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Response of Fungal Communities and Microbial Processes
to Forestry Practices in Mixedwood Forests

by

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Abstract

Response of the decomposer fungal community and microbially-mediated processes to harvesting and vegetation management were examined in three mixedwood forests in Ontario, Canada. Seven to 9 years following harvesting and 2 years after vegetation management was initiated, organic and mineral soil was sampled from each of five treatments; 1. unharvested, 2. harvested, 3. glyphosate application, 4. triclopyr application and 5. brushsaw use. Harvesting and vegetation management had no significant effect on basal respiration, microbial biomass C, metabolic quotients (qCO_2), $C_{mic}:C_{org}$ and nitrogen mineralization in either organic or mineral soil. Fungal community structure as indicated by rank abundance curves and fungal species richness, diversity, evenness and dominance also were not impacted in either soil layer, although harvesting caused fungal community richness and diversity in organic and mineral soil to become more similar. Vegetation management decreased the isolation frequencies of two fungal species (*Mortierella vinacea*, *Paecilomyces carneus*).

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Table of Contents

Approval page.....	ii
Abstract.....	iii
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vi
List of Figures.....	vii
 1. INTRODUCTION.....	 1
1.1 Literature Review.....	1
1.2 Thesis Rationale.....	11
1.3 Study Objectives.....	13
 2. RESPONSE OF MICROBIAL PROCESSES AND FUNGAL COMMUNITY STRUCTURE TO CLEAR-CUTTING AND SITE PREPARATION IN MIXEDWOOD FOREST SOILS.....	 14
2.1 Introduction.....	14
2.2 Methods.....	17
2.3 Results.....	26
2.4 Discussion.....	44

Table of Contents concluded

3. RESPONSE OF MICROBIAL PROCESSES AND FUNGAL COMMUNITY STRUCTURE TO VEGETATION MANAGEMENT IN MIXEDWOOD FOREST SOILS.....	50
3.1 Introduction.....	50
3.2 Methods.....	54
3.3 Results.....	57
3.4 Discussion.....	68
4. CONCLUSIONS.....	75
5. BIBLIOGRAPHY.....	79
6. APPENDICES.....	86

List of Tables

Table	Page
2.1 Abiotic parameters in organic and mineral soil layers of two mixed-wood forest sites, 7 to 9 years after clear-cutting and site preparation.....	27
2.2 Microbial processes in organic and mineral soil layers of two mixedwood forest sites, 7 to 9 years after clear-cutting and site preparation.....	29
2.3 Sorenson's similarity coefficient for fungal communities in organic and mineral soil layers of unharvested and clear-cut and prepared forest soil.....	35
2.4 The most frequently isolated fungal species (overall frequency > 2%) from the organic and mineral soil layers of two mixedwood forest sites, 7 to 9 years following clear-cutting and site preparation.....	36
3.1 Abiotic parameters in organic and mineral soil layers of three harvested forest sites, 2 years following application of triclopyr, glyphosate or using brushsaws.....	58
3.2 Microbial processes in organic and mineral soil layers of three harvested forest sites, 2 years after imposing vegetation management procedures (glyphosate, triclopyr, brushsaw use).....	59

List of Tables concluded

Table		Page
3.3	Sorenson's similarity coefficient for fungal communities in organic and mineral soil layers of clear-cut and site prepared, and vegetation managed sites.....	69
3.4	The most frequently isolated fungal species (overall frequency >2%) from the organic and mineral soil layers of three clear-cut and prepared mixedwood forest sites, 2 years after using glyphosate, triclopyr or brushsaws.....	65
6.1	Fungal species isolated from the organic and mineral layers of two mixedwood forest soils, 7 to 9 years following clear-cutting and site preparation.....	86
6.2	Fungal species isolated from the organic and mineral layers of three harvested forest soils, 2 years after using glyphosate, triclopyr or brushsaws.....	93

List of Figures

Figure		Page
2.1	Rank abundance curves for all fungal species isolated from the organic and mineral layers of two undisturbed mixedwood forest and adjacent harvested sites, 7 to 9 years after clear-cutting and site preparation, a. organic layer species, b. mineral layer species.....	31
2.2	Fungal community indices for all fungal species isolated from the organic and mineral soil layers of two undisturbed mixedwood forest and adjacent harvested sites, 7 to 9 following clear-cutting and site preparation, a. species richness (no. fungal species/ 20 particles, b. species diversity (1/ Simpson's index), c. species evenness (Shannon's index), d. species dominance (Berger-Parker).....	33
2.3	A comparison of rank abundance curves at the species and genus level for all fungi isolated from the organic soil layers of two undisturbed mixedwood forest and adjacent sites, harvested 7 to 9 years previously, a. species level, b. genus level.....	41
2.4	A comparison of rank abundance curves at the species and genus level for all fungi isolated from the mineral soil layers of two undisturbed mixedwood forest and adjacent sites, harvested 7 to 9 years previously, a. species level, b. generic level.....	43

List of Figures (concluded)

Figure		Page
3.1	Rank abundance curves for all fungal species isolated from the organic and mineral soil layers of three mixedwood sites which were clear-cut and prepared, and two years prior to sampling were treated with herbicides (glyphosate or triclopyr), manual brushsaws or left untreated, a. organic layer species, b. mineral layer species.....	62
3.2.	Fungal community indices for all fungal species isolated from the organic and mineral soil layers of three mixedwood sites which were clear-cut and prepared, and two years prior to sampling were treated with herbicides (glyphosate or triclopyr), manual brushsaws or left untreated, a. species richness (no. fungal species/ 20 particles), b. species diversity (1/ Simpson's index), c. species evenness (Shannon's index), d. species dominance (Berger-Parker).....	64

1. Introduction

This introduction contains three sections; 1.1 a literature review of clear-cutting, site preparation and vegetation management effects on plant communities, forest soils and soil microorganisms 1.2 thesis rationale 1.3 study objectives.

1.1 Literature Review

Response of forest soils, plant communities and soil microbial communities to clear-cutting and site preparation.

Clear-cutting is the primary method of forest harvesting utilized in Canada (Jewett et al. 1995) and involves the complete removal of over and understory trees in an area (Keenan & Kimmins 1993). Clear-cutting in conjunction with ground skidding, where cut logs are dragged to a central log pile, can damage unharvested vegetation (Oswald 1990) and disturb the soil through compaction and exposure of mineral soil (Johnson et al. 1991a; Keenan 1987).

Canopy removal during clear-cutting increases amounts of precipitation and solar radiation reaching the soil surface and decreases evapotranspiration which can result in summer increases in soil temperature (Frazer et al. 1990; Marra & Edmonds 1996) and moisture (Frazer et al. 1990). Increased surface run-off and water movement through the soil combined with decreased evapotranspiration following clear-cutting and the suppression of vegetative re-growth can increase streamflow, soil erosion (Likens et al. 1970; Bormann et al. 1974) and may make steeper forest sites more vulnerable to

landslides.

Organic soil is the major source of leached nutrients following clear-cutting (Dahlgren & Driscoll 1994). Concentrations of nitrate, ammonium and mineralizable N decrease in the organic soil (Schmidt et al. 1996) as the production and leaching of ammonium and nitrate increases following clear-cutting (Dahlgren & Driscoll 1994). Total phosphorus is reduced in the organic soil (Schmidt et al. 1996) but phosphate concentrations are unaffected (Dahlgren & Driscoll 1994) or decrease (Schmidt et al. 1996) following clear-cutting. Leached sulphate, phosphate and ammonium are retained in the mineral soil through adsorption to clay particles (Dahlgren & Driscoll 1994; Maynard 1995) but nitrate is rapidly lost as clear-cutting results in tree root senescence and the primary method of nitrate immobilization is biological retention in the rooting zone (Maynard 1995). Carbon and nitrogen content (Bauhus 1996; Chang et al. 1995; Olsson et al. 1996b; Schmidt et al. 1996) and the C:N ratio may decrease in the organic soil and increase in the mineral soil (Olsson et al. 1996b), although, Schmidt et al. (1996) found clear-cutting to increase C:N in organic soil. Potassium (Dahlgren & Driscoll 1994; Likens et al. 1970; Romanowicz et al. 1996), sodium, aluminum, magnesium and calcium ions increase in soil solutions following harvesting (Dahlgren & Driscoll 1994; Likens et al. 1970); the leaching of these ions has been correlated to increases in leachate nitrate concentrations (Likens et al. 1970). Clear-cutting may also reduce potassium, calcium (Olsson et al. 1996a; Schmidt et al. 1996), magnesium (Olsson et al. 1996a), sulfur and manganese in forest mineral soil (Schmidt et al. 1996), base saturation (Johnson et al. 1991b; Olsson et al. 1996a; Schmidt et al. 1996) and pH

(Dahlgren & Driscoll 1994; Johnson et al. 1991b; Likens et al. 1970; Schmidt et al. 1996).

Harvesting improves the light, moisture and nutrient conditions for unharvested vegetation by removing the competition from trees. Clear-cutting affects plant community structure (Carleton 1994; Harrington & Edwards 1996; Mou et al. 1993) although the impacts vary with the intensity and method of harvesting used (Carleton 1994). The density of most regenerating tree species increases or decreases depending on their requirements and mode of reproduction (Mou et al. 1993). Reiners (1992) found clear-cutting to not affect plant species composition, although the relative abundances of plant species are altered with species evenness at a maximum immediately following clear-cutting and decreasing with time. Harrington & Edwards (1996) found clear-cutting continued to promote tree species evenness and diversity after three years.

Following clear-cutting, cut blocks are often re-planted with conifer seedlings. To facilitate the establishment of planted conifers, efforts are made to reduce competition from faster growing non-crop vegetation. In general, the major competitors of coniferous crop trees are grasses during early establishment and hardwood trees and shrubs during later stages in conifer growth. A technique for improving conifer establishment is mechanical site preparation which is performed on clear-cut blocks before conifer seedlings are planted (Ehrentraut & Branter 1990). Machines available for site preparation are designed to disrupt the seed bed and existing root systems by removing the organic soil and exposing the mineral soil beneath. Conifer seedlings are often planted on exposed mineral soil where they have a competitive advantage over non-

crop vegetation (Oswald 1990). In the present study, site preparation involved the use of Young's teeth and disk trenchers, machines which create furrows in the organic and upper mineral soil layers.

The disruption of soil layers during site preparation causes the vertical and horizontal redistribution of organic and surface mineral soils (Johnson et al. 1991a) and can result in soil erosion (Oswald 1990) and increased soil temperature and moisture (Ohtonen et al. 1992). Total nitrogen (Ohtonen et al. 1992; Schmidt et al. 1996), carbon (Schmidt et al. 1996) and calcium (Ohtonen et al. 1992), and the concentrations of nitrate (Ohtonen et al. 1992), ammonium, mineralizable N (Schmidt et al. 1996) and phosphate (Ohtonen et al. 1992) have been found to decrease following site preparation. In addition, site preparation can increase pH and base saturation (Schmidt et al. 1996).

The method of site preparation used determines the impact on the plant community. Machines which remove most of the organic layer have greater impacts on the regenerating vegetation than machines which expose the mineral soils in furrows metres apart (Strong et al. 1995). Forest floor disturbance has been found to decrease above-ground biomass, increase plant tissue nutrient concentrations, increase spatial variation in plant composition and density (Mou et al. 1993), and reduce basal diameters of regenerating vegetation (Harrington & Edwards 1996; Strong et al. 1995). Pre-existing seedlings are often eliminated by site preparation and reproductive propagule availability is altered (Mou et al. 1993). Soil profiles disturbed by site preparation often do not maintain species richness (Strong et al. 1995), dominance (Strong et al. 1995) or diversity of the regenerating vegetation (Harrington & Edwards 1996; Strong et al.

1995), but improve survival, health/vigour (Strong et al. 1995), growth (Ehrentraut & Branter 1990; Harrington & Edwards 1996; Strong et al. 1995) and volume (Harrington & Edwards 1996) of crop conifers. In addition to the impacts of clear-cutting and site preparation on forest soils and the plant communities they support, these practices also have an effect on the community structure and function of soil microorganisms.

During organic matter decomposition, saprotrophic soil microorganisms break down complex organic material and release mineral nutrients such as phosphate, ammonium and nitrate for microbial and plant uptake (Killham 1994). In addition to organic material furnished by plants and animals, microbial biomass in the soil is an important source of organic matter. In forest soils the microbial biomass is dominated by fungi which are the primary decomposers of organic matter. Decomposer soil fungi may also affect forest systems by functioning as faunal predators, plant pathogens and food sources for some species of mites and Collembola (Kendrick 1992).

Soil moisture, temperature, pH and the availability and quality of organic substrates are the primary soil characteristics controlling soil microbial communities and the processes they mediate (Keenan & Kimmins 1993). Clear-cutting and site preparation can potentially affect all of these soil characteristics, consequently affecting the soil microbial community.

Increased soil moisture and temperature following clear-cutting and site preparation may enhance decomposition (Bormann et al. 1974; Trettin et al. 1996). The quality and quantity of organic substrates available for decomposition may be altered following clear-cutting and site preparation by; 1. leaving plant remains such as leaves

and stems on site 2. changing the plant community which will affect the amounts and types of leaf litter available to the decomposers 3. redistributing and compacting organic and surface mineral layers and 4. the senescence of rooting systems which will provide organic substrate and decreases the amount of rhizodeposition (Ohtonen et al. 1992). Clear-cutting can increase nitrification (Frazer et al. 1990), nitrogen mineralization (Frazer et al. 1990; Olsson et al. 1996b), basal respiration (Sundman et al. 1978) and cellulose decomposition (Trettin et al. 1996), as well as, seasonal fluctuations in basal respiration (Marra & Edmonds 1996). Subsequent site preparation further increases cellulose decomposition (Trettin et al. 1996). In contrast, Bauhus (1996) found the rate of soil carbon and nitrogen mineralization to decrease following clear-cutting.

Clear-cutting can decrease soil microbial biomass (Bååth et al. 1995; Chang et al. 1995; Chang & Trofymow 1996) or have no impact (Entry et al. 1986). Clear-cut soil covered with a layer of slash material may have greater summer and winter microbial biomass due to the insulating effects of organic material (Entry et al. 1986). Bååth (1980), however, found slash amount had no impact on soil fungal biomass. Subsequent site preparation appears to have no additional effects on microbial biomass (Ohtonen et al. 1992).

Impacts of clear-cutting on fungal community structure are indicated by changes in species isolation frequencies (Bååth 1981; Wicklow & Whittingham 1978) and reduced fungal biomass (Bååth 1980; Bååth et al. 1995). Increases in numbers of the nitrifying bacteria *Nitrosomonas* and *Nitrobacter* (Likens et al. 1970), greater bacterial biomass

(Entry et al. 1986) and changes in the biochemical characteristics of bacterial populations (Niemelä & Sundman 1977) indicate that clear-cutting may also alter bacterial community structure. Site preparation can also change microbial community structure as indicated by increased microbial C: microbial N ratios, but does not affect the relative proportions of soil fungi and bacteria (Ohtonen et al. 1992).

Response of forest soils, plant communities and soil microbial communities to vegetation management

The goal of vegetation management is the same as that of site preparation - facilitating coniferous seedling establishment by decreasing the competition from non-crop vegetation. Vegetation management is usually performed within two years of planting conifer seedlings and can be chemical, motor-manual or mechanical (Ehrentraut & Branter 1990). The use of chemical herbicides (glyphosate and triclopyr) and manually operated brushsaws for non-crop vegetation control are discussed here.

The herbicide glyphosate (Vision®, Roundup®) is non-selective and phytotoxic to most annual, biennial and herbaceous plants (Anderson 1977) at a field concentration of 1.5 kg active ingredient (a.i.)/ ha (Bell et al. 1997). Glyphosate is often applied to plant stems or foliage during early stages of forest regeneration and is translocated throughout the plant where it inhibits the aromatic amino acid biosynthetic pathway (Anderson 1977), resulting in impaired plant growth, respiration and photosynthesis (Sprankle et al. 1975b).

Reduced groundcover following the application of glyphosate to a clear-cut and prepared mixedwood forest has been shown to increase light availability, soil temperature and moisture (Reynolds et al. 1997b). Repeated applications of glyphosate can also increase soil nitrate concentrations while pH (mineral soil), and levels of total magnesium and potassium (organic soil) decrease (Ohtonen et al. 1992). Simpson et al. (1997) showed that the application of glyphosate does not significantly affect the movement of total organic N, ammonium, nitrate, calcium or potassium in the soil. Glyphosate mobility in soil is very limited (Sprankle et al. 1975a).

Glyphosate application alters plant community structure by selectively reducing the cover and height of target plants (Bell et al. 1997). Glyphosate application to a clear-cut forest system decreases plant volume, species richness, diversity of some vegetation groups (Sullivan et al. 1996), aspen biomass and the stem density of aspen and shrubs (Perala 1985). Glyphosate reduces the percent cover of deciduous trees, shrubs and ferns, increases the cover of conifers, forbs, grasses and sedges (Bell et al. 1997) and decreases the leaf area index of non-crop vegetation (Reynolds et al. 1997a).

Triclopyr (Garlon®, Release®) is a selective herbicide phytotoxic to most deciduous, woody and broad-leaf plant species (Campbell 1990) with very low activity in monocots. Triclopyr is applied to plant foliage or stems at field concentrations of 1.9 kg a.i./ ha (Bell et al. 1997) and produces auxin-like responses in affected plants (Perala 1980).

Triclopyr in the soil is resistant to leaching, especially in the organic layer (Choon et al. 1986; Perala 1980) and shows little lateral movement (Stephenson et al. 1990).

Although triclopyr application can increase soil temperature, moisture and the amount of photosynthetically active solar radiation (Reynolds et al. 1997b), nutrient movement in the soil remains unaltered (Simpson et al. 1997).

Like glyphosate, triclopyr affects plant community structure by selectively reducing plant cover and height (Bell et al. 1997). Triclopyr application at field concentration decreases deciduous tree and shrub cover, increases conifer, forb, grass, sedge, fern and horsetail cover (Bell et al. 1997) and reduces the leaf area index of non-crop vegetation (Reynolds et al. 1997a).

Motor-manual and mechanical forms of vegetation management are often used at later stages in forest development when the majority of competitors to crop conifers are hardwood trees (Ehrentraut & Branter 1990). This review discusses the use of motorized brushsaws which are used to manually remove the above-ground, vegetative parts of non-crop, woody plants (Oswald 1990). Brushsaw use can increase soil moisture and the amount of solar radiation reaching the soil surface (Reynolds et al. 1997b) and has no impact on soil nutrient movement (Simpson et al. 1997). Brushsaw use affects plant community structure by reducing deciduous tree cover (Bell et al. 1997) and the leaf area index of competing vegetation (Reynolds et al. 1997a) while increasing conifer, shrub, forb and grass cover (Bell et al. 1997). Strong et al. (1995) found that brushsaws, in comparison with other vegetation methods, are intermediate at maintaining plant species richness and do not preserve community structure or diversity well.

The application of herbicides such as glyphosate and triclopyr has the potential for altering decomposition and nutrient cycling processes by altering biological soil

parameters. However, glyphosate applied at field concentration is readily inactivated (Perala 1985) and degraded by soil microorganisms (Sprankle et al. 1975a) and no significant effects on microbial biomass (Olson & Lindwall 1991; Wardle & Parkinson 1991), microbial respiration (Olson & Lindwall 1991; Wardle & Parkinson 1991), metabolic quotients (qCO_2) (Wardle & Parkinson 1991), bacterial biomass: fungal biomass ratio (Wardle & Parkinson 1991), ammonification (Tu 1994), denitrification (Tu 1994), nitrification (Olson & Lindwall 1991), sulfur oxidation (Tu 1994) or bacterial, fungal and actinomycete counts (Rosylycky 1982) have been demonstrated. For a few days following application, field dosages of glyphosate can alter the isolation frequency of some fungal species (Abdel-Mallek et al. 1994; Wardle & Parkinson 1990b) and reduce some negative interspecific fungal interactions (Wardle & Parkinson 1992).

