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Influence of fire, logging, and overstory composition on understory abundance, diversity, and composition in boreal forests, Ontario Canada

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INFLUENCE OF FIRE, LOGGING, AND OVERSTORY COMPOSITION ON UNDERSTORY ABUNDANCE, DIVERSITY, AND COMPOSITION IN BOREAL FORESTS, ONTARIO, CANADA

By

Stephen A. Hart

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ABSTRACT

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Keywords: Understory vegetation, composition, diversity, vascular plants, bryophytes and lichens, time since fire, timber harvesting, boreal forest, fire.

Understory vegetation is the most diverse and least understood component of North American boreal forests and are important as they influence overstory succession and nutrient cycling. The objectives of this thesis were to (1) review the current understanding of boreal understory vegetation dynamics in the literature and (2) examine the effect of stand age, overstory composition, and logging versus fire on understory vegetation communities in northwestern Ontario, Canada.

Understory vegetation abundance and diversity increase rapidly after fire, in response to abundant resources and an influx of disturbance adapted species. The highest diversity occurs within the first 40 years after fire, and declines indefinitely thereafter as a result of decreasing productivity and increased dominance of a small number of late successional pleurocarpous mosses and woody plant species. Vascular plant and bryophyte/lichen communities undergo very different successional changes. Vascular plant communities are dynamic and change more dramatically with time since fire, whereas bryophyte and lichen communities are much slower to establish and change over time. Considerable variations exists depending on canopy composition, site condition, regional climate, and frequently occurring non-stand-replacing disturbances. Forest management practices represent a unique disturbance process and can result in different understory vegetation communities from those observed for natural processes, with potential implications for overstory succession and long-term productivity. Because of the importance of understory vegetation on nutrient cycling and overstory composition, post-harvest treatments emulating stand-replacing fire are required to maintain understory diversity, composition, and promote stand productivity in boreal forests.

Understory vegetation communities were sampled in 68 forest stands of conifer, mixedwood, and deciduous overstory types ranging from seven to 201 years since fire for fire origin stands, and 7 to 31 years old for logging origin stands. For fire origin stands, total species richness and cover followed similar trends for the three overstory types and were highest in the intermediate aged stands (72-90 years old). Trends in richness and cover, however, differed significantly for vascular and nonvascular plant groups. Vascular plant diversity and cover was generally higher under deciduous stands, and was lower on older stands, while nonvascular species diversity was highest under conifer stands and increased with time since fire. Neither alpha nor beta diversity was higher under mixedwood stands while mixedwood stands were compositionally intermediate to conifer and deciduous stands. Multivariate analysis using multiple response permutation procedures indicated that understory communities were compositionally distinct for all overstory types and showed no convergence with increasing time since fire. Compared with post-fire stands of similar ages, post-logged stands had similar total understory cover and diversity. Vascular cover and richness, however, were higher on post-logged stands, and nonvascular cover and diversity lower. Stands of logging and fire origin were

compositionally distinct for all overstory types and ages. Compositional differences appeared to be driven by higher levels of preestablished rhizomatous species and the prevalence of pleurocarpous mosses on fire origin stands.

Understory vegetation communities in the central boreal shield appear to support the intermediate disturbance hypothesis. Understory richness, however, was not negatively affected by high cover values as predicted by the intermediate disturbance hypothesis. Moreover, richness appears to be highest on sites with high resource availability, suggesting that boreal understory communities are influenced more by plant tolerances for low resources, rather than competition.

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Finally, I would like to thank my parents to whom I bear an uncanny resemblance, owe a great deal of money, and have put through untold amounts of stress.

NOTE TO THE READER

Considerable effort has been made to integrate chapters 2 and 3. These chapters have been written with the intention of submission for publication as distinct manuscripts, and as such, there is some overlap of term definitions. Chapter 2 has been published in Critical Reviews in Plant Sciences, and chapter 3 will be submitted shortly.

Chapter 2:
Hart, S.A. and H.Y.H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25: 115-137.

CHAPTER ONE GENERAL INTRODUCTION

Boreal understory vegetation plays a critical role, influencing overstory succession and nutrient cycling (Zavitkovski 1975, Messier *et al.* 1998, Wardle *et al.* 2004, Nilsson and Wardle 2005). Despite its important effect on ecosystem processes, boreal understory vegetation remains relatively understudied and is poorly understood when compared to temperate and tropical ecosystems. A proper understanding of the dynamics of boreal understory vegetation is necessary to address concerns for biodiversity and conservation and forest management.

The objectives of this thesis were to (1) review the current understanding of boreal understory vegetation dynamics in North America and (2) examine the dynamics of understory vegetation in Northwestern Ontario, Canada. Chapter two presents a literature review of the dynamics of understory vegetation in the North American boreal forest. The review focuses on the development of vegetation communities following stand replacing fire, and the relationship of overstory composition, minor disturbances, site conditions, and geographic variation on species abundance, diversity, and composition.

Chapter three is an empirical study of the relationship of time since fire, logging, and overstory composition on the abundance, diversity and composition of understory vegetation communities in the central boreal shield of northwestern Ontario, Canada. The study focuses on the intermediate disturbance hypothesis, as well as the environmental heterogeneity hypothesis, as potential mechanisms driving understory communities.

CHAPTER TWO UNDERSTORY VEGETATION DYNAMICS OF NORTH AMERICAN BOREAL FORESTS

INTRODUCTION

Boreal forests, or taiga, have a circumpolar distribution, spanning the complete breadths of both Eurasia and North America. At their widest, they stretch over 1000 km from north to south, and cover over 14.7 million km^2 (Bonan and Shugart 1989), making the boreal forest the largest forest ecosystem on earth (Kuusela 1992). Despite its size, vegetation diversity is relatively low, supporting only 291 vascular plant species from 47 families in boreal North America (La Roi 1967), in mixtures ranging from 39 to 77 species (Qian *et al.* 1998). The lack of vegetation diversity of the boreal forest can be attributed to its northern distribution and the general trend of decreasing diversity with increasing latitude. Most boreal plant species have wide ranges in habitat tolerance, resulting in very few narrow range endemics, and considerable overlap between habitats (Carleton and Maycock, 1981; Qian *et al.*, 2003). This overlap is evident in the similarity between Eurasian and North American boreal vegetation communities. Many species of lower plants (bryophytes and lichens) are common to both continents, as are some species of vascular plants, while most shrubs and all trees belong to the same genus (Gordon 1996).

Boreal understory vegetation is the most diverse and least understood component of boreal plant communities (Roberts 2004). At their most diverse, boreal overstory communities may be made up of six tree species, whereas up to 77 plant species may be present in the understory (La Roi 1967, Qian *et al.* 2003). Understory vegetation acts as a forest ecosystem driver (Nilsson and Wardle 2005), affecting canopy succession

(Zackrisson *et al.* 1996, Messier *et al.* 1998), nutrient cycling (Weber and Van Cleve 1981, Brumelis and Carleton 1989, Knops *et al.* 1996), and wildlife (Økland and Eilertsen 1996, Gunnarsson *et al.* 2004). Forest management has, however, tended to focus on overstory structure and composition, and does not often address potential changes to understory vegetation communities, which can result in long term shifts in forest communities, and have long lasting effects over the boreal landscape (Rees and Juday 2002, Chapin, III *et al.* 2004a).

Understory vegetation communities are dynamic (Rees and Juday 2002, Chipman and Johnson 2002) and change considerably with overstory structure and composition and soil substrate status (De Grandpré *et al.* 1993, Klinka *et al.* 1996, Qian *et al.* 2003, Chen *et al.* 2004). For example, old growth forests support unique understory vegetation communities (Thompson *et al.* 2003) and are of increasing concern for their contribution to regional biodiversity (Frelich and Reich 2003). The transient nature of all boreal forests, a result of fire cycles ranging from 100 to 500 years depending on precipitation, topography, and vegetation (Johnson 1992, Hély *et al.* 2001, McRae *et al.* 2001, Lesieur *et al.* 2002), (Johnson, 1992; Hély *et al.*, 2001; McRae *et al.*, 2001; Lesieur *et al.*, 2002), causes vegetation communities of widely varying ages to occur in close proximity to one another (Pojar 1996, Cyr *et al.* 2005). As a result, understory communities form a diverse mosaic across the boreal forest contributing to both temporal and landscape diversity (Weber and Stocks 1998, Weir *et al.* 2000).

A proper understanding of boreal understory community dynamics is vital to address concerns for biodiversity conservation and forest management. This review will focus on the successional dynamics of understory vegetation communities of the North

American boreal forests. Of particular interest will be patterns of abundance, composition, and diversity as succession proceeds towards old-growth (gap dynamics) stages, environmental factors driving these changes, including understory light environment, substrate, and site productivity, and implications for overstory regeneration and long term productivity. This review will begin by describing trends in understory vegetation succession following stand-replacing fire. It will then discuss how overstory composition, site condition, and regional climate may affect understory vegetation dynamics. Next, it will address how understory vegetation may respond to non-stand replacing disturbances such as insect outbreaks and windthrow. A discussion of the implications of forest management, in particular the practices of clearcutting and site preparation, for the succession of boreal vegetation communities will follow. The review will conclude by identifying areas for future research as well as a summary of major points.

UNDERSTORY VEGETATION DYNAMICS WITH TIME SINCE FIRE

Boreal stand dynamics refer to changes in stand structure and composition over time with associated changes in the biotic and abiotic environment (Chen and Popadiouk 2002). Given the strong effect of stand structure and composition on understory vegetation composition and diversity (Saetre *et al.* 1997, Kneeshaw *et al.* 1998, Økland *et al.* 1999, Légaré *et al.* 2002), it is important to discuss boreal understory vegetation dynamics with respect to overstory stand dynamics.

Overstory Composition and Structure

In boreal mixedwood forests, following a stand replacing fire, the fast growing, shade intolerant species, trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula* *papyrifera* Marsh.) on mesic sites (Gauthier *et al.* 2000), .), and jack pine (*Pinus banksiana* Lamb.) on xeric sites colonize available growing space (Lavoie and Sirois 1998, De Grandpré *et al.* 2000b). These species form dense, single-storied canopies, inhibiting their own regeneration, and allowing the establishment of understories having shade tolerant white and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill) BSP, respectively), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white cedar (*Thuja occidentalis* L.) (Carleton and Maycock 1978, Bergeron 2000), which are often present within the first few years following wildfire. As the shade intolerant canopy breaks down, shade tolerant conifers gradually occupy gaps, forming uneven-aged, structurally heterogeneous stands. Some birch often remains in the canopy because of its ability to rapidly fill the gaps (Syrjanen *et al.* 1994, Bergeron 2000). Chen and Popadiouk (2002) described the dynamics of boreal mixedwoods in four structurally distinct stand development stages: 1) stand initiation; 2) stem exclusion; 3) canopy transition; and 4) gap dynamics. These stages are applicable to changes in structure and composition of other mesic boreal forest stands.

Change in the Understory Environment

Development of overstory structure and composition alters the understory environment, particularly that of light availability, substrate, temperature, soil nutrients, and pH.

Light

Understory light availability decreases with stand development following fire. This decrease is most severe following closure of the initial post-fire cohort of shade intolerant deciduouss and pines, but continues as shade tolerant conifers become increasingly dominant in the overstory. Under a closed-canopy forest stand, light transmission is controlled at the following three layers: 1) overstory (above shrub layer – 1 to 3 m and up); 2) shrub layer (above 50 cm); 3) herbaceous layer (forest floor up – 50 cm). Increases in overstory light transmission are often compensated by decreases in light transmission through lower canopy layers (Constabel and Lieffers 1996, Messier *et al.* 1998), (Constabel and Lieffers, 1996; Messier *et al.*, 1998), resulting in 2-5.9% of light reaching the forest floor under close canopy boreal forests. Increases in the number and size of gaps in late seral stands can increase in light transmission to the understory somewhat (De Grandpré *et al.* 1993, Pham *et al.* 2004).

Light is usually the most limiting resource affecting understory tree and other vascular plant establishment and growth (Chen *et al.* 1996, Chen 1997, Strengbom *et al.* 2004). However, non-vascular plants are often more limited by throughfall precipitation than by light, both of which are reduced under dense canopies (Busby *et al.* 1978).

Soil Nutrients and pH

Soil nutrient availability and pH generally decrease with time due to fire and increasing conifer content. Fires reduce forest floor thickness, liberating nutrients previously immobilized in organic compounds (Brais *et al.* 2000, Simard *et al.* 2001). Release of the base cations calcium (Ca), magnesium (Mg), potassium (K), and phosphorus (P) increases pH, while associated increases in soil temperature increase mineralization rates (Binkley 1984). Because of volatilization, total nitrogen (N) may decrease following intense fires. However mineralized N usually increases because of increased mineralization in the first 20 years following fire (Flanagan and Van Cleve 1983, Dyrness *et al.* 1989, Brais *et al.* 2000, White *et al.* 2004, Smithwick *et al.* 2005).

As the time after a fire increases, soil nutrients become immobilized in organic compounds, many of which are slow to decompose, partially because of their high carbon (C) to N ratios; this immobilization decreases pH and thereby available soil nutrients, as well as pH (Paré *et al.* 1993, Paré and Bergeron 1995, Brais *et al.* 1995, Driscoll *et al.* 1999). Although total nitrogen may not change considerably with time after the fire, the form of N changes from NO_3 to NH_4 (Deluca *et al.* 2002, Zackrisson *et al.* 2004, Nilsson and Wardle 2005) as a result of N fixation, which has been found to increase linearly with time since fire, primarily from cyanobacteria on the moss *Pleurozium shreberi* (Brid.) Mitt (Flanagan and Van Cleve 1983, Zackrisson *et al.* 2004).

Higher C:N ratios and acidity found in conifer litter decrease available soil nutrients and pH, as base cations are immobilized in the lignicolous litter, decreasing pH, which is further lowered by the acidity of the litter (Van Cleve *et al.* 1983, Wardle *et al.* 2003). As time since fire proceeds, increasing conifer content is likely to cause pH to decrease further and increase rates of nutrient immobilization, resulting in an overall trend of decreasing soil fertility with time since fire (Roberts 2004).

Forest Floor Heterogeneity

The forest floor is heterogeneous with microsites in the form of decaying wood, tip up mounds, and exposed mineral soil. The heterogeneity is particularly important for a number of bryophyte and shade tolerant tree and herbaceous species, which variously require decaying wood as a substrate, low competition, and/or exposed mineral soil for successful establishment (Jonsson and Esseen 1990, Crites and Dale 1997, Delong *et al.* 1997, Lee and Sturgess 2001, Brassard and Chen 2006).

Following fire, the forest floor changes considerably from exposed mineral soil with abundant charcoal to increasing organic matter. Much later, a moss layer forms decreasing available colonizing sites for a number of species, and promoting species capable of vegetative reproduction (McIntyre *et al.* 1995, Nilsson and Wardle 2005). Charcoal, abundant following fire, contributes to long-term soil productivity by stimulating nitrification (Nilsson *et al.* 2000, DeLuca *et al.* 2002) and adsorbing the phenolic compound batastasin-III, produced by ericaceous vegetation and having allelopathic effects on establishment and growth of a number of tree species (Zackrisson *et al.* 1996, Wardle *et al.* 1998). The adsorptive capability of charcoal can remain for up to 100 years (Mills and Macdonald 2004, Mills and Macdonald 2005).

Decaying wood volumes follow a U-shaped distribution along a post-fire chronosequence (Lee *et al.* 1997). Volumes of decaying wood are high following fire (Crites and Dale 1997), the result of contributions from the pre-fire overstory, and increase in abundance and size again towards the gap dynamics stage as the initial overstory post-fire cohort is replaced (McIntyre *et al.* 1995, Hély *et al.* 2000, Chen and Popadiouk 2002, Pothier *et al.* 2004).

Overstory tree mortality, the result of canopy replacement and natural dieback (Harper *et al.* 2003) causes an increase in tip up mounds, forming a hump and hummock topography on the forest floor, exposing mineral soil, as well as depressions and elevated microsites. Soil heterogeneity is increased by reversing the podzolization process, thus increasing soil fertility (Kuuluvainen 1994). This process becomes more prevalent as stands age (Shafi and Yarranton 1973, De Grandpré *et al.* 1993, Peltzer *et al.* 2000, Rees and Juday 2002), resulting in high microsite heterogeneity at the gap dynamics stage of stand development in boreal forests.

As time since fire increases, the nature and availability of resources change considerably. Despite an increase in microsite heterogeneity and no decrease in total available N, there is an overall decrease in light transmission, other soil nutrients, and pH, resulting in a much more resource-limited environment in later successional stages.

Understory Vegetation

Colonization

Following stand replacing fire, resources and growing space are abundant. Colonization is rapid with communities dominated by fast growing vascular plants (Greene *et al.* 1999). Plant biomass increases rapidly on exposed mineral soil and charcoal to almost continuous plant cover within five to seven years, occupying virtually all microsites (De Grandpré *et al.* 1993, White *et al.* 2004) (Figure 2-1a). Plant cover is, in part, due to intense layering by vascular plants in response to high light availability, making plant cover highest during the first 20 years following fire (Figure 2-1) (De Grandpré *et al.* 1993, Lynham *et al.* 1998, Rees and Juday 2002).

Species composition of early successional communities are typically dominated by shade intolerant, nutrient demanding species such as *Epilobium angustifolium* L., *Rubus idaeus* L., *Pteridium aquilinum* L. Kuhn, and *Calamagrostis canadensis (Michx.) Beauv.* (De Grandpré *et al.* 1993, Whittle *et al.* 1997a, Rees and Juday 2002). These species colonize from seeds or regenerate from underground rhizomes, and can remain dormant for up to 100 years (Martin 1955, Archibold 1979, Whittle *et al.* 1997a), and grow rapidly in response to the abundant resources present.

