The correlations between understory plants and EM morphotypes could also indicate similar preferences for site types, such as would be determined by drainage and soil chemistry. Reviewing the evidence linking host diversity, species composition and stand age to regulating ectomycorrhizal communities, Johnson et al. (2005) found that there was no consistent evidence to substantiate the relationships. Rather it is suggested that non-EM fungal species associated with the understory would be competing with EM for resources, and therefore EM diversity is being regulated by indirect effects, such as, litter chemistry rather than by more direct effects such as carbon allocation.

The ericaceous understory plants also show more direct interactions with mycorrhizae. Certain species of ericaceous understory plants, such as *Arctostaphylos uva-ursi* (Bear berry) may act as reservoirs of ectomycorrhizal inoculum after disturbances (Dahlberg 2002; Dahlberg 2001; Bradbury et al. 1998). If there is a die-off of tree roots, patches of EM hyphae may establish relationships with available understory plants and re-establish with tree host species as regeneration occurs. Ericoid plant roots, although typically located in the top layers of soil and therefore susceptible to fires, form rhizomes that tend to survive (Dahlberg 2002). Bergero et al. (2000) have shown that a *Quercus* species found in the Mediterranean forms ericoid mycorrhizal symbioses that usually form on an ericaceous shrub. It is suggested by sharing mycorrhizae that not only are reservoirs of inoculum present but that hyphal linkages between these species may allow nutrient transfer (Bergero et al. 2000).

Mycorrhizal fungal partners may show differing abilities to absorb, retain and use nutrients in boreal environments (Perez-Moreno and Read 2000; Pellissier and Souto 1999) and these differences could play a role in the understory plant/EM relationship. The fungal partners may also have different tolerances to the allelopathic chemicals produced by ericaceous plants. Phenolic compounds produced by ericaceous plants have been shown to be inhibitory to conifer EM species (Mallik 2000; Yamaski et al. 1998) although more tolerant fungi can metabolise phenolic compounds (Pellissier and Souto

1999). *Cenococcum geophilum* is associated with both types of plot (see Results; ordination Tables 2, 3 & 4, Ch. 3, ISA Ch. 4) and has been shown to be tolerant to phenolic compounds (Pellissier and Souto 1999). The *Piloderma sp. 2/Piloderma sp. 3* were associated with *Sphagnum* plots and *Piloderma sp. 1* was associated with ericoid/lichen plots. This may reflect varied tolerances and abilities to metabolise phenolics between different species or genotypes within the *Piloderma* genus.

This separation of species or genotypes into two distinct vegetation types and the other correlations of EM with plot types or associated plants, points to the possibility of unique and specific relationships between understory plants and EM fungi. Read and Perez-Moreno (2003) state that because in boreal systems fungal partners are responsible for nutrient supply to their plant partners, the symbiosis is responsible for control over nutrient cycles, species composition and productivity in this biome.

Understory Plant Community and Nutrient Supply Rates. Understory plants essentially become the dominant vegetation temporarily in areas where disturbances have removed the tree canopy. The understory therefore acts as a dynamic pool for nutrient uptake and cycling during the canopy recovery and regrowth (Palviainen et al. 2005).

Several nutrient supply rates are associated with specific plot types. Levels of Pb and K are higher in a group of ericoid/lichen plots (Fig. 1a). This group of plots has an average pH that is low at 3.8 (acidic), however, other factors such as ectomycorrhizal type, specific plants species or decomposition rates in these plots show no other obvious differences when compared to other plots. In general only weak relationships exist between pH, specific nutrients and either plant cover or EM abundance (ordination, results not shown).

The ericoid/lichen plots tended to be drier, and the association of Pb and K with these sites may be linked to the conditions in the well drained soil. As water logged soils tend to be anoxic to microbes, levels of nutrients in the soil may not reflect their availability (Bhatti et al. 2002) and water logged soils often experience structural damage (Ballard 2000). Laiho et al. (2004) found that K concentrations were lower in drained peatland sites. However, K in peatlands is mostly soluble and moves freely with water (Starr and Westman 1978) and this may explain its retention in drier plots.

Sites with higher percent cover of ericaceous plants normally have higher levels of Fe, Zn, K, Ca, Mg and Mn, which can lead to longer term deterioration of a site, and lower N due to the forming of protein-phenolic complexes (Mallik 2003). Plants in these sites may therefore also be adapted for different nutrient regimes or more tolerant of the conditions produced by the ericaceous plant themselves. Zn is associated with *Sphagnum* plots from our study (Fig. 1a biplot; Classification Tree, see Results). The influence of the *Sphagnum* cover should be a more important factor than disturbance type for the classification tree, as the results include all plots within fire transects, not only those in the disturbed areas. The common presence of the ericaceous shrubs *L. groenlandicum* and *G. hispidula* in *Sphagnum* plots may in part explain the higher levels of Zn normally associated with soils with ericaceous shrubs.