Glyphosate when applied repeatedly (Ohtonen et al. 1992) or at greater than recommended field concentration (Wardle & Parkinson 1990a) can reduce microbial biomass. Multiple applications of glyphosate increase nitrogen mineralization and alter microbial community structure by reducing the fungal component of microbial biomass more than the bacterial component (Ohtonen et al. 1992). Glyphosate at greater than field concentration also alters microbial community structure by changing the relative frequency of fungal species (Abdel-Mallek et al. 1994; Wardle & Parkinson 1990b), increasing bacterial (Rosylycky 1982; Wardle & Parkinson 1990b) and actinomycete counts (Rosylycky 1982) and affecting the interactions between pairs of fungi (Wardle & Parkinson 1992). Research on the impacts of triclopyr application or the use of brushsaws on microbial processes or community structure is lacking although reductions

in plant cover following vegetation management may allow greater amounts of solar radiation and precipitation to reach the soil surface which can potentially affect microbial activities.

1.2 Thesis Rationale

Although microbial activities in decomposition and nutrient cycling are essential to the productivity and maintenance of forest systems, studies examining the impacts of clear-cutting, site preparation and mechanical and chemical vegetation management practices on plant communities and soil properties are far more abundant than those examining the impacts of these forestry practices on soil microorganisms. The literature compiled for this review included studies investigating the impacts of clear-cutting and glyphosate application on soil microorganisms, but only two studies examined site preparation impacts and none addressed the effects of triclopyr or brushsaw use. All of the forestry practices discussed in this review are currently being utilized by the forestry industry, and an attempt to understand their impact on soil microorganisms should be made.

The response of soil microorganisms to forestry practices has generally been studied at the process level where measurements of microbial activities and biomass are used to indicate treatment effects (eg. Bauhus 1996; Chang & Trofymow 1996; Frazer et al. 1990; Olson & Lindwall 1991; Tu 1994). Forest soil is dominated by fungal biomass, and while some researchers have investigated the response of fungal community

structure to forestry practices (eg. Bååth, 1981; Wicklow & Whittingham 1978), studies which investigate the impacts on both microbially-mediated processes and fungal community structure in the soil are lacking. Examining the impacts of forestry practices on the soil fungal community in conjunction with microbial process measurements may provide greater understanding of disturbance impacts. In addition, insight into the relationship between microbial processes, microbial biomass and fungal community structure, which is not presently well understood (Wander et al. 1995), may be provided.

Of the studies examining the impacts of vegetation management in this review, the majority investigated the impact of glyphosate application on soil microorganisms through direct application of glyphosate to agricultural soil and used higher than recommended dosages under laboratory conditions (eg. Rosylycky 1982; Wardle & Parkinson 1990a). In addition, most studies concentrated on the immediate, direct effects of glyphosate application (eg. Rosylycky 1982; Tu 1994; Wardle & Parkinson 1990a) on microbial communities. Only the study by Ohtonen et al. (1992) was conducted in the field and used a forest soil to examine the impacts of glyphosate application on soil microorganisms. To understand the impacts of forestry practices on microbially-mediated processes and fungal community structure, studies must be conducted under field conditions using operational techniques. For these reasons it was proposed that research be conducted to examine the longterm impacts of clear-cutting, site preparation and vegetation management techniques (glyphosate, triclopyr and brushsaws) on microbially-mediated processes and fungal community structure in a mixedwood forest soil.

1.3 Study Objectives

This research forms one component of a larger, integrated study called the Fallingsnow Ecosystem Project. The project commenced in 1993 with the objective of examining the effects of clear-cutting, site preparation and various methods of vegetation management on ecosystem processes of spruce plantations in Ontario, Canada (Bell et al. 1997). The specific objectives of the present study were; 1. to examine the effects of clear-cutting and subsequent site preparation on parameters important to decomposition and nutrient cycling in forest soil, specifically basal respiration, nitrogen mineralization; parameters related to these processes such as microbial biomass carbon, metabolic quotients (qCO_2) and the ratio of microbial carbon: organic soil carbon ($C_{mic}:C_{org}$); and the structure of decomposer fungal communities. 2. to examine the response of the microbial parameters listed above to three vegetation management procedures (glyphosate, triclopyr and brushsaw use) which were applied following clear-cutting and site preparation. 3. to provide insight into the possible relationship between fungal community structure and microbially-mediated processes following soil disturbance caused by harvesting and/ or vegetation management practices. It was hypothesized that clear-cutting, site preparation and vegetation management practices would have a negative impact on the microbial community and that alterations in the fungal community would be reflected in microbially-mediated process measurements.

2. Response of microbial processes and fungal community structure to clear-cutting and site preparation in mixedwood forest soils

2.1 Introduction

The roles of soil microorganisms in decomposition and nutrient cycling are important to the productivity and maintenance of ecosystems. Saprotrophic soil microorganisms break down complex organic matter and release mineral nutrients for microbial and plant uptake (Killham 1994). The microbial biomass in the soil is an additional and important source of organic matter. Microbial communities and the processes they mediate are controlled primarily by soil moisture, temperature and the availability and quality of organic substrates (Keenan & Kimmins 1993) - all factors which can be significantly altered by the silvicultural practices of clear-cutting and site preparation.

Clear-cutting and site preparation have been shown to increase soil temperature and moisture (Frazer et al. 1990), increase soil density, redistribute organic material from the soil surface (Johnson et al. 1991a), and alter plant community composition and structure (Strong et al. 1995) thereby affecting the types and amounts of plant residues available to the decomposer community. By altering those factors which are known to regulate decomposer communities and processes, clear-cutting and site preparation potentially could have significant impacts on soil decomposers.

Many studies have investigated clear-cutting and site preparation impacts on soil characteristics and the plant community; however, relatively few studies have concentrated on how these impacts translate to soil microorganisms and the processes they mediate. Frazer et al. (1990) and Olsson et al. (1996b) reported increases in nitrogen mineralization following clear-cutting. Sundman et al. (1978) observed clear-cutting to increase basal respiration while Marra & Edmonds (1996) found exaggerated seasonal fluctuations in carbon mineralization and Trettin et al. (1996) reported increased cellulose decomposition. Site preparation can further increase cellulose decomposition (Trettin et al. 1996). In contrast, Bauhus (1996) found clear-cutting to reduce the rate of carbon and nitrogen mineralization. Microbial biomass may decrease (Bååth 1980; Bååth et al. 1995; Chang et al. 1995; Chang & Trofymow 1996) or remain the same following clear-cutting (Entry et al. 1986). Subsequent site preparation appears to have no additional impact on microbial biomass (Ohtonen et al. 1992).

Altered microbial community structure is indicated by changes in the relative abundances of microorganisms. Clear-cutting has been found to alter both fungal (Wicklow & Whittingham 1978; Bååth 1981) and bacterial (Niemelä & Sundman 1977; Likens et al. 1970) community structure and can also reduce the fungal component (Bååth 1980; Bååth et al. 1995) and increase the bacterial component of the microbial biomass (Entry et al. 1986; Sundman et al. 1978). Site preparation does not appear to alter the relative proportions of soil fungi and bacteria, but may affect microbial community structure as indicated by increases in the microbial C: microbial N ratio (Ohtonen et al. 1992).

The response of soil fungi to clear-cutting and site preparation generally has been studied at the process level using measurements of microbially mediated processes and microbial biomass to indicate treatment effects. While Wicklow and Whittingham (1978) and Bååth (1981) examined clear-cutting impacts at the fungal species level, these studies did not include measurements of microbially-mediated processes. Because forest soil microbial biomass is dominated by fungi (Killham 1994), studying the fungal community at the species level may provide more specific and subtle evidence for treatment effects than would be evident from soil process measurements alone. In addition, this information may provide insight into the relationship between fungal community structure, microbially mediated processes and microbial biomass which is not presently well understood (Wander et al. 1995).

Seven to nine years after clear-cutting and site preparation, organic and mineral soil from two spruce plantations and their adjacent uncut mixedwood forest were compared as part of the Fallingsnow Ecosystem Project (Ontario, Canada). The objectives of this study were: 1. to examine the longterm effects of clear-cutting and site preparation on microbially mediated processes including basal respiration, microbial biomass C, metabolic quotients (qCO_2), the ratio of microbial carbon: soil organic carbon ($C_{mic}:C_{org}$) and nitrogen mineralization. 2. to examine harvesting impacts on the structure of the soil fungal community and the possible relationship between species level and process level measurements. 3. to determine the relative sensitivity of community indices to treatment effects at fungal species and genus taxonomic levels.

It was hypothesized that physical disturbance of the organic soil layer following clear-cutting and site preparation would impact fungal community structure by altering the relative abundance of some species; reduce basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization, and increase metabolic quotients (qCO_2). Due to the lesser amount of disturbance caused by clear-cutting and site preparation in the mineral soil compared to the organic soil, it was hypothesized also that fungal community structure, carbon and nitrogen mineralization rates, microbial biomass C, $C_{mic}:C_{org}$ and qCO_2 would not be impacted in the mineral soil. Also it was expected that fungal community indices at the species level would be more sensitive to treatment effects than if those indices were expressed at the genus level.

2.2 Methods

Site description

The experimental sites are located approximately sixty kilometers southwest of Thunder Bay, Ontario, in the transition zone between the Great Lakes - St. Lawrence and boreal forest regions. The mean annual temperature for this area is 2.4°C, with an annual precipitation of 703 mm and 2183 h of sunshine (Canadian Climate Normals, 1993).

The experimental design is a randomized block design using three clear-cut sites ranging in size from 27.7 to 51.8 ha. Each site contains four blocks ranging in size from

3.3 to 12.4 ha and each block represents one of four treatments; 1. clear-cut and prepared control 2. glyphosate treated 3. triclopyr treated 4. manual brushsaw treated. Two sites had adjacent uncut forests which represented treatment 5. uncut controls. This chapter examines the impacts of clear-cutting and site preparation through comparison of the uncut and clear-cut controls. The impacts of glyphosate, triclopyr and brushsaw release on soil microbial processes and fungal community structure will be presented in the following chapter.

No uncut control was available for site 3 so this study deals only with sites 1 and 2. Site 1 (48°12' north/89°49' west) was created in 1988 when a 101 year old stand (27.7 ha) consisting of *Populus tremuloides* Michx. (trembling aspen) (60%), *Abies balsamea* (L.) Mill. (balsam fir) (20%), *Picea glauca* (Moench) Voss (white spruce) (10%) and *Betula papyrifera* Marsh. (white birch) (10%) was harvested. Site 1 was seven years old when samples for this study were taken. Site preparation using Young's teeth was performed in June of 1989 (Bell et al. 1997). The following spring white spruce seedlings were planted (approximately 1,700 seedlings/ ha). The soil is a well drained, silt loam (Simpson 1996).

A 75 year old trembling aspen stand (51.8 ha) with *Picea mariana* (Mill.) B.S.P. (black spruce) and balsam fir in the understory, was harvested in 1986 to create site 2 (48°9' north/89°50' west). Site 2 was nine years old when samples for this study were taken. In October 1986, site 2 was prepared using Young's teeth. White spruce seedlings were planted the following spring at a density of 1,700 seedlings/ ha (Bell et al. 1997). The soil is an imperfectly drained, silt loam containing clay (Simpson 1996).

Corylus cornuta Marsh. (beaked hazel), *Cornus stolonifera* Michx. (red-osier dogwood), *Diervilla lonicera* Mill. (bush honeysuckle), *Prunus pensylvanica* L. f. (pin cherry), *Pteridium aquilinum* (L.) Kuhn (bracken fern), *Rubus parviflorus* Nutt. (thimbleberry) and *Rubus idaeus* L. spp. *melanolasius* (red raspberry) were common in the shrub and understory layers of all sites (Bell et al. 1997).

Sampling Regime

In July 1995, three soil cores (20cm diam., 10cm deep) were sampled randomly from each harvested and unharvested area of sites 1 and 2 (3 cores/ 2 treatments/ 2 sites; total=12). Each core was separated into organic (litter, fermentation and humus) and mineral soil, passed through a 4 mm mesh sieve and stored at 4°C. The organic and mineral fractions of each soil sample were used in all physical, chemical and biological measurements.

Measurements

Soil Moisture and Organic Matter Contents

Soil moisture was determined gravimetrically by drying each sample to a constant weight in an 80°C oven. The difference in mass between fresh and dry soil was used to calculate percent moisture on a dry weight (dwt) basis.

Organic matter was estimated by placing oven dried soil from the moisture determinations in a 105°C oven for 24 h then transferring the soil to a muffle furnace for 24 h at 400°C. The difference in soil mass at 105°C and after organic matter combustion was used to calculate percent loss on ignition (adapted from Nelson & Sommers 1982).

Soil pH and Electrical Conductivity

Distilled water was mixed with soil subsamples to create a slurry. The ratio of soil (g dwt):water (g) used was 1:5 for organic and 1:2 for mineral soil. Slurry pH was measured after one hour using a digital pH meter (Markson model 1096, Amber science, San Diego, USA). Soil slurries were then vacuum filtered using Whatman #42 filters, and the electrical conductivity of the soil filtrate was measured using a digital conductivity meter (Orion Research model 701A, Cambridge, USA).

Basal and Substrate Induced Respiration

Basal respiration rate ($\mu\text{g CO}_2\text{-C/g soil dwt/h}$) was determined using an infrared gas analyzer (Analytical Development Co. Ltd. ADC-225-MK3, Huddlesdon, England) to measure the amount of $\text{CO}_2\text{-C}$ respired (carbon mineralized) by soil microorganisms incubated for three hours. Five grams dwt equivalent of field moist organic soil or 100 g dwt equivalent of field moist mineral soil were adjusted to 150% and 20% moisture content respectively, and placed in one litre glass jars. CO_2 efflux was measured by

sealing the jars and analyzing headspace CO_2 after one and four hours of incubation. The difference in CO_2 concentration between the two measurement times was used to calculate the rate of CO_2 evolution ($\mu\text{g CO}_2\text{-C/ g dwt soil/ h}$). The following day, soil used to measure basal respiration was amended with ground glucose and used to determine substrate induced respiration.

Soil microbial biomass was estimated using the substrate induced respiration method developed by Anderson and Domsch (1978). Glucose response curves using 8, 16, 32, 64 and 128 mg glucose/ g dwt soil determined that amending organic subsamples with 32 mg glucose/ g dwt soil and mineral subsamples with 8 mg glucose/ g dwt soil resulted in maximal respiration rates. After measuring basal respiration each sample was supplemented with 32 mg glucose/g organic soil or 8 mg glucose/g mineral soil, mixed thoroughly, returned to the one liter jars and CO_2 evolution monitored hourly for eight hours. Microbial biomass was based on the lowest respiration rate prior to the commencement of microbial growth which often occurred at six hours for the organic soil and at four hours for the mineral soil. CO_2 evolution rates ($\mu\text{g CO}_2\text{-C / g dwt soil/ h}$) were converted to $\text{ml CO}_2/ 100 \text{ g dwt soil/ h}$ and the formula $x=40.4y+0.37$, where x =microbial biomass ($\text{mg C}_{\text{mic}}/ 100 \text{ g dwt soil}$) and y =glucose induced respiration ($\text{ml CO}_2/ 100 \text{ g dwt soil}$), was used to estimate microbial biomass C (Anderson & Domsch 1978).

Quotients

Using Odum's (1969) theory of the bioenergetics of ecosystem succession, Anderson and Domsch (1990) state that as the amount of substrate carbon used for respiration diminishes more carbon will be incorporated into microbial biomass. This theory forms the basis of the metabolic quotient (qCO_2) which is calculated using basal respiration and microbial biomass C data ($\mu g CO_2-C / h : \mu g$ microbial biomass C) (Anderson & Domsch 1985). Stressful environments (e.g. increased organic substrate recalcitrance, reduced availability etc.) increase qCO_2 as microorganisms respire more CO_2 to meet energy demands and incorporate less organic substrate into their biomass (Anderson & Domsch 1990).

The ratio of microbial biomass C (mg): soil organic C (g) was calculated using microbial biomass C and organic matter data. Since organic carbon content was not measured in the present study, organic C was assumed to compose 58% of soil organic matter (Hausenbuiller 1978). Greater substrate quality and availability or the shift to a microbial community with a more economic metabolism can increase $C_{mic}:C_{org}$, indicating that more of the organic carbon present in a soil is being converted into microbial biomass (Anderson & Domsch 1990).

Nitrogen Mineralization

The nitrogen mineralization rate ($\mu\text{g N/ g dwt soil/ day}$) was determined by measuring the amount of ammonium-N and nitrate-N evolved by soil microorganisms during a six week laboratory incubation. Five grams dwt equivalent of field moist organic or 10 g dwt equivalent of field moist mineral soil was adjusted to 150% or 20% moisture, respectively. Moisture contents were monitored gravimetrically twice weekly and maintained throughout the incubation. Soil was incubated at room temperature in plastic bags closed with a foam stopper to allow gas exchange. The soil extraction procedure consisted of shaking each sample in 2N KCl (40 ml for organic samples; 25 ml for mineral samples) for one hour. After shaking, the slurry was filtered and the filtrate analyzed for ammonium and nitrate content using a Technicon Autoanalyzer (Technicon Instruments, Tarrytown, USA) (adapted from Frazer et al. 1990). Measurement of ammonium and nitrate concentrations were performed initially and after six weeks incubation and the difference between the two measurement times was used to calculate the rate of mineral nitrogen production.

Soil Fungal Community

Actively growing fungi were isolated from one gram dwt organic and five grams dwt mineral soil which had been given 15, two minute washes with distilled water to remove the majority of spores (Parkinson 1982). Twenty organic and twenty mineral

particles from each washed sample were transferred aseptically to 2% malt extract agar (1 particle/ plate) containing the antibiotics, streptomycin sulfate (0.10 g/ L) and chlorotetracycline (0.05 g/ L). Plates were incubated for two weeks at room temperature and then stored at 5°C. Fungi were identified to species level. Some fungal isolates which remained sterile in culture, as well as, those for which no taxonomic description was found could not be identified and were classified as 'unidentified'.

Fungal community structure was examined using rank abundance curves and indices of community structure including species richness, diversity, evenness and dominance. In a rank abundance curve the relative abundance of each species (y-axis) and a ranked list of species (x-axis) are plotted, utilizing all of the information gathered from a community. The resultant curve represents community structure which can be further characterized by fitting mathematical distribution series (Magurran 1988).

Species richness indices measure the number of species in a defined sampling unit. Species richness (S) is the number of fungal species/ sample (20 particles). S is very simple to calculate, widely used and has a high discriminant ability, however, it is very sensitive to sample size (Magurran 1988). The inverse of Simpson's non-parametric diversity index of heterogeneity was calculated using the formula

$1/D = 1 / \sum p_i^2$, where D is Simpson's index and p_i is the proportion of individuals in the *i*th species. Simpson's index is largely unaffected by species richness or sample size and is widely used (Magurran 1988). Simpson's diversity index was used in this study because it is a measure of dominance (weights common species more heavily than rare ones) and most communities are dominated by relatively few abundant species and many

rare ones. The present study concentrated more on frequently isolated fungal species than rare ones.