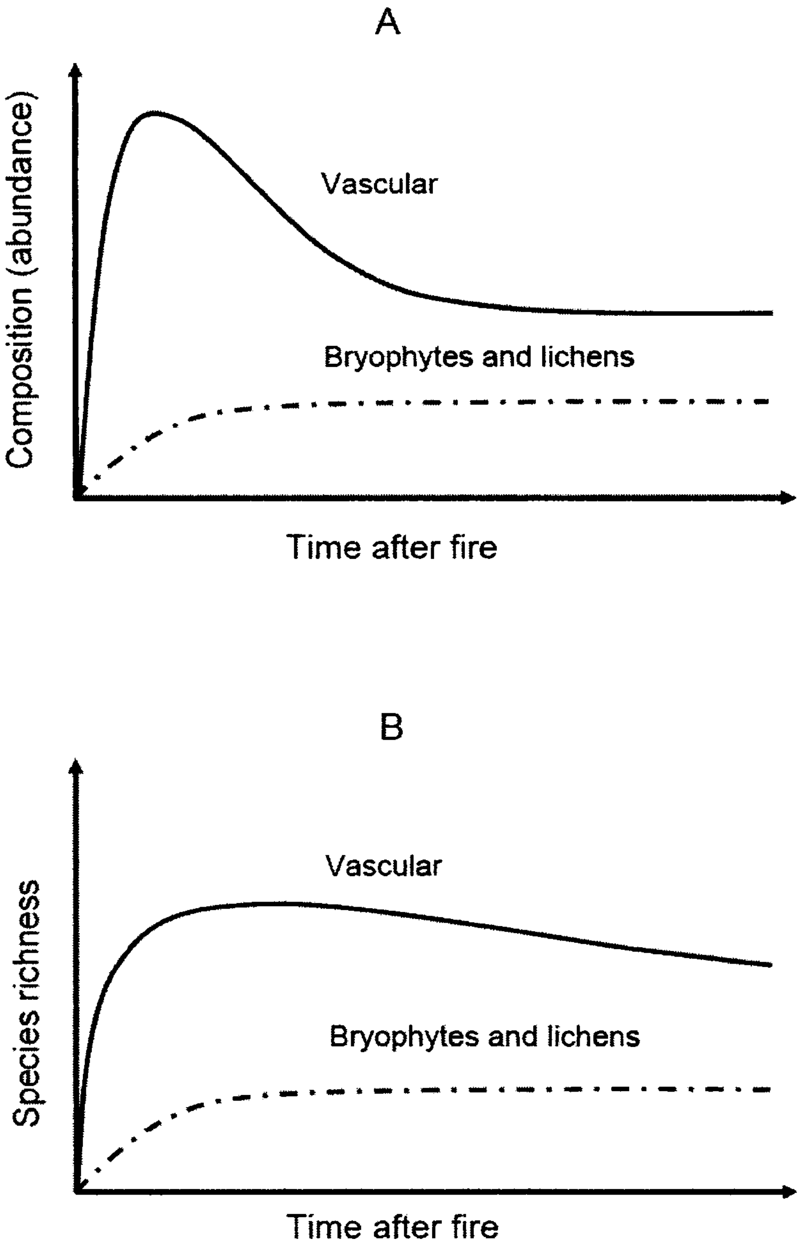

Figure 2-1. Change in understory vegetation with time since fire: (a) composition (relative abundance of vascular plants (solid line) and bryophytes and lichens (dashed line)) and (b) species richness (After De Grandpré *et al.* 1993, Rees and Juday 2002, Uotila and Kouki 2005).

Species present following fire are mostly the result of local colonization from buried propagules and rhizomes located in the humus layer (Granstrom 1982, Rydgren and Hestmark 1997). Rydgren and Hestmark (1993) identified the presence of viable seed populations of 14 of 34 taxa not found in the above ground community of an old-growth *Picea abies* forest in southeastern Norway. In Canadian boreal forests, De Grandpré *et al.* (1993) found that up to 70% of all species present after fire were present before fire, but species dominant before were not usually abundant following fire (Peltzer *et al.* 2000). Similarly, differences between prefire and post-fire compositions were reported in other boreal forest ecosystems (e.g., Moore and Wein 1977, Tellier *et al.* 1995).

The types of species present following fire are also affected by fire severity (Purdon *et al.* 2004). Intense fires cause a shift from herbaceous to shrub layer species, as the reproductive tissues of many herbaceous species are found in the humus layer and are susceptible to fire, whereas those of shrubs such as *Vaccinium spp.* are rooted deeper and therefore not as vulnerable (Purdon *et al.* 2004). Periods of intense, recurrent fires can also exhaust local seed sources, inhibiting seedling establishment and promoting the establishment of a lichen-heath community more typical of northern boreal forests (Lavoie and Sirois 1998).

Following fire, the number of species, *i.e.*, the species richness, increases quickly, and continues to increase throughout the early stages of post-fire succession (Figure 2-1b), as a large number of plant species colonize growing spaces initially free of competition (Greene *et al.* 1999). Rees and Juday (2002) have reported the presence of 80 species on burned stands in Alaska, while Abrams and Dickman (1982) recorded 89 species on burned stands in Northern Michigan.

Bryophyte and lichen species are not a large component of vegetation communities during the earlier stages of post-fire succession (Figure 2-1). However, a few post-fire specialists do occur. *Ceratodon purpureus* (Hedw.) Brid., *Marchantia polymorpha* L. and *Leptobryum pyriforme* (Hedw.) Wils. were found exclusively on burned sites during the early stages of post-fire succession (Rees and Juday 2002). Non-vascular species are not a large part of early post-fire vegetation communities because of their inability to grow rapidly in response to increased resources following disturbance (Frego and Carleton 1995a) and intense competition from vascular plants (Shropshire *et al.* 2001).

Understory vegetation plays an important role during the early stage of stand development. Overstory species have very little influence on the early post-fire light environment and only affect the understory light environment at the end of this stage when canopy closure occurs. Aggressive vascular plant species exert primary control over light penetration to the forest floor (Messier *et al.* 1998), decreasing light levels to as little as 2% of photosynthetically active radiation (PAR) (Zavitkovski 1975, Lieffers and Stadt 1994, Messier *et al.* 1998). These species also exert control over nutrient cycling. The majority of biomass production and leaf turnover is performed by the understory community (Zavitkovski 1975), which rapidly takes up abundant nutrients following fire, releasing them slowly through decomposition, thus slowing nutrient loss following fire (Schläpfer and Schmid 1999).

Canopy Closure

Following canopy closure, light availability in the understory decreases to less than 15% PAR (Økland *et al.* 2003). Resulting in a pronounced shift in understory composition as shade intolerant species are quickly replaced by more shade tolerant species (De Grandpré *et al.* 1993). Increasing mass of overstory species also increases competition for soil nutrients, while microsite heterogeneity continues to increase.

Cover and biomass are higher in early successional stands and peak within the first 20 years following fire, declining shortly thereafter (White *et al.* 2004) (Figure 2-1a). Early successional species with high leaf area indices (*e.g.*, *Rubus idaeus*, *Pteridium aquilinum*) decline in response to lower light levels and decreasing soil nutrients and pH, and are replaced by species with lower leaf area indices (*e.g.*, *Coptis trifolia* (L.) Salisb and *Clintonia borealis*) (De Grandpré *et al.* 1993, Shropshire *et al.* 2001). This decline in cover continues from 26 to 74 years, with fluctuations from 120 to 230 years after fire (De Grandpré *et al.* 1993). Most of the decline in understory biomass is the result of the decline in vascular plant biomass. De Grandpré *et al.* (1993) recorded the lowest vascular plant abundance on very old sites. Bryophyte cover, however, increased with time since fire (Carleton 1982, Taylor *et al.* 1988, Nygaard and Odegaard 1999).

After canopy closure, understory composition shifts to the dominance of shade tolerant species. Shade intolerant species such as *Rubus idaeus* and *Solidago rugosa* P. Mill. disappear soon after canopy closure and shade created by an aspen overstory can virtually eliminate *Epilobium angustifolium* and *Calamagrostis canadensis* (Lieffers and Stadt 1994). De Grandpré *et al.* (1993) found that the greatest shift in composition occurred within the first 26 years following fire, after which time most changes in composition were the result of shifts in the relative abundance of species. The appearance of new species is inhibited by dense understory vegetation cover and increasing forest floor litter and organic matter, as well as the decline in resource availability in the understory, which acts as a filter on light and nutrient requiring species (Paré *et al.* 1993, George and Bazzaz 1999, Charron and Greene 2002). Ericaceous vegetation, however, continuously increases with time since fire (Skre *et al.* 1998). Further, a few vascular species only appeared more than 46 years after fire, such as *Cornus canadensis* L., *Circaea alpina* L., and *Goodyera tesselata* Lodd., and *Linnea borealis* L. (De Grandpré *et al.* 1993, Wardle and Zackrisson 2005).

Understory diversity is greatest between 30 and 38 years after fire (Rees and Juday, 2002), when dominant species such as *Aster macrophyllus* (L.) *Cass.*, *Aralia nudicaulis* L., *Acer spicatum* Lam., and *Corylus cornuta* Marsh. are somewhat evenly distributed (De Grandpré *et al.* 1993) (Figure 2-1b). Diversity declines slowly over the following 200 years (De Grandpré *et al.* 1993, Rees and Juday 2002, Chipman and Johnson 2002). The peak in vascular species diversity coincides with time of maximum understory cover, which occurs between 13 and 18 years (De Grandpré *et al.* 1993), and declines considerably after 74 years (Wardle *et al.* 2003). Lichen and bryophyte species diversity continues to increase throughout post-fire succession (Rees and Juday 2002), somewhat offsetting the decline in vascular species diversity (Figure 2-1b). The increase in bryophyte and lichen diversity with time since fire is the result of poor colonizing ability of many of these species, as well as an increase in microsite heterogeneity in the form of tip up mounds and coarse woody debris (Lee *et al.* 1997, Mills and Macdonald 2004, Wardle *et al.* 2004, Brassard and Chen 2006).

The decline in understory vascular plant diversity is the result of a long-term decrease in soil nutrients and pH (Wardle and Zackrisson 2005), light (Lieffers and Stadt 1994, Messier *et al.* 1998), and increased dominance of a few understory species (De

Grandpré *et al.* 1993). As soil nutrients and pH decline, a number of nutrient demanding species decrease in abundance, and slow growing ericaceous species become more prevalent (Skre *et al.* 1998, Nygaard and Odegaard 1999, Mallik 2003). Increased stand basal area and conifer content decreases understory light availability, inhibiting the growth of all but the most shade tolerant understory species, thus lowering understory diversity (Ross *et al.* 1986). De Grandpré *et al.* (1993) found the decline in understory diversity was related to a shift in overstory composition from deciduous to conifer species.

VARIATION AS AFFECTED BY OVERSTORY COMPOSITION, SITE CONDITION, AND CLIMATE

Variation in understory vegetation communities has been attributed to canopy composition, site conditions, and both longitudinal and latitudinal factors. Carleton and Maycock (1981) found 120 of 410 species in the boreal forests south of James Bay to have an affinity for specific overstory species, whereas species such as *Cornus canadensis* and *Maianthemum canadense* Desf. are virtually ubiquitous, occurring alongside different overstory species as a result of similar site requirements (Carleton and Maycock 1980, Carleton and Maycock 1981). It is generally thought that canopy composition plays the greatest role in determining understory composition, with other site characteristics such as soil texture and slope of secondary importance, as well as some noticeable trends across longitudinal and latitudinal gradients (Qian *et al.* 1998, Légaré *et al.* 2002, Chipman and Johnson 2002, Lamarche *et al.* 2004).

Overstory Composition

The number of overstory species in North American boreal forests is relatively low compared to tropical or temperate forests. There are, however, significant differences in the effects each species can have on the understory environment. This is primarily the result of differences in light transmission, litter composition and leaf morphology.

Considerable differences in light transmission exist between stand types (deciduous and conifer) and stand composition (shade tolerant and shade intolerant). Transmission of PAR is higher under deciduous stands than coniferous stands, with aspen and birch having higher light transmission than that of pine and spruce-fir stands (Canham and Burbank 1994, Messier *et al.* 1998). Shade tolerant species have lower light transmission than shade intolerant species because of increased canopy depth, resulting in a continued decrease in light transmission as stands age (Messier *et al.* 1998, Lieffers *et al.* 1999). This decline in light transmission can be summarized by genus as follows: *Betula* > *Populus* > *Pinus* > *Picea* > *Abies* > *Thuja* (Messier *et al.*, 1998). Before leaf expansion, and following leaf senescence, deciduous canopies have much higher light transmission than all other stand types (Ross *et al.* 1986). Despite having the highest light transmission of any closed canopy forest in the world, light availability plays a major role in determining the composition of boreal understory vegetation communities (Messier *et al.* 1998).

Deciduous tree species create conditions favorable for the growth of vascular plants and inhibit the growth of mosses and lichens. Deciduous leaf litter is much higher in base cations and pH, increasing soil fertility (Paré and Bergeron 1996). Deciduous litter also decomposes more rapidly than coniferous litter, increasing rates of nutrient cycling (Coté *et al.* 2000). Flanagan and Van Cleve (1983) found birch litter to have respiration rates 11.5 times higher than black spruce litter. These conditions are more favorable for fast growing herbaceous species (Sydes and Grime 1981), which readily outcompete slower growing groups such as terricolous bryophytes (Frego and Carleton 1995b) and ericaceous vegetation (Skre *et al.* 1998). Humus types, as affected by litter type, have been hypothesized as an important factor in controlling herbaceous layer composition since many boreal herbaceous species root directly in the humus layer (Qian *et al.* 2003). While likely very important to a number of species, this area remains underinvestigated.

Morphology of deciduous and coniferous litter can also affect the type of vegetation communities present. Deciduous leaf litter represents a large physical barrier for bryophytes, which have been found to be much less vigorous under deciduous leaf litter (Beatty and Scholes 1988). Conifer litter, however, represents a small physical barrier, and does not inhibit capture of light and throughfall precipitation by bryophytes. Herbaceous plants are well adapted to penetrate leaf litter, and have a competitive advantage over bryophytes under deciduous canopies. As a result, terricolous bryophytes and lichens are a much larger component of tolerant and intolerant conifer stands than they are of deciduous stands (Carleton and Maycock 1981, Carleton 1982), where they are often represented by only a few species, and typically on the least productive sites, or are restricted to decaying wood (Crites and Dale 1997, Chen *et al.* 2004).

The high light transmission and soil nutrients typical of deciduous canopies favor fast growing shrubs such as *Acer spicatum* and *Corylus cornuta*. (Légaré *et al.*, 2002). These shrubs in turn have a significant effect on understory composition, as well as canopy succession (Vincent 1965, Messier *et al.* 1998, Lieffers *et al.* 1999). Light transmission can decrease from 15% below the overstory to less than 5% under *A. spicatum* cover. Shrub leaf litter can have the same effect as that of overstory deciduous species, increasing nutrient cycling rates, and inhibiting bryophyte growth (Timoney 2001).

Few studies have compared the understory diversity of different stand types of similar ages. Reich *et al.* (2001) reported a decrease in understory diversity from aspen stands, to jack pine, to black spruce, as well as large compositional differences. Qian *et al.* (2003), however, found aspen and black spruce stands in British Columbia to have similar numbers of understory plant species (168 and 157 species, respectively). Differences, however, occurred in the contribution of vascular and non-vascular plant groups to understory diversity. Aspen stands supported much higher vascular plant diversity, whereas black spruce stands had much higher non-vascular diversity.

Mixed-species stands, those composed of conifer and deciduous overstory species, may support higher understory diversity than pure conifer and deciduous stands. Conifer stands having greater amounts of birch also had higher understory diversity, as a result of increased herbaceous species (Pitkanen 2000). The increase in herbaceous species is likely because of increased light penetration through the canopy, creating a more heterogeneous light environment, with areas of high light availability, which are more favorable for herbaceous species, as well as the higher nutrient content of birch leaf litter. Saetre *et al.* (1997) also found mixed stands of spruce and birch to have more diverse vascular communities than pure stands of spruce, although bryophyte diversity was reduced. These effects were attributed to the higher nutrient content and pH of birch litter and its effect on soil productivity. To date, no study has compared understory diversity of mixed stands to both conifer and deciduous stands. Some mixed species stands may support higher understory diversity by creating higher resource heterogeneity in the understory, allowing resource requiring vascular plants to coexist with much more tolerant, though less competitive, species such as ericaceous shrubs and bryophytes. The degree to which diversity is increased is also likely to depend on the proportions of the overstory species to one another, and may also depend on stand age.

Vascular plant cover is highest under deciduous stands and decreases with increasing conifer content (Saetre *et al.* 1997, Légaré *et al.* 2002). *Acer spicatum* biomass is highest under birch and aspen stands and decreases under conifer stands, although it is still higher under jack pine than under shade tolerant conifers such as spruce. Jack pine stands have a high light transmission to the understory but are likely to be too nutrient poor to be ideal for *Acer spicatum* (Légaré *et al.* 2002), although this may also depend on substrate, as some jack pine stands can support healthy *Acer spicatum* layers. Herbaceous layer cover is not as affected by canopy composition as the shrub layer, where changes in cover with canopy composition are easily observed (Carleton and Maycock 1981, Légaré *et al.* 2002). Bryophyte cover, however, is much lower under deciduous canopies (Timoney 2001), where high resource conditions favor vascular plant growth, and leaf litter inhibits bryophyte growth.

Canopy composition has been found to be the largest factor affecting understory vegetation communities in the southern boreal forest of Quebec (De Grandpré *et al.* 1993, Légaré *et al.* 2002). Changes in canopy composition as a result of disturbance severity and management may have an associated effect on understory vegetation communities.

Site Conditions

Although light is considered to be the most important environmental factor affecting understory vegetation (Légaré *et al.* 2002), soil type and slope position can affect soil fertility and, therefore, affect understory abundance, composition, and diversity.

Soil fertility, although affected by overstory composition, is largely a factor of mineral soil type (till or clay), as well as slope and slope position. Till has lower pH, base cation saturation, and C mineralization than clay, although mineralization rates of N have been found to be lower on clay soils (Coté *et al.* 2000, Lamarche *et al.* 2004).

Changes in understory biomass are pronounced between clay and till substrates. Clay soils have a higher biomass of *Acer spicatum* (Légaré *et al.* 2002), as well as a number of early successional species such as *Salix humilis* Marsh., *Alnus crispa* (Chaix) DC., *Rubus idaeus*, and *Aster macrophyllus* (Shropshire *et al.* 2001). Soil depth also affects cover, with deeper tills supporting higher vascular plant biomass than shallow soils (Harvey *et al.* 1995). Soil effects on understory abundance are particularly important for forest management as a number of the aforementioned species have been associated with decreasing understory light transmission, and inhibiting overstory regeneration (Messier *et al.* 1998).

Sites with higher fertility are generally favored by vascular plant communities (Nieppola and Carleton 1991). Chen *et al.*(2004) found more productive aspen stands to have a higher vascular component, particularly of the herbaceous species *Cornus sericea* and *Galium trifidum*; whereas, aspen stands of lower productivity had more non-vascular and ericaceous species such as *Polytrichum juniperinum*, *Pleurozium shreberi*, and

Vaccinium vitis-idaea and *V. myrtilloides*. Composition of large dominant shrubs does not vary as much between soil types, with *Alnus* spp. replacing *Acer spicatum* and *Corylus cornuta* only on more infertile soils (Lamarche *et al.* 2004).

Understory diversity in boreal forests appears to be similar between stand types (Qian *et al.* 2003), with only the least productive sites showing noticeable declines in diversity (Harper *et al.* 2003). This is because declines in vascular species richness are often offset by increases in non-vascular species diversity (Qian *et al.* 2003). Within plant groups, however, there are noticeable effects of site fertility on understory diversity. Vascular plants, particularly the herbaceous layer, are more diverse on productive sites (Chen *et al.* 2004), which are often upland sites with a glaciofluvial surface geology (clay) (Lamarche *et al.* 2004). Chipman and Johnson (2002) found glaciofluvial sites to have a much higher diversity in the herbaceous layer than did sites found on glacial till. The increase in species diversity was found to be the result of an increase in species with narrow tolerance ranges, indicating increased resource partitioning and lack of dominance by any one species. The authors also found slope position to affect diversity, with upper slope sites more diverse than those lower down the slope. Changing overstory composition from jack pine on upper slopes to black spruce on lower slopes may influence the decline in diversity from upper to lower slopes, as light penetration and forest floor nutrients are likely to decline with the increase in black spruce.

Climate

Changes in North American boreal forest understory vegetation dynamics across latitudinal and longitudinal gradients remain poorly understood. To date, no study has directly compared vegetation in the southern and northern boreal forest, and only Qian *et* *al.* (1998) has studied longitudinal variation across North America. Despite the relatively low plant diversity of the boreal forest, variation in precipitation and temperature, and their effect on fire regime, overstory composition, and productivity are likely to have an effect on the understory vegetation community.