Understory Plant Community and Decomposition Rates. A group of *Sphagnum* plots have higher wood decomposition rates (Table 5, Ch.3; Fig 1a). In general *Sphagnum* plots have a greater abundance of *Piloderma sp. 2* and *Piloderma sp. 3*. However specific plots with higher rates of woody decomposition do not necessarily have an abundance of these Pilodermas, which have been associated with the decomposition of woody substrates (Hagerman et al. 1999b; Cairney and Burke 1998). The average pH level in S*phagnum* plots with high rates of wood decomposition was found to be higher (4.15 pH) than the overall transect average, however no significant correlations between decomposition and pH were found (ordinations, results not shown). The most notable difference in soil conditions between *Sphagnum* and ericoid/lichen plots is the water logged nature of the moss dominated plots. Normally large amounts of moisture cause oxygen deficiencies in soil, and when combined with a cool climate, these factors have been found to cause accumulation of organic matter in boreal peatlands (Prescott et al. 2000b). However the *Sphagnum* plots with high wood decomposition were largely in fire transects (Fig. 1b), which had uneven edges with partial burns into the forest. This may have resulted in these *Sphagnum* plots being less likely to be water logged. Localized conditions such as pH levels and soil moisture and temperature may therefore be affecting wood decomposition rates at a microsite level. Decomposition rates near forest edges are determined largely by soil temperature and soil moisture regimes (Chen et al. 1995).

Litter characteristics, which would be different between plot types, have been shown to affect soil biota (Conn and Dighton 2000). Small local variations in soil biota could also be playing a role in increased wood decomposition rates in some *Sphagnum* plots.

The Underground Components and the Understory Plant Community's Response to the Disturbances (logging and fires). The understory plant community has been shown to have some significant effects on the belowground variables in this study. A study by Harper et al. (2004) within the same transects showed that the understory plant community was significantly affected by the disturbances in these transects.

Mosses are sensitive to trampling and damage by machinery (Palviainen et al. 2005), however, Harper et al. (2004) found that *Sphagnum* moss cover had the highest Depth of Edge Influence (DEI, see Appendix for definition) for moss species for the burned edges at our sites and that a persistent *Sphagnum* layer found in the cuts could in part be responsible for the slow regeneration of spruce seedlings in the logged areas (Boudreault et al. 2002; Harper et al. 2004).

Ericaceous plants tend to re-establish quickly and vigorously from surviving underground root structures (Mallik 2000) especially in burned areas. Harper et al. (2004) suggest that slow shrub recovery (*C. calyculata, K. angustifolia, K. polifolia* and *L. groenlandicum*) in these logged sites may be due to damage by machinery and changes in the microclimate and soil conditions at the forest edges and that two shrub species (*V. myrtilloides* and *L. groenlandicum*) with positive edge of influence might have been caused by increased light and nutrient availability after fires or regeneration from rhizomes.

Fewer understory species were affected on the forest side of the fire edges with the exception of shrubs (*C. calyculata, K. angustifolia, K. polifolia* and *L. groenlandicum*), which had greater DEIs (see appendix for definitions) at these edges. Most shrubs (*C. calyculata, K. angustifolia, K. polifolia*, *L. groenlandicum*, *Salix* spp., *V.angustifolium, V.myrtilloides*), and herbs (*Carex* spp., *C.groenlandica, Equisetum* spp., *G.hispidula, L borealis, P.palmatus, R.chamaemorus, S.trifolia, V.oxycoccos)* had greater MEIs at the cut edges, however, the absolute value of MEI was larger at fire edges for a number of moss and lichen species.

Harper et al (2004) found that in general the influence of the edge was greater in burned transects (up to 40m into the forest from the edge), than in cut transects (5m into the forest from the edge). Fire edges had a more gradual change in canopy cover and were less even from partial burning into the forest, and this was still apparent at the time of our study. At logged edges, however, more species were affected, with greater DEI measurements. Many of the plant species with significant percent cover in our plots were affected negatively by influence of edge effect such as lichens, *Sphagnum*, *G. hispidula*, *L. groenlandicum*, *P. mariana* and *C. calyculata* (Harper et at. 2004).