Shannon's index of evenness was chosen to measure fungal community evenness using the formula $E = H' / H_{\max}$ where H' is the observed value of Shannon's diversity index and H_{\max} is the maximum diversity that could occur in a community ($H' = -\sum p_i \ln p_i$ and $H_{\max} = \ln S$). Shannon's index of diversity takes the evenness of species' abundances into account, thus comparing H' to the maximum evenness possible is a useful measurement of community evenness (Magurran 1988)

The Berger-Parker index of dominance is calculated using the formula $d = N_{\max} / N$ where N_{\max} is the number of times the most abundant species in a sample was isolated and N is the total number of isolates. This index expresses the proportional importance of the most abundant species and has low sensitivity to sample size (Magurran 1988).

Sorenson's similarity index was used to compare fungal communities. This binary index was used because it weights matches in species composition more heavily than mismatches (Krebs 1989). Mismatches may occur frequently between samples taken from very large communities such as the soil fungal community. In addition, this index is useful when examining communities where many of the species present are not present in a sample from that community (Krebs 1989).

Community indices were compared at the species and genus level to evaluate the usefulness of identifying fungi to the lowest taxonomic level possible for assessing clear-cutting and site preparation impacts in the present study.

Statistical Analysis

A three factor analysis of variance was used to test differences among the means of each variable (pH, electrical conductivity, moisture, organic matter, basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 , nitrogen mineralization, indices of community richness, diversity, evenness and dominance, isolation frequencies of frequently found fungal species), and to assess variation attributable to site location, soil layer and treatment. Because the organic and mineral layers of each sample were not independent, a repeated measure was included in the three factor ANOVA. Assumptions of normally distributed errors and homogeneity of variances were tested; violating data were transformed. SAS was used to perform all statistical analyses (SAS institute Inc. 1985).

2.3 Results

Soil Characterization

There was no significant effect of clear-cutting and site preparation on soil moisture or organic matter in the organic and mineral layers, although treatment appeared to reduce these measurements slightly in the organic layer (Table 2.1). Soil moisture and organic matter contents in the organic layer remained significantly higher than in the mineral soil following treatment. Soil pH and electrical conductivity were not affected by clear-cutting and site preparation and did not differ between soil layers.

Table 2.1 Abiotic parameters in organic and mineral soil layers of two mixedwood forest sites, 7 to 9 years after clear-cutting and site preparation. Values shown are means (s.e.).

Soil Layer	Treatment	% Moisture (dwt)	% Organic Matter	pH	Electrical Conductivity (dSm ⁻¹)
Organic	uncut	251.3 ^{a1}	73.9 ^a	5.0 ^a	1.7 ^a
		(10.6)	(2.7)	(0.1)	(0.1)
	clear-cut	191.1 ^a	63.3 ^a	4.9 ^a	1.5 ^a
		(11.8)	(3.0)	(0.1)	(0.2)
Mineral	uncut	44.5 ^b	8.0 ^b	4.9 ^a	0.9 ^a
		(15.1)	(3.4)	(0.1)	(0.1)
	clear-cut	31.3 ^b	5.0 ^b	4.6 ^a	0.9 ^a
		(2.9)	(0.8)	(0.1)	(0.1)

¹Within each column different letters indicate significant differences between means ($p=0.05$; $n=2$).

Microbial Processes

Clear-cutting and site preparation had no significant impact on microbial processes in either the organic or mineral soil layers after seven to nine years. Basal respiration, nitrogen mineralization, microbial biomass C and $C_{\text{micr}}:C_{\text{org}}$ remained significantly higher in the organic soil than in the mineral soil (Table 2.2). $q\text{CO}_2$ was not altered by clear-cutting and site preparation, and was similar in organic and mineral soil. Although not significant, measurements of carbon mineralization, nitrogen mineralization, microbial biomass C and the quotient $C_{\text{micr}}:C_{\text{org}}$ tended to be lower in the organic layer following clear-cutting, this slight reduction was also seen in moisture and organic matter.

Fungal community

Clear-cutting and site preparation did not change the fungal community structure in organic (Figure 2.1a) or mineral soil (Figure 2.1b). In general the fungal communities were characterized by one very abundant species, four or five moderately abundant species and many species of low abundance. Shannon's index of evenness was high for both soil types before and after treatment as the majority of species in the community were rare (relative abundance <2%) (Figure 2.2c).

Fungal richness decreased by approximately two species in the organic and increased by three species in the mineral layer following clear-cutting and site preparation (Figure 2.2a). Species richness in the organic layer was significantly higher than in the

Table 2.2 Microbial processes in organic and mineral soil layers of two mixedwood forest sites, 7 to 9 years after clear-cutting and site preparation.
Values shown are means (s.e.).

Soil Layer	Treatment	Carbon Mineralization ($\mu\text{gC/gdwt/h}$) ²	Nitrogen Mineralization ($\mu\text{gN/gdwt/day}$) ³	Microbial Biomass (mgC/gdwt)	$C_{\text{mic}}:C_{\text{org}}$ ² (mg:g)	$q\text{CO}_2$ ($\times 10^{-3}$)
Organic	uncut	12.1 ^{a1}	17.6 ^a	8.5 ^a	3.7 ^a	1.5 ^a
		(1.4)	(4.9)	(0.5)	(0.3)	(0.2)
	clear-cut	8.4 ^a	12.2 ^a	6.0 ^a	2.2 ^a	1.1 ^a
		(0.7)	(1.8)	(0.4)	(0.2)	(0.1)
Mineral	uncut	0.7 ^b	0.9 ^b	0.4 ^b	0.1 ^b	1.4 ^a
		(0.3)	(0.4)	(0.1)	(0.03)	(0.1)
	clear-cut	0.4 ^b	0.8 ^b	0.4 ^b	0.01 ^b	1.1 ^a
		(0.1)	(0.2)	(0.1)	(0.0)	(0.1)

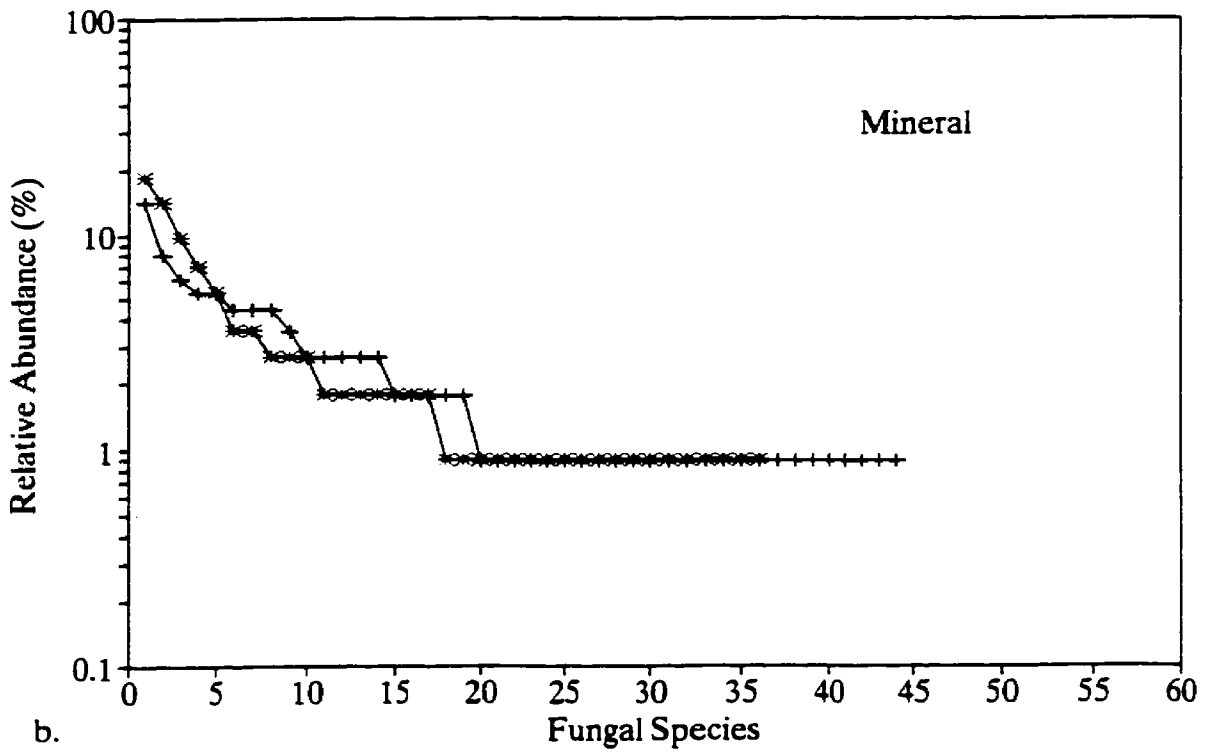
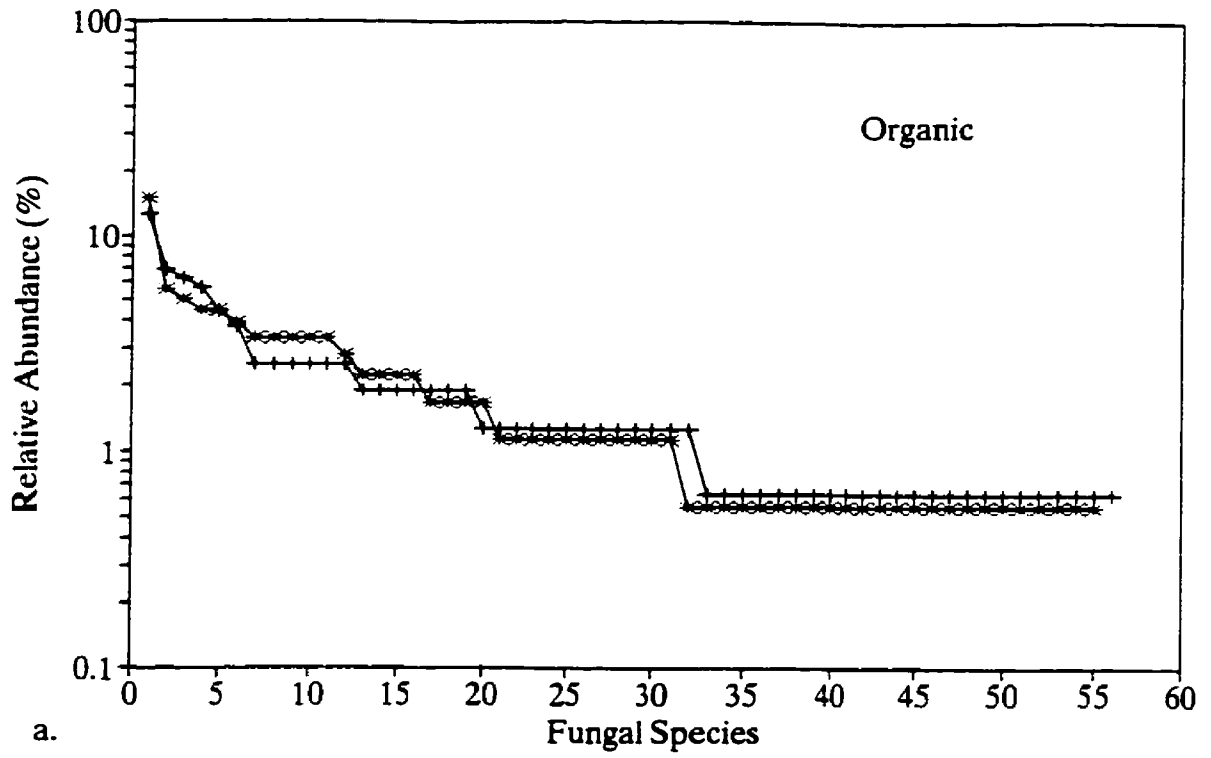
¹Within each column, different letters indicate significant differences between means ($p=0.05$; $n=2$).

²Data were square root transformed to satisfy ANOVA assumptions.

³Data were log transformed to satisfy ANOVA assumptions.

Figure 2.1 Rank abundance curves for all fungal species isolated from the organic and mineral soil layers of two undisturbed mixedwood forest and adjacent harvested sites, 7 to 9 years after clear-cutting and site preparation ($n=2$).

- a. organic layer species
- b. mineral layer species



—*— uncut —+— clear-cut

Figure 2.2 Fungal community indices for all fungal species isolated from the organic and mineral soil layers of two undisturbed mixedwood forest and adjacent harvested sites, 7 to 9 years following clear-cutting and site preparation. Values shown are means (s.e.) (n=2).

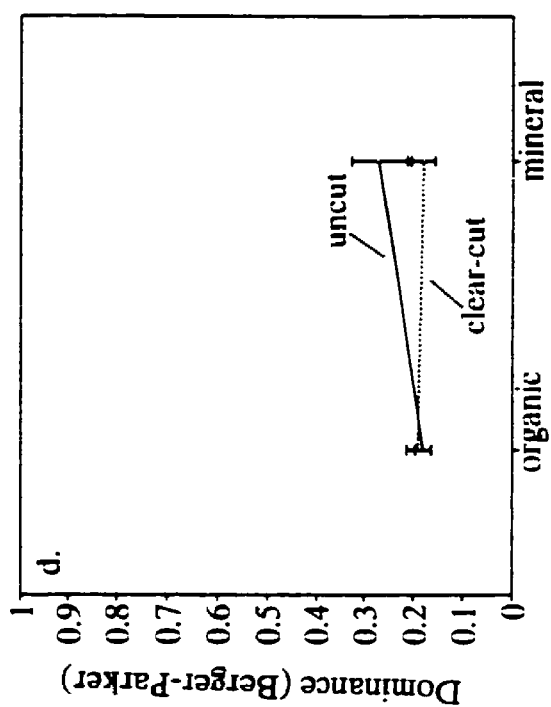
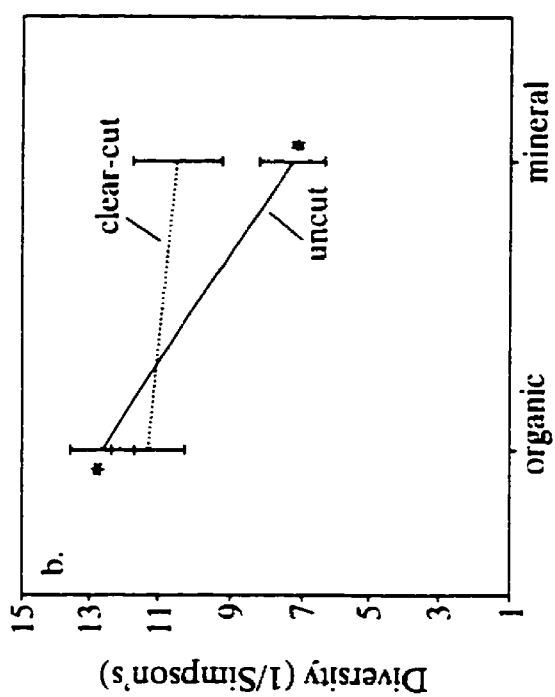
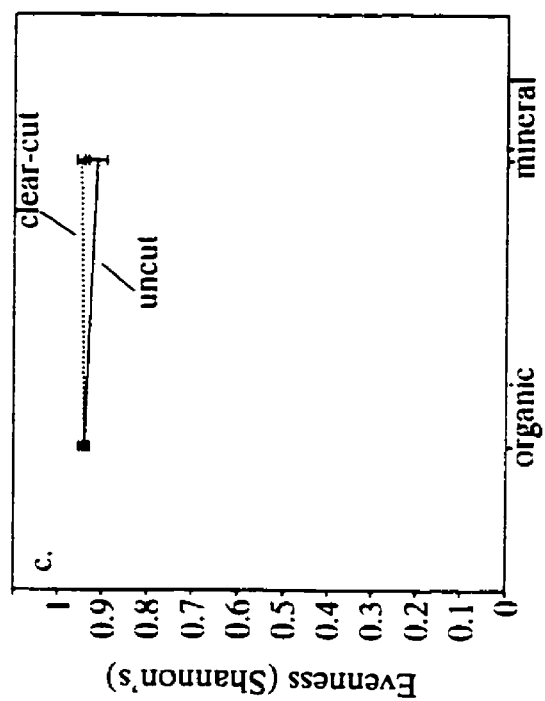
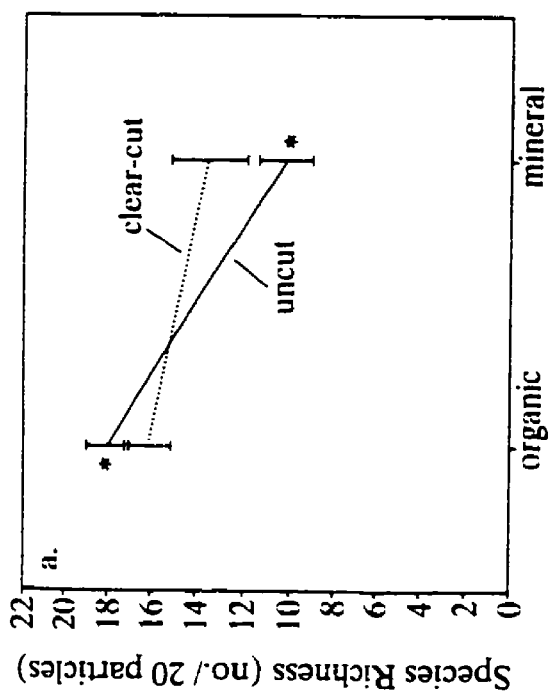
a. species richness (no. fungal species/ 20 particles)

b. species diversity (1/ Simpson's index)

c. species evenness (Shannon's index)

d. species dominance (Berger-Parker)

* indicate significant differences between soil layers ($p=0.05$)



mineral layer prior to treatment but not afterward. Fungal species diversity showed the same trend (Figure 2.2b); while $1/\text{Simpson's index}$ in the uncut organic layer was significantly higher than in the uncut mineral layer, no difference was found following treatment.

Fungal community similarity between organic and mineral layers increased from 0.37 to 0.44 following harvesting and site preparation. The greatest similarity occurred between the cut and uncut communities of the same soil layers. In general, low similarity values indicated different fungal community compositions within soil profiles and between treatments (Table 2.3). Regardless of whether unidentified fungi are included or excluded during calculation of Sorenson's index, similar trends in community composition at the species and genus level were evident.

When the fungal data from both treatments and soil layers were combined, fourteen fungal species had isolation frequencies greater than 2%. The fourteen most frequently isolated fungal species are presented in Table 2.4. In organic soil from clear-cut and uncut treatments and mineral soil from the clear-cut treatment, *Mortierella vinacea* was the most frequently isolated fungus making up 14.1% of all isolations. *Mortierella vinacea* was the second most frequently isolated species in the control mineral soil where *Phialocephala* sp. dominated. Dominance of the most frequently isolated fungus (*Mortierella vinacea* or *Phialocephala* sp.) in the fungal community was low in both soil layers and was not significantly affected by clear-cutting and site preparation (Figure 2.2d). Clear-cutting and site preparation did not significantly affect the frequency of occurrence of the 14 most isolated fungal species (Table 2.4). A

Table 2.3 Sorenson's similarity coefficient for fungal communities in organic and mineral soil layers of unharvested and clear-cut and prepared forest soil

Treatment Comparison	Similarity Value <i>species</i> level (includes all fungal isolates)	Similarity Value <i>species</i> level (excludes unidentified fungi) ¹	Similarity Value <i>genus</i> level (excludes unidentified fungi)
uncut organic to clear cut organic	0.59	0.64	0.68
uncut mineral to clear-cut mineral	0.55	0.67	0.72
uncut organic to uncut mineral	0.37	0.46	0.50
clear-cut organic to clear-cut mineral	0.44	0.49	0.58

¹Unidentified fungi include those isolates which did not sporulate in culture or for which no taxonomic description was found.

Table 2.4 The most frequently isolated fungal species (overall frequency > 2%) from the organic and mineral soil layers of two mixedwood forest sites, 7 to 9 years following clear-cutting and site preparation.
Values shown are mean isolation frequencies (s.e.).