Climatic factors change with increasing latitude and longitude in the North American boreal forest. Decreasing temperatures and increasing presence of permafrost with increasing latitude results in declining productivity from reduced nutrient cycling rates and paludification (Van Cleve *et al.* 1981, Bonan and Shugart 1989). There is also a decline in deciduous species with increasing latitude, such that forest stands in the far north are composed exclusively of black spruce, white spruce and tamarack, causing a decline in nutrient cycling and reducing understory resource heterogeneity (Rowe 1972, Canham and Burbank 1994).

Longitudinally, the most important change across the North American boreal forest is change in precipitation and subsequently fire regime. The increase in precipitation, from 300-500 mm per year in the western boreal forest to 800-1000 mm in the eastern boreal forest, results in an increase in the fire return interval from 75 years in the western boreal forest to 150 years or more in the eastern boreal forest (Kneeshaw *et al.* 1998, Weir *et al.* 2000, Lesieur *et al.* 2002, Chipman and Johnson 2002, Thompson *et al.* 2003). The longer fire cycle in the eastern boreal forest in turn leads to much older stands and an increase in shade tolerant conifers and decline in productivity (Lesieur *et al.* 2002, Wardle *et al.* 2004).

The majority of boreal forest research has occurred in the southern range, where commercial activity and human population are relatively high. Very few studies have examined understory vegetation in northern latitudes of the boreal forest, making comparisons between the southern and northern boreal forest very difficult. The less productive, conifer dominated, northern boreal forest has a much lower herbaceous species composition, and is dominated by bryophytes, lichens, and ericaceous species (Carleton 1979, Nieppola and Carleton 1991). Black and Bliss (1978) found very little change in vascular species composition along a post-fire chronosequence in the North West Territories, although there were declines in species abundance, whereas the composition of cryptogamous species changed markedly between successional stages, along with increases in *Vaccinium uliginosum* L. and *V. myrtilloides* Michx., indicating that northern boreal understory vegetation communities are driven primarily by bryophyte and lichen composition. The persistence of some early successional herbaceous species in the northern boreal forest may also be attributable to the broken canopies of less productive black spruce stands, allowing much higher light penetration to the understory.

No studies have compared understory diversity along latitudinal gradients. Diversity is generally lower at higher latititudes, in part because of declining productivity. The loss of a number of species with affinities for deciduous canopies may also decrease diversity (Carleton and Maycock 1981). At least some of this decline, however, may be made up for by an increase in bryophyte and lichen richness, which can offset declines in vascular plant diversity in the southern boreal forest (Qian *et al.* 2003).

Longitudinal changes in vegetation composition and diversity are likely to be less pronounced from those found along latitudinal gradients. Most boreal bryophyte and lichen species have a circumpolar distribution, and virtually all understory species are found across North America (La Roi 1967). This is particularly true for black spruce dominated ecosystems that have very little change in understory composition across North America, likely the result of similar site requirements and very low productivity, preventing a number of species from establishing (Carleton and Maycock 1980, Qian *et al.* 1998). Qian *et al.* (1998) found understory diversity to be highest in the central boreal region and higher in the western boreal than in the eastern boreal. These differences were primarily the result of changes in the vascular flora, whereas bryophyte diversity changed very little.

Higher floristic diversity in the central boreal region may be explained by the diversity of overstory species comprising these stands. For example, balsam fir is largely absent from the western boreal forest, whereas trembling aspen and jack pine are much less abundant in the eastern boreal forest (La Roi 1967, Rowe 1972), possibly limiting the distribution of associated understory species (Carleton and Maycock 1981). The intermediate disturbance hypothesis may also account for higher diversity in the central boreal region (Huston 1979). The intermediate fire cycle found in the central boreal region allows for stands of widely varying ages to occur alongside each other, whereas the longer fire cycle of the eastern boreal forest results in stands that are much older, and less diverse (Chipman and Johnson 2002). The shorter fire cycles of the western boreal forest prevents stands from reaching late successional stages, potentially inhibiting a number of understory species (De Grandpré *et al.* 1993).

A major difference in understory composition between the eastern and western boreal forest is the absence of the tall shrub *Acer spicatum* in the western boreal forest (La Roi 1967). Although common on upland sites in the eastern and central boreal regions, *A. spicatum* is much less abundant in the western boreal forest and is completely absent west of Saskatchewan. *Acer spicatum* affects canopy succession in the central and eastern boreal forest by decreasing light availability under aspen and birch canopies to levels inhibiting the growth of all but the most shade tolerant conifers, likely resulting in changes to overstory successional dynamics across the North American boreal forest.

EFFECTS OF MINOR DISTURBANCES ON UNDERSTORY VEGETATION

Stand-replacing fire is the most widely recognized disturbance factor in the boreal forest and is associated with maintaining diversity (Chipman and Johnson 2002). Minor disturbances such as windthrow, insect outbreaks, and canopy dieback also play a major role in maintaining understory diversity and composition by increasing resource availability, heterogeneity, and removing dominant species (Jonsson and Esseen 1990, De Grandpré *et al.* 1993). These disturbances become increasingly important in controlling forest dynamics as stands age (De Grandpré *et al.* 2000b).

Changes in Understory Environment with Minor Disturbances

Minor stand disturbances such as windthrow, insect outbreaks, and canopy dieback occur between stand replacing fires, and are prevalent when the fire return interval is sufficiently long to allow stochastic events, disease, and canopy succession to occur, respectively (Gromtsev 2002). Windthrow and insect outbreaks can result in large canopy gaps of 0.1ha or more. The two disturbance types often occur together as stands with a number of dead canopy trees are very susceptible to windthrow. Insect outbreaks in the eastern North American boreal forest are usually caused by spruce budworm (*Choristoneura fumiferana* (Clemens)), which reaches pest levels when the amount of balsam fir in the canopy is very high (MacLean 1980).

Large canopy gaps created by windthrow and spruce budworm outbreaks affect resource availability in the understory environment. Increased light transmission to the forest floor increases PAR, soil temperatures, and mineralization rates. Large inputs of decaying wood also increase nutrient availability. Paré *et al.* (1993) found that spruce budworm-induced gaps increased available Ca and N, whereas Van Cleve and Dyrness (1983) reported increases in pH, Ca, and Mg after experimental canopy removal. Large canopy gaps are very important in high latitude boreal forests because the low solar angle can prevent direct sunlight from reaching the forest floor in small canopy gaps (Bonan and Shugart 1989).

Small canopy gaps, created by natural canopy dieback of a few dominant individuals as stands of early successional species such as trembling aspen, are replaced by shade tolerant conifers and do not increase understory light transmission and nutrient availability to the same extent as large canopy gaps. Small canopy gaps are often too small to allow direct light transmission to the forest floor (Bonan and Shugart 1989, Kneeshaw and Bergeron 1998) and organic matter inputs from decaying wood are limited.

Canopy gap formation increases considerably with time since fire (Hill *et al.* 2005). Kneeshaw and Bergeron (1998) found canopy gaps increased from 7.1% in 50-year-old stands to 40.4% in 234-year-old stands. Canopy gaps in early successional stands are caused by single tree mortality, whereas late stage gaps are primarily caused by spruce budworm and windthrow (Kneeshaw and Bergeron 1998, Harper *et al.* 2002, Hill *et al.* 2005). Secondary canopy disturbance is most prevalent between 100 and 300 years following fire. Harper *et al.* (2002) found that, after 300 years, shifting stand composition from balsam fir to black spruce resulted in stands that were much more open and less susceptible to windthrow and spruce budworm.

All forms of secondary disturbance increase forest floor heterogeneity by tip-up mound and hummock formation when root balls are upturned. This process exposes and mixes mineral soil, and creates new microsites, as well as increasing soil fertility by reversing the podzolization process (Kuuluvainen 1994).

Response of Understory Vegetation to Minor Disturbances

Changes in vegetation community composition are controlled by disturbance severity, with more severe disturbances causing greater changes in understory composition (Roberts 2004). Larger canopy disturbances, windthrow and insect outbreaks, result in large shifts in understory composition (Figure 2-2a). In general, these changes are the result of increased abundance of vascular species already present in the understory. De Grandpré *et al.* (1993) found increases in the abundance of *Aster macrophyllus*, *Aralia nudicaulis*, *Acer spicatum*, *Clintonia borealis*, and *Rubus pubescens* Raf. between 120 and 230 years since fire. Large canopy gaps also allow some early successional species to reoccupy a stand. *Rubus idaeaus* is particularly successful at occupying canopy gaps, likely because of its prevalence in the persistent seed bank (Moore and Wein 1977, De Grandpré *et al.* 1993), and is often the only species to colonize canopy gaps, as other species already present simply increase in abundance (Hughes and Fahey 1991). Changes in composition are not applicable to all stands. Rydgren *et al.* (2004) found young stands to be less susceptible to composition changes from gaps than older stands, because of an already similar floristic composition. Richer sites also change less in composition, likely because potential colonizers are already present, and competition more severe. Canopy gap formation is most important in old stands by allowing early successional species to coexist with late successional species, temporarily reversing the trend of declining floristic diversity (De Grandpré and Bergeron 1997).

Single-tree canopy gaps represent much less severe disturbances, and do not cause the same shifts in understory composition. Very little change in vascular composition has been found for small canopy gaps. However, important shifts in the non-vascular community can occur. Small canopy gaps, while not increasing direct light penetration, increase throughfall precipitation, promoting the growth of bryophytes (Økland *et al.* 1999). Frego (1996) found *Pleurozium shreberi* to be very effective at occupying small forest floor gaps because of the species' abundant propagules and rapid growth.

Tip-up mounds and hummocks are very important in controlling bryophyte diversity, by increasing bryophyte composition. Viable seed populations decrease with soil depth (Moore and Wein 1977, Rydgren and Hestmark 1997, 1998), and exposed mineral soil from uprooting is likely to be relatively low in viable seeds, as well as vegetative propagules. Small disturbance patches are readily colonized by bryophytes because of the proximity of potential sources of bryophyte diaspores (Jonsson and Esseen 1990).

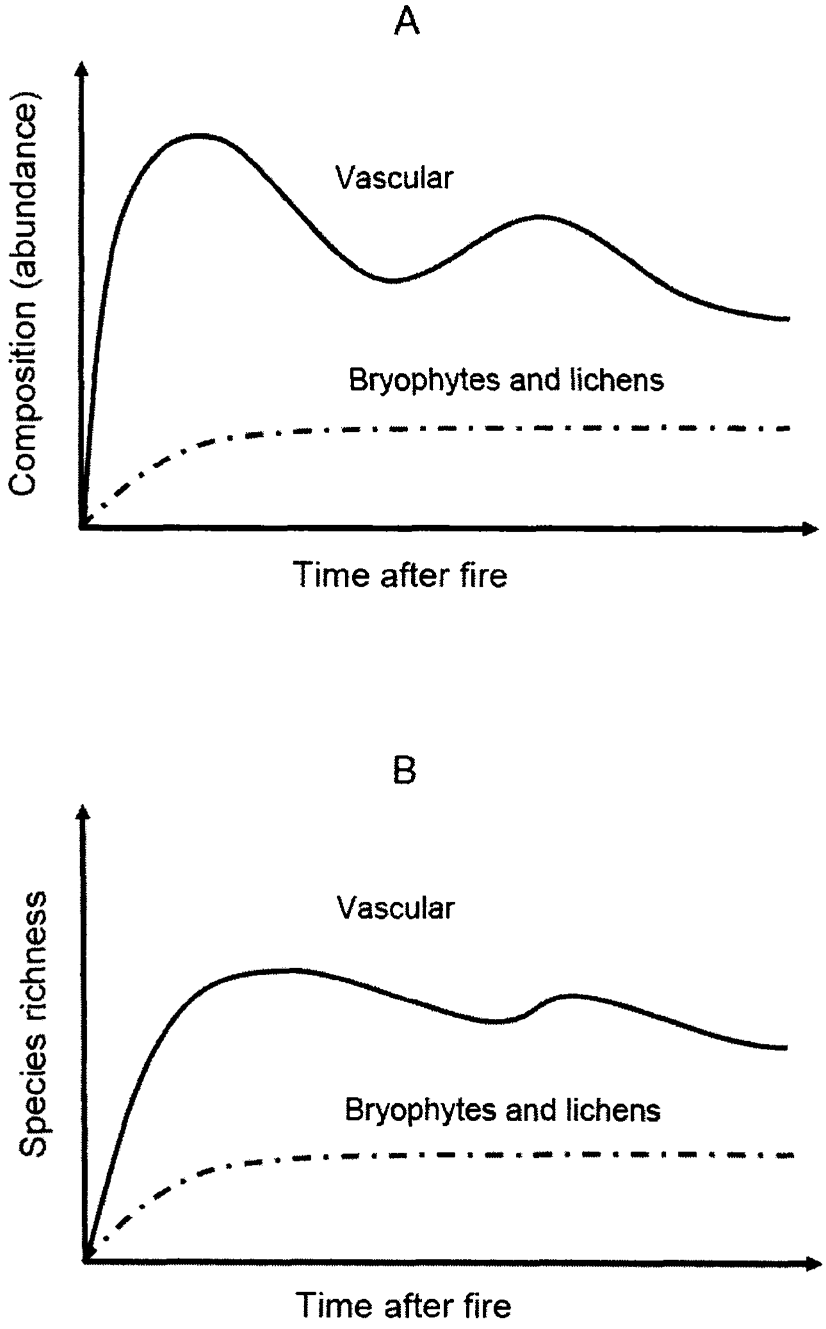

Figure 2-2. Effect of minor canopy disturbance on understory vegetation: (a) composition and (b) species richness (After De Grandpré *et al.* 1993, Roberts and Gilliam 1995, Rydgren *et al.* 1998).

Increased abundance of early successional vascular species, as well as bryophytes on specific microsites, such as tip-up mounds, increases understory diversity (Figure 2-2b), much of which is owed to more even abundance of species. Roberts and Gilliam (1995) found richness to be highest three years after disturbance, decreasing thereafter. The rate of decrease in diversity and composition (Fig. 2-2a) is a result of the degree of vegetation change. Severe disturbances causing large changes in composition and diversity may have effects lasting up to 25 years, whereas less severe disturbances may only last 5 years (Rydgren *et al.* 1998). Changes in the lichen and bryophyte communities, however, are much slower.

Minor canopy disturbances are not nearly as severe as stand replacing fire in causing change. As a result, resource availability does not increase to the same extent, which prevents the colonization of a number of early successional and opportunistic species. Understory diversity does not increase to the same extent as that following fire (Figure 2-2b). Stands older than 300 years after fire do not have the same fluctuations in understory diversity; instead, diversity decreases gradually over time (De Grandpré *et al.* 1993). This is because declining productivity promotes stands composed primarily of well-spaced black spruce that are less susceptible to windthrow and insect damage (De Grandpré *et al.* 2000).

Minor canopy disturbances, especially those caused by spruce budworm outbreaks are thought to be very important in maintaining understory composition and diversity, as well as controlling overstory dynamics, in the eastern boreal forest of North America, where fire cycles are relatively long and balsam fir is a large component of the overstory (De Grandpré and Bergeron 1997, Harper *et al.* 2002). Minor canopy disturbances are likely to be much less important in the western boreal forest of North America because of much shorter fire cycles, which inhibit the growth of balsam fir and decrease the extent to which canopy succession occurs (Rowe 1961). Although minor canopy disturbances play an important role in increasing understory diversity in late successional stands, the long-term trend for all stands is a decline in understory diversity (Figure 2-2b), and dominance of a few late successional species, with increasing time since fire.

IMPLICATIONS FOR FOREST MANAGEMENT

Environmental Differences between Harvesting and Wildfire

Although somewhat similar in appearance, the different effects of wildfire and forest harvesting on a number of environmental factors result in different physical and soil chemical properties (McRae *et al.* 2001). Similar to wildfire, the removal of the overstory and subsequent increase in soil temperatures and decaying wood, stimulate nutrient release. As pH rises, availability of Ca, Mg, K, and P increases as does nitrification and nitrogen mineralization (Binkley 1984, Brais *et al.* 2002, Frey *et al.* 2003, Palvainen *et al.* 2004). The amount of forest floor and organic matter removal is much less following logging (Rees and Juday 2002), resulting in less soil disturbance and thereby preventing soils from warming up as much; this decreases the available nutrient pool bound in organic matter. Increases in nutrients and pH are relatively small, with nutrient releases and increase in pH much less than those following wildfire, and making the effects of increased resources more short lived (Simard *et al.* 2001). Salvage harvesting has been found to have a negative effect on long term base cation availability (Brais *et al.* 2000). The loss of activated carbon is another important difference between the two disturbance types likely to affect nutrient cycling and productivity because of its ability to adsorb phenolic compounds and stimulate nitrification. The short term increases in resources following harvesting are not as pronounced as those following wildfire, potentially resulting in decreased site productivity (Dussart and Payette 2002).

Composition

Understory vegetation communities following wildfire and harvesting can be considerably different. Post-logging understory communities are more similar compositionally to the pre-disturbance communities compared to those resulting from wildfire (Rees and Juday 2002). These communities are dominated primarily by tolerant bryophytes and vascular plants such as *Cornus canadensis*, *Acer spicatum* and *Rosa acicularis*, and *Kalmia angustifolia* (Mallik 2003, Økland *et al.* 2003, Bourgeois *et al.* 2004, Haeussler and Bergeron 2004), most of which are present in late successional communities prior to clear-cutting. Carleton and Maclellan (1994) found that logging promotes tall broadleaved shrubs, which may affect overstory regeneration because of their effect on understory light availability (Messier *et al.* 1998). These species reproduce primarily by vegetative propagules and are able to increase their presence considerably in response to increased resources following cutting (Vincent 1965, Maundrell and Hawkins 2004).

Notably absent from most of these stands are a number of pioneering species, many of which are adapted to post-fire conditions of exposed mineral soil, charcoal substrates, and seedbed recruitment. Early successional burned stands support known pyrophilic non-vascular flora of lichens and mosses, such as *Marchantia polymorpha* L., *Leptobryum pyriforme* (Hedw.) Wils., *Ceratodon purpureus* (Hedw.), and *Ptilidium* *ciliare* (L.) Hampe in much greater abundance than logged stands (Whittle *et al.* 1997b, Nguyen-Xuan *et al.* 2000). Similar trends have also been observed for a number of vascular species such as *Erigeron canadensis* L., *Viola adunca* J.W. Smith., *Rubus allegheniensis* Porter, and *Epilobium angustifolium*, all of which require extensive soil disturbance to create seedbeds and expose dormant seeds (Whittle *et al.* 1997b).

Logged stands do not support similar numbers of exclusive species (Nguyen-Xuan *et al.* 2000). Whittle et al. (1997b) found *L. borealis* to be the only species to occur solely on logged jack pine sites, compared to 40 species exclusive to burnt sites. *L. borealis* is a species normally found exclusively in late successional stands and is vulnerable to fire because it roots in the humus layer (De Grandpré *et al.* 1993). Rees and Juday (2002) reported similar trends in Alaska with 17 species exclusive to wildfire sites and only 8 species exclusive to logged sites. Lower species diversity in later successional stands may also explain some of the lack of exclusive species following logging, as the later successional communities present prior to harvesting are less diverse and have a much smaller species pool of potential colonizers.

Logged stands may also be predisposed to shifts in species composition. Post-logged mesic to hydric sites were found to support higher cover of ruderal and introduced species than drier sites with sand and till substrates (Harvey *et al.*, 1995). As well, increased composition of primarily xeric and meso-xeric species, such as *Aralia hispida* Vent., on logged stands was attributed to increased soil moisture losses from logging, which were attributed to complete canopy removal, allowing more airflow over harvested stands (Bourgeois *et al.* 2004).