Conclusions. Harper et al. (2004) have shown that the understory plant community at this site was indeed affected by the disturbances and that the effect was different between disturbance types. The fire edges were more gradual and cut edges tended to be more abrupt (see above discussion).

Results from this study show a consistent and strong association between understory vegetation plot types and/or their associated plant species and specific ectomycorrhizal species. *Piloderma sp. 2/Piloderma sp. 3* were more abundant in *Sphagnum* plots and correlated with plant species associated with these plots, that is *Sphagnum, G. hispidula* and *P. mariana*. The *Piloderma sp. 1* are more abundant in ericoid/lichen plots and positively correlated with species found in these plots, that is lichens and *V. angustifolium*. *Cenococcum geophilum* is found abundantly in both plot types, however, it is correlated with lichen and closely associated with *V. angustifolium*. This relationship exists not only with EM species that occurred abundantly and frequently but also with a number of the more rare EM morphotypes and species characterized in this study. This relationship between the understory plants and EM fungi could be driven by similar site preferences, such as drainage, soil chemistry and temperature, and litter characteristics, which would be in part be mediated by the plants and fungi themselves. In this ecosystem where the canopy is dominated by a single tree species, the understory may play a more integral role in EM community structure. The patchy yet ubiquitous presence of ericaceous plants means the presence of phenolic compounds in the soil; spatial distribution of EM may in part be regulated by the varying tolerance of EM species to metabolize these compounds.

The relationships between the understory plant community and nutrient supply rates and decomposition rates were generally found to be weak.

General Conclusions

The main goals of this study were to 1) describe the EM community in the black spruce forest of Northern Québec, 2) determine if any effect of disturbance type (logging and fires) was detectable on EM abundances, nutrient supply rates and decomposition, and 3) determine if plot type (*Sphagnum* or ericoid/lichen) and plant species percent cover had an effect on EM abundances, nutrient supply rates and decomposition. In general the EM community had low diversity compared with other studies of boreal systems, with several species typical of mature northern conifer forest, dominating the assemblage. The disturbances were found to have a minimal impact upon all the belowground components studied and differences between disturbance types were also negligible. The most interesting findings were the associations between both plot types and plant species percent cover and specific EM abundances.

In Chapter 2, I showed that the plant community is composed of a continuous mosaic of dry ericoid/lichen and wetter *Sphagnum* dominated patches. The EM community appears to be unique, showing an unusually high dominance of *C. geophilum,* although this may have been overestimated, a recognized problem when morphotyping this species. A number of *Piloderma* species are also abundant as well as occurring frequently in soil samples. *Russula,* an EM genus typically common in many forest types, was detected by morphotyping, however not abundantly, and was not detected by sequencing.

In Chapter 3, where the effects of logging and forest fires on the underground components in this study were investigated, there was no strong evidence that the disturbances had a significant effect on EM abundance, nutrient supply rates or decomposition rates, either as differences between disturbance types or as gradients along the transects. Any differences detected appear to be between transects. The EM community may therefore be defined by local and micro site conditions, and perhaps, like other organisms in this forest system, are adapted to disturbances. Wood decomposition was slightly higher for a small number of plots in fire transects F1 and F2, but shows no association with the burned portions of the transects. Some nutrients also show higher values in cut (Ca, Mg and B) or burned transects (N) and again there are no significant effects of the disturbances. Differences between transect types may be associated with the structure of the fire edges, which are less abrupt, with many snags and partial burns into the forest and the fairly extensive edge effect in regards to understory plants (Harper et al. 2004). Differences between transects may therefore indicate that local transect conditions, such as stand characteristics, drainage, edge orientations and physical soil properties could have more of an effect on EM abundances, nutrient supply and decomposition rates than direct effects of the disturbances.