Fungal species	Treatment and Soil Layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Cladosporium cladosporioides</i> (Fres. de Vries)	8.3 ^{1,2} (2.3)	2.5 ^a (1.6)	3.3 ^a (2.3)	2.5 ^a (1.0)
<i>Cylindrocarpum magnusianum</i> (Sacc. Wollenw.)	3.3 ^a (1.5)	3.3 ^a (1.5)	9.2 ^b (4.2)	7.5 ^b (1.6)
<i>Gymnoascus reessii</i> Baran	2.5 ^a (1.6)	5.8 ^a (2.2)	2.5 ^a (1.6)	0.8 ^a (0.8)
<i>Mortierella alpina</i> Peyronel	7.5 ^a (3.5)	3.3 ^a (1.5)	6.7 ^a (3.3)	4.2 ^a (1.8)
<i>Mortierella vinacea</i> Dixon-Stewart	22.5 ^a (3.9)	16.7 ^a (5.6)	13.3 ^a (3.0)	13.3 ^a (3.7)

¹Frequency of isolation (%) = (no. of times species isolated/20 soil particles plated) X 100

²Within each row, different letters indicate significant differences between means ($p=0.05$; $n=2$)

Table 2.4 continued.

Fungal species	Treatment and Soil Layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Oidiodendron tenuissimum</i> (Peck) Hughes	5.8 ^{a2} (2.7)	0 ^a	1.7 ^a (1.0)	4.2 ^a (1.4)
<i>Paecilomyces carneus</i> (Duche & Heime) A.H.S. Brown & G. Sm.	4.2 ^a (1.8)	8.3 ^a (3.7)	0.8 ^a (0.8)	0.8 ^a (0.8)
<i>Penicillium canescens</i> Sopp	0 ^a	7.5 ^a (4.7)	1.7 ^a (1.5)	0.8 ^a (0.8)
<i>Penicillium janthinellum</i> Biourge	6.7 ^a (1.9)	2.5 ^a (1.6)	0.8 ^a (0.8)	0 ^a
<i>Penicillium montanense</i> Christensen & Backus	5.0 ^a (2.9)	2.5 ^a (1.0)	5.0 ^a (2.9)	2.5 ^a (1.6)
<i>Phialocephala</i> sp.	0.8 ^a (0.8)	0 ^a	17.5 ^b (3.1)	4.2 ^b (2.2)

²Within each row, different letters indicate significant differences between means ($p=0.05$; $n=2$)

Table 2.4 concluded.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Pseudogymnoascus roseus</i> Raïllo	1.7 ^{a2} (1.0)	1.7 ^a (1.0)	0.8 ^a (0.8)	5.0 ^a (1.7)
<i>Trichoderma polysporum</i> (Link:Fr.) Rifai	5.0 ^a (1.7)	5.0 ^a (3.1)	1.7 ^a (1.0)	2.5 ^a (1.6)
<i>Trichoderma viride</i> aggr. sensu Rifai	5.0 ^a (2.9)	9.2 ^a (1.8)	1.7 ^b (1.5)	0 ^b

²Within each row, different letters indicate significant differences between means ($p=0.05$; $n=2$)

complete list of all fungi isolated in the present study and their isolation frequencies are included in Appendix Table 6.1.

Comparing results at the fungal species and genus level

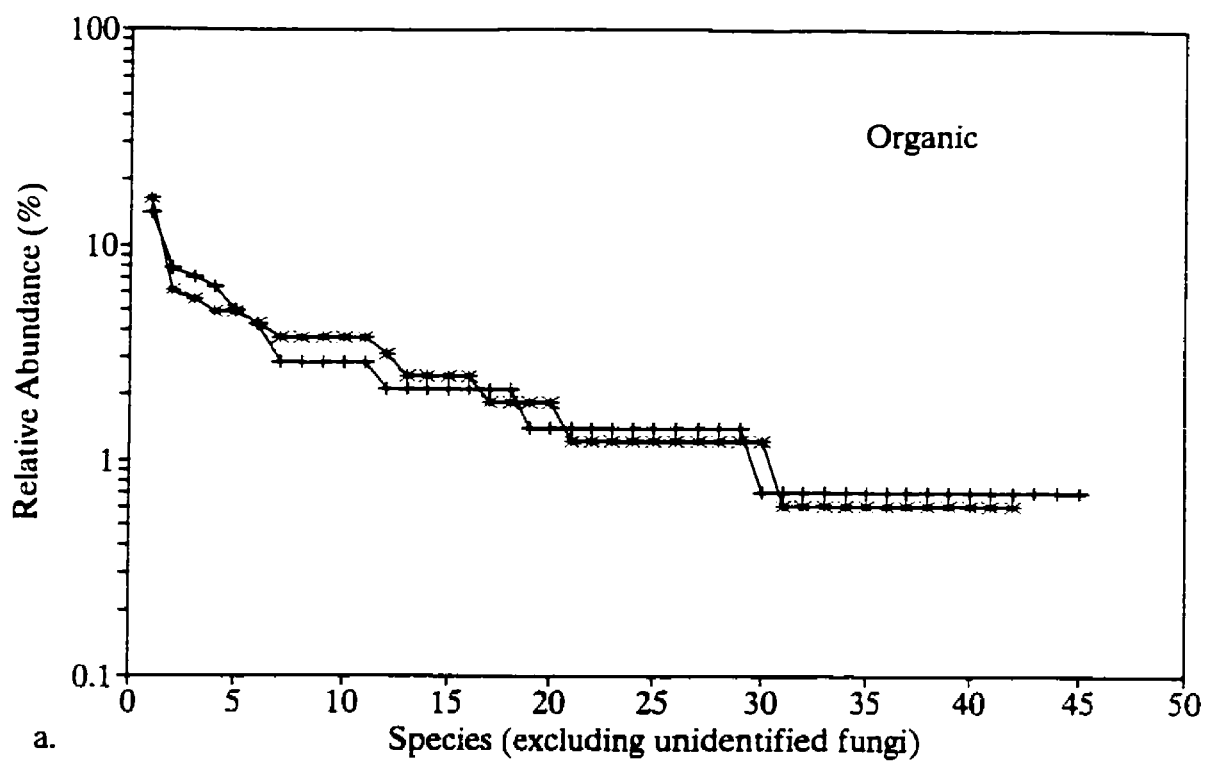
As the genera of unidentified isolates could not be determined, only fungi identified to the species level were used in this comparison. Rank abundance curves indicated that fungal community structure at the species and genus level were similar (Figure 2.3a & b, Figure 2.4a & b). In the organic layers of both treatments, one species (*Mortierella vinacea*) and two genera (*Mortierella* and *Penicillium*) dominated the fungal community; at the genus level, clear dominance of the community by one taxonomic group was no longer evident (Figure 2.3a, Figure 2.3b). In the mineral soil *Mortierella vinacea* dominated the community at the species level which coincided with the dominance of *Mortierella* at the genus level (Figure 2.4a, Figure 2.4b). At both species and genus levels the majority of species and genera isolated from the organic and mineral layers were of low abundance.

At the species level, fungal richness was significantly greater in the organic soil than in the mineral soil prior to clear-cutting, but these differences were not detectable at the genus level. The values for species similarity (Sorenson's index) of fungal communities within a soil profile and between treatments increased when examined at the genus level, but the general trend remained the same (Table 2.3). The analysis of species data at the genus level was less sensitive to changes in community richness,

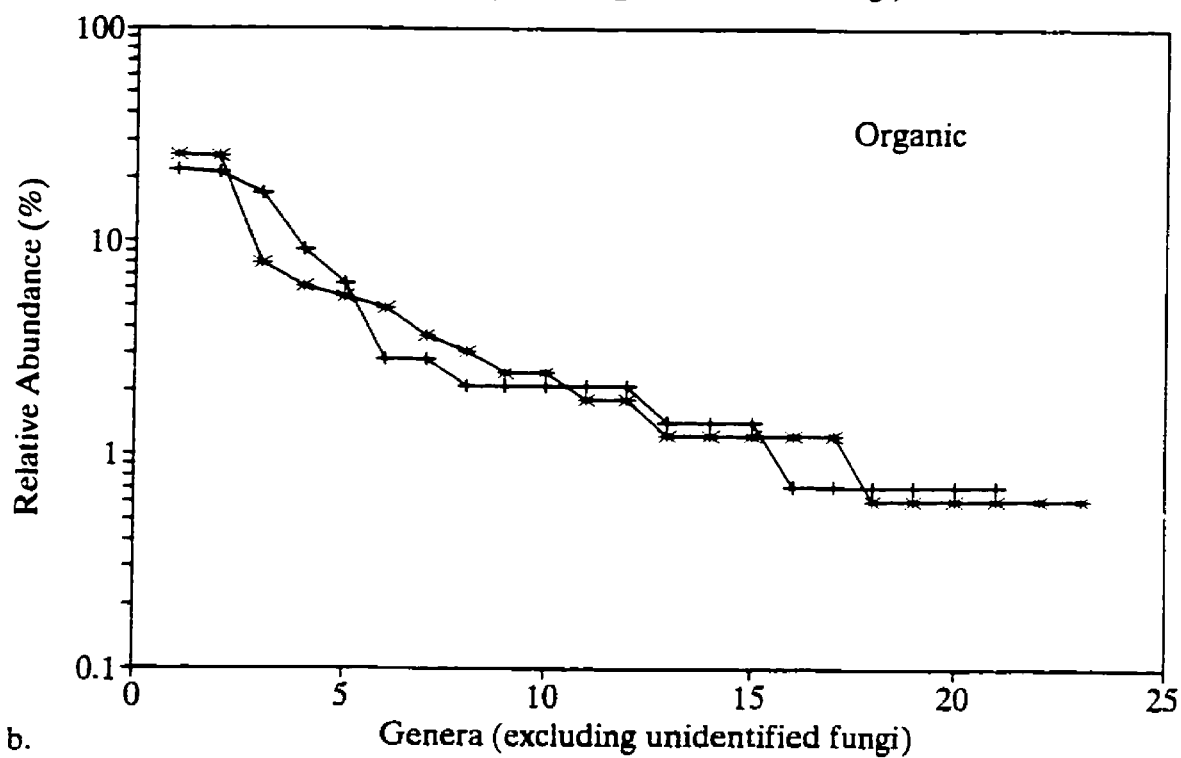
Figure 2.3 A comparison of rank abundance curves at the species and genus level for all fungi isolated from the organic soil layers of two undisturbed mixedwood forest and adjacent sites, harvested 7 to 9 years previously ($n=2$).

a. species level

b. generic level



a.

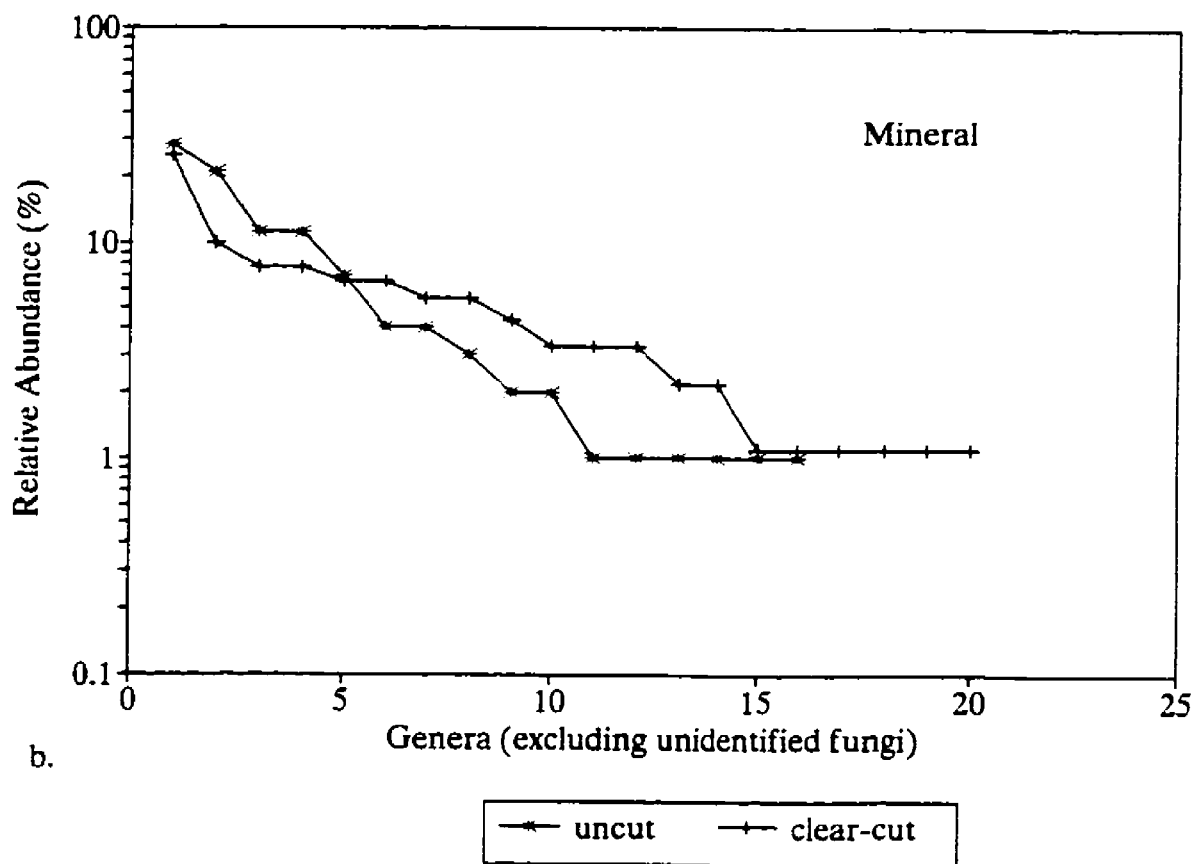
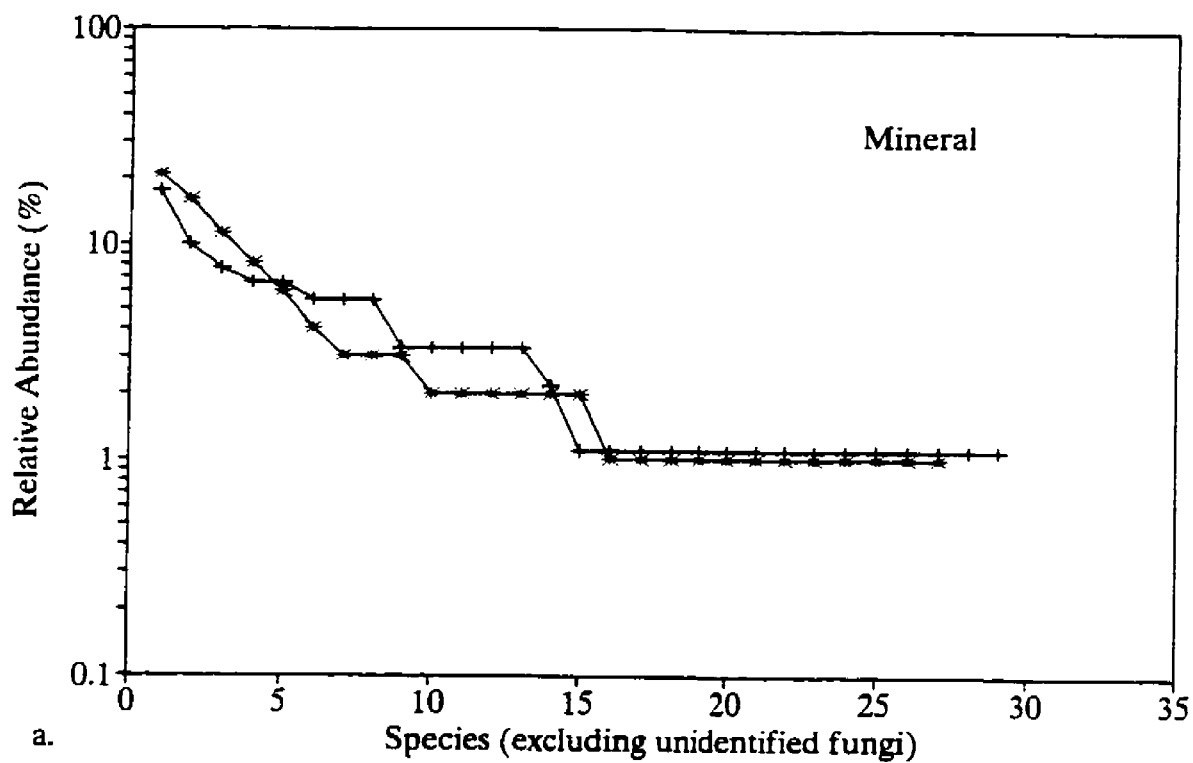


b.

—*— uncut —+— clear-cut

Figure 2.4 A comparison of rank abundance curves at the species and genus level for all fungi isolated from the mineral soil layers of two undisturbed mixedwood forest and adjacent sites, harvested 7 to 9 years previously ($n=2$).

- a. species level
- b. generic level



caused fungal communities to appear more similar, and created significant site differences in fungal community evenness and dominance.

2.4 Discussion

Through physical disturbance and alteration of the plant community, the amounts and types of organic matter in the soil can be altered by clear-cutting and site preparation. Tree residues remaining on the soil surface following clear-cutting are a source of organic material to decomposers. Following clear-cutting in this study, residues were mechanically pushed into large slash piles making this additional organic matter unavailable to the majority of soil saprotrophs. During clear-cutting compaction of the organic layers and relocation of organic material may occur (Johnson et al. 1991). Machines available for site preparation remove the organic soil and expose the mineral soil beneath. Many of the soil cores sampled in this study had disturbed profiles where mineral soil was mixed into the organic layer or where the organic layer was very thin. However, no significant longterm reductions in soil organic matter or $C_{mic}:C_{org}$ were found seven to nine years after harvesting, indicating the amount of organic material or organic carbon available to soil decomposers had not been decreased.

Summer increases in soil moisture were detected by Marra & Edmonds (1996) three to four years after clear-cutting and by Ohtonen et al. (1992) five years after the disruption of the upper soil horizons by site preparation; however, data from the present study found no significant impact of clear-cutting and site preparation on soil moisture

after seven to nine years.

pH is frequently reduced by clear-cutting (Dahlgren & Driscoll 1994; Johnson et al. 1991b; Likens et al. 1970; Schmidt et al. 1996) and can be increased following site preparation (Schmidt et al. 1996); however, in the present study no significant impacts of harvesting on soil pH was detected.

Microbial activity is controlled primarily by the availability and quality of organic substrates, soil moisture, temperature and pH (Keenan & Kimmins 1993). Thus, the lack of significant longterm changes in basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 and nitrogen mineralization following harvesting is not unexpected. Seven to 9 years after clear-cutting and site preparation in the present study, microbial activities were not different from pre-harvested levels. However, most studies on clear-cutting impacts have reported increased or decreased basal respiration rates (Bauhus 1996; Chang & Trofymow 1996; Sundman et al. 1978), nitrogen mineralization rates (Bauhus 1996; Frazer et al. 1990) and microbial biomass C (Bååth 1980; Chang et al. 1995; Chang & Trofymow 1996; Entry et al. 1986) depending on the time since harvest and the methodology utilized. Chang et al. (1995), Frazer et al. (1990) and Sundman et al. (1978) state that following clear-cutting, soil microbial activities eventually approach pre-cut levels. Microbial processes in the present study may indicate that microbial systems have recovered to pre-cut levels within 7 to 9 years following harvesting.

The tendency for basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization to be slightly reduced in the organic layer 7 to 9 years after clear-cutting may indicate that the recovery of microbial systems was not complete at the time of

sampling; Sundman et al. (1978) predicted biological conditions similar to unharvested soil would be re-established within 8 to 13 years. Although microbial systems may not have recovered completely after 7 to 9 years, qCO_2 results indicate that microorganisms were not stressed metabolically under these conditions.