Understory communities resulting from wildfire and harvesting begin to converge after 20 years (Bergeron and Dubuc 1989, Rees and Juday 2002), and are likely to converge completely after 100 years (Rees and Juday 2002). Current rotation ages, however, are often shorter than the time required for convergence of the two disturbance types, resulting in vegetation communities that may remain permanently altered in the presence of continued forest harvesting. Of concern also is the possibility of permanent changes in vegetation communities as a result of changes in the abundance of certain species. For example, logging in central Siberia creates conditions more favorable for grasses, preventing tree reestablishment, resulting in the permanent conversion of forest to grassland, in the absence of fire (Vlassova 2002, Chaping, III *et al.* 2004b). In Quebec, the grass *Calamagrostis canadensis* can inhibit the rate at which stand composition converges, by preventing colonization by other species (Tellier *et al.* 1995). Allelopathy by the ericaceous shrub *Kalmia angustifolia* has been identified as the cause of the failure of black spruce to regenerate following harvesting, resulting in the conversion of coniferous forests to a lichen-heath dominated ecosystem (Mallik 2003). Fire and insect outbreaks after logging have also been associated with the conversion of black spruce stands in Quebec to lichen-heath parkland as a result of a reduction in seed bearing trees (Lavoie and Sirois 1998, Dussart and Payette 2002, Payette and Delwaide 2003).

Differences in understory composition between burnt and logged stands are primarily the result of the failure of forest harvesting to provide conditions suitable for colonization and germination of early successional species, while also failing to remove or inhibit late successional species (Nguyen-Xuan *et al.* 2000, Rees and Juday 2002). Early post-logged communities are much closer in composition to late successional communities. These stands have lower turnover indices, and therefore, change much less in composition over time (Rees and Juday 2002). As a result, harvesting can result in a decrease in both beta and temporal diversity.

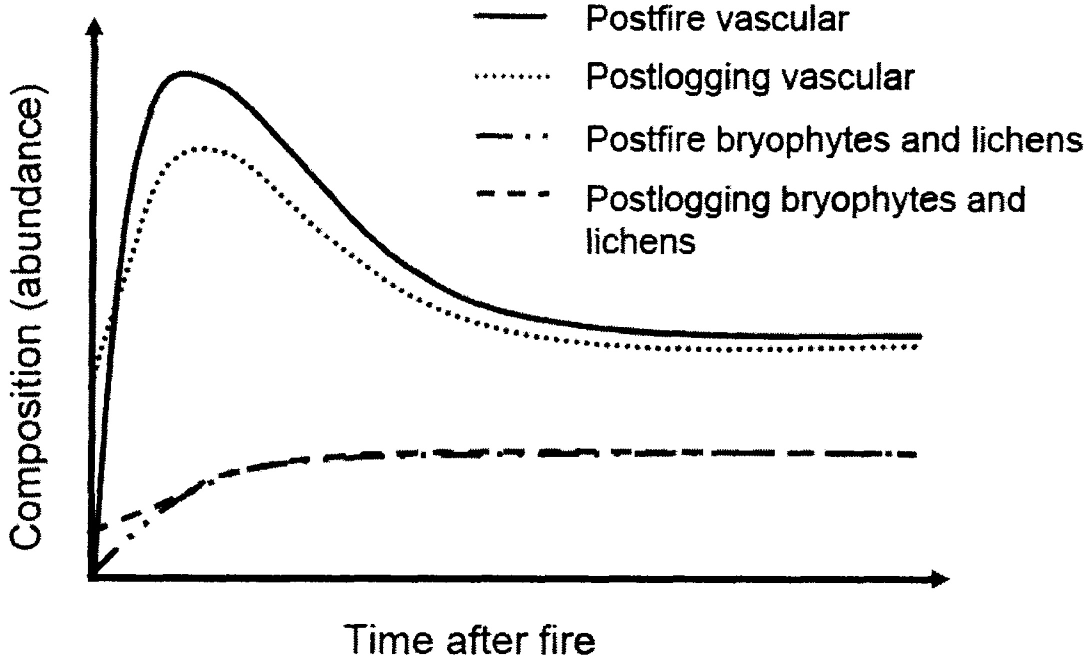

Figure 2-3. Comparison of understory vegetation diversity in communities resulting from wildfire and harvesting (After De Grandpré *et al.* 1993, Rees and Juday 2002).

Diversity and Abundance

Boreal plant communities are disturbance dependant. Following forest harvesting, understory diversity increases in response to increases in resource availability and colonisable microsites (Peltzer *et al.* 2000, Rees and Juday 2002, Haeussler *et al.* 2002). Increases in diversity are initially caused by increases in herbaceous species diversity, which can double following logging (Bradbury 2004, Pykala 2004). The diversity of bryophyte and lichen species also increases, but at a much slower rate, requiring five to six years to double (Tellier *et al.* 1995).

A number of studies have compared the effects of logging and wildfire on boreal forest understory vegetation diversity. Although harvesting results in an increase in understory diversity, it is only very rarely higher than that found in communities resulting from wildfire (Whittle *et al.* 1997b, Nguyen-Xuan *et al.* 2000) (Figure 2-3). Rees and Juday (2002) found floral diversity on burned stands to be higher than on stands that had been logged (146 species vs. 111, respectively). Some of the increased diversity can be explained by the higher number of exclusive species found on burnt stands, as well as a more even distribution of species in the initial post-fire communities. The rapid increase in pre-established species following logging may lead to dominance of only of few species, a condition more typical of later successional stands (De Grandpré *et al.* 1993, Peltzer *et al.* 2000).

In situations where harvesting removes very few species and recruitment following fire is low, understory diversity can be higher on harvested stands (Bergeron and Dubuc 1989). This discrepancy may be explained by disturbance intensity. Very intense fires can destroy much of the seedbed, as well as many species relying on vegetative propagation. Harvesting and site preparation intensity also affect understory diversity. Increased intensity of harvesting and treatment increases soil disturbance, thereby exposing buried seeds and exposing mineral soil for colonization, as well as increasing soil temperatures; such conditions favoring vascular plant establishment and growth. Scarification following harvesting has also been found to increase vascular plant diversity (Nguyen-Xuan *et al.* 2000, Bradbury 2004, Haeussler and Bergeron 2004).

Biomass of understory species is very high following logging because of the presence of well established residual species. Many late successional species are shade tolerant and are not physiologically suited to increase growth rates in response to abundant light resources in the understory. The tall shrubs *A. spicatum*, *Amelanchier alnifolia*, and *C. cornuta*, however, are well adapted to reproduce vegetatively and can grow rapidly in response to abundant light (Vincent 1965, Bock and Van Rees 2002). The same is also true for the herbaceous species *Clintonia borealis*, *Cornus canadensis*, and *Aralia nudicaulis*, which are not normally part of early successional post fire communities, but can increase in abundance rapidly through vegetative means. The grass *Calamagrostis canadensis* can reach very high abundance within a few years of clearcutting, despite having been present in very small numbers prior to harvesting (Lieffers and Macdonald 1993). Moss cover, particularly by pleurocarpous mosses, is often higher following harvesting that wildfire (Rees and Juday 2002). Long-term vascular understory cover is, however, not likely to remain as high on logged stands because of lower increases in soil nutrients, resulting in reduced vigor for a number of vascular species that are likely to decline to levels of abundance more typical of late successional communities. Bryophyte cover, however, is higher through all early successional stages and does not converge with wildfire for 80 to 100 years (Fig. 2-3) (Rees and Juday 2002, Haeussler and Bergeron 2004).

Forest harvesting results in understory communities intermediate to those of post-fire communities and minor canopy disturbances. Increases in early succession species composition and diversity are not as high as those found following wildfire, resulting in earlier declines in these communities similar to that found shortly after minor canopy disturbance.

Long-term Implications

In much of the southern boreal forest, increased harvesting activity and fire suppression has allowed logging to replace wildfire as the principal disturbance factor. Large-scale logging, however, has occurred in the North American boreal forest for less than 100 years. Much of such logging is still occurring on primary forests, making it difficult to understand the long term impact on understory communities and productivity.

Immediate differences in understory composition and decreased diversity on early successional stands have serious long-term consequences as fire origin communities are gradually replaced by post-harvest communities. A number of early successional and pyrophilic species, particularly mosses and lichens, may be at risk of large scale declines in abundance as conditions favoring their establishment become increasingly rare (Whittle *et al.* 1997b, Rees and Juday 2002). Herbaceous species diversity is also likely to decline significantly when site preparation following harvesting fails to provide exposed mineral soil and when soil nutrients decline. Harvesting activities also decrease microsite heterogeneity, resulting in fewer colonizing sites for late successional bryophytes and a decline in forest floor heterogeneity (De Grandpré *et al.* 2000a, Kuuluvainen and Laiho 2004, Wardle and Zackrisson 2005). Despite the tendency of harvesting to create larger numbers of early successional stands across the forest landscape, increased bryophyte, tall shrub, and ericaceous composition of the stands, as well as their lower diversity makes them more similar to late successional communities, potentially decreasing community heterogeneity across the North American boreal forest.

The loss of many early successional herbaceous species and their replacement by pleurocarpous mosses and woody vegetation also has serious implications for long term stand productivity (Dussart and Payette 2002). Early successional species have higher foliar nutrient content than many late successional species (especially ericaceous species) (Wardle and Zackrisson, 2005). Pleurocarpous mosses, while promoting nitrogen fixation, have sufficiently slow decomposition rates that they inhibit nutrient cycling, as well as insulate the soil, inhibiting further decomposition of the humus layer (Zackrisson *et al.* 2004). Allelopathy by abundant ericaceous vegetation will decrease nitrogen fixation as well as overstory regeneration (Nilsson *et al.* 2000). These changes in composition and nutrient dynamics are likely to result in increased rates of retrogressive succession compared to communities originating from wildfire (Boudreault *et al.* 2002, Wardle *et al.* 2004).

Management Options

Two main objectives exist for understory vegetation management in the boreal forest. The first is to minimize harvest intensity in order to minimize disturbances to the understory community in the hope of maintaining later successional communities. By minimizing forest floor disturbance this method will likely fail to increase soil nutrient availability and does not remove bryophyte cover or late successional vascular plant species. Later successional species have lower foliar nutrient status, further decreasing nutrient cycling rates and increasing the likelihood of retrogressive succession, while also failing to provide conditions suitable for a number of early successional species.

Emulating natural forest succession processes is of increasing interest in boreal forest management (Bergeron *et al.* 2002). Increased soil disturbance following harvesting increases soil nutrient cycling and promotes the establishment of early successional species, particularly herbaceous species with high foliar nutrient status, thereby increasing productivity (Whittle *et al.* 1997b, Wardle and Zackrisson 2005). Establishing early successional communities will also result in greater species turnover over time since fire, thereby increasing stand temporal diversity and landscape diversity (Rees and Juday 2002). Controlled burning of logged stands is likely to be the best management option because it will consume more of the forest floor, thereby increasing nutrient availability, as well as promoting more pyrophilic species (Whittle *et al.* 1997b, Rees and Juday 2002). Creating activated charcoal is also very important because of its ability to inhibit the effects of ericaceous vegetation, while also promoting nitrification (Wardle *et al.* 1998).

CONCLUSIONS

1. Understory vegetation cover and diversity increase rapidly after fire because of an increase of resources and an influx of disturbance adapted species. Diversity is highest within the first 40 years following fire and declines indefinitely after as a result of declining productivity and increased dominance of a small number of late successional pleurocarpous mosses and woody plant species.
2. Vascular plant and bryophyte communities undergo very different successional changes. Vascular communities are more dynamic and change considerably with time since fire, overstory composition, climate, and soil type, whereas bryophyte communities are much slower to establish and change over time. Vascular plant diversity and cover peak much earlier than bryophyte diversity and cover, which increase indefinitely with time since fire.

3. Overstory composition has a strong effect on understory composition. Deciduous stands tend to support primarily vascular communities whereas conifer stands favor the establishment of bryophytes. Total species richness, however, is roughly equivalent between stand types. Mixedwood canopies support understory communities intermediate between conifer and deciduous stands, which may be more diverse than other understory communities, depending on the proportions of conifer and deciduous overstory species.

4. Changes in understory diversity, composition, and abundance occur across latitudinal and longitudinal gradients. Overall diversity is likely to be higher in the southern boreal forest where vascular species are abundant and form a much larger component of the understory communities, whereas bryophytes appear to play a larger role in northern boreal forests. Understory diversity is highest in the central boreal region and higher in the western boreal forest than in the eastern boreal forest. Most of the differences are attributable to the changes in the vascular flora, and indicate the importance of fire cycles in maintaining understory diversity in North American Boreal forests. To date, however, this area remains under investigated, as no studies have directly compared understory diversity of southern and northern boreal forests in North America.

5. Site conditions affecting understory vegetation communities are primarily the result of differences in soil nutrients between till and clay substrates. Clay soils are more fertile than till and can support higher vascular plant diversity, increasing nutrient cycling rates. Abundance of vascular species is much higher on clay soils with potential consequences for overstory regeneration.

6. Minor disturbances such as windthrow, spruce budworm outbreaks, and single tree canopy gaps increase understory resource availability, causing shifts in composition and

increasing species diversity and abundance. Windthrow and insect outbreaks represent larger disturbances and cause shifts in the vascular community by increasing abundance of some early successional species. This process maintains diversity and productivity of late successional stands.

7. Forest management does not emulate the ecological effects of wildfire on understory vegetation. Resulting communities are compositionally different, lacking a number of pyrophilic species while supporting a large number of late successional bryophytes and woody plants. They are not as diverse as those resulting from wildfire. These changes in composition and diversity are intermediate between those observed for wildfire and minor canopy disturbances and have long term consequences for landscape diversity as well as forest productivity.

8. Emulation of natural forest succession should include soil disturbance and prescribed burning to promote the establishment of productive early successional and pyrophilic species, inhibit the presence of ericaceous species and pleurocarpous mosses, as well as create activated charcoal.

CHAPTER THREE INFLUENCE OF FIRE, LOGGING, AND OVERSTORY COMPOSITION ON UNDERSTORY ABUNDANCE, DIVERSITY, AND COMPOSITION IN BOREAL FORESTS, ONTARIO, CANADA

INTRODUCTION

In the boreal forest, understory vegetation plays a critical role in ecosystem processes, influencing overstory succession, nutrient cycling, and long term stand productivity (Zavitkovski 1975, Zackrisson *et al.* 1995, Messier *et al.* 1999, George and Bazzaz 1999, Wardle *et al.* 2004, Nilsson and Wardle 2005, Kolari *et al.* 2006). Understanding factors that affect understory diversity, abundance, and composition, is important for sustainable management of boreal forests, in which overstory regeneration and biodiversity conservation are of concern. Three primary factors affecting understory vegetation communities in boreal forests are stand replacing fires, clearcut harvesting and overstory species composition.

In the boreal forest of North America, stand replacing fire is the principal natural disturbance factor (Johnson 1992). Understory vegetation diversity and cover are highest following moderate, stand replacing fires, which remove aboveground vegetation and consume some of the forest floor, increasing understory light and nutrient availability as well as colonizing opportunities favorable to herbaceous plants and pyrophilic bryophytes (Ross *et al.* 1986, Dyrness *et al.* 1989, Brais *et al.* 1995, Lynham *et al.* 1998), and decline with canopy closure and soil nutrient immobilization (De Grandpré *et al.* 1993, Økland and Eilertsen 1996, Rees and Juday 2002). The abundance of species tolerant of low nutrient conditions, such as woody vegetation and bryophytes, increases with declining resource availability (Rees and Juday 2002). Old growth boreal forests typically support understory communities with low diversity and productivity (De Grandpré *et al.* 1993, Wardle *et al.* 2003, Uotila and Kouki 2005, Wardle and Zackrisson 2005). Intense fires, however, can decrease diversity by destroying the propagules of herbaceous species and dormant seeds found in the humus layer of the forest floor, reducing the number of potential recolonizing species following stand replacing fire (Bergeron and Dubuc 1989, Whittle *et al.* 1997a, Lavoie and Sirois 1998, Roberts 2004). Low intensity disturbances (e.g., surface fires and canopy gap formation), however, do not increase understory resource availability as much as stand replacing fires; resulting in smaller and shorter lived increases in diversity and cover, as well as minor shifts in composition, driven primarily by changes in the relative abundance of previously established species (Van Cleve and Dyrness 1983, Bonan and Shugart 1989, Paré *et al.* 1993, De Grandpré *et al.* 1993).

Overstory species composition affects understory resource availability and therefore understory vegetation. Aspen (*Populus* spp.) and birch (*Betula* spp.) have high foliar nutrient content and produce litter high in base cations and pH, while also having high light transmission to the understory (Ross *et al.* 1986, Brais *et al.* 1995, Paré and Bergeron 1996, Messier *et al.* 1998). Conifer litter is much lower in base cations and pH, canopy light transmission, especially under spruce (*Picea* spp.) and fir (*Abies* spp.), is lower than under deciduous canopies, resulting in reduced resource availability (Messier *et al.* 1998, Ste-Marie and Paré 1999). Understory vegetation affinities for specific overstory types is low in the boreal forest, but large differences in community composition occur between deciduous and conifer overstories (Carleton and Maycock 1981, Reich *et al.* 2001). Vascular plant cover and diversity are highest under deciduous stands, whereas conifer stands, particularly spruce and fir, support higher cover and diversity of bryophytes (Økland and Eilertsen 1996, Saetre *et al.* 1997, Légaré *et al.* 2002, Qian *et al.* 2003). There is, however, some evidence that diversity may remain similar between overstory types, depending on the relative contribution of plant groups in the understory (Qian *et al.* 2003). As a result, it may be possible for mixed species stands to have higher diversity by providing a heterogeneous understory environment favorable to the establishment of a number of plant groups (Canham and Burbank 1994, Saetre *et al.* 1997, Pitkanen 2000, Hart and Chen 2006, Lenière and Houle 2006).

Increased forest harvesting activities in the southern boreal forest have resulted in logging becoming a major stand replacing disturbance. In the absence of severe post-harvest treatments (e.g., disk trenching), logging is rarely as severe a disturbance as stand replacing fire because it merely removes the overstory, with relatively little disturbance to the understory, consuming very little of the organic layer (Nguyen-Xuan *et al.* 2000, Rees and Juday 2002). Logging represents a relatively minor disturbance to understory vegetation communities, and can result in altered understory community composition, diversity and abundance (Whittle *et al.* 1997b, Nguyen-Xuan *et al.* 2000, Rees and Juday 2002, Bock and Van Rees 2002).

To date, studies of boreal understory vegetation communities have individually examined time after disturbance, overstory type, and harvesting, or have been limited in the range of stand ages and overstory types examined (Nguyen-Xuan *et al.* 2000, Reich *et al.* 2001, Rees and Juday 2002, Qian *et al.* 2003, Chen *et al.* 2004). As well, no study has examined the effects of mixed species overstory types on understory vegetation diversity, heterogeneity, cover, and composition in the North American boreal forest. However, a number of conceptual models have been proposed to explain patterns of terrestrial plant diversity relating to disturbance and resource availability (e.g., Huston 1979, Tilman and Pacala 1993, Roberts and Gilliam 1995, Sarr *et al.* 2005). Diversity is generally highest in communities where disturbances are intermediate in intensity, providing new colonizing opportunities while allowing some previously established species to remain (Grubb 1977). Tilman's resource ratio hypothesis states that diversity is highest in habitats of low to intermediate resource availability where the requirements of a number of species are likely to be met without allowing any one species to dominate and exclude other species. The environmental heterogeneity hypothesis predicts that diversity is highest in habitats with high resource heterogeneity as the resource and competitive requirements of more species are likely to be met (Huston 1979), while others showed that resource quantity, not heterogeneity, maintains plant diversity (Stevens and Carson 2002).