The understory plant community at this site was indeed affected by the disturbances and the effect was different between disturbance types (Harper et al. 2004). In Chapter 4, the most significant and interesting results showed a consistent and strong association between understory vegetation plot types and/or their associated plant species and specific ectomycorrhizal species. A persistent *Sphagnum* layer was found in the disturbance at logged sites and the highest Depth of Edge Influence (DEI) for *Sphagnum* was found at burned edges (Harper et al. 2004). The correlations between *Sphagnum* and the *Piloderma* sp. 2 and sp. 3 could indicate that the disturbances affected abundances of these Pilodermas negatively in burned sites and positively in cut sites. *G. hispidula* was also found to be negatively affected by both logged and burned disturbance areas (Harper et al. 2004). The association of *Piloderma* sp. 2 and sp. 3 with *G. hispidula* could indicate this species was negatively affected in both logged and burned sites. Lichen cover was negatively affected in both logged and burned disturbance areas although overall DEI values were more significant at cut edges (Harper et al. 2004). The correlations between *Piloderma* sp. 1 and lichen may mean that the abundances of this EM species was negatively affected by both logging and forest fires, although perhaps more notably at cut edges. *C. geophilum* may also have been negatively affected in both logging and forest fires in the same manner, as it was also correlated with lichen. This relationship between the understory plants and EM fungi could be driven by similar site preferences, such as drainage, soil chemistry and temperature and litter characteristics, which would in part be mediated by the plants and fungi themselves. In this ecosystem where the overstory is dominated by a single tree species, the understory may play a more important role in EM community structure. The patchy yet ubiquitous presence of ericaceous plants ensures the presence of phenolic compounds in the soil and spatial distribution of EM may in part be regulated by the varying tolerance of EM species to these compounds. Further investigation into the mechanisms that cause these associations between EM abundances and the understory plant community would contribute to understanding these findings.

The understory plant community correlates less with nutrient supply rates. Our results show that only a few nutrients show associations with plot types or associated plant species and these are either weak correlations or only occur in a small number of plots. Zn is the possible exception to this, as the ordinations show higher Zn levels in a group of *Sphagnum* plots, largely from adjacent transects F1 and F2.

In general a weak relationship exists between the understory plot types and associated plant species and decomposition rates. Wood decomposition was higher in a group of *Sphagnum* plots, largely from fire adjacent transects F1 and F2, where local site conditions may again be playing a role in the results. Higher pH levels, the possible influence of high soil moisture in *Sphagnum* plots, and differences in soil biota due to different litter characteristics may be playing a role in the slight increase in wood decomposition in these plots. Both disturbances and the understory plant community appear to have a minimal effect on nutrient supply rates and decomposition. It should be noted that the effects of the disturbances on nutrient supply and decomposition rates may have been more apparent closer to the time of the disturbances. Further studies into what important factors are affecting in these vital components of the boreal ecosystem are needed to understand the role they play in long term forest health.

This study showed that although EM, nutrients and decomposition in the black spruce boreal forest may not have been directly affected by disturbances, there were important indirect effects on the EM community via the changes in the plant community caused by logging and forest fires. This emphasises the importance of considering both above and below ground factors when establishing viable sustainable forestry practices.

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Appendix 1. Definitions

Magnitude of edge influence (MEI): is a measure of the strength of edge influence,

MEI= $(x_d-x_i)/(x_d+x_i)$

x_d is the mean of a variable at distance d from the edge, x_i is the mean of a variable in interior forest at distances 100, 150 and 200m from the edge. The MEI varies from -1 to 1 and positive values indicate positive responses to edge influence (that is values greater at the edge than in interior forest) and negative values indicate negative responses (values lower at the edge than in interior forest), a result of zero indicates no edge influence (Harper et al. 2004).

Depth of edge influence (DEI): a critical values approach was used in this study to calculate DEI, where mean values of response variables at different distances from the edge are compared with critical values of interior forest conditions derived from re-sampling values from the interior forest. A full explanation of the critical values approach to measuring DEI can be found in Harper et al. (2004.

Appendix 2. Monte Carlo Test for NMDS ordination: Stress in Relation to Dimensionality (Number of Axes)

Stress in real data (50 runs)				Stress in randomized data Monte Carlo test (50 runs)			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	34.798	47.323	57.252	40.447	45.035	57.252	0.0196
2	21.417	22.671	24.948	21.373	23.536	26.417	0.0392
3	15.532	15.784	16.509	15.302	16.336	17.670	0.0588
4	11.911	12.097	12.703	11.263	12.311	12.998	0.1765

p = proportion of randomized runs with stress < or = observed stress
i.e., p = (1 + no. permutations <= observed)/(1 + no. permutations)

Appendix 3. Broken-stick Eigenvalues for PCA ordination: Variance extracted from the first 10 Axes.

Axis	Eigenvalue	Percent of Variance	Cumulative Percent of Variance	Broken-stick Eigenvalue
1	24.579	24.623	24.623	14.798
2	11.653	11.674	36.297	10.959
3	8.489	8.504	44.801	9.039
4	7.750	7.764	52.565	7.759
5	4.827	4.835	57.400	6.800
6	4.492	4.437	61.837	6.032
7	4.172	4.179	66.016	5.392
8	3.822	3.829	69.845	4.843
9	3.550	3.557	73.402	4.364
10	3.348	3.354	76.756	3.937