Based on rank abundance curves, and indices for community evenness and dominance, fungal community structure did not appear to be altered by clear-cutting and site preparation. Seven to nine years after harvesting, the fungal community was dominated by one species with the majority of isolated species in low abundance, a pattern indicative of an undisturbed community (Christensen 1969). Fungal community structure appears to be fairly stable following clear-cutting (Bååth 1981), and ordinations performed by Wicklow and Whittingham (1978) suggested a fungal community altered by clear-cutting approximately seventy years before eventually becomes similar to uncut fungal communities. The fungal community in the present study may have recovered to pre-cut levels within 7 to 9 years of disturbance or may not have been impacted by harvesting.

Only fungal species richness and diversity were affected significantly by clear-cutting and site preparation since these indices were reduced in the organic and increased in the mineral layers following harvesting. Disturbances of intermediate intensity which do not destroy all of the organisms present in an area, may create new habitat conditions which allow new organisms to colonize. Thus, following an intermediate disturbance increases in species richness and diversity may be observed (Connell 1978). In the organic soil, clear-cutting and site preparation may have been disruptive enough to reduce

fungus diversity and richness while less intense disturbance in the mineral soil increased fungus diversity and richness. The hypothesis that disturbance of the mineral soil 7 to 9 years after clear-cutting would be less than in the organic soil was not upheld by any fungus community measurements other than richness and diversity. However, the tendency for basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization to be slightly reduced in the organic soil but not the mineral soil may also suggest that upper soil horizons were more disturbed by harvesting than those further beneath the surface.

The significance of changes in fungus species richness and diversity to a forest soil system are unknown. It is argued that much of the species variation in fungus communities may result in functional redundancy, where many organisms perform the same functions e.g. degrade cellulose (Hawskworth 1991). Functional redundancy may reduce the importance of fungus species diversity (Gitay et al. 1996) and lessen the impact of diversity-reducing disturbance on forest systems (Hawskworth 1991). In the present study, functional overlap in the decomposer community may have in part prevented trends in fungus species diversity and richness following harvesting from being translated into changes in microbial processes and metabolic quotients.

As the differences in fungus diversity and richness in organic and mineral soil narrowed following harvesting, Sorenson's similarity index indicated the fungus community composition also became more similar. Principal-component analysis and humus phospholipid fatty acid analysis performed by Bååth (1981) and Bååth et al. (1995) indicated slight changes in organic soil fungus community structure following

clear-cutting and the removal of tree residues was a result of altered organic substrate availability. In the present study, alterations in organic matter which could not be detected by the loss on ignition technique may have resulted in lower similarity values between fungal communities in clear-cut and uncut soil, especially in the organic layer. However, in the same soil layers of both treatments fungal community similarity was greater than between the organic and mineral layers of a single treatment which indicated a drastic change in community composition had not occurred.

In this study, clear-cutting and site preparation did not significantly affect isolation frequencies of the fourteen most abundant fungal species. *Mortierella vinacea* was the dominant fungal species in clear-cut organic and mineral soil and uncut organic soil. *Mortierella vinacea* was also one of the principal fungi isolated by Christensen (1969) in mixedwood forests of Wisconsin. Following clear-cutting *Phialocephala* sp. no longer dominated the mineral soil fungal community, however, its isolation frequency was not significantly reduced. Although fungal species may be more sensitive to and indicative of disturbance than measurements of microbial processes, this was not observed in the present study. After 7 to 9 years, impacts of clear-cutting and site preparation on fungal community structure and microbial process measurements (with the exception of fungal species richness and diversity) were absent.

In the present study, the response of fungal community structure to clear-cutting was very similar at species and genus levels; with the exception of fungal richness and diversity where impacts detected at the species level were not evident at the genus level. Widden (1978) concluded that statements regarding generic abundances represented by

many different species are not valid unless the major species are known. However, in the present study identifying fungi to the genus level instead of the species level would have changed very few conclusions.

Conclusions

1. This study suggests that soil microbial processes and the fungal community had almost recovered to pre-cut levels within 7 to 9 years of harvesting disturbance.
2. Significant impacts on basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 and nitrogen mineralization were not evident following clear-cutting and site preparation, although all parameters (except qCO_2) tended to be slightly lower in the organic soil layer of the harvested sites.
3. Overall, fungal community structure and individual species abundances were not altered 7 to 9 years after clear-cutting and site preparation; however the differences in fungal richness, diversity and community composition seen between uncut organic and mineral soil were narrowed following harvesting.
4. Microorganisms in the organic layer may be impacted more than in the mineral layer due to the greater disturbance of clear-cutting and site preparation to the organic layer.
5. At both the species and genus levels fungal response patterns to harvesting were very similar; exceptions were species richness and diversity where effects were detected at the species level, but not the genus level.

3. Response of microbial processes and fungal community structure to vegetation management in mixedwood forest soils

3.1 Introduction

Following clear-cutting, vegetation management is used to facilitate the establishment of planted coniferous seedlings by decreasing the competition from non-coniferous vegetation (Ehrentraut & Branter 1990). Vegetation management is considered necessary for economic wood production (Bell et al. 1997) and can be chemical, motor-manual or mechanical (Ehrentraut & Branter 1990).

While clear-cutting and site preparation had little significant impact on microbial processes and fungal community structure in the present study (see Chapter 2), the additional disturbance caused by vegetation management may directly affect soil microorganisms (e.g. herbicide acting as a toxin or resource) or indirectly affect them by altering factors which control decomposer activities (e.g. moisture, temperature, organic substrate quantity and type) (Wardle 1989). Decreased canopy or ground cover following the application of herbicides (glyphosate, triclopyr) or the use of manually operated brushsaws can increase soil temperature and moisture (Reynolds et al. 1997b) and alter plant community composition and structure (Bell et al. 1997), thereby impacting the amount and type of organic substrates available to the microorganisms.

Glyphosate is a broad spectrum, non-selective herbicide toxic to most annual, biennial and perennial herbaceous plants (Anderson 1977) and has been used extensively

for vegetation management (Bell et al. 1997). At field concentration in agricultural soil, glyphosate does not appear to affect microbial biomass (Olson & Lindwall 1991; Wardle and Parkinson 1991), microbial respiration (Olson & Lindwall 1991; Wardle & Parkinson 1991), metabolic quotients (qCO_2) (Wardle & Parkinson 1991), bacterial biomass: fungal biomass ratio (Wardle & Parkinson 1991), ammonification (Tu 1994), denitrification (Tu 1994), nitrification (Olson & Lindwall 1991), sulfur oxidation (Tu 1994) or bacterial, fungal and actinomycete counts (Roslycky 1982). Field doses of glyphosate initially may alter the isolation frequency of some fungal species (Abdel-Mallek et al. 1994; Wardle & Parkinson 1990b) and occasionally affect interspecific fungal interactions (Wardle & Parkinson 1992), thus impacting fungal community structure. Direct impacts of glyphosate on microbial activities and community structure are often only evident immediately after application (Wardle & Parkinson 1990a; Wardle & Parkinson 1990b), at greater than field dosages (Roslycky 1982; Wardle & Parkinson 1990a) or following repeated applications (Ohtonen et al. 1992).

The majority of studies investigating glyphosate effects have been conducted in agricultural systems; research on the impact of this herbicide in forest soils is scarce. Ohtonen et al. (1992) examined microbial processes in a clear-cut forest following repeated glyphosate applications and observed reduced microbial biomass C , $C_{mic}:C_{org}$ and decreased fungal biomass relative to bacterial biomass. However, Ohtonen et al. (1992) did not specifically examine fungal community structure at the species level which may be more sensitive to disturbance than microbial processes.

Triclopyr is a selective herbicide toxic to most deciduous, woody plant species (Campbell 1990) with low activity in monocots and has been used successfully for vegetation management (Perala 1980). Brushsaws are used to manually remove non-coniferous woody vegetation and their use is more publically accepted than chemical vegetation management methods (Bell et al. 1997; Strong et al. 1995). Research on the impacts of triclopyr application and brushsaw use on soil microbial processes and community structure is lacking.

The effects of herbicides on soil microbial activities and fungal communities generally have been studied by direct application of the herbicide, often at concentrations exceeding those recommended for field application. Direct soil applications do not consider the response of soil microorganisms to indirect herbicide impacts which may occur in a field situation. Relating the results from such studies to response in the field can be difficult e.g. Olson & Lindwall (1991) found high dosages of glyphosate to reduce nitrification rate in laboratory studies while no effects were observed in the field. Thus a more relevant approach to understanding the repercussions on forest soil microorganisms is to conduct field studies using recommended treatment intensities and dosages. The scarcity of information on the impacts of vegetation management practices on forest soils, particularly under field conditions using treatments relevant to the field, prompted the present study which aimed to determine the effects of chemical herbicides (glyphosate and triclopyr) and manually operated brushsaws on microbially-mediated processes and fungal community structure. This study forms one component of the Fallingsnow Ecosystem Project (Ontario, Canada).

The soils used in the present study were obtained from three mixedwood sites which were clear-cut and prepared seven to nine years previously and planted with *Picea glauca* (Moench) Voss (white spruce). In 1993 (three to six years after planting), vegetation management procedures including 1. glyphosate, 2. triclopyr and 3. brushsaw use were utilized on each site. The objectives of this study were; 1. to examine the impacts of glyphosate, triclopyr and brushsaw use on microbially-mediated processes including basal respiration, microbial biomass C, nitrogen mineralization, metabolic quotients (qCO_2) and the ratio of microbial carbon: soil organic carbon ($C_{mic}:C_{org}$) in a harvested soil two years after treatment. 2. to examine the repercussions of glyphosate, triclopyr and brushsaw use on the structure of the soil fungal community in a harvested soil two years after treatment.

It was hypothesized that two years after vegetation management was performed to a clear-cut and prepared forest soil, the use of glyphosate, triclopyr and manually operated brushsaws would; 1. alter microbially-mediated processes including basal respiration, microbial biomass C, qCO_2 , $C_{mic}:C_{org}$ and nitrogen mineralization. 2. affect soil fungal community structure through changes in the relative abundance of some species.

3.2 Methods

Study Area

The study design, location and climate for the Fallingsnow Ecosystem Project have been described previously. Three clear-cut and prepared sites were used in this study. Sites 1 and 2 were mixedwood stands which were harvested seven to nine years prior to sampling in summer 1995. More detail on sites 1 and 2 is provided in Chapter 2. Site 3 (48° north/89°50' west) was created in 1987 when 32 ha of an 85 year old *Populus tremuloides* Michx. (trembling aspen) and *Abies balsamea* (L.) Mill. (balsam fir) forest were harvested. Site preparation using Young's teeth was performed in the summer of 1988 (Bell et al. 1997). The following spring, white spruce seedlings were planted (approx. 1,700/ ha). In general, the soil in site 3 was poorly drained with a silt loam texture (Simpson 1996).

Corylus cornuta Marsh. (beaked hazel), *Cornus stolonifera* Michx. (red-osier dogwood), *Diervilla lonicera* Mill. (bush honeysuckle), *Prunus pensylvanica* L. f. (pin cherry), *Pteridium aquilinum* (L.) Kuhn (bracken fern), *Rubus parviflorus* Nutt. (thimbleberry) and *Rubus idaeus* L. spp. *melanolasius* (red raspberry) were common in the shrub and understory layers of sites 1, 2 and 3 (Bell et al. 1997).

The project has a randomized block design using three clear-cut and prepared sites, each containing four treatment blocks (3.3 to 12.4 ha), each block corresponding to one of the following treatments: 1. clear-cut and prepared control, 2. glyphosate (1.5

kg active ingredient (a.i.)/ ha), 3. triclopyr (1.9 kg a.i./ ha) and 4. brushsaw. In all three sites vegetation management was performed in the summer of 1993; glyphosate and triclopyr were aerially applied in August 1993 while manual brushsaw release was performed two months later. Vegetation management impacts were assessed by comparing the results from glyphosate, triclopyr and brushsaw treated blocks to those obtained from clear-cut and prepared control blocks.

Sampling regime

In July 1995, three soil cores (20cm diam., 10cm deep) were sampled randomly from each of the four blocks (clear-cut and prepared control, glyphosate, triclopyr, and brushsaw) in each site (3 cores/ 4 blocks/ 3 sites; total=36). As described in the previous chapter, each soil core was separated into organic and mineral layers, passed through a 4 mm sieve and analyzed.

Measurements

Soil moisture, organic matter, pH and electrical conductivity were measured for the organic and mineral layers of each soil core. Microbial processes examined included; 1. basal respiration rate using CO₂ evolution, 2. microbial biomass C using substrate induced respiration (Anderson & Domsch 1978), 3. $C_{mic}:C_{org}$ (Anderson & Domsch 1990), 4. qCO₂ (Anderson & Domsch 1985) and 5. nitrogen mineralization rate using

laboratory incubations (adapted from Frazer et al. 1990).

The fungal community was examined through plating washed soil particles and identifying fungi to the species level wherever possible. Fungal community measurements included; 1. plotting rank abundance curves 2. calculating community indices including species richness (no. of species), diversity ($1/\text{Simpson's index}$), evenness (Shannon's index) and dominance (Berger-Parker index) 3. calculating similarity (Sorenson's index) of fungal communities. Methodologies were identical to those described in Chapter 2.

Statistical Analysis

A three factor analysis of variance was performed to test differences among the means of each measurement (moisture, organic matter, pH, electrical conductivity, microbial process measurements (including basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 and nitrogen mineralization), fungal community indices (including species richness, diversity, evenness, dominance), as well as, isolation frequencies of individual fungal species) and to assess variation caused by site location, soil layer and treatment. A repeated measure was included in the three factor ANOVA as the organic and mineral layers of each soil core were not independent. Data violating the ANOVA assumptions of normally distributed errors and homogeneity of variances were transformed. SAS was used to perform all the statistical analyses in this chapter (SAS Institute Inc. 1985).

3.3 Results

Soil characterization

Application of glyphosate and triclopyr, and brushsaw use did not significantly affect the organic matter or moisture content in either organic or mineral soil relative to that measured in the clear-cut and prepared control soil (Table 3.1). In all treatments, organic matter and moisture were significantly higher in the organic than in the mineral soil. Electrical conductivity and pH were similar in organic and mineral layers and were not altered two years after triclopyr, glyphosate or brushsaw use (Table 3.1).

Microbial processes

Relative to untreated clear-cut and prepared soil, glyphosate, triclopyr and brushsaw use had no impact on basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 or nitrogen mineralization two years after treatment (Table 3.2). All these parameters were significantly higher in the organic soil than in the mineral soil, regardless of treatment. In the organic layer, basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization tended to be slightly increased following glyphosate application.

Table 3.1. Abiotic parameters in organic and mineral soil layers of three harvested forest sites, two years following application of glyphosate, triclopyr or using brushsaws. Values shown are means (s.e.).

Soil Layer	Treatment	% Moisture (dwt)	% Organic Matter	pH	Electrical Conductivity (dSm ⁻¹)
Organic	clear-cut	167.1 ^{a1}	60.9 ^a	5.0 ^a	1.4 ^a
	control	(15.1)	(2.9)	(0.1)	(0.2)
	brushsaw	155.3 ^a	56.8 ^a	5.1 ^a	1.2 ^a
		(15.1)	(4.8)	(0.2)	(0.1)
	triclopyr	129.7 ^a	45.8 ^a	5.3 ^a	1.4 ^a
		(22.5)	(6.4)	(0.1)	(1.2)
Mineral	glyphosate	136.5 ^a	52.9 ^a	5.4 ^a	1.4 ^a
		(14.9)	(4.3)	(0.1)	(0.1)
	clear-cut	31.4 ^b	5.2 ^b	4.7 ^a	0.8 ^a
	control	(2.3)	(0.6)	(0.2)	(0.1)
	brushsaw	31.4 ^b	5.0 ^b	4.8 ^a	1.1 ^a
		(2.2)	(0.4)	(0.1)	(0.1)
	triclopyr	58.2 ^b	11.5 ^b	4.9 ^a	1.2 ^a
		(3.5)	(7.1)	(0.1)	(0.1)
	glyphosate	33.3 ^b	5.9 ^b	4.9 ^a	1.2 ^a
		(4.3)	(1.5)	(0.1)	(0.2)

¹Within each column different letters indicate significant differences between means (p=0.05; n=3).

Table 3.2. Microbial processes in organic and mineral soil layers of three harvested forest sites, 2 years after imposing vegetation management procedures (glyphosate, triclopyr, brush saw use). Values shown are means (s.e.).

Soil Layer	Treatment	Carbon Mineralization ($\mu\text{gC/gdw}/\text{h}$) ²	Nitrogen Mineralization ($\mu\text{gN/gdw}/\text{day}$) ²	Microbial Biomass (mgC/gdw) ²	$C_{\text{mic}}:C_{\text{org}}$ ³ (mg:g)	qCO_2 ($\text{X}10^{-3}$) ²
Organic	clear-cut control	7.6 ¹ (0.6)	11.7 ^a (1.4)	5.5 ^a (0.4)	1.9 ^a (0.2)	1.0 ^a (0.1)
	brush saw	8.0 ^a (1.2)	10.2 ^a (1.7)	5.2 ^a (0.7)	1.8 ^a (0.3)	2.0 ^a (0.3)
	triclopyr	7.0 ^a (1.5)	11.3 ^a (1.1)	4.0 ^a (0.8)	1.3 ^a (0.4)	2.0 ^a (0.2)
	glyphosate	15.3 ^a (3.8)	19.2 ^a (2.8)	8.1 ^a (1.5)	2.7 ^a (0.6)	2.0 ^a (0.3)
Mineral	clear-cut control	0.5 ^b (0.1)	0.5 ^b (0.3)	0.4 ^b (0.1)	0.02 ^b (0.01)	1.0 ^b (0.1)
	brush saw	0.4 ^b (0.1)	0.9 ^b (0.2)	0.5 ^b (0.1)	0.10 ^b (0.03)	0.9 ^b (0.2)
	triclopyr	1.2 ^b (0.8)	1.5 ^b (0.6)	0.8 ^b (0.3)	0.2 ^b (0.2)	1.0 ^b (0.1)
	glyphosate	0.4 ^b (0.1)	0.8 ^b (0.2)	0.5 ^b (0.1)	0.03 ^b (0.02)	0.9 ^b (0.1)

¹Within each column, different letters indicate significant differences between means ($p=0.05$; $n=3$).

²Data were square root transformed to satisfy ANOVA assumptions.

³Data were log transformed to satisfy ANOVA assumptions.