The forests of the central boreal shield are mosaics of different ages and overstory compositions, supporting the most diverse understory vegetation communities in the North American boreal forest (Qian *et al.* 1998), as a result of frequently occurring disturbances of wildfire and relatively large number of overstory species. This study addresses the question of how abundance, diversity, and composition of understory vegetation changes with time since fire, and if these age-related dynamics differ with overstory composition. Further, do wildfire and logging support different levels of understory diversity, abundance, and composition? It is hypothesized that (1) plant diversity peaks at intermediate stand ages, and (2) understory diversity is highest under mixedwoods because both conifer and broadleaf associated specialists can co-exist, *i.e.*

the resource heterogeneity. In association with diversity measures, it is expected that stand age, overstory composition and disturbance origin are related to understory vegetation abundance and composition.

METHODS

Study area and stands

The study was conducted in the boreal mixedwood forest region approximately 100 km north of Thunder Bay, Ontario (Figure 3-1), between 49°38' N and 49°27' N and from 89°54' W to 89°29' W. The closest meteorological station is located in Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m elevation). The area has a moderately dry, cool climate with short summers. Mean annual temperature is 2.5° C and mean annual precipitation is ca. 710 mm (Environment Canada 2006). Soils on upland sites are relatively deep glacial tills of the Brunisolic order (Soil Classification Working Group 1998). The study area lies within the English River forest forest section level (B.11) (Rowe 1972), where *Pinus banksiana* Lamb., *Picea mariana* (Mill.) BSP, *Populus tremuloides* Michx. and *Betula papyrifera* Britt. occur in mixed dominance with *Picea glauca* (Moench) Voss and *Abies balsamea* (L.) Mill. also present. The average fire frequency for the region is unknown, but is likely to be approximately 90 years as the fire frequency in the Saskatchewan boreal forest has been estimated to be 75 years (Weir *et al.* 2000), and that of western Quebec 99 years (Bergeron 1991).

All selected sites were located on flat midslope positions, with no slope exceeding 5%, on well drained glacial moraines greater than 50 cm in thickness, which is the prevailing site type in the region. In the field, site condition was determined by topographic characteristics and soil profile determined from a soil pit dug in the centre of the plot for measurements described below. All stands selected were greater than 1 ha in area and were visually homogeneous in structure and composition.

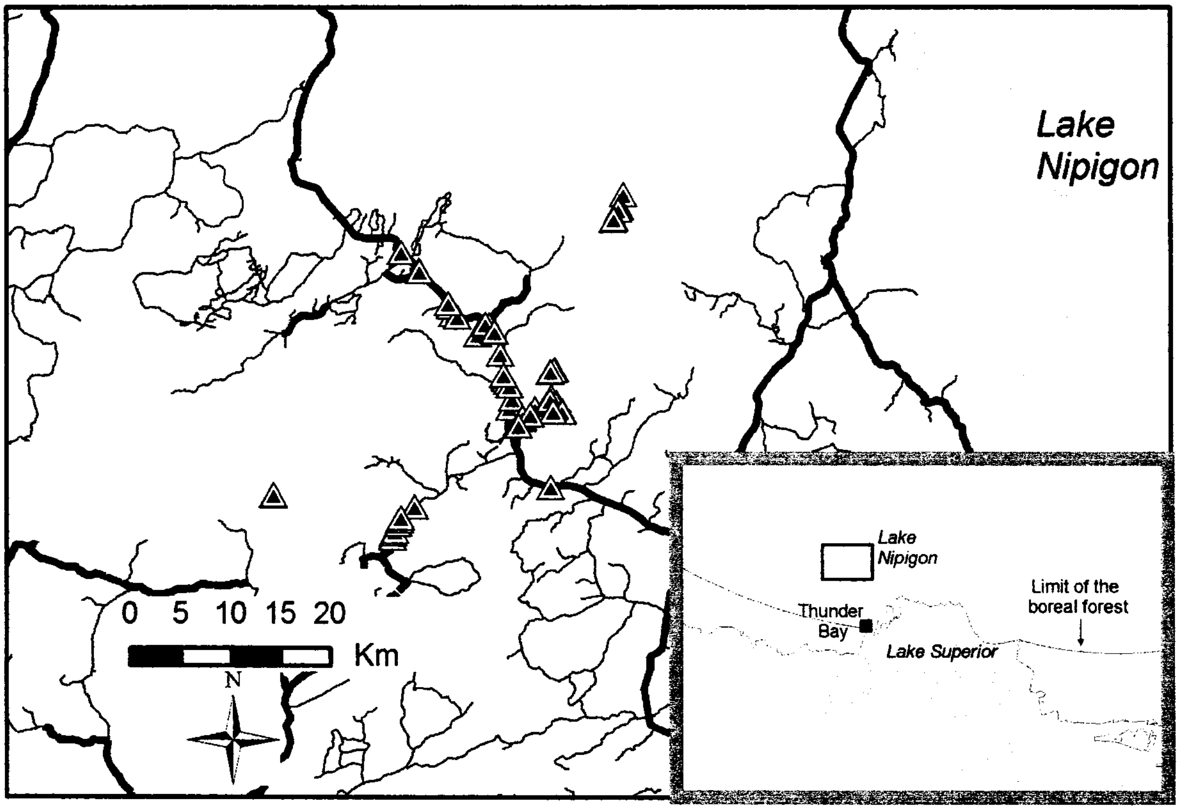

Figure 3-1. Map of the study area showing the location of study sites (triangles).

Sampling design

To determine the effect of time since last disturbance, stands of fire origin were selected using stand development stages according to Chen and Popadiouk (2002) to ensure a wide range of stand ages ranging from seven to 201 years time since fire (TSF). Stands of harvest origin were sampled for only stand initiation and stem exclusion stages as commercial harvesting of the study area did not begin until the early 1970s.

For each mode of stand origin, three overstory types were sampled: conifer, deciduous, and mixedwood. Deciduous and conifer stands were defined as stands having an overstory composed of > 70% deciduous or conifer species by tree stem density, mixedwoods were defined as having mixtures of conifer and deciduous species in relatively equal proportions. Fire origin stands greater than 25 years old were classified based on the basal area of conifer and deciduous tree species (Table 3-1). Seven year old stands of fire origin were classified based on pre-fire overstory composition, from forest inventory maps. Logging origin stands were classified based on pre-harvest forest inventory maps, and by stem count of conifer and deciduous tree species.. Each stand origin, overstory type, and stand age class was replicated a minimum of three times. For mixedwood type, however, it was not possible to sample stands of canopy transition stage, approximately 139 years of age in the study area (Table 3-1). The infrequency of fire in the study area is likely to have narrowed sampling possibilities.

Although site conditions were controlled as much as possible a number of successional pathways exist for any forest stand (Oliver and Larsson 1996). Depending on stand history, as well as the patchy recruitment of late successional tree species, the overstory composition of a boreal forest stand can change considerably over time (Bergeron 2000; Chen and Popadiouk 2002). As a result, it is not possible to conclude that late successional stands studied are the natural progression of younger aged stands. In this study the influence of time since fire and overstory composition on understory vegetation are treated as separate variables to avoid confound results with different stand successional pathways.

Time since last disturbance was determined for each stand sampled. Detailed fire and harvesting records were available for stands younger than 70 years. For stands older than 70 years, however, tree ages were used to estimate TSF (Bergeron 1991). Of all the sampled stands, either post-fire jack pine or trembling aspen trees were selected for the determination of time since fire. No fewer than three canopy stems were sampled for each stand. For each selected tree, a core or disk at breast-height was taken and brought to the laboratory. In the laboratory, the cores mounted on constructed core strips and disks were transversely cut and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Tree ages were corrected to time since fire by adding seven years using the model developed by Vasiliauskas and Chen (2002). For the oldest burnt area, i.e., 201 year-old stands, one live jack pine tree and seven jack pine snags were sampled and disks were cut at the base of stems. The ring count of live trees was 201 years and that of snags ranged 140 to 180 years. We used the live tree age as TSF for the area.

Every effort was made to intersperse stands sampled, to avoid sampling stands of the same class in close proximity to one another. In trying to control for site conditions, stand age, and overstory composition, however, some clumping of stand types occurred.

Measurements of understory vegetation

Both the shrub and ground layers were sampled within a circular 400 m^2 plot (radius 11.28 m) that represents a selected stand using the count-plot method (Mueller-Dombois and Ellenberg 1974). The shrub layer was defined as any species having a height between 1.3 m and 4 m (*sensus* Carleton and Maclellan 1994). Species less than 1.3 m in height were sampled as part of the ground layer vegetation. The shrub layer was sampled separately because of larger spatial requirements in sampling and because of its effect on understory resource availability; as such, the species found in the shrub layer were also found in the ground layer (Mueller-Dombois and Ellenberg 1974, Messier *et al.* 1998, Légaré *et al.* 2001). Shrub layer species were sampled by visually estimating the percent cover of each species within three 25 m^2 circular plots (radius of 2.82 m). These subplots were located at random distances from the plot centre. The first subplot direction was randomly selected and the other two were 120 degrees apart. Ground layer vegetation (all species <1.3 m in height) was sampled by visually estimating the percent cover of all plant species within 10 randomly located 1 m^2 (1 x 1m) subplots (Mueller-Dombois and Ellenberg 1974).

Table 3-1. Study sampling regime. Total of 68 sites sampled.

Overstory type	Age (yrs)	Origin	N	Basal area (m^2/ha)	Stand composition by basal area					
					Jack pine	Black spruce	White spruce	Balsam fir	Aspen	Birch
Conifer	7	Fire	3	-	-	-	-	-	-	-
Conifer	25	Fire	3	2.7 (1.4)	2.7 (1.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
Conifer	72-90	Fire	5	34.0 (2.8)	23.3 (3.2)	4.7 (2.1)	1.6 (0.7)	1.9 (0.8)	0.0 (0.0)	2.4 (1.3)
Conifer	139	Fire	3	19.0 (2.1)	3.5 (0.2)	6.9 (1.8)	4.7 (2.8)	2.9 (1.1)	0.0 (0.0)	1.0 (1.0)
Conifer	201	Fire	3	31.3 (.07)	0.0 (0.0)	0.4 (0.4)	12.8 (3.8)	14.4 (3.6)	0.4 (0.4)	3.2 (1.0)
Conifer	7	Logging	3	-	-	-	-	-	-	-
Conifer	25-31	Logging	3	-	-	-	-	-	-	-
Mixedwood	7	Fire	3	-	-	-	-	-	-	-
Mixedwood	25	Fire	3	4.1 (1.0)	3.5 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.6 (0.2)	0.0 (0.0)
Mixedwood	72-90	Fire	7	32.2 (2.0)	10.2 (2.0)	2.5 (0.9)	0.3 (0.2)	1.9 (0.8)	13.7 (3.2)	3.4 (2.2)
Mixedwood	201	Fire	3	30.6 (2.6)	0.0 (0.0)	1.1 (1.1)	9.9 (5.0)	6.5 (3.2)	0.0 (0.0)	13.1 (2.0)
Mixedwood	7	Logging	3	-	-	-	-	-	-	-
Mixedwood	25-31	Logging	3	-	-	-	-	-	-	-
Deciduous	7	Fire	3	-	-	-	-	-	-	-
Deciduous	25	Fire	3	8.8 (1.8)	0.4 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8.4 (1.6)	0.0 (0.0)
Deciduous	72-90	Fire	5	33.8 (1.4)	0.0 (0.0)	1.3 (1.2)	0.8 (0.7)	0.6 (0.4)	30.9 (1.0)	0.3 (0.3)
Deciduous	139	Fire	3	37.3 (4.5)	0.7 (0.7)	2.7 (2.7)	1.2 (1.2)	7.3 (2.0)	24.3 (4.4)	1.2 (0.7)
Deciduous	201	Fire	3	29.3 (2.1)	0.5 (2.4)	0.0 (0.0)	1.7 (1.6)	0.7 (0.4)	2.4 (2.4)	24.0 (2.0)
Deciduous	7	Logging	3	-	-	-	-	-	-	-
Deciduous	25-31	Logging	3	-	-	-	-	-	-	-

Notes: Data are total mean basal area and basal area by overstory species (1 standard error in parentheses). N = number of stands and '-' denote no data.

Analyses

Abundance was calculated as the mean percent cover (relative abundance) from all ten subplots of a species within a stand. Understory vegetation diversity was calculated using species richness and beta diversity. Richness was measured as the total number of species recorded within a plot. Beta diversity was measured using the Bray-Curtis measure of dissimilarity between all possible pairs of subplots within a plot. Bray-Curtis values range between 0 and 1.0 with 0 indicating no difference and 1.0 no similarity between subplots. This method has been recommended for use with ecological data in part because rare species have very little influence on the index and it incorporated the relative abundance of species as well as the absolute number of species in a given subplot (McCune and Grace 2002).

Because of the difference in age range between stands of fire origin and those of logging origin, analyses were conducted in two steps. First, changes in abundance, diversity, and composition with time after fire were determined for post-fire stands and then the difference and similarity were compared for fire origin *vs*. logging origin stands. The effects of stand age and overstory type on cover and diversity of fire origin stands were examined using the following model:

$$[3.1] \quad Y_{ijk} = u + A_i + S_j + A \times S_{ij} + e_{(k)ij}$$

where Y_{ijk} is cover, species richness, or beta diversity, A is age class (i = 1, 2, …5), S is overstory type (j = 1, 2, 3), and e is error.

Stands of both fire and logging origin were compared among the two youngest age classes (7 and 25-31 years after disturbance) to determine the effects of stand origin on cover, species richness, and beta diversity, as well as the effects of age and overstory type:

$$[3.2] \quad Y_{ijkl} = u + A_i + S_j + A \times S_{ij} + O_k + A \times O_{jk} + A \times S \times O_{ijk} + e_{(l)ijk}$$

where Y_{ijkl} is cover, species richness, or beta diversity, A is age class ($i = 1, 2, \ldots 5$), S is overstory type ($j = 1, 2, 3$), O is stand origin ($k = 1, 2$), and *e* is error. Normality and homogeneous variances were confirmed following Neter et al. (1996)

Multivariate analyses were performed using the statistical package PC-Ord version 4. The hypothesis of no significant difference in understory vegetation composition among overstory types, time since fire, and stand origins was tested using multiple response permutation procedures (MRPP) (Smouse *et al.* 1986). MRPP is a nonparametric procedure that avoids distributional assumptions of normality and homogeneity of variance, which are not commonly met in ecological community data. Trends in the compositional data were examined using Non-Metric Multidimensional Scaling (NMS), a nonparametric ordination technique well suited for data on discontinuous scales (Kenkel and Orloci 1986). The ordination was run using the autopilot program, on the slow and thorough analysis, using Euclidean distance measures. To identify species with high affinities for particular overstory types, stand age classes, and origins, an Indicator Species Analysis was performed. The analysis calculates indicator values for all species by multiplying the proportional abundance of a species in a group by the proportional frequency of the species in a group. Species occurring in only one site were eliminated from the analyses to avoid identifying rare species as having specific affinities for a given overstory type. The statistical significance of the indicator values were evaluated using a Monte Carlo method with 1000 runs. In each run, species were randomly assigned to groups and indicator values calculated.

RESULTS

Abundance, diversity, and composition with time since fire

Significant differences ($P<0.10$) were not detected between age classes nor overstory types, for total understory cover, but there were siginificant differences for understory cover of individual plant groups (Table 3-2; Figure 3-2). Vascular plant cover was highest in the seven year age class (68.6%), which was significantly higher than those in the 25, 72-90, and 201 age classes (40.7, 51.2, and 40.4%, respectively) while the cover in the 139 age class (60%) did not differ between them. Cover values were significantly higher under deciduous stands (58.4%) than conifer stands (41.7%) for all age classes except the 7 year old stands (Figure 3-2). Mixedwood stands had the highest cover in the 7 year old age class but had a mean cover intermediate to that of conifer and deciduous overstory types in all other age classes (53.7%) and did not differ significantly from the two other overstory types.

Nonvascular cover was significantly different between stand ages and overstory types with a significant interaction between them (Table 3-3, Figure 3-2). Nonvascular cover was much lower in the seven year old age class (2.8%) than in all other age classes. Cover was higher in the 25 and 139 year old stands (21.6% and 25.3%, respectively) than in the 72-90 and 201 year old stands (15.2 and 15.3%, respectively). Conifer stands supported significantly higher nonvascular cover (28.1%) than mixedwood (12.2%) and deciduous (5.2%) stands with mixedwood stands having significantly higher cover than deciduous stands for all stands except at age 7.

Shrub layer cover did not vary significantly with stand age, but was significantly different between overstory types (Table 3-2). Deciduous stands had significantly higher mean shrub layer cover (61.9%) than either mixedwood (48.3%) and conifer stands (36.5%). There was a significant interaction between stand age and overstory type, with differences in overstory types being driven by the higher shrub layer cover in the 72-90 and 139 year old deciduous stands (Figure 3-2).

Total understory species richness was significantly lower in the two youngest age classes than in stands of the three older age classes (Table 3-3; Figure 3-3). Richness increased with age and peaked at age 139 and then declined at age 201 for all overstory types except a missing mixedwood at age 139. There was a marginally significant interaction between stand age and overstory type ($P = 0.082$) and among overstory types, mixedwoods had a greater richness than other types at age 72-90, but not at other age classes (Table 3-4, Fig 3-3A).

Greater differences in understory richness occurred among overstory types when plant groups were examined. Vascular species richness was highest in late successional stands; the two youngest age classes had lower mean species richness (19.8 and 17.1, respectively) than the three older age classes (22.6, 21.5, and 22.7, respectively). Vascular species richness was higher in deciduous stands (22.2) than in conifer stands (18.5) with mixedwoods (21.5) supporting an intermediate vascular species richness between conifer and deciduous overstory types (Table 3-3; Figure 3-3).

Nonvascular species richness was significantly lower in the youngest age class (7.2) than in the four older age classes (12.4, 10.8, 14.8, and 10.8, respectively) (Table 3-3; Figure 3-3). Richness did not differ significantly between older age classes except a decline in richness occurred from the 139 to 201 year-old class. Nonvascular species richness was significantly higher under conifer stands (12.4) than under deciduous stands (10.0), with a significant interaction indicating greater nonvascular plant richness in mixedwoods than other types at 72-90 year-old age class.

Table 3-2. Analysis of variance summary for understory cover for stands of fire origin as a function of stand age (A_i, $i = 1, 2, \ldots 5$) and overstory type (S_j, $j = 1, 2, 3$). P values are shown for main effects and interaction. Bold type indicates $p < 0.10$. Source is explained in eq. 1.

		Total cover			Vascular cover			Nonvascular cover			Shrub layer cover		
Source	Df	MS	F	*P*	MS	F	P	MS	F	*P*	MS	F	P
A_i	4	0.024	1.922	0.128	0.108	5.253	**0.004**	0.73	17.42	**<0.001**	0.005	0.185	0.906
S_j	2	0.014	1.129	0.334	0.092	4.48	**0.018**	1.56	37.15	**<0.001**	0.24	9.616	**<0.001**
$A \times S_{ij}$	7	0.006	0.504	0.826	0.01	0.502	0.847	0.15	3.457	**0.006**	0.039	1.556	0.173
Error	36	0.013			0.021			0.04					

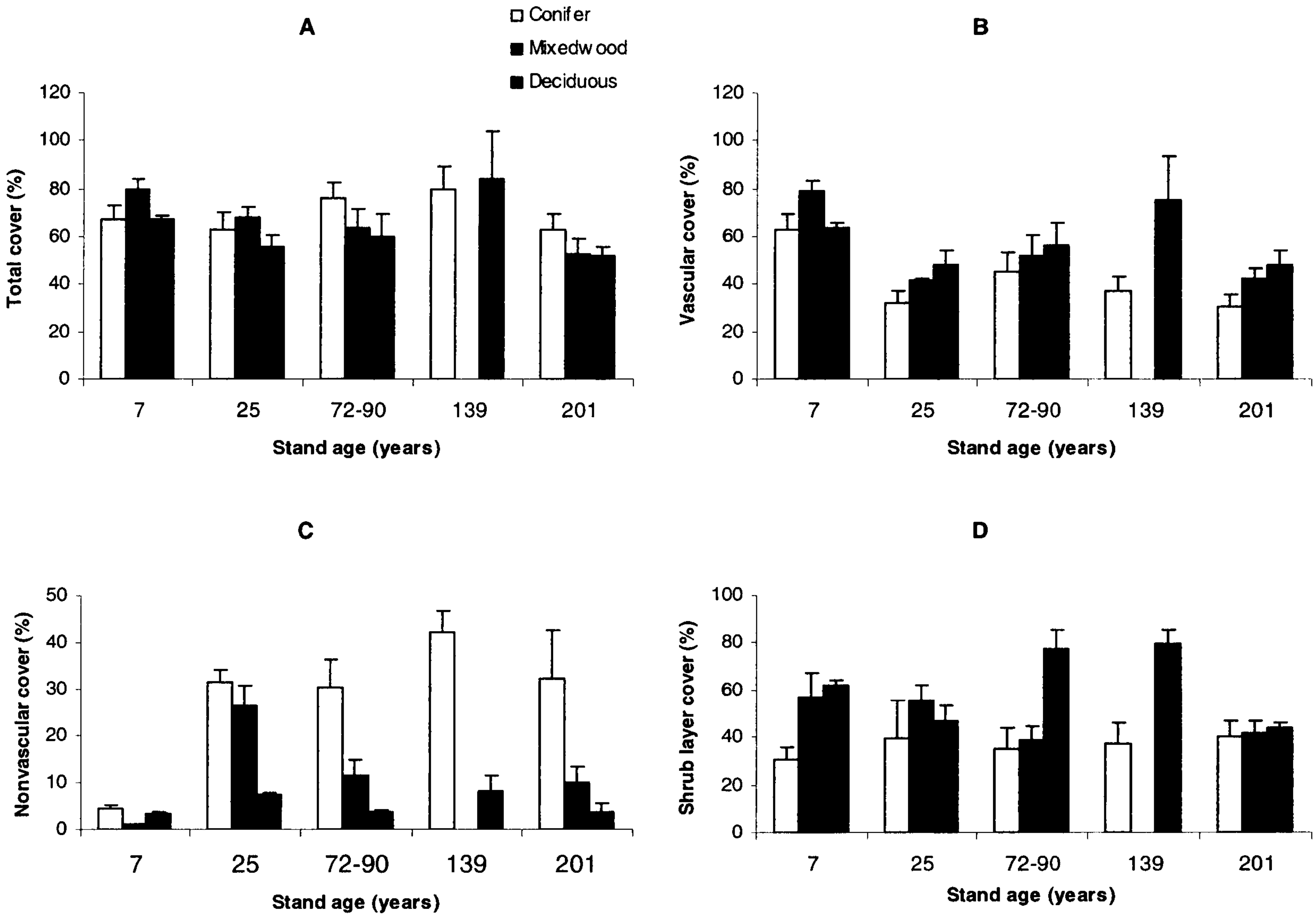

Figure 3-2. Effects of stand age and overstory type on (A) total cover, (B) vascular cover, (C) nonvascular cover, and (D) shrub layer cover (%) (mean + 1 SE) of fire origin stands.

Shrub layer species richness exhibited a different pattern from that observed for other understory plant groups. Shrub layer species richness was lower in the oldest age class (3.6) than in the three youngest age classes, but did not differ between stands of different overstory composition (Table 3-3, Figure 3-3). Within plot beta diversity ranged from 0.483 to 0.754, but did not differ between stands of different overstory type nor age (Table 3-3; Figure 3-4).

MRPP analysis (Table 3-4) confirmed the observations from the ordination (Fig. 3-5). All stand ages and overstory types supported significantly different understory communities ($p < 0.001$). The distance values showed separation between groups and the A value (0.26988) was relatively high, indicating low heterogeneity within groups (McCune and Grace 2002).

Table 3-3. Analysis of variance summary for understory species richness and beta diversity for stands of fire origin as a function of stand age (A_i, $i = 1, 2, \ldots 5$) and overstory type (S_j, $j = 1, 2, 3$). P values are shown for main effects and interaction. Bold type indicates $p < 0.10$. Source is explained in eq. 1.

Source	Df	Total richness			Vascular richness			Nonvascular richness			Shrub layer richness			Beta		
		MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
A_i	4	0.019	6.242	**0.001**	0.023	4.175	**0.007**	0.06	3.729	**0.012**	0.06	5.187	**0.002**	0.016	4.092	**0.008**
S_j	2	0.002	0.788	0.462	0.026	4.884	**0.013**	0.04	2.61	**0.087**	0.007	0.606	0.441	0.005	1.221	0.307
$A \times S_{ij}$	7	0.006	2.004	0.082	0.002	0.337	0.931	0.04	2.689	**0.024**	0.006	0.779	0.624	0.01	2.421	**0.039**
Error	36	0.003			0.005			0.02			0.012			0.004		

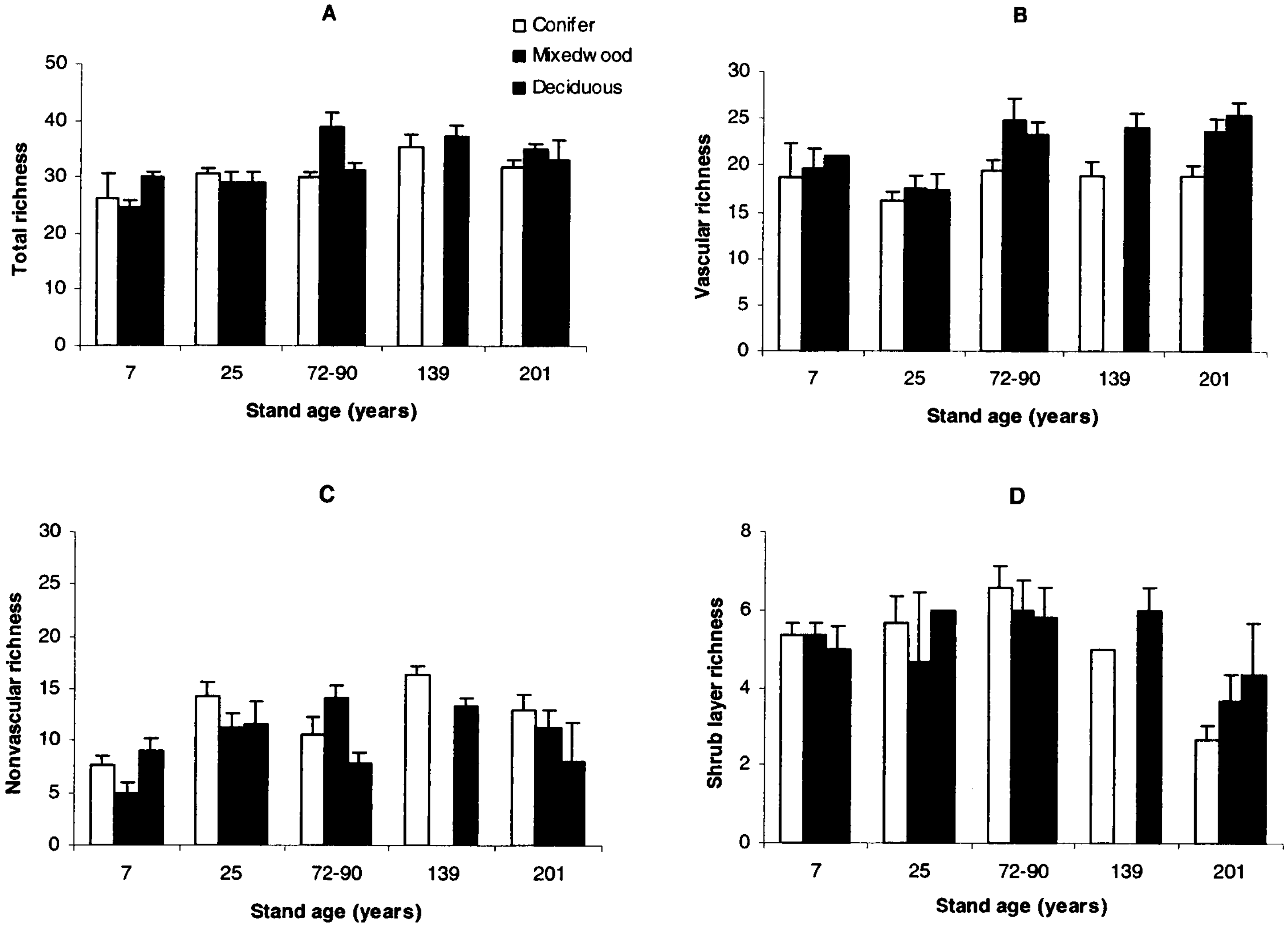

Figure 3-3. Effects of stand age and overstory type on (A) total richness, (B) vascular richness, (C) nonvascular richness, and (D) shrub layer richness (mean + 1 SE) of fire origin stands.

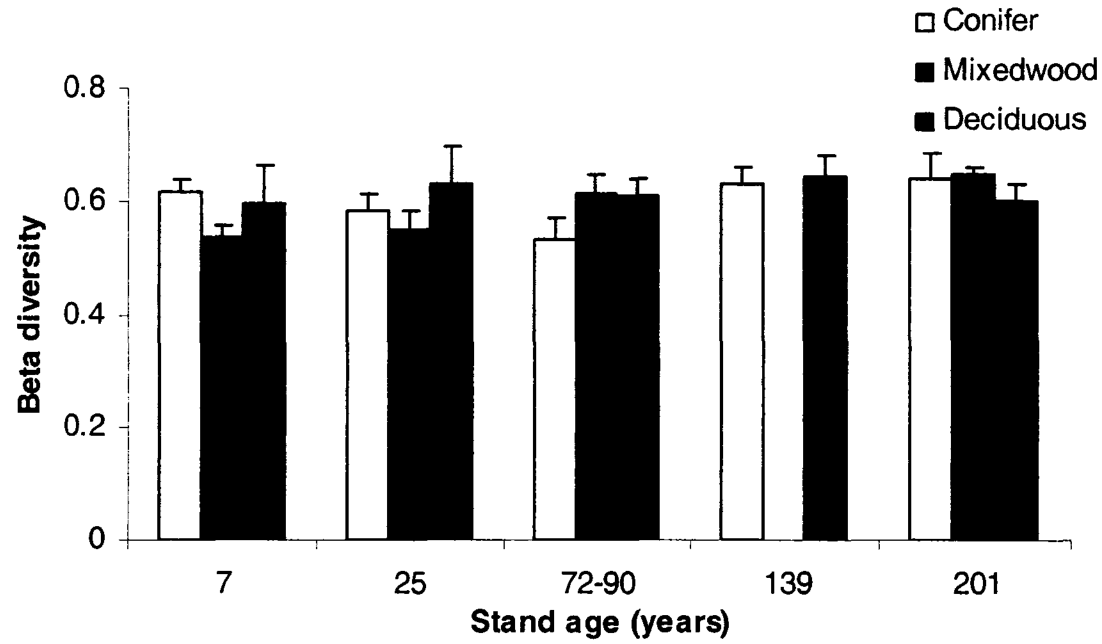

Figure 3-4. Effect of stand age and overstory type on beta diversity (mean + 1 SE) of fire origin stands.

Stands of different ages and overstory types differed significantly in understory composition (Table 3-4; Figure 3-5). NMS ordination (Figure 3-5) identified axes 2 and 3 as having the highest r^2 values (0.264 and 0.455, respectively), resulting in a cumulative r^2 value of 0.719. Stands of different ages separated in ordination space with stands of very different ages further apart than stands of similar ages. Almost no overlap occurred between conifer and deciduous stands while mixedwood stands were compositionally intermediate between the two overstory types.

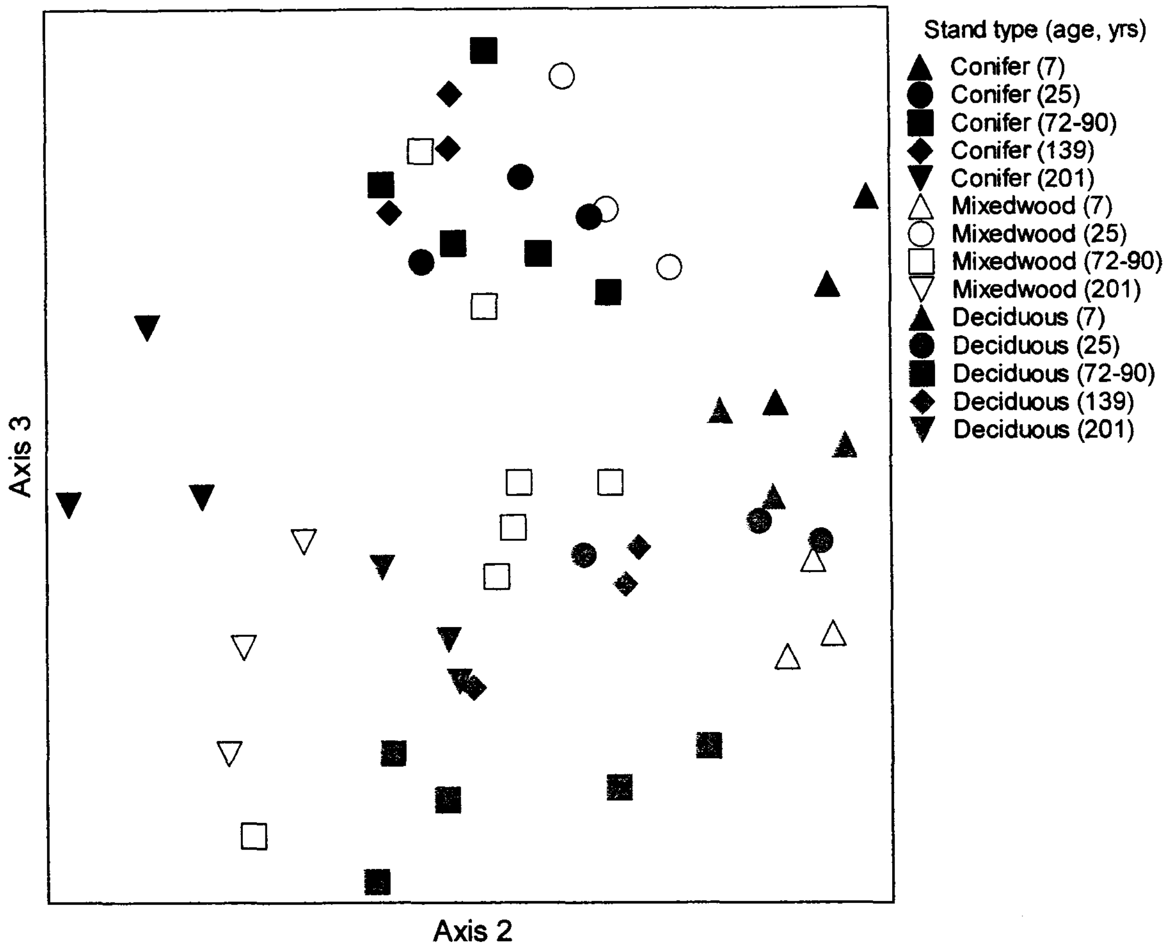

Figure 3-5. NMS ordination of understory vegetation community composition for conifer, mixedwood, and deciduous stands of 7, 25, 72-90, 139, and 201 years since fire (shown in brackets). Stands nearest each other on the graph have similar floristic assemblages, while those located farther apart are less similar. Axis 2 separates stands from young (right) to old (left) while axis 3 separates stands of different overstory composition.

Table 3-4. Results of the MRPP testing the effects of overstory type and stand age on understory composition of fire-origin stands.

Overstory type (stand age, yrs)	Average distance	N	MRPP statistics
Conifer (7)	204.99	3	Observed delta = 205.45735
Conifer (25)	172.24	3	Expected delta = 281.40244
Conifer (72-90)	230.12	5	$T = -11.535595$
Conifer (139)	145.71	3	$A = 0.2698807$
Conifer (201)	192.27	3	$p < 0.001$
Mixedwood (7)	294.24	3	
Mixedwood (25)	232.69	3	
Mixedwood (72-90)	230.48	7	
Mixedwood (201)	171.74	3	
Deciduous (7)	218.65	3	
Deciduous (25)	164.2	3	
Deciduous (72-90)	202.14	5	
Deciduous (139)	225.53	3	
Deciduous (201)	143.79	3	

Significant compositional differences between overstory types were found by indicator species analysis (Table 3-5). Conifer and deciduous stands had similar numbers of indicator species (21 and 25, respectively) whereas mixedwood stands had only eight species, and none in the 72-90 year old age class. Although conifer and deciduous stands had a similar number of nonvascular indicator species (9 and 8, respectively), those associated with deciduous stands were species of small stature, primarily found on decaying wood (i.e., *Brachythecium reflexum* and *Sanionia uncinata*), whereas large ground dwelling pleurocarpous mosses (*Pleurozium shreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquestrus*, and *Hylocomium splendens*) were restricted to conifer stands. Vascular species associated with deciduous stands were primarily herbaceous (i.e., *Mertensia paniculata* and *Trientalis borealis*), whereas coniferous stands were associated with more tolerant woody vegetation such as the ericaceous species *Vaccinium myrtilloides*, *V. angustifolium*, and *Ledum groenlandicum*.

Table 3-5. Indicator and randomized indicator values for species that are significant (P < 0.10) indicators of stands of different ages and overstory types.