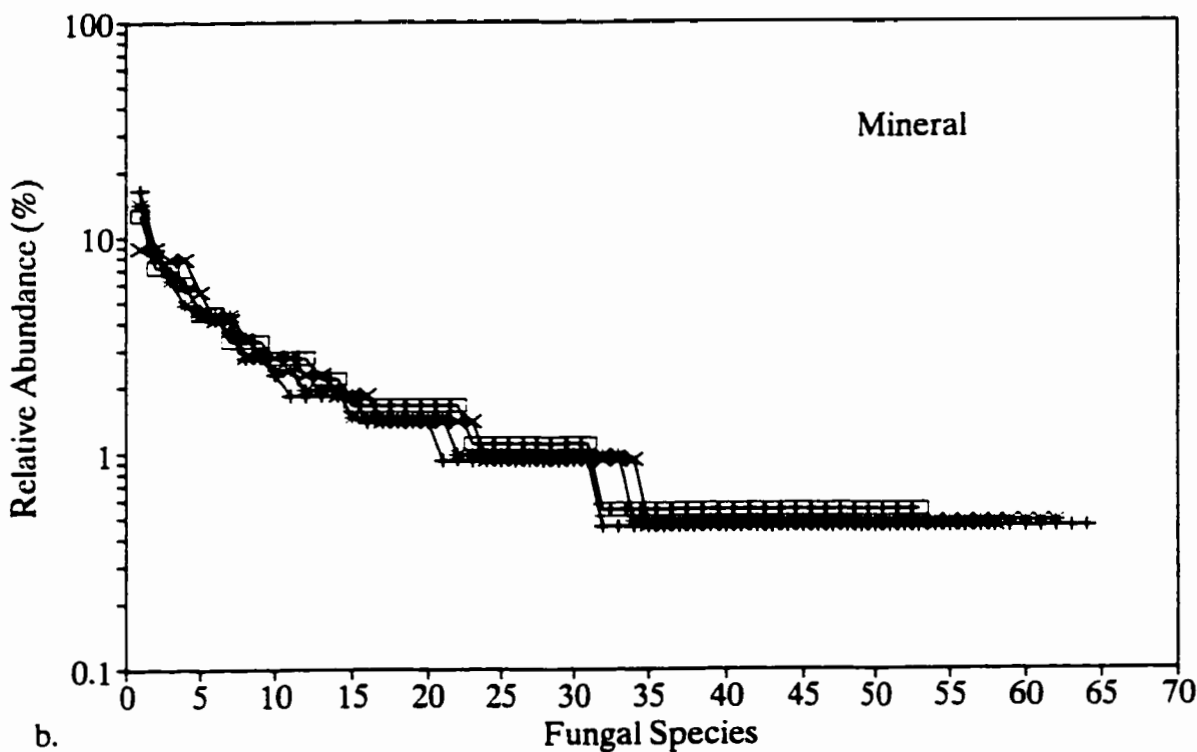
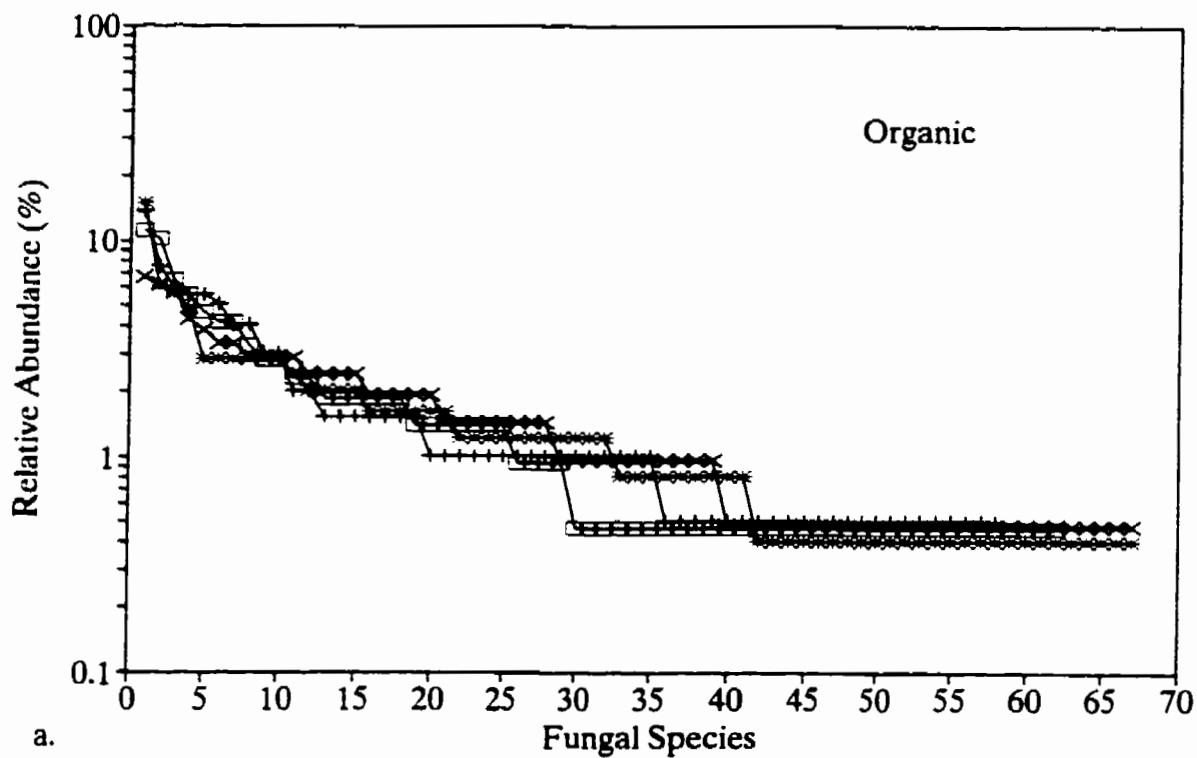
Fungal community

The use of glyphosate, triclopyr and brushsaws to suppress vegetation did not affect fungal community structure in the organic or mineral soil according to rank abundance curves (Figure 3.1a, Figure 3.1b) or indices of community structure (Figure 3.2a-d). Based on rank abundance curves the fungal community was characterized by one or two relatively abundant species, 5 or 6 moderately abundant species, and many rare species (relative abundance <2%) (Figure 3.1a, Figure 3.1b). The low relative abundance of most isolated fungal species resulted in high values for community evenness in the organic and mineral layers of all treatments (Figure 3.2c). Species richness and diversity were similar in the fungal communities of harvested organic and mineral soil and were not altered significantly two years after glyphosate, triclopyr or brushsaw use (Figure 3.2a, Figure 3.2b).

When the fungal data from all treatments and soil layers was combined, thirteen fungal species were found with frequencies of 2% or greater (Table 3.4). *Mortierella vinacea* was the most abundant species in the organic and mineral layers of all treatments except the glyphosate treatment where *Trichoderma viride* dominated in the organic layer and was as abundant as *Mortierella vinacea* in the mineral layer. The application of glyphosate and triclopyr significantly reduced the isolation frequency of *Mortierella vinacea*, however, fungal community structure was not affected; Berger-Parker dominance, which examines the dominance of the most frequently found fungal species (eg. *Mortierella vinacea* or *Trichoderma viride*), was not significantly reduced by

Figure 3.1 Rank abundance curves for all fungal species isolated from the organic and mineral soil layers of three mixedwood sites which were clear-cut and prepared, and two years prior to sampling were treated with herbicides (glyphosate or triclopyr), manual brushsaws or left untreated ($n=3$).

- a. organic layer species
- b. mineral layer species



—*— clear-cut —+— brushsaw —□— triclopyr —x— glyphosate

Figure 3.2 Fungal community indices for all fungal species isolated from the organic and mineral soil layers of three mixedwood sites which were clear-cut and prepared, and two years prior to sampling were treated with herbicides (glyphosate or triclopyr), manual brushsaws or left untreated. Values shown are means (s.e.) (n=3).

- a. species richness (no. fungal species/ 20 particles)
- b. species diversity (1/ Simpson's index)
- c. species evenness (Shannon's index)
- d. species dominance (Berger-Parker)

No significant treatment impact found ($p=0.05$)

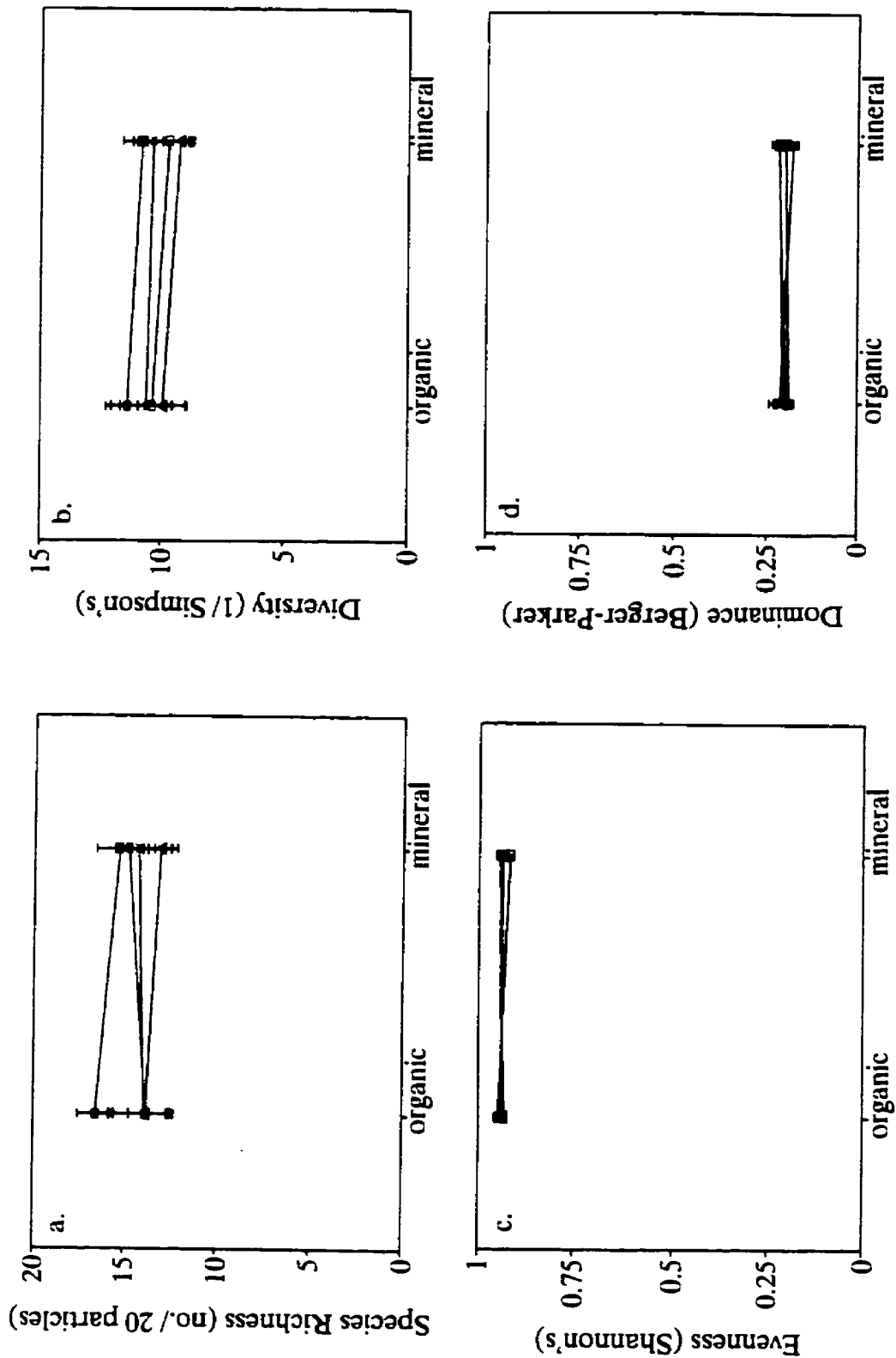


Table 3.4. The most frequently isolated fungal species (overall frequency > 2%) from the organic and mineral soil layers of three clear-cut and prepared mixedwood forest sites, 2 years after using glyphosate, triclopyr or brushsaws. Values shown are mean isolation frequencies (s.e.)

Fungal species	Treatment and Soil Layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Cladosporium cladosporioides</i> (Fres. de Vries)	3.3 ^{1 a2} (1.8)	6.1 ^a (2.7)	6.7 ^a (1.8)	3.9 ^a (1.5)	1.7 ^b (0.8)	1.7 ^b (0.8)	0.6 ^b (0.5)	0 ^b
<i>Cylindrocarpon magnusianum</i> (Sacc. Wollenw.)	2.2 ^a (1.1)	1.1 ^a (0.7)	1.1 ^a (0.7)	0.6 ^a (0.5)	9.4 ^b (3.3)	10.6 ^b (2.4)	4.4 ^b (1.2)	9.4 ^b (2.8)
<i>Gliocladium roseum</i> Bain.	2.2 ^a (1.1)	3.3 ^a (2.1)	3.3 ^a (2.2)	4.4 ^a (2.1)	1.1 ^a (1.1)	2.2 ^a (1.6)	7.2 ^a (2.9)	6.1 ^a (2.9)
<i>Gymnoascus reessii</i> Baran	3.9 ^a (1.7)	1.7 ^a (0.7)	6.7 ^a (3.0)	1.7 ^a (1.1)	0.6 ^a (0.5)	0.6 ^a (0.5)	4.4 ^a (1.5)	1.7 ^a (1.1)
<i>Mortierella alpina</i> Peyronel	2.8 ^a (1.1)	3.3 ^a (1.4)	2.8 ^a (1.1)	5.1 ^a (1.1)	5.0 ^a (1.6)	2.8 ^a (1.6)	1.1 ^a (0.7)	3.3 ^a (1.6)

¹Frequency of isolation (%) = (no. of times species isolated/20 soil particles plated) X 100

²Within each row, different letters indicate significant differences between means ($p=0.05$; $n=3$)

Table 3.4 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Mortierella</i> <i>vinacea</i> Dixon-Stewart	20.6 ^{c2} (3.9)	15.0 ^{b,c} (2.5)	13.3 ^{a,b} (4.0)	6.7 ^a (2.8)	16.1 ^c (3.2)	20.0 ^{b,c} (3.0)	12.8 ^{a,b} (4.0)	10.6 ^a (2.8)
<i>Paecilomyces carneus</i> (Duche & Heime) A.H.S. Brown & G. Sm.	8.3 ^a (2.7)	1.7 ^b (1.1)	5.6 ^{a,b} (2.0)	2.8 ^{a,b} (1.8)	1.1 ^{a,b} (0.7)	1.1 ^{a,b} (0.7)	0 ^{a,b}	1.7 ^{a,b} (1.1)
<i>Penicillium canescens</i> Sopp	7.8 ^a (3.5)	5.6 ^a (2.1)	2.8 ^a (0.8)	2.2 ^a (1.6)	1.1 ^b (0.7)	0 ^b	1.1 ^b (1.1)	0 ^b
<i>Phialocephala sp.</i>	0 ^a	0 ^a	0 ^a	0 ^a	5.0 ^b (1.6)	7.2 ^b (2.9)	7.2 ^b (2.9)	5.0 ^b (3.1)
<i>Pseudogymnoascus</i> <i>roseus</i> Raillo	1.1 ^a (0.7)	1.1 ^a (0.7)	0 ^a	1.1 ^a (0.7)	5.0 ^a (1.4)	8.3 ^a (2.6)	3.3 ^a (1.6)	3.3 ^a (1.1)
<i>Trichoderma</i> <i>harzianum</i> Rifai	1.7 ^a (0.8)	6.1 ^a (2.1)	3.3 ^a (1.4)	3.9 ^a (2.7)	1.7 ^a (1.1)	4.4 ^a (3.1)	1.7 ^a (1.1)	2.2 ^a (1.4)

²Within each row, different letters indicate significant differences between means (p=0.05; n=3)

Table 3.4 concluded.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Trichoderma polysporum</i> (Link:Fr.) Rifai	3.9 ^{a2} (2.2)	8.3 ^a (1.4)	1.7 ^a (1.1)	3.3 ^a (1.6)	2.8 ^a (1.4)	3.3 ^a (2.1)	1.7 ^a (0.8)	3.3 ^a (3.1)
<i>Trichoderma viride</i> aggr. sensu Rifai	6.7 ^a (2.1)	8.3 ^a (1.4)	12.2 ^a (2.6)	7.2 ^a (2.1)	7.2 ^a (3.2)	5.0 ^a (2.1)	6.1 ^a (3.2)	10.6 ^a (4.4)

²Within each row, different letters indicate significant differences between means (p=0.05; n=3)

glyphosate, triclopyr or brushsaw use (Figure 3.2d). Brushsaw use significantly reduced the isolation frequency of *Paecilomyces carneus*. In the clear-cut control, the occurrence of *Paecilomyces carneus* was significantly higher in the organic than mineral soil. However, this difference was not evident in the glyphosate, triclopyr and brushsaw treatments (Table 3.4).

Although most of the fungal species analyzed were not impacted by vegetation management, low values for Sorenson's similarity index indicate that fungal community composition may have been affected. Similarity values obtained were similar when fungal communities among treatments and between soil layers were compared (Table 3.3). A complete list of all fungi isolated and their frequency of isolation during the present study is included in Appendix Table 6.2.

3.4 Discussion

Bell et al. (1997) found deciduous tree cover to be reduced significantly one year after glyphosate, triclopyr and brushsaw use in the Fallingsnow Ecosystem Project. Shrub cover was reduced significantly by both glyphosate and triclopyr application and glyphosate also reduced fern cover (Bell et al. 1997). However, increased deposition of plant residues (e.g. litter, stems, roots) resulting from vegetation management was not sufficient to increase the amount of organic matter present in the soil after two years. Every autumn this soil system receives a large influx of organic material in the form of leaf litter, thus organic inputs resulting from glyphosate, triclopyr and brushsaw use may

Table 3.3. Sorenson's similarity coefficient for fungal communities in organic and mineral soil layers of clear-cut and site prepared, and vegetation managed soil.

Soil Layer	Treatment	Organic				Mineral			
		clear-cut	brushsaw	triclopyr	glyphosate	clear-cut	brushsaw	triclopyr	glyphosate
Organic	clear-cut	-	0.48	0.53	0.69	0.59	0.41	0.42	0.50
	brushsaw	-	-	0.55	0.51	0.50	0.41	0.40	0.45
	triclopyr	-	-	-	0.47	0.48	0.38	0.37	0.42
	glyphosate	-	-	-	-	0.50	0.36	0.39	0.46
Mineral	clear-cut	-	-	-	-	-	0.41	0.46	0.52
	brushsaw	-	-	-	-	-	-	0.56	0.47
	triclopyr	-	-	-	-	-	-	-	0.50
	glyphosate	-	-	-	-	-	-	-	-

not have been detected.

One growing season following vegetation management, reduced soil moisture was detected by Reynolds et al. (1997), however, this was not evident two years after treatment. Vegetation management reduced the percent cover of deciduous trees, shrubs (glyphosate and triclopyr) and ferns (glyphosate) within one year of treatment, but the cover of conifers, forbs, grasses, shrubs (brushsaw), sedges (glyphosate and triclopyr), ferns (triclopyr) and horsetails (triclopyr) increased (Bell et al. 1997). The rapid recovery of vegetation following herbicide and brushsaw use may account for the lack of a treatment effect on soil moisture observed after two years. Ohtonen et al. (1992) found multiple applications of glyphosate to have no significant impact on pH in forest organic soil, a result also found in the present study. However, contrary to the present study, Ohtonen et al. (1992) found the pH in the mineral soil to be significantly reduced by glyphosate.

Two years after vegetation management was implemented, no significant changes to soil microbial processes, $C_{mic}:C_{org}$ or metabolic quotients were detected indicating little impact of herbicide or brushsaw treatment on microbial activities. Single applications of glyphosate to agricultural soil at field concentrations were reported to have few direct effects on microbial biomass, basal respiration, qCO_2 (Wardle and Parkinson 1990a) or nitrogen mineralization (Olson & Lindwall 1991). In the present study, field applications of glyphosate at recommended concentrations to a mixedwood forest soil also had no impact on basal respiration, microbial biomass C, $C_{mic}:C_{org}$, qCO_2 or nitrogen mineralization.

Two years following the application of glyphosate basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization in the organic soil tended to be slightly higher than in the organic soil of the clear-cut controls. It is unlikely that the higher microbial biomass and activity rates were a direct result of the application of glyphosate two years prior to sampling since glyphosate is rapidly degraded (Newton et al. 1984) by soil microorganisms (Sprankle et al. 1975a) and would have been completed by the time this study was initiated.