Overstory type (stand age, yrs)	Species	Indicator value	Randomized indicator value	*P*
Conifer (7)	*Aralia hispida*	100.0	21.0	0.001
	Ceratodon purpureus	87.8	23.1	0.003
	Ledum groenlandicum	51.8	22.4	0.023
	Pinus banksiana	75.9	19.4	0.001
	Vaccinium angustifolium	56.4	22.8	0.018
	Vaccinium myrtilloides	37.5	19.5	0.021
Conifer (72-90)	*Maianthemum canadense*	18.2	13.7	0.028
	Picea mariana	38.8	18.5	0.023
	Ptilium crista-castrensis	36.3	22.2	0.030
Conifer (139)	*Abies balsamea*	34.6	18.4	0.018
	Betula papyrifera	28.7	17.0	0.095
	Dicranum flagellare	38.5	17.3	0.022
	Dicranum fuscescens	37.2	17.7	0.018
	Dicranum polysetum	51.8	24.6	0.001
	Jamesoniella autumnalis	40.8	17.8	0.010
	Pleurozium shreberi	24.9	17.1	0.017
Conifer (201)	*Hylocomium splendens*	56.3	21.2	0.004
	Lonicera canadensis	48.6	20.8	0.016
	Mitella nuda	52.3	20.7	0.006
	Rhytidiadelphus triquestrus	72.9	23.7	0.001
	Viola renifolia	22.2	15.5	0.050
Mixedwood (7)	*Clintonia borealis*	19.0	13.7	0.009
	Epilobium angustifolium	66.5	24.1	0.004
	Polygonum cilinode	85.7	20.2	0.001
	Rubus idaeus	44.2	21.3	0.020
Mixedwood (25)	*Cladina mitis*	51.3	16.1	0.005
	Cladonia sp.	21.0	15.9	0.082
	Polytrichum juniperinum	31.4	16.8	0.050
Mixedwood (201)	*Acer spicatum*	28.5	16.3	0.030

Deciduous (7)	*Apocynum androsaemifolium*	58.3	26.3	0.059
	Carex brunnescens	66.7	20.7	0.026
	Cornus canadensis	15.7	13.0	0.086
	Polytrichum commune	39.4	17.0	0.021
	Polygonum sp.	66.7	22.8	0.026
	Prunus pensylvania	48.9	20.2	0.014
Deciduous (25)	*Actaea rubra*	58.0	22.4	0.008
	Diervilla lonicera	22.2	16.7	0.095
Deciduous (72-90)	*Anemone quinquefolia*	34.5	18.6	0.046
	Aster macrophyllus	43.3	21.3	0.033
	Galium triflorum	23.7	16.4	0.092
	Mertensia paniculata	67.1	20.4	0.007
	Trientalis borealis	23.8	16.1	0.042
Deciduous (139)	*Brachythecium reflexum*	46.2	21.0	0.071
	Corylus cornuta	36.3	19.8	0.046
	Lycopodium lucidulum	48.0	20.6	0.004
	Orthotrichum obtusifolium	29.9	16.5	0.052
	Peltigera horizontalis	41.7	18.0	0.070
	Peltigera neopolydactyla	66.7	20.7	0.034
	Plagiomnium cuspidatum	33.2	18.0	0.020
	Populus tremuloides	89.7	28.1	0.002
	Sanionia uncinata	22.2	16.0	0.069
Deciduous (201)	*Brachythecium velutinum*	45.7	20.9	0.026
	Equisetum pratense	79.0	19.3	0.002
	Streptopus roseus	20.5	15.0	0.037

Effects of logging vs. fire on understory vegetation abundance, diversity, and composition

Total understory cover did not differ significantly between stands of logging and fire origin while it declined from seven to 25-31 year old age classes on stands of both fire and logging origin and differed marginally between overstory type (Table 3-6; Figure 3-6). Vascular species cover, however, was significantly higher on logging origin stands than fire origin stands in the 25-31 year old age class, but declined significantly from the seven to 25-31 year old age class on all overstory types of both origins except conifer stands of logging origin (Table 3-6; Figure 3-6).

Nonvascular species cover was significantly affected by stand origin, age, and overstory type (Table 3-6). Fire origin stands in the 25-31 year old age class had significantly higher nonvascular species cover than logging origin stands, particularly in deciduous and mixedwood types, but there was no difference between the two stand origins in the 7 year old age class (Table 3-6; Figure 3-6). Between the two age classes, nonvascular cover was higher in the older age class for all overstory types of both origins except deciduous stands of logging origin (Figure 3-6). Shrub layer cover in the seven year old age class was significantly higher on logged stands than fire origin stands for all overstory types, but was not significantly different between stand origins on 25-31 year old stands (Table 3-6; Figure 3-6).

Table 3-6. Analysis of variance summary for understory cover of stands of both fire and logging origin as a function of (A_i, i = 1, 2), overstory type (S_j, j = 1, 2, 3), and stand origin (O_k, k = 1, 2). P values are shown for main effects and interactions; bold type indicates p < 0.10. Source is explained in eq. 2.

		Cover			Vascular cover			Nonvascular cover			Shrub layer cover		
Source	Df	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
A_i	1	0.035	7.25	**0.012**	0.225	40.746	**<0.001**	1.904	47.146	**<0.001**	0.083	5.715	**0.024**
S_j	2	0.015	3.152	**0.059**	0.019	3.462	**0.046**	0.293	7.258	**0.003**	0.288	19.767	**<0.001**
O_k	1	0	0.097	0.758	0.061	11.01	**0.003**	0.586	14.513	**0.001**	0	0.001	0.972
AxO_{ik}	1	0	0.005	0.946	0.047	8.522	**0.007**	0.727	17.989	**<0.001**	0.042	2.886	0.101
SxO_{jk}	2	0.001	0.116	0.891	0.006	1.085	0.353	0.027	0.672	0.519	0.032	2.184	0.133
$AxSxO_{ijk}$	2	0.009	1.898	0.17	0.032	5.838	**0.008**	0.04	0.986	0.386	0.034	2.334	0.117
Error	26	0.005			0.006			0.04			0.015		

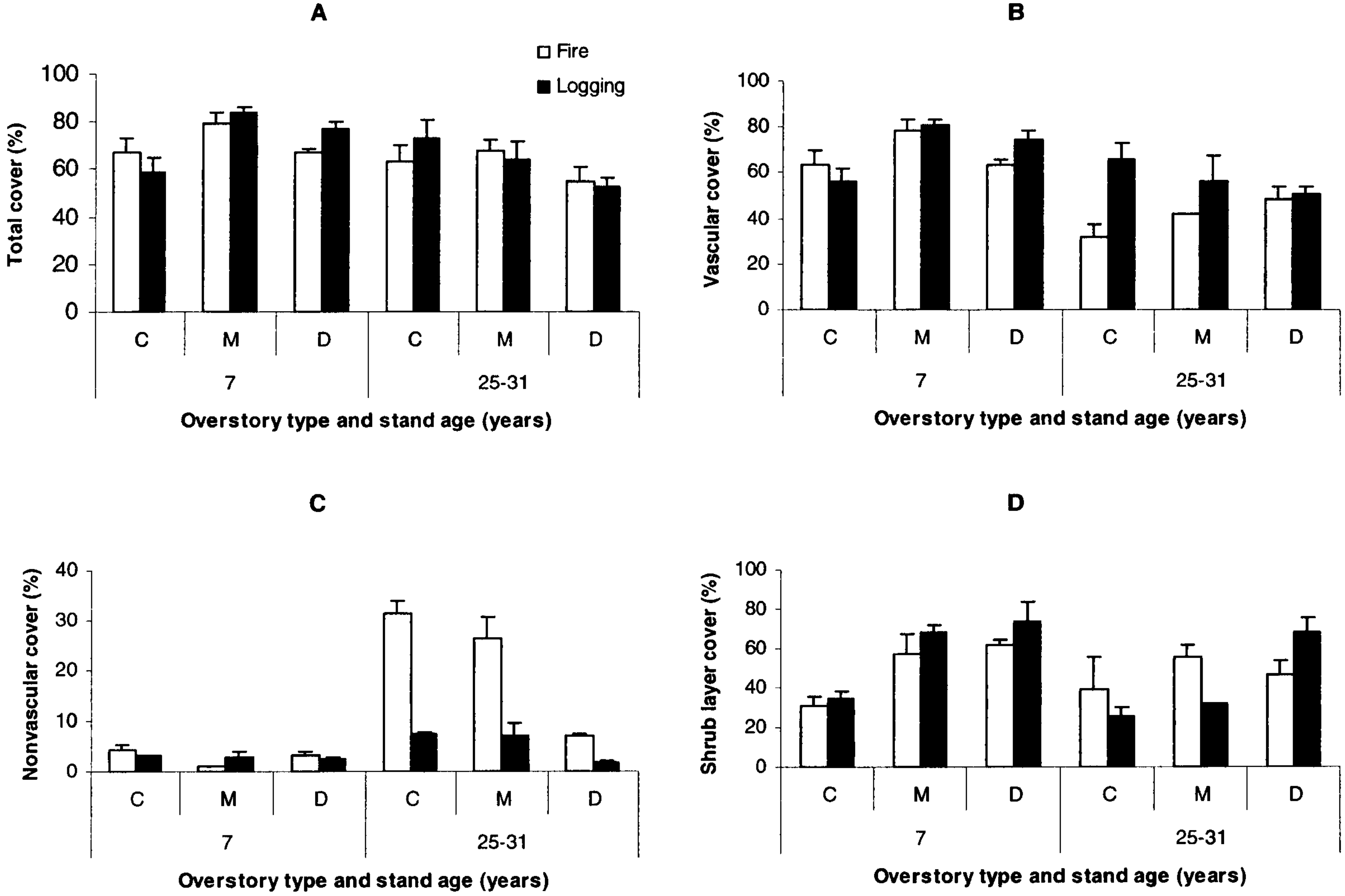

Figure 3-6 Effects of stand origin, age, and overstory type (Conifer (C), Mixedwood (M) and Deciduous (D)) (A) total cover, (B) vascular cover, (C) nonvascular cover, and (D) shrub layer cover (%) (mean + 1 SE) of young stands.

Total species richness differed with overstory type, age, and origin with significant two-way interactions between them, indicating higher richness on logged stands than on those of fire origin, and highest richness in mixedwoods within the seven year old age class (Table 3-7; Figure 3-7A). No differences occurred within the 25-31 year old age class or between overstory types (Table 3-7; Figure 3-7B). Vascular species richness was higher on logged stands in both age classes and under all overstory types with greatest richness in mixedwoods at seven year old age class (Figure 3-7B). Richness declined on both logging and fire origin stands from the seven to 25-31 year age classes.

Nonvascular species richness was significantly higher on fire origin stands than logging origin stands for the 25-31 year old age class, but no significant differences was observed for the seven year old age class or between overstory types (Table 3-7; Figure 3-7C). Shrub layer species richness was only affected by stand origin, indicating logging origin stands had significantly higher shrub layer species richness than fire origin stands (Table 3-7; Figure 3-7D). Within plot beta diversity did not differ significantly between stands of different origins, age classes, or overstory types (Table 3-7; Figure 3-8).

Table 3-7. Analysis of variance summary for species richness and beta diversity data of stands of both fire and logging origin as a function of (A_i, $i = 1, 2$), overstory type (S_j, $j = 1, 2, 3$), and stand origin (O_k, $k = 1, 2$). P values are shown for main effects and interactions; bold type indicates $p < 0.10$. Source is explained in eq. 2.

		Total richness			Vascular richness			Nonvascular richness			Shrub layer richness			Beta		
Source	Df	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
A_i	1	0.004	0.935	0.342	0.070	11.270	**0.002**	0.059	1.818	0.189	0.0001	0.017	0.897	0.009	1.403	0.247
S_j	2	0.006	1.379	0.270	0.010	1.629	0.216	0.001	0.035	0.966	0.002	0.160	0.853	0.011	1.666	0.209
O_k	1	0.028	7.001	**0.014**	0.130	21.660	**<0.001**	0.122	3.752	**0.064**	0.084	7.882	**0.009**	0.020	3.019	**0.094**
AxO_{ik}	1	0.035	8.664	**0.007**	0.010	1.406	0.246	0.181	5.561	**0.026**	0.0001	0.017	0.897	0.051	7.660	**0.010**
SxO_{jk}	2	0.011	2.785	**0.080**	0.000	0.121	0.886	0.065	1.985	0.158	0.011	1.056	0.362	0.014	2.110	0.141
$AxSxO_{ijk}$	2	0.009	2.347	0.116	0.020	3.043	**0.065**	0.003	0.092	0.913	0.003	0.293	0.749	0.014	2.165	0.135
Error	26	0.004			0.010			0.033			0.011			0.007		

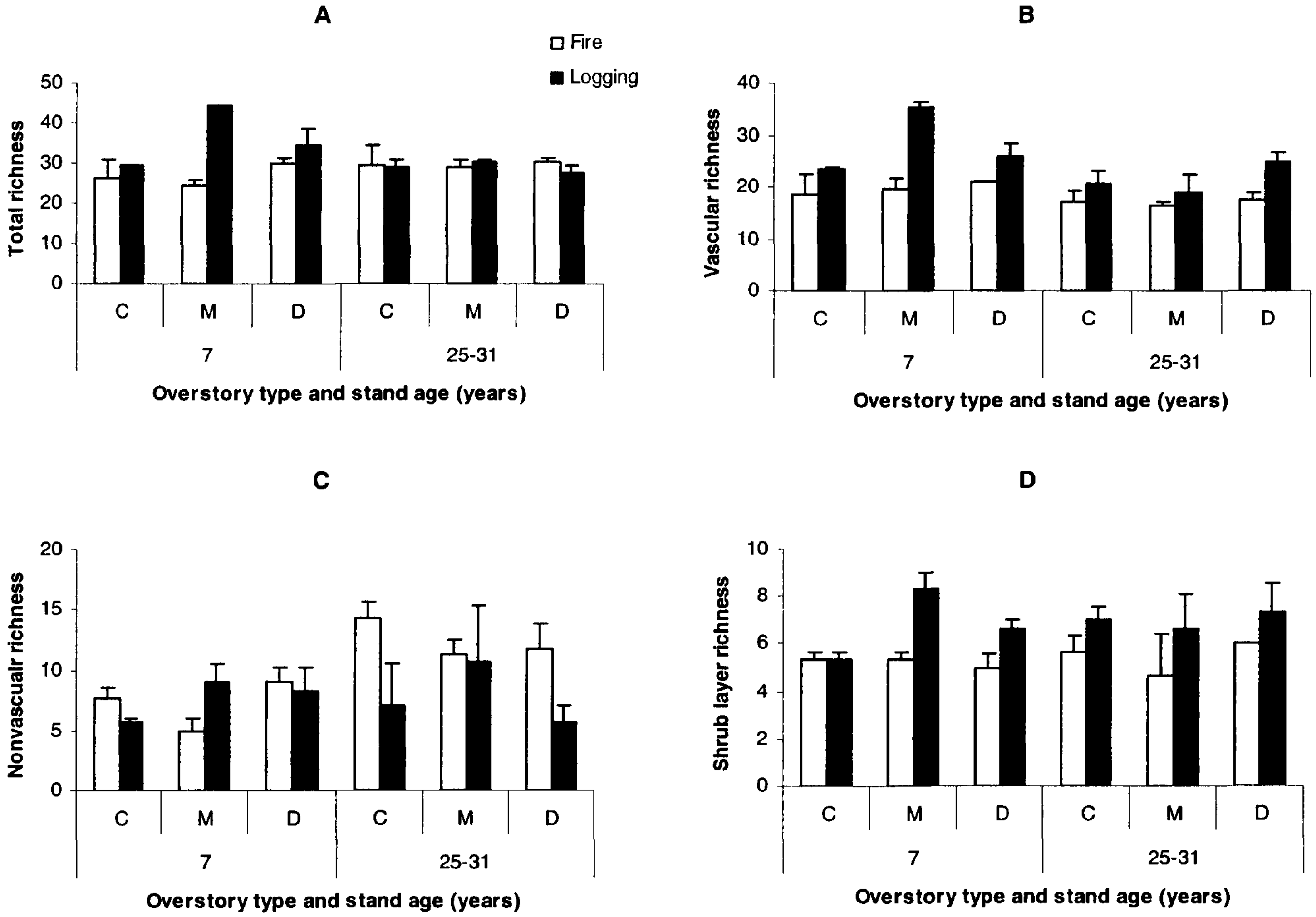

Figure 3-7. Effects of stand origin, age, and overstory type (Conifer (C), Mixedwood (M) and Deciduous (D)) on (A) total richness, (B) vascular richness, (C) nonvascular richness, and (D) shrub layer richness (mean + 1 SE) of young stands.

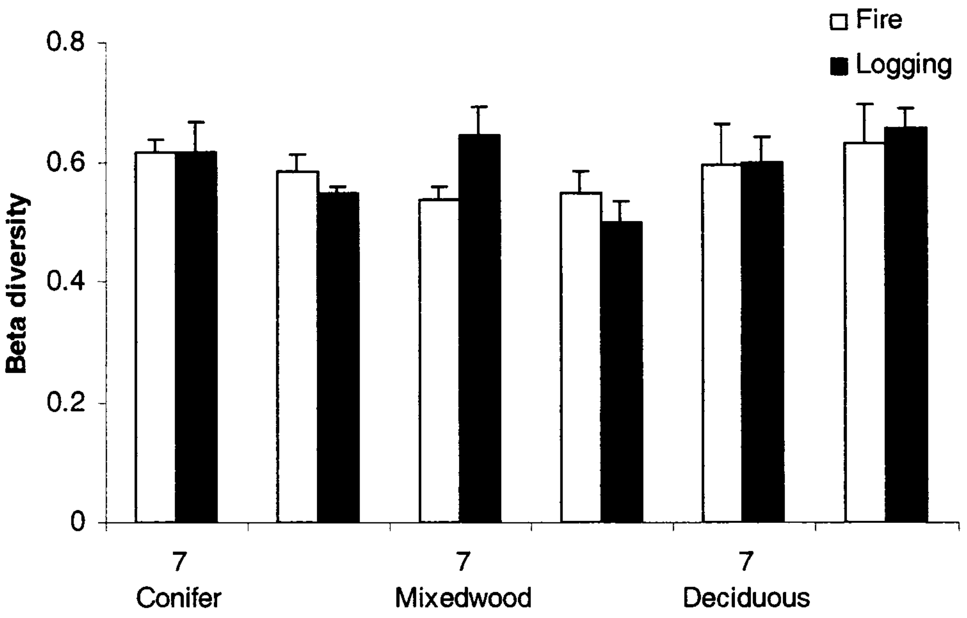

Figure 3-8. Effect of stand origin, age, and overstory type on beta diversity (mean + 1 SE) of young (7 and 25-31 years old) fire and logging origin stands.

Ordination, tests of similarity indices, and indicator species analysis found differences in understory community composition between stands of logging and fire origin, as well as differences in stand age and overstory type (Table 3-8; Figure 3-9). NMS ordination found a two-dimension optimal solution. Axes 2 and 3 had the highest r^2 values (0.278 and 0.473, respectively) with a cumulative r^2 of 0.751, which offered a good separation in ordination space. Overstory type and stand age mirrored trends observed in NMS ordination of fire origin stands (*see* Figure 3-5 *vs.* Figure 3-9). Stands of logging and fire origin showed partial separation in ordination space; however, stands of the same age class segregated stand origin.