Two years following the use of glyphosate, triclopyr and brushsaws there was no evidence of either direct or indirect impacts on fungal community structure in mixedwood forest soil based on rank abundance curves and indices of community structure. Rosylycky (1982) also found microbial community structure (measured using relative population sizes of actinomycetes, bacteria and fungi) in an agricultural soil to be unaffected by glyphosate application at field concentration. The fungal communities in all treatments appeared stable and resembled those found in undisturbed forest soils as indicated by rank abundance curves dominated by a few species with the majority of species having low relative abundances (Christensen 1969)). Even though the isolation frequency of *Mortierella vinacea* (most frequently isolated species) was reduced significantly by both the application of glyphosate or triclopyr, dominance (Berger-Parker), and thus community structure, was not affected. Bååth (1981) concluded that changes in vegetation cover may not have immediate effects on fungal community structure and in this study, vegetation cover may not have been reduced sufficiently or may have recovered quickly enough to prevent significant changes to fungal community

structure two years after herbicide or brushsaw treatment.

While vegetation management had no significant impacts on microbial processes, $C_{mic}:C_{org}$, metabolic quotients or fungal community structure, significant alterations in the isolation frequency of two fungal species were detected two years after treatment. The isolation frequencies of *Mortierella vinacea* (glyphosate and triclopyr) and *Paecilomyces carneus* (brushsaw) were reduced significantly by vegetation management in clear-cut and prepared organic soil, and it is also possible that some rare species with isolation frequencies too low for statistical analysis were impacted. The presence or absence of fungal species is used to calculate Sorenson's similarity index, thus the low community similarity found between treatments (often values were lower among treatments than between soil horizons) may have resulted from undetected shifts in the community composition of infrequently isolated fungal species.

Glyphosate directly applied to soil at field concentration can affect fungal species. Wardle and Parkinson (1990b) showed that alterations in the percent occurrence of individual fungal species can occur for up to nine days following application and increases and decreases in the density of fungal species were reported by Abdel-Mallek et al. (1994) when soil was incubated in the presence of glyphosate for 10 weeks. Also reduced competition between two fungal species were observed by Wardle and Parkinson (1992) in agricultural soil treated with glyphosate in the lab. However, in field experiments indirect impacts of herbicide application on fungal species may also occur through alterations in the microbial habitat e.g. reduced plant cover, altered soil nutrient levels (Wardle 1989). As mentioned previously for the soil process measurements, the

significant reduction in isolation frequency of *Mortierella vinacea* observed two years following glyphosate and triclopyr application was probably not the result of direct herbicide impacts on this species since glyphosate (Newton et al. 1984) and triclopyr (Johnson et al. 1995) have fairly rapid decay rates in soil. As brushsaw use results in very little soil disturbance, selective cutting of deciduous trees using manually operated brushsaws also may have decreased indirectly the isolation frequency of *Paecilomyces carneus*. *Paecilomyces carneus* was isolated significantly more frequently from the harvested organic soil than the mineral soil, a difference not found two years after vegetation management was performed. Slight alterations in microbial habitat such as changes in plant cover, soil nutrient levels or dead plant residues may have affected *Mortierella vinacea* and *Paecilomyces carneus* even though the fungal community as a whole was unaffected by treatment. Both *Mortierella vinacea* and *Paecilomyces carneus* appear to be generalist saprotrophs, they are globally distributed species which have been isolated from the soil beneath many different types of vegetation (Domsch et al. 1980). The response of *Mortierella vinacea* and *Paecilomyces carneus* to vegetation management treatments had very little impact on microbial decomposition, evidenced in this study by basal respiration, qCO_2 and nitrogen mineralization measurements. Wardle & Parkinson (1990b) state that in comparison to other factors which influence the soil system (e.g. spatial variation, seasonality) herbicide effects in the field are most likely unimportant. The majority of fungal species in the present study were unaffected by vegetation management as was the case for the microbial activity and fungal community parameters. Although a small number of fungal species appeared to be sensitive to the use of

glyphosate, triclopyr and brushsaws.

Conclusions

1. Two years following glyphosate, triclopyr or brushsaw use in clear-cut and prepared, mixedwood forest soils, basal respiration, microbial biomass C, qCO_2 , $C_{mic}:C_{org}$ and nitrogen mineralization were not affected significantly relative to that measured in untreated controls.
2. Fungal community structure, as determined by rank abundance curves and community indices (richness, diversity, evenness, dominance), was not altered two years after vegetation management was carried out on a clear-cut and prepared forest soil.
3. 11 of the 13 most frequently isolated fungal species were unaffected by vegetation management; however, herbicide application reduced the isolation frequency of *Mortierella vinacea* and manually operated brushsaws reduced the isolation frequency of *Paecilomyces carneus*. Occurrence of *Paecilomyces carneus* was significantly greater in the organic soil than in the mineral soil in the harvested control but this difference was not detectable in the blocks which had undergone vegetation management. As indicated by values for Sorenson's similarity, vegetation management may have altered the isolation frequencies of rare fungal species resulting in changes to fungal community composition.

4. Conclusions

Studies examining the repercussions of forestry practices such as clear-cutting, site preparation and vegetation management on soil microorganisms are not abundant, especially in comparison to the large amount of literature available on the impact of forestry practices on plant communities and soil properties. Understanding the response of soil microorganisms to disturbance caused by forestry practices is necessary as decomposition and nutrient cycling are very important to ecosystem productivity and maintenance. Most studies examining the impacts of forestry practices on soil microorganisms have concentrated on microbial activities such as decomposition and nutrient cycling. The fungal component of the microbial biomass is dominant in forest soils but information on the response of the fungal community to clear-cutting, site preparation and vegetation management in addition to microbially-mediated processes is lacking, especially at the fungal species level.

Ohtonen et al. (1992) completed a study which examined the effect of site preparation and vegetation management (glyphosate application) on forest soil microorganisms. The response of soil microorganisms to glyphosate application has been studied primarily in agricultural soils using both laboratory and field situations. Although glyphosate is used frequently as a method of vegetation management, forest field studies are lacking. Studies examining microbial responses to triclopyr and manually operated brushsaws in forest soil are also wanting.

The present study was conducted in the field using mixedwood forest sites located in Ontario, Canada. The impact of clear-cutting, site preparation and vegetation

management on microbially mediated processes and fungal community structure was examined. The specific objectives of this study were: 1. to determine fungal community structure, basal respiration, microbial biomass C, qCO_2 , $C_{mic}:C_{org}$ and nitrogen mineralization in two sites, 7 to 9 years after clear-cutting and site preparation 2. to determine the response of the fungal community and microbial processes (basal respiration, microbial biomass C, qCO_2 , $C_{mic}:C_{org}$ and nitrogen mineralization) in three clear-cut sites, 2 years after applying glyphosate and triclopyr, and the use of brushsaws 3. to provide information on the possible relationship between microbial process level and fungal species level measurements 4. to compare the sensitivity of community indices at the fungal species and genus levels.

The results indicate that there were relatively few long term (7 to 9 year) effects of clear-cutting and site preparation on microbial processes or fungal communities. Also, 2 years following herbicide or brushsaw utilization there was very little evidence of adverse impacts on soil microorganisms. It is suggested that other factors such as seasonality and spatial variation may have a stronger influence on microbial response than disturbance caused by harvesting and vegetation management. Basal respiration, microbial biomass C, qCO_2 , $C_{mic}:C_{org}$ and nitrogen mineralization were not significantly affected by clear-cutting or vegetation management, however, similar tendencies for reduced basal respiration, microbial biomass C, $C_{mic}:C_{org}$ and nitrogen mineralization values in organic soil following harvesting indicated that 7 to 9 years later, soil microorganisms almost had recovered. Microorganisms in the organic soil may have been disturbed more by harvesting than those in the mineral layer.

Clear-cutting and site preparation had no impact on indices of evenness and dominance, and did not affect fungal species isolation frequency. However, differences in fungal richness, diversity and community composition between the organic and mineral soil were narrowed 7 to 9 years after harvesting.

Vegetation management did not alter community indices or the isolation frequencies of 11 of the 13 most frequently isolated fungal species. *Mortierella vinacea* and *Paecilomyces carneus* were the only two fungi significantly affected by vegetation management in that their isolation frequencies were reduced by herbicide application and brushsaw use, respectively. Also, *Paecilomyces carneus* was significantly more frequently isolated from clear-cut organic soil than mineral soil; a trend no longer evident following vegetation management. Through impacts on rare fungal species, vegetation management may have changed the composition of the fungal community as evidenced by values for Sorenson's similarity.

The response of the fungal community to clear-cutting and site preparation was similar at both the genus and species levels; except for fungal community richness and diversity where impacts at the species level were no longer detected at the genus level. In the present study, identifying fungi to the genus level instead of the species level would not have required the modification of any overall conclusions.

While this study found that there were few impacts on soil microorganisms, 7 to 9 years after clear-cutting and site preparation and two years after vegetation management, many different methods and intensities of clear-cutting, site preparation and vegetation management are currently utilized by the forestry industry. The response of

forest systems to different forestry practices can be altered by seasonality, site characteristics, plant community composition and management strategies, thus, the results of this study may be specific to the sites examined and the forestry techniques used.

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6. Appendices

Appendix Table 6.1. Fungal species isolated from the organic and mineral layers of two mixedwood forest soils, 7 to 9 years following clear-cutting and site preparation. Values shown are mean isolation frequencies¹ (s.e.).

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Absidia glauca</i> Hagem	1.7 (1.0)	0.8 (0.8)	0	0
<i>Acromonium butyri</i> (van Beyma) W. Gams.	0	2.5 (1.6)	0	0
<i>Acromonium potronii</i> Vuill.	0.8 (0.8)	0	0	2.5 (1.0)
<i>Aspergillus</i> sp. 1	2.5 (2.3)	0	0	0
<i>Aspergillus fumigatus</i> Fres.	0	0	0.8 (0.8)	0.8 (0.8)
<i>Aureobasidium pullulans</i> (de Bary)	0	1.7 (1.5)	0	0.8 (0.8)
Arnaud				
<i>Botrytis cinerea</i> Pers. ex Nocca & Balb.	0.8 (0.8)	0	0	0.8 (0.8)
<i>Chaetosphaeria vermicularioides</i> (Sacc. & Roum.) W. Gams & Hol.-Jech.	0.8 (0.8)	0.8 (0.8)	0	0.8 (0.8)
<i>Chrysosporium pannorum</i> (Link) Hughes	0.8 (0.8)	1.7 (1.5)	0	2.5 (1.0)

¹Frequency of isolation (%) = (no. of times species isolated/20 soil particles plated) X 100

Table 6.1 continued.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Cladosporium cladosporioides</i> (Fres. de Vries)	8.3 (2.3)	2.5 (1.6)	3.3 (2.3)	2.5 (1.0)
<i>Coelomycete</i> sp. 1	0.8 (0.8)	0	0	0
<i>Cylindrocarpon magnusianum</i> (Sacc. Wollenw.)	3.3 (1.5)	3.3 (1.5)	9.2 (4.2)	7.5 (1.6)
<i>Eupenicillium shearii</i> Stolk & Scott	1.7 (1.5)	0	0	0
<i>Fusarium avenacea</i> Wollenw.	0	0.8 (0.8)	0	0
<i>Gliocladium roseum</i> Bain.	0	3.3 (1.5)	0	0
<i>Gymnoascus reessii</i> Baran	2.5 (1.6)	5.8 (2.2)	2.5 (1.6)	0.8 (0.8)
<i>Humicola fuscoatra</i> Traaen	0	0	0.8 (0.8)	5.8 (2.2)
<i>Mariannaea elegans</i> (Corda) Samson.	0	0.8 (0.8)	0	0
<i>Monodictys castaneae</i> (Wallr.) Hughes	0	0	0.8 (0.8)	0
<i>Mortierella alpina</i> Peyronel	7.5 (3.5)	3.3 (1.5)	6.7 (3.3)	4.2 (1.8)

Table 6. 1 continued.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Mortierella horticola</i> Linnem.	0	0.8 (0.8)	0	0
<i>Mortierella isabellina</i> Oudem.	1.7 (1.0)	1.7 (1.5)	0	0.8 (0.8)
<i>Mortierella parvispora</i> Linnem.	0	0.8 (0.8)	2.5 (1.6)	0.8 (0.8)
<i>Mortierella ramamiana</i> (Naumov) Linnem var. <i>angulispora</i>	3.3 (1.5)	3.3 (1.5)	3.3 (1.5)	3.3 (1.5)
<i>Mortierella ramamiana</i> (Moller) Linnem var. <i>ramamiana</i>	1.7 (1.5)	0 (1.5)	1.7 (1.5)	0
<i>Mortierella vinacea</i> Dixon-Stewart	22.5 (3.9)	16.7 (5.6)	13.3 (3.0)	13.3 (3.7)
<i>Mucor hiemalis</i> Wehmer f. <i>hiemalis</i>	0.8 (0.8)	0	0	0
<i>Mucor hiemalis</i> f. <i>silvaticus</i> (Hagem) Schipper	1.7 (1.0)	0	0	0
<i>Mycogone perniciosa</i> Link	0	0	1.7 (1.0)	0.8 (0.8)
<i>Oidiodendron</i> sp. 1	0	0.8 (0.8)	0	0
<i>Oidiodendron chlamydosporicum</i> Morrell	1.7 (1.5)	0.8 (0.8)	0	0.8 (0.8)

Table 6.1 continued.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Oidiodendron tenuissimum</i> (Peck) Hughes	5.8 (2.7) 0	0	1.7 (1.0) 0	4.2 (1.4) 0
<i>Paecilomyces</i> sp.1		0.8 (0.8)		
<i>Paecilomyces</i> sp.2	0.8 (0.8) 0	0	0	0
<i>Paecilomyces</i> sp.3		0	0	0.8 (0.8)
<i>Paecilomyces carneus</i> (Duche & Heim) A. H. S. Brown & G. Sm.	4.2 (1.8) 1.7	8.3 (3.7) 1.7	0.8 (0.8) 0	0.8 (0.8) 0
<i>Paecilomyces farinosus</i> (Holm ex Gray) A. H. S. Brown & G. Sm.	(1.0) 0	(1.5) 0.8	0	0
<i>Penicillium</i> sp. 1		(0.8) 0		
<i>Penicillium arenicola</i> Chalabuda.	0.8 (0.8) 0		0	0
<i>Penicillium canescens</i> Sopp		7.5 (4.7) 2.5	1.7 (1.5) 0.8	0.8 (0.8) 0
<i>Penicillium janthinellum</i> Biourge	6.7 (1.9) 2.5	(1.6) 0	(0.8) 0	
<i>Penicillium melinii</i> Thom	(1.6)			0

Table 6.1 continued.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Penicillium montanense</i> Christensen & Backus	5.0 (2.9)	2.5 (1.0)	5.0 (2.9)	2.5 (1.6)
<i>Penicillium purpurogenum</i> Stoll	5.0 (3.1)	3.3 (1.5)	0	0
<i>Penicillium raistrickii</i> G. Smith	0	0	0.8 (0.8)	0
<i>Penicillium spinulosum</i> Thom	3.3 (1.5)	0.8 (0.8)	0	0
<i>Penicillium steckii</i> Zaleski	0.8 (0.8)	2.5 (1.6)	0	0
<i>Penicillium thomii</i> Maire	3.3 (1.5)	3.3 (2.3)	0.8 (0.8)	0.8 (0.8)
<i>Penicillium variabile</i> Sopp	6.7 (1.0)	1.7 (1.5)	0	0
<i>Phialocephala</i> sp. 1	0.8 (0.8)	0	17.5 (3.1)	4.2 (2.2)
<i>Phialophora fastigiata</i> (Lagerb. & Melin) Conant	5.0 (2.4)	1.7 (1.0)	0	0.8 (0.8)
<i>Phialophora malorum</i> (Kidd & Beaum.) McColloch	0	0.8 (0.8)	0	0
<i>Polyscytalum</i> sp.	1.7 (1.0)	0	0	0

Table 6.1 continued.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Pseudogymnoascus roseus</i> Raillo	1.7 (1.0)	1.7 (1.0)	0.8 (0.8)	5.0 (1.7)
<i>Rhinocladiella</i> sp. 1	3.3 (2.3)	2.5 (2.3)	0	0
<i>Sporothrix schenkii</i> Hektoen & Perkins	1.7 (1.0)	0.8 (0.8)	0	0
<i>Tetrasporium</i> sp. 1	0	0	0.8 (0.8)	0
<i>Tolypocladium cylindrosporum</i> W. Gams	0	0.8 (0.8)	0	0
<i>Tolypocladium niveum</i> (Rostrup) Bissett	0	1.7 (1.0)	0	0
<i>Trichocladium opacum</i> (Corda) Hughes	0	0	2.5 (1.0)	5.0 (2.4)
<i>Trichoderma fertile</i> Bissett	0	1.7 (1.0)	0	0
<i>Trichoderma harzianum</i> Rifai	0.8 (0.8)	1.7 (1.0)	0.8 (0.8)	0.8 (0.8)
<i>Trichoderma longipilis</i> Bissett	0	2.5 (1.0)	0	0
<i>Trichoderma polysporum</i> (Link:Fr.) Rifai	5.0 (1.7)	5.0 (3.1)	1.7 (1.0)	2.5 (1.6)

Table 6.1 concluded.

Fungal species	Treatment and soil layer			
	uncut Organic	clear-cut Organic	uncut Mineral	clear-cut Mineral
<i>Trichoderma strictipilis</i> Bissett	0	0	1.7 (1.0)	0
<i>Trichoderma viride</i> Pers.:Fr.	0	0	1.7 (1.0)	0
<i>Trichosporon beigelli</i> (Kuchenm. & Rabenh.) Vuill.	1.7 (1.0)	0	0	1.7 (1.5)
<i>Troposporella fumosa</i> Karst.	0	0	0.8 (0.8)	0
<i>Truncatella truncata</i> (Lev.) Stey.	0	0.8 (0.8)	0	0
<i>Verticillium lecanii</i> (Zimm.) Viegas.	0	0	0	0.8 (0.8)
Yeast sp. 1 (dark hyphal)	0	0.8 (0.8)	0	0
Sterile dark (total)	10.0 (2.4)	9.2 (3.2)	8.3 (3.3)	14.2 (5.2)
Sterile hyaline (total)	0.8 (0.8)	3.3 (1.5)	2.5 (1.6)	4.2 (1.8)

Appendix Table 6.2. Fungal species isolated from the organic and mineral layers of three harvested forest soils, 2 years after using glyphosate, triclopyr or brushsaws. Values shown are mean isolation frequencies¹ (s.e.).