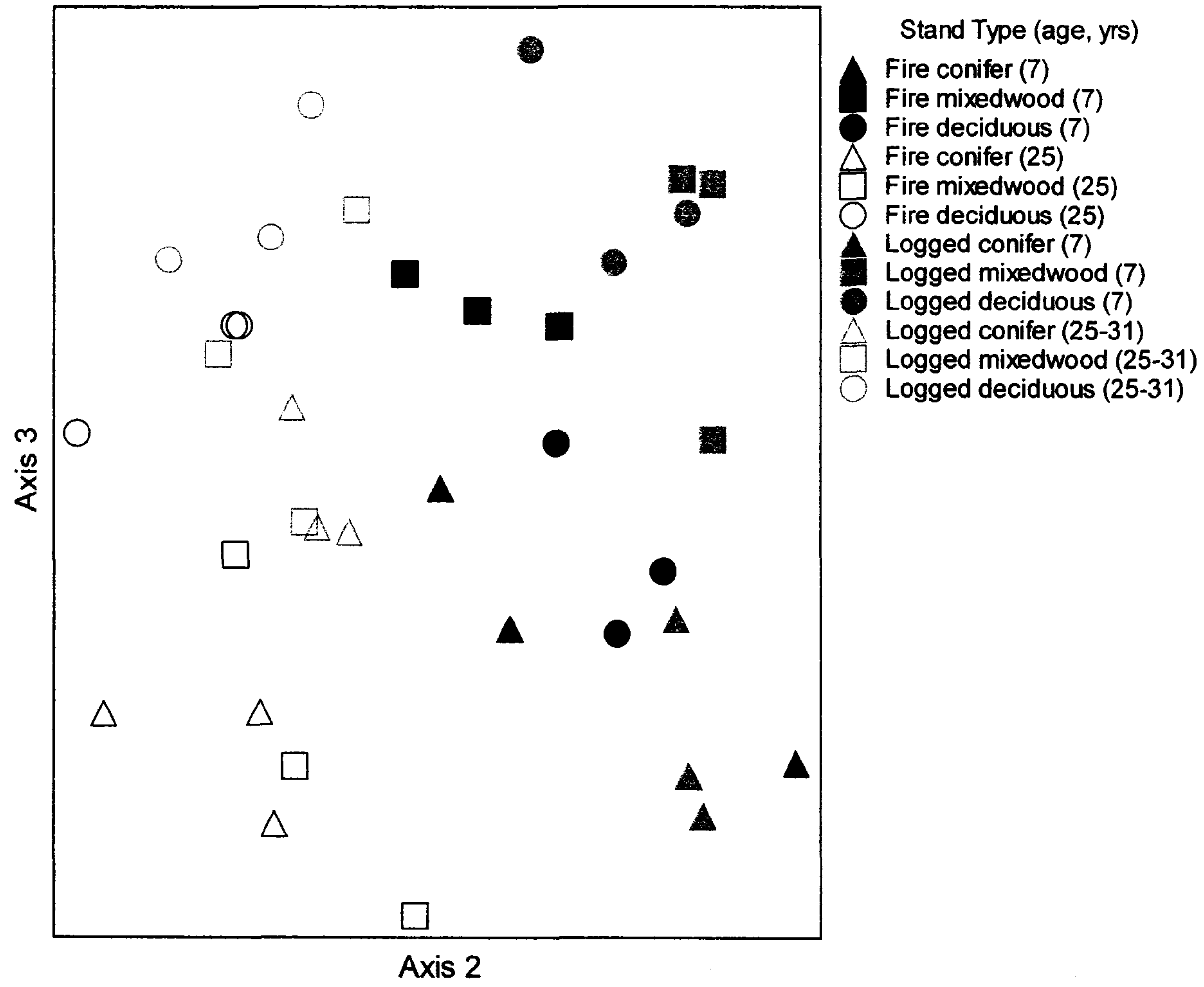

Figure 3-9. NMS ordination of understory vegetation community composition for conifer, mixedwood, and deciduous stands of 7 and 25-31 years old, fire and logging origin. Axis 2 separates young (right) and older (left) stands while axis 3 separates stands of conifer (top), mixedwood, and deciduous (bottom) overstory types and fire (top) and logging (bottom) origin.

MRPP analysis (Table 3-8) found stands of different origin, age, and overstory type supported significantly different understory communities ($p < 0.001$). Observed distance values showed a good separation between groups while the relatively high *A* value (0.23111) indicated that heterogeneity within groups of similar overstory types was low.

Table 3-8. Results of the MRPP testing the null hypothesis of no significant difference in community composition between stands of logging and fire origin, young and older age class, and overstory composition.

Overstory type (stand age, yrs)	Average distance	N	MRPP statistics
Fire conifer (7)	204.97565	3	Observed delta = 217.18358 Expected delta = 282.46330 T = -7.1430533 A = 0.23110867 p < 0.001
Fire 1 mixedwood (7)	294.24089	3	
Fire 1 deciduous (7)	218.61993	3	
Fire conifer (25-31)	172.16345	3	
Fire mixedwood (25-31)	232.68756	3	
Fire deciduous (25-31)	164.19673	3	
Log conifer (7)	227.12783	3	
Log 1 mixedwood (7)	237.31577	3	
Log 1 deciduous (7)	286.30459	3	
Log 2 conifer (25-31)	212.20995	3	
Log 2 mixedwood (25-31)	222.97898	3	
Log 2 deciduous (25-31)	122.25043	3	

Indicator species analysis identified a number of species with affinities for specific overstory types. All ages and overstory types of post-logged and post-fire stands had at least one significant indicator species (Table 3-9). Logged stands had more indicator species (22) than post-fire stands (12) although this was due in part to the large number of species significantly associated with post-logged seven year old mixedwoods. Post-logged stands were significantly associated with a number of grasses and sedges such as *Calamagrostis canadensis* and *Carex brumelis* as well as other herbaceous species such as *Aster macrophyllus* and *Polygonum commune.* Most of these species are rhizomatous and were probably present on the stands prior to logging. Post-fire stands were significantly associated with ericaceous shrubs and the pleurocarpous mosses such as *Pleurozium shreberi* and *Ptilium crista-castrensis*, with *Clintonia borealis* while *Polygonum* sp. was the only herbaceous species significantly associated with post-fire stands.

Table 3-9. Indicator and randomized indicator values for species that are significant ($p < 0.10$) indicators of stands of different origins, ages, and overstory types.

Overstory type (stand age, yrs)	Species	Indicator value	Randomized indicator value	*P*
Fire conifer (7)	*Ceratodon purpureus*	63.7	26.5	0.009
	Ledum groenlandicum	55.1	26.6	0.054
	Pinus banksiana	69.8	22.8	0.011
	Vaccinium angustifolium	62.4	32.2	0.025
	Vaccinium myrtilloides	26.7	20.2	0.073
Fire mixedwood (7)	*Clintonia borealis*	22.8	15.9	0.011
Fire deciduous (7)	*Polygonum* sp.	66.7	24.6	0.055
Fire conifer (25)	*Pleurozium shreberi*	38.9	24.8	0.011
	Ptilium crista-castrensis	64.7	30.2	0.004
Fire mixedwood (25)	*Cladonia* sp.	25.5	17.9	0.034
Fire deciduous (25)	*Brachythecium* sp.	24.7	17.3	0.019
	Plagiomnium cuspidatum	35.7	19.2	0.039
Logged conifer (7)	*Calamagrostis canadensis*	93.2	35.2	0.002
	Cladina mitis	47.9	26.3	0.092
	Oryzopsis pungens	57.8	22.0	0.054
	Viola adunca	66.7	22.3	0.050
Logged mixedwood (7)	*Acer spicatum*	42.2	21.4	0.045
	Aster macrophyllus	38.9	22.1	0.050

	Betula papyrifera	85.9	37.1	0.008
	Carex brumelis	55.6	24.6	0.060
	Carex houghtoniana	87.3	30.9	0.003
	Carex sp.	74.4	27.5	0.003
	Osmunda claytoniana	87.5	22.7	0.005
	Picea glauca	34.4	21.2	0.066
	Polygonum cilinode	78.8	20.7	0.003
	Polytrichum commune	54.5	20.5	0.011
	Ribes hirtellum	66.7	25.0	0.064
Logged deciduous (7)	*Amelanchier alnifolia*	60.3	22.4	0.006
	Epilobium angustifolium	38.8	24.6	0.045
	Populus tremuloides	45.8	21.0	0.057
Logged mixedwood (25-31)	*Maianthemum canadense*	16.2	13.5	0.062
Logged deciduous (25-31)	*Aralia nudicaulis*	21.1	17.2	0.097
	Fragaria vesca	38.1	19.5	0.091

DISCUSSION

Influence of TSF and overstory type on understory vegetation

Understory cover of individual plant groups was significantly influenced by overstory composition and time since fire. However, there is complexity since vascular and nonvascular species exhibited opposing responses to overstory type and stand age. Vascular species cover was highest under deciduous overstories and in the seven year old age class, whereas nonvascular cover was highest under conifer overstories and was higher on older stands. The reciprocal relationship between the two plant groups is consistent with other studies, and appears to be proportionate enough that no differences in total understory richness were detected. Many nonvascular species, particularly the pleurocarpous mosses, are very tolerant of low light and nutrient conditions typical under conifer and later successional stands, whereas the majority of vascular species are herbaceous and relatively intolerant of low light and nutrient conditions (Frego and Carleton 1995b, Roberts 2004). The low cover of nonvascular species under deciduous stands is also explained by the slow growth of most nonvascular species and their inability to grow above leaf litter (Beatty and Scholes 1988). In this study nonvascular species found under deciduous canopies were species of small stature and were primarily limited to decaying wood (personal observation).

Increases in vascular plant cover in the 139 year old deciduous stands, however, are likely the result of higher resource availability following canopy breakup as this age class represents a canopy transition stage in which overstory structural heterogeneity was very high. Under these stand conditions, both light penetration and nutrient availability (Paré *et al.* 1993, Lieffers *et al.* 1999) as well as vascular species cover of already established species can increase (De Grandpré *et al.* 1993). As well, the effect of overstory type on understory cover in the seven year old stands differed from those of other age classes. This result is expected, as canopy closure has yet to occur on these stands.

Shrub layer cover exhibited a different pattern from that of the vascular species group. Although shrub layer cover was generally higher under deciduous stands, this was limited to the 72-90 and 139 year old stands, likely because of the increased time required for the relatively large species *Acer spicatum* and *Corylus cornuta* to become dominant and to achieve high cover values in the understory. The lower light transmission occurring in the 25 year old stands as a result of stem exclusion processes (Ross *et al.* 1986) may explain the difference in shrub layer cover between age classes.

The overall trend for understory species richness is different from that observed in other studies in the boreal forest. Both Rees and Juday (2002) and De Grandpré et al. (1993) found species richness to be highest in the first 40 years after fire and to decline thereafter. Although a slight decline in vascular species richness was observed between the seven and 25 year old stands, the richness of all plant groups was highest in the 72-90 and 139 year old age classes. These differences may be the result of dissimilarity among study regions. The central boreal shield, a transitional region between the eastern and the western regions, has been found to be more floristically diverse than either the western or eastern regions of the boreal forest (Qian *et al.* 1998). The study area, therefore, is likely to have a greater species pool available to colonize a given site and there are likely to be more potential species for a given set of site conditions. The southern boreal forest of the central boreal shield has much better drained soils than those found in the eastern boreal forest and experiences much warmer summers than in Alaska and the clay belt region of Quebec. Thus, potentially maintaining higher resource availability on later successional sites, delaying the onset of retrogressive succession which is common in both the clay belt and Alaska (Van Cleve *et al.* 1981, Taylor *et al.* 1988).

The effect of overstory type on understory richness was limited to plant groups. Total and shrub layer species richness did not differ between overstory types, whereas vascular species richness was generally higher under deciduous stands, and nonvascular richness higher under conifer stands. Of interest is the compensation by vascular and nonvascular species in maintaining similar levels of richness between overstory types. To date, most studies of boreal understory vegetation have found richness to be higher under deciduous stands than conifer stands (Reich *et al.* 2001, Qian *et al.* 2003). This study, however, demonstrates that under certain conditions a decline in the richness of one plant group can be compensated by an increase in the other. This observation may help to explain the higher understory richness of intermediate aged stands, as declines in early successional vascular species may be compensated by increases in the number of nonvascular species.

Understory species richness does not appear to be driven by cover. The resource ratio hypothesis predicts that increasing dominance of a few species in late successional and high resource communities causes a decline in species richness as less competitive species are eliminated. This study, however, found richness and cover to follow very similar patterns, even among plant groups. Species richness was found to be highest when cover was also highest for total, vascular, and nonvascular species groups. These results are supported by Chen et al. (2004), who found understory diversity increased with site quality under aspen stands in northern British Columbia, suggesting that boreal understory vegetation dynamics are influenced more by the ability of species to tolerate declining resource availability than by competition. It must be remembered, however, that resource availability was inferred, based on a results from previous studies (e.g. Reich et al. 2001), preventing one from drawing more meaningful conclusions.

The shrub layer behaved somewhat differently from the ground layer. Shrub layer richness was only affected by stand age. Despite being comprised of vascular species, the shrub layer showed no decline in richness with increasing conifer content. Shrub layer cover, however, declined significantly with increasing conifer content in the overstory. These results are consistent with other studies in the boreal forest which have found species like *Acer spicatum* Lamb. to be most abundant under deciduous canopies than coniferous canopies (Légaré *et al.* 2002). The behavior of the shrub layer also suggests that species cover and abundance are not necessarily related and can have reciprocal relationships.

Mixedwood stands appear to be compositionally intermediate between conifer and deciduous overstory types. Understory vegetation cover for all plant groups was intermediate between conifer and deciduous stands. This is likely because of intermediate light transmission to the understory as both conifer and deciduous overstory species have different light transmission levels to the understory (Messier *et al.* 1998). The NMS ordination shows mixedwoods stands to be compositionally intermediate to conifer and deciduous overstory types. As well, mixedwoods were found to have very few indicator species, compared to conifer and deciduous stands.

There was some support for the environmental heterogeneity hypothesis as some mixedwood stands had greater species richness than conifer and deciduous overstory types. Mixedwood stands in the 72-90 year old age class had higher total, vascular, and nonvascular species richness than conifer and deciduous stands. No trend was apparent in any other age class, suggesting that mixedwoods may only increase understory resource heterogeneity and richness under specific circumstances. As well, resource heterogeneity was inferred, based on results from other studies and not actual field measurement. The missing mixedwood sites from the 139 year old age class prevent drawing more concrete conclusions, but it is possible that high structural diversity of stands at canopy transition stage in the 72-90 to 139 year old age classes promote understory heterogeneity (Chen and Popadiouk 2002, Brassard and Chen 2006). Stands in the seven and 25 year old age classes have overstories composed of jack pine and aspen, which have similar light transmission levels (Messier *et al.* 1998), whereas stands in the 72-90 year old age class have some tolerant conifers in the overstory, possibly creating more heterogeneous light conditions favorable to increasing understory species richness (Saetre *et al.* 1997, Messier *et al.* 1998, Pitkanen 2000, Chen and Popadiouk 2002). Overstory structural diversity is also much higher in these age classes than in younger age classes as canopy succession and gap formation processes increase (Chen and Popadiouk 2002, Pham *et al.* 2004, Hill *et al.* 2005, Brassard and Chen 2006). Leniere and Houle (2006) found herbaceous species diversity to be higher under more structurally diverse sugar maple (*Acer saccharum* Marsh) stands.

Differences in species richness do not appear to be related to heterogeneity of understory communities. No difference in heterogeneity, measured by beta diversity, was found between overstory types or age classes, suggesting that differences in species richness are not driven by the heterogeneity of microsite communities in the understory. These results are similar to those of Saetre et al. (1997), who found no difference in understory heterogeneity between stands of Norway spruce (*Picea abies* (L.) Karst) and mixed stands of Norway spruce and birch (*Betula pendula* Roth). Alternatively, it is possible that the size (1 m^2) and number of subplots (10) used in this study were insufficient to detect community differences at the microsite level (Sarr *et al.* 2005), as De Grandpré et al. (2000a) and Shafi and Yarranton (1973) found differences in understory heterogeneity between sites using 100 and 120 subplots per overstory type, respectively.

Compositional differences between both stand ages and overstory types suggest parallel succession between stands (Figure 3-5). The distribution of stands along axis 2 shows changing understory composition of all overstory types with increasing time since fire. Similar results have been reported in the Ontario clay belt where old-growth black spruce stands were found to continue to undergo changes in understory composition (Harper *et al.* 2003). Further, NMS ordination showed no sign of convergence in understory composition with increasing time since fire, suggesting different overstory types can remain compositionally distinct well beyond the length of traditional fire cycles.

Influence of forest harvesting on understory vegetation richness, abundance, and composition

Understory cover was higher on post-logged stands while nonvascular cover was much higher on post-fire stands, but only in the 25-31 year old age class. Vascular species cover appears to be related to richness as the two measures follow a similar trend. The high nonvascular cover in the 25 year old post-fire stands is likely be the result of the very high stem densities typical of post-fire stands at the stem exclusion stage . Competition for light is very intense at this stand development stage, resulting in low canopy light transmission levels, favoring the growth of shade tolerant nonvascular species (Ross *et al.* 1986).

Forest harvesting was found to increase species richness. The increase appears to be driven by an increase in vascular species richness for all overstory types and age classes. The same was also found for the shrub layer, whereas a decline in nonvascular species diversity was observed for most overstory types within the 7 and 25-31 year old age classes. The increase in vascular species richness was found on stands seven and 25-31 years after disturbance, whereas the increase in total species richness was only found on stands in the seven year old age class. An increase in nonvascular species richness on fire origin stands appears to compensate for the lower vascular species richness in this case.

Studies comparing species richness between stands of fire and logging origin have found both declines and increases in richness following logging (e.g., Abrams and Dickmann 1982, Nguyen-Xuan *et al.* 2000, Rees and Juday 2002, Haeussler and Bergeron 2004). Discrepancies between studies are likely the result of the type of predisturbance communities and different disturbance intensities as intense fires can destroy seedbeds, whereas a number of species can propagate vegetatively and remain on a stand after minor disturbances (Haeussler and Bergeron 2004). Studies that have found lower richness on post-logged stands compared to post-fire stands attributed much of the differences to the absence of pyrophilic species on post-logged stands, in particular a number of bryophytes (Peltzer *et al.* 2000, Rees and Juday 2002). Alternately, cases of higher richness on post-logged stands have been the result of preestablished vascular species, primarily herbaceous species (Haeussler and Bergeron 2004, Roberts 2004).

This study supports the findings of similar boreal understory vegetation research. Indicator species analysis shows a large number of herbaceous and clonal sedges and forbs are associated with post-logged stands. This is particularly true for the seven year old age class, whereas only a few species are significantly associated with the 25-31 year old logging origin stands, although the absence of older post-logged stands prevents drawing more concrete conclusions.

The convergence of species richness and cover between post-fire and post-logged stands in the 25-31 year old age class is driven by an increase in nonvascular species richness on fire origin stands. Compositional differences, however, are evident in the NMS ordination, supported by MRPP analysis, that found stands of different origins and age classes to be compositionally distinct from one another. The strong effect of overstory composition and time since fire on understory composition is likely to cause conversion in understory composition over time, making alternative compositional pathways unlikely. Bergeron and Dubuc (1989) found understory communities began to converge 20 years after disturbance and converged completely after 100 years. Current forest rotation ages, however, occur in much less than 100 years, as a result, observed differences in understory community composition may persist somewhat throughout the life of the forest stand, affecting landscape and temporal diversity.

CHAPTER FOUR GENERAL CONCLUSIONS

Understory richnes,was not negatively affected by high cover values as predicted by the intermediate disturbance hypothesis. Moreover, richness appears to be highest on sites with high resource availability, suggesting that boreal understory communities are influenced more by plant tolerances for low resources rather than competition.

Vascular and nonvascular species appear to compensate for each other under different site conditions, resulting in similar total understory cover and richness under most overstory types and stand ages. Mixedwood stands do not appear to support higher understory species richness, despite being compositionally intermediate between deciduous and coniferous stands. Community composition, however, was different for all overstory types as stands of different overstory composition and time since fire were found to support distinct communities with some species found to be specific to each overstory type.

Post-logged stands support similar richness and cover to post-fire stands. The cover and richness of vascular species, however, was much higher on post-logged stands while the richness and cover of nonvascular species was lower. These differences resulted in significantly different community composition, driven primarily by the large number of late successional rhizomatous species already established on post-logged stands and pleurocarpous mosses on fire origin stands.

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