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Absidia glauca</i> Hagem	1.7 (0.8)	0	0.6 (0.5)	1.7 (0.8)	0	0	2.2 (1.6)	0.6 (0.5)
<i>Acremonium</i> sp.		0	0.6 (0.5)	0	0	0	0	0
<i>Acremonium butyri</i> (van Beyma) W. Gams.	1.7 (1.1)	0.6 (0.5)	2.2 (1.1)	2.8 (1.6)	0	1.7 (1.1)	0.6 (0.5)	0
<i>Acremonium murorum</i> (Corda) W. Gams.	0	1.1 (0.7)	0.6 (0.5)	0	0	1.7 (1.6)	1.7 (1.1)	2.8 (1.4)
<i>Acremonium potronii</i> Vuill.	1.1 (1.0)	0	1.1 (0.7)	1.7 (1.1)	1.7 (0.8)	0	0	0
<i>Acremonium strictum</i> W. Gams.	1.1 (1.0)	1.1 (0.7)	0	1.7 (0.8)	0	0	0	0
<i>Alternaria alternata</i> (Fr.) Keissler	0	0	0	0	0	0.6 (0.5)	0	0
<i>Alysidium resinae</i> (Fr.) M. B. Ellis	0	0	0.6 (0.5)	0.6 (0.5)	0	0	0	0

¹Frequency of isolation (%) = (no. of times species isolated/20 soil particles plated) X 100

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Aspergillus</i> sp. 1	0	0.6 (0.5)	1.7 (0.8)	0	0	0	0	0
<i>Aspergillus</i> sp. 2	0	0	0.6 (0.5)	0	0	0	0	0
<i>Aspergillus fumigatus</i> Fres.	0	1.1 (0.1)	0	0	0.6 (0.5)	1.1 (0.7)	0	0
<i>Aspergillus sydowii</i> (Bain. & Sart.) Thom & Church	0	0.6 (0.5)	0	0	0	0	0	0
<i>Aureobasidium</i> <i>pullulans</i> (de Bary) Arnaud	1.1 (0.1)	0	0	0	0.6 (0.5)	0	0	1.1 (0.1)
<i>Basidiomycete</i> sp.	0	0	0.6 (0.5)	0.6 (0.5)	0	0	0	0
<i>Botrytis cinerea</i> Pers. ex Nocca & Balb.	0	0.6 (0.5)	0.6 (0.5)	0 (0.5)	0.6 (0.5)	0	0	0
<i>Chaetodiplodia</i> sp.	0	0	0	3.3 (2.6)	0	0	0	0
<i>Chaetosphaeria</i> <i>vermicularioides</i> (Sacc. & Roum.) W. Gams & Hol.-Jech.	0.6 (0.5)	0.6 (0.5)	1.1 (0.7)	0.6 (0.5)	0.6 (0.5)	0	0	0.6 (0.5)

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Chloridium</i> <i>clavaeformes</i> (Preuss) W. Gams & Hol. Jech.	0	0	0	0.6 (0.5)	0	0	0	0
<i>Chrysosporium</i> <i>pannorum</i> (Link) Hughes	2.8 (1.4)	0	2.2 (1.4)	0.6 (0.5)	2.8 (1.1)	0	0	0
<i>Cladosporium</i> <i>cladosporioides</i> (Fres. de Vries)	3.3 (1.8)	6.1 (2.7)	6.7 (1.8)	3.9 (1.5)	1.7 (0.8)	1.7 (0.8)	0.6 (0.5)	0
<i>Coelomycete</i> sp. 1	0	0	1.1 (0.1)	0	0	0	0	0
<i>Cylindrocarpon</i> <i>magnusianum</i> (Sacc. Wollenw.)	2.2 (1.1)	1.1 (0.7)	1.1 (0.7)	0.6 (0.5)	9.4 (3.3)	10.6 (2.4)	4.4 (1.2)	9.4 (2.8)
<i>Eupenicillium</i> <i>crustaceum</i> Ludwig	0.6 (0.5)	0	0.6 (0.5)	0.6 (0.5)	0	0	0	0
<i>Eupenicillium shearii</i> Stolk & Scott	0	1.7 (1.1)	0.6 (0.5)	0.6 (0.5)	0.6 (0.5)	0	0	0
<i>Fusarium avenacea</i> Wollenw.	0.6 (0.5)	0	0	1.7 (1.1)	0	0.6 (0.5)	0	1.1 (0.7)

Table 6.2 continued.

Fungal species	Treatment and soil layer									
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral	brushsaw Organic	clear-cut Organic
<i>Fusarium redolens</i> Wollenw.	0	0	0	0.6 (0.5)	0	0	0	0		
<i>Gliocladium roseum</i> Bain.	2.2 (1.1)	3.3 (2.1)	3.3 (2.2)	4.4 (2.1)	1.1 (1.1)	2.2 (1.6)	7.2 (2.9)	6.1 (2.9)		
<i>Gymnascus reessii</i> Baran	3.9 (1.7)	1.7 (0.7)	6.7 (3.0)	1.7 (1.1)	0.6 (0.5)	0.6 (0.5)	4.4 (1.5)	1.7 (1.1)		
<i>Humicola fuscoatra</i> Traaen	0	0	0	0	5.0 (1.4)	2.2 (1.1)	2.8 (1.1)	5.0 (2.6)		
<i>Leptosphaeria coniothyrium</i> (Fuckel) Sacc.	0	0	0	1.1 (0.7)	0	0	0	0		
<i>Mortierella alpina</i> Peyronel	2.8 (1.1)	3.3 (1.4)	2.8 (1.1)	5.1 (1.1)	5.0 (1.6)	2.8 (1.6)	1.1 (0.7)	3.3 (1.6)		
<i>Mortierella horticola</i> Linnem.	0.6 (0.5)	3.3 (1.4)	2.8 (1.1)	5.1 (1.1)	5.0 (1.6)	2.8 (1.6)	1.1 (0.7)	3.3 (1.6)		
<i>Mortierella humicola</i> Oudemans & Koning	0	0	0	1.1 (0.7)	0	0	0	0		
<i>Mortierella isabellina</i> Oudem.	1.7 (1.1)	0.6 (0.5)	2.2 (0.8)	0	1.1 (0.7)	1.7 (0.8)	0	0		
<i>Mortierella parvispora</i> Linnem.	0.6 (0.5)	0	0	1.1 (0.7)	2.2 (0.8)	0.6 (0.5)	0	2.2 (0.8)		

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Mortierella</i> <i>ramanniana</i> (Naumov) Linnem var. <i>angulispora</i>	3.9 (3.1)	0	0.6 (0.5)	2.2 (1.1)	0	0.6 (0.5)	0	0
<i>Mortierella</i> <i>ramanniana</i> (Moller) Linnem var. <i>ramanniana</i>	1.7 (1.1)	0	0	0.6 (0.5)	0	0	0	0
<i>Mortierella vinacea</i> Dixon-Stewart	20.6 (3.9)	15.0 (2.5)	13.3 (4.0)	6.7 (2.8)	16.1 (3.2)	20.0 (3.0)	12.8 (4.0)	10.6 (2.8)
<i>Mucor hiemalis</i> Wehmer f. <i>hiemalis</i>	0	0.6 (0.5)	0	1.1 (0.7)	0	0	0	1.1 (1.0)
<i>Mucor hiemalis</i> f. <i>silvaticus</i> (Hagem) Schipper	0	0	0	0	0.6 (0.5)	0	0	0
<i>Mycogone perniciosa</i> Link	0	0	0	0	1.7 (0.8)	1.1 (0.7)	0.6 (0.5)	0.6 (0.5)
<i>Oidiodendron</i> sp. 1	0.6 (0.5)	0	0	0	0	0	0	0
<i>Oidiodendron</i> <i>chlamydosporicum</i> Morrall	1.7 (0.8)	1.7 (1.1)	1.1 (0.1)	3.3 (1.4)	0.6 (0.5)	0.6 (0.5)	0	1.1 (0.1)

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Oidiodendron rhodogemum</i> Robak	0	0.6 (0.5)	0	0	0	0	0	0
<i>Oidiodendron tenuissimum</i> (Peck) Hughes	0.6 (0.5)	0.6 (0.5)	2.2 (1.1)	0	3.3 (1.1)	1.1 (0.7)	3.3 (1.1)	1.1 (0.7)
<i>Paecilomyces</i> sp.1	0.6 (0.5)	0	0	0	0	0	0	0
<i>Paecilomyces</i> sp.2	0	0	0	0	0.6 (0.5)	0	0	0
<i>Paecilomyces</i> sp.3	0	0	0.6 (0.5)	0	0	0	0	0
<i>Paecilomyces carneus</i> (Duche & Heim) A. H. S. Brown & G. Sm.	8.3 (2.7)	1.7 (1.1)	5.6 (2.0)	2.8 (1.8)	1.1 (0.7)	1.1 (0.7)	0	1.7 (1.1)
<i>Paecilomyces farinosus</i> (Holm ex Gray) A. H. S. Brown & G. Sm.	2.2 (1.4)	0	0	1.1 (0.7)	0	0	0	0.6 (0.5)
<i>Paecilomyces marquandii</i> (Masse) Hughes	1.1 (0.7)	1.7 (1.1)	0.6 (0.5)	0.6 (0.5)	0.6 (0.5)	0	1.7 (1.1)	1.7 (1.1)
<i>Penicillium</i> sp. 1	1.1 (0.7)	1.7 (1.1)	0	0	0	0	0	0

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Penicillium</i> sp. 2	0.6 (0.5)	0	0	0	0	0	0	0
<i>Penicillium</i> sp. 3	0	1.1 (1.0)	0	0	0	0.6 (0.5)	0	0
<i>Penicillium</i> sp. 4	0	0	0.6 (0.5)	0	0	0	0	0
<i>Penicillium</i> sp. 5	0	0	0.6 (0.5)	0	0	0	0	0
<i>Penicillium</i> sp. 6	0	0	0	0	0	0	0.6 (0.5)	0
<i>Penicillium arenicola</i> Chalabada.	0	0	0	0	0	0	0.6 (0.5)	0
<i>Penicillium canescens</i> Sopp	7.8 (3.5)	5.6 (2.1)	2.8 (0.8)	2.2 (1.6)	1.1 (0.7)	0	1.1 (1.0)	0
<i>Penicillium claviforme</i> Bainier	0	0	0	0.6 (0.5)	0	0	0	0
<i>Penicillium janthinellum</i> Biourge	3.9 (1.7)	1.1 (0.7)	2.2 (1.6)	2.2 (1.1)	1.1 (0.7)	1.7 (1.1)	1.7 (1.1)	0
<i>Penicillium lanosum</i> Westling	0.6 (0.5)	0	0.6 (0.5)	0	0.6 (0.5)	0	0.6 (0.5)	0
<i>Penicillium melinii</i> Thom	0	1.1 (0.7)	0.6 (0.5)	0	1.1 (0.7)	0	0	0

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Penicillium montanense</i>	2.2 (0.8)	0.6 (0.5)	0	0.6 (0.5)	2.2 (1.1)	2.2 (1.1)	1.7 (1.1)	1.7 (1.1)
Christensen & Backus								
<i>Penicillium purpurogenum</i> Stoll	3.9 (1.3)	4.4 (1.7)	3.9 (1.0)	1.7 (1.1)	0	0	1.1 (1.0)	2.2 (1.6)
<i>Penicillium spinulosum</i> Thom	2.8 (2.1)	4.4 (2.1)	2.2 (1.1)	0.6 (0.5)	1.1 (0.7)	1.1 (0.7)	0.6 (0.5)	0
<i>Penicillium steckii</i>	1.7	1.7	1.7	1.7	0	0	0	0.6
Zaleski	(1.1)	(0.8)	(0.8)	(0.8)				(0.5)
<i>Penicillium thomii</i>	2.2	2.2	1.7	2.2	0.6	0	0	0
Maire	(1.6)	(1.1)	(0.8)	(1.6)	(0.5)			
<i>Penicillium variabile</i>	1.7	6.1	5.0	0.6	0	0	0	0.6
Sopp	(1.1)	(2.6)	(3.1)	(0.5)				(0.5)
<i>Petriellidium</i> sp. 1	0	0	0	0	0	0	0.6 (0.5)	0.6 (0.5)
<i>Phialocephala</i> sp. 1	0	0	0	0	5.0 (1.6)	7.2 (2.8)	7.2 (2.8)	5.0 (3.1)
<i>Phialophora americana</i>	0	0	0	0	0	0.6 (0.5)	0	0
(Nannf.) Hughes								

Table 6.2 continued.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Phialophora fastigiata</i> (Lagerb. & Melin) Conant	1.7 (0.8)	0	0	0.6 (0.5)	0.6 (0.5)	1.1 (1.0)	1.7 (1.1)	0
<i>Phialophora malorum</i> (Kidd & Beaum.) McColloch	0.6 (0.5)	0	0	0	0	0	0	0
<i>Phoma pomorum</i> Thum	0.6 (0.5)	0	0	2.8 (1.8)	0	0.6 (0.5)	0.6 (0.5)	0
<i>Pseudogymnoascus</i> <i>roseus</i> Raillo	1.1 (0.7)	1.1 (0.7)	0	1.1 (0.7)	5.0 (1.4)	7.8 (2.2)	3.3 (1.6)	3.3 (1.1)
<i>Rhinocladiella</i> sp. 1	1.7 (1.6)	0.6 (0.5)	1.7 (0.8)	1.1 (0.7)	0	0	0	0
<i>Rhinocladiella</i> sp. 2	0	0	0	0	0	0.6 (0.5)	0	0
<i>Sporothrix schenckii</i> Hektoen & Perkins	1.7 (1.1)	0.6 (0.5)	1.7 (1.1)	0	0.6 (0.5)	0	0	0.6 (0.5)
<i>Stachybotrys</i> <i>chartarum</i> (Ehrenb. ex Link) Hughes	0	0.6 (0.5)	0	0.6 (0.5)	0	0	0	0

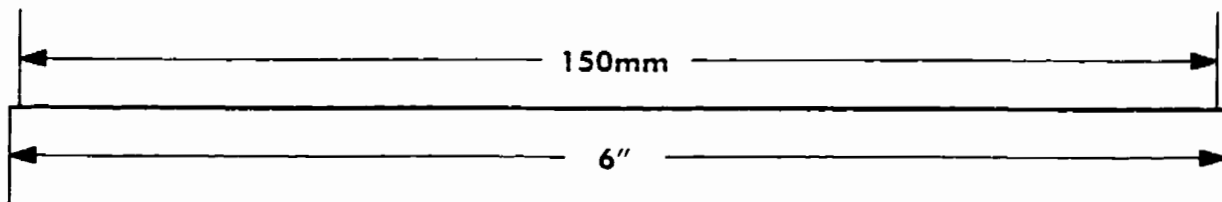
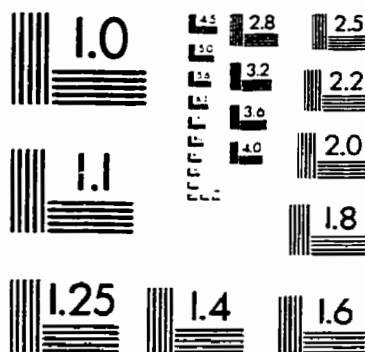
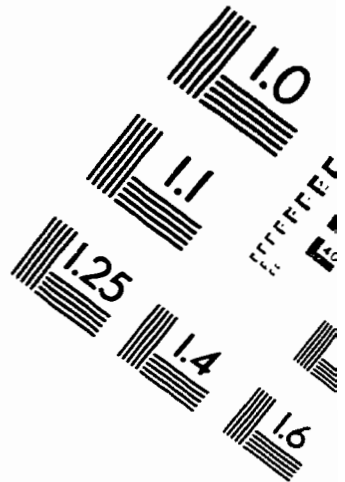
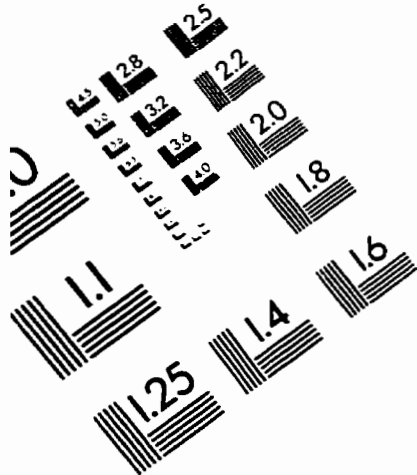
Table 6.2 continued.

Fungal species	Treatment and soil layer																	
	clear-cut		brushsaw		triclopyr		glyphosate		clear-cut		brushsaw		triclopyr		glyphosate			
	Organic	Mineral	Organic	Mineral	Organic	Mineral	Organic	Mineral	Organic	Mineral	Organic	Mineral	Organic	Mineral	Organic	Mineral		
<i>Tolypocladium cylindrosporium</i> W. Gams	0.6 (0.5)		0		0.6 (0.5)		0		0		0	0.6 (0.5)		0		0		
<i>Tolypocladium niveum</i> (Rostrup) Bissett	2.2 (0.8)		0		0		0.6 (0.5)		1.1 (0.7)		1.1 (0.7)		0.6 (0.5)		0		0	
<i>Torulomyces lagena</i> Delitsch	0.6 (0.5)		0		0		0		0		0		0		0		0	
<i>Trichocladium opacum</i> (Corda) Hughes	0		0.6 (0.5)		0		0		3.9 (1.7)		0.6 (0.5)		1.1 (1.0)		1.1 (0.7)		1.1 (0.7)	
<i>Trichoderma fertile</i> Bissett	1.1 (0.7)		0		0		1.1 (0.7)		0		0		0		0		0	
<i>Trichoderma harzianum</i> Rifai	1.7 (0.8)		5.6 (1.7)		3.3 (1.4)		3.9 (2.7)		1.7 (1.1)		4.4 (3.1)		1.7 (1.1)		2.2 (1.4)		2.2 (1.4)	
<i>Trichoderma longibrachiatum</i> Rifai	0		0		0.6 (0.5)		0		0		0.6 (0.5)		0		0.6 (0.5)		0.6 (0.5)	
<i>Trichoderma longipilis</i> Bissett	2.8 (1.1)		0		0		3.3 (2.1)		0		0		0		1.7 (1.1)		1.7 (1.1)	
<i>Trichoderma polysporum</i> (Link:Fr.) Rifai	3.9 (2.2)		2.2 (1.1)		1.7 (1.1)		3.3 (1.6)		2.8 (1.4)		3.3 (2.1)		1.7 (0.8)		3.3 (3.1)		3.3 (3.1)	

Table 6.2 concluded.

Fungal species	Treatment and soil layer							
	clear-cut Organic	brushsaw Organic	triclopyr Organic	glyphosate Organic	clear-cut Mineral	brushsaw Mineral	triclopyr Mineral	glyphosate Mineral
<i>Trichoderma strictipilis</i> Bissett	0.6 (0.5)	0	0.6 (0.5)	0	1.7 (1.1)	1.7 (0.8)	3.3 (1.8)	3.3 (1.6)
<i>Trichoderma viride</i> Pers.:Fr.	6.1 (2.2)	8.3 (1.4)	12.2 (2.6)	7.8 (2.1)	7.2 (3.2)	5.0 (2.1)	6.1 (3.2)	10.6 (4.4)
<i>Trichosporon beigelli</i> (Kuchenm. & Rabenh.) Vuill.	0	1.1 (0.7)	0	0.6 (0.5)	1.1 (1.0)	0	0	0
<i>Trichurus spiralis</i> Hasselbr.	0	0	0.6 (0.5)	0	0	0	0	0
<i>Truncatella truncata</i> (Lev.) Stey.	0.6 (0.5)	1.1 (1.0)	0	0	0	0	0	0
<i>Verticillium lecanii</i> (Zimm.) Viegas.	0	1.1 (0.7)	1.7 (0.8)	0.6 (0.5)	0.6 (0.5)	1.1 (0.7)	0.6 (0.5)	9.4 (4.8)
<i>Verticillium psalliotae</i> Treschow	0	0.6 (0.5)	0	0	0	0.6 (0.5)	0	0.6 (0.5)
<i>Volutella ciliata</i> Alb. & Schw. ex Fr.	0	0.6 (0.5)	0	0	0	0.6 (0.5)	1.1 (1.0)	1.7 (0.8)
Yeast (dark hyphal)	0	0	0	0	0.6 (0.5)	0	0	1.1 (1.0)
Sterile dark (total)	8.9 (2.6)	8.3 (1.6)	15.0 (3.2)	17.8 (2.6)	11.1 (4.1)	16.7 (2.7)	7.8 (1.8)	11.7 (3.3)
Sterile hyaline (total)	2.2 (1.1)	-	2.2 (1.1)	2.2 (1.1)	1.7 (1.1)	6.1 (1.9)	2.8 (2.1)	1.7 (0.8)